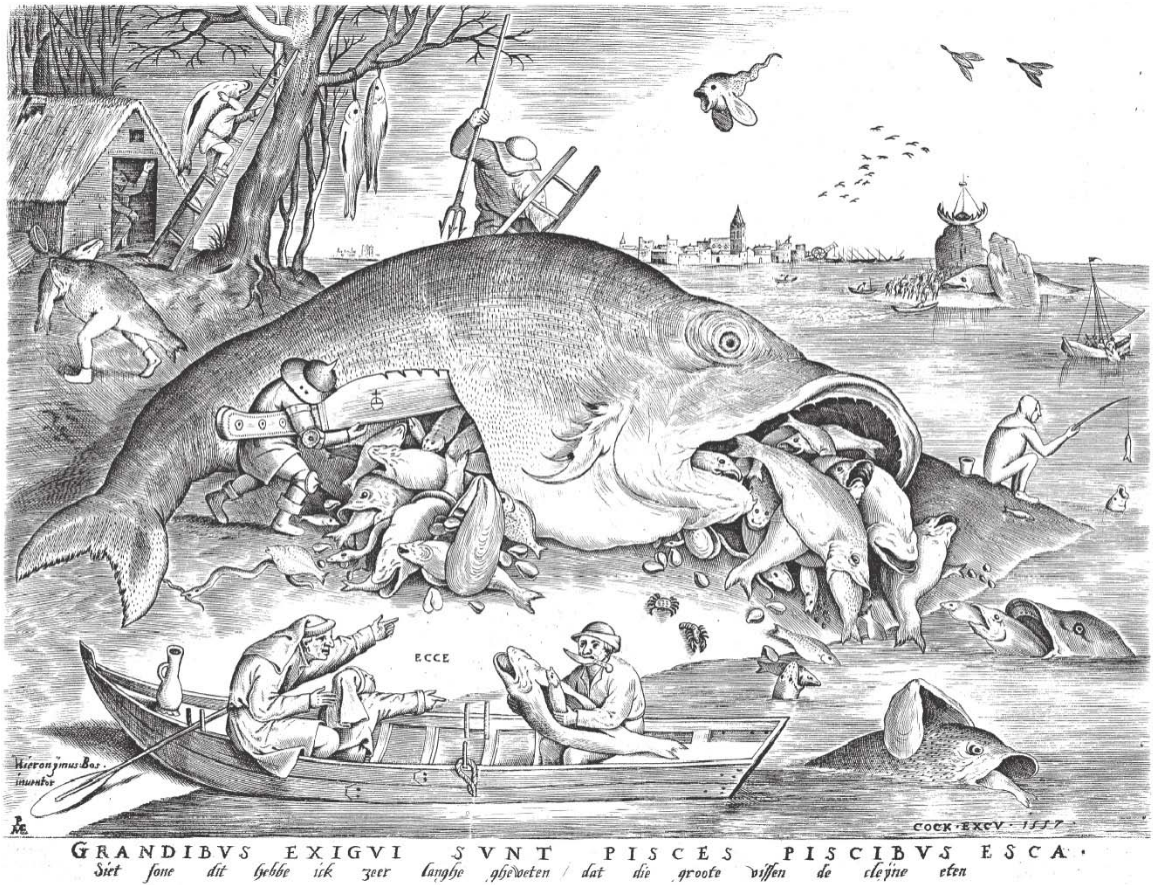
Columbia River Food Webs:
Developing a Broader Scientific Foundation for Fish and Wildlife Restoration



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Cover image: *The Big Fish Eat the Small Ones*, Peter Brueghel the Elder, 1556

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Unit Conversion Tables

Metric to English Units	**English to Metric Units**
Length	**Length**
1 kilometer = 0.62 miles	1 inch = 0.025 meters
1 kilometer = 3,280.8 feet	1 inch = 2.54 centimeters
1 meter = 0.00062 miles	1 inch = 25.4 millimeters
1 meter = 1.09 yards	1 foot = 0.31 meters
1 meter = 3.28 feet	1 foot = 30.48 centimeters
1 meter = 39.37 inches	1 yard = 0.91 meters
1 centimeter = 0.033 feet	1 yard = 91.44 centimeters
1 centimeter = 0.39 inches	1 mile = 1.61 kilometers
Area	**Area**
1 square kilometer = 247.11 acres	1 acre = 0.0041 square kilometers
1 square kilometer = 0.39 square miles	1 acre = 4,046.9 square meters
1 square meter = 0.00025 acres	1 square mile = 640 acres
1 square meter = 10.76 square feet	1 square mile = 2.59 square kilometers
Volume	**Volume**
1 cubic kilometer = 810,713 acre feet	1 acre foot = 0.0000012 cubic kilometers
1 cubic meter = 0.00081 acre feet	1 acre foot = 1,233.5 cubic meters
1 cubic meter = 35.32 cubic feet	1 cubic yard = 0.77 cubic meters
1 cubic meter = 1.31 cubic yards	1 cubic foot = 0.028 cubic meters
1 cubic meter = 61024 cubic inches	1 gallon = 0.0038 kiloliters
1 kiloliter = 35.32 cubic feet	1 gallon = 3.79 liters
1 liter = 0.26 gallons	1 quart = 0.95 liters
1 liter = 1.06 quarts	1 quart = 946.35 milliliters
1 liter = 2.11 pints	1 pint = 0.47 liters
1 liter = 33.81 ounces	1 ounce = 0.03 liters
1 milliliter = 0.034 ounces	1 ounce = 29.57 milliliters
Rate	**Rate**
1 cubic meter/second = 0.035 thousand cubic feet/second	1 thousand cubic foot/second = 28.32 cubic meters/second
1 cubic meter/second = 35.31 cubic feet/second	1 cubic foot/second = 28316847 cubic millimeters/second
1 cubic meter/second = 61023.74 cubic inches/second	1 cubic foot/second = 0.028 cubic meters/second
1 cubic meter/second = 264.17 gallons/second	1 cubic foot/second = .7 cubic meters/minute
1 cubic meter/second = 1000 liters/second	1 cubic foot/second = 101.94 cubic meters/hour
1 cubic meter/minute = 0.59 cubic feet/second	1 cubic inch/second = 0.000016 cubic meters/second
1 cubic meter/hour = 0.0098 cubic feet/second	1 liter/second = 0.001 cubic meter/second
1 cubic millimeter/second = 0.000061 cubic inch/second	1 cubic inch/second = 16 387.064 236 cubic millimeter/second
Weight	**Weight**
1 metric ton =1.1 U.S. tons	1 U.S. ton = 0.9 metric tons
1 kilogram = 0.0011 tons	1 ton = 907.18 kilograms
1 kilogram = 2.2 pounds	1 pound = 0.45 kilograms
1 gram = 0.0022 pounds	1 pound = 453.59 grams
1 gram = 0.035 ounces	1 ounce = 0.028 kilograms
1 milligram = 0.0000022 pounds	1 ounce = 28.35 grams
1 milligram = 0.000035 ounces	1 ounce = 28,350 milligrams

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Executive Summary

Food Webs: Key Components of Ecosystem Resilience and Productivity

Food webs describe pathways by which energy, nutrients and other materials make their way to species of cultural and economic interest. Food webs are often thought of as reflections of habitat, yet many other factors shape the internal organization, linkages, productivity and resilience.[1] Species diversity, the mix of native and non-native species, chemical contaminants, habitat carrying capacity, nutrient delivery and cycling, competition, predation, disease and associated system-scale processes are all deeply involved in shaping food webs. Nevertheless, highly complex food webs have been successfully manipulated at large scales to improve water conditions as well as recreational fisheries while, at the same time ill-advised manipulations have resulted in serious environmental issues – the introduction of mysids being one example.

The concept of a food web remains one of the most useful – and most challenging – ideas in ecology. It describes feeding habits and food (trophic) relationships between species within an ecosystem or within a particular place. Although actual trophic relationships are sometimes difficult to sample, measure, describe and model, they are of immense practical and theoretical importance. They characterize, in a relatively simple way, how energy, nutrients, toxins and biomass are transferred from producers to consumers. There are several well known approaches to describing and quantifying trophic relationships within communities. Food chains and food webs traditionally illustrate only connections between species, whereas food networks or food budgets illustrate the relative transfer rates of energy, nutrients, toxins or biomass through thousands of connections. Collectively, these can be quantified and modeled to produce an understanding of how nutrients and energy are assimilated into productive fisheries or, at the other extreme, how they contribute to degraded environmental conditions.

Food webs relate directly to the Northwest Power and Conservation Council's (NPCC or Council) Columbia River Fish and Wildlife Program, which seeks to establish and maintain an ecosystem that sustains an abundant, productive and diverse community of fish and wildlife (NPCC 2009-09:6). Food webs fuel that ecosystem, providing the theme for this review. Incorporating a food web perspective into management efforts helps sustain the ecological system and provide for more productive and resilient fisheries.

The objectives of this report are to provide a fundamental understanding of aquatic food webs in the Columbia River Basin and to illustrate and summarize their influences on native fish restoration efforts. The spatial scope addresses tributaries, impoundments, the free-flowing Columbia and Snake rivers, as well as the estuary and plume. Achieving the Council's vision for the Columbia River Fish and Wildlife Program (NPCC 2009-09) of sustaining a "productive and diverse community" that provides "abundant" harvest, is best accomplished through a time-prioritized action plan, one that complements other approaches while addressing important challenges and uncertainties related to the Basin's food webs. Note that the oceanic food webs, although of immense importance in sustaining fish populations, are not considered beyond the plume since they involve an additional set of complex and rapidly evolving issues. An analysis of oceanic food webs of relevance to the Columbia River requires a separately focused effort (e.g., Hoegh-Guldberg and Bruno 2010).

Implications for Restoration

Food webs reveal insights into basic properties underpinning productivity and resilience that cannot be obtained from an exclusive focus on hydrosystem, habitat, hatcheries and harvest (the four H's). Restoration activities have traditionally focused on physical habitat, an approach that assumes local habitat structure and quality dictate fish production. Physical characteristics of riverine habitats traditionally have been thought to constrain fish production. More importantly, traditional freshwater food web illustrations have typically conveyed the notion that most fish food is produced within the local aquatic habitat itself. In reality, much of the food comes from external or very distant sources – including subsidies from marine systems borne by adult returns of anadromous fishes, from fishless headwater tributaries that transport prey downstream, and from adjacent

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[1] Resilience is the ability of the biotic system to absorb and recover from perturbations

streamside and estuarine vegetation and associated riparian and terrestrial habitats. Key trophic pathways and food sources vary over time and space throughout watersheds. When restoration activities are not successful, it is often because they do not take a sufficiently broad view of watershed drivers, including food webs and the processes that regulate food availability. It is well recognized that many fishes use an array of habitat types to complete their life cycles, and thereby encounter a diverse array of important prey resources – and this is fundamental to effective restoration.

Food web structure and processes associated with them determine how system components act collectively – sometimes synergistically – to underpin the resilience and productivity of the larger ecosystem. Each food web component, whether a primary producer, an external input of organic matter, a microbial decomposer or a tertiary consumer, responds to changes in environmental conditions. Further, when a predator impacts its prey, the influence can extend well beyond the prey, reverberating throughout the entire food web as a "cascading trophic interaction."

The Council's vision of restoring and maintaining ecosystems that sustain an abundant, productive and diverse community of fish and wildlife through the Fish and Wildlife Program (NPCC 2009-09) is an important challenge. The ISAB's assertion is that prospects for doing that can be improved through a food web perspective. Implementing a food web perspective for the Columbia River would complement other approaches, such as the focus on habitat restoration, and thereby enhance our collective ability to meet the Council's vision.

Report Structure and Rationale

The report has five complementary sections. General concepts and applications related to food webs are examined initially (Section A), followed by a brief description of the physical setting (Section B), a detailed discussion of key environmental processes affecting food web characteristics (Section C), an examination of food webs in typical habitats (Section D) and a system perspective integrating our findings with contemporary and emerging issues (Section E). The four appendices describe a variety of methods used in food web investigations (Appendix A), the legal and policy web surrounding restoration activities in the Basin (Appendix B), pesticides used in the Basin (Appendix C), and give a list of common and scientific names used in the report (Appendix D).

The ISAB proposes a systematic action plan dealing with three thematic concerns. The first is to address key threats to the resilience and productivity of the Basin's food webs. There is a need to understand the aggregate capacity of the Basin to produce fish while restoring degraded ecosystems and food webs to a healthy state. This means moving in many cases toward food webs containing both new and old elements (i.e., hybrid food webs) and able to persist under a set of environmental conditions that have changed substantially over the last century. The second thematic concern is to fill a very large number of perplexing information gaps and critical uncertainties impeding progress. Efforts are needed to fill those gaps progressively and systematically, as we work our way forward. The third concern is to protect the healthy ecosystems and productive food webs we currently have, while reclaiming and restoring those that are degraded. That means identifying what is still healthy and what is not, and characterizing why and how those that continue to function well do so.

Addressing Key Threats to Resilience and Productivity

Foods webs of the Columbia River are productive yet potentially fragile. Human presence in the region is growing rapidly, hatchery production of fishes is nearly ubiquitous, chemical use is widespread, expansion of non-native species continues unabated, and the climate is changing inexorably. The net result is that the Basin's food webs continue to change, and there is a considerable range of challenges to be faced. During the course of this evaluation, three critical and several highly important threats were consistently identified by the ISAB. These require proactive efforts, but there are three particular issues in need of immediate attention:

Uncertainty about the Aggregate Carrying Capacity of the Columbia River. Massive annual releases of juvenile fish from hatcheries affect wild food webs and stocks of *wild* fish. There are approximately 130-150 million hatchery salmon and steelhead added to the system annually. The thousands of metric tons of food used to raise them, as well as the natural foods required to maintain them in the river, affect the capacity of the Columbia River to support naturally-produced native fishes. Additionally, since nutrients and organic matter constitute the basic fuels for food webs, changes to the amounts and forms can significantly affect food web productivity and resilience. These changes result from the continuing losses of marine- and riparian-derived nutrients, altered land-based leaching of nutrients and organic matter, and increasing atmospheric deposition of nitrogen and micro-nutrients. The ISAB recommends that new work should:

> Determine the ability of the system to provide sufficient food to support viable populations of fishes and other organisms for the long term. Data on the seasonal consumption demand and energetic carrying capacity of major habitat types are currently lacking or inaccessible for juvenile fishes, and the information is needed for system-wide planning purposes. A monitoring strategy is needed that tracks the food demands of *wild* native, artificially propagated native and non-native organisms as well as the spatial and temporal movement of nutrients and organic matter relative to what comes in and from whence it has come. Collectively, these determine the aggregate carrying capacity of the Basin for aquatic organisms.

Proliferation of Chemicals and Contaminants. There has been widespread and abundant introduction of synthetic chemicals into the Basin, and the amounts and diversity of those chemicals are stunning as well as of great concern. Bioaccumulation and biomagnification of chemical contaminants can reduce or eliminate critical components of the food web, leading to food shortages for higher trophic levels. Further, it can reduce the ability of species and individuals to cope with normal environmental stresses due to behavioral deficiencies, slower somatic growth rates and increased disease susceptibility. This problem is rapidly expanding and could negate many of the restoration efforts. Further, fish migrating from the oceans to fresh water transport persistent industrial pollutants acquired at sea. The positive feedback of nutrient additions from spawning adults is important, but there is also some negative feedback from pollutant delivery from the ocean. The net balance is unclear and needs careful documentation. Consistent with the Council's 2009 Fish and Wildlife Program (Sections D.1.g., p. 16 and D.2, p. 42), but not currently being fully implemented, the ISAB recommends that further work should:

> Engage with regional partners in pinpointing, quantifying and mapping the spatial patterns of these chemicals within the Basin, in measuring their transfer and accumulation rates, and in understanding the vulnerabilities of the region's food webs to them. The Council should continue to work diligently with other regional agencies to implement the recently completed interagency Columbia River Basin Toxics Reduction Action Plan and update it regularly, so that we can deal with current and future chemical insults to the system in timely fashion, before they become even more serious problems. This has to be a large, ongoing and collective regional effort.

Consequences of Non-native Species: Hybrid Food Webs. Continuing introduction and proliferation of non-native species, and their still poorly understood impacts on the native biota heighten the need to manage "novel, hybrid or no-analogue" food webs[2] in the future, those for which we have no historical reference. The Western Governors' Association Policy Resolution 10-4 on Combating Invasive Species has moved this issue forward for the western Region. The ISAB recommends that further work should:

> Mount a region-wide monitoring program on the temporal pace and spatial extent of non-native introductions, indentifying impending problems while they are still small and manageable. Once indentified, we should intervene quickly whenever and wherever invasive problems are likely to emerge, averting problems when possible, or slowing them down, when not completely avoidable. It is also timely to reevaluate our stocking practices for non-native species, in the larger context of the regional concern for production and conservation of its native biota. Some policy changes may be in order.

Beyond meeting these pressing threats, we need to anticipate and head off a variety of others that are impending, before they too become urgent. In general, we need to understand the consequences of:

Altered Nutrient Organic Matter (Energy), Water, and Thermal Sources and Flows. Nutrients and organic matter constitute the fuels for food webs. Water flow and temperature directly control their availability and incorporation into food webs. Continuing losses of marine-derived nutrients and riparian-derived organic matter, in addition to increased land-based leaching of nutrients and organic matter, accelerating eutrophication, ongoing atmospheric deposition of

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[2] The terms "novel, hybrid, and no-analogue" are used synonymously in this report when referring to existing and future food webs for which there is no historical reference.

nitrogen and micro-nutrients, as well as water storage, extraction and flow manipulation, collectively threaten to alter the Basin's food webs (Chapters D.4, D.6, and D.8). The ISAB recommends that further work should:

- Assess the magnitude of these problems and be able to predict the consequences of such alterations.

Disconnects among Critical Habitats and their Food Webs. Connectivity and timing impact the availability of the preferred foods of migrating juvenile fishes. Broad-scale changes in temperature, nutrient and chemical regimes, hatchery programs and habitat restoration affect the connectivity and timing of organisms with their food supplies. The Fish and Wildlife Program has already begun to address this issue in its restoration activities, but we need to extend those efforts considerably. The larger point is that we need to manage for total system productivity, rather than attempting to optimize each of a great many local system components independently. There are three related needs for effective reconnection of critical habitat, and the ISAB recommends further work should:

- Identify and quantify the critical connections between place-based production of foods and the timing of seaward movements by juvenile anadromous fishes, based on mechanistic understanding of their relationships within the Basin.
- Mount large-scale catchment projects, in both rural and urban locations, bringing diverse scientific and resource management expertise to bear, and delivering science of real management value. The Fish and Wildlife Program currently funds some floodplain restoration work, but a systematic campaign to restore floodplain food webs and reconnect them to the main channel is also needed.
- Establish the links between river discharge, floodplain inundation and fish production, and evaluate the food-web effects of large scale and seasonally appropriate floodplain inundation. The supplemental BiOp calls for NOAA to develop a life-cycle model, which should evaluate how to deliver the fish to the right place at the right time, with the right blend of food resources.

Plan for Environmental Change and Expect Some Surprises. Substantial habitat and other changes will continue over the remainder of this century. Management decisions made in this next decade (including the implementation of an FCRPS Biological Opinion) will affect food webs and other resources for the next several decades. Canadian and regional authorities are already planning for large scale water and power management needs for the next half a century. The ISAB recommends further work should:

- Insert the region's biota into the list of planning targets from the outset, ameliorating those changes we can do something about in the short run, and mitigating others over the long run. Provide forecasts over the next several decades, taking into account the anticipated climatic and anthropogenic changes that will impact the Basin's environment.
- Establish the planning goals for the Basin's complex biota and food webs, and mount modeling exercises to project the impact of alternative policy choices on all components. If accumulated experience is any guide, we can also anticipate that the Columbia River will continue to see unanticipated challenges from time to time.
- Establish a response system that can absorb short term ecological surprises readily, with strong rebound capacity. The ISAB urges the Council to set aside some funding for such challenges and for exploratory activities, to remain alert to impending challenges, and to provide early detection and proactive intervention when needed.

Fill Specific Knowledge Gaps

Proactive management of food webs can only be effective if we clear up several serious information gaps. Sadly, our base-level understanding of the Basin's food webs remains rudimentary. This report highlights a collection of vignettes on ecosystem and food web structure, but even those relatively well-studied exemplars reveal substantial and critical information gaps (see Chapter E.5). The ISAB suggests the Council consider extending current studies and projects to gather some of this much needed (additional) information as well as devote some resources and remedial attention to filling knowledge gaps. The challenges fall in four general areas: data gathering and synthesis, modeling, experimental testing of models, and evaluation of alternative policies. Specifically, we need to:

Data Gathering and Synthesis

- Determine the ability of the system to produce foods to support proposed or anticipated numbers of both wild and hatchery reared fishes at a level promoting adequate growth and/or successful migration.
- Fully understand the trophic consequences of adding hatchery fish to the system as well as the imported foods used to grow them and the waste products produced during rearing.
- Quantify incremental improvements in available foods and fish production derived from habitat-specific restoration activities, with special emphasis on floodplains.
- Mount a region-wide monitoring program to quantify the temporal pace and spatial extent of non-native introductions and continuing invasions, and to spot impending problems while still minor and manageable.
- Establish a monitoring strategy to track constituents and sources of contaminants, nutrients and organic matter, spatially and temporally. Further, determine the extent to which marine-derived nutrients are helpful, and, which pollutants and artificial chemicals are helpful and/or harmful.
- Identify the nutrients that enhance the productivity of food webs, and determine whether existing concentrations are limiting productivity. Keep in mind that ratios of nutrients also shape the structure of communities, and an imbalance of essential nutrients hampers productivity.

Modeling

- Quantify critical connections between place-based production of foods and the timing of movements by juvenile fishes, thereby establishing a mechanistic understanding of their relationships.
- Initiate directed studies and modeling of the impacts of the increasing chemical load on the organisms and thus on the structure, resilience and productivity of the aquatic food webs.
- Model how to get the fish where they need to be, when they need to be there, with the right blend of available food resources, thermal regimes and interactions with predators and competitors. Incorporate connected system thinking into management planning and coordinate agency efforts to improve total Basin productivity.
- Evaluate a broader application of seasonal environmental flows[3] to connect habitats, mitigate disruption and benefit ecological functions of food webs downstream.

Restoration Actions and Experiments to Test Model Predictions and Assumptions

- Determine where and when fish growth is density dependent as well as when hatchery fish may displace or otherwise cause wild juveniles to move downstream due to food limitations. Experimental manipulation of the number and timing of hatchery releases is a logical method to quantify this.
- Use large-scale experiments to evaluate the relationships between survival (smolt to adult) during years of different ocean productivities and river conditions. Consider the impact of altering hatchery releases during years of predicted poor ocean or river survival. Survival in the ocean is perhaps density dependent, and may be related to food availability and predation intensity. Survival in the river may be as well. Further, experiments should consider stage-specific size and growth to identify critical life stages and periods that impose important constraints on survival.
- Using a food web perspective, mount multidisciplinary, subbasin-scale catchment projects, including both rural and urban locations, to promote concentrated collaborative efforts among scientific investigators and resource managers. Use the projects to test predictions about the most effective food webs to sustain and enhance species of interest.

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[3] The quality and quantity of water necessary to protect aquatic ecosystems and their dependent species and processes in order to ensure sustainable development of water resources (Arthington et al. 2010).

- Restore the floodplains (including those in the estuary) and floodplain-supported food webs, and reconnect them with the main channel. While doing so, establish the relationships between river discharge, floodplain inundation, food webs and fish production. Experiment with large scale and seasonally appropriate floodplain inundation, and evaluate the food web effects.

Evaluation of Alternative Policies with Models

- Reevaluate stocking practices for non-native species, in the context of the regional concern for production and conservation of native biota. Some policy changes may be in order.
- Model scenarios of different policy options with respect to nutrient additions (e.g., direct fertilization, carcasses) or reductions as a guide to future management efforts. The process to date has been guided more by perceptions of benefit than by hard proof of success.
- Establish planning goals for the biota and food webs for the foreseeable future, taking into account anticipated climatic and anthropogenic changes impacting the Basin's environment. Mount modeling exercises to project the impact of alternative policy choices on all components.

A Strategy for Protecting the Best and Restoring the Rest

The ISAB agrees with the 2009 Fish and Wildlife Program's habitat strategies of "building from strength" and identifying "stronghold areas," restoring ecosystems and protecting areas. It is clear that biotic conservation is most successful where actions are aimed at protecting ecosystems rather than by attempting to restore or reclaim them after the damage is done. For the Columbia River Basin, the realization is growing that a concerted effort to protect the food webs of critical environments will be needed, and Congress is considering legislation (H.R. 2055 and S. 817) that would direct federal, state, local and private stakeholders to develop conservation plans that make new investments in the healthiest salmonid runs. To accomplish that, we need to preserve the most productive food webs, even while steering degraded systems to a more productive status. Specifically:

Identify Properties Sustaining Desired Ecosystem States. In deciding which habitats to preserve and which to restore, we need a sense of what our desirable end-targets are to be. Initial identification of "desired end states" was part of the Subbasin Planning exercise (ISRP & ISAB 2004-13), and that process should be expanded to include consideration of the constituent food webs. We need to:

> Determine sustainable food web structures for each of the eight broad habitat types enumerated in Section D of this report. For each broad type of habitat, execute carefully matched comparisons (healthy versus degraded), developing a blueprint for what to protect and what to restore; and develop reasonable targets for measureable outcomes, so that we can gauge ongoing success as we move forward with the preservation and reclamation effort.

Sustaining Resilient Communities. Food webs are resilient to some perturbations and vulnerable to others. Changes of some species and sensitivity to some abiotic factors have little impact, but changes in others have drastic effects. We need to:

> Identify rapidly changing habitats that are matched with stable reference sites, and then examine how biotic components and abiotic parameters differ between them, translate those differences into "real time" and "real world" sensitivity analyses, by characterizing the changes that occur in the food webs, and extrapolate from these empirical comparisons to wider predictions, and from there to policy choices.

Hybrid Food Webs as Legitimate Targets, while Maintaining Productivity. Rather than insisting on pristine food webs as targets, we need to move toward productive and resilient food webs containing both new and old biotic elements and resistant to mild perturbations. We need to:

> Synthesize what we know about biotic and abiotic factors, as well as processes, governing food web structure and function. We then need to build them into a very general food web modeling platform, such as the life-cycle model envisioned by NOAA, and then challenge the structure and resilience / sensitivity of the resulting food webs in the face of changing inputs. We envisage an effort on the pattern and scale of the COMPASS effort. We also

need to ground-truth (benchmark) model predictions against empiric reality for the cases used to construct the model, as well as for others that it should be able to mimic.

Restore for a Changing World. Water quantity/quality, seasonal flow patterns, and non-native species introductions will respond to ongoing climate, population, chemical inputs and land use changes, and their effects are likely to conflict with some of the Council's restoration goals. Most current restoration plans implemented under the Fish and Wildlife Program or under the NMFS FCRPS Biological Opinion make little or no allowance for changing conditions and rarely address their influence on food webs. The Council and NOAA Fisheries, through the action agencies, should consider a targeted solicitation for proof-of-concept proposals that deal with conserving food webs in a changing environment. We need to:

- Build consideration of the likely effects of such changes into future habitat restoration projects; insist that restoration proposals explain (on the Taurus Proposal form) how the proposed actions will accommodate or otherwise respond to future conditions, especially as these relate to food webs; and develop landscape-based strategies that emphasize food web restoration in high impact areas and conservation in low impact areas.
- Carry out management experiments at a scale and control level similar to the habitat restoration experiments now being evaluated in intensively monitored watersheds (IMWs). Through the Integrated Status and Effectiveness Monitoring Program (ISEMP), establish meaningful long-term monitoring on all food web-related restoration/reclamation projects, and evaluate successes and failures. There are many uncertainties and threats to project success, and we need to assess the conditions under which success or failure is likely if we are to be effective. Further, initiate controlled proof-of-concept restoration demonstrations at a scale that is sufficient to provide confidence of benefits, rather than concentrating on "targets of opportunity" as choices for restoration/reclamation projects.

The Case for a Comprehensive Food Web Model. It is critical to connect growth performance in freshwater, estuarine and marine habitats. If fish have a difficult season in terms of growth during one or more freshwater habitats, can they compensate during later life stages? Throughout this report, the need for better quantitative food web and related bioenergetic models has arisen repeatedly. The need for a major modeling effort to build a "total system model" of the Basin is abundantly clear. The effort would be large and would need to be sustained, but necessary for understanding the Basin as an integrated system. It is unclear how to model a system as large or complex as the Columbia River Basin, but that is the challenge facing habitat restoration and management. The model could be developed in parallel with the life-cycle model envisioned by NOAA (Crozier et al. 2008).

A Time-Prioritized Action Plan

The ISAB suggests that the Council consider a systematic action plan addressing the concerns outlined above. We envision a concerted 12-year plan with an estimated *total* cost of at least $20-25 M. This estimate is given only to provide an initial sense of the scope and scale of the food web issues. The food web activities could be nested within the existing Fish and Wildlife Program, representing on the order of 1% of annual budget. Some of the suggested projects fall naturally under the Monitoring section of the Program, as they involve determination of the state of the system, both in advance of intervention and for progressive monitoring as the effort unfolds. Some fall under the Habitat section of the Program, as they involve efforts at habitat manipulation and/or restoration/reclamation. Some fall under the Production section of the Program, as they may involve adjustments to which fish are reared and released, in what numbers, and where. The rest of the suggested projects fall under the Research portion of the Program, particularly those aimed at filling information gaps.

Collectively, these investigations and activities need to be well integrated with the accelerating landscape-scale changes taking place, as well as being well coordinated with complementary research and management activities by agencies and Tribes. As we know so well, this is not a trivial task. Nevertheless, a focus on food webs provides a strong complement to the ongoing emphases on hydrosystem, habitat, hatcheries and harvest (the four H's).

A. Food Webs: Concepts and Applications

It is through the food relation that animals touch each other and the surrounding world at the greatest number of points, … the struggle for existence becomes sharpest and most deadly; and, finally, it is through the food relation almost entirely that animals are brought in contact with the material interests of man.

Stephen A. Forbes, *The Food of Fishes*, 1880

A.1. Food Webs and Restoration of Columbia River Fish and Wildlife

The vision for the Northwest Power and Conservation Council's (Council or NPCC) Columbia River Fish and Wildlife Program is to establish and maintain an ecosystem that sustains an abundant, productive, and diverse community of fish and wildlife (NPCC 2009-09:6). This vision further embraces the concept that the Columbia River ecosystem provides opportunities for tribal trust and treaty-right harvest as well as for non-tribal harvest. Achieving this multi-faceted vision involves actively mitigating across the Basin for the adverse effects of hydrosystem development and operation on fish and wildlife and re-establishing conditions that allow for fish and wildlife recovery. In general, species recovery includes but is not limited to those species listed under the Endangered Species Act.

This report reviews the contemporary knowledge about food webs, especially those in the Columbia River Basin. In discussions of how to best achieve the Fish and Wildlife Program vision, the ISAB noted that many studies have been conducted in the past three decades on local or site-specific questions involving food habits, predation, and other food-related species interactions in the Basin and elsewhere. The ISAB also found considerable scientific evidence, through past research by its members and many other scientists, to suggest that a broader scientific foundation incorporating food web concepts as well as detailed studies would significantly benefit basinwide restoration efforts, help sustain the ecological system and provide for more productive fisheries. The Report makes the case for broadening our scientific foundation to more consistently include a food web perspective in our thinking, in applied research and restoration approaches, and in the evaluation of the benefits of research activities proposed for funding by agencies, tribes and NGOs. An adequate consideration of the food web perspective complements other perspectives and thereby enhances our scientific foundation to meet the vision of the Fish and Wildlife Program.

What is a Food Web?

The concept of a food web is one of the most useful, but most challenging, ideas in ecology. Food webs describe pathways by which energy, nutrients and other materials make their way to species of ecological, social, cultural and economic interest. A food web reflects in a general way the range of environmental factors encountered in a community. These include habitat conditions, habitat carrying capacity, species diversity, the mix of native and non-native species, chemical contaminants, nutrient delivery and cycling, competition, predation, parasitism, disease and other ecological processes. Food webs, although highly complex, have been successfully manipulated at large scales to improve water quality as well as recreational fisheries (e.g., Carpenter et al. 1985, 1995). Ill-advised manipulations of food webs have resulted in serious environmental issues – the introduction of *Mysis,* a freshwater shrimp, in the Basin being one example (Spencer et al. 1991, Nesler and Bergersen 1991).

All life is linked by food web processes such as photosynthesis, decomposition and feeding. Collectively, these provide and transfer energy for living, growing and reproducing. The tangible expression of these processes will vary with scale. At the ecosystem scale food web processes help shape the biotic structure of communities as well as the overall productivity and resilience of the ecosystem. At the community scale, food webs linking similar species assemblages can function quite differently as a consequence of physiological and behavioral responses by individuals – especially those at higher trophic levels – to different environmental conditions, habitat, and natural or human perturbations. At the species scale, food preferences and requirements can shift during ontogeny such that older individuals consume different foods than juveniles.

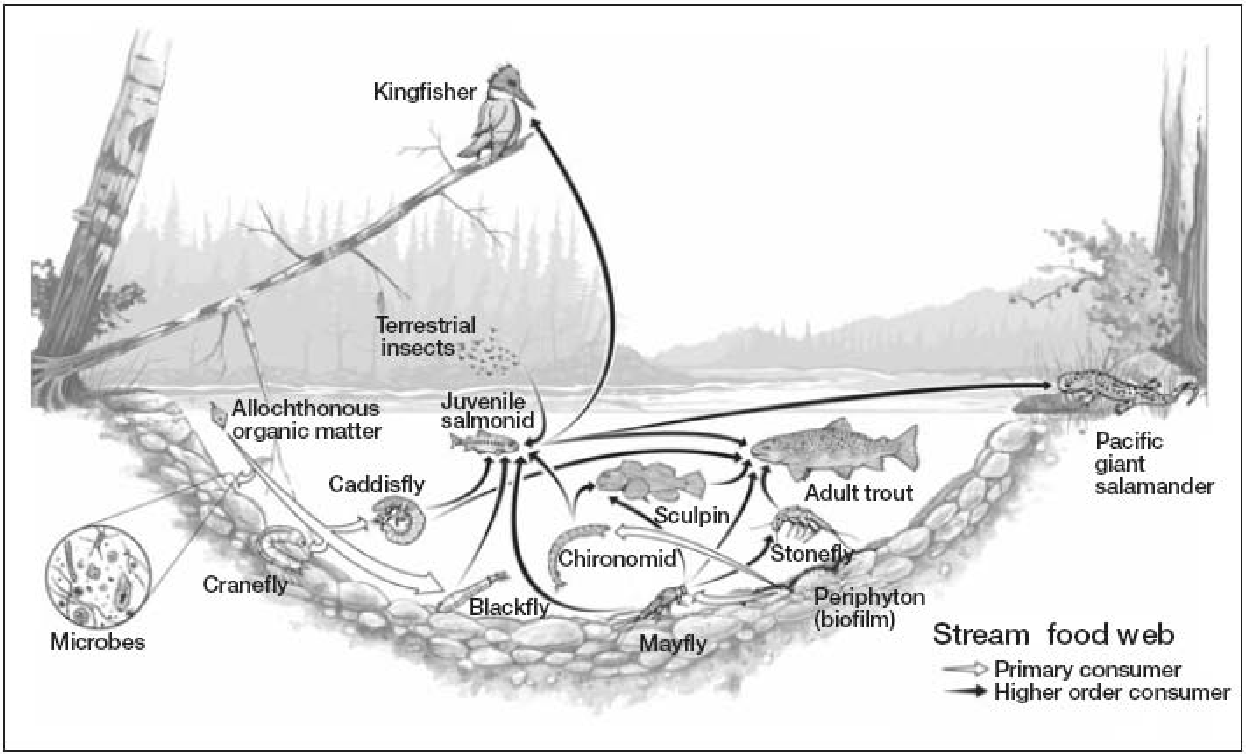


Figure A.1.1. A simple food web for a representative Pacific Northwest salmonid community (from Macneale et al. 2010)

A Definition. Food webs describe trophic relationships between the species within an ecosystem or within a particular place (Figure A.1.1). Although these trophic relationships are difficult to sample, measure, describe and model, they are of central practical and theoretic importance because they characterize how energy and biomass are transferred from producers to consumers. There are several important facets to food webs. Whereas, food chains and food webs illustrate only connections between species, food networks or food budgets illustrate the relative quantity of energy, nutrients, toxins or biomass being transferred through many (tens to thousands) connections. Collectively, these can be quantified and modeled to produce a clearer understanding of how nutrients and energy are assimilated into productive fisheries or, at the other extreme, into degraded environmental conditions. Further, understanding food webs from an ecological or quantitative perspective, and more broadly the ecological networks they represent, is central to understanding the response of ecosystems to perturbations (Pascual and Dunne 2006b). One key response variable is that of resilience, the ability of the biotic system to absorb and recover from perturbations.

A Brief History. Broad descriptions of food webs first appeared in the late 1600s, but it was not until the early 1700s that the concept was generalized (Egerton 2007). Detailed accounts of fish feeding first appeared in the late 1800s (e.g., Forbes 1880, and others), but feeding relationships among species had been conceptualized many decades earlier by scientific visionaries such as Charles Darwin. The earliest formalized food webs were published in the 1910s and became somewhat quantitative by the 1920s (e.g., Pierce et al. 1912, Petersen 1915, Hardy 1924). The pioneering population ecologist Charles Elton (1927) coined the term food chain, and termed all the food chains in a community a food cycle, which we now call a food web. With the proliferation of new techniques and modeling approaches, the ability to quantify food webs and their internal processes has expanded exponentially in recent years (Pascual and Dunne 2006a; Appendix A). In recent decades food webs have been effectively used to trace radioactive chemicals (Odum 1959) and pesticides (Carson 1962, Woodwell 1967), and raise public awareness for legislative actions toward pollutants.

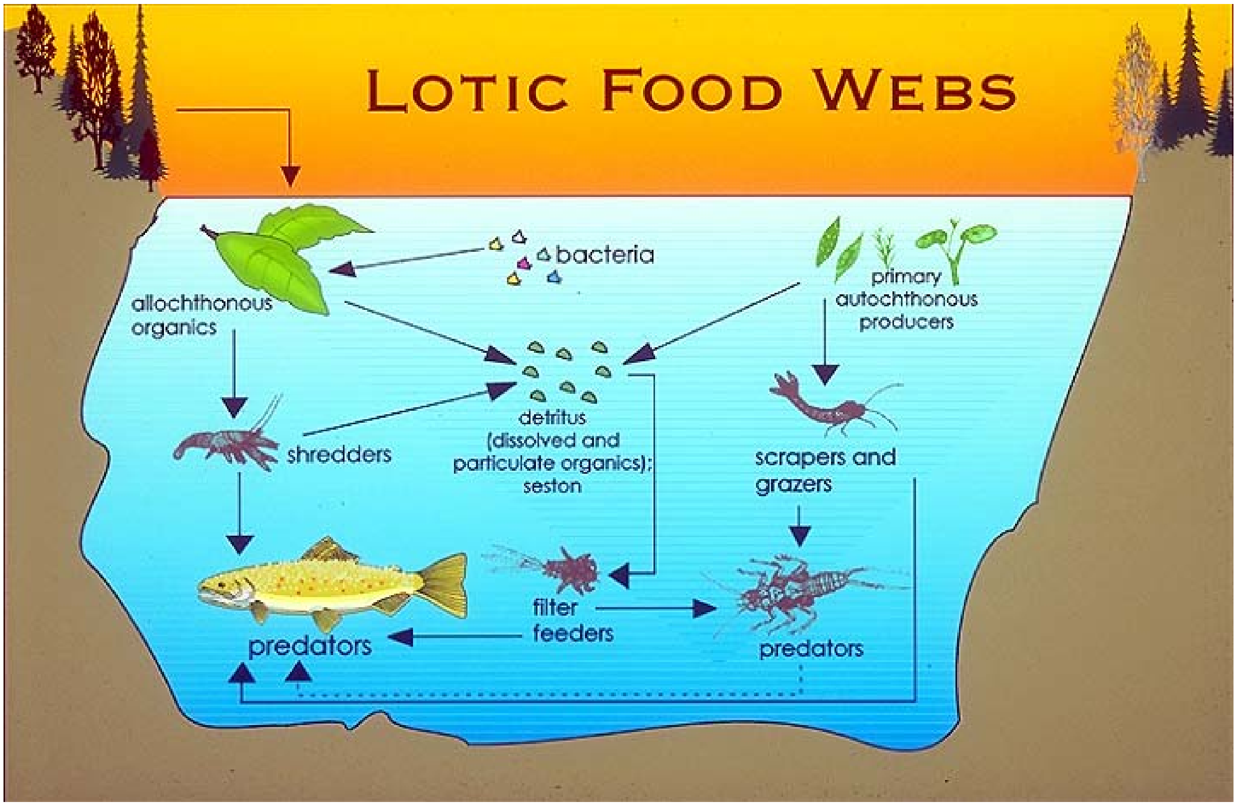


Figure A.1.2. A traditional conceptual food web for a small forested stream showing important functional nodes regulating the production and transfer of organic matter and nutrients. Inputs of organic matter and nutrients from the riparian forest, as well as in-stream primary production, are consumed by a variety of microbes and invertebrates which, in turn, are consumed by insect and fish predators. This conceptualization, although instructive, has been shown to be too simple for a comprehensive understanding of stream systems. Contemporary and more comprehensive food webs, with their inherent complexity, are described throughout this report.

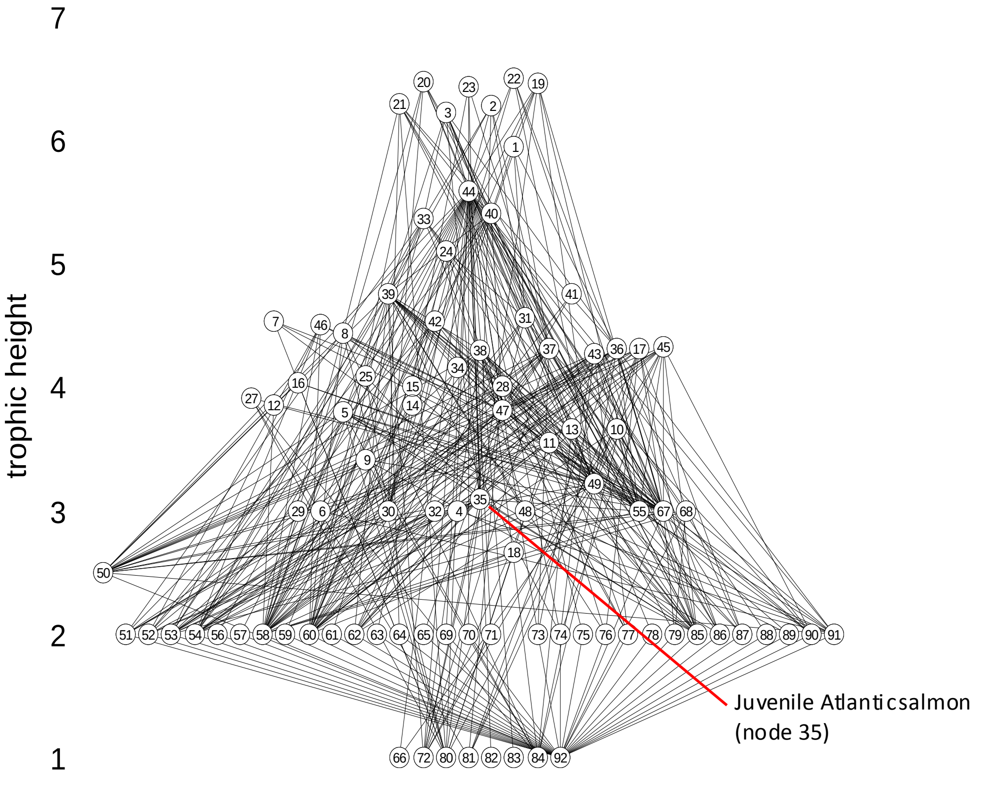
Why Food Webs are Important. The structure of food webs and processes associated with them are important because they determine how the many different system components act collectively – and sometimes synergistically – to support the resilience and productivity of ecological systems (Figure A.1.2). Each component of the food web, whether it is a primary producer such as an algae, an external (allochthonous) input of organic matter such as leaf litter, a microbial decomposer such as a bacterium, or a tertiary consumer such as a fish, possesses intricate physiological and behavioral dynamics that enable it to respond to slight changes in environmental conditions. Further, when a predator has a pronounced effect on its prey population, its influence can extend beyond the prey and reverberate throughout the food web – a process known as a trophic cascade.

A food web can be viewed as a "complex adaptive system" (Levin 1998) in that it exhibits structure (a sustained diversity of individual components), function (the components interact through localized connections), and behavior (inputs and outputs), and it adapts to the environment as natural selection reinforces particular subsets of local interactions. Thinking about food webs in this way can help us explore their stability and persistence, and thus, improve our understanding of factors that make ecosystems resilient or sensitive to human related perturbations (Pascual and Dunne 2006b).

Food Web Structure, Function and Dynamics

Initially, energy enters the food web from the sun via primary producers, or autotrophs, which synthesize complex organic substances (carbohydrates) from light, carbon dioxide and nutrients. These organisms are typically photosynthetic plants such as macrophytes, mosses, diatoms and algae that use sunlight as an energy source. A few, such as those found under anaerobic conditions, are chemotrophic, using chemical energy from methane, nitrate and other molecules instead. Organisms acquiring their energy by consuming organic substances are referred to as heterotrophs. Heterotrophs include microbes (predominantly bacteria and fungi), which obtain energy from dissolved and particulate organic compounds; herbivores, which obtain energy by consuming live plants; carnivores, which obtain energy from eating live animals. Ultimately detritivores, scavengers which consume dead biomass and associated microbes, derive energy from the remains of animals and plants.

A food web is a set of interconnected food chains by which energy and biomass circulate within an ecosystem from one organism to the next and to the next and so on (Figure A.1.3). Organisms in a food web are often grouped into trophic levels, based on the number of links that separate them from the primary producers. Trophic levels may contain either a single species or a group of species that are presumed to share both predators and prey. They usually start with a plant and end with a carnivore. Riparian plants, instream algae and diatoms, dissolved organic matter, and occasionally phytoplankton, form the base of most riverine food chains. The total biomass of each trophic level generally decreases from the base of the chain to the top. This is because energy is lost to the environment with each transfer. On average, only 10% of the organism's energy is passed on to its consumer. The other 90% is used for the organism's life processes or is lost as heat to the environment. Directly linked to this are pyramids of numbers; as the energy and biomass are transferred along trophic pathways, the number of consumers at each level declines significantly so that a single top consumer (e.g., a salmon or a seal) will be supported by literally millions of separate producers (e.g., diatoms). However, it should be noted that some producers with low biomass, especially periphyton, are so productive and have such a high turnover rate that they can actually support a larger



Juvenile Atlantic salmon (node 35)

Figure A.1.3. The food web of the Ythan estuary, Scotland (Montoya et al. 2006). Each numbered node refers to a specific organism or a functional grouping of organisms. Note number 35, near the middle of the food web, is juvenile Atlantic salmon. The trophic height (y-axis) concept is described in Chapter C.3

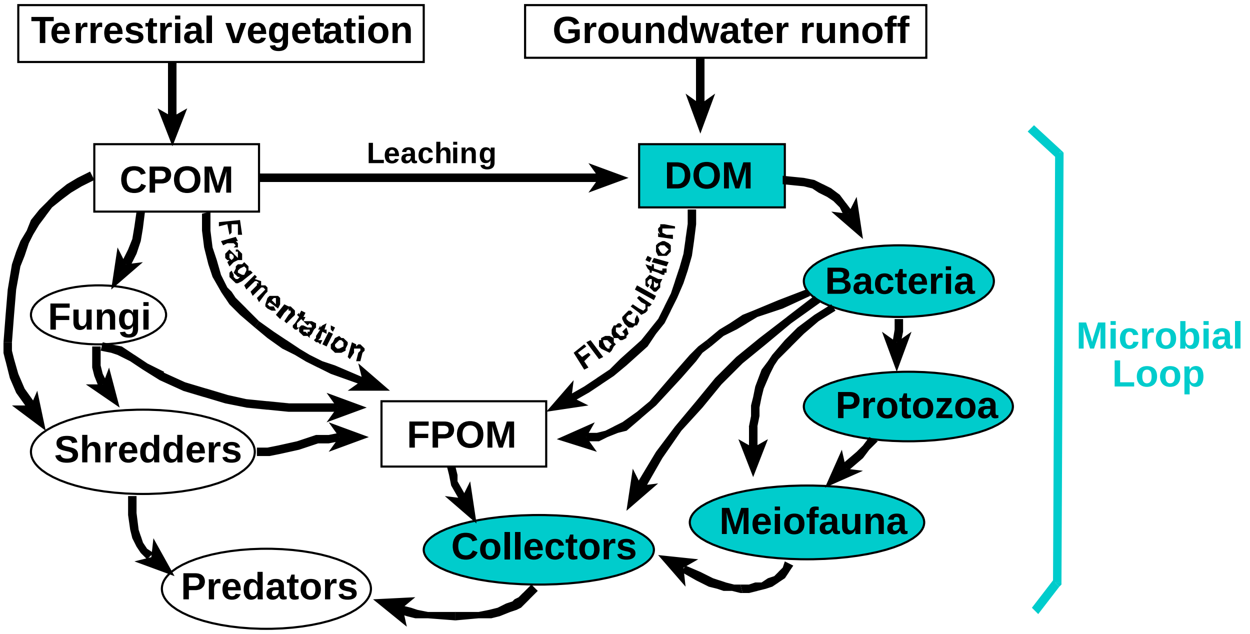


Figure A.1.4. The microbial loop. This pathway plays a vitally important role in food webs as dissolved organic matter and nutrients are assimilated into forms that can fuel higher trophic levels. CPOM = coarse particulate organic matter, FPOM = fine particulate organic matter, and DOM = dissolved organic matter.

biomass of grazers.[4]

Graphically displayed food webs, such as that for the Ythan estuary in Scotland (Figure A.1.3), are simplified representations of what actually happens in nature. The food web as it is drawn may only show a fraction of all actual pathways to emphasize those that are considered most important for the transfer of nutrients and organic matter. In reality, most consumers feed on multiple species and are, in turn, fed upon by multiple other species. Further, the relations of detritivores and parasites are seldom adequately characterized in such illustrations. The number of species and links described in the food web of even a depauperate stream or lake of low productivity will contain at least a hundred species with nearly a thousand links (Woodward et al. 2005, Woodward 2009). More productive streams or lakes will have over a thousand species with an, as yet, undetermined number of links (Allan 1995).

A food web is typically divided into two broad realms: the grazing web, which typically begins with algae, or periphyton, and the microbial web, which begins with organic detritus. These webs are comprised of individual food chains. In a grazing web, materials typically pass from plants to plant eaters (herbivores) to flesh eaters (carnivores). In a microbial web, materials pass from plant and animal matter to bacteria and fungi (decomposers), then to detrital feeders (detritivores), and then to their predators (carnivores; Figure A.1.4). Generally, there are numerous omnivores that consume a diversity of materials and prey. The more steps between producer and final consumer, the less energy remains available. In a food web there are seldom are more than four links along any pathway between base and top, or five levels (however, see Figure A.1.3 for the Ythan estuary, Scotland).

Importance of Food Webs in Sustaining Resilience and Productivity

Since Sir Alister Hardy's pioneering work in the 1920s on the feeding relationship of North Sea herring with planktonic assemblages, investigators have tried to understand how food web complexity affects community stability and ecosystem productivity. Nearly four decades later, the relationship between the number of links in food webs and community stability remained contentious (e.g., MacAuthur 1955). Recent theoretical advances, however, have allowed development of more sophisticated mathematical models that better predict the dynamics of food webs and their roles in maintaining ecosystem properties (see

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[4] There is an important distinction between standing crop of biomass and productivity. Standing crop (biomass) refers to the amount of organic matter or nutrients existing at a specific location; productivity refers to the rate at which the biomass is accumulated (or depleted) over time.

Sidebar A.1.1). Today there is increasing evidence that greater complexity (more species and/or links) can increase the stability of a food web – but only if most links are weak (e.g., relatively little energy flows through the link; McCann et al. 1998). Evidence from natural systems reveals that most links are weak because many species feed opportunistically on a variety of prey. Experiments in streams often demonstrate that even though predators occasionally can have strong impacts on a few prey species, they have much weaker effects on many others (e.g., Woodward and Hildrew 2002), and these effects can reverberate throughout the system in strong and surprising ways (e.g., Baxter et al. 2007). Nevertheless, researchers agree that food webs are a cornerstone for sustaining ecosystem resilience and productivity. It is the inherent taxonomic complexity, the numerous linkages, the strength of those linkages, and the structural variability of food webs over space and time that sustain species of economic and cultural interest.

Food chain length, which is the number of energy transfers from the base of a food web to the top, is a central characteristic of food webs and of great importance to ecological communities (Sabo et al. 2010; see Chapter C.3). Food-chain length has attracted considerable attention for nearly a century because it strongly affects community structure, ecosystem processes including nutrient cycling and biomagnification of contaminants, and the productivity of many species of commercial and cultural interest. Conventional wisdom holds that more than just resource availability determines food chain length (Post 2002). What, then, determines food chain length? Evidence points toward a complex and contingent framework of interacting constraints that includes the history of community organization, resource availability, the type of predator-prey interactions, disturbance and ecosystem size. Within this framework, current investigations are centered upon when and where the different constraints operate to determine food chain length.

Sidebar A.1.1. Food Webs and the Internet

In addition to food web networks, there has been considerable examination in recent years of other complex networks, and these have important lessons for natural resource management. One such network is the Internet (Bascompte 2009). Network-related research has been motivated by the belief that the structure of a network will greatly affect its resilience (e.g., ability to overcome perturbations) and "robustness" (e.g., ability to effectively handle huge amounts of information). Understanding that structure and the mechanisms that contribute to robustness could support more effective management of other kinds of networks.

Understanding the extent to which the Internet (and food webs) is resilient to failure of an individual node is important and is an issue that must be addressed at the level of the entire network. In the case of the Internet, robustness is not so much a property of each of the servers, but of the overall network of relationships among servers. Early on it was thought that a resilient and robust network would have nodes that are equally connected – in other words, it would be "homogeneous". However, in reality the Internet is very heterogeneous with the bulk of nodes having a small number of connections, but a few nodes having many more connections than would be expected by chance.

Researchers are exploring the consequences of this heterogeneous Internet structure. Computer simulations seeking the point of failure in the Internet show that homogeneous networks are quite fragile. When a few nodes are removed the network collapses (Albert et al. 2000). Heterogeneous networks are much more robust and resilient to the random loss of nodes. In this case, the highly connected nodes act as the "glue" bringing robustness and resilience to the whole network. However, these nodes also can be the network's "Achilles heel"; if these highly connected nodes are seriously damaged or removed, the network may collapse.

The implications for natural resource management, and food webs, are obvious. Even though natural systems can evolve and respond to some changes, simplifying system-scale properties can have fundamental implications for the entire system. This example illustrates why understanding the structure and dynamics of food webs is so important for assessing their behavior.

These constraints become an especially important consideration in systems where environmental conditions have been substantially altered, possibly permanently, by human actions (Sabo et al. 2010). Factors that influence food chain length significantly influence abundance and productivity of high trophic level species that are of interest to humans, such as salmon and marine mammals.

Key Uncertainties and Technical Challenges with Food Webs

Food webs are difficult to quantify. Even ones that are perceived to be "simple" are, in reality, highly complex and vary by habitat type as well as over time. Moreover, the taxonomy of the myriad organisms in a food web is often poorly known. Although techniques for quantifying food web connections are developing rapidly, few contemporary descriptive models can provide accurate predictions of future conditions (Appendix A). Rarely do reasonably complete quantitative food webs exist for aquatic systems, especially spatially extensive and diverse ones. The key challenge for developing a comprehensive understanding of the Basin's food webs is to address the complexity in terms of space, time and taxonomy using the best contemporary techniques and emerging models.

Perhaps the greatest technical task is unraveling the taxonomy, especially for smaller organisms. Despite centuries of investigations of the Earth's biota, the taxonomy of freshwater organisms and their distributional patterns are only just beginning to become clear (Dudgeon et al. 2006, Balian et al. 2008). Adequate data on the diversity of most invertebrate groups in fresh waters do not exist, but high levels of local endemism and species richness seem typical of several major groups, including decapod crustaceans, molluscs and aquatic insects such as caddisflies and mayflies (Balian et al. 2008). Studies using a combination of approaches show that numerous protists (e.g., ciliated protozoans) may have restricted geographic distributions (Foissner et al. 2003), implying they could be richer in species than is currently supposed. It is highly likely that the richness of freshwater fungi, bacteria and microalgae has been equally underestimated (Gessner and Van Ryckegem 2003).

Fortunately, new techniques are helping to elucidate food webs. Two important ones are (1) the use of naturally-occurring stable isotopes of carbon (C), nitrogen (N), and sulfur (S), among others, to track the movement of nutrients within food webs; and (2) the use of molecular genetics (e.g., "bar-coding") to identify the organisms in food webs, especially smaller organisms that are otherwise difficult to collect, sort or directly observe (Avise 2004, Fry 2008; Appendix A). The use of stable isotopes to quantify food webs is predicated on the observation that organisms acquire a distinct signature because the ratios of stable isotopes of C, N, and S in body tissues reflect both location of origin and trophic history. Subtle environmental influences such as resorption of nutrients from senescing leaves or even plant age can complicate interpretation of stable isotope data (Fry 2008). Nevertheless, this approach is providing reasonably quick, accurate and routine analyses for general food web characteristics. Molecular genetic identification of species, even with inherent technical pitfalls, is another promising approach for deciphering food web structure since so few aquatic organisms are readily identifiable to species (Moritz and Cicero 2004, Avise 2004).

The grand challenge in understanding aquatic food webs is, however, to integrate molecular (genomic), biogeochemical, environmental and economic information into a general model quantifying ecological networks (Belgrano et al. 2005). If successful, we could begin to elucidate mechanisms governing ecosystem dynamics across scales, levels of biotic organization and biological diversity, and their relative roles in driving the complex network of interactions among the abiotic and biotic components of ecosystems.

Why are Food Webs Important in Columbia River Basin Fish and Wildlife Restoration?

Recent ISAB reports, such as those on climate change, non-native introductions, estuarine conditions and spill-transport, have included some discussion of food webs (See Chapter A.2). This ISAB food web review compiles those findings and builds upon them to address food web dynamics at primary (e.g., microbial and primary production), secondary (e.g., consumers of microbial and primary production), and tertiary (e.g., predators) levels. A diverse literature has been compiled and reviewed to produce a coherent summary that identifies future directions for research to improve strategies for the restoration of fish and wildlife in the Columbia River Basin.

Many answers to our most fundamental questions regarding fish and wildlife restoration in the ensuing decades require an adequate understanding of the relevant food webs. For example, with regard to effects on abundance, productivity diversity and spatial structure in the Basin, we can ask:

- What are the ecological consequences of changing the river from a primarily benthic-based production system to one that is now predominantly pelagic-based?
- How do intensive and selective fisheries (e.g., those for northern pikeminnow) reverberate through food webs?
- What are the ecological consequences of the large numbers and consistent annual levels of salmonid hatchery releases?
- Are the preferred foods of migrating juvenile salmon available in sufficient quantities, and at the right times?
- How vulnerable are existing salmonid food webs to near term climate-induced changes?
- Do marine-derived nutrients released from the bodies of spawning salmon contribute to the survivorship and productivity of the subsequent generation, as well as enhance the productivity of the entire biotic community?
- What are the quantifiable, system-scale impacts of sea lion and bird predation?

- How might projected changes in agricultural land use and water withdrawals impact food web structure?
- Can a general model be developed to predict the food web consequences of proliferating non-native species (e.g., shad, bivalves) on the foods of native species?
- What is the magnitude of chemical contamination and the consequences for food webs?
- How has habitat restoration activities affected food webs, especially in comparison to those in comparable natural habitats?

During the scoping phase of this report, the Council, NOAA Fisheries, and the Columbia River Basin Indian Tribes agreed that the above questions were important to Basin's fish and wildlife restoration efforts. Food web processes underlie limitations on native fish production and thereby have implications for fish and wildlife restoration efforts. In addition to density effects, food webs underlie a wide range of trophic interactions, including accumulation and biomagnifications of toxins, species competition and predator-prey relations, all of which are important considerations for restoration.

Objectives of this Report

This report is intended to provide a fundamental understanding of aquatic food webs in the Basin and their effects on native fish restoration efforts. The spatial scope includes tributaries, impoundments and the mainstem Columbia and Snake rivers, as well as the estuary and plume. The open ocean, although of immense importance in sustaining salmonid populations (e.g., Ruggerone et al. 2010), is not considered here because it involves an additional set of complex issues requiring a separate focused effort. Nevertheless, there is urgency in developing a better understanding of food webs underpinning the growth and vitality of native fishes in the freshwater and estuarine portions of the Basin. That urgency relates to rapidly changing, and in many cases declining, populations of native fishes despite massive efforts to sustain and restore suitable habitats.

This review comprises five complementary sections. General concepts and applications related to food webs are examined first (Section A), followed by a brief description of the physical setting of the Basin (B), a detailed discussion of key environmental processes affecting food web characteristics (C), an examination of food webs in typical habitats (D) and, finally, a system perspective on Basin's food webs that integrates our findings with contemporary and emerging issues (E).

A.2. Why Understanding Food Webs is Important

It is widely acknowledged that sustaining[5] freshwater habitat for salmonid abundance or viability, especially when ocean productivity is low, is vitally important (Naiman et al. 1995, Ruggerone et al. 2009). Freshwater habitat not only provides living space, it provides the foods needed for growth and survival. This has been broadly acknowledged by the ISAB for the Columbia River. Since 1995, food web issues have figured substantially in at least 22 ISAB/ISRP reports as well as the book Return to the River (Williams 2006; Table A.2.1).

Outside of the estuary, the plume and a few other restricted habitats, surprisingly little is known about food webs in the Columbia River Basin, or their influence on the survival and production of native fishes and wildlife. Most studies have been at relatively small scales, such as individual stream reaches or single reservoirs, and most examined interactions among very few species. Further, attempts to understand how food webs will change with projected shifts in environmental conditions or community composition, or even descriptions of how food webs change progressively from the tributaries downstream to the ocean, are extremely rare. This is despite food web processes being central to the survival of migrating juvenile fishes as well as system productivity. With the proliferation of contaminants and non-native species, and the greatly modified riverine, estuarine and lake environments, food webs have been substantially and fundamentally altered from those existing prior to extensive hydropower, agricultural and other human developments. Are contemporary food webs functioning in a manner that can support viable ecological systems for native fishes, or have they been so fundamentally altered as to impede (or even preclude) costly restoration efforts? How have changes in the mainstem and estuarine food webs altered the capacity of the system to produce salmon and sustain native fishes?

Since food web processes underpin native fish production, they have strong implications for fish and wildlife restoration efforts. These implications relate to trophic interactions, accumulation and biomagnifications of toxins, species competition and predator-prey relations, all of which are integral to productive and resilient populations. Understanding food web interactions should inform management and restoration actions, including an understanding of their likely impacts, opportunities and outcomes.

Management Applications

Sustaining and improving native fish populations in the Basin requires a comprehensive understanding of the biophysical environment supporting them, including pathways by which the fish are nourished. Understanding properties that sustain ecosystems and their functions is critical at this time of rapid environmental change and habitat loss, when perturbations to ecological structure are unavoidable (Pascual et al. 2006).

There are many implicit and untested assumptions in habitat restoration efforts, one of which is that habitat restoration will improve food supplies. However, other changes associated with hydropower development, land use, contaminants and invasive species may effectively neutralize any localized habitat restoration for economically and culturally important species. Given present environmental conditions - it is not yet clear how food webs underpinning native fishes might best be restored. Knowledge of the spatial and temporal characteristics of aquatic food webs could improve efforts to manage the sustainability of a highly altered and complex system. At a minimum, it would improve understanding of the present day environment, and reveal how current conditions fundamentally impact fish survivorship and fish production.

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[5] The ability to thrive or endure under changing conditions.

Table A.2.1. ISAB and ISRP reports containing references to the importance of food webs in the Columbia River Basin

Report Number	Title
ISRP 2009-16	ISRP Review of Lake Roosevelt Fisheries Guiding Document
ISAB 2008-5	ISAB Snake River Spill-Transport Review
ISAB 2008-4	Non-native Species Impacts on Native Salmonids in the Columbia River Basin
ISAB 2008-2	ISAB Review of the Estuary Recovery Module
ISAB 2007-3	Human Population Impacts on Columbia River Basin Fish and Wildlife
ISAB 2007-2	Climate Change Impacts on Columbia River Basin Fish and Wildlife
ISAB 2007-1	Latent Mortality Report
ISRP/ISAB 2005-20 Pt 2	Example Summary Research Plan 2007-2013
ISRP 2005-14	ISRP Retrospective Report 1997-2005
ISAB 2005-4	Harvest Report
ISRP/ISAB 2004-13	Subbasin Plan Review
ISAB 2004-2	ISAB Findings from the Reservoir Operations / Flow Survival Symposium
ISAB 2003-3	Review of Salmon and Steelhead Supplementation
ISAB 2003-2	Review of Strategies for Recovering Tributary Habitat
ISAB 2003-1	Review of Flow Augmentation: Update and Clarification
ISAB 2001-7	A Review of Salmon Recovery Strategies for the Columbia River Basin
ISAB 2001-3	Hatchery Surplus Letter
ISRP 2000-10	Review of Fiscal Year 2001 Innovative Proposals
ISAB 2000-5	The Columbia River Estuary and the Columbia Basin Fish and Wildlife Program
ISAB 2000-3	Report on the Council’s Artificial Production Review
ISAB 99-5	Lake Pend Oreille Kokanee Net Pen Alternative: Response to Questions from the Northwest Power Planning Council
ISAB 99-3	Looking for Common Ground: Comparison of Recent Reports Pertaining to Salmon Recovery in the Columbia River Basin

Complexity and System-scale Processes

Food web interactions in the Basin encompass a complex array of habitats spanning a network of headwater streams, tributaries, lakes (which may contain resident-only or mixed resident and anadromous fish communities), mainstem river reservoirs and free-flowing reaches, freshwater and brackish estuaries, river plume and coastal ocean habitats. Myriad organisms are linked trophically within these inter-connected habitats, but not all linkages are equal. The challenge is to filter the immense array of potential connections down to a tractable subset of interactions significantly influencing the structure and function of the food web as a whole. That subset can be modeled to understand, and perhaps predict, the population dynamics of species of interest (Sidebar A.2.1).

Sidebar A.2.1. Network Analysis of Food Webs

Network analysis of food webs is not new. MacArthur (1955) suggested that the stability of food webs might be roughly proportional to the logarithm of the number of links in the web. In contrast, May (1972) suggested that in general food webs, those assembled randomly by assigning links to species, many species with stronger connections between them weaken the system. Of course, food webs are not randomly assembled. Much of the following 30+ years has been devoted to the underlying topology of food webs and the effects of species removals on stability, to understanding differences (or the lack of them) between terrestrial and aquatic webs (Dunne et al. 2004), and to what sort of topology contributes to stability.

A number of procedures have been proposed to simulate food webs that result in webs with differing topological characteristics (Dunne and Williams 2009). It is not clear which, or if, any of these procedures produce webs that truly mimic those in nature, or if there is a basic underlying topological structure that mimics real food webs (Dunne et al 2002a). This is a critical issue since there are few empirical food webs available, and thorough studies of such processes as cascading extinctions and community collapse require many examples.

The most critical issue in the theoretical study of food webs (and most critical to the persistence of the Columbia River ecosystem) could be the impact of primary species loss or substitution on the potential for secondary species extinctions, and extinction cascades. In many simulated food webs, hierarchical feeding – a basic feature of food web structure – appears to reduce the resilience and stability of the system; while for empirically derived food webs it seems to increase stability (Dunne and Williams 2009).

Recent studies have concentrated on the role of species richness and web complexity (or connectance) in the resilience and stability of food web networks. Species richness is simply the number of nodes in the network (in many cases one node may represent a number of closely related species, e.g., all spiders). Connectance is defined as the fraction of possible links among species that are actually realized. Dunne et al. (2002b) found no relationship between species richness and stability of 16 high quality empirical webs in simulated species removal experiment models; however in removal experiments with simulated, but supposedly realistic networks, they found a strong positive relationship between resilience and stability and both species and connectance when the experiments involved removing the most highly connected or randomly chosen species first. They also found cases where network stability was surprisingly sensitive to sequential removal of the least connected species. One general result that seems to follow from these model based analyses is that stability of a network impacted by species loss increases with species richness. An unknown outcome is what happens when native species are displaced by invasive species, as is happening in the Basin today.

A second area of study has focused on the positional importance of species in food web networks (keystone species). There are many different indices that can be used to quantify positional importance and thus provide a ranking of a species influence. Additionally, there is a promising analytical approach that ranks the importance of species to the stability of a network (Allesina and Pascual 2009). Removing the highest ranked species will wreak the most havoc on a system. That is, removal will lead to the most efficient collapse of the system. All model based results should be regarded as scenarios since extinction of a species is defined to result from loss of all of its resources (a predator losing all of its prey). These analyses do not provide for extinctions that may result from dynamics within the population like low population abundance. Also most model experiments were performed with networks represented by matrices which merely indicated the existence or non-existence of a link (a zero – one matrix). In most cases no attempt was made to introduce the strength of interaction between species. However, the Allesina and Pasqual approach provides an avenue for moving from qualitative to quantitative analysis of networks since their basic network matrix and procedure for analysis should work equally well if zeroes and ones are replaced by interaction strengths, once sufficient field data exists to actually evaluate these interaction strengths.

Understanding the removal of a particular species is vital in the management of an ecosystem like the Columbia River where threats of extinction due to habitat loss, overexploitation, alien invasion, and climate change are ongoing realities. The fact that extinction of a single species can cascade into multiple co-extinctions make it difficult to predict the patterns, making it imperative that techniques like that of Allesina and Pascual (2009) be developed. Application of their procedure could provide a ranking of species where loss of the most highly ranked (perhaps they can be called keystone species) will likely lead to the most catastrophic losses in the ecosystem.

In order to do this, it is first necessary to identify and quantify major trophic interactions. Only then is it possible to identify potentially important species. Species may be directly important to humanity because of their cultural, commercial, recreational, or esthetic value, or indirectly through the ecological services they provide (typically involving food webs) or the problems they present (e.g., toxin consumption via consumption of fish). Direct importance is self explanatory but indirect importance is indicated by the following criteria:

1. Species with high biomass or production (based on assessments, literature, historical records);
2. Species exhibiting a key ecological function as prey, predators, competitors or parasites/pathogens of other important species.
3. Species that accumulate or biomagnify toxic chemicals.

These criteria can then be applied to identify species within the habitat continuum to identify a subset of focal species with connections radiating out to include associated prey, predators, parasites and competitors. Pacific salmon, steelhead, bull trout, native resident trout, sturgeon and lamprey satisfy the criteria for focal species and, by extension, their key prey, predators, parasites and competitors would be explicitly included in an examination of the Basin's food webs. Although salmonids are used extensively in this report to demonstrate the various elements of food webs, other species of interest need to be examined in a similar fashion.

Size-selective predation and timing of life history (and feeding) transitions are strong determinants of survival for one or more critical life stages in many fish species (e.g., Marschall and Crowder 1995, Biro et al. 2005, Farley et al. 2007, Cross et al. 2008). Therefore, food web interactions need to be organized and examined within a spatial-temporal framework. The framework includes life stage-specific trophic and environmental processes affecting growth, timing and survival of key species living and moving within and among habitats (Moss et al. 2005, Cross et al. 2008, Duffy et al. 2009). Moreover, this approach provides a framework for methodically examining trade-offs associated with contrasting life history strategies, and examining how the relative cost and benefits associated with a particular behavior or habitat might shift as environmental conditions and management actions change.

The effects of food web processes on a specific life stage are essential for understanding effects on growth and survival through subsequent life stages (Biro et al. 2005). Growth associated with a particular habitat is determined by the availability and energy content of food, thermal conditions, and consumer body size (Beauchamp 2009). Food web-related effects on survival are related primarily to predation or starvation, both of which are mediated by environmental conditions, and perhaps exacerbated by competition (Sidebar A.2.2). It is fundamental that an assessment of food supply should not only consider species and sizes of prey that are exploited by consumers, and also consider what fraction of the forage base is available (spatial-temporal overlap with consumers) and vulnerable (detection and capture). Therefore, the food supply must be considered within the context of the habitat occupied and at spatial-temporal scales relevant to consumers while foraging.

Sidebar A.2.2. The Role of Parasites in Aquatic Food Webs

Parasitism is the most common animal lifestyle, yet food webs rarely include parasites. Parasites are fundamentally important in shaping the structure of food webs as well as resulting pathways and processes (Lafferty et al. 2010). Even though much is known about the life cycles of aquatic parasites, the subject has received scant attention from a food web perspective. A few early studies indicate that including parasites leads to obvious increases in species richness, number of links, and food chain length. Recent studies suggest that about 75% of the links in food webs involve a parasitic species; these links are vital for regulation of host abundance and potentially for reducing the impact of toxic pollutants (Dobson et al. 2008). In essence, parasites increase food web connectance and resilience, sometimes dramatically. In addition, parasites greatly affect other food web properties, such as nestedness (asymmetry of interactions), chain length, and linkage density. Furthermore, whereas most food web studies find that top trophic levels are least vulnerable to natural enemies, the inclusion of parasites revealed that mid-trophic levels, not low trophic levels, suffer the highest vulnerability to natural enemies. The results to date – albeit from a few studies – show that an understanding of food webs will be very incomplete unless parasites are included. Most notably, recognition of parasite links may have important consequences for ecosystem stability and resilience because they increase connectance and nestedness.

Food web processes affecting the availability of food for native fishes have physiological consequences too. Energy reserves stored in lipids and proteins change over time and through migration and reproduction. Timing of migration and reproduction, temperature regimes, and the metabolic costs of feeding and predator avoidance affect energy reserves which, in turn, affect subsequent performance and survival. Physiological indicators of nutrition and stress can help define energy deficient or stressful reaches of the hydrosystem, and lead to more beneficial management decisions (Wagner and Congleton 2004).

Within each life stage of every species, food web processes can be identified and potentially quantified using a variety of existing sampling and analytical procedures and modeling (summarized in Appendix A). An ultimate objective of any food web investigation is to link population dynamics of key species to food web processes by identifying factors limiting production during specific life stages and environmental conditions. These factors may be identified by resolving trophic linkages through diet, stable isotope or fatty acid analyses; describing distribution, movement and habitat use at appropriate ontogenetic, temporal (diel, seasonal, inter-annual) and spatial (vertical, horizontal, habitat-specific, landscape) scales within prevailing environmental conditions (vertical-horizontal thermal structure, DO, turbidity, light); evaluating stage-specific growth through cohort tracking; and quantifying trophic interactions and growth performance through bioenergetics models or alternative mass-balance approaches when data are limited.

Relationship to the Columbia River

Habitat specific. Aquatic systems in the Columbia River Basin encompass an array of distinct habitats from an ecological perspective. Each habitat supports a relatively unique food web with inherently different trophic interactions and rates of energy and nutrient transfers. Many native fishes utilize several of these during their lives, with critically important consequences for growth, mortality and reproductive success. A better understanding of each food web and interactions among habitat-specific food webs yield insights into the integrated functioning of a highly complex system. Further, it establishes the basis for predicting changes from current and emerging human alterations to the land and climate.

A general theory of fish feeding, which has included the use of models, has been sought by many researchers (e.g., Ivlev 1961, Keeley and Grant 2001, Esteban and Machetti 2004). Yet, there are still problems identifying what fish will eat from the suite of potential prey. Fish are not totally opportunistic and will not always feed on the most abundant food organism. A range of factors affect availability of prey to fish, including abundance, size, color, habitat and behavior (Vogel and Beauchamp 1999). As well, non-native organisms that are not part of the natural ecosystem but are suitable prey, lead to the formation of novel or hybrid food webs (see Chapters C.5 and E.4). A crucial issue in this regard is whether or not the non-native prey are as important for fish growth and survival as are the native food species.

Potential changes from human activities. Humans have greatly altered the aquatic food webs in the Columbia River Basin, both from historical and current actions. Further, it is expected that population growth, economic expansion and global warming will create increasing demands for water, food and power – further impacting aquatic systems. Many of these impacts will be potentially severe from an ecological perspective. It is of urgent concern to establish the food, space and migratory conditions required for sustaining fish species and communities, and to quantify the environmental conditions that will allow them to thrive in the coming decades. Several options are available to do this – such as establishing environmental flow requirements for food and space (e.g., Poff et al. 2010) and determining the temperature requirements for the integrity of species, communities and food webs (Olden and Naiman 2010).

Regulatory obligations to protect endangered species. Many species of fish and wildlife inhabit, migrate through, or use the Columbia River. Some of those species are listed as threatened or endangered under the Endangered Species Act (ESA[6]). The ESA restricts the "taking"[7] of endangered species as well as by protecting species' critical habitats[8] which include food webs essential to the conservation of the species.

In addition to the ESA, other laws, regulations, and treaties give rise to obligations to protect listed as well as non-listed species that interact in Basin's ecosystems and food webs. Such legal obligations can be found in treaties and executive orders of the Basin's tribes; the Northwest Power Act;[9] the Clean Water Act;[10] the Marine Mammal Protection Act;[11] the Migratory Bird Treaty Act;[12] and state endangered species acts. These directives require actions to restore and protect fish and wildlife populations that interact in complex food webs. Successful implementation of these directives is complicated by food web interactions. For example, when a Caspian tern colony protected under the Migratory Bird Act preys on and significantly impacts ESA-listed steelhead. These are complicated food-web related issues, and in Appendix B we describe an illustrative subset of the laws affecting food web management and restoration.

Links to restoration. Food availability can limit fish production without being directly lethal. Poor growth within a particular habitat can compromise survival in other habitats and subsequent life stages. Unfortunately, habitat is often mistakenly equated with food availability and food production, perhaps because actually estimating the abundance of food resources is difficult. Field experiments in the Pacific Northwest have shown repeatedly that trophic manipulations (e.g., nutrient additions or salmon carcass introductions) that boost the abundance of potential prey organisms also subsequently boost fish growth (e.g., Warren et al. 1964, Shortreed et al. 1984, Slaney et al. 1986, Bilby et al. 1998). In contrast, despite many attempts to restore physical habitats by creating pools or adding cover structures, there exists only ambiguous evidence that such restoration efforts can increase fish abundance and biomass (House and Boehne 1985, Frissell and Nawa 1992, Hilborn and Winton 1993, Reeves et al. 1997, Ward 2000, Thompson 2006, Stewart et al. 2009, Whiteway et al. 2010). Even though it may be premature to conclude from these studies that food availability is somehow more limiting to fish populations than the quality of the physical environment, evidence is mounting that many habitat restoration activities are not always effective in meeting stated goals.

This may be because few quantitative studies have evaluated the *effectiveness* of stream restoration structures to improve fish habitat (Whiteway et al. 2010). Their meta-analysis of 211 stream restoration projects did show a significant increase in pool area, average depth, large woody debris, and percent cover, as well as a decrease in riffle area, following the installation of in-stream structures. A significant increase in salmonid density and biomass also was

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[6] Endangered Species Act. 16 U.S.C. §§ 1531-1544

[7] ESA §3(19) defines "take" as "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct."

[8] ESA §3(5) defines "critical habitat" for a threatened or endangered species as: "(i) the specific areas within the geographical area occupied by the species, at the time it is listed…on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed…upon a determination by the Secretary that such areas are essential for the conservation of the species."

[9] Pacific Northwest Electric Power Planning and Conservation Act (aka Northwest Power Act). 16 U.S.C. §§ 839-839h

[10] Clean Water Act. 33 U.S.C. § 1251 *et seq.*

[11] Marine Mammal Protection Act. 16 U.S.C. §§ 1361-1421h

[12] Migratory Bird Treaty Act. 16 U.S.C. §§ 703-712

shown. However, there were large differences between species, with rainbow trout showing the largest increases in density and biomass. The analyses highlight the potential of in-stream structures to create better habitat for increasing the abundance of salmonids, but the scarcity of long-term monitoring of the effectiveness of in-stream structures and the inconsistency of results remain problematic.

In the end, the relative importance of food and space depends on site-specific circumstances (Chapman 1966). However, the availability of food does warrant further examination, given that it has been demonstrated in field studies to be an important limiting factor, yet it is often overlooked in restoration because there are no easily measured indices of food abundance, availability or fish growth. Efforts to assess the spatial-temporal availability of prey could be better focused by first identifying the prey species, and their sizes, that contribute most significantly to the energy budgets of salmonids and other key species. These and closely related topics, such as hydroelectric alterations, non-native species in food webs and food demands by hatchery reared fish, are further explored in subsequent chapters of this report.

B. The Physical Setting

B.1. The Columbia River Ecosystem: Characterization of Pre-Development Food Webs

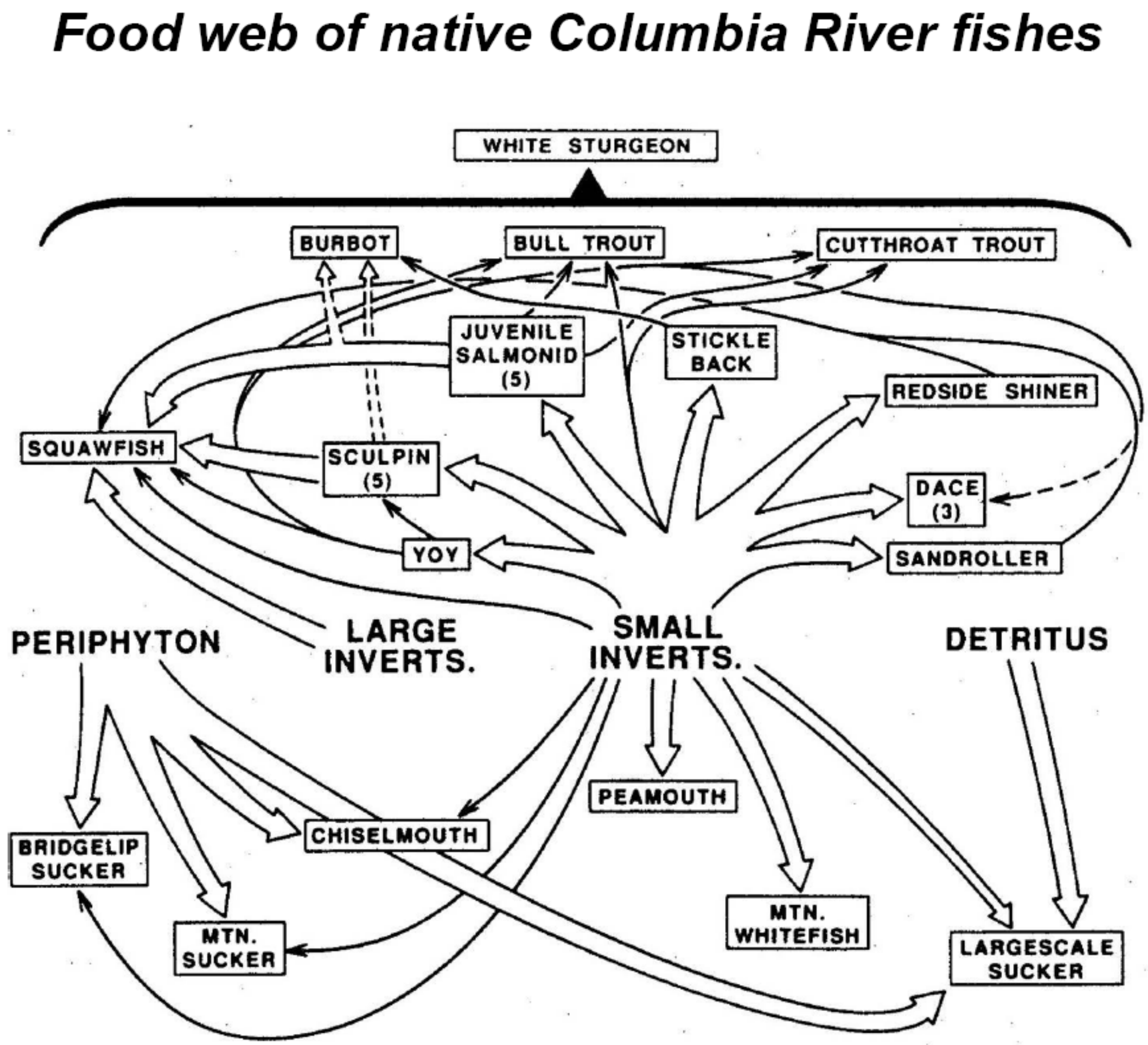
Today's Columbia River and its tributaries are only ecological vestiges of the historical ecosystem, its estuary and its watershed (Dietrich 1995, Lee et al. 1997). Even though detailed historical information on the environment of the Columbia River and its tributaries is surprisingly sparse, glimpses of the region and the nature of the river begin to emerge by the late 1700s. A general view of the river and surrounding lands can be pieced together from explorer's journals, from early economic activities and from paleoenvironmental investigations. The scarcity of scientific information should not be surprising since the Basin covers numerous ecological zones over an area roughly the size of France, and written records prior to 1800 AD on environmental conditions are generally rare.

Most early descriptions of the Pacific Northwest are found in the journals of British citizens and personnel of the U.S. Army (Maser and Sedell 1994). These descriptions tell of valleys so wet, especially west of the Cascades, that early travel by land was confined to hills along their edges. Peter Skene Ogden, of the British-owned Hudson Bay Company, noted considerable flooding resulting from extensive beaver dams, sediment accumulations, fallen trees, and abundant live vegetation within stream channels in the early 1800s (Ogden 1961). Many lowland rivers contained large areas of cottonwood forests, sloughs, forested wetlands, swamps and grassy marshes before 1900 (Secretary of War 1922). For example, in 1854 the Willamette River flowed in five separate channels between Eugene and Corvallis, Oregon, with a massive floodplain forest surrounding the channels (Sedell and Froggatt 1984). Similarly, the name of the "Boise" River in Idaho was derived following English (the "wooded river") and French ("les bois") trappers' descriptions of the broad expanse of floodplain forests encountered there (ISHS 1971).

These and other scenes from the past give important insights into the physical and ecological characteristics of the Columbia River, and thereby into the food webs that existed prior to extensive development of the Basin's resources. There are a number of historical observations on physical and biological characteristics that are known with reasonable certainty, and these can be used to envision food webs based on contemporary research. These observations, which are occasionally quantitative, relate to the basic features of the river and tributaries (e.g., annual runoff, floods, sediment transport, water clarity, water temperature, dead wood, biota) and the resources used by Native Americans and early European settlers (e.g., locations of villages and towns, economic activities, resource exploitation).

The Early Food Webs

Illustrations of food webs prior to wide-scale development of the Basin are mere sketches of their actual complexity. They are based almost completely on fish assemblages thought to exist at the time (Li et al. 1987). White sturgeon were most likely a top predator because of its broad range of foods (Figure B.1.1). Burbot, bull trout and cutthroat trout ate a variety of other fishes and invertebrates, as they do today. However, beyond the foods of the key fishes, and some important fishes such as juvenile lamprey, there is only speculation about the foods of other fish species. This is because the invertebrate communities of that time period are not known with much certainty, the microbial and periphyton communities are not known at all, and the detrital pathways were not described until more than a century later. In fact, the foods of many important Columbia River fishes were not described until 1896 and, even then, it was only a limited examination (Evermann and Meek 1896).



Food web of native Columbia River fishes

Figure B.1.1. Hypothetical food web of the lower and middle Columbia River before 1800. The width of the trophic link represents the relative importance of the prey to its predator. Dashed arrows denote the assumption that burbot prey mostly in deep lakes in the Basin. Sturgeon are capable of eating a variety of prey. From Li et al. (1987).

Historical Observations of the River and Estuary

Insights from Descriptions of Physical Structure and Hydrology. Historically the Columbia River and tributaries were well known for the numerous rapids, falls, and reaches of fast moving water. The explorers Lewis and Clark travelled many kilometers in a single day with heavily laden canoes, except for reaches where they were forced to portage around dangerous rapids and falls (DeVoto 1953, Ambrose 1996). Their accounts, and those from other early American and European explorers, create a vision of a dynamic and high energy river that provided longitudinal connectivity for migration as well as transport of organic matter and sediments.

Lengthy streamflow records are essential for accurately characterizing runoff patterns. The flow record of the Columbia River at The Dalles is of special interest, because it is the longest continuous daily record on the Pacific Coast of North America. Annual peak flows were recorded beginning in 1858, and daily U.S. Geological Survey (USGS) flow observations began in June 1878 (Henshaw and Dean 1915). The U.S. Geological Survey has published monthly averaged river flows at The Dalles for 1879–1999 that account for the effects of flow regulation (Naik and Jay 2005). Further, the Bonneville Power Administration has estimated monthly averaged virgin flows— flows in the absence of both regulation and irrigation depletion—for the years 1929–1989 (BPA 1993). Monthly virgin flows at The Dalles for the missing early years from 1879 to 1928 were estimated by Naik and Jay (2005) from records of irrigation water use. Changes in the hydrologic pattern over the last 125 years are evident (Figure B.1.2).

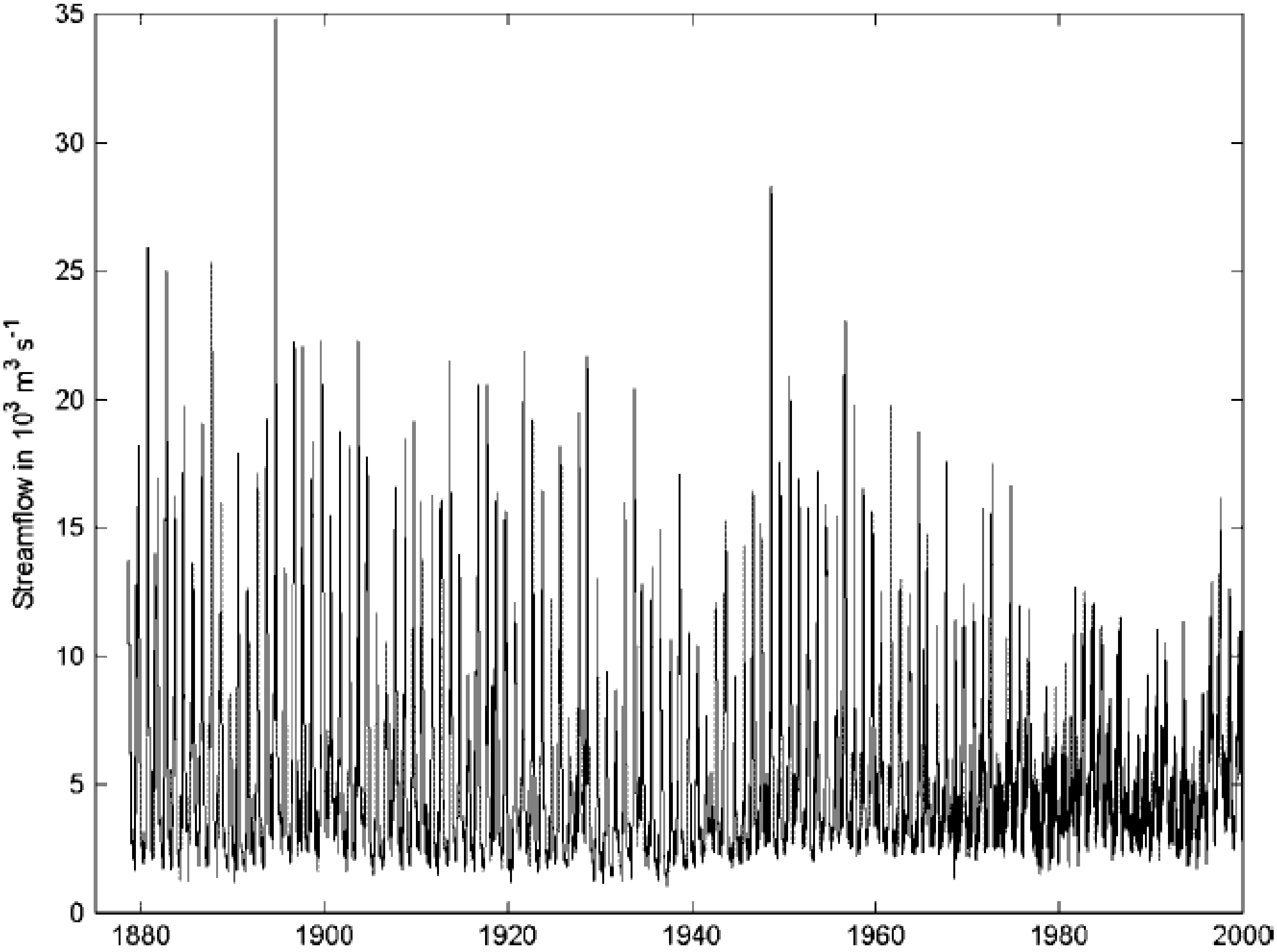


Figure B.1.2. Daily observed Columbia River flow at The Dalles, 1878-1999 (from Naik and Jay 2005).

Examination of the virgin flow record shows that annual average flow volume has decreased by approximately 15% since the late 19th century. These changes reflect human and climatic alterations to the natural flow regime (see Chapter B.2 and Naik and Jay 2005).

Prior to 1900 the annual flow pattern of nearly all streams in the Columbia River Basin was one of strong spring freshets, with the main river peaking at The Dalles on about 12 June (~ 13,610 m^3 s^{-1}), followed by annual low flows in late summer. The autumn months generally experienced slightly elevated flows as the rainy season began with the arrival of powerful storms from the North Pacific. Sediment transport was spatially uneven depending on the underlying geology and channel confinement. Nevertheless, under historical conditions the river delivered ~21 million metric tons of sediment to the estuary annually (Naik and Jay 2010). In the estuary there was 45 km^2 of shallow water habitat during freshets and ~30 km^2 at other times of the year (Kukulka and Jay 2003; Figure B.1.3). There is no estimate of the amount of habitat available historically in the river and tributaries because existing records do not adequately describe the extensive braiding, lateral marshes and beaver dams. Collectively, however, the observations of flow patterns and sediment transport suggest that the spring freshet and the late summer low flows were important in setting up a diversity of food webs in different parts of the system. Many stream organisms cue their life histories to flow and sediment transport regimes (Hershey and Lamberti 1998, Williams 2006), and there was a great diversity of life histories throughout the Basin due to the local effects of climate, topography and lithology. Further, shallow water habitat with quieter waters encouraged the deposition of fine organic matter, setting up food webs fundamentally different from those in faster waters.

Other key variables associated with water discharge and affecting food webs are temperature and clarity. Temperature is a master variable in determining life history strategies for most aquatic invertebrates and fish (Brannon et al. 2004, Olden and Naiman 2010). Unfortunately, there does not appear to be any systematic measurements of water temperatures from historical times. Further, there are no systematic measurements of water clarity. However, Lewis and Clark, and other early explorers reported seeing the river's bottom nearly everywhere above the estuary (Ambrose 1996). These observations are important because they suggest that primary production by diatoms and other benthic algae and by macrophytes played strong roles in supporting food webs. Contemporary studies indicate that where abundant light reaches the substrate, even in fast flowing rivers, benthic plants are quite productive (Naiman and Sedell 1980) and support a rich diversity of scraping and herbivorous invertebrates (Hershey and Lamberti 1998).

Insights from Large Dead Wood. Large pieces of dead wood are fundamentally important in structuring aquatic food webs. The large wood influences water hydraulics, creating substantial habitat heterogeneity and providing places for attachment and resting. There are a number of historical observations of large wood that are consistent with characteristics of relatively unaltered rivers in the Pacific Northwest. Lewis and Clark noted repeatedly that the "trails" they followed along upland tributaries were choked with dead wood making passage extremely difficult (DeVoto 1953, Ambrose 1996).

Further downstream, along the mainstem Columbia, there was no mention of dead wood in the channel, which is a bit surprising at first. The large wood could have been piled on the banks near high water marks and not easily noticed, or it may have decayed. In the coastal region we now know that much of the large wood is broken into fragments within a decade or so of entering the channel, and decays relatively quickly if exposed to the air (Naiman et al. 2010). Further downstream in the upper estuary, Lewis and Clark observed extremely large trees being transported by floods (Ambrose 1996), which is indicative of active lateral migration of the channel into fringing forests (Naiman et al. 2010). However, they also mention having difficulty in finding dry wood for fires. This is especially puzzling considering that the U.S. Army Corps of Engineers later mounted a massive snag removal program in this section of the river (and the lower tributaries) to improve navigation (Maser and Sedell 1994).

Snag removal programs were of high priority in the 1800s, fundamentally changing food web structure in the river. As an example, reports of the Secretary of War (1922) for the years 1875-1921 document obstacles to navigation in the Willamette River above Corvallis where the river flowed in a complex pattern within an extensive floodplain forest. More than 5500

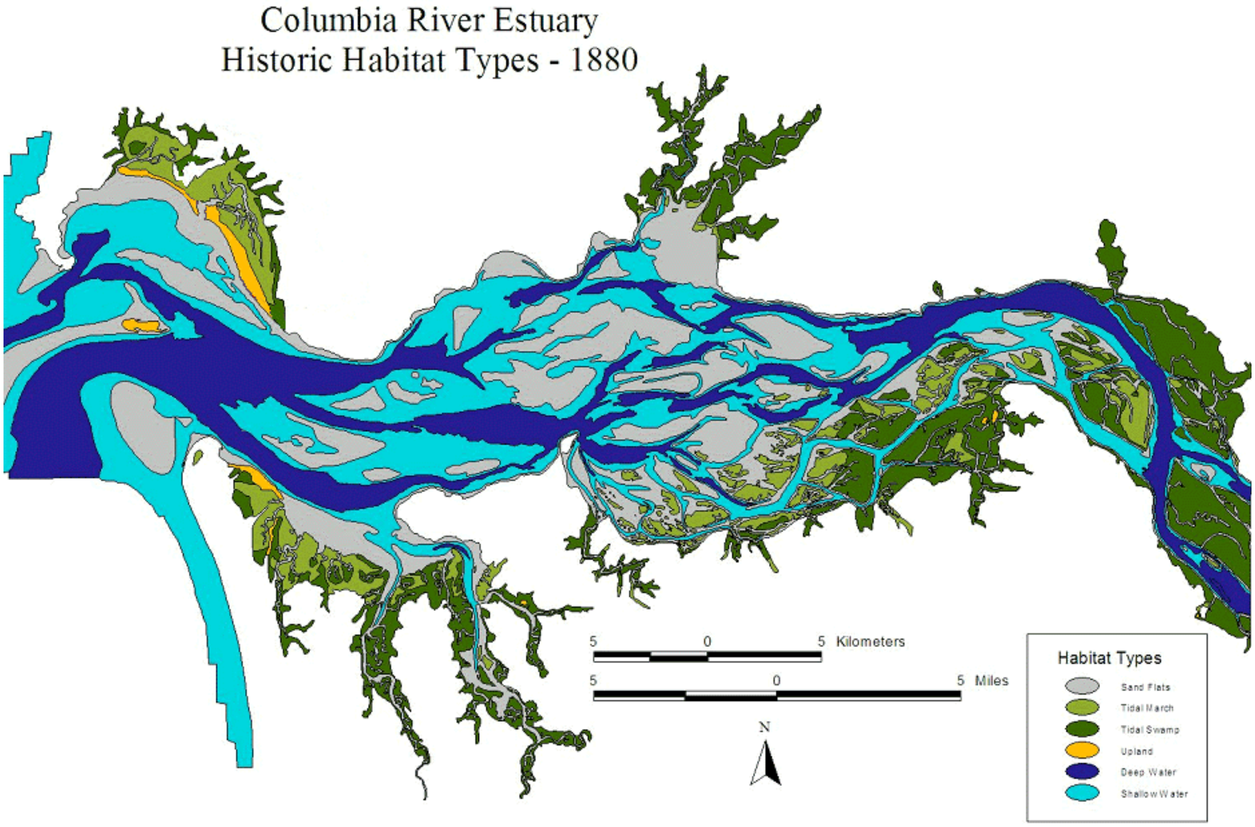


Figure B.1.3. Historic habitat types of the Columbia River estuary in 1880 (from Russell 2009).

snags were removed from 89 km of the river within a decade. The snags ranged from 1.5 - 2.7 m in diameter and 6 - 37 m long. The river was later confined by diking and other engineering activities to one channel, as it remains today (Secretary of War 1922).

Although no region-wide systematic survey of vegetation removal in the riparian zone is available, adequate historical documentation for some areas shows major simplification of channel and floodplain habitat during the period of agricultural settlement, early logging (Sedell and Luchessa 1982, Sedell et al. 1982) and floodplain clearing tied to hydraulic modifications and in-channel mining for gold. This simplification resulted in large changes to the amount of dead wood, the volumes of pools, and the amount of sediment stored in streams (Salo and Cundy 1987, Lee et al. 1997). Collectively, this resulted in a severe impoverishment of thousands of kilometers of fish habitat and fundamental alterations to food webs. Sedell and Luchessa (1982), for instance, documented how the removal of large woody obstructions, the blocking of tributary channels, and the practice of releasing large volumes of wood and impounded water from logging-related "splash dams" caused straightening and simplification of channel morphology, and a reduction of connectivity between the main channels and the smaller, more productive, channels on the adjacent floodplains.

West of the Cascades, tributary junctions, riparian zones and the estuary have undergone extensive modification from removal of large Sitka spruce, western hemlock and western red cedar (Thomas 1983, Graves et al. 1995, Diefenderfer and Montgomery 2009). For example, there has been a loss of 77% of forested wetland since 1880 in the lower estuary as well as other major changes to the channel and fringing marshes (see Chapter D.7). These were done to improve navigation and to sustain expanding agriculture. It is well documented that early settlers converted fertile bottom land to agriculture by logging, stump removal and diking (Martin 1997).

Historical Observations of Resource Use

Insights from Local Economies. Economic activities in the Basin centered on trapping, logging, fishing, agriculture and mining in the 1800s. Today it is difficult to envision the extent of these enterprises but, when coupled with modern investigations of relatively natural systems without similar activities, they provide good insights into ecological conditions existing prior to their initiation.

An important enterprise was beaver (*Castor canadensis*) trapping, which also drove the early exploration of western North America. Beaver were widely distributed in the Basin, often in dense concentrations, and actively sought by European and American trappers and Native Americans for their own uses as well as for barter with traders. The key roles of beaver in shaping stream dynamics are well documented, with the effects varying as functions of channel size and local environmental conditions (Morgan 1868, Naiman et al. 1988). Beaver impacted streams have food webs fundamentally different, and much more productive, than streams without beaver (Naiman et al. 1994, Naiman and Rogers 1997). Political and economic competition between nations for the fur resource and the desire for initial settlement in the Northwest led to the intentional depletion of beaver populations. Indeed it was an official policy of the Hudson Bay Fur Company to "scour" beaver from the Snake River Basin to prevent American settlement in the Oregon Territory (Gibson 1997). The widespread removal of beaver – they were nearly extinct in North America by 1900 – undoubtedly changed the food webs of the Basin, not only in the tributary streams and rivers but also in the fringing marshes and riparian zones. The effects of beaver on hydrology and sediment routing are a function of scale. Certainly the tens of thousands of beaver dams held substantial water and retained massive amounts of sediment. The volumes were probably minor when compared to the annual volumes carried by the Columbia River at its mouth but, at the local scale, the beaver dams created marshes, retained water during low flow periods, recharged local aquifers and maintained productive food webs. In other words, they provided and maintained high quality habitat as well as diverse and productive food webs.

Mining quickly followed beaver trapping as a main economic activity. It was widespread along streams and rivers through much of the basin in the mid 1800s. The need for food, fuel and building materials to support mining, smelting and transportation (Conley 1984) led to expanding agriculture and extensive conversion of riparian forests. The fact that tree harvest was so active suggests riparian and floodplain trees were large, high quality and plentiful. Upstream, the riverside forests were among the first to be cut because logs could be floated to markets and mills when other transportation was not available. From the mid-1800s to ~1915 hundreds of rivers were cleaned of dead wood so that logs could be floated to mills without impediment (Maser and Sedell 1994). The net effect of stream cleaning and splash damming resulted in significant changes to physical conditions in the channels as well as the food webs.

Insights from Fisheries and Fish Biologists. Commercial fisheries flourished for sturgeon, salmon and steelhead starting around 1850 and continued until ~1920. Harvest of white sturgeon alone peaked at nearly 2.5 million kg in 1892 (Cleaver 1951). Pre-development total run sizes for adult salmon and steelhead likely ranged from 5 million during unfavorable survival years to nearly 20 million during favorable years.[13] In aggregate, this possibly represented the world's largest run of Chinook salmon, as well as very large runs of sockeye, coho, steelhead, and possibly chum. The very large numbers of sturgeon, salmon and other species would not have been possible without productive food webs, both in freshwaters as well as in the estuary and ocean.

As fisheries dwindled biologists and managers grew increasingly concerned about production areas and the access of fishes to spawning and rearing habits. Many fishery biologists believed that dead wood in streams restricted fish passage, and further cleaning of the streams commenced (Bisson et al. 1987). It is now known that the stream cleaning of dead wood and the removal of beaver dams have been ecologically disastrous. The net effects of forest harvest, hydraulic and dredge mining, log sluicing and stream cleaning on the hydrology are, again, scale dependent. Locally, as the basic retention devices for nutrients and organic matter were removed, the productivity of food webs was severely degraded.

Insights from Agriculture. Irrigated agriculture was also an early economic activity in the Basin, but not widespread until about a century ago (Naik and Jay 2005). The earliest irrigation was carried out by missionaries settling in the Walla Walla and Clearwater River drainages prior to 1840 (Simons 1953). The settlers were able to divert water from tributary streams to adjacent lands with little effort. By 1860 the human population was still very sparse, and there was only 9 km^2 of land under irrigation. The period 1860–80 saw an influx of settlers because mining as well as cattle, sheep and hog raising activities spread rapidly in the Pacific Northwest. Railroads were constructed, bringing additional settlers and expanding the markets for farm products. In 1870 there were about 130,000 people living in Washington, Oregon and Idaho and ~200 km^2 of land were being irrigated above The Dalles (Simons 1953). By 1880, the population had increased to 400,000, and there was ~800 km^2 of irrigated agriculture. Also in 1880, a transcontinental rail connection was completed between Chicago and the ocean ports of the Pacific Northwest. This opened new markets for products from farmlands, mines and forests. Larger irrigation projects were then undertaken in the Snake and Yakima river valleys. Between 1880 and 1890, the population increased by 170% and the irrigated lands to ~2,100 km^2. By 1990 irrigated agriculture represented about 28,000 km^2 (Lee et al. 1997).

Collectively, early agricultural activities may not have had much effect on annual runoff and sediment transport at the Basin scale, but it was locally devastating on small tributaries. By 1890 losses of historical salmon runs were already attributed to irrigation dams and intermittent flows in important spawning areas (Gilbert and Everman 1894, U.S. Census Office 1896). Even now agricultural conversion represents only about 16% of land area in the Basin, but the influence is disproportionate to the areal footprint because the focus is often on low elevation, valley bottoms and floodplain areas which hold the bulk of riparian zones and streams (Lee et al. 1997). Agricultural activities also include extensive grazing effects on private and public lands that are not considered when estimating land areas converted to agricultural use (Lee et al. 1997). Grazing has been directly linked to the extensive loss of riparian vegetation, channel widening and entrenchment, loss of bank stability and the erosion and drying of once productive wet meadows systems. Like beaver removal, forest harvest and wood snagging, the food web effects of agriculture at the local scale were likely profound as water was removed from channels during the drier months of the year, small channels were eliminated, and mainstem channels isolated from the floodplains by channelization and diking. Furthermore, sedimentation increased with erosion and inputs of organic matter from riparian vegetation declined. Early agriculture did not depend on the use of pesticides or other artificial chemicals that are abundant and widespread today and likely impairing contemporary food webs (Chapter C.7). Nevertheless,

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[13] Chapman (1986) estimated 7,505,000 adult salmon in peak years. The Council's Program gives an estimated average of 10-16 million returning to the Basin annually (NPCC 2009).

mercury and cyanide were commonly used in mining activities in earlier years and often mining ditches and canals dumped directly to rivers or became irrigation canals, so contaminants may have been important even then.

Insights from Paleolimnology. Paleolimnology, the study of lake histories through analysis of sediments, has proven to be an important tool for addressing prehistoric variability in aquatic systems (Smol 2002). Such analyses are relatively rare for lakes within the Basin. However, Redfish Lake, Idaho, has been examined in some detail and offers insights into the pelagic food webs existing in oligotrophic lakes prior to widespread human interventions, starting with commercial fisheries at the mouth of the Columbia River in 1860 (Selbie et al. 2007). The data suggest that the planktonic *Daphnia* assemblage in Redfish Lake, a preferred and more valuable food source for juvenile sockeye, switched to a small, less visible *Bosmina*-dominated cladoceran zooplankton assemblage in response to stronger predation of *Daphnia* by resident kokanee and later by the stocking of other salmonids. This switch fundamentally changed the food web for juvenile salmon, a change that has persisted to this day.

There is ample paleolimnological and other evidence that the later blocking of lakes to fish migration, stocking of lakes with non-native species, and active management for selected fish species fundamentally altered historical food webs (Rieman and Falter 1981, Drake and Naiman 2000). In most cases, there was a decline in overall productivity as nutritionally superior species of crustaceans, insects and other small-bodied species were replaced by less nutritious or less available species, and the structure of the food webs shifted to other configurations.

Insights from Archeology. For several thousand years the Columbia River has been a key source of food, fiber and water for Native Americans. Numerous villages were located along the river at points allowing for the harvest of fish, mussels, and other water-derived resources (Bulter and O'Connor 2004). Middens associated with villages tell a story of extensive exploitation of abundant riverine resources that are nearly non-existent today. Freshwater mussels are, in particular, important as indications of ecological conditions in the river. Abundant mussel shells in middens adjacent to boulder-stabilized reaches of the Snake River suggest that Native American tribes selectively exploited high-density, old-aged mussel beds (Vannote and Minshall 1982).

Different mussel species are widely varied in their habitat requirements but all, as adults, are filter feeders. Investigations in the early 1800s describe the abundant native mussels (Lea 1839) that have now largely disappeared. It is now recognized that river lithology and fluvial geomorphic processes interact to regulate both population size structure and relative abundance of the two dominant mussels, *Margaritifera falcata* (Gould) and *Gonidea angulata* (Lea) (Vannote and Minshall 1982). Species of *Margaritifera* appear largely dependent upon salmonids for basinwide distribution of the parasitic, 3- to 5-week juvenile glochidium stage, although glochidia have been found on other fish. The extreme longevity (40-100 years) of *M. margaritifera*, a closely related species from the northeastern USA and eastern Canada, has been widely reported and longevity is apparently similar for *M. falcata* in the Salmon River. Collectively, the past abundance and wide distribution of mussels suggests an extensive influence of these filter feeders on riverine processes.

Locally, many tributaries of the Columbia River are aggrading with sand and gravel due to a 100+ year episode of mining, irrigation diversion, and grazing. In addition, massive slope failure and erosion from hydraulic mining, road construction and forest harvest have contributed substantial materials to the upstream ends of watersheds. The increased influx of sediments in the Snake River appears to have shifted the historical community structure from predominance by *M. falcata* to increased numbers of *G. angulata*. Where sand replaces or covers interstitial gravels, *G. angulata* progressively replaces *M. falcate* because it has the ability to migrate vertically (Vannote and Minshall 1982). The specific consequences for the historical mussel-based food web are unclear in this case as both species are filter feeders taking their nutrition from particles suspended in the water; it is not known if other species prey on the mussels.

Insights from Native Americans. The writing of Lewis and Clark, and others, are replete with descriptions of many Native Americans living in proximity to the river. It is clear that Native Americans made extensive use of the river and its resources. In the densities described it is clear that the local people used the riparian areas for a variety of purposes including those related to food. Certainly wood was gathered for fires and construction, fibers and roots were collected for a variety of uses (Turner 1995, 1997), and fish and game were captured for nutrition (Butler and O'Connor 2004). Unfortunately, the exact nature and the spatial extent of those uses are not known with certainty. Nevertheless, the uses suggest that riparian zones were diverse and productive.

It is interesting that the large river mussels were apparently of limited importance to Native Americans in terms of volumes consumed (Spinden 1908, Ray 1933) but they appear to have been utilized in small numbers in many areas of the Basin (Lyman 1984). Mussels were, however, of importance for survival of these peoples as they staved off starvation in the late winter and early spring when stored foods were in short supply or began to spoil (Ray 1933, Post 1938). When people in a winter village began to disperse in early spring, some would move to the river and camp by mussel beds, gathering mussels with a forked stick through holes in the ice if wading was impossible.

Conclusions

These lines of evidence offer clear glimpses that historical food webs of the Basin have been profoundly modified since the arrival of the first Europeans. Any one of these activities would have had important consequences for food web structure and productivity but, collectively, they suggest that the historical food webs of the Columbia River show little resemblance to those existing today. This new ecological system with its unique configurations, and now-limited longitudinal and lateral connectivities, has deep implications – from a food web perspective – for the type of restoration actions to be performed and for the success of those actions.

B.2. Contemporary Flow Characteristics – the Hydrosystem

The relatively recent and widespread construction of water impoundments throughout the Columbia River Basin has attenuated peak springtime river flows, which historically transported large quantities of sediments, nutrients, cold water, and associated materials downstream. This basic alteration has fundamentally altered food web processes as impoundments now trap large quantities of sediment and store water, heat and nutrients while altering supplies and timing to downstream environments. As a result, sediment deposition on floodplains has been largely eliminated, and deposition in the estuary and on the continental shelf, where replacement of sediments is essential for the maintenance of benthic habitat, has been reduced. Operation of the storage reservoirs has flattened the hydrograph by increasing low late-summer and fall flows and decreasing spring flows, altering the timing of delivery of nutrients supporting primary producers — the base of aquatic food webs — in the river, estuary and marine environments. Storage of spring snowmelt, decreased flow velocities and increased surface areas of reservoirs have altered water temperatures throughout the year. Water temperature has a primary influence on basic processes like solute chemistry, nutrient cycling and metabolic rates; therefore, changing temperature regimes has important effects on aquatic food webs (Ward and Stanford 1982).

In this chapter we describe changes in discharge, sediment and nutrient transport, and temperature regimes brought about by water impoundment in the Columbia River, and we identify the general consequences of these changes for aquatic food webs. Specific food web effects are discussed in greater detail in later chapters of the report.

Effects of Water Storage and Irrigation

Water availability is a vital concern for farmers and cities in the Basin. Rainfall is sparse east of the Cascade Mountains, in contrast with the well-watered lands to the west. Irrigation water is obtained largely from melting snow, requiring collection and storage of spring runoff for use throughout the growing season. To address this need, the water storage capacity was increased to about 21 billion m^3 (17 million acre-feet) during the first half of the 20th century. By the 1960's, the hydroelectric system was also expanding. Planners recognized that power generation would be constrained by low flows in late summer, fall and winter, and that realization of the full potential of the hydropower system would require increased upstream water storage to flatten the seasonal flow cycle, as well as provide protection against flooding. Signing of the Columbia River Treaty with Canada (1964) cleared the way for construction of four large storage reservoirs in British Columbia and Montana, more than doubling total storage capacity in the Basin and almost equalizing summer and winter average flows. Total active water storage capacity was about 25 billion m^3 (20 million acre-feet) prior to construction of the Columbia River Treaty dams (Volkman 1997); it is currently about 69 billion m^3 (56 million acre-feet). Thus the large variations in seasonal and annual natural flows that caused power and flood control regulation problems in earlier years have been largely dampened (Figure B.2.1).

Average annual flow of the Columbia River measured at The Dalles, Oregon has decreased by about 15% over the past century (Naik and Jay 2005). About one-half of this decrease is attributed to irrigation withdrawals, and one-half to changes in climate and land use (Naik and Jay 2005). The effects of irrigation on Columbia River flows are largely due to increased water use in the middle Columbia region; average annual flows in the lower Snake River, the largest tributary to the Columbia, did not trend downward from 1900 through the mid-1980s (Rood et al. 2010). Much of the surface water in the upper Snake Basin was appropriated prior to 1900, and irrigation withdrawals in the middle and lower basins are small. In recent years (1988 to present), reduced precipitation has produced a series of below-average flow years in the Snake River.

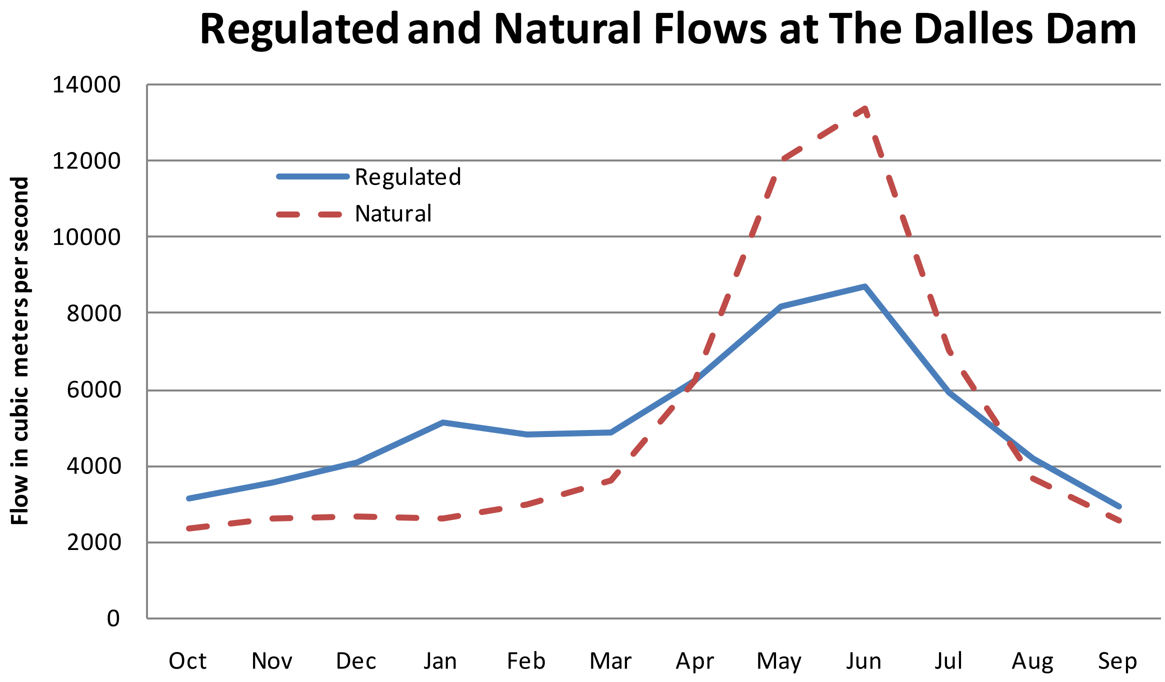

Figure B.2.1. Monthly average flow hydrograph for the Columbia River at The Dalles showing natural (unregulated) and regulated flows, both modified to reflect the 2000 level of irrigation depletion (from the Northwest Power and Conservation Council).

Minimum flows are reduced by irrigation withdrawals, but increased by the release of stored water for hydropower generation or to assist fish migrations. The net effect varies among subbasins. Release of water from storage reservoirs has increased minimum flows of the Columbia River at The Dalles by 33% over the past 100 years (K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data; see also Figure B.2.1). Much of this increase in late summer and fall flows occurred after the large expansion of storage capacity due to the Columbia River Treaty in the 1960s and early 1970s. The Snake River, in contrast, shows minimum flows decreasing since the early 1960s (K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data). Although 25 large water storage reservoirs with a working capacity of approximately 7.5 billion m^3 (6 million acre-feet) have been constructed in the middle and upper Snake River Basin, the stored water is used primarily for irrigation rather than for power generation or in-stream flow augmentation.

Peak flows for the mainstem Columbia River have been dramatically reduced by expanded water storage capacity (Figure B.2.1). Maximum flows at The Dalles in recent years have averaged 44% less than during the first half of the 20th century (K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data). Irrigation withdrawals and precipitation trends have had relatively small effects on peak flows (Bottom et al. 2005). The last major flood on the Columbia River, in 1948, occurred when basinwide storage capacity was only about one-quarter of that today. On the other hand, peak spring flows in the lower Snake River, heavily influenced by flows from the free-flowing Salmon, Grand Ronde, and Clearwater Rivers, have remained unchanged over the past century, while peak flows in the undammed John Day River have increased by 40% (K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data), possibly as a consequence of deforestation and loss of native rangeland vegetation.

In addition to flattening the annual flow cycle, increased upstream water storage has moved the *average time of peak flow* in the lower Columbia River back by about three weeks, from mid-June in earlier years to late May at present (Figure B.2.2). Predictions of changes in mountain snowfall and spring snow-melt timing with climate change over the remainder of the 21st century suggest that the timing of peak river discharge will continue to come earlier, and will increasingly deviate from the historical timing of the spring freshet (Hamlet and Lettenmaier 1999; see also ISAB 2007-2). These changes in peak runoff timing and accompanying temperature changes may affect the timing of

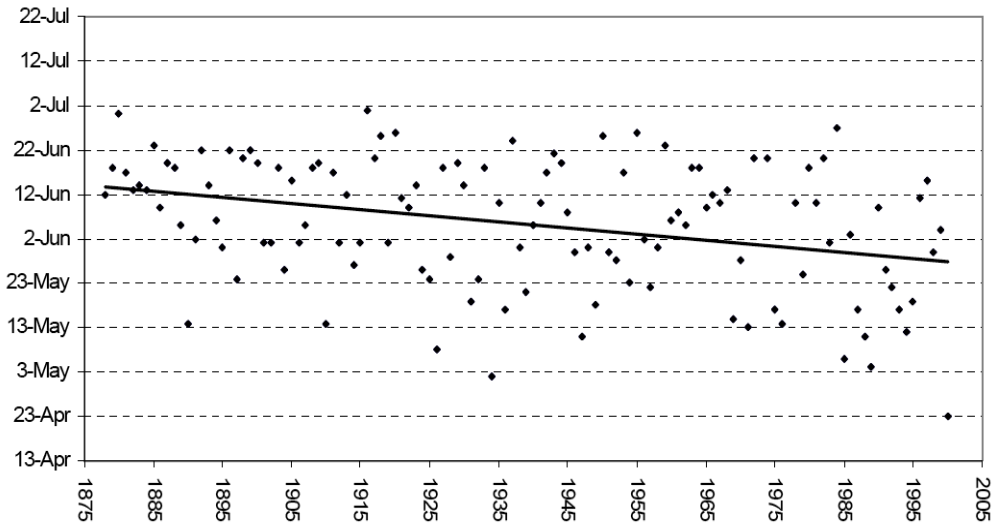

Figure B.2.2. Dates of peak annual flows in the lower Columbia River, 1878 to 2001 (Bottom et al. 2005; data adapted from USGS records).

reproduction and other key life-history events for organisms at all trophic levels, consequently altering food-web relationships. One example is an anticipated change in the timing of downstream migration and ocean entry for juvenile salmonids (Muir et al. 2006). Earlier migration may expose the juvenile fish to longer periods of low food availability in the river and ocean.

Effects of Hydroelectric Power System

After World War II, rapidly increasing economic activity and growing urban populations provided impetus for expansion of the federal hydropower system to the present-day total of 22 major and 36 smaller dams.[14] In addition, most of the large dams in the Basin that function primarily for water storage and flood control also generate electricity (Chapter D.5). The hydropower capacity of the Columbia Basin (39 GW; estimate by NPCC staff) is the largest of any river basin in North America.

Impoundment of hydroelectric power and storage reservoirs transformed the original lotic (flowing water) ecosystems into lentic (standing-water) ecosystems. Food webs associated with lotic and lentic ecosystems differ profoundly, in ways that will be detailed in other chapters of this report. Successional changes in dominant species at all trophic levels may continue for many years after impoundment and often are driven by the introduction, either deliberately or accidentally, of non-indigenous species. Many native fishes that occurred in lotic environments before impoundment survive in reservoirs but they may not thrive because food webs have become highly altered. Important changes can include a shift from benthic or terrestrial food sources to planktonic sources and highly varying food supplies (Chapters D.5, D.6). Native fishes can also be constrained by introduced competitors and predators (Chapters C.3, C.5, D.5). Reservoirs can have other deleterious effects on native fishes that are not directly related to changes in food webs.[15] Changes in aquatic ecosystems also have far-reaching effects on associated terrestrial ecosystems, most importantly the riparian zone (Chapter D.8).

Within the U.S. portion of the Basin, hydroelectric dams on the mainstem Columbia and Snake rivers are, with the exception of Grand Coulee and Brownlee, run-of-the-river dams with limited storage capacity. Unlike

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[14] Of the 22 major dams, 13 are operated by the Federal government (Corps of Engineers or Bureau of Reclamation) and 9 by public or private utilities.

[15] Water-storage dams typically do not provide for fish passage and block access of anadromous and other stream-adapted fishes to upstream spawning and rearing areas. Moreover, blocked access results in isolation from, and fragmentation of, suitable habitat for native stream fishes, thereby increasing the vulnerability of local populations to extirpation (Fausch et al. 2009).

upstream water-storage reservoirs, these dams have little effect on maximum and minimum flows. Flow through powerhouses at the dams is, however, coordinated systemwide to provide for peak power production during the daylight and early evening hours when it is most needed. One consequence of this "load following" power production is that flows vary daily and weekly over a considerable range. Studies have shown that migrating juvenile salmon encountering a dam during a period of low flow are confused by the lack of directional cues, and may even swim back upstream (Venditti et al. 2000). Fluctuating water levels also prevent the colonization of shallow-water areas by benthic algae and invertebrates and discourage the establishment of aquatic macrophytes (Chapters D.3, D.6), important drivers of food production.

Reduced flow velocities in hydroelectric power reservoirs and reduced flow volumes due to upstream water storage can slow the downstream migration of juvenile salmon by several weeks (Smith et al. 2002; Chapter E.4). Replenishment of body energy reserves by feeding during the migration is therefore potentially more important now than under pre-development conditions. Feeding by migrating juvenile salmon in reservoirs has not received much attention to date, but some evidence suggests that the availability of suitable prey is limited during spring months (Chapter D.6). A protracted migration also prolongs exposure of juvenile salmon to introduced and native predators. Reduced flow velocities and volumes also change habitat conditions which favor non-native invertebrates and aquatic plants, leading to development of hybrid food webs (Chapter C.5).

Sediment Transport and Deposition

Sediment deposition and transport influence food webs through effects on benthic substrates and habitat structure as well as the flux of nutrients and toxic materials. Rivers naturally erode and transport large quantities of sediment and associated materials at higher flows. An indirect effect of increased flow regulation on the Columbia River has been to decrease sediment transport and the size of the plume. The consequences for sediment deposition in the estuary are described in Chapter D.7.

Except under extreme freshet conditions, reduced flow velocities in run-of-river (ROR) reservoirs allow much of the sediment load to settle out. Consequently, dredging is necessary to maintain shipping channels in the upper reaches of the reservoirs. About one-third of the 2 to 3 million m^3 of sediment transported annually by the Snake River is deposited at the upstream end of Lower Granite reservoir (the uppermost of the four dams on the lower river), requiring regular dredging to maintain the 4.3 m deep shipping channel at Lewiston, Idaho. On-land disposal of the dredging spoils is judged to be economically infeasible, and in-river disposal smothers benthic biota and disrupts, at least temporarily, benthic food webs important to juvenile salmonids and other fishes (Bennett et al. 1993).

Many trace elements – including heavy metals such as lead, copper, cadmium, and mercury – are readily adsorbed to sediment particles (Horowitz et al. 2001). Therefore, sediment deposits in the Basin's reservoirs can be a source of contamination for aquatic biota (Delistraty and Yokel 2007). Introduction of metals into food webs is greatly accelerated by chemical reactions involving the microbial community living at the interface between the water column and oxygen-depleted sediments (Chapter C.7). The half-life of metals bound to deposited sediments is on the order of decades (Johnson et al. 2005); consequently, transfer of heavy metals from sediments to the biota can continue for years after metal releases have been terminated. Synthetic organic chemicals such as pesticides, PCBs (polychlorinated biphenyls, previously used as insulator fluid in electric transformers and capacitors), and PBDEs (polybrominated diphenyl ethers, used as flame-retardants in a wide range of products) also bind to sediment particles. These toxic organic chemicals persist in the aquatic environment for short (organophosphate pesticides) to long (PCBs and PBDEs) time periods, and have been identified in sediments, at high concentrations in some locations, in the Columbia River. Contaminated sediments that have been accumulating in hydroelectric reservoirs for several years may be re-suspended and transported to new downriver deposition sites by large spring freshets.[16] These considerations are further discussed in Chapter C.7.

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[16] Although water-storage projects have eliminated the most extreme spring freshets, sediment transport is proportional to river discharge raised to a power of 3.5. Sediment transport is therefore increased during even moderate freshets.

Nutrient Transport

The growth of phytoplankton, periphyton, and macrophytes – the primary producers that constitute the foundation of aquatic food webs[17] – is largely influenced by availability of the major nutrients nitrate and phosphate. Silicate is also an essential nutrient for diatoms, a prominent component of phytoplankton and periphyton. Water storage reservoirs can act as traps for suspended sediments and nutrients (Ward and Stanford 1983, Thornton et al. 1990, Melillo et al. 2003), reducing availability to downstream areas. In addition to sedimentation of particulate material at low flow velocities, nutrients are removed from reservoirs by phytoplankton and periphyton, enter planktonic/nectonic and benthic food webs, and may be eventually sequestered in sediments. Relatively low nutrient concentrations in Columbia River water at Vernita Bar, above the confluence with the Snake River, are due in part to nutrient removal by ten large upstream water storage projects on the mainstem Columbia River and on the Kootenai, Pend Oreille, Clark Fork and Duncan rivers. For example, the annual average flow at Vernita Bar in 2000 was 52% of the flow in the lower Columbia (89 km above the river mouth), but total nitrogen (TN) transport at Vernita Bar was only 25% and total phosphorus (TP) transport only 15% of transport at the lower river site (water year 2000; Wise et al. 2007).[18] By comparison, the Snake River in the same year contributed 20% of flow, 30% of TN, and 24% of TP, and the Willamette River contributed 15% of flow, 28% of TN, and 30% of TP. The relatively high nutrient contribution by the Willamette River reflects the extensive conversion of land to agricultural use there (Prahl et al. 1997).

Loss of nutrients in upper-basin water storage reservoirs, as well as reduced nutrient release from salmon carcasses as a consequence of declining wild salmon populations and blocked access to previously used spawning grounds, has reduced nutrient inputs to some Columbia River tributaries. However, agricultural development and urbanization have greatly increased nutrient inputs at other locations. Of these two factors, agriculture is by far the most important. In 2000, agricultural use of chemical fertilizers and manure introduced 660,000 metric tons (mt) of nitrogen and 126,000 mt of phosphorus into Basin watersheds (Wise et al. 2007), exceeding point-source release of these nutrients (largely from urban centers) by 50-fold or more. A mass-balance comparison of net nutrient inputs to Basin streams prior to and after human settlement has not been attempted, but it is highly likely that nutrient transport by the river overall is much higher now than prior to settlement, despite some removal of nutrients in upstream storage reservoirs.

Although run-of-river hydroelectric reservoirs on the mainstem Columbia and Snake rivers trap sediments, they have little or no effect on downstream transport of dissolved nutrients. Nitrate, soluble reactive phosphorus, and silica concentrations increase 20% to 40% as water passes through the series of four reservoirs on the lower Columbia River (1996-1998; Kelly 2001). The increases are attributed to inputs from tributary streams which carry high nutrient concentrations (Prahl et al. 1997).

Temperature Regimes

Water temperature has a primary influence on basic processes like solute chemistry, nutrient cycling, and metabolic rates, and can thereby has important effects on aquatic food webs. Collectively, hydrologic alteration and other human development across the Basin have had an important influence on water temperature regimes (Sidebar B.2.1). Temperature controls on physiology and growth of aquatic organisms translate to effects on development, life history, behavior, distribution in time and space, and ultimately to predator-prey and competitive interactions (e.g., Reeves et al. 1987, Reese and Harvey 2002, ISAB 2007-2, McCullough et al. 2009). Temperature influences the production, distribution and availability of species at all levels of organization (McCullough et al. 2009, Olden and Naiman 2010) and so influences the abundance, distribution, dynamics, productivity and persistence of salmonids and other species feeding, consuming or interacting with them (Coutant 1999, Poole and Berman 2001, McCullough et al. 2009, Olden and Naiman 2010).

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[17] A second "foundation" of lesser importance in the mainstem Columbia River is provided by organic material imported from upstream terrestrial sources.

[18] Nutrient loads are low relative to flow at Vernita Bar despite the introduction a few km upstream of drainage water from 2,700 km^2 of irrigated land in the Columbia Basin Project.

Sidebar B.2.1. Alteration of Temperature Regimes in the Columbia River

Temperature has a fundamental influence on physical and biotic processes that directly affect aquatic food webs. Therefore, any change in temperature regimes is important to consider. Changes in water temperatures related to the development of water storage and hydropower facilities can be characterized in three ways: *moderation of seasonal variability*, *general warming*, and *altered temporal and spatial variability* at finer scales.

Moderation by water storage reservoirs – Large storage reservoirs moderate flow (i.e., shift the relative volume of winter and summer flows) and temperature regimes. They do this by storing much of the cold spring flood and releasing it later from reservoir hypolimnia that remain cold through the summer season. As a result, for rivers below larger storage impoundments, summer flows are often cooler and winter flows warmer than occurred naturally (Coutant 1999, Stanford et al. 2006). The extent of temperature moderation depends on the volume of storage, depth and timing of releases, and relative volume of discharge and receiving flow. Discharges from Grand Coulee Dam, for example, moderate summer temperatures of the Columbia River (Ebel et al. 1989) as far downstream as the mouth of the Snake River (~ 435 km; Quinn et al. 1997, Coutant 1999), and even to Bonneville Dam (ISAB 2003-1). Dworshak Reservoir releases to the Clearwater River reduce summer temperatures in the Snake River by as much as 9-10^o C below the Clearwater confluence, and even beyond Lower Granite Dam (~ 144 km; Coutant 1999, Tiffan et al., 2009). Brownlee Dam in Hells Canyon warms fall, winter and early spring flows, and cools summer flows in the Snake River (Geist et al. 2006, Williams et al. 2008). Reservoirs formed by other dams throughout the Basin, including Hungry Horse on the South Fork Flathead River, Koocanusa on the Kootenay River, Deadwood on the Payette River, and several on the Boise River also alter downstream temperatures substantially in both summer and winter.

Warming trends – In the lower mainstem Columbia River a trend toward earlier warming, later cooling, and higher maximum temperatures (average increase >1.8^o C in summer maximum since the 1940s) was first noted in the mid 1990s (Quinn and Adams 1996, NRC 1996, Quinn et al. 1997, Robards and Quinn 2002). The trends are associated with declining summer flows linked to water extraction, warmer irrigation return flows, changes in tributaries related to climate change (NRC 2004, ISAB 2007-2), and upstream storage effects (D. Jay, Portland State University, personal communication). Air temperatures are increasing with a warming climate, while summer base flows in tributaries are declining (Hidalgo et al. 2009, Luce and Holden 2009). Climate-related warming has become apparent in a number of tributary streams where detailed examination has occurred (e.g., Isaak et al. 2010).

Altered spatial and temporal variability – The spatial and temporal variability of temperatures within and among reaches of streams and rivers are altered by dams and flow regulation. In general the river downstream of cold storage reservoir discharges has an altered (relative to the natural river) gradient of increasing temperature that can extend from a few km to hundreds of km downstream. Hourly flow fluctuations associated with load-following power production can produce rapid expansion and contraction of that "equilibration zone" (Coutant 1999). Even constant discharge can produce substantial diel variation because of heating and cooling associated with normal air temperature fluctuations (CaIssie 2006). Mixing zones at the confluences of tributaries produce complex spatial patterns as well. Summer water releases from Dworshak Reservoir to the Clearwater River, for example, produce sharp vertical and horizontal gradients in temperature that extend at least to Lower Granite Reservoir (Tiffan et al. 2009; Figure B.2.3). Similar gradients exist below the confluence of the warmer Snake River with the cooler Columbia River, and may be modified by complex channel topography (Coutant 1999).

The cold-water plumes of smaller tributaries produce thermal gradients that serve as refugia for aquatic organisms that might not normally persist in the food webs of warmer mainstem rivers (Keefer et al. 2007, 2008; McCullough et al. 2009). However, the extent and quality of these refugia may be declining with water resource development and land use changes. Fluctuations in discharge associated with run-of-river or storage impoundments also influence hydraulic gradients associated with hyporheic (subsurface) discharge, which may be either colder or warmer than ambient river temperatures. Since dams are often built at channel constrictions, reservoirs often inundate the upstream alluvial floodplains, thereby blocking hyporheic exchange and eliminating thermal refugia for some species (Poole and Berman 2001, Sauter et al. 2001). Dams can alter hyporheic conditions downstream as well. For instance, increased flow and depth associated with power peaking *reduces* the hydraulic gradients at the river bed below Bonneville Dam, essentially blocking hyporheic discharge and reducing or eliminating thermal gradients important for reach-scale habitat segregation between chum and Chinook (Geist et al. 2008). Flow fluctuations associated with load following may produce highly complex temperature patterns differing markedly from those occurring in natural systems, and with other food web implications as well.

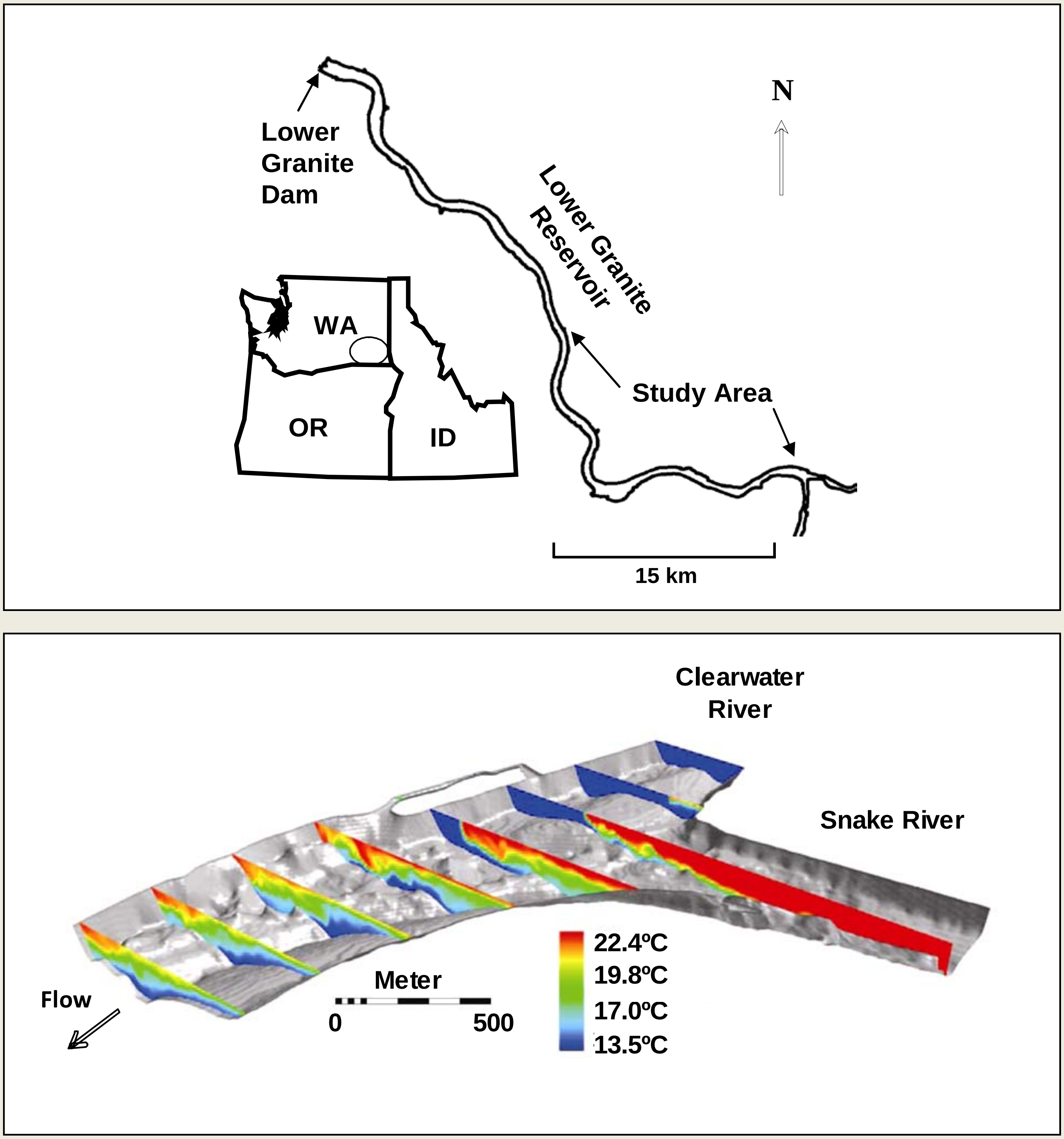

Figure B.2.3. Map showing the thermal structure of the Snake and Clearwater rivers above and below their confluence (Tiffan et al. 2009, reproduced from Cook et al. 2006)

The actual effects of temperature alteration on Columbia River food webs and on the salmonid populations linked to them are not well documented, but there are some clues in recent work. Researchers have shown complex changes in the migration timing of adult salmon, steelhead and shad with warming and declining flows (e.g., Quinn and Adams 1996, Quinn et al. 1997, Robards and Quinn 2002, Keefer et al. 2007). Similarly, thermally driven changes in juvenile migrations are anticipated and could result in important mismatches between critical points in life history tied to forage availability (NRC 1996, Quinn and Adams 1996, Coutant 1999, Geist et al. 2006; ISAB 2004-2, 2007-2).

Warming also has been associated with an expansion of non-native populations of American shad in mainstem reservoirs. Juvenile shad may compete with juvenile fall Chinook for zooplankton prey, which are an important food resource for both species in mainstem reservoirs (ISAB 2007-2). Warming is anticipated to result in expansion of populations of some species, and in food consumption by native and non-native fishes that prey on juvenile salmonids (Petersen and Kitchell 2001, Heino et al. 2009), as well as the vulnerability of salmonids to that predation (Quinn and Adams 1996, Petersen and Kitchell 2001; ISAB 2004-2, 2007-2). The loss or shifting distribution of thermal refugia might exacerbate effects like these throughout the Basin (Sauter et al. 2001, McCullough et al. 2009, Isaak et al. 2010).

Moderated thermal regimes below many storage reservoirs in the West have resulted in the reorganization of fish communities, often with the expansion of non-native species (Lee et al. 1997). Introduced rainbow trout have expanded in tail-waters below larger impoundments, and introduced warm and cool-water species have expanded in many of the impoundments themselves. The general expectation has been for cascading effects through food webs that may threaten traditional fisheries and native populations (Eby et al. 2006). Moderated thermal regimes also may have positive aspects, such as the expansion of native rainbow trout below Arrow Rock Reservoir in the South Fork Boise River, or the potential to use regulated flows to partially mitigate the effects of future climate change (Nelitz et al. 2007, Olden and Naiman 2010). The dominant life history and relative success of fall Chinook in the Snake River may be changing towards a life history that overwinters in reservoirs, in part due to changes in thermal and forage conditions that influence early growth and survival in the hydropower system reservoirs (Connor et al. 2002, 2003, 2005; Chandler 2007, Tiffan et al. 2009).

Conclusions

Impoundment of hydroelectric reservoirs on the mainstem Columbia River and many of its tributaries, and of water storage reservoirs throughout the Basin, has had far-reaching effects on aquatic food webs. In addition to the elimination of almost all mainstem riverine and floodplain habitat (Chapter D.6), water storage alters the magnitude and timing of historical seasonal flow cycles, and power-peaking releases of water from hydroelectric dams result in unnatural short-term flow and depth fluctuations. Retention of water in reservoirs also alters seasonal temperature cycles, resulting in elevated temperatures during the summer months. These changes are generally unfavorable for native aquatic biota adapted to cool running waters, but favorable to many non-indigenous species better adapted to impoundments (Chapter C.5). Some non-indigenous species have proven to be effective predators on or competitors with native invertebrate animals and fishes (Chapters C.3, C.5, D.5, D.6).

Changes in the hydrograph have also altered transport of sediments and nutrients to the estuary and coastal shelf, with consequences for food webs in those environments (Chapter D.7). Changes in aquatic food webs related to development of the hydropower system will be further amplified in the future as long-term trends in climate conditions, land use, release of chemicals, and introduction of non-indigenous species continue (Chapters C.5, C.7, E.1). Thoughtful and durable restorative measures will be required to protect native species and maintain beneficial uses of Columbia Basin waters (Chapters E.3).

C. Environmental Processes Affecting Food Web Characteristics

C.1. Importance of Marine-Derived Nutrients

Annual spawning migrations provide a mechanism for transporting nutrients from the fertile northern Pacific Ocean to freshwaters and associated riparian zones (Stockner 2003, Naiman et al. 2009). This phenomenon has been recognized for centuries. Returning salmon were widely regarded by aboriginal peoples as vessels of nutrition, and it was accepted that Nature would be fundamentally different, and poorer, without them (Roche and McHutchison 1998).

These basic insights have not changed. Returning fish replenish and help sustain aquatic ecosystems, although in recent decades their numbers have diminished greatly in the southern part of their range in North America (Stouder et al. 1997, Gresh et al. 2000). The marine-derived nutrients (MDN) fuel an amazingly complex process that is surprisingly sensitive to climate, latitude, land use, species and individual stock characteristics. Nevertheless, with continued exploitation of Pacific salmon and declines in other anadromous species, and with projected changes in climate and land use, it is not yet clear how the story will ultimately unfold.

The accumulation of knowledge about salmon-borne nutrients and ecosystem processes is impressive (summarized in Stockner 2003, Naiman et al. 2002, 2009) and has been discussed briefly in previous ISAB reports (ISAB 2003, 2005; Table A.2.1). Here we review major pathways, mechanisms and consequences of fish-borne MDN in estuarine, freshwater and riparian ecosystems. In so doing, we describe the breadth of the MDN influence on the long-term viability of fish populations and on the structure and dynamics of coupled aquatic-riparian food webs, and identify gaps in understanding these processes.

Major Roles and Processes of MDN in Aquatic and Riparian Ecosystems

It has been long recognized that nutrients from salmon carcasses may be a significant factor in the support of freshwater production (Juday et al. 1932). However, relatively little quantitative information on the nutrient contribution by salmon to stream ecosystems existed until the development of stable isotope analysis. Over time, the biogeochemical cycling of elements results in a predictable distribution of heavy and light isotopes in nature. For example, carbon (C) in marine systems is enriched with the heavier isotope of carbon (i.e., a higher $^{13}C/^{12}C$ ratio) relative to terrestrial organic matter in plants and soils. Similarly, stable isotope ratios for nitrogen (N) and sulfur (S) differ between terrestrial and marine ecosystems. The difference in these isotopic ratios enables the fate of marine-derived C, N, S and other elements to be tracked in food webs through analyses of naturally occurring stable isotopes (see Appendix A).

Estuaries. Little is known about the potential impacts of fish-borne MDN on trophic interactions or fish growth in estuaries, and the reports are mixed. On one hand, this is not surprising considering the tidal influences and the variability in estuarine residence times among salmon species. On the other hand, one might expect a clear MDN impact, given that pink and chum salmon frequently spawn short distances upstream, and that fish-borne nutrients and carcasses are washed downstream (Brickell and Goering 1970, Goering and Brickell 1972). Furthermore, estuaries are used extensively by juvenile chum and ocean-type Chinook, and all anadromous fish spend some portion of their life cycle there.

There is some documentation, however, that estuarine invertebrates utilize MDN. Two clam species in the high intertidal zone near abundant salmon spawning exhibit elevated $\delta^{15}N$ values relative to the same species located in the mid-intertidal zone (Chow 2007)[19]. Further, harpacticoid copepods consume the macroalgae *Ulva* sp. as a primary food source, and *Ulva* utilizes MDN when available (Fujiwara and Highsmith 1997). Since foods of juvenile chum in the estuary are often dominated by harpacticoid copepods, there may

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[19] The heavier isotope of nitrogen (^{15}N), as compared to the more common form (^{14}N), is present in relatively higher abundance in the oceans and also accumulates as trophic level increases. Isotopic ratios, typically expressed as δ values, represent the parts per thousand deviation in a sample from a international isotope standard. For example, the international N standard is atmospheric N_2, which contains 0.3663% ^{15}N, or $\delta^{15}N = 0‰$. In general, N in salmon tissues contain slightly more of the heavier isotope (^{15}N), frequently in the range of 0.3707% ^{15}N, or $\delta^{15}N = 12‰$.

be an indirect link between adult and juvenile chum when MDN inputs enhance algal and harpacticoid production, ultimately increasing food availability and juvenile chum growth and survival.

Nevertheless, according to other studies, MDN appear to have little effect on growth of juvenile salmonids in estuaries. For example, decomposition of adult salmon carcasses result in increased concentrations of organic N in Iliuliuk Bay, Alaska, but no beneficial effects are observed for juvenile salmon (Brickell and Goering 1970). Similarly, application of urea fertilizer to the Yakoun River estuary in the Queen Charlotte Islands, British Columbia, does not result in appreciable enhancement of salmonid growth or survival (Stockner and Levings 1982).

Several factors may account for the lack of influence of MDN on juvenile salmon in estuaries. Estuaries may have sufficient nutrients from other sources because they receive inputs from the entire catchment, as well as the ocean. They are typically among the most nutrient-rich environments in the Basin. Moreover, nutrient inputs might be sequestered by estuarine sediments before they can be incorporated into the food web. Even though salmon carcass decomposition results in increased dissolved organic N concentrations, there may be no change in NH_4^+ concentration, the form of N most useful to primary producers, as estuarine sediments can sequester organic N before it is mineralized (Brickell and Goering 1970). This process is exacerbated by the fact that estuaries typically have fine sediments with high capacities for adsorption of organic compounds. In addition, dry-wet cycles result in alternating oxidizing and reducing conditions, causing specific adsorption of dissolved elements onto hydrous oxides of iron (Fe) and aluminum (Al) and thereby transforming dissolved nutrients into less soluble and less bioavailable forms (Faulkner and Richardson 1989).

Lakes. Nutrient inputs from returning fish have been long known to affect the N and P status of oligotrophic lakes (e.g., Juday et al. 1932, Barnaby 1944, Donaldson 1967). Lake studies have focused primarily on sockeye. MDN are transferred to lakes via downstream movement from spawning tributaries and via in situ decomposition of beach spawners. Sockeye-producing lakes are typically oligotrophic, and primary production is often severely nutrient-limited (Goldman 1960, Hyatt and Stockner 1985, Wurtsbaugh et al. 1997, Hyatt et al. 2004). Consequently, MDN inputs, depending on the physical setting, have significant potential to stimulate overall lake productivity (Stockner and Ashley 2003).

Since flushing rates tend to be low in lakes, MDN inputs may be comparatively high in relation to losses. For example, in Iliamna Lake, Alaska, annual salmon-borne inputs are equivalent to 50 – 100% of total annual dissolved N losses via flushing (Kline et al. 1993) and comprise >50% of total lake P (Donaldson 1967). Similarly, on the Kamchatka Peninsula of northeastern Russia, spawning sockeye contribute an estimated 30 – 40% of total annual P inputs (Krohkin 1975). In contrast, simulation models of sockeye-producing lakes in Idaho indicate that MDN historically has been of minimal importance, contributing only 3% of annual P budgets, much of which is quickly lost due to high flushing rates and P export by smolts (Gross et al. 1998). Regardless of flushing rates, the significance of MDN inputs may be reduced by dilution in large volume lakes (Krohkin 1967, Durbin et al. 1979). However, effective concentrations may be greater in localized habitats such as near nesting colonies of avian scavengers (Payne and Moore 2006), the mouths of spawning tributaries, or in the vicinity of beach spawning. In general, MDN inputs are more likely to influence production in lakes where spawning densities and contributions of salmon-derived nutrients are high relative to lake nutrient pools, and where flushing rates are low.

Alaskan and Russian lakes show a link between MDN, primary production, and plankton composition. Sockeye-producing lakes show increased phytoplankton biomass and primary production in years of high salmon escapement (e.g., Schindler et al. 2003), while lakes to which anadromous access is blocked show significantly lower P concentrations and phytoplankton standing stocks (Kyle 1996). These latter results, however, are confounded as most non-salmon lakes sit high in the hydrologic landscape and salmon lakes are generally low in the landscape. MDN inputs also influence species composition as well as productivity and biomass in lake algal communities. Analyses of fossilized diatoms and $\delta^{15}N$ signals in sediment cores show strong historical correlations between diatom assemblages and salmon spawning densities in Alaskan lakes (Finney et al. 2000, 2002; Gregory-Eaves et al. 2003, 2009). Periods of high salmon abundance correlate with increased abundance of mesotrophic to eutrophic indicators such as *Stephanodiscus minutulus/parvus* and *Fragilaria crotonensis*, whereas periods of low salmon abundance are marked by more oligotrophic taxa such as *Cyclotella comensis* and *C. ocellata*. These responses are similar to those seen following lake fertilization in other coastal systems (Ennis et al. 1983).

Responses of zooplankton to MDN inputs are less consistent than those for phytoplankton. The inconsistencies are most likely due to bottom-up effects of MDN fertilization being confounded by top-down effects of foraging by juvenile sockeye and other fishes on zooplankton (Burgner 1991). Some of the increased algal production in sockeye lakes may be due to reductions in grazing by zooplankton (cf. Carpenter et al. 1985). Whereas there are reports of increased zooplankton production associated with high escapements (Krohkin 1975, Sweetman and Finney 2003), and positive correlations between spawner density and zooplankton δ^{15}N (Finney et al. 2000), others report that foraging by juvenile sockeye results in decreased zooplankton biomass (Schmidt et al. 1998), possibly minimizing the positive effects on zooplankton abundance of increased algal production (Hardy et al. 1986). This appears to be caused by recruitment exceeding system carrying capacity and thereby depressing edible zooplankton, and eventually resulting in density-dependent growth reduction.

Feedbacks to salmon production. Juvenile sockeye production is correlated with lake primary production and forage resources (Burgner 1987, Koenings and Burkett 1987, Hume et al. 1996). Therefore, it has been suggested that MDN from returning fish may provide an important feedback for future stocks (Mathisen 1972, Mathisen et al. 1988). Accordingly, N and P fertilization projects have been undertaken by various agencies to enhance production of sockeye (LeBrasseur et al. 1979, Stockner 1981, 1987; Hyatt and Stockner 1985, Griswold et al. 2003, Hyatt et al. 2004) and other salmon species that forage as juveniles on zooplankton in oligotrophic lakes (Kyle 1994). Nonetheless, it is difficult to establish an unequivocal link between MDN and salmon production in lakes. Lake to lake comparisons suggest that juvenile salmon obtain MDN through the lake food web, and that enhanced lake productivity is associated with increased smolt production, but it is not clear that increased recruitment is a result of MDN enrichment of nursery habitat or a result of increased spawning. Within a single lake, the relationship between amount of MDN and juvenile salmon production is not clear either. As MDN increase, so does primary production, but it does not necessarily produce more fish (Schindler et al. 2003). The lack of a clear relationship may be in part due to the fact that, over a minimum threshold, all salmon populations show strong negative density dependence in growth and survival. Additionally, even where MDN inputs enhance primary and secondary production in nursery lakes, these effects will not be necessarily translated to increased smolt production where other factors (e.g., spawning habitat availability) are limiting.

Rivers. Spawning and subsequent decomposition of carcasses create seasonal pulses of dissolved and particulate nutrients in streams, which are thought to be important in food web dynamics. These pulses typically are measured as N (NH_4^+, NO_3^-, total N) or phosphorus (PO_4^{-2}, soluble reactive P, total P) concentrations, relative to background levels. The nutrient pulses generally increase with run size or carcass abundance (e.g., Johnston et al. 2004, Mitchell and Lamberti 2005, Hood et al. 2007). Their duration varies; most studies report concentrations returning to background levels within 1–3 months of the pulse onset (Sugai and Burrell 1984, Johnston et al. 2004, Claeson et al. 2006).

Several mechanisms have been proposed to explain how salmon alter stream nutrient concentrations (summarized in Moore et al. 2007). The excretion of dissolved nutrients from dead and dying salmon and the decomposition of salmon carcasses are perhaps the primary source of these nutrients. However, the construction of redds by the fish also has the potential to contribute nutrients. Redd construction can release antecedent dissolved nutrient pools trapped in sediments, resuspend nutrient-laden sediments and organic matter, and reduce nutrient uptake by scouring or burying periphyton that would otherwise sequester dissolved nutrients. Redd construction may be sufficient to cause significant changes in water chemistry on its own.

The response of periphyton to the annual influx of MDN is highly variable. It is often quantified as a change in chlorophyll *a* or ash-free dry mass per unit area, and it may be as great as a 15-20x increase (Mitchell and Lamberti 2005, Wipfli et al. 1998). In other cases, redd creation decreases primary production (e.g., Moore et al. 2004), or no significant change in production parameters is observed (e.g., Claeson et al. 2006). The variability may also be due to other biotic and abiotic factors, including: 1) run timing, magnitude and distribution, 2) stream temperature, discharge and shading, 3) background nutrient levels, 4) carcass retention capacity, 5) nutrient storage capacity and 6) composition of the biological community (Ambrose et al. 2004).

As fish die, macroinvertebrates rapidly colonize the carcasses, with densities of some taxa increasing relative to areas without MDN (Minakawa and Gara 2003, Walter et al. 2006). In their attraction to dead salmon, macroinvertebrates are selective, choosing carcasses higher in fat and nutrient content where available. Analyses of δ^{13}C and δ^{15}N confirm that macroinvertebrates consume and assimilate MDN, either directly from salmon tissue or indirectly via grazing of algae and fungi containing MDN, or via predation on other MDN-enriched invertebrate taxa (e.g., Bilby et al. 1996, Claeson et al. 2006). Evidence from natural streams and artificial microcosms indicates that macroinvertebrate density, standing stock and individual growth rate are increased in the presence of salmon carcasses (Chaloner and Wipfli 2002, Minakawa et al. 2002).

MDN are incorporated into freshwater fishes, resident or anadromous, through several trophic pathways (Kline et al. 1990, 1993; Bilby et al. 1996). Nutrients and organic matter from spawning salmon may be incorporated into stream food webs through autotrophic or heterotrophic uptake and subsequently eaten by invertebrates that serve as a food source for the fish (Chaloner and Wipfli 2002). Fishes also directly incorporate MDN by consuming salmon eggs and carcass flesh (Bilby et al. 1998). Direct consumption of salmon eggs and carcasses are important for Dolly Varden and rainbow trout in Alaska (Denton et al. 2009, 2010), and bull trout in the Skagit River, Washington (Lowery 2009). While MDN might stimulate growth of juvenile salmon, this food subsidy might also prop up predator populations. MDN subsidies also may affect the growth, condition, biomass, density and lipid content of resident freshwater fishes (Bilby et al. 1998, Wipfli et al. 2003, 2004, Denton et al. 2010). The duration of effects vary; some persist only as long as carcasses are available, while others last for months after decomposition. Unfortunately, these analyses tend to have small sample sizes (n = 1 or 2 streams). Therefore, the consistency of the responses seen in these studies is unknown.

There are positive feedbacks on fish populations via MDN-enhanced productivity within streams. For example, spawning salmon deliver a pulse of energy and nutrients, and actively modify the physical stream bed, all of which influence stream productivity. Local densities of juvenile salmon increase during spawning and, as juvenile and resident salmonids consume spawner tissue and eggs, their lipid content, condition factor, growth rate and survivorship also increase (Bilby et al. 1998, Wipfli et al. 2003). These feedbacks often occur in winter, a critical period when other food sources are limited, and likely influence life-histories since larger fish have a greater propensity to out-migrate to marine systems (Jonsson and Jonsson 2005) and generally survive at a higher rate when they do (Bilton et al. 1982, Bilton 1984, Ward and Slaney 1988, Holtby et al. 1990; but see Holtby and Healey 1986).

The link between stream productivity and salmonid production, as evidenced by the results of river fertilization experiments (e.g., Johnston et al. 1990, Deegan and Peterson 1992), suggests that depleted fish populations risk spiraling toward further depletion, exacerbating the challenge of recovery efforts (Larkin and Slaney 1997, Scheuerell et al. 2005), and necessitating the development of nutrient restoration programs (e.g., Pearsons et al. 2007, Kohler et al. 2007). For this reason, MDN effects on stream productivity should be considered in setting fisheries escapement numbers, for example to a level above which an increase in MDN transfer is no longer observed (Bilby et al. 2001).

There are, however, potential adverse effects of MDN in the contemporary world. Salmon transport not only nutrients from marine to freshwater systems, but also persistent industrial pollutants (also see Chapter C.7). These pollutants include methylmercury (MeHg; Zhang et al. 2003), polybrominated diphenyl ethers (PBDEs; Hites et al. 2004a), and various organochlorine contaminants, such as polychlorinated biphenyls (PCBs; Krümmel et al. 2003, Hites et al. 2004b, Kelly et al. 2007) and polychlorinated dibenzodioxin and dibenzofuran (PCDD/F; Kelly et al. 2007). Such compounds are lipophilic and biomagnified in relatively fatty fish that occupy higher trophic levels, such as salmon (Thomann et al. 1992). Because salmon species differ in marine distribution and diet, they also differ in their contaminant levels (O'Neill et al. 2006, O'Neill and West 2009), with higher tissue concentrations typically found in species with coastal distributions and feeding at higher trophic levels (e.g., Chinook) than in those with more oceanic distributions and feeding at relatively lower trophic levels (e.g., pink). Pollutants transported upstream by salmon can exceed background levels from atmospheric deposition (Zhang et al. 2003, Krümmel et al. 2003, Kelly et al. 2007). Even in heavily urbanized and industrial watersheds such as the Fraser River, British Columbia, the majority of some contaminants may originate from marine sources (Kelly et al. 2007). Not surprisingly, pollutant concentrations in lake sediments near spawning grounds correlate with spawner densities (Krümmel et al. 2003). The positive feedback of nutrient cycling between spawning adults and their progeny may be counterbalanced by a negative feedback of pollution, a complication that is relatively recent in their evolutionary history.

Riparian Zones. The influence of riparian vegetation on the quality of salmonid habitat has been well documented; there are strong feedbacks on salmon populations via enhanced riparian functions. Riparian forests partially regulate instream primary production through shading, while providing allochthonous organic matter in the form of litter inputs (Naiman and Décamps 1997, Naiman et al. 2005). These processes affect the species composition and production of aquatic invertebrates, which provide an essential food source for juvenile fishes (Meehan et al. 1977). In some systems, riparian canopy effects may exert a greater influence on fish biomass, density and growth than do direct inputs of nutrients and organic matter in the form of salmon carcasses (Wilzbach et al. 2005). However, MDN enrichment of riparian invertebrates does affect juvenile salmon production, as terrestrial invertebrates often support a substantial proportion of fish diets (Wipfli 1997, Baxter et al. 2005).

MDN transfer mechanisms. In natural systems animals play important roles in mediating MDN transfer from spawning streams to riparian ecosystems. Bears in particular can consume a large proportion of total spawner biomass (e.g., Gende et al. 2002), with the number of salmon killed determined largely by spawner density (Quinn et al. 2003). MDN are subsequently transferred to riparian soils via dissemination of partially-eaten carcasses and salmon-enriched wastes. In southwestern Alaska, total annual N inputs to riparian ecosystems are significantly increased by the presence of salmon and bear together, but not by either species individually (Helfield and Naiman 2006).

Although bear are the most visible consumers of salmon, MDN are also disseminated by other salmon-eating mammals and birds (e.g., Ben-David et al. 1998, Hilderbrand et al. 2004, Christie and Reimchen 2005, Payne and Moore 2006). Nutrients are also carried from streams to adjacent riparian areas via the metamorphosis of aquatic insects into winged adults and their subsequent death and consumption by terrestrial insectivores (Jackson and Fisher 1986). Terrestrial flies and carrion beetles also are suspected to play an important role in distributing and diffusing MDN via colonization and consumption of salmon carcasses by larvae and subsequent dispersal of adult insects within the riparian zone (Meehan et al. 2005, Hocking and Reimchen 2006).

MDN are also transferred to riparian habitats through abiotic processes. While flooding deposits salmon carcasses on stream banks in larger rivers (Cederholm et al. 1989, Ben-David et al. 1998) dissolved nutrients from decomposing carcasses may enter hyporheic flowpaths in streams with hydraulically conductive substrates. Increased concentrations of NH_4^+ and soluble reactive P have been observed in streams following entry of spawning sockeye salmon in peak run years, and the nutrient-enriched surface water subsequently downwells into the hyporheic zone beneath the riparian forest (O'Keefe and Edwards 2003). The relative importance of these pathways varies in time and space with salmon escapement and predator abundance, as well as climate, channel morphology, flow and vegetative characteristics (Helfield and Naiman 2006).

Soil-plant nutrient processes. Most pathways for the movement of salmon-derived nutrients in riparian areas are mediated through soils. Riparian soils adjacent to streams show significant ^{15}N enrichment when spawning densities are high (Reimchen et al. 2003, Bartz and Naiman 2005). Although ^{15}N enrichment can be potentially caused by biogeochemical processes unrelated to MDN (e.g., Pinay et al. 2003), the inference that MDN inputs contribute to soil nutrient pools is supported by the results of experimental additions of salmon carcasses to riparian soils. In western Washington NH_4^+ and NO_3^-, bound mainly in the soft tissues of salmon, enter bioavailable soil pools within weeks to months of death; whereas calcium (Ca^{+2}) and P, bound largely in slowly decaying bone, are released over months to years (Drake et al. 2005).

Foliar ^{15}N enrichment in riparian plants growing near spawning streams is well documented (Naiman et al. 2009). Although patterns of foliar isotopic composition may be influenced by edaphic factors unrelated to MDN (e.g., Handley and Scrimgeour 1997), the weight of evidence suggests that most riparian plants assimilate MDN. Consistent ^{15}N enrichment has been quantified at sites with high spawning densities relative to comparable sites without salmon (summarized in Naiman et al. 2009). The relationship between MDN and foliar ^{15}N enrichment has been corroborated by experimental fertilization studies (e.g., Koyama et al. 2005) and by empirical observations above and below salmon-blocking waterfalls (Bartz and Naiman 2005). Additionally, an N isotope tracer study examining the fate of labeled NH_4^+ (the primary product of carcass decay) in riparian soils and trees showed that ~30% of labeled NH_4^+ was found in riparian trees within 6 months of addition (Drake et al. 2006).

Foliar nutrient concentrations are often higher in plants receiving MDN inputs (Helfield and Naiman 2001, 2002; Bilby et al. 2003, Mathewson et al. 2003, Wilkinson et al. 2005), although this is not always the case (Drake et al. 2006). MDN subsidies might not enhance foliar nutrient concentrations in cases where increased growth rates result in increased foliar biomass and diluted nutrient concentrations, or where nutrients are translocated from foliage. Alternatively, at sites where soil nutrients are abundant, MDN additions might have little effect on the nutrient status of plants. For example, salmon-derived N subsidies appear to be less important to riparian ecosystems where symbiotic N_2-fixation by alder is prevalent (Helfield and Naiman 2002).

Dendrochronological analyses indicate that MDN inputs may enhance the productivity of riparian trees, thereby shaping food web characteristics. In coastal rainforests of southeast Alaska, enhanced growth of Sitka spruce has been reported in areas where MDN inputs are greatest (Helfield and Naiman 2001). Among trees within 25 m of the stream channel, basal area growth rates are more than three times greater at sites with spawning salmon relative to comparable sites without spawning salmon. As a result, there is a disproportionate occurrence of large trees and productive forest in close proximity to spawning streams (Kirchhoff 2003, Helfield and Naiman 2003).

Short term (annual) relationships between salmon escapement and tree-ring growth have been demonstrated for various salmon and tree species throughout the Pacific Northwest (Drake et al. 2002, Drake and Naiman 2007). Although trees receiving MDN might not always grow faster than their counterparts at reference sites, tree-ring chronologies suggest that trees grow faster when salmon are abundant than they would in the absence of salmon more than half of the time. Additionally, in one Columbia River tributary, riparian tree-ring growth rates decreased concomitantly with the construction of a dam and consequent extirpation of salmon (Drake 2005). This trend was statistically significant at only one of the tributaries examined, but the technique (i.e., intervention analysis) holds promise for assessing the importance of MDN to riparian tree growth and the system-scale consequences of declining salmon runs.

Emerging Issues

Only one investigation has attempted to evaluate potential sources of variability among studies in stream ecosystem responses to salmon-borne nutrients (Janetski et al. 2009). Results obtained from 37 publications, which collectively included 79 streams, revealed positive, but highly inconsistent, overall effects of salmon on dissolved nutrients, sediment biofilm, macroinvertebrates, resident fish and isotopic enrichment. Variation in the response variables was commonly influenced by salmon biomass, stream discharge, sediment size, and whether nutrients were provided by salmon or artificial carcass treatments. Further, benthic macroinvertebrates and biofilm associated with small sediments (<32 mm) display a negative response to salmon, while those associated with large sediments (>32 mm) show a positive response. Identifying sources of variation in salmon–stream interactions is a critical step toward understanding why engineering and subsidy effects vary so dramatically over space and time, and assist in developing management strategies that will preserve the ecological integrity of salmon streams. There are, however, other important issues embedded in the observed variability:

Effects of En Masse Spawners vs. Other Species. Nearly all results to date are from Pacific salmon spawning in large and dense aggregations (i.e., pink, chum, sockeye), and the effects of MDN are readily apparent. Other species of Pacific salmon (i.e., coho, Chinook, and steelhead) often spawn in lesser numbers, even though they may be locally dense. A comparison of marine-derived N in riparian vegetation along streams in two western Washington watersheds clearly shows marine N at locations adjacent to stream reaches supporting chum salmon but not at sites supporting coho, which spawn at much lower densities (Bilby et al. 2003). There are equally compelling questions about whether, after considering the nutrient content of outmigrating juvenile salmonids rearing and growing for some time in fresh water, there is a net import or export of nutrients.

The ecosystem-scale effects of MDN from coho, Chinook, and steelhead on food webs require additional quantification. Even though MDN derived from these species can be detected in riparian vegetation (Bilby et al. 1996) it is not clear if the food web responses to the added nutrients are locally significant or spatially extensive. This latter point emphasizes that the importance of MDN is context-dependent. Its influence on food web structure and productivity depends on temporal and spatial variations in climate, channel morphology, escapement, predator density, and other local biophysical characteristics.

Artificially Placed Carcasses vs. Natural Spawning. Restoration of MDN via the artificial placement of carcasses, as is often done by hatcheries, may not directly mimic the role of natural spawners in stream food webs and may not be very effective (Shaff and Compton 2009). Although δ^{15}N of juvenile coho increases with salmon carcass mass in the stream channel, this relationship is only significant for natural spawners. Artificially placed carcasses do not appear to increase MDN utilization by juvenile coho. Quantitative information is lacking but possible explanatory factors include the restricted spatial and temporal distribution of artificially placed carcasses, general absence of eggs, and lack of substrate bioturbation. Further, dissolved nutrients are positively related to salmon biomass per unit discharge but the slope of the relationship for natural runs is five to ten times higher than for carcass additions (Janetski et al. 2009). Mean effects on ammonium and phosphorus concentrations are also greater for natural runs than for carcass additions, an effect attributable to excretion by live salmon. In contrast, larger positive effects are observed on benthic macroinvertebrates for carcass additions than for natural runs, likely because disturbance by live salmon is absent.

MDN Effects on Smolt Production and Adult Returns. The overarching concept that MDN enhances smolt size and production appears to be well established. However, ecological mechanisms supporting the enhanced growth of juvenile salmon are complex and not completely understood. As well, it is not clear how the relative availability of MDN translates into increased numbers of returning adults, especially given future uncertainties regarding climate change and other factors affecting salmon survivorship in the ocean. Although smolt size is typically positively associated with survival within a given year (Holtby et al. 1990), year-to-year variation in marine survival is only weakly correlated with smolt size, and often not at all (Quinn 2005). Indeed, marine survival may be better predicted by oceanic food web conditions, such as the intensity of coastal upwelling (Scheuerell and Williams 2005).

Conclusions

Conceptually, there is general understanding of the importance and complexity of MDN in freshwater and riparian ecosystems. Collectively, the data suggest that MDN is often important in fueling food webs and shaping ecosystem processes, thereby providing significant links between marine, freshwater and riparian ecosystems. However, there are significant exceptions and these need to be noted for specific situations (Schindler 2008). Nevertheless, the linkage is strong in many cases and, therefore, the long-term viability of fish populations, riparian plant communities and terrestrial predators and scavengers may be mutually dependent. Such findings clearly illustrate the complexity of interactions in freshwater and riparian ecosystems and the importance of food web linkages across ecosystem boundaries (Naiman and Latterell 2005). Sustainable management of fisheries requires a holistic approach that treats salmon population dynamics, ocean climatic cycles, riparian vegetation, predators and scavengers as an integrated food web. Failure to maintain the MDN requirements of the entire system will eventually result in subtle but persistent declines in system-scale integrity, leading to loss of fundamental ecological characteristics.

Finally, one must consider that there are potentially many nutrient sources available for aquatic systems. In most cases the relative importance of MDN with respect to other nutrient sources remains to be quantified. In this chapter we focused on MDN – and it is certainly an important nutrient source – especially so because of its bioavailability. Nonetheless, one should not ignore other nutrient sources for freshwater and riparian systems that also underpin the productivity of food webs. These include riparian litterfall that may add many times more in total amounts of nutrients than MDN per unit area (O'Keefe and Naiman 2006; Chapter D.8), riparian epiphytes that fix N_2 (Naiman et al. 2005), the capture of marine micronutrients in aerosols and precipitation (R. Van Pelt and R.J. Naiman, University of Washington, unpublished data), long range atmospheric transport of nutrients (e.g., N) and translocation of nutrients from upslope regions of the catchment dissolved in subsurface water flows (e.g., N from N_2-fixation by upslope alder and nutrients associated with river-borne silts; Bechtold and Naiman 2006). Collectively, the importance of other nutrient sources relative to MDN also requires quantification in terms of impacts on the overall productivity of freshwater and riparian habitats. Nevertheless, the marine environment is a highly important nutrient source and, with major alterations to salmon abundance throughout the North Pacific, the consequences for continental systems may be problematic for the continued long-term vitality of many oligotrophic freshwater systems.

C.2. Effects of Seabird and Marine Mammal Predation on Food Webs and Salmonids

Seabirds and marine mammals are top predators in food webs of the estuary, plume and ocean, and thereby may affect the abundances and species composition of lower trophic levels. They prey on salmonids, both juvenile migrants to the estuary and ocean and returning adults, as well as many other organisms in the estuary. Millions of migrating smolts and thousands of returning adults are consumed by seabirds or marine mammals every year. Thus predation by these animals has a significant impact on the survival of salmonids returning to the Columbia River.

This chapter examines the roles and effects of the dominant species on the associated food webs and identifies key uncertainties in our understanding of their relationships in the ecological system.

Seabirds

Among the piscivorous waterbirds, Caspian tern (*Hydroprogne caspia)*, double-crested cormorant (*Phalacrocorax auritus)*, white pelican (*Pelecanus erythrorhynchos*), gulls (*Larus* spp.), and common merganser (*Mergus merganser*) are all known to prey on juvenile salmonids. However, Caspian tern and double-crested cormorant are the major piscivorous predators on juvenile salmonids in the estuary and mainstem Columbia River. Figure C.2.1 shows the locations of nesting sites of piscivorous birds in the Columbia River basin. The most significant impact of avian predation on juvenile salmonids occurs in the estuary by these two species (Collis et al. 2009). The losses of juvenile salmonids to these two species of fish-eating birds nesting on East Sand Island were 15-20 million smolts, or about 15% of all juvenile salmonids estimated to reach the estuary during the 2009 out-migration (Roby and Collis 2009). The estimated total annual consumption of juvenile salmonids by species/run types are compared for Caspian terns and double-crested cormorants nesting on East Sand Island in Figure C.2.2 (Roby and Collis 2009). This shows that smolts consumed by cormorants have increased and since 2008 have exceeded the numbers consumed by Caspian terns.

Caspian Terns. Colonial nesting seabirds have increased dramatically in the Columbia estuary in recent years. Currently, East Sand Island supports the largest colony of Caspian terns in the world (~ 10,000 pairs) and the

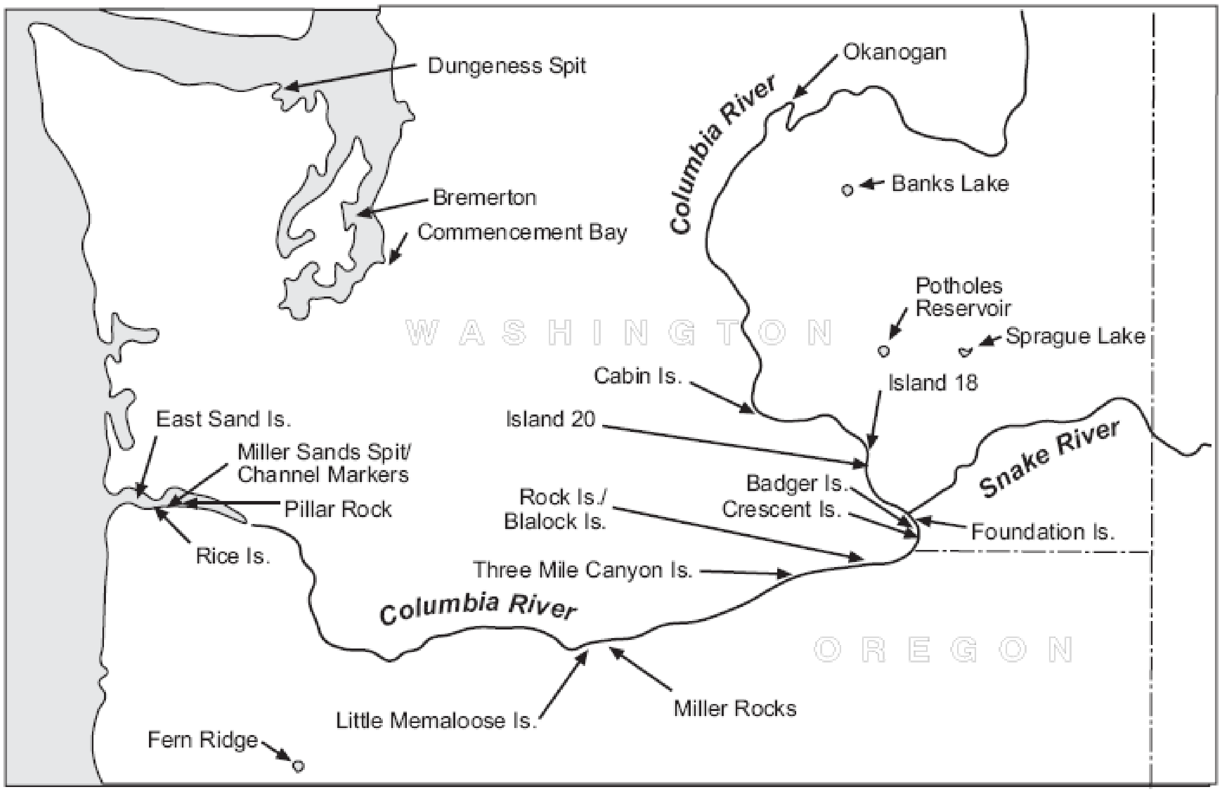


Figure C.2.1. Locations of active and historic bird colonies in the Columbia River Basin (from Roby and Collis 2009).

largest breeding colony of double-crested cormorants in western North America (~ 12,000 pairs; D. Roby, Oregon State University, personal communication). In 1980 there were no Caspian terns, only a few hundred double-crested cormorants, and many fewer gulls nesting in the estuary as compared to 2009. Several factors contributed to the large increases in seabirds during the last three decades. Foremost, these seabirds prefer to nest on low-lying, exposed islands, which are readily available today. Prior to hydropower dam construction, spring freshets scoured the islands during the nesting season. The advent of dredge spoil islands provided secure nesting habitat, free of mammalian predators. Rice Island, a dredge spoil island in the freshwater part of the estuary, was colonized by terns, cormorants and gulls in the 1980s, more than 20 years after being created. Other factors contributing to seabird increases are the large numbers of juvenile salmonids from hatcheries (Chapter C.4), and the loss of breeding habitats in other locations, such as islands in Willapa Bay, Grays Harbor and Puget Sound, Washington (D. Roby, Oregon State University, personal communication).

Caspian terns nesting on East Sand Island rely primarily on marine fishes for food. Juvenile salmonids (smolts) comprise about 30% of prey items, ranging from about 47% in 2000 to 17% in 2004, as based on direct observations of prey items carried in their bills back to the colony (Collis et al. 2009). Anchovy, Pacific herring, shiner perch, and smelt were also prevalent in the diet, together averaging 60% of tern bill loads.

Based on bioenergetic estimates, the total consumption by Caspian terns on East Sand Island in 2008 was 6.7 million smolts (95% CI= 5.8 – 7.5 million). Since 2000, the average has been 5.2 million smolts consumed annually by terns from this colony (Figure C.2.2a). This amount is less than half of the annual consumption of juvenile salmonids by Caspian terns in the late 1990s, when their breeding colony was located on Rice Island in the upper estuary (Roby et al. 2003). The difference is explained in part by a greater reliance on northern anchovy, Pacific herring, and other marine forage fishes by the East Sand Island tern colony (Lyons et al. 2005, Collis et al. 2009).

Predation rates by birds vary over time and depend on the timing of smolt outmigration and the breeding seasons of the birds (Roby et al. 2008, Ryan et al. 2003). Most salmonids are consumed from mid-April through mid-June, corresponding to the peak of coho, yearling Chinook and steelhead out-migration (Figure C.2.2a).

Based on PIT tag recoveries from the colonies, corrected for biases of detection efficiency and deposition rate, ~ 2% of the 2.4 million PIT-tagged fish released in 2008 were recovered on the Caspian tern colony at East Sand Island. Of fish identified by recovered tags, about 50% were steelhead, 34% Chinook, 2% coho and <1% sockeye, with predation rates consistently higher for hatchery than wild smolts. Minimum predation rates on PIT-tagged steelhead passing Bonneville Dam averaged ~8% for wild fish and ~ 11% for hatchery smolts (Collis et al. 2009).

Caspian terns nesting on Crescent Island in the mid-Columbia (rkm 509) also exhibit a high proportion of juvenile salmonids in their diet. About 66-68% of prey items consumed by terns in 2009 were salmon (230,000-460,000 smolts), followed by bass, other sunfish, carp and minnows. As in previous years, ~ 2% of the in-river PIT-tagged juvenile salmonids released above McNary Dam in 2008 were recovered on the Crescent Island tern colony, with steelhead being by far the most vulnerable to predation, possibly because of their size and orientation near the surface (Collis et al. 2009, Roby et al. 2008).

East Sand Island Cormorants. East Sand Island it also home to the largest double-crested cormorant colony in western North America. The total population of double-crested cormorants in the estuary has fluctuated between 10,000 and 14,000 nesting pairs since 2002 (Roby et al. 2008, Collis et al. 2009). Total smolt consumption by double-crested cormorants was about 9.3 million (95% CI: 7.1 – 11.5 million) in 2008 and 11.1 million in 2009 (Figure C.2.2b), similar to or greater than that of Caspian terns nesting on East Sand Island in those years (Roby and Collis 2009). Based on undigested fish tissue in foreguts, juvenile salmonids comprised 11% of the diet of cormorants nesting on East Sand Island, similar to other years. Anchovy was generally the most common prey type in the cormorant diet. Of the approximately 9.3 million smolts consumed by cormorants nesting in 2008, subyearling Chinook, coho, yearling Chinook and steelhead were the most prevalent juvenile salmonids, in order of decreasing prevalence (Figure C.2.2b, Roby and Collis 2009).

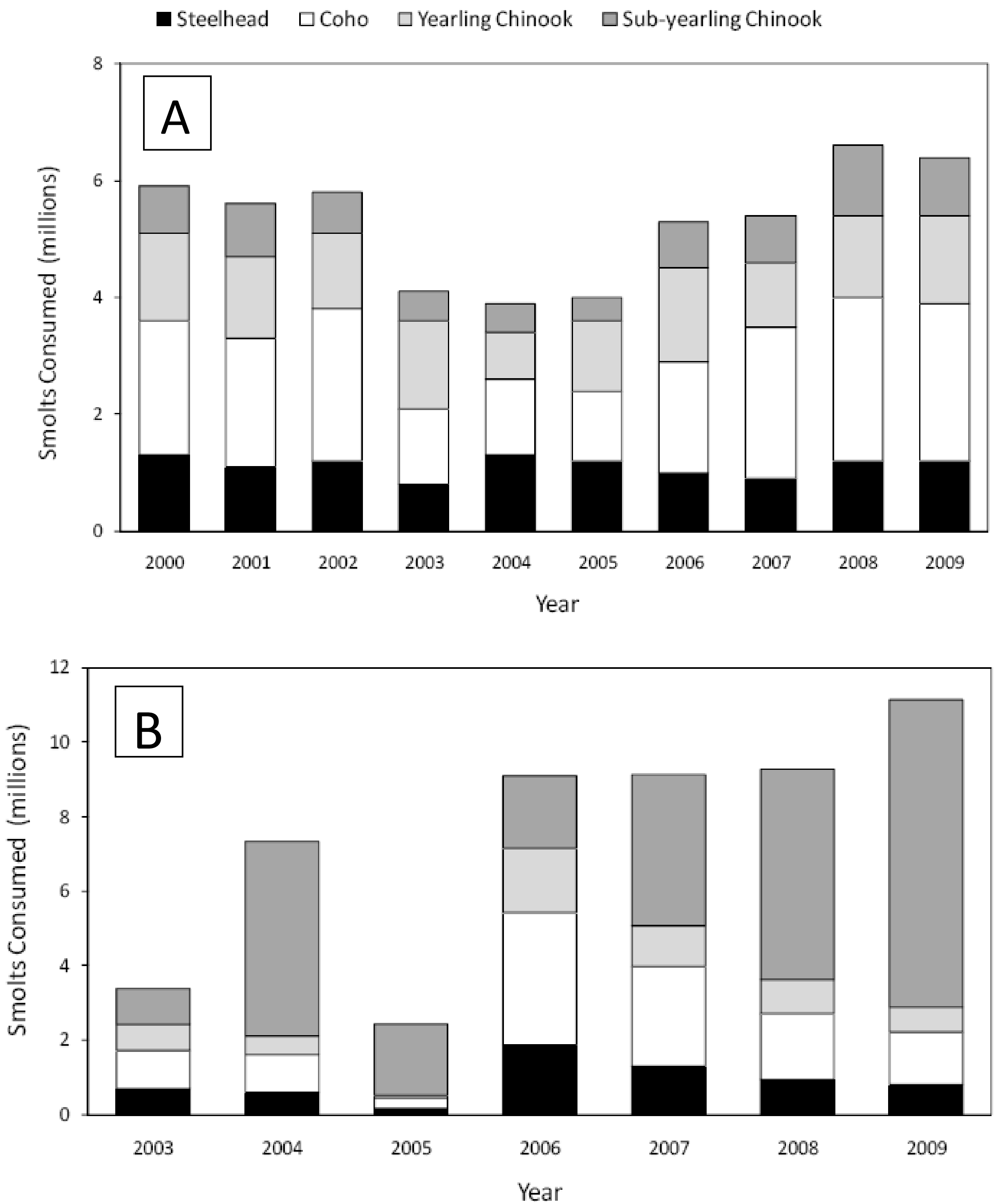


Figure C.2.2. Total annual consumption of juvenile salmonids from four species/run types by (A) Caspian terns nesting on East Sand Island during 2000-2009 and (B) double-crested cormorants during 2003-2009 (from Roby and Collis 2009).

Survival of juvenile salmonids from Bonneville Dam to the Pacific Ocean also has been estimated from acoustic and radio tags. Tracking with radio tags indicates that smolt survival is high from Bonneville Dam to the estuary (rkm 46 and salt water intrusion), but drops to 83 - 89% due to bird predation in the estuary (Schreck et al. 2006). Survival of Snake River spring Chinook and two steelhead groups tracked with acoustic tags from Bonneville Dam to the Astoria Bridge ranged from 62 - 76% (Welch et al. 2008). However, survival estimates of juvenile Chinook salmon tagged with JSATS acoustic tags, released from the Bonneville Dam bypass through the estuary, averaged only ~ 55% for yearlings and ~ 8 - 15% for subyearling fish in 2005 (McMichael et al. 2007). The greater loss of spring Chinook smolts was in the lower 50 km portion of the estuary (McMichael

2009) with avian predation accounting for only ~ 10% of the fish loss. SARs of PIT-tagged yearling Chinook and steelhead released at rkm 225 (Skamania) and in the estuary at rkm 10 (Astoria) provide interesting insights into bird predation (Marsh et al. 2008). All Astoria releases were made after dark on an outgoing tide to reduce avian predation from nearby colonial nesting birds. Based on tag recoveries after the nesting season, this release strategy was apparently successful, as avian predation rates were about 3 times higher for Chinook and about 7 times higher for steelhead released at Skamania versus Astoria. However, data indicate that transportation and release in the estuary provided only modest improvement in SARs for steelhead, and none for Chinook.

Other Piscivorous Birds. California brown pelicans have a large post-breeding roost site on East Sand Island, reaching over 7,000 birds in some years. Breeding colonies of glaucous-winged/western and ring-billed gulls are also found in the estuary, as well as small colonies of Brandt's and pelagic cormorants (Roby and Collis 2007).

Mid-Columbia River. Caspian terns and double-crested cormorants are also responsible for most losses of salmonid smolts to avian predators along the mid-Columbia River, specifically Caspian terns nesting on Crescent Island and double-crested cormorants nesting on Foundation Island, both in McNary Pool. Salmon smolts were 64% of the prey items for terns nesting on Crescent Island in 2009, or about 360,000 smolts (Roby and Collis 2009).

On the Columbia River plateau, gull colonies are found nesting on six islands between The Dalles and Rock Island dams (Figure C.2.1). California gulls nesting near Caspian tern colonies have a negative effect on the survival of juvenile salmonids because some gulls kleptoparasitize juvenile salmon from terns. Collis et al. (2002) concluded that the majority of gulls nesting on the Columbia River plateau pose little risk to salmonid survival, with the exception of California gulls nesting on Miller Rocks. Over 3,500 PIT tags (expanded estimate) were recovered from Crescent Island and Miller Rocks gull colonies in 2007 and over 4,000 PIT-tagged smolts from Miller Rocks in 2008 (Collis and Roby 2008). Consumption estimates for these two colonies suggest that gulls consume far fewer PIT-tagged fish per capita compared to nearby tern and cormorant colonies (Roby and Collis 2007, Roby and Collis 2009). However, Ruggerone (1986) estimated that the number of juvenile salmonids consumed by gulls below Wanapum Dam during a 25-day period of peak migration was over 115,000, or about 2% of the estimated spring migration. Since then the gull colony was eliminated at Cabin Island and no other colonies are near Wanapum Dam (D.Roby, pers. comm.).

Food Webs Effects. Seabirds can affect top down changes by influencing the number and sizes of prey species below them in the food web and by preying on forage fishes and intermediate consumers. For example, predation on bass and pikeminnow may mediate predation by these species on juvenile salmonids in parts of the Basin (Weise et al. 2008). High predation mortality on anchovy by seabirds may result in prey switching by other predators in the estuary or coastal ocean. Seabirds often respond functionally (through changes in their individual feeding rate) and numerically (through aggregation or reproduction) where and when appropriate sized prey is abundant.

Climate conditions also have an important influence on bird predation rates on juvenile salmonids during outmigration (Lyons et al. 2009). The diet of Caspian terns in the estuary varied among years and was related to river flows and the Pacific Decadal Oscillation (PDO). High flows and negative PDOs (cool ocean) are associated with a larger tern colony size and a greater proportion of salmonids in the diet, presumably because marine forage fishes are less available. Conversely, low flows and positive PDOs (and warm and poor ocean conditions) are related to smaller colony size, reduced salmonid consumption, and higher predation on marine fishes such as northern anchovy because anchovy move into the estuary in greater numbers during low-flow, warm years (Figure C.2.3). Thus tern predation on juvenile salmonids may be lower during years of warm PDOs and low flows when their ocean survival is usually low compared to years of cool PDOs and high river flows.

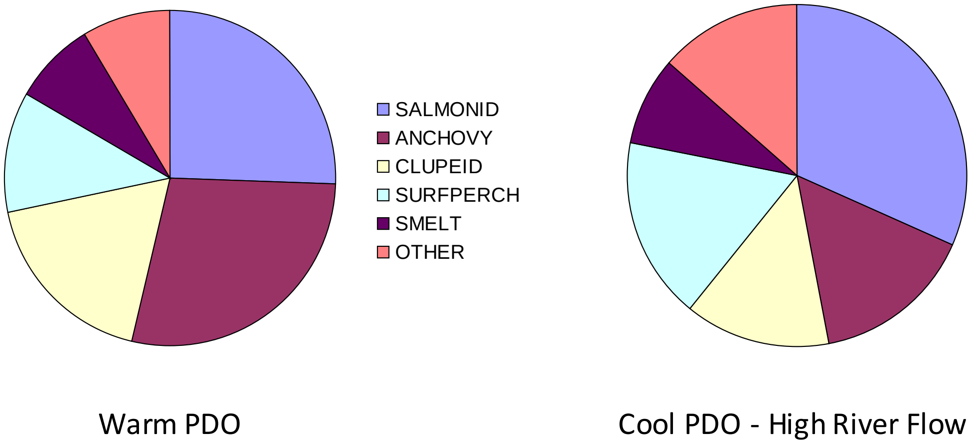


Figure C.2.3. Diet composition of Caspian terns from East Sand Island during years of contrasting PDOs and Columbia River flows (Lyons 2010).

Marine Mammals

Marine mammals also prey on both juvenile and adult salmonids, and their numbers have been increasing in the Columbia River estuary. Pinnipeds and man are the top carnivores in lower Columbia River food webs in terms of consuming large quantities of adult salmonids and other fishes (Tackley et al. 2008, Stansell et al. 2009). Three species of pinnipeds frequent the estuary and adjacent ocean: Pacific harbor seal (*Phoca vitulina richardsoni*), California sea lion (*Zalophus californianus*) and Steller sea lion (*Eumetopias jubata*).

Recent censuses estimate about 28,000 to 34,000 harbor seals along the coasts of Oregon and Washington (Scordino 2010). With the passage of the Marine Mammal Protection Act in 1972 the harbor seal population increased 4 – 7% per year until 1990; thereafter, their total population size leveled off (Jeffries et al. 1997, Carretta et al. 2007). They are present year-round near the mouth of the Columbia River, with peak numbers exceeding 3,000 from mid-December through March (NMFS 2009). Harbor seals typically are found less than 80 km upriver, but a few have been observed at Bonneville Dam.

The population of California sea lions has also increased since the mid-1970s. Population size was estimated to be about 238,000 in recent years (NMFS 2008, unpublished data). About 300-500, nearly all males or subadult males, are present in the Columbia River during most of the year. In summer, many return to breeding rookeries in southern California, where pup counts have increased to a maximum of about 50,000 per year since 2000, with declines during strong El Niño periods. California sea lions are present upriver as far as Bonneville Dam (rkm 235) and into the Willamette River up to Willamette Falls, also ~ 200 km from the ocean (NMFS 2009).

Steller sea lions in the northeast Pacific stock number about 31,000, with about 6,000 individuals in Washington and Oregon (Angliss and Allen 2009). Some are present year-round at the mouth of the Columbia River and, in recent years, 10 or more have been seen at Bonneville Dam, with a maximum of 17 in 2008 (Tackley et al. 2008).

The numbers of pinnipeds observed at Bonneville Dam have increased dramatically during the last decade. The maximum daily number of pinnipeds estimated from visual observations increased from 83 between 2002 and 2007 to 124 per year during the last three years (Figure C.2.4; Stansell et al. 2009, 2010). The mean and maximum number of days that California sea lions are present at Bonneville Dam has increased steadily from 2002 to 2008, averaging 76 per year before 2008 and 75 per year during the last three years, with peak daily abundances during late March to early May (Tackley et al. 2008, Stansell et al. 2010). Some stay in fresh water for several days, some longer. In recent years, California sea lions have been observed preying on adult fall Chinook in the Bonneville tailrace during fall and winter (Stansell et al. 2009a,b). The number of Steller sea lions observed at Bonneville Dam also increased rapidly from 2002 to 2009, averaging 5 per year before 2008 and 47 from 2008 to 2010 (Stansell et al. 2010). In 2010 the number of sea lions observed at the Bonneville tailrace was the highest since 2002 and the estimated consumption was over 6,000 adult salmonids, about 2% of the run, indicating that the impact on salmonids in the Basin is increasing (Stansell et al. 2010).

Food Web Effects. Harbor seals and sea lions are opportunistic feeders, preying both in the Columbia River and nearshore marine areas on a variety of prey, including Pacific lamprey, Pacific herring, American shad, flatfishes, smelt, surfperch, hake, rockfishes, salmonids and squid. During the spring migration of smelt, shad, lamprey, salmon and steelhead, seals and sea lions follow their prey upstream to Bonneville Dam and Willamette Falls (NMFS 2008, unpublished data). Based on scat analyses in the Columbia River and nearby estuaries, salmon generally make up to 10-30% of the diets by weight. In the Columbia River, eulachon, salmonids, rockfishes, Pacific herring, lamprey and sand lance (in that order) were identified from the gastrointestinal tracts of sea lions (Brown et al. 1995).

Fishes caught by the three pinniped species produced estimates of 0.4 to 4.2% of the salmon run taken January 1 to May 31, 2002-2009 (Table C.2.1). These estimates are based on surface observations at the tailrace of Bonneville Dam, expanded to hours when marine mammals were not being monitored and then adjusting the unknown fish catch proportionally by the known predation of fishes. Adult salmon were the primary prey. Most of the prey was adult Chinook caught by California sea lions during early March through mid-May (Tackley et al. 2008, Stansell et al. 2009b; Table C.2.1). In 2010 the “expanded” predation of Chinook salmon was 3,435 through April 28, the highest on record since 2002 (Columbia Basin Bulletin, 30 April 2010).

White sturgeon are the most commonly observed prey of Steller sea lions. The adjusted catch of white sturgeon was about 400 to over 1,700 during 2005 through 2009 (Table C.2.2; Stansell et al. 2009b). Estimated lengths of sturgeon ranged from 0.6 to 2.7 m. Hundreds of Pacific lamprey adults were also observed taken at Bonneville, comprising 1-25% of the expanded total observed fish eaten by seals and sea lions (Tackley et al. 2008, Stansell et al. 2009b).

Salmon often survive contacts with predaceous pinnipeds, leaving scars from bites and scratches. In the Columbia River, 16% of the spring Chinook and 24% of the summer steelhead passing Bonneville Dam have marks (NMFS 1997). Scarred fish are observed at Lower Granite Dam as well. The subsequent effects of these encounters on survival and successful reproduction are unknown.

The large number of seals and sea lions in the Columbia River raises concerns about their impacts on salmonids migrating upriver as adults and downriver as juveniles, especially during March through June, as well as

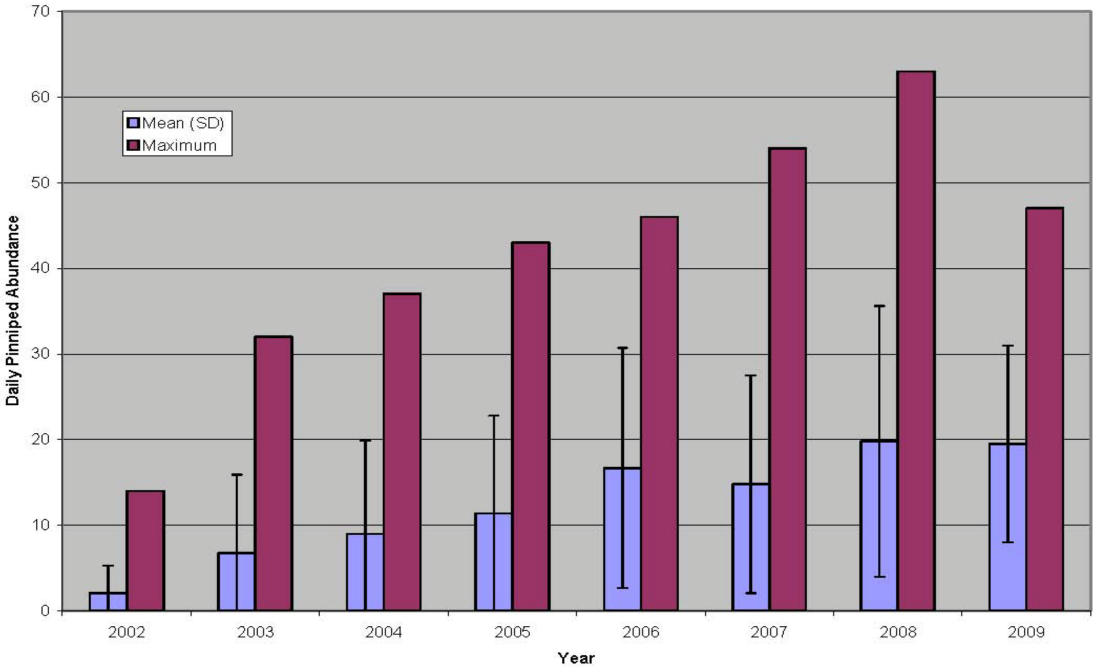


Figure C.2.4. Mean (and standard deviation) and maximum daily estimated number of pinnipeds present at Bonneville Dam between 1 January and 31 May, 2002 to 2009

Table C.2.1. Consumption of salmonids by California sea lions, Steller sea lions, and harbor seals at Bonneville Dam, from surface observations conducted between 2002 and 2009. Total salmonid passage counts include all adult salmonids that passed Bonneville Dam from January 1 through May 31. From Stansell et al. (2009b).

Year	**Bonneville Dam salmonid passage (Jan. 1-May 31)**	**Expanded salmonid consumption estimate**[1]		**Adjusted salmonid consumption estimate**[1]	
		Estimated consumption	**% of run (Jan. 1 to May 31)**	**Estimated consumption**	**% of run (Jan. 1 to May 31)**
2002	284,733	1,010	0.40%	-	-
2003	217,185	2,329	1.10%	-	-
2004	186,804	3,533	1.90%	-	-
2005	82,006	2,920	3.40%	-	-
2006	105,063	3,023	2.80%	3,401	3.10%
2007	88,474	3,859	4.20%	4,355	4.70%
2008	147,543	4,466	2.90%	4,927	3.20%
2009	186,060	4,489	2.40%	4,960	2.70%

1. Expanded consumption estimates are adjusted to time when observations were not made and for the observed proportion of fishes preyed upon. Adjusted consumption estimates include unidentified fish based on the proportion of known catch.

impacts on other fishes that reside in the estuary. In 2010 the “expanded” sea lion take of Chinook near the Bonneville Dam was the highest since 2002, over 3,400 fish (The Columbia Basin Bulletin, April 30, 2010). The numbers of pinnipeds actually residing in the lower Columbia River and the estuary and the impacts of resident pinnipeds on salmonids and other fishes and food webs are unknown.

The impact of pinniped predation on salmonids in the Columbia and Willamette rivers, on wild versus hatchery fish, on different stocks and runs, and on their productivity is still unknown or largely speculative when compared to other limiting factors or threats. There are no reliable estimates of total pinniped abundances in the estuary, integrated over all seasons. Moreover, the impact of predation on out-migrating smolts is poorly understood and difficult to assess. Losses to predation early in the life history might be compensated for by reduced losses during later life stages. Such compensation would be expected if predators selectively remove the most vulnerable individuals. The impacts are much more obvious for predation on mature salmon than on juveniles, since the adults have already survived multiple threats in multiple environments, and they are all valuable for harvest or escapement. However, the natural selection imposed by predators at any life stage prior to spawning could enhance (and may even be necessary to maintain) the fitness of wild salmon populations in the longer term.

As top predators in the ocean and estuary, pinnipeds potentially influence the dynamics and structure of food webs by altering community composition, regulating and affecting the growth and survival of prey or other predators, and in transferring nutrients among habitats. Pinniped predation on some species may benefit salmon. For example, harbor seals feed on hake, a

Table C.2.2. Consumption of white sturgeon by pinnipeds at Bonneville Dam from 1 January through 31 May, 2002 to 2009 (from Stansell et al. 2009b).

Year	**Total Hours Observed**	**Observed Sturgeon Catch**	**Expanded Sturgeon Consumption Estimate**	**Adjusted Sturgeon Consumption Estimate**
2005	1,108	1	-	-
2006	3,647	265	315	413
2007	4,433	360	467	664
2008	5,131	606	792	1,139
2009	3,455	758	1,241	1,710

species that preys on juvenile salmonids (Trites 1997). Hake are also preyed upon by sea lions off Oregon and Washington. Other fishes eating juvenile salmon, such as rockfish, are also eaten by pinnipeds. Lamprey, another favored prey of pinnipeds, may parasitize adult salmonids. Forage fishes, like herring, smelts and anchovy, when abundant, may provide a buffer to predation on juvenile salmonids (Holtby et al. 1990, Pearcy 1992). However, the effects of these linkages on food web structure and salmonid survival are largely speculative. Since adult salmonids do not feed during migration in the estuary and river, they have little direct top-down effect on lower trophic levels, but influence consumption rates by other animals that feed on salmon. They have indirect effects on lower trophic levels through the decomposition of salmon carcasses, however.

Conclusions and Key Uncertainties

Seabirds and pinnipeds are top predators in the food web in the Columbia River estuary and their influence of the dynamics and structure of lower trophic levels should be considered in future research and management. One major uncertainty of predation on salmonids by seabirds and marine mammals is the impact on spawning abundances and productivity of salmonid Evolutionarily Significant Units (ESUs). Mortality, especially on juvenile salmonids, could be either additive with a direct effect on the number of returning adults or compensatory, especially where seabird predation is compensated by increased ocean survival with little or no effect on the number of returning spawners. Predation by marine mammals, on the other hand, has a more direct effect as mature fish are killed, spawning escapement is reduced, and this may result in too few spawners to fully seed some streams. Efficient predators like pinnipeds, whose abundance is constrained by other factors (haulout sites, rookeries, prey availability in other seasons), pose a much greater threat to small salmon populations than to large populations because, typically, they kill a higher *proportion* of the population as salmon abundance decreases (i.e., the mortality is depensatory).

C.3. Food Web Consequences of Fish Predation

Fishes dramatically affect the ecological characteristics of freshwater ecosystems because they are abundant, ecologically diverse creatures that span multiple trophic levels (see Sidebar C.3.1). Moreover, they are often highly mobile or migratory, and capable of influencing the interconnectedness of food webs in different habitats (Chapter E.4). Since most fishes are carnivorous and continue to grow throughout their life, the long-lived species tend to be top predators capable of imposing significant top-down controls on food webs. Factors modifying the relative abundance of fishes at different trophic levels affect a wide variety of ecological services such as photosynthesis, water quality, nutrient cycling and the viability of other species. Predation effects are discussed throughout the report. Dams, fisheries, hatcheries and the introduction of non-native species are additional factors altering fish communities and their trophic interactions, and are further addressed in subsequent chapters.

This chapter provides an overview of the complexity of food web interactions involving fish predation, the diversity and history of fish communities in the Columbia River, and the ways in which human activities threaten those natural fish communities and the ecological services they provide. Fish predation on juvenile anadromous salmonids within the Basin is considered in more detail in Sidebar C.3.2 (for native fishes) and in Chapter C.5 (for non-native fishes). Fish predation on lake resident salmonids is reviewed in Sidebar C.6.3 and Chapter D.4.

Feeding Behavior of Fishes

Energetics and Trophic Levels. An analysis of the diet of 600 species of freshwater and marine fishes (compiled by Love 1980) shows that 85% are carnivores, 6% are herbivores, 4% are omnivores, 3% are detritivores and 2% are scavengers or filter feeders (Pandian and Vivekananan 1985). Most carnivorous fishes eat invertebrates (invertivores) and/or fish (piscivores). Carnivory is advantageous in fishes whose diet must be 2 to 4 times richer in protein than terrestrial homeotherms (Love 1980), typically exceeding 40% of total food intake. A protein rich diet meets both nutrient and energy requirements, in part because fishes require less energy to maintain body temperature than do homeotherms but also because fishes excrete nitrogenous wastes rapidly and continuously, mostly through their gills (Pandian 1975). In contrast, mammals suffer reduced growth when restricted to a high protein diet because of the energy required to eliminate nitrogenous waste (Just 1980). For example, the optimal ratio of total energy to protein energy is 2:1 in Atlantic salmon (Lee and Putnam 1973) compared with around 10:1 in terrestrial ruminants (Williamson and Payne 1980).

To meet their high requirement for protein, herbivorous and detritivorous fishes require specialized feeding and digestive adaptations. They need much higher daily rations and must spend more time foraging than carnivorous fish. Daily time costs for feeding to satiation range from 1-3 h among carnivores, 8-14 h among herbivores, 12-24 h among detritivores, and up to 24 h among filter feeders (Pandian and Vivekandandan 1985). Herbivorous and detritivorous fishes probably rely on the microorganisms attached to plants and detritus to meet their protein requirements (Goldman and Kimmel 1978).

Ontogenetic Shifts in Trophic Level. Food webs involving fishes can be especially challenging to construct because of ontogenetic changes in feeding ecology. Fish growth is indeterminate, and preferences for size and type of prey (hence trophic level) tend to change as fish grow larger. Many fishes, including most salmonids, begin life as invertivores, but they become piscivores as they grow larger (Keeley and Grant 2001). Migratory life histories such as anadromy are also common in fishes, and migration can lead to changes in diet and trophic level. For example, the Pacific lamprey is a “life history omnivore” which spends most of its life as a filter-feeding ammocoete (trophic level 2.0), but after metamorphosis, it migrates to sea where it parasitizes piscivorous fish (trophic level 4.5; see Sidebar C.3.1 for an explanation of numeric trophic levels).

Sidebar C.3.1. Numeric Trophic Level

Food webs can be organized such that members are assigned numerical ranks based on their trophic level. Trophic level 1 is for primary producers or detritus at the base of the food web; trophic level 2 for primary consumers that feed exclusively on primary producers or detritus; trophic level 3 for carnivores that feed exclusively on primary consumers (e.g., invertivores); and trophic levels 4 or higher for carnivores that feed on secondary or higher level consumers. Consumers that feed on a mix of trophic levels are assigned a fractional trophic level. For instance, a lake trout might reside at trophic level 3.5 if feeding 50% on planktivorous fish and 50% on herbivorous zooplankton, but would be at trophic level 4.0 if feeding exclusively on planktivorous fish. Among adult fishes native to the Columbia River, trophic levels range from 2.3 for the omnivorous mountain sucker to 4.3 for the piscivorous northern pikeminnow and 4.5 for the parasitic Pacific lamprey (Table C.3.2). Stable isotope analysis (see Appendix A) is a useful tool for identifying trophic level and the primary (i.e., pelagic, benthic, or detrital) pathway of energy flow for different species or life stages within a food web, as long as a baseline isotope signature can be established for the primary consumers (Vander Zanden and Rasmussen 1999).

Feeding habits can also change during ontogeny because predation risk diminishes as fish grow larger (reviewed by Ward et al. 2006, Beauchamp et al. 2007). Small fish are vulnerable to more predators than their larger conspecifics, and consequently, juveniles are often found in habitats that afford some protection from predators, such as vegetated littoral zones or deep water. Cannibalism is also common, and juvenile fishes often seek refuge from larger conspecifics. In contrast, large fish have greater opportunities than small fish to forage in less protected (and perhaps less crowded) habitat, such as the pelagic zone. Such movements to new habitat, mediated by growth and predation risk, affect competitive interactions (Mittelbach 1986, Biro et al. 2003a,b) and can shift the trophic level of any particular species, if food items differ between those habitats.

Similarly, introduction of a new competitor or predator can alter habitat use and shift the trophic level of native fishes. Stable isotope analyses (see Appendix A) have revealed that the trophic level of lake trout declined from 3.9 to 3.3 after smallmouth bass and rock bass were introduced into Canadian lakes; bass now inhabit the littoral zone and have reduced the opportunity for lake trout to subsidize their pelagic (primarily zooplankton) diet with fish from the littoral zone (Vander Zanden et al. 1999). Trophic changes observed in Flathead Lake, Montana, following the introduction of non-native lake trout may be particularly relevant to other areas of the Columbia Basin and are described in detail in Sidebar C.6.3 and Chapter D.3. Over the longer term, such trophic interactions within fish communities can lead to adaptive changes in morphology and behavior, resulting in greater resource partitioning. For example, after alewife became abundant in Lake Michigan, gill rakers in the bloater became shorter and fewer, apparently a morphological shift toward greater foraging efficiency in benthic habitats (Crowder 1986).

Trait-Mediated Interactions. Variation in feeding behavior and associated morphology (trophic polymorphism) is common among populations of the same species, or among individual fish within the same population (Ward et al. 2006). Such polymorphism is particularly well known in salmonids and sticklebacks, and typically reflects genetic adaptation to local feeding opportunities. In some species, however, individual fish may switch from one morphotype to another in response to environmental conditions (Proulx and Magnan 2004). Trophic interactions that differ among individuals within the same population are said to be “trait-mediated” (Abrams 2007). Trait-mediated interactions appear to be common and significantly affect the complexity and properties of food webs (Peacor et al. 2006). Simulation studies of simple food webs indicate that trait-mediated interactions can have a stabilizing influence, and can promote the co-existence of competing species (Peacor et al. 2006).

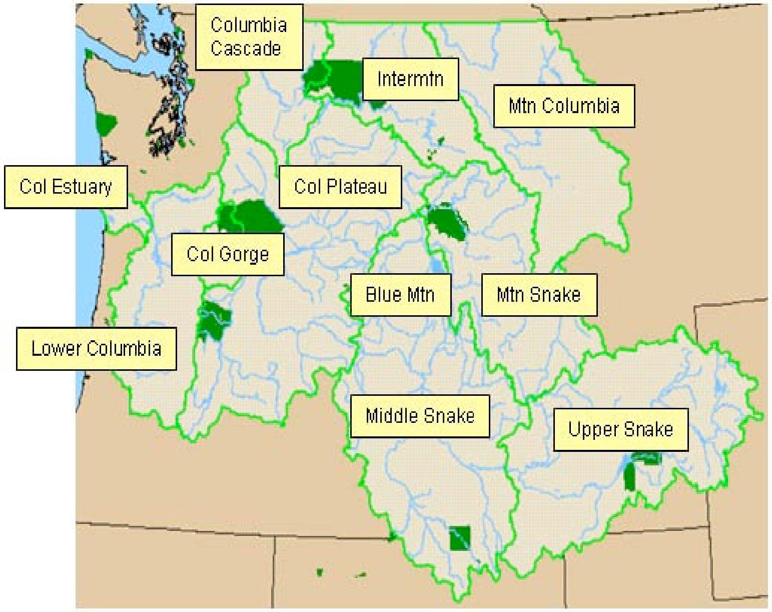
Fish Communities in the Columbia River

Native Fishes. Approximately 53 native species of freshwater and anadromous fishes occur in the Basin; an additional 44 marine species occur in the estuary (Tables C.3.1 and C.3.2). The distribution and relative abundance of these species varies considerably among the 12 provinces in the Basin, with each province typically supporting about 30 native species. Suckers, sculpins, cyprinids (pikeminnow, chubs, daces), and salmonids are the most widely distributed and abundantly represented families of native fishes. The average trophic level of the native adult freshwater and anadromous species is 3.4 (range: 2.3 to 4.5) and 25 (47%) are piscivorous.

Non-native Fishes. Approximately 45 non-native species of freshwater and anadromous fishes also inhabit the Basin, accounting for 46% of the total number of freshwater and anadromous fishes (Table C.3.3; Chapter C.5). Non-native fishes occur in all provinces, with an average of about 24 non-native species in each. Centrarchids (bass, crappie, and other sunfish), cyprinids (carp), percids (yellow perch and walleye), catfishes and salmonids are the most widely distributed and abundantly represented families of non-native fishes. The average trophic level of non-native fish species is 3.3 (range 2.0 to 4.5) and 23 species (51%) are piscivorous. Although these (unweighted) average trophic values are similar for native and non-native species, simple averaging across species does not account for the relative abundance of species. Some non-native piscivorous fishes have become exceptionally abundant. For example, in Roosevelt Lake upstream of Grand Coulee Dam, piscivorous walleye and yellow perch are the numerically dominant fishes (Harper et al. 1981). Piscivorous bass and crappie are relatively abundant in most provinces (Table C.3.3). At least nine of these species have been stocked intentionally in recent years (see Chapter C.5 for details). Additionally, species native to the Basin have been stocked into provinces that did not previously support those species.

Table C.3.1. Legend to Tables C.3.2 and C.3.3

	Occurrence		Province	Description
-	Unlikely	1	Columbia Estuary	Including all tributaries downstream of Cowlitz River
+	Confirmed	2	Lower Columbia	Including all tributaries below Bonneville down to & including the Cowlitz River
++	Common	3	Columbia Gorge	Bonneville Dam to The Dalles Dam
		4	Columbia Plateau	The Dalles Dam to Wanapum Dam, Yakima, Crab, Palouse, Tucannon, Walla Walla, & lower Snake: Pasco to Clarkston
	Habitats	5	Blue Mountain	Clarkston thru Hells Canyon, Grande Ronde, Imnaha, Asotin
A	Small tributaries	6	Mountain Snake	Clearwater & Salmon rivers only
B	Large rivers (Snake, Willamette, Yakima, etc.)	7	Middle Snake	Snake River above Hells canyon near Weiser, Boise R, Malheur, Payette, Powder, etc.
C	Free flowing reaches, excluding below Bonneville	8	Upper Snake	Above Shoshone Falls
D	Lakes	9	Columbia Cascade	Wanapum Dam to Chief Joseph Dam
E	Storage Reservoirs	10	Intermountain	Begins with Grand Coulee Dam--Spokane, Pend Oreille, Coeur d'Alene
F	Run-of -river Reservoirs	11	Mountain Columbia	Clarkfork, Bitterroot, Flathead, Kootenai
G	Estuary	12	Canadian Columbia	Portion of the Columbia River in Canada



Trophic Level	Description
1	Plants and algae make their own food and are called primary producers.
2	Herbivores eat plants and are called primary consumers.
3	Carnivores which eat herbivores are called secondary consumers.
4	Carnivores which eat other carnivores are called tertiary consumers.
5	Apex predators which have no predators are at the top of the food chain.

Table C.3.2. Native fish species in the Columbia River basin by province, trophic level, and habitat type.
See legend in Table C.3.1. Special features including piscivory (eating other fish), anadromy (spawning in freshwater but migrating to sea), and hatchery supplementation are noted. Some are not native to all provinces shown (e.g., sport fish stocking); others were extirpated from some provinces. Relative abundance data (“present” versus "common") are not available for all areas. Presence in the Canadian Columbia Province is inferred from presence in adjacent provinces (9, 10, or 11). Information was compiled from subbasin reports provided by the Northwest Power and Conservation Council and the Columbia Basin Fish and Wildlife Authority.

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
Acipenseridae	Green sturgeon	*Acipenser medirostris*	3.3	-	+	-	G	+	+										
	White sturgeon	*Acipenser transmontanus*	3.2	+	+	+	BG	+	+	+	+	++	+	+	+	+	+		+
Catostomidae	Utah sucker	*Catostomus ardens*	3.2	-	-	-	BCF							+	+				
	Longnose sucker	*Catostomus catostomus*	2.5	-	-	-	BCF				+				+	+	++	+	+
	Bridgelip sucker	*Catostomus columbianus*	2.8	-	-	-	ABCEF				+	++	++	++	++	+	++		+
	Largescale sucker	*Catostomus macrocheilus*	3.1	-	-	-	ABCDEF	+	++	+	+	++	++	++		+	++	+	+
	Mountain sucker	*Catostomus platyrhynchus*	2.3	-	-	-	ABCEF	+	++		+	++	+	+	+	+	+		+
	White sucker	*Catostomus commersoni*	2.8	-	-	-	A											+	+
Cottidae	Coastrange sculpin	*Cottus aleuticus*	3.1	+	-	-	ABG	+	+										
	Prickly sculpin	*Cottus asper*	3.1	+	-	-	BDEF	+	++	+	+					+	+		+
	Mottled sculpin	*Cottus bairdii*	3.3	+	-	-	ABCEF			+	+	++	++	++	+	+	+	+	+
	Paiute sculpin	*Cottus beldingi*	3.2	+	-	-	BCF				+	++	+	++			+		+
	Slimy sculpin	*Cottus cognatus*	3.4	+	-	-	AD					+	+			+	+	+	+
	Shorthead sculpin	*Cottus confusus*	3.7	+	-	-	ABCF					++	+	++	+	+	+		+
	Shoshone sculpin	*Cottus greenei*	3.2	+	-	-	ABF							+					
	Riffle sculpin	*Cottus gulosus*	3.2	+	-	-	AB												
	Wood River sculpin	*Cottus leiopomus*	3.2	+	-	-	A							+					
	Reticulated sculpin	*Cottus perplexus*	3.2	+	-	-	AB	+	++		+								
	Torrent sculpin	*Cottus rhotheus*	3.4	+	-	-	ABCDEF	+	++		+	+	++	+	+	+	+		+

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
	Sculpin	*Cottus spp*	3.3	+	-	-	ABCDEF								+	++	++		+
Cyprinidae	Chiselmouth	*Acrocheilus alutaceus*	2.4	-	-	-	ABCDEF	+	++	+	+	++	++	++	+	+	++		+
	Utah chub	*Gila atraria*	2.8	-	-	-	BDE							++	+				+
	Peamouth	*Mylocheilus caurinus*	3.5	-	-	-	ABCDEFG	+	++	+	+	++	+	+	+	+	++	+	+
	Oregon chub	*Oregonichthys crameri*	2.9	-	-	-	A		+										
	Lake chub	*Couesius plumbeus*	3.4	+	-	-	DE										+		+
	Northern pikeminnow	*Ptychocheilus oregonensis*	4.3	++	-	-	ABCDEF	+	++	+	+	++	++	++		+	++	+	+
	Longnose dace	*Rhinichthys cataractae*	3.2	-	-	-	ABCEF	+	++		+	++	++	++	+	+	++	+	+
	Leopard dace	*Rhinichthys falcatus*	2.7	-	-	-	A	+	+		+	+	+	+	+	+	+		+
	Speckled dace	*Rhinichthys osculus*	2.9	-	-	-	ABCDEF	+	++	+	+	++	++	++	+	+	++		+
	Umatilla dace	*Rhinichthys umatilla*	2.9	-	-	-	BCF									+			+
	Redside shiner	*Richardsonius balteatus*	3.4	-	-	-	ABCDEF	+	++	+	+	++	++	++	+	++	++	+	+
	Leatherside chub	*Snyderichthys copei*	2.9	-	-	-	A								+				
Gadidae	Burbot	*Lota lota*	4.0	+	-	-	BD				+					+	+		+
Gasterosteidae	Threespine stickleback	*Gasterosteus aculeatus*	3.5	-	+	-	ABCDEFG	+	++	+	+					+	+		+
Osmeridae	Eulachon	*Thaleichthys pacificus*	3.3	-	+	-	BG	+	+										
	Longfin smelt	*Spirinchus thaleichthys*	3.2	-	+	-	BG	+	+										
Percopsidae	Sand roller	*Percopsis transmontana*	3.3	-	-	-	AB	+	+	+	+		+			+	+		+
Petromyzontidae	River lamprey	*Lampetra ayresi*	4.5	+	+	-	ABG	+	+		+								
	Western brook lamprey	*Lampetra richardsoni*	4.0	-	-	-	AB	+	+		+	+							

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
	Pacific lamprey	*Lampetra tridentata*	4.5	+	+	-	ABFG	+	++		+	+	+	+		+			+
Salmonidae	Cutthroat trout	*Oncorhynchus clarki*	4.0	++	+	+	ABCDEFG	+	++	+	+	++	+	+	+	++	+	+	+
	Pink salmon	*Oncorhynchus gorbuscha*	4.2	-	+	-	AG												
	Chum salmon	*Oncorhynchus keta*	3.5	-	+	+	AG	+	+										
	Coho salmon	*Oncorhynchus kisutch*	4.2	++	+	++	ABCDEFG	+	+	+	+		+		+			+	+
	Rainbow trout	*Oncorhynchus mykiss*	4.4	+	-	++	ABCDEF	+	++	+	+	++	++	++	+	++	++	+	+
	Steelhead	*Oncorhynchus mykiss*	4.4	+	+	++	ABCEFG	+	+	+	+	+	+	+		++			+
	Redband trout	*Oncorhynchus mykiss gibbsi*	4.4	+	-	-	ABCDEF					+	+	+			+		+
	Sockeye salmon	*Oncorhynchus nerka*	3.7	-	+	++	DG	+	+	+	+	+	+			++			
	Kokanee	*Oncorhynchus nerka*	3.7	-	-	++	D	+	+		+	+	+	+			++	+	
	Chinook salmon	*Oncorhynchus tshawytscha*	4.4	+	+	++	ABG	+	++	+	+	+	+	+		+	+	+	
	Pygmy whitefish	*Prosopium coulterii*	3.1	-	-	-	AD									+	+	+	
	Mountain whitefish	*Prosopium williamsoni*	3.2	-	-	-	ABCDEF	+	++	+	+	++	++	+	+	+	+	+	
	Bull trout	*Salvelinus confluentus*	3.1	++	+	-	ABCDEFG	+	+	+	+	+	+	+	+	+	+	+	
Marine species	Bay goby	*Lepidogobius lepidus*	3.3	-	-	-	G	+											
	Bay pipefish	*Syngnathus leptorhynchus*	3.2	-	-	-	G	+											
	Big skate	*Raja binoculata*	3.9	+	-	-	G	+											
	Buffalo sculpin	*Enophyrs bison*	3.3	+	-	-	G	+											
	Butter sole	*Isopsetta isolepis*	3.6	-	-	-	G	+											
	Cabezon	*Scorpaenichthys marmoratus*	3.6	++	-	-	G	+											
	C-O sole	*Pleuronichthys coenosus*	3.2	-	-	-	G	+											
	English sole	*Parophrys vetulus*	3.4	-	-	-	G	+											

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
	Goby	*Rhinogobius brunneus*	3.4	-	-	-	G	+											
	Kelp greenling	*Hexogrammus decagrammus*	3.6	-	-	-	G	+											
	Lingcod	*Ophiodon elongatus*	4.3	++	-	-	G	+											
	Night smelt	*Spirinchus starksi*	3.5	-	-	-	G	+											
	Northern anchovy	*Engraulis mordax*	3.0	-	-	-	G	+											
	Pacific hake	*Merluccius productus*	4.3	+	-	-	G	+											
	Pacific herring	*Clupea harengus pallasi*	3.2	-	-	-	G	+											
	Pacific sand lance	*Ammodytes hexapterus*	3.1	-	-	-	G	+											
	Pacific sanddab	*Citharichthys sordidus*	3.5	+	-	-	G	+											
	Pacific sandfish	*Trichodon trichodon*	3.7	+	-	-	G	+											
	Pacific staghorn sculpin	*Leptocottus armatus*	3.5	+	-	-	G	+											
	Pacific tomcod	*Microgadus proximus*	3.6	-	-	-	G	+											
	Padded sculpin	*Artedius fenestralis*	4.0	+	-	-	G	+											
	Piked dogfish	*Squalus acanthias*	4.3	++	-	-	G	+											
	Pile perch	*Rhacochilus vacca*	3.7	-	-	-	G	+											
	Pricklebreast poacher	*Stellerina xyosterna*	3.2	-	-	-	G	+											
	Redtail surfperch	*Amphistichus rhodoterus*	3.4	-	-	-	G	+											
	Ringtail snailfish	*Liparis rutteri*	3.3	-	-	-	G	+											
	Saddleback gunnel	*Pholis ornata*	3.6	-	-	-	G	+											
	Sand sole	*Psettichthys melanostictus*	4.1	+	-	-	G	+											
	Shiner perch	*Cymatogaster aggregata*	3.0	-	-	-	G	+											
	Showy snailfish	*Liparis pulchellus*	3.6	-	-	-	G	+											
	Silver surfperch	*Hyperprosopon ellipticum*	3.4	-	-	-	G	+											
	Slipskin snailfish	*Liparis fucencis*	3.5	-	-	-	G	+											

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
	Snake prickleback	*Lumpenus sagitta*	3.1	-	-	-	G	+											
	Speckled sanddab	*Citharichthys stigmaeus*	3.4	-	-	-	G	+											
	Spotfin surfperch	*Hyperprosopon anale*	3.3	-	-	-	G	+											
	Starry flounder	*Platichthys stellatus*	3.3	-	-	-	BG	+											
	Striped seaperch	*Embiotoca lateralis*	3.4	-	-	-	G	+											
	Surf smelt	*Hypomesus pretiosus*	3.4	-	-	-	G	+											
	Tubenose poacher	*Pallasina barbata*	3.2	-	-	-	G	+											
	Walleye Pollock	*Theragra chalcogramma*	3.5	+	-	-	G	+											
	Walleye surfperch	*Hyperprosopon argenteum*	3.5	-	-	-	G	+											
	Warty poacher	*Ocella verrucosa*	3.2	-	-	-	G	+											
	White seaperch	*Phanerodon furcatus*	3.4	-	-	-	G	+											
	Whitebait smelt	*Allosmerus elongatus*	3.2	-	-	-	G	+											

Table C.3.3. Non-native fish species in the Columbia Basin by province, trophic level, and habitat type. See legend in Table C.3.1. Special features are noted, including piscivory (eating other fish), anadromy (spawning in freshwater but migrating to sea), and hatchery supplementation. Relative abundance data (“present” versus "common") are not available for all areas. Presence in the Canadian Columbia Province is inferred from presence in adjacent provinces (9, 10, 11), except for Atlantic salmon that are not known to successfully spawn anywhere in the Basin. Information was compiled from subbasin reports provided by the Northwest Power and Conservation Council and the Columbia Basin Fish and Wildlife Authority.

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
Centrarcidae	Green sunfish	*Lepomis cyanellus*	3.5	+	-	-	ADE	+	+								++	+	+
	Pumpkinseed	*Lepomis gibbosus*	3.1	+	-	-	BDEF	+	++	+	+	+	+	+	+	+	+	+	+
	Warmouth	*Lepomis gulosus*	3.3	+	-	-	BCDEF	+	+		+	+		+					
	Bluegill	*Lepomis macrochirus*	3.2	-	-	-	BDEF	+	++	+	+	+	+	+	+	+	+	+	+
	Redear sunfish	*Lepomis microlophus*	3.4	-	-	-	BD	+	+										
	Smallmouth bass	*Micropterus dolomieui*	3.2	++	-	+	ABCDEF	+	++	+	+	+	++	++	+	+	++	+	+
	Largemouth bass	*Micropterus salmoides*	3.8	++	-	+	BCDEF	+	++	+	+	+	+	+	+	+	++	+	+
	White crappie	*Pomoxis anularis*	4.4	++	-	-	BCDEF	+	++	+	+	+		++	+	+	++		+
	Black crappie	*Pomoxis nigromaculatus*	4.2	++	-	-	BCDEF	+	++	+	+	+	+	++	+	+	++	+	+
Cichlidae	Tilapia	*Tilapia sp.*	2.1	-	-	-	DF							+					
Clupeidae	American shad	*Alosa sapidissima*	3.5	-	+	-	BG	+	++	+	+								
Cobitidae	Oriental weatherfish	*Misgurnus anguillicaudatus*	3.2	-	-	-	D	+	+					+					
Cyprinidae	Goldfish	*Carassius auratus*	2.0	-	-	-	D	+	+		+								
	Grass carp	*Ctenopharyngodon idella*	2.0	-	-	-	BDEF	+	+	+	+			+	+			+	+
	Carp	*Cyprinus carpio*	3.0	-	-	-	BDEF	+	++	+	+	+	++	++	+	+	+		+
	Tui chub	*Gila bicolor*	2.8	-	-	-	ACDEF							+	+				
	Golden shiner	*Notemigonus crysoleucas*	2.6	-	-	-	D	+	+										
	Spottail shiner	*Notropis hudsonius*	2.5	-	-	-	D							+	+				
	Fathead minnows	*Pimephales*	2.1	-	-	-	DEF	+	+					+	+			+	+

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
		promelas																	
	Tench	*Tinca tinca*	3.5	-	-	-	DEF	+	+	+	+				+	+	+		+
Cyprinodonidae	Banded killifish	*Fundulus diaphanus*	3.2	-	-	-	DEF				+			+					
Esocidae	Tiger muskie	*Esox lucius x masquinongy*	4.5	++	-	+	BDEF						+	+			++		+
	Grass pickerel	*Esox americanus vermiculatus*	3.7	++	-	-	D										+		+
	Northern pike	*Esox lucius*	4.4	++	-	-	BDEF										+	+	+
Gasterosteidae	Brook stickleback	*Culaea inconstans*	3.1															+	+
Ictaluridae	White catfish	*Ameiurus catus*	3.8	+	-	-	BDEF	+	+							+			+
	Yellow catfish	*Ameiurus natalis*	3.3	+	-	-	BDEF	+	+		+			+			+		+
	Blue catfish	*Ictalurus furcatus*	3.4	+	-	-	BDEF							+	+				
	Black bullhead	*Ictalurus melas*	3.7	-	-	-	BDEF			+	+		+	+		+	+	+	+
	Brown bullhead	*Ictalurus nebulosus*	3.4	+	-	-	BDEF	+	+	+	+	+	+	+	+	+	+	+	+
	Channel catfish	*Ictalurus punctatus*	3.9	++	-	+	ABCEF	+	+	+	+	+	++	++	+	+	++		+
	Tadpole madtom	*Noturus gyrinus*	3.3	-	-	-	ABF				+			+					
	Flathead catfish	*Pylodictis olivaris*	3.8	+	-	-	BDEF				+	+		+					
Percidae	Yellow perch	*Perca flavescens*	3.7	+	-	-	ABCDEF	+	+	+	+	+	+	++	+	+	++	+	+
	Walleye	*Sander vitreus*	4.5	++	-	-	BCDEF	+	+	+	+			+	+	+	++	+	+
Poecillidae	Mosquito fish	*Gambusia affinus*	3.1	-	-	-	BCDEF	+	++		+			+	+				
Salmonidae	Lake whitefish	*Coregonis clupeaformis*		-	-	-	DE				+					+	++	+	+
	Golden trout	*Oncorhynchus aquabonita*	3.3	-	-	+	AD						+		+			+	+
	Atlantic salmon	*Salmo salar*	4.4	+	-	-	AB				+				+	+			
	Brown trout	*Salmo trutta*	3.6	+	-	+	ABCDEF	+	+	+	+			+	+	+	++	+	+
	Brook trout	*Salvelinus fontinalis*	3.1	+	-	+	ABCDEF	+	+	+	+	+	+	+	+	++	++	+	+

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	piscivory	anadromy	hatchery		1	2	3	4	5	6	7	8	9	10	11	12
	Lake trout	*Salvelinus namaycush*	4.3	++	-	-	DE	+	+			+	+		+		+	+	+
	Arctic grayling	*Thymallus arcticus*	3.3	-	-	+	AB						+	+	+			+	+
	Tiger trout	*S. trutta x S. fontinalus*	-	+	-	+	ABCDEF										++		+
Umbridae	Central mudminnow	*Umbra limi*	3.2	-	-	-	AD											+	+

Production of Native Fishes. Production of many native fishes has significantly declined during recent decades. This decline is most apparent among salmonids with many populations of Chinook, coho, chum, sockeye, steelhead bull trout, and Pacific eulachon/smelt protected by the Endangered Species Act. Additionally, the green sturgeon is a Species of Concern and anxiety has surfaced about the decline in abundance of Pacific lamprey (see ISAB 2009-3). In contrast, the northern pikeminnow, a major native piscivore, has become exceptionally abundant. These declines in production of native fish species, and the spectacular increase in northern pikeminnow can be linked to human activities which have changed the trophic structure and productivity of fish communities.

How Human Interventions Change the Trophic Structure of Fish Communities

Dams. Hydrological changes associated with dams significantly change freshwater fish assemblages, both above and below dams in the Columbia River Basin (Paragamian 2002) and elsewhere (Quinn and Kwak 2003, Greathouse et al. 2006, Propst et al. 2008). Specific dams also change the trophic structure of fish communities in different ways, depending on the context. Closure of the Petit-Saut Dam in French Guiana increased the number of detritivorous fish species but decreased the number of omnivorous, herbivorous and carnivorous fish species downstream (de Merona et al. 2005). In contrast, a (short-term) increase in the number of piscivorous fish species, at the expense of detritivorous species, was observed following closure of the Tucurui Dam in Brazil (de Merona et al. 2001).

In the Columbia and Snake rivers, dams have changed food web interactions both directly and indirectly. Impoundments have directly increased predation risk for anadromous salmon smolts by delaying their downstream migration (Chapters B.2 and D.6), thereby prolonging their exposure to piscivorous birds and fishes (Chapter C.2). Impoundments have also changed trophic interactions indirectly by creating extensive new habitat that favors some native piscivorous fishes like the northern pikeminnow, and providing new opportunities for non-native piscivores like walleye and centrarchids (Chapter C.5).

Fisheries. Overfishing threatens biodiversity, trophic structure, productivity and resilience in freshwater and marine ecosystems around the world (Worm et al. 2009). Since fisheries often target the largest fish, which are typically top predators, overfishing can alter the trophic structure of fish communities and entire ecosystems. Progressive overfishing that leads to serial depletion of the highest trophic levels is called “fishing down the food web” (Pauly et al. 1998), a phenomenon that is widespread in the North Atlantic Ocean and has been reported worldwide (Worm et al. 2006, Gascuel and Pauly 2009). An alternative phenomenon in which fisheries expand to exploit increasingly lower trophic levels without first depleting the higher trophic levels is called “fishing through the food web”; this trend is also common in marine fisheries throughout the world, and can lead to conflicting and unsustainable demands on ecological services delivered by food webs (Essington et al. 2006).

In the Columbia River Basin, people kill more large fish than any other predator, and such selective predation must affect the food webs. Each year, on average over the past decade, fisheries within the Basin have killed approximately 500,000 Pacific salmon and steelhead, 47,000 sturgeon, 51,000 American shad, 200,000 northern pikeminnow (bounty program), plus other fishes (Figure C.3.1). These removals imply a fishing mortality rate of about 30% for salmonids (of both hatchery and wild origin) but only about 1% for the non-native shad population. In comparison, total predation mortality on anadromous salmonids by avian and mammal predators is unlikely to exceed 20% (see Chapter C.2).

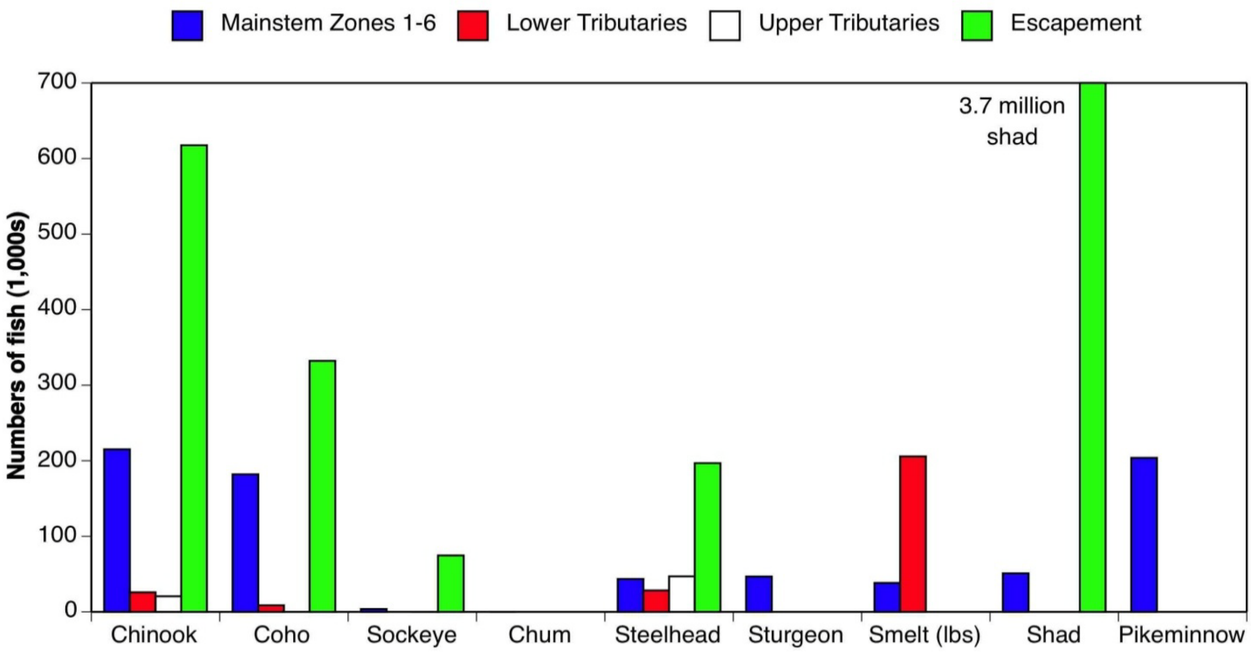


Figure C.3.1. Average catches and spawning abundances of salmon and other species in the Columbia River Basin, 1999-2008. Some catches in upriver tributaries may not be included (JCRMS 2009a,b; CBFWA). From Pacific Fishery Management Council. 2010. Review of 2009 Ocean Salmon Fisheries. Pacific Fishery Management Council, Portland, Oregon. Available by the Northwest Power and Conservation Council.

Fisheries for salmonids target hatchery-origin fish whenever possible, and although hatchery-origin fish clearly account for most of the salmonid harvests, the relative contributions of wild and hatchery-origin salmonids to the yearly harvest is not documented (C. LaFleur, WDFW, personal communication; Columbia Basin Fish and Wildlife Authority). Most shad are captured from the mainstem river below McNary Dam (Zones 1-6), but some are removed from tributaries throughout the Basin. Walleye, a non-native piscivore, is an exceptionally popular sport fish in the mainstem Columbia and in storage reservoirs; about 120,000 walleye are harvested per year in Lake Roosevelt alone (Beckman et al. 1985).

Species Introductions and Hatchery Stocking. The trophic structure of fish communities can be dramatically altered by the introduction of non-native species. For example, the non-native piscivorous Nile perch was introduced into Lake Victoria in 1954; by 1980, Nile perch accounted for 90% of the lake's fish community and replaced most of the native planktivorous or detritivorous haplochromine cichlids and catfish (Goldschmidt et al. 1993). The interaction between the native cichlids and the non-native Nile perch is thought to have been similar to that between the native walleye and the invasive rainbow smelt in the Great Lakes (Carpenter and Scheffer 2009), despite the reversed provenance of the prey and predator species. In parts of the Columbia River Basin, and elsewhere in western North America, non-native lake trout and brook trout are displacing native bull trout (Donald and Alger 1993, Nakano et al. 1998, Gunckel et al. 2002; see Chapter C.5).

When non-native predators do not replace native predators, they increase the number and diversity of top predators, which can alter trophic pathways, increase top-down control and total consumption by predators, or change connectivity among habitats (Eby et al. 2006). The effects on community structure will depend on the nature of interactions among the predators, and the complementarities of their diets and feeding behavior (Nilsson et al. 2008).

In the Columbia River, the introduction of non-native species has expanded the range of trophic levels among fishes, decreasing the lower bound from 2.5 to 2.0 when several herbivorous carps and tilapias became established, and increasing the upper bound from 4.3 (excluding the parasitic lamprey) to 4.4 or 4.5 when the piscivorous white crappie, northern pike and walleye became established (Table C.3.3). Currently, 51% of non-native species in the upper Columbia River are piscivores and their impact on native salmonids, and on

Columbia River food webs, has been considerable (Chapter C.5).

Intensive hatchery stocking of any species (native or non-native) affects food webs by increasing the number of fish feeding at a particular trophic level. Increased abundance at one trophic level will increase consumption of organisms at lower levels, while providing feeding opportunities for higher trophic levels. Each year, about 140 million hatchery-reared juvenile anadromous salmonids are released into the Columbia River, accounting for over half the total salmonid smolt migration. The magnitude of hatchery releases and their implications for food webs in the Columbia River are reviewed in Chapter C.4.

Consequences of Changing the Trophic Structure of Fish Communities

Trophic Cascades. An increasing number of studies in freshwater ecosystems (reviewed by Eby et al. 2006) and more recently in marine ecosystems (e.g., Baxter et al. 2007, O'Gorman et al. 2008, Baum and Worm 2009) have demonstrated that adding or removing top fish predators produces "trophic cascades," effects on other trophic interactions which reverberate down through the food web. Experimental studies with stream enclosures show that adding a top fish predator can indirectly decrease algae growth by releasing invertebrate grazers from predation by minnows, whose foraging had been constrained in the presence of bass (Power et al. 1985, Power 1990). Similar experiments in the Baltic Sea show that algal blooms associated with nutrient loading are exacerbated by overfishing piscivorous fishes (Eriksson et al. 2009).

Trophic cascades are particularly well documented for freshwater lakes and can have dramatic consequences for lake ecosystems (Chapters D.4, E.4). For example, human activities have caused shallow lakes in the North American prairie pothole region to become deeper and more connected, which has improved conditions for the planktivorous fathead minnow. The minnows have reduced algal grazing by zooplankton and macroinvertebrates, leading to more algae and turbid water, and consequently, fewer macrophytes, and ultimately fewer waterbirds and other wetland-dependent species (Potthoff et al. 2008).

Other Consequences for Ecosystems. Fishes play a significant role in recycling nutrients within ecosystems and moving nutrients between ecosystems. Because of their relatively large biomass, fish store a large proportion of the nutrients in some (especially tropical) ecosystems and they can transport these nutrients faster and farther than most other taxa (McIntyre et al. 2007). Moreover, they excrete dissolved nutrients in a form readily available to primary producers. Reducing planktivorous fish biomass decreases total excretion by fishes; conversely, adding fishes to fishless lakes increases the rate of nutrient recycling (Schindler et al. 1993, 2001). Changes to food webs that alter nutrient turnover time probably alter ecosystem resilience (Eby et al. 2006). It has been documented that overfishing certain species has disproportionate effects on nutrient recycling because of the great variation among fish species in relative rates of recycling N versus P (McIntyre et al. 2007).

Species with migratory life histories often couple ecosystems. One consequence is that local interactions affecting predator abundance in one ecosystem have reverberating effects in another (Chapter E.4). For example, fish can increase terrestrial plant production by eating dragonfly nymphs, thereby decreasing the number of adult dragonflies that eat pollinating insects (Knight et al. 2005). Anadromous salmon are considered keystone species for their ability to transfer nutrients from the ocean to freshwater habitats, thereby enhancing the ecological luxuriance of both freshwater and terrestrial ecosystems (Chapter C.1). Similarly, fishes that forage in the littoral zone of lakes can transfer nutrients to the pelagic zone (Vanni 2002), and this coupling of habitats can be diminished by the stocking of top predators (Eby et al. 2006).

Trophic interactions between piscivorous and planktivorous fishes in lakes can also determine whether a lake is a source or sink for atmospheric carbon dioxide. Lakes dominated by planktivorous fishes are typically sinks for carbon dioxide, because phytoplankton are released from grazing by zooplankton, which allows gross primary production to exceed respiration (Cole et al. 2000).

Loss of functional diversity in food webs is thought to make ecosystems less resilient (Gunderson and Holling 2002), but the importance of functional diversity in fishes rarely has been considered. Experimental manipulations of whole lakes in Canada have shown that lakes with greater functional redundancy of invertebrates and cyprinid fish species are more resilient to the effects of acid stress than are lakes without functional redundancy (Schindler 1990).

Opportunities for Managing the Trophic Structure of Fish Communities

The trophic structure of fish communities in the Basin is not understood sufficiently well to manage or reliably predict changes in those fish communities. Simulation models based on food webs and bioenergetics (Chapter C.6) have been developed to quantify existing interactions and can be used to guide construction of ecosystem models (e.g., *Ecopath*, Christensen in press; *Atlantis*, Fulton et al. 2007) to explore and evaluate alternative scenarios for managing community structure and ecosystem services. Early applications of these models in other ecosystems appear promising (e.g., Fulton 2010). However, such models require more comprehensive information about community composition and food web interactions than is currently available for the Columbia River.

These concerns and knowledge gaps lead to a number of general recommendations (Chapter E.5). Efforts to develop ecosystem models would improve our perspective of the relative impact on salmonid production from predation by fishes, birds, humans (fisheries) and other mammals, and the significance of competition with non-native fishes and salmonids released from hatcheries. Experimental studies are also needed to test and confirm the predictive and explanatory power of alternative ecosystem models. Once validated, ecosystem models could predict and evaluate the outcome of alternative management strategies or interventions with a view to controlling undesirable changes in food webs.

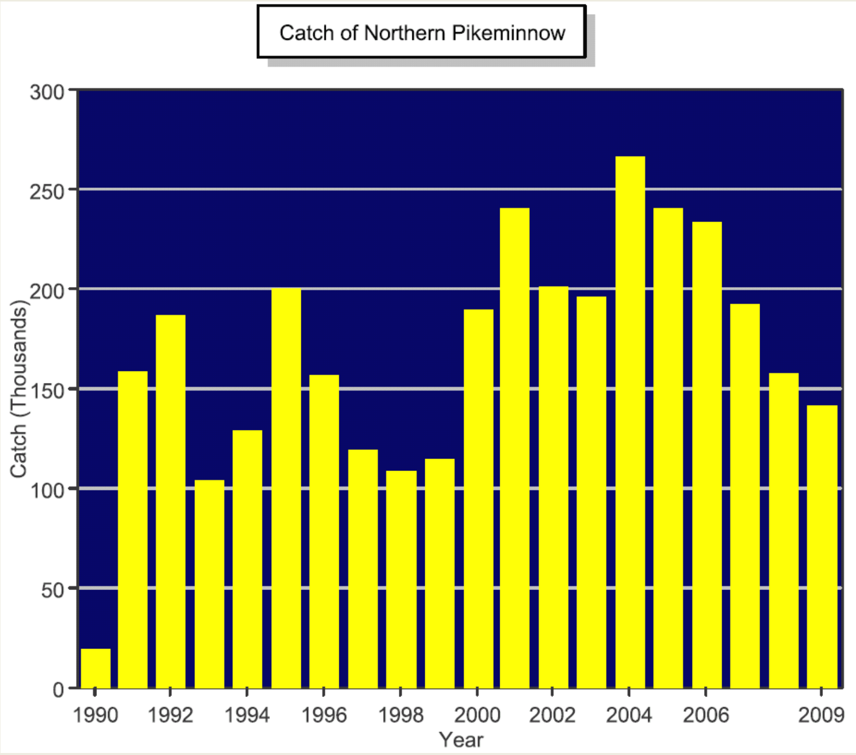
The following studies of fish communities and their trophic interactions are recommended to facilitate the development of ecosystem models:

- Determine the relative abundance and biomass of species in Columbia River fish communities. Intensive studies conducted in large reservoirs in the 1990s are likely out of date, as non-native species continue to spread and little is known about fish communities in some major habitats.
- Investigate the trophic interactions within existing fish communities, with an emphasis on estimating parameters required for ecosystem models.
- Develop bioenergetic models to quantify (or bound) the reduction in productivity of target populations that could be expected from predation and competition by other fish species, or other populations (especially hatchery releases) of the same species.
- Create opportunities to test predictions of bioenergetic models by monitoring changes in productivity of target populations due to predation by and competition with other populations.

Sidebar C.3.2. Fish Predation of Juvenile Pacific Salmon in the Columbia Basin

The Columbia River is home to five species of Pacific salmon and the anadromous steelhead trout. Populations of these species were once among the largest in the world with estimated annual adult returns to the river mouth of 5 million salmon and steelhead during unfavorable survival years to nearly 20 million during favorable years, but this abundance has declined to just under two million adults in the recent decade. Much of the decline can be attributed to dams and development of the hydrosystem, which among other impacts, delays the downstream migration of salmon smolts and makes them more vulnerable to fish predation. This sidebar and Table C.3.4 are intended to provide a summary of what is known about the extent of fish predation on juvenile salmon during downstream migration.

Fish predation on juvenile salmonids has been studied most extensively in impounded reaches of the lower Columbia and Snake rivers. Reservoirs provide favorable habitat for a number of piscivorous species, but the most important predators of juvenile salmon are native northern pikeminnow and non-native smallmouth bass and walleye (Table C.3.4). Comparisons of the diets and relative abundances of northern pikeminnow, smallmouth bass, and walleye in both impounded and non-impounded reaches of the Snake and Lower Columbia rivers between 1990 and 1996 show that northern pikeminnow ate primarily juvenile salmonids, whereas smallmouth bass and walleye ate primarily non-salmonid fishes (sculpins, cyprinids, suckers, and percopsids; Zimmerman 1999). Diets varied widely among species and river reaches in terms of both the proportion of fish and non-fish prey and the proportion of salmonid and non-salmonid fish prey. Smallmouth bass were dramatically more abundant in impounded reaches of the Snake River than in the non-impounded reaches of the lower Columbia River. Walleye, on the other hand, appear to be restricted to the Columbia River (Zimmerman and Parker 1995). These investigations provide strong evidence that the impacts of non-native predator species on juvenile salmon can vary greatly among habitats.



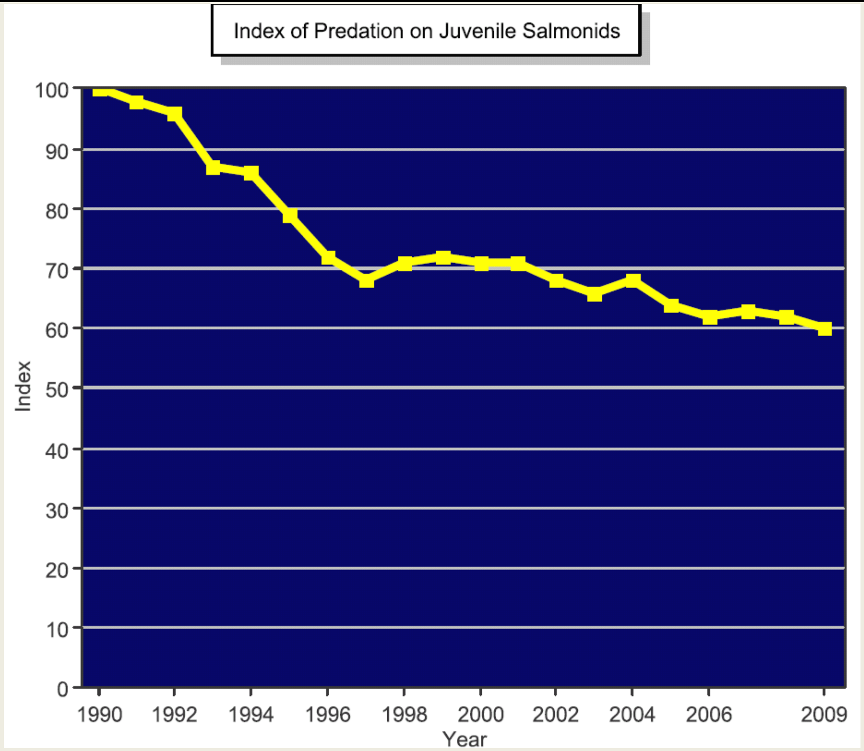


Figure C.3.2. Removals of northern pikeminnow from the lower Columbia River and trends in the index of predation on juvenile salmonids (from CBFWA).

The northern pikeminnow is clearly the most abundant and significant fish predator of juvenile salmonids in the lower Columbia River above Astoria (Friesen and Ward 1999). Pikeminnow appear to aggregate in the tailraces of dams, where they feed on disoriented salmon smolts (McNary Dam, Poe et al. 1991; and elsewhere, Ward et al. 1995), and at sites in Bonneville Pool where hatchery-origin salmonids are released (Collis et al. 1995). An intensive study of fish predation in the John Day Reservoir between 1983 and 1986 (Beamesderfer et al. 1991, Poe et al. 1991, Rieman et al. 1991, Vigg et al. 1991) revealed that, on average, salmonids accounted for 67% (by weight) of the diet of pikeminnow, and Petersen (1994) later estimated that pikeminnow killed ~ 7% of all juvenile salmon entering the reservoir. Ward et al. (1995) concluded that pikeminnow caused similar or higher mortality of juvenile salmonids downstream of Bonneville Dam. Raymond et al. (1996) estimated that prior to initiation of a control program pikeminnow killed 8% of the roughly 200 million juvenile salmonids that migrated downstream in the Basin each year. The pikeminnow removal program, initiated in 1990, appears to have progressively reduced mortality on juvenile salmonids by 25% after 5 to 6 years (Friesen and Ward 1999) and by 40% (CBFWA 2010) after 19 years (Figure C.3.2). To date, there is no evidence of compensation in predation, growth, or reproduction by surviving pikeminnow, or by other resident fish predators (CBFWA 2010).

Smallmouth bass in the John Day Reservoir eat relatively few salmonids (< 4% of the diet by weight, Poe et al. 1991) and cause relatively low mortality to migrating salmonid smolts (< 1% mortality, Rieman et al. 1991; see Table C.3.4). In contrast, smallmouth bass in the McNary Reservoir eat juvenile salmon at a higher rate (1 to 1.4 salmon per bass per day, accounting for 59% of their diet by weight) than do northern pikeminnow (0.3 to 0.6 salmon per pikeminnow per day, accounting for only 29% of their diet; Tabor et al. 1993). However, total removals from McNary Reservoir cannot be estimated without information on the relative abundances of predator species.

Channel catfish are voracious predators of juvenile salmon, with salmon accounting for 33% of the catfish's diet in the John Day Reservoir, but catfish are probably not abundant enough in the Basin to cause significant mortality of salmonids (Rieman et al. 1991). White sturgeon are known to eat moribund or injured salmon but are not considered to be significant predators of healthy salmon in reservoirs (Rieman et al. 1991).

In the Middle Columbia River (upstream of its confluence with the Yakima River, but below Chief Joseph Dam), 54% of resident fish species are piscivorous, and 59% are non-native species (data from subbasin report). Of these, northern pikeminnow, smallmouth bass and walleye have the greatest potential for significantly affecting salmonids. Sculpin also may cause significant mortality to salmonids during the egg and fry stages (Hillman et al. 1989). Adult salmonids including bull trout, rainbow trout, cutthroat trout and brook trout are known to prey on juvenile Chinook and steelhead; some instances are reported in the upper Wenatchee River basin (Hillman and Miller 2002).

Recent studies indicate that fishes eating salmon are relatively rare in the Columbia River estuary downstream of Astoria (L. Weitkamp and R. Emmett, NOAA Fisheries, Montlake and Newport facilities, personal communication). Consequently, fish predation in the lower estuary cannot account for significant mortality of juvenile salmon. Pacific hake and jack mackerel eat juvenile salmon migrating seaward from the Columbia River, but the rate of predation appears to be extremely low – only 7 Chinook smolts were observed in the stomachs of 5320 hake and 2082 mackerel examined between 1998 and 2004 (Emmett and Krutzikowsky 2008). The low rate of predation on salmon reflects the fact that juvenile salmonids account for a very small proportion of the small forage fishes in that area. Nevertheless, because hake can be very abundant in some years (billions of fish), they likely contribute to salmon mortality to some degree.

Table C.3.4. Major fish predators of juvenile anadromous salmonids in the Columbia River Basin

Location	Fish Predator	Relative Abundance	% Salmon in Diet (by weight)	% of Available Salmon Killed	Sources
Middle Columbia					
Tributaries	Sculpins (several species)	+	Primarily eggs		
	Bull Trout	+			
	Cutthroat Trout	+			
	Rainbow/Steelhead Trout				
Mainstem	Northern Pikeminnow	++			
	Smallmouth Bass	+			
	Walleye	+			
	Channel Catfish	-			
Lower Columbia					
McNary Reservoir	Northern Pikeminnow	++	29% Salmon		Tabor et al. (1993)
	Smallmouth Bass	+	59% Salmon	Moderate?	
	Walleye	+			
	Channel Catfish	+			
John Day Reservoir	Northern Pikeminnow	++	67% Salmon	High (7.3%)	Poe et al. (1991), Rieman et al. (1991), Petersen (1994)
	Walleye	+	14% Salmon	<2%	
	Smallmouth Bass	+	4% Salmon	Low (<1%)	
	Channel Catfish	+	33% Salmon	<<1%[1]	
Bonneville Reservoir	Northern Pikeminnow	++		High?	Collis et al. (1995), Ward et al. (1995), Zimmerman (1999)
	Smallmouth Bass	+			
	Walleye	+			
	Channel Catfish	+			
Lower Snake					
Unimpounded reach upstream of Lower Granite Reservoir	Northern Pikeminnow	++			Zimmerman (1999)
	Smallmouth Bass	++			
	Walleye	-			
	Channel Catfish	+			
Little Goose Reservoir	Northern Pikeminnow	++			Curet (1993), Zimmerman (1999)
Lower Granite Reservoir	Smallmouth Bass	++	70% Fish[2]	Moderate?	

Location	Fish Predator	Relative Abundance	% Salmon in Diet (by weight)	% of Available Salmon Killed	Sources
Columbia Estuary	Walleye Channel Catfish Northern Pikeminnow Smallmouth Bass	- + ++ +	74 - 83% Fish[2]	High Low?	Ward et al. (1995)
Columbia Plume	Walleye Pacific Hake Jack Mackerel	- ++ +	<<1% Salmon <<1% Salmon	<<1% <<1%	Emmett and Krutzikowsky (2008)

Notes:

[1] abundance so low that impact is likely negligible

[2] mostly non-salmonid fishes

C.4. Hatchery Releases and Food Webs

Fish released from hatcheries in the Columbia River Basin enter natural food webs and affect native fish communities and their trophic interactions. Concerns about ecological interactions between hatchery-reared and naturally produced (wild) salmonids have been expressed for many years (Reisenbichler and McIntyre 1977, Nickelson et al. 1986). Evidence is growing that such ecological interactions reduce the productivity (Fresh 1997, Chilcote 2003, Kostow et al. 2003, Kostow and Zhou 2006) and carrying capacity (Buhle et al. 2009) of wild salmonid populations. The unintended consequences of hatchery releases can have serious implications for the recovery of endangered salmonid populations.

This chapter provides perspective on the scope of current hatchery releases by summarizing the numbers and biomass of hatchery fish released by species and release location (Table C.4.1). We focus on trophic interactions between hatchery-reared and wild salmonids, summarizing the evidence that hatchery-reared salmonids prey upon or compete for food with wild salmonids. We then attempt to determine how the overall burden that juvenile anadromous salmonids impose on Columbia River food webs has changed since the development of the hydrosystem (Table C.4.2). Finally, we provide some general guidelines to reduce the undesirable impacts of hatchery releases on food webs.

Scope of Hatchery Releases

Anadromous salmonids. Most anadromous salmonids in the Basin originate from hatcheries. Overall proportions of wild and hatchery-reared salmon are not known with precision, because not all hatchery fish are marked, monitoring is incomplete and some fisheries target hatchery fish. Even so, the aggregate release of hatchery-reared smolts to the Columbia River is well over half the total smolt abundance (as estimated from adult returns and discussed in greater detail below; Table C.4.2). This conclusion is also supported by recent sampling of juveniles during downstream migration. Juvenile Chinook, steelhead and coho from the open waters of the estuary in 2007 to 2009 were primarily hatchery-reared (range 89 -100%, L. Weitkamp, NOAA Fisheries, personal communication). In contrast, juveniles in rearing areas off the main channel in restored and reference wetlands from 2005 to 2007 were predominantly wild (Roegner et al. 2010). In 2009, hatchery-reared fish accounted for at least 85% of the total adult catch of spring/summer Chinook and steelhead, 80% of coho, and 34% of fall Chinook, but less than 10% of sockeye (Figure C.4.1).

Salmon hatcheries were built primarily to maintain fisheries in the face of a continuing decline in production from wild populations, caused in large part by dam construction between 1907 and 1975. An estimated 8.25 billion hatchery-reared anadromous salmonids have been released into the Columbia River

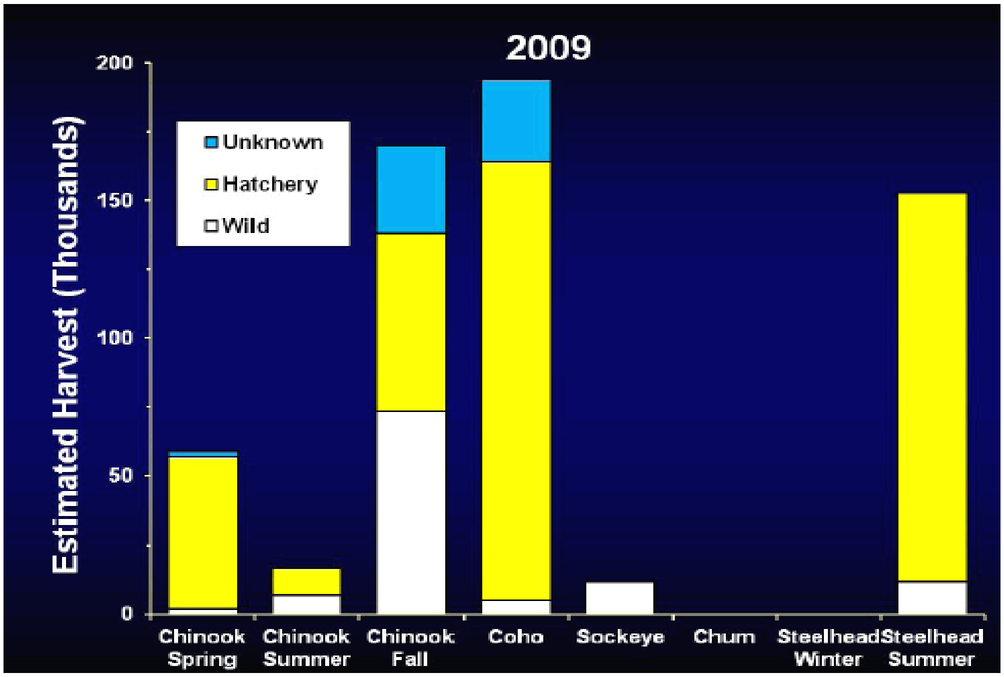


Figure C.4.1. Relative contributions of wild and hatchery origin fish to the total catch of anadromous salmonids in the Columbia River Basin in 2009. From CBFWA (2010).

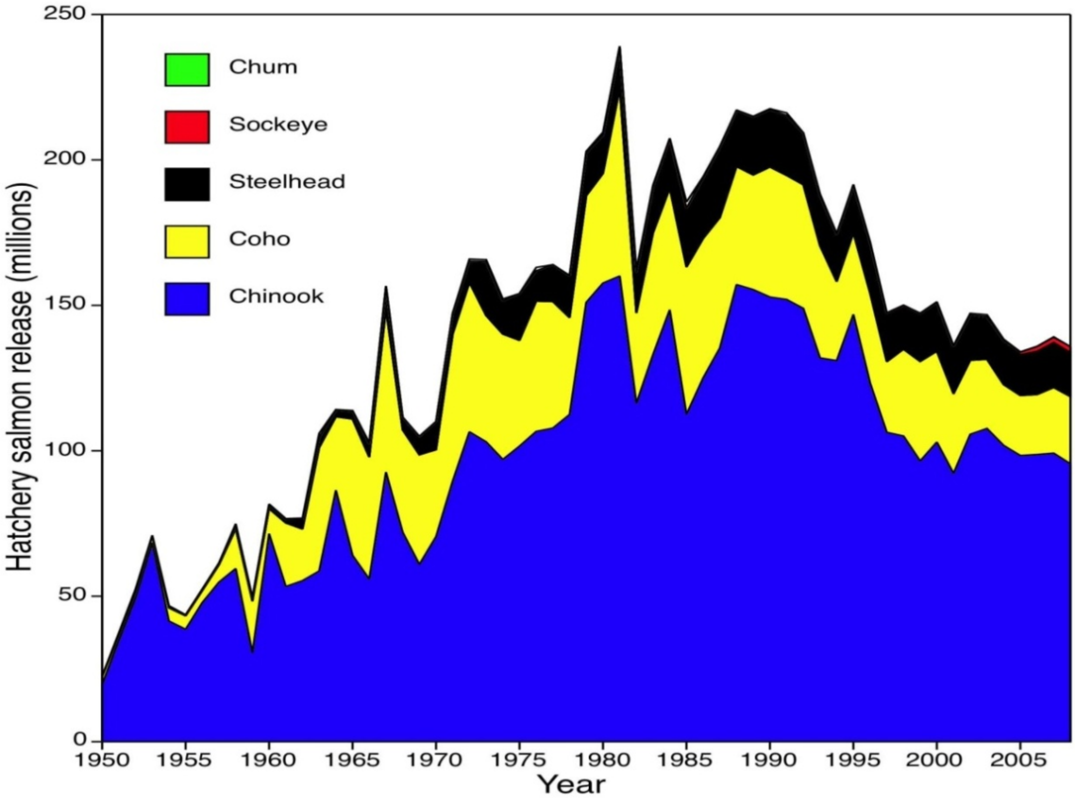


Figure C.4.2. Numbers of juvenile salmonids released from hatcheries into the Columbia River Basin, 1950-2008. Data sources: Mahnken et al. (1998), Fish Passage Center (2009).

Basin since 1950 (Figure C.4.2). Total annual releases of anadromous salmonids increased from approximately 50 million fish in the 1950s to approximately 200 million fish in the 1980s, and then declined to an average of 141 million fish during the most recent 10-yr period (1999-2008).

Releases during the recent 10-yr period (1999-2008) were mostly Chinook (71% of the total number), coho (18%), and steelhead (11%), with much smaller proportions of other anadromous salmonid species including sockeye, chum, and sea-run cutthroat trout (all < 1%). Chinook and coho were released into all four “mega-reaches” of the Basin (see definitions in Figure C.4.3), primarily downstream of McNary Dam. Among Chinook, approximately 28% were spring run, 5% summer run, and 67% fall run salmon. Steelhead were also released into all four mega-reaches, but mostly in the Snake River. Sockeye were released primarily into rearing lakes (Skaha and Wenatchee) in the Columbia River above the Snake River confluence. Chum salmon and sea-run cutthroat trout were released only below Bonneville Dam.

Size at release differs greatly among species and sometimes within species. Chum spend little time in fresh water and are released as fed fry (average weight 1.4 g). Coho, steelhead and sea-run cutthroat trout, which naturally rear in fresh water for a prolonged period, are typically released as yearlings with average weights ranging from 26.6 g (coho) to 118.7 g (cutthroat). During the recent 10-yr period, 32% of Chinook were released as yearlings (average weight 32.7 g) and 68% as subyearlings (average weight 7.7 g). Sockeye are typically planted into rearing lakes as fed fry (average weight 1 to 2 g), but yearling smolts (average weight 18.5 g) have been released into the Snake River.

Numerically, hatchery releases of Chinook are greater than the combined releases of all other salmonid species, and this is true in all four mega-reaches of the Columbia River (Figure C.4.4). In terms of biomass, hatchery Chinook are dominant in all mega-reaches except the Snake River, where steelhead account for about 75% of the total biomass. Below Bonneville Dam, hatchery coho and Chinook account for about one third and one half of the total biomass, respectively.

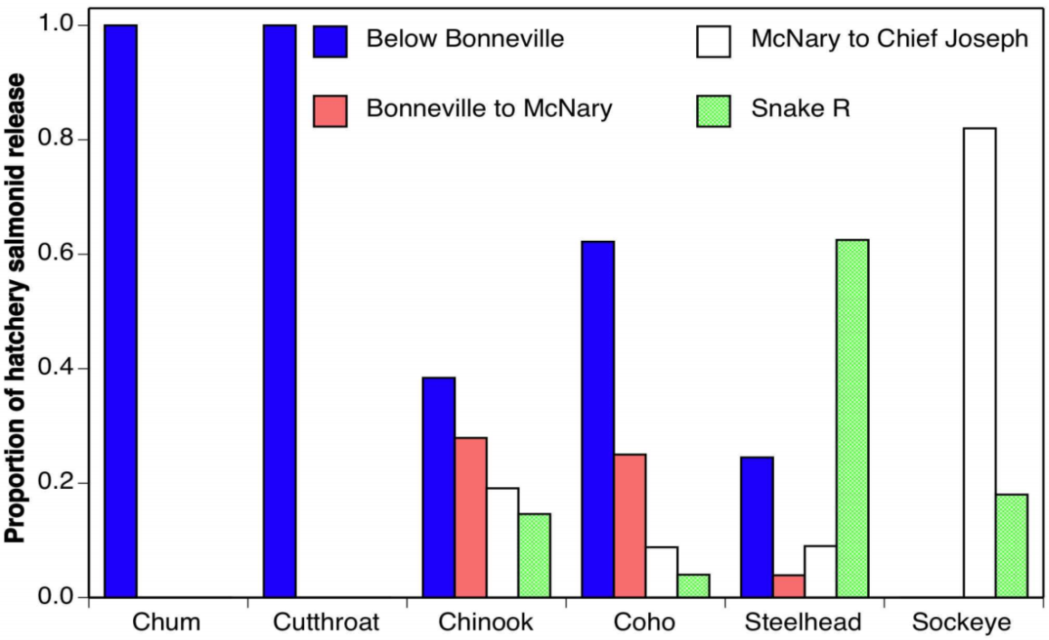


Figure C.4.3. Average proportion of the total hatchery-raised juvenile anadromous salmonids released into each of four "mega-reaches" of the Columbia River Basin, 1999-2008 (data source: Fish Passage Center 2009).

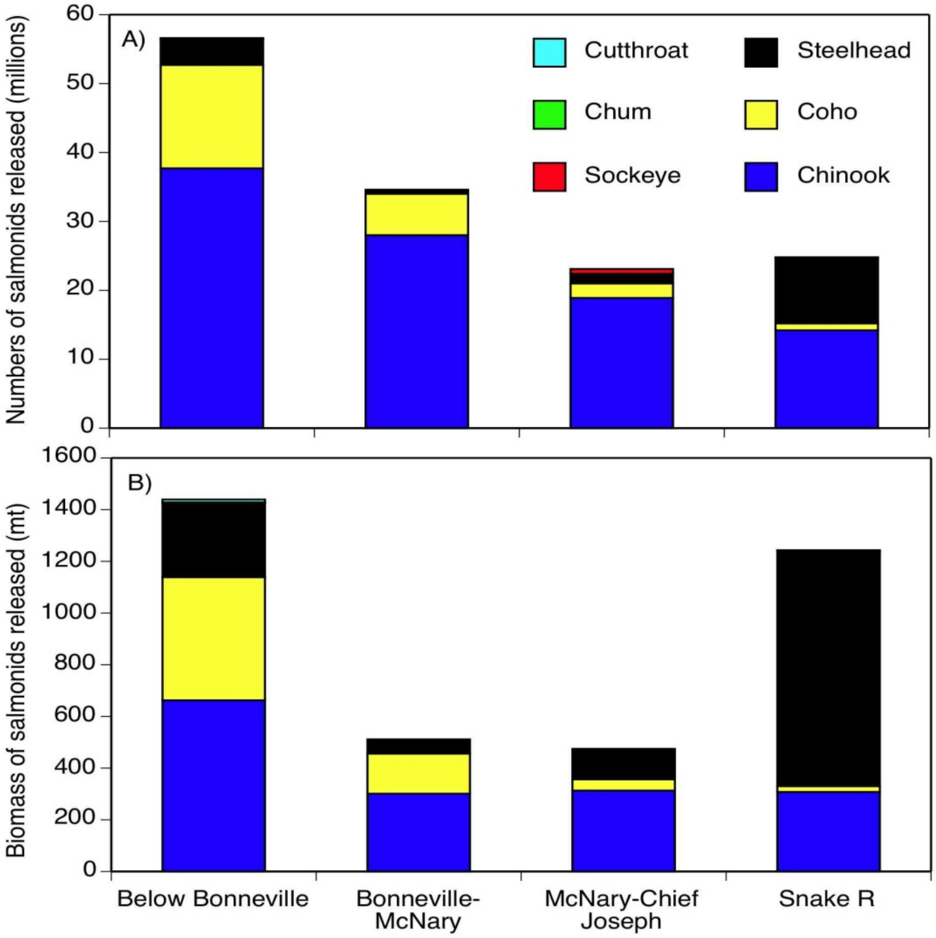


Figure C.4.4. Annual average numbers (A) and biomass (B) of hatchery-reared juvenile anadromous salmonids released into each of four mega-reaches of the Columbia River Basin, 1999-2008 (data source: Fish Passage Center 2009).

White sturgeon. The white sturgeon is facultative anadromous in the lower Columbia River below Bonneville Dam, but substantially dam-locked elsewhere in the Basin. It is the only native non-salmonid released from hatcheries in the Basin (Table C.4.1). Releases to supplement the mid-Columbia population between the Grand Coulee and Revelstoke dams and the Kootenai River population totaled about 300,000 yearlings and 1.4 million larvae (both fed and unfed) between 1992 and 2010. The hatchery releases are intended to support recovery of dam-locked populations endangered by their lack of natural recruitment following hydrosystem development (Sidebar C.4.1).

Sidebar C.4.1. Scope and Impact of Hatchery Releases of White Sturgeon

Food limitation and competitive interactions leading to density-dependent mortality may frustrate plans to recover white sturgeon in the upper Columbia Basin. Existing recovery plans involve releasing significant numbers of hatchery-reared sturgeon to mitigate for lost natural recruitment. Hatchery releases to support the mid-Columbia River population between Grand Coulee and Revelstoke dams have totaled almost 150,000 yearlings (123,716 of these in Canada since 2002, Ken Scheer, Freshwater Fisheries Society of British Columbia, personal communication; and 24,630 in Washington since 2004, Jason McLellan, WDFW, personal communication), and 1.4 million fed or unfed larvae (all released in Canada between 2008 and 2010, Ken Scheer, Freshwater Fisheries Society of British Columbia, personal communication). Hatchery stocking to support the Kootenai River population totaled about 120,000 sturgeon between 1992 and 2006, released primarily as yearlings with an average length of 20 cm (Justice et al. 2009). There is now compelling evidence of density-dependent mortality of hatchery-reared white sturgeon, which is attributed to limitation of food supply and to predation on juveniles by larger white sturgeon (Justice et al. 2009; Figure C.4.5).

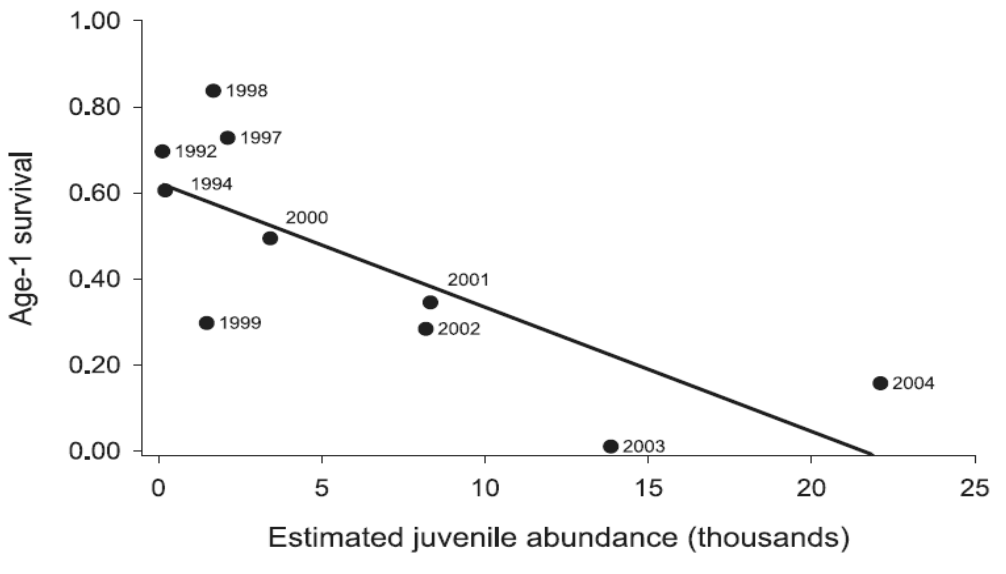


Figure C.4.5. Relationship between annual estimates of juvenile sturgeon abundance and age-1 survival estimates derived from the best-fitting non-covariate model (from Justice et al. 2009).

Food habits of juvenile white sturgeon in the upper Columbia River have not been investigated, but data from lower reaches give some insight into the food web supporting this species. In the lower Columbia River and in the reservoirs above Bonneville and The Dalles dams, juvenile white sturgeon eat primarily benthic invertebrates (McCabe et al. 1993, Sprague et al. 1992). The amphipods *Corophium salmonis* and *C. spinicorne*, the non-native bivalve *Corbicula fluminea*, chironomid larvae, and *Neomysis spp*. are the most abundant items in sturgeon stomachs. Larger fish are piscivorous, and kokanee are widely cited as an important food source. All of these species are also eaten by other native and non-native fishes (Chapters D.6, D.7). The key feature of rearing habitat for sturgeon in Kootenay Lake appears to be the abundance of food resources, especially kokanee, mountain whitefish and mysid shrimp (Hatfield 2009). Food production in the Kootenai River appears to be degraded. Impoundments and water storage reservoirs in other parts of the upper Columbia River have reduced food supply for benthic feeding fish such as sturgeon (see Chapter D.5).

Resident species. Hatchery programs annually release over 30 million resident (or landlocked) salmonids within the Basin. Native kokanee are released primarily within the Intermountain province and account for 51% of all resident fish releases. Native rainbow trout (including redband trout) and native cutthroat trout are stocked widely and account for 42% and 4% of resident fish releases, respectively (Table C.4.1). About 15% of the stocking of resident salmonids is intended to substitute for lost opportunities to harvest anadromous salmonids (Figure C.4.6).

A variety of non-native resident species are also stocked from hatcheries but in much smaller numbers. These include brown trout (1.7%), brook trout (0.6%), the sterile hybrid of brown and brook trout known as the "tiger trout" (0.4%), grayling (0.5%), largemouth bass (0.2%), and several other species in much lower proportions. The implications of stocking non-native species are examined in Chapter C.5. It is also worth noting that some fish species native to the Basin have been introduced into drainages or provinces where they did not previously occur.

Trophic Interactions with Native Species

Once released, hatchery-reared fish interact trophically with wild salmonids and other native species. Whether hatchery-reared fishes are predators, competitors or prey in these interactions, and thus their trophic level, is largely determined by size at release relative to wild species. Surprisingly little is known about the impact of hatchery releases on natural food webs within the Basin. In the paragraphs that follow, we focus primarily on hatchery salmonids because they account for the vast majority of all artificially-reared fish released. However, in Sidebar C.4.1, we also summarize some recent evidence and concerns about the effects of releasing hatchery-reared white sturgeon.

Predation of wild fish. The impact of predation by hatchery salmonids on native fishes depends on the vulnerability and abundance of the prey species (as determined by the predator's functional response to prey density; Holling 1959), the abundance of hatchery-reared predators (determined by the numerical response to prey density; Holling 1966), and the extent of spatial and temporal overlap between the prey and predator populations (which determines the duration of exposure to predation).

Hatchery-reared salmonids are capable of consuming fish up to approximately 50% of their own length, although prey are typically much smaller. This means that hatchery-reared salmonids longer than 70 mm can feed on newly emerged salmon. When given a suitable size range of prey fish, yearling coho and cutthroat trout tend to be more piscivorous than yearling steelhead or Chinook (Beauchamp 1990, 1995; Ruggerone 1992, Ruggerone and Rogers 1992, Nowak et al. 2004). Predation by coho has caused significant mortality in pink salmon populations (Parker 1971, Hargreaves and LeBrasseur 1986). Even so, hatchery-reared steelhead and cutthroat trout raise greater concern because they are typically the largest salmonids released, and thus feed on a wide range of wild salmonids (Hawkins and Tipping 1999). Studies in western Washington indicate that the actual incidence of predation by hatchery steelhead on sub-yearling wild fall Chinook is generally low (range 0 to 0.01 fry/steelhead stomach), but the incidence varies considerably between streams and years (Sharpe et al. 2008).

The spatial and temporal overlap between wild and hatchery-reared salmonids generally increases as hatchery fish are released earlier and farther upstream. Rates of predation by hatchery-reared steelhead on fall Chinook fry in the Trinity River, California were higher than in western Washington streams (6.4% vs. 0.3%), and this difference was attributed to differences in the timing and location of steelhead releases (Naman and Sharpe, presentation, NOAA Fisheries). Salmonid fry emerging from spawning areas or rearing nearby tend to be particularly vulnerable to predation by larger hatchery-reared salmonids. As well, hatchery smolts released in upper reaches have more opportunities than smolts released farther downstream to encounter and prey upon wild salmonids during their downstream migration. In general, however, hatchery-reared salmonids probably pose a greater threat to wild populations and food webs through competition than predation (HSRG 2009).

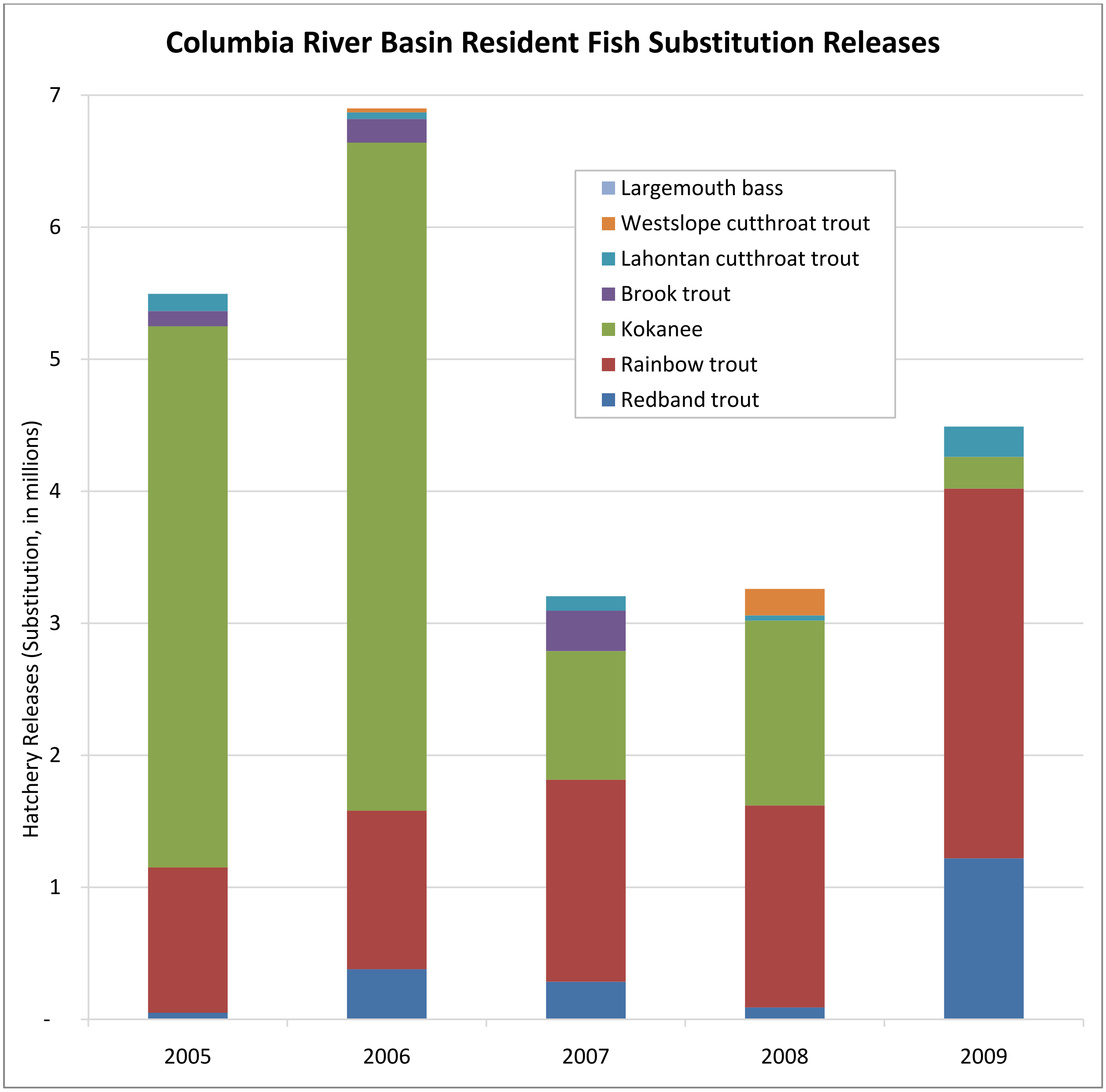


Figure C.4.6. Recent trends in numbers of resident fish released from hatcheries in the Columbia River Basin as a “substitution” for lost anadromous fish harvest opportunities. Data source: adapted from CBFWA (2010). Not all species and numbers of fishes are represented (see Table C.4.1 for a complete list).

Competition. Hatchery-reared salmonids often compete with wild salmonids for food resources and space, which in turn can reduce the survival of the wild fish (reviewed by ISAB 2003-3, Naish et al. 2007, Kostow 2008, HSRG 2009). For example, the productivity of wild steelhead in the Clackamas River, Oregon, declined by approximately 50% when hatchery steelhead were released in numbers exceeding (by about 300%) the estimated carrying capacity of the habitat (Kostow and Zhou 2006). In the Snake River, low survival rates of wild spring Chinook are significantly associated with large releases of hatchery-reared steelhead from the same region, suggesting competitive interactions in the mainstem Columbia and/or estuary (Levin and Williams 2002). Survival rates for juvenile spring- and summer-run Chinook in the Salmon River, Idaho, are almost 50% lower in streams with non-indigenous brook trout than in streams without brook trout (Levin et al. 2002). Collectively, these and other studies implicate competition for food between hatchery-reared (or non-native) and wild native salmonids as an important factor limiting the productivity and carrying capacity of wild populations.

The potential for competition between hatchery and wild salmonids depends on the extent of overlap in behaviors that determine diet and relative competitive ability, and on the extent of spatial and temporal overlap between the competing populations. Since fish of the same species are likely to have similar behavior, intraspecific competition (i.e., between hatchery-reared and wild fish of the same species) has the potential to exceed interspecific competition. The actual intensity of competition depends on the availability of food relative to the number of competing fish, or more generally, on the extent to which food webs limit growth and survival of wild fish.

Hatchery-reared salmonids are fed prior to release. Therefore, they tend to be larger than their wild conspecifics. Larger size in juveniles is known to confer a competitive advantage in coho (Nickelson et al. 1986, Rhodes and Quinn 1998, 1999), steelhead (Berejikian et al. 1996, McMichael et al. 1997) and Chinook (Peery and Bjornn 2004). Large or aggressive hatchery juveniles may displace wild juveniles from their feeding territories, perhaps forcing them into marginal habitats where growth suffers and they are exposed to greater risk from predators (Nielsen 1994), or perhaps displacing them into different habitats (with different food webs).

Hatchery-reared salmonids released as putative smolts often fail to migrate to sea, and instead remain in fresh water for another year or for the rest of their lives. These "residual" male hatchery fish pose a particular concern because they compete with wild resident fishes for a prolonged period; they also become larger and more piscivorous with age (Kostow 2008). Reduced growth of wild rainbow trout in the Yakima River was attributed to competition with hatchery steelhead that residualized (McMichael et al. 1997). Residual hatchery-reared Chinook, known as "mini-jacks," have been documented in the Hood River (up to 25% of the hatchery fish returning in 2006) and in the Willamette River (up to 14% of fish returning in 2007) (Kostow 2008). In the Yakima River (Cle Elum Hatchery), mini-jacks represented 41% of the yearling male Chinook salmon released during 1997-2007, and in the Lostine and Imnaha rivers (Lookingglass Hatchery) they represented 52% of the release in two recent years when data were collected (Beckman and Larsen 2005, Larsen et al. 2010). Residual behavior appears to be correlated with size and condition factor at release (Mullan et al. 1992, Viola and Schuck 1995) and with premature release (Evenson and Ewing 1992).

Most research on competitive interactions focuses on the period of stream residence. Much less is known about competition between hatchery and wild salmonids during downstream migration, and in particular, during migration through the estuary. The ISAB previously indicated that more attention should be devoted to the potential impact of large releases of hatchery fish on food availability for wild salmonids in the Columbia River estuary (ISAB 2008-2). If rearing habitat in the estuary limits the survival of juvenile salmonids, then massive pulses of large hatchery fish could cause significant mortality in wild juveniles that become displaced into suboptimal habitat with less food. As yet, there is no compelling evidence of density-dependent growth of salmonids in the estuary. However, it is difficult to study growth in estuaries, and even more difficult to determine whether food supply is limiting in these relatively open ecosystems – a necessary step to demonstrate competition (Fresh 1997). Unfortunately food supply is often overlooked as a factor affecting survival in the estuary, especially for hatchery fish.

Ration-dependent growth rates have not been measured in the Basin, and would have to be inferred from studies in other estuaries; such extrapolation is inherently risky given the variability among estuaries (D. Beauchamp presentation). Bioenergetics models have been used to estimate total food consumption needed to account for the observed growth of juvenile salmonids. For example, in the small (1.8 km^2) Salmon River estuary, Oregon, intraspecific competition for food is suggested by the fact that daily ration is directly related to observed stomach fullness, which in turn, is weakly but significantly negatively correlated with the density of juvenile Chinook in the tidal marsh (Bieber 2005, Gray 2005). Similarly, the size of wild Chinook fry rearing in the Campbell River estuary, British Columbia, is negatively correlated with the total biomass of salmonids in the estuary, suggesting that growth has been reduced by competitive interactions (Korman et al. 1997, following McAllister and Brown 1994; Figure C.4.7).

Table C.4.1. Approximate annual releases of hatchery-reared anadromous and resident fishes by species and province of the Columbia River Basin in recent years. A zero value indicates that a release target has been established, but no fish were released in this period. Fishes are classified as native to the Columbia River (N) or introduced (I), but some fishes native to the Columbia River were introduced into provinces where they did not occur naturally. Releases of hatchery-reared fishes into the upper Snake Province have not been reported. In recent years, about 0.7 million anadromous sockeye salmon fry (<1 g) have been released annually into the Okanagan River (Skaha Lake, Canada). Data sources: Columbia Basin Fish and Wildlife Authority, FPC 2009.

		Number of Hatchery Fish Released Annually (1000's of fish)										
Species	**Native?**	**Columbia Estuary**	**Lower Columbia**	**Columbia Gorge**	**Columbia Plateau**	**Blue Mountain**	**Mountain Snake**	**Middle Snake**	**Columbia Cascade**	**Inter-mountain**	**Mountain Columbia**	**Total**
Anadromous Fishes												
Chum	N	229	66									295
Coho	N	5,070	11,626	1,071	3,216		860	496	1,060			23,399
Spring/Summer Chinook	N	1,058	8,496	2,898	4,841	1,084	11,746	350	6,771			37,245
Fall Chinook	N	13,203	16,006	16,512	20,498		705	125				67,048
Sockeye	N						184		366			550
Sea-run Cutthroat	N		151									151
Summer Steelhead	N	66	1,819	0	1,502	1,281	9,580	767	883			15,897
Winter Steelhead	N	273	1,824	37								2,134
White Sturgeon	N									3	17	20
All anadromous		19,899	39,988	20,518	30,057	2,365	23,075	1,738	9,080	3	17	146,740
Resident Fishes												
Cutthroat Trout	N		8	11	90			3				111
Westslope Cutthroat	N				12		5		157	523	231	928
Rainbow Trout	N	71	1,568	218	2,667		665	2,602	1,149	3,750	530	13,220
Kokanee	N		0		715		5	930	319	13,253	864	16,086
All native resident		71	1,576	229	3,484	0	675	3,535	1,625	17,526	1,625	30,345
Introduced Resident												
Golden Trout	I		0		0				0			0
Brook Trout	I		11	18	83				26	46	0	185
Brown Trout	I	35	51	12				23	80	336		538
Lahontan Cutthroat	I							157	0	63		221
Atlantic Salmon	I				2							2
Grayling	I						4	1		3	136	144

Largemouth Bass	I									11	63	75
Smallmouth Bass	I							<1			13	13
Channel Catfish	I						2	16		25	2	45
Tiger Muskie	I						6	2		<1	<1	10
Tiger Trout	I			12					9	109		130
All introduced resident		35	62	42	85	0	12	42	115	531	215	1,142
Grand Total		20,005	41,626	20,789	33,626	2,365	23,762	5,629	10,820	18,186	1,857	178,666

Juvenile salmonids reared in hatcheries (or other artificial facilities such as spawning channels, which are now rare in the Basin) probably dominate the main estuary as they migrate seaward. In 2008 for example, a total of 95.5 M Chinook, 15.1 M steelhead, 23.1 M coho, 0.10 M chum, and 0.18 M cutthroat trout were released either upstream of Bonneville Dam or directly into the estuary. Reliable data on the relative abundance of wild and hatchery-reared salmonids in the estuary are not available, but hatchery-reared smolts appear to dominate in terms of biomass, as they are typically larger than wild smolts. Based on adipose fin clip rates reported for hatcheries and observed in field-caught fish, juvenile salmonids collected from the open waters of the Columbia River estuary between 2007 and 2009 were mostly of hatchery origin, with hatchery fish accounting for 89% of subyearling Chinook (n = 1,510), 94% of yearling Chinook (n = 934), 89% of steelhead (n = 630) and 100% of coho (n = 740; Laurie Weitkamp, NOAA Fisheries, personal communication). In contrast, most juvenile salmonids collected from restored and reference wetland sites from 2005 to 2007 were wild fish (Roegner et al. 2010). Yearling hatchery smolts are thought to rapidly move through the estuary and out into the plume, traveling from the Bonneville Dam to the ocean in about two or three days (Magie et al. 2010). This migration speed implies that their food consumption in the estuary will be less than that in upstream reservoir habitats. On the other hand, subyearling hatchery Chinook smolts and chum fry appear to rear for longer periods in the estuary, and may compete with their wild counterparts to a greater extent (McMichael et al. 2010, Bottom et al. 2008).

Stable isotope analyses (SIA, Appendix A) provide a promising opportunity to learn more about the extent of competition between hatchery and wild salmonids. For example, SIA has revealed considerable variability in the ultimate energy sources supporting subyearling Chinook in the Columbia estuary, indicating that juveniles exploit a wide range of different food webs and habitats (Chapter D.7). Much of the body

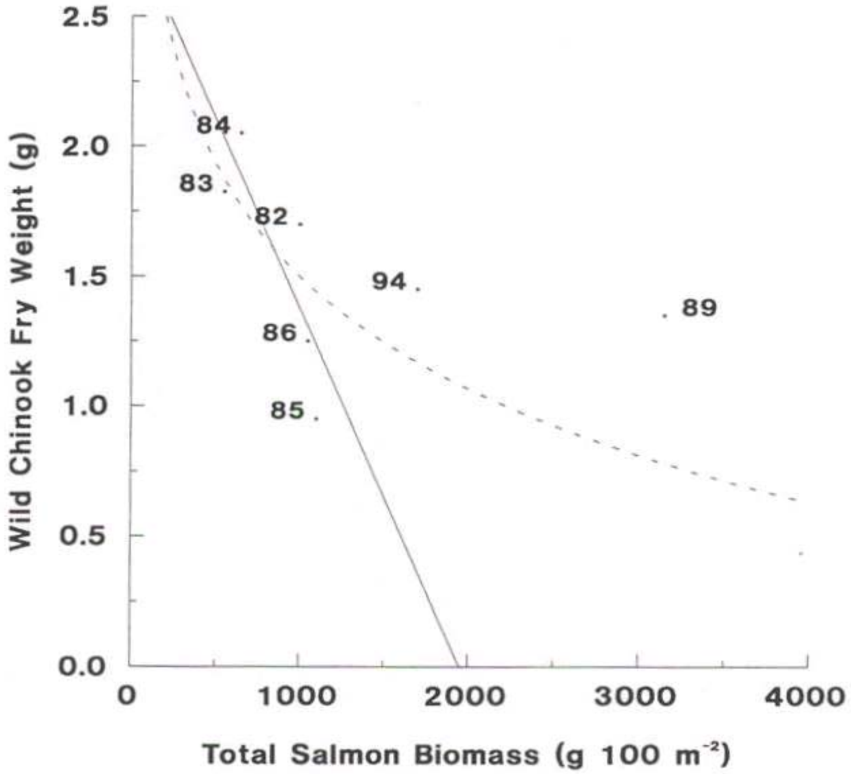


Figure C.4.7. Evidence of possible density-dependent growth of wild Chinook fry in the Campbell River estuary, British Columbia. The weight of fry in mid-May is shown versus the estimated total biomass of all juvenile salmonids (i.e., other Chinook, coho, chum, pink including hatchery and wild fish, but hatchery fish likely accounted for the majority of the biomass each year). From Korman et al. (1997).

composition of subyearling Chinook is derived from hatchery food, but this contribution ranges widely from 0% to 100% (average 32%). These percentages reflect the fact that food eaten in the hatchery is supplanted by energy from natural foods within a few weeks of release. Evidently, some hatchery fish lose the hatchery isotope signal while feeding during their seaward migration from the release site to the river mouth. This evidence of feeding during migration suggests that the extent of competition with wild salmonids will be proportional to the distance from the hatchery to the ocean, but this interpretation may be overly simplistic (Maier and Simenstad 2009).

Juvenile salmonids in the Columbia estuary eat primarily crustaceans and other invertebrates (McCabe et al. 1983). Fish are also eaten, but never exclusively. All salmonids (excluding steelhead) from pelagic areas exhibit a broad overlap in diet in the spring. The diet of salmonids overlaps that of threespine stickleback in the upper estuary and American shad in the lower estuary. In intertidal areas during spring, the diet of subyearling Chinook overlaps that of starry flounder with two species of amphipods (*Corophium salmonis* and C. *spinicorne*) being important prey items. No significant diet overlaps have been detected among these fishes in summer months.

In the lower estuary exploitative competition is unlikely to occur between juvenile Chinook and threespine stickleback in the tidal marshes, because the availability of benthic prey is unlikely to be limited by the foraging behavior of either stickleback or Chinook (Spilseth and Simenstad 2011). Competition between the two species is diminished by habitat partitioning: Chinook display a greater tendency to feed near the surface and in mid-water, whereas stickleback feed mostly on benthic prey. These findings reinforce the need to maintain and restore a diverse suite of habitats in the estuary.

The density of juvenile American shad, a non-native species, in the Columbia River estuary has not been assessed. However, juvenile shad are likely very abundant given the large number of adults returning to spawn each year. Another 20 non-native species also occur in the estuary (Chapter C.5), but their feeding habits and interactions with native salmonids are unknown.

Competition at sea. Many hatcheries were originally built on the premise that the ocean has an unlimited capacity to support salmon and other anadromous fishes. Evidence has been accumulating over several decades that competition for food at sea, both intraspecific and interspecific, can alter the growth, age at maturation and survival of salmonids (e.g., Cooney and Brodeur 1998, Ruggerone and Nielsen 2004, Holt et al. 2008, Ruggerone et al. 2010). Because salmon migrate long distances at sea, depressed Columbia River populations may be negatively affected by competitive interactions with more abundant populations from other regions. For example, many coded-wire tagged Chinook from Washington, Oregon, California and Idaho have been captured in fisheries along the south side of the Alaska Peninsula and in the Bering Sea (Myers et al. 1996, Celewycz et al. 2009). An especially productive region for Chinook from all regions is the “horseshoe,” which is located in the Bering Sea along the continental slope just north of Unimak Pass.

A key concern with regard to large scale hatchery production is that the number of salmon released from hatcheries is not adjusted to suit changing ocean conditions. For example, competitive interactions in the marine environment may explain findings that large aggregate releases of hatchery-reared spring Chinook in the upper Basin significantly contribute to poor survival of wild spring Chinook in the Snake River, but only during years of poor ocean conditions (Levin et al. 2001).

Diversion of nutrients. The role of anadromous salmon in conveying marine derived nutrients back to food webs in spawning tributaries is described in Chapter C.1. Hatchery-reared salmon may be less effective at supplying marine-derived nutrients to headwater spawning streams because they typically return to hatcheries downstream of natural spawning areas. To the extent that hatchery-reared salmon replace wild salmon, food webs in natural spawning habitats may become impoverished. However, this potential reduction in marine-derived nutrients from wild spawning salmon may be offset or overwhelmed by the external subsidy of nutrients in hatchery fish food originating largely from other marine food webs (see below).

Are Hatchery Releases Straining Food Webs?

Long-term trend in abundance of anadromous salmonids. Most hatchery releases are primarily intended to compensate fisheries for the loss of wild production. Thus, it is not immediately obvious whether hatchery salmon are merely replacing wild salmon, or whether hatchery fish place an additional burden on food webs in the Basin. To assess the overall impact on food webs, we attempted to reconstruct the average annual abundance of salmonid smolts before and after hydropower development.

Average adult returns of each species were estimated over three different periods: the recent 10-yr period (1999-2008); a corresponding 10-yr period eighty years ago (1919-1928); and the 10-yr period that produced the maximum average returns (based on Chapman's 1986 estimates of harvest rate and catch since 1889 for Chinook, steelhead and sockeye, 1892 for coho, and 1899 for chum; Table C.4.2). The maximum 10-yr period in this time series varies by species, ending in 1899 for sockeye, 1901 for steelhead, 1919 for chum, 1921 for Chinook (with life history types combined), and 1930 for coho. We note, however, that aggregate Chinook abundance was likely highest in years prior to 1889 (Chapman 1986). Recent adult abundances of Chinook and coho are from the Columbia Basin Fish and Wildlife Authority.

Smolt abundances were back-calculated from average adult abundances based on assumed values for smolt-to-adult survival. The survival rates shown in Table C.4.2 were estimated based on data from coded-wire tag studies and historical estimates by Chapman (1981); smolt survival rates for 1999-2008 were adjusted so that the proportion of hatchery smolts correspond with recent estimates of the proportion of hatchery adult returns. These "adjusted" survival rates reflect observations that rates were generally higher in the pre-development period. For comparison, we also back-calculated smolt abundances based on constant survival rates (those documented by Bradford 1994). Note that assuming constant survival generates higher estimates of smolt abundances in the pre-development period. We caution readers that these reconstructed smolt estimates are very imprecise.

Although an approximation, reconstruction of smolt abundances indicates that considerably more smolts are migrating down the Columbia River now than before hydropower development. This conclusion holds for both of the 10-yr periods and for both scenarios of smolt-to-adult survival, but the pattern varies across species. Smolt abundance has increased most for steelhead (by 4 to 8 times) and fall Chinook (3 to 7 times), less for coho (2 to 3 times), and least for spring/summer Chinook (up to 2 times; Figure C.4.8). Trends in sockeye smolt abundance are especially uncertain; estimated historical abundance was lower than current abundance under the adjusted survival rate scenario but higher under the constant survival rate scenario.

In summary, total salmonid smolt abundance appears to have increased since 1930, and this increase may have significant implications for food webs. However, the extent of the increase is much less than might be inferred by simply examining trends in hatchery releases. Moreover, several other factors might reduce the burden that hatchery fish exert on food webs in the Columbia River. Hatchery-reared smolts are typically larger than their wild conspecifics, and likely spend less time rearing in the Basin once they begin migrating downstream. This conclusion is supported by the fact that hatchery fish are relatively more abundant than wild fish in samples from open channel habitat and relatively less abundant in off channel habitat in the estuary. Finally, wild fish rely on food webs from the moment they begin feeding as fry whereas hatchery fish rear on feed that largely originates outside the Basin. In the next section, we consider the magnitude of that food subsidy.

Table C.4.2. Estimated 10-yr average abundance of anadromous salmonid smolts in the Columbia River Basin before hydropower development began (i.e., before 1930) compared with the most recent 10-yr average (1999-2008).

The first scenario is based on the 10-yr period that produced the peak average returns of adults (based on catch records and harvest rates reported by Chapman (1986) for years since 1899); note that the peak period varies by species, ending in 1899 for sockeye, 1901 for steelhead, 1919 for chum, 1921 for Chinook (smolt ages combined), and 1930 for coho. The second scenario is based on a single 10-yr period (1919-1928) that was 80 years before the recent period. Recent adult abundances are from CBFWA. Smolt abundances were back-calculated from adult abundances based on assumptions about smolt-to-adult survival. The survival rates in this table are adjusted to reflect observations that survival rates were higher in the pre-development period (see text for details).

		Peak Adults in 10-yr Pre-development Period			1919-1928 (10-yr Period Pre-development)			1999-2008 (Most Recent 10-yr Period)				
		Assumed Smolt Survival	Estimated number (millions)		Assumed Smolt Survival	Estimated number (millions)		Assumed Smolt Survival	Estimated number (millions)			
Species	**Type**		**Adults**	**Smolts**		**Adults**	**Smolts**		**Adults**	**Total Smolts**	**Hatchery Smolts**	**Percent Hatchery**
Chum		2.5%	0.32	13	2.5%	0.30	12	2.0%	0.01	0.5	0.28	57%
Chinook		3.1%	1.60	51				0.46%	0.88	192.3	99.8	52%
Fall	Subyearling	2.5%	0.53	21	2.5%	0.46	18	0.39%	0.52	133.3	66.4	50%
Spring	Yearling	3.6%	0.21	6	3.6%	0.18	5	0.59%	0.30	50.8	28.0	55%
Summer	Yearling	3.6%	0.85	24	3.6%	0.73	20	0.70%	0.06	8.1	5.4	66%
Subtotal		3.1%	1.60	51	3.1%	1.37	44	0.46%	0.88	192.3	99.8	52%
Coho	Yearling	10.0%	1.07	11	10.0%	0.96	10	1.9%	0.51	26.7	25.0	94%
Sockeye	Yearling	10.0%	0.57	6	10.0%	0.22	2	1.0%	0.08	8.1	0.81	10%
Steelhead	Yearling	10.0%	0.36	4	10.0%	0.28	3	2.1%	0.44	21.6	15.3	71%
All Yearlings		6.2%	3.07	50	5.9%	2.37	40	1.2%	1.39	115.4	68.2	59%
All Subyearlings		2.5%	0.85	34	2.5%	0.76	30	0.4%	0.53	133.8	73.0	55%
Total			3.92	84		3.13	70		1.92	249.2	141.2	57%

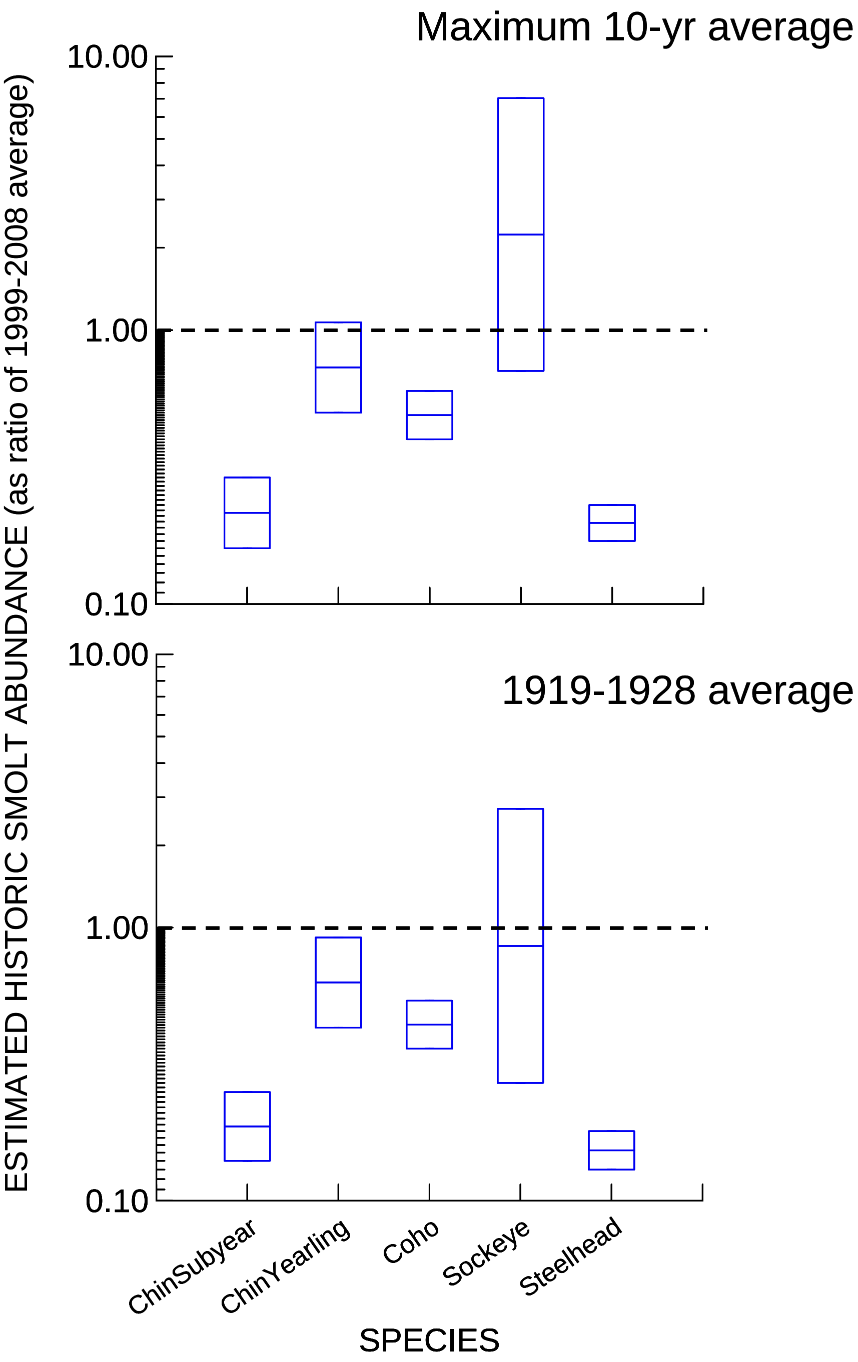


Figure C.4.8. Estimated abundance of anadromous salmonid smolts in the Columbia River Basin before hydropower development began (i.e., before 1930) expressed in ratio to the most recent 10-yr average (1999-2008; dashed line). Top frame refers to the 10-yr period that produced the maximum average returns of adults for each species (not including years before 1899) whereas the bottom frame refers to a single 10-yr period 80 years ago (1919-1928) (see Table C.4.2 for details). Ranges in the box plots illustrate the sensitivity to assumptions about smolt survival rate, with upper ranges based on constant smolt survival (values from Bradford 1995) and lower ranges based on declining smolt survival as specified in Table C.4.2.

Subsidies from other food webs. The Columbia River hatchery program receives significant energy and nutrient input in hatchery salmon feed originating from sources external to the Basin. This external subsidy is needed to produce the large numbers of hatchery salmonids released each year. The subsidy enters Columbia River food webs and is transferred to the multitude of species that now depend on hatchery salmonids, including pikeminnows, terns, gulls, and eagles, pinnipeds and fishermen.

We estimated the amount of hatchery food imported to Basin hatcheries from external marine food webs. Roughly 4,000 mt of anadromous hatchery salmon are being released into the Columbia River basin each year (Table C.4.1). After accounting for the weight of fry at emergence, about 99% of this biomass is gained while consuming feed in hatcheries. About 0.85 to 1.0 kg of feed is required to produce 1 kg of salmon following recent improvements in feed composition (R. Hardy, University of Idaho, presentation; Tacon 2005). This exceptional conversion rate is related to the high lipid and protein content of the feed, and to its low water content. The feed is derived largely from marine forage fishes, such as anchovy, herring, pilchards, sprats, sardines and menhaden. Approximately 50% of the feed consists of non-marine derived ingredients such as canola meal and oil, soybean meal and crystalline amino acids. Although the composition of feeds varies slightly depending on the source, about 3 kg of forage fish is needed to produce 1 kg of salmon smolts (Tacon 2005). Therefore, roughly 10,000 mt of marine forage fish is required to produce the 3,100-3,600 mt of feed fed to salmon smolts released into the Basin each year. That quantity of forage fish would fill about four Olympic swimming pools (each 50x25x2 m).

Most salmon fisheries in the Columbia River depend on hatchery production maintained by the external food subsidy. The total annual catch by tribal, non-tribal commercial and sport fisheries was estimated at 671,000 salmon and steelhead in the Basin during 2002-2006 (NMFS 2010). These values do not include Columbia River salmon harvested in fisheries outside the Basin, including fisheries in southeast Alaska, British Columbia and the coast of Washington and Oregon, nor do they include adult hatchery salmon returning to hatcheries or straying to spawning grounds. The percentage of harvests produced by hatcheries is not documented in NMFS (2010), so we are assuming an overall hatchery contribution of 81% to the fisheries (based on estimates by species available from CBFWA). After applying average weights per adult salmon reported by Chapman (1986), we estimate the total biomass of hatchery salmon and steelhead harvested annually in the Columbia River during 2002-2006 to be approximately 3,000 mt. This biomass would fill 1.2 Olympic swimming pools and is only about three quarters of the total biomass of smolts released from hatcheries. Such a loss of biomass from the smolt stage to harvest of adults seems to be a unique feature of the Basin.

Juvenile hatchery salmon in the Basin consume a small portion of the total world production of salmon feed, which goes primarily to support caged salmon farming. The total quantity of fishmeal and oil consumed by hatchery and farmed salmon throughout the world was approximately 982,000 mt in 2003, which is equivalent to approximately 1.96 million mt of salmon feed (assuming 50% of the diet is fishmeal and oil). Thus, the salmon feed delivered to Columbia River hatcheries represents less than 1% of the world total.

Strategies to Control Undesirable Impacts

Ecological risks posed by hatchery releases can be managed by actions that decrease interactions between hatchery-reared and wild fish in shared environments and across life cycles. The following five general guidelines to control undesirable impacts on food webs are adapted from 12 more specific strategies for reducing ecological risks (Kostow 2008):

1) *Integrate hatchery activities with other watershed objectives*. Hatcheries should not be implemented as isolated activities, and their benefits should be evaluated against goals for the entire watershed. Hatchery programs no longer serving clear social or biological needs should be discontinued. This guideline is consistent with NOAA's draft Environmental Impact Assessment to Inform Columbia River Basin Hatchery Operations and the Funding of Mitchell Act Hatchery Programs.

2) *Reduce the scale of hatchery activities to match carrying capacity.* Reducing the number of hatchery-reared fish reduces ecological risks to wild fish communities and food webs. Consideration should be given to carrying capacity of food webs at both local and regional scales. As ocean climate and freshwater productivity models improve, it may also become

feasible to match hatchery releases to predicted ocean and freshwater conditions to avoid excessive releases when feeding conditions are poor.

3) *Adopt release procedures that reduce competition with wild fish.* Releasing smaller hatchery smolts will help to reduce their competitive advantage over wild counterparts. However, steps also should be taken to ensure that hatchery smolts are ready for seaward migration. Acclimation ponds and voluntary releases are useful for reducing the number of hatchery fish residualizing in fresh water and competing with wild fish.

4) *Choose the timing and location of hatchery releases to minimize interactions with wild fish.* Interactions with wild fish generally increase as hatchery-reared salmonids are released earlier and farther upstream, closer to natural spawning areas.

5) *Mark all fish released and monitor the effects of hatchery programs*. Marks are necessary to monitor the interactions between hatchery and wild fish. Marks also allow estimation of survival and straying rates of hatchery fish, evaluation of benefits from hatchery programs, and removal of hatchery fish from natural rearing or spawning habitats if desired.

C.5. Non-Native Species

Background

Humans have greatly accelerated the movement and establishment of non-native species into the Columbia Basin, and some have profoundly altered the structure and productivity of the Basin's food webs. This chapter reviews information on the food web-related impacts of non-native species and the consequences for fish and wildlife conservation and restoration. In a previous report on non-native species (ISAB 2008-4), we covered the topic from a general ecological and management viewpoint. In this chapter we delve deeper into the food-web aspects of the issue and update the literature review.

Non-native species arrive via many routes associated with movements and activities of people including 1) trade (biofouling of ships and ballast, transport via sport boats, shoes and clothing); 2) deliberate stocking for recreation and esthetics (fish, birds, plants); 3) commerce (plants, fish, bivalves); 4) accidental or intentional release of pets (fish, reptiles, amphibians); and 5) biocontrol of other nuisance species (Pimentel et al. 2005, Simberloff et al. 2005).

The pace of introduction has quickened, particularly since 1900, with the number of non-native species in Washington, Oregon and Idaho exceeding 1,000 (Figure C.5.1). These organisms are present throughout the Basin, with most watersheds hosting many well-established non-native species from a great variety of taxonomic groups (Figure C.5.2). While detailed introduction histories for a large number of these non-native species can be obtained from references tabulated by Sanderson et al. (2009), organized databases for taxonomic groups such as insects, parasites and pathogens, and the diseases they cause, are not yet available. Non-natives from these groups are underreported, though undoubtedly present in large numbers. In general, introductions, coupled with environmental degradation and overharvesting of some populations, have profoundly altered numerous North American freshwater and estuarine ecosystems (Richter et al. 1997, Wilcove et al. 1998).

The region's lakes and, in more recent times, reservoirs have been a prime target of introductions. Before European arrival, the Basin's lakes supported a suite of fishes that included a variety of native salmonids, whitefishes, minnows, suckers, and sculpins. Since European arrival, introductions and invasions of non-native species have expanded to include American shad, basses, sunfishes, perches, minnows, catfishes, northern pike, lake whitefish, brook trout, brown trout, Atlantic salmon and lake trout (Chapter C.3). In addition to new species from outside the Basin, a number of fishes that occurred naturally in restricted areas of the Basin have been widely introduced to other areas. Kokanee salmon and rainbow trout, for example, have been introduced to or invaded virtually every lake or reservoir having the potential to support coldwater species, while cutthroat trout, coho and Chinook have been dispersed on a more limited basis (Chapter C.4). At least one invertebrate, *Mysis relicta,* has been widely introduced to coldwater lakes as well (Nesler and Bergersen 1991).

Many introductions are attempts to augment sport fisheries. After the fact, it is realized that these constitute significant food-web manipulations. Often the introductions are invertebrate-feeding or planktivorous fishes that support high yields (e.g., lake whitefish and kokanee) or piscivores that might attain large sizes (e.g., rainbow trout, lake trout, walleye, black bass). Other intentional introductions enhance forage availability for introduced or native predators (Wydoski and Bennett 1981). Introductions also occur illegally by anglers seeking to establish favorite species such as walleye and northern pike in new areas or through the use of live bait. Some species subsequently invade other lakes that are not targets of the original introduction. For instance, mysids, kokanee and lake trout all have moved from lakes where they were introduced to downstream lakes. In fact, lake trout have invaded most of the accessible lakes upstream from Flathead Lake, in some cases moving over 100 km to the highest reaches of the Basin (Martinez et al. 2009). The net effects on food webs have been dramatic, as explained below.

With the exception of the mysid and lake trout introductions, there has been relatively limited examination of food-web effects of the widespread introductions and invasions by non-native species. Species occurrence records indicate that expansion of non-native forms has not led to widespread extinctions of native species (Lee et al. 1997). However, substantial declines in native species such as mountain whitefish, westslope cutthroat trout and bull trout have been linked at least anecdotally to the establishment of kokanee, lake trout (Martinez et al. 2009), and other species. The best evidence of the profound effects

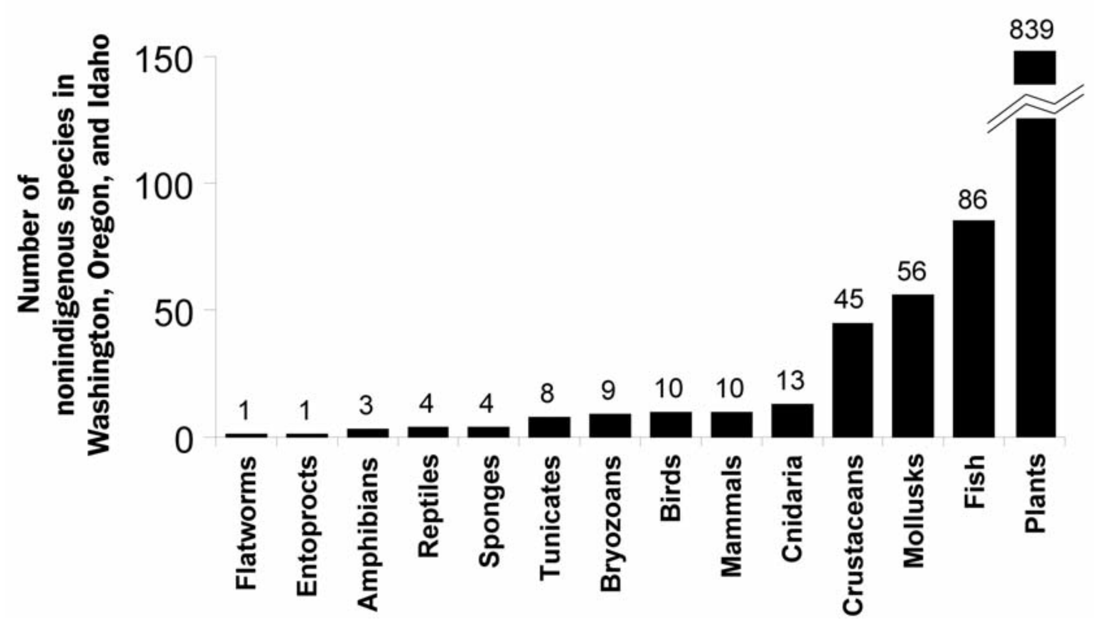


Figure C.5.1. Numbers of non-native species, by major taxonomic group, currently present in the Pacific Northwest states of Washington, Oregon and Idaho (from Sanderson et al. 2009).

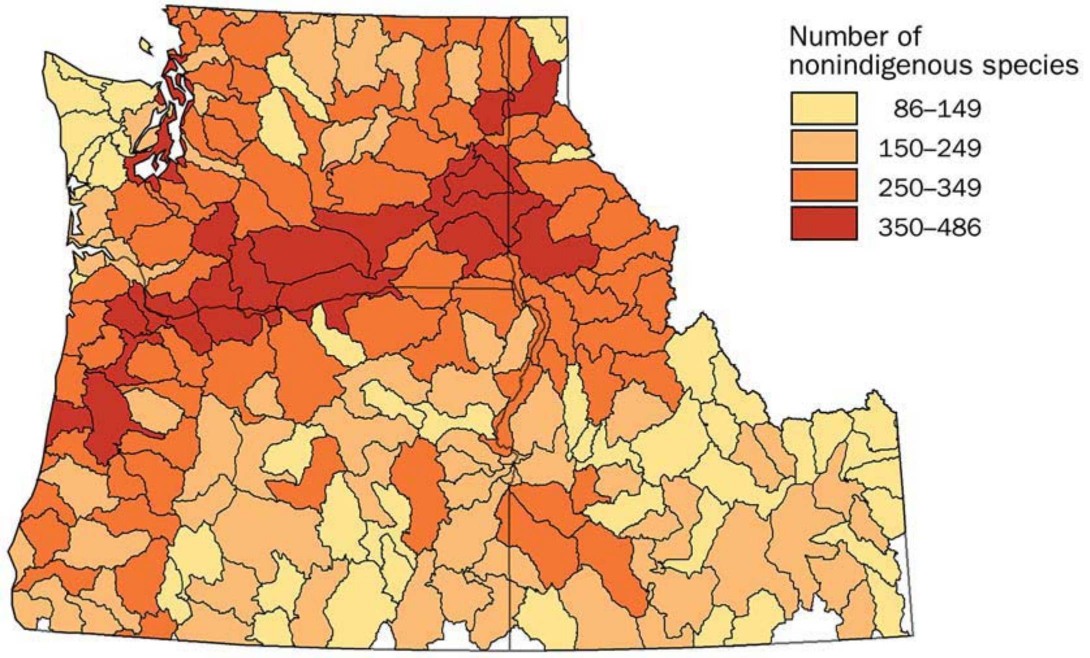


Figure C.5.2. Numbers of non-native species per watershed (4th field Hydrologic Unit Code) in Washington, Oregon and Idaho, for 2007 (from Sanderson et al. 2009).

following species introductions comes from food web investigations of Pend Oreille, Flathead, and other lakes following the establishment of *Mysis relicta* (Sidebar C.5.1). Lake trout introductions also have been linked to similar trophic cascades in other ecosystems (Ruzycki et al. 2003, Koel et al. 2005). One result is that fisheries managers now expend substantial resources attempting to reduce expanding lake trout populations and their effects on other valued fisheries (Hansen et al. 2008, Martinez et al. 2009). More subtle changes in phytoplankton communities, nutrient cycling and other trophic levels have occurred (Chipps 1997, Chipps and Bennett 2000), but understanding of those processes is still limited.

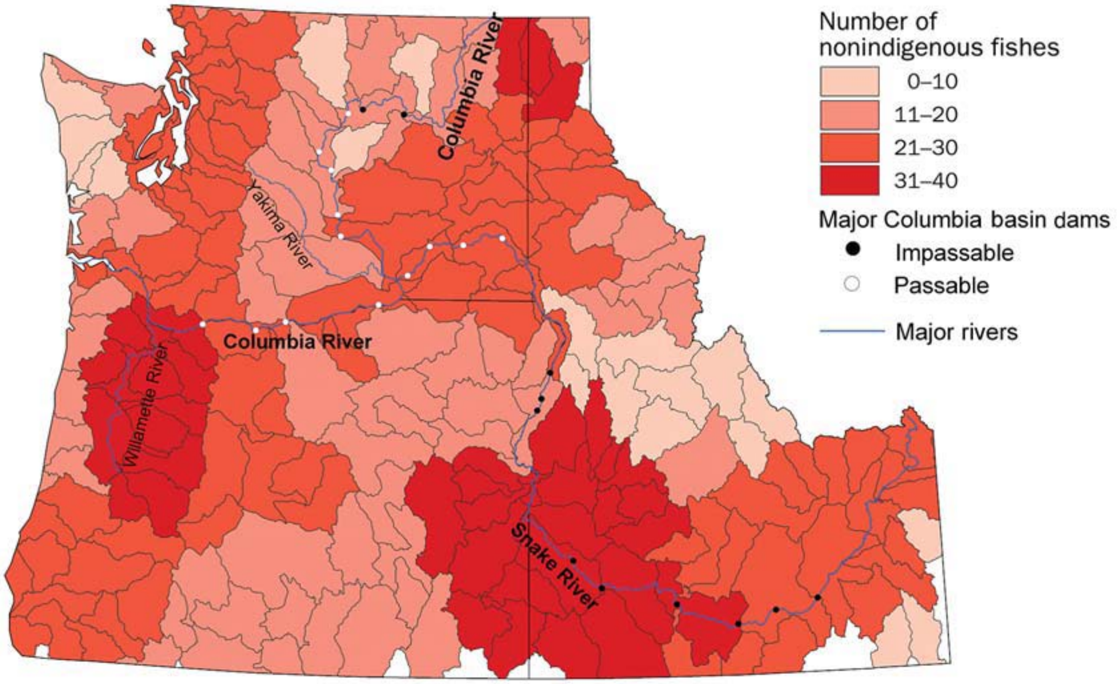


Figure C.5.3. Number of non-indigenous fish species per watershed (4th field Hydrologic Unit Code) in Washington, Oregon and Idaho. Dots represent major dams along the Columbia and Snake rivers. HUCs with less than 50% of their area in one or more of the three states were excluded from the spatial analyses and are not shaded (white). From Sanderson et al. (2009).

Non-Native Fish

Approximately 45 non-native species of freshwater and anadromous fishes now inhabit the Basin, accounting for 46% of the total number of fishes (Table C.3.3). The balance between native and non-native fish species has shifted dramatically in some parts of the Basin. There is an average of about 24 non-native species in each province; the more heavily invaded watersheds have as many as 31 (Table C.3.3; Schade and Bonar 2005). In 1985, for example, the littoral fish composition in John Day reservoir was dominated by natives; a decade later, non-native species dominated (Barfoot et al. 2002). By 2003, 41 of 91 inland fish species recorded in Washington State were non-natives (Wydoski and Whitney 2003). Above Hell's Canyon Dam and the other total blockage dams, densities of non-natives are particularly high, and there are well-established populations of non-native channel catfish, smallmouth bass, yellow perch and walleye. Dams and impoundments have been identified elsewhere as a major cause of transformation to food webs dominated by non-native species; not only fishes but many other aquatic groups as well (Johnson et al. 2008). This physical restructuring is a major cause of the hybrid food webs that are becoming common. At least 54% of the resident fish species in Washington, 50% in Oregon, and 60% in Idaho are non-natives (Sanderson et al. 2009; Figure C.5.3). In these three states, 26 native fish species are federally listed, including 17 Pacific salmon ESUs, three species of chub (Cyprinidae), three species of sucker (Catostomidae), Foskett speckled dace, bull trout, and Lahontan cutthroat trout. Most listings cite non-native fishes as the cause of endangerment, typically involving changes in the food web, increases in predation and competition, and infection by non-native pathogens or parasites (Mack et al. 2000, Simberloff et al. 2005). The threat of these non-native taxa is further increased by the changes in environmental conditions from ongoing climate change (Rahel et al. 2008).

Predation by Non-Native Fish

Predation is the best documented of all non-native impacts on salmon in the Pacific Northwest, with non-native fishes consuming significant numbers of emigrating juvenile salmon in some habitats (Sanderson et al. 2009; Chapter C.3). Most studies have been relatively small scale, sampling single stream reaches or single reservoirs, and they often examine the impact of a single non-native. Collectively, the available data suggest that cumulative impacts could be massive. Consider the following examples:

In the John Day reservoir from 1983-86, the impact of non-native predators on emigrating juvenile salmonids was significant. Walleye, smallmouth bass, and channel catfish consumed thousands of juvenile salmon and steelhead, but native northern pikeminnow accounted for the largest losses of smolts (Riemanet al. 1991, Vigg et al. 1991, Poe et al. 1991). Other non-native fishes also have been documented to prey on juvenile salmonids, including largemouth bass, yellow perch and crappie (Bennett et al. 1983, Poe et al. 1994). In Lake Washington, smallmouth bass are more effective predators on juvenile Chinook than largemouth bass (Tabor et al. 2007).

Largemouth and smallmouth bass also contribute to the decline of some native fishes, frogs and salamanders (Fuller et al. 1999). Smallmouth bass, in particular, sometimes replace native pikeminnow. They consume 35% or more of juvenile salmon outmigrants in some regions, preying on smaller size classes than do pikeminnow (Fritts and Pearsons 2004, 2006). Walleye, now self-sustaining, consume between 250,000 and 2,000,000 outmigrating salmonids annually in the Columbia River (Tinus and Beamesderfer 1994).

Stocking of hatchery-raised brook trout has been widespread in the Pacific Northwest, and it has led to the decline of bull and cutthroat trout through hybridization (with the former), predation and competition (Gunckel et al. 2002, Dunham et al. 2004, Peterson et al. 2004). Precise mechanisms have not been explored thoroughly, but the presence of brook trout is associated with a 12% reduction in survival of juvenile salmon in several upper Snake River tributary streams (Levin et al. 2002).

The effects of predation and other food-web interactions can be indirect. For instance, spawning American shad, introduced into the Columbia River in 1871, outnumber returning salmon 5:1 (Peterson et al. 2003). In excess of 5,000,000 juvenile shad may benefit salmon by serving as alternative prey, or harm salmon by subsidizing total food supply and boosting reproduction of large predators, since they are eaten by both native (e.g., northern pikeminnow) and non-native (e.g., walleye) predators that also consume juvenile salmon (Petersen et al. 2003). Given the complexity of the interactions of non-native species in food webs, formal modeling explorations are likely to play a useful role in evaluating threats presented by non-native introductions. As examples of such a formal approach, the likely consequences of management of various non-native predators on juvenile salmonids can be evaluated using the modeling framework EcoPath (Harvey and Kareiva 2005). Similarly, field-integrated bioenergetics models (Chapter C.6) can be applied and are apt to be more useful for anadromous species that spend only a fraction of their lives within a modeled habitat or food web.

Competition for Food and Habitat. Most studies have not involved enough of the biota to conclusively demonstrate direct competition for food. Such a demonstration requires data on the food species themselves, as well as on the spatial and temporal overlap of the various players (Fresh 1997). Nevertheless, either depleting or changing the composition of local food webs is expected to seriously affect native fishes and wildlife in the Basin’s habitats.

In the estuary, feeding and other competitive interactions between native and non-native fish have not been adequately examined. However, the matter is now beginning to receive the attention it warrants, especially as the number of non-native fish species peaks in the tidal regions (33 non-native fish at about rkm 200; Sanderson et al. 2009). There is some diet overlap between steelhead smolts and non-native shad (McCabe et al. 1983); however, species eat the non-native bivalve Asian clam, providing a good example of a hybrid food web. In addition to shad, it will be important to examine salmonid diet overlaps and possible competition with basses (e.g., Centrarchidae; nine non-native species) and minnows (Cyprinidae; eight non-natives), which dominate the non-native community in the estuary (Table C.3.3). Although there is little information on feeding habits of non-native fish, the descriptive information on their diets in Sytsma et al. (2004, appendices therein) gives a good starting point.

Food competition in the reservoirs may be equally strong. It is known that planktivorous American shad reduce both abundance and size of *Daphnia* in the mainstem reservoirs (Haskell et al. 2006). *Daphnia* are important food resources for subyearling Chinook, which rear in the reservoirs (Rondorf et al. 1990). Further, this hybrid food-web illustrates the sensitivity of food-web interactions to climate change (discussed by Rahel 1996). Temperature increases and flow decreases in summer alter food-web dynamics by causing abundances of zooplankton, primarily cladocerans and copepods, to peak progressively earlier in summer, thereby enabling juvenile shad to deplete this important food source before subyearling Chinook arrive (Haskell et al. 2006). Future increases in water temperature, which are expected from both climate and land use changes (ISAB 2007-2, 2007-3), will probably favor further expansion of shad in the reservoirs, and would likely have negative food-web consequences for juvenile salmonids.

Competition for food by brown trout and Atlantic salmon, two other non-native salmonids, is also a possibility that has not been investigated. Prospects for competition with Atlantic salmon may be limited, since this species has not yet reproduced naturally in the Basin and is only stocked from a hatchery into topographically isolated Hosmer Lake in the coastal mountains of Oregon. Periodic and isolated records are present from other areas too (Table C.3.3). Brown trout have colonized many streams (ISAB 2008, Sanderson et al. 2009) and are likely more of a threat, as they use similar habitat to rainbow trout, including boulder emplacements (Shuler et al.1994), where they prey on drifting insects. Brown trout consume an estimated 15% of the juvenile spring-summer Chinook rearing in North Fork reservoir on the Clackamas River (Lowery and Beauchamp 2010).

As further caution, the impacts of non-native fish on food webs may not be reversible by removing the non-natives. For example, introduction of brook trout into a fishless lake in the Rocky Mountains eliminated two important plankton species, only one of which recovered after removal of the trout (Parker et al. 2001). Removal of non-native trout from alpine lakes around Mt. Rainier, Washington, resulted in a change of the food webs, but not a reversion to the original trophic states (Drake and Naiman 2000).

Other Non-Native Vertebrates

There are far fewer non-native taxa from other vertebrate groups (birds, mammals, reptiles and amphibians) resident in the Basin. Nevertheless, vertebrates often have major effects on food webs. There are at least 42 non-native species of birds, mammals, reptiles and amphibians in Oregon and Washington (O'Neil and Johnson 2001, Witmer and Lewis 2001). Fortunately, many are not associated with aquatic or riparian ecosystems.

Birds. There are 18 recorded non-native bird species in Washington and Oregon, most of which were introduced for hunting or cultural-esthetic reasons (Witmer and Lewis 2001). They tend to be either upland game birds (e.g., ring-necked pheasant, California quail) or birds that are associated with people and cities throughout the United States (e.g., European starling, house sparrow). Only three are water birds, trumpeter swan, mute swan, and American black duck. None is widespread or abundant, though some negative interactions with native species are reported (e.g., mute swans can be aggressive to other water birds).

Aquatic Mammals**.** The only non-native aquatic mammal is the nutria or coypu; O'Neil and Johnson 2001). This species is semi-aquatic, inhabiting stream banks and wetland-marshlands, where it burrows, rests and feeds on vegetation (see Figure D.7.1 for a Basin food web containing nutria). Nutria are rodents native to South American and were brought to Oregon and Washington for fur farming in the 1930s. Feral nutria were recorded not long after (Larrison 1943, Witmer and Lewis 2001). Nutria consume or remove vegetation so thoroughly as to convert marsh ecosystems to open water, and they are considered major pests in northeastern and southern coastal areas. Nutria carry pathogens and parasites that infect many native species (as well as humans and domestic animals).

Reptiles and Amphibians**.** There are two non-native reptiles in the aquatic-riparian ecosystems of Oregon and Washington (O'Neil and Johnson 2001). The snapping turtle and the red-eared slider are native to the eastern United States. Snapping turtles prey on native species, compete for food with native turtles, and carry parasites and pathogens that negatively impact native turtles. The red-eared slider competes with native turtles for food and nest sites (Oregon Department of Fish and Wildlife).

One non-native amphibian, the American bullfrog, is particularly problematic for the Basin's food webs. Native to the United States east of the Rockies, it is now widely established. Bullfrogs have commonly been farmed, escape regularly, readily become feral in diverse environments, and are difficult to eradicate (Garner et al. 2006). They are voracious predators, as well as carriers of the chytrid pathogen causing chytridiomycosis (see below), and are believed to be partially responsible for declines in many native amphibians (e.g., Pearl et al. 2004, Hayes et al. 2009). In fact, non-native fish, crayfish and bullfrogs all are thought to hold some blame for declines in native amphibians, as well as for other aquatic food web changes (Kats and Ferrer 2003). Bullfrogs also are predators of fishes, including juvenile salmonids (Garwood et al. 2010).

Non-native species can increase the likelihood that other non-native species will establish, via a process generally referred to as “invasional meltdown” (Simberloff and Von Holle 1999). There is evidence that bullfrogs may positively benefit from the presence of non-native centrarchid sunfishes, which share their native eastern habitat (Adams et al. 2003). In the Willamette Valley, Oregon, bullfrog tadpoles have higher survivorship where bluegill sunfish are present, presumably because sunfish limit the abundance of macroinvertebrates that prey on tadpoles. Reducing non-native centrarchids might reduce the abundance of bullfrogs in their non-native range (Adams et al. 2003).

Non-Native Aquatic Invertebrates

Potential modes of introduction are more diverse for invertebrates than for fish and other vertebrates. In addition to the movement of freshwater organisms via recreational boats and cargo barges/tugs and the intentional or accidental release of bait, numerous non-native invertebrates have been introduced via oceanic shipping, seafood operations and releases from home aquaria. Oceanic ships transport non-native invertebrates via hull fouling and in ballast tank water and sediment. Sampling of 134 stations in the lower Columbia River and estuary revealed 269 aquatic invertebrate species and 55 other unknown taxa (Sytsma et al. 2004). Of those identified, 21% were introduced, 34% were native, and 45% were of uncertain origin but probably non-native. Unfortunately, the ecological and food web effects of non-native invertebrates have received limited attention, and their potential effects on the Basin’s native fishes are still poorly described. Given that aquatic invertebrates constitute much of the food of native fish and wildlife (McCabe et al. 1997) it seems obvious that a changing array of invertebrate biota will affect growth and survival of native fish and wildlife. Several examples indicate the scope of the problem:

- New Zealand Mud Snail – This small, single-shelled mollusk can blanket streambeds with huge densities (e.g., 500,000 m^{-2}), representing up to 95% of the invertebrate biomass in some areas. They feed primarily on bottom-dwelling algae and detritus, consume 75% of autochthonous primary production (Hall et al. 2003, 2006), outcompete native macroinvertebrates such as larval mayflies, stoneflies, and caddisflies, which normally serve as salmon prey (Kerans et al. 2005). Mud snails have been observed in the diets of juvenile Chinook from the estuary, but are thought to be a poor nutritional source for salmon and other native fish species (Vinson and Baker 2008). The total food web impact of the mud snail on juvenile salmonids has not been determined, but it seems clear that its mode of feeding and volume of consumption must have strongly negative effects.
- Freshwater Asian Clam – First appearing in the Basin in 1938 (Burch 1944, cited by Cordeiro et al. 2007), this species is a major ecosystem engineer, changing both structure and function. Besides altering existing habitats, it affects trophic interactions and the availability of food for pelagic species and other benthos, and impacts ecosystem processes such as nutrient mineralization, oxygen availability and sedimentation (Karatayev et al. 2005). In high densities, it significantly reduces phytoplankton abundance, displaces native bivalve species feeding on phytoplankton, increases ammonia levels and clogs cooling water intakes (Boersma et al. 2006). The species is one of the two most abundant benthic invertebrates of the lower Columbia River, where it has been reported as prey for steelhead (Bottom and Jones 1990), serves as a seasonal food source for white sturgeon (McCabe et al. 1997), and is a prominent food item for raccoon and surf scooter (Simenstad et al. 1984). The presence of the Asian clam does have some positive aspects; it reduces turbidity and restores submerged aquatic vegetation (Phelps 1994). Taken as a whole, impacts by the Asian clam remain somewhat ambiguous but there is no doubt that its presence results in consequences that ripple through the food web, affecting the biotic community in largely unpredictable ways.

- *Mysis* – the consequences of invasion by the mysid shrimp are particularly well documented (Sidebar C.5.1).
- Northern crayfish – This species has been recently recorded from several sites in Washington and Oregon (Larson et al. 2010). Although the food web effects of northern crayfish are not known yet, non-native crayfish are well-documented to have had major reorganizing effects on food webs elsewhere, including displacement of native crayfish via competition and transmission of disease and reduction of native aquatic plants (e.g., Lodge et al. 2000). Northern crayfish may threaten Washington's only native crayfish, the signal crayfish; Larson et al. 2010), and they also are considered a cause of decline of some native amphibians (Katz and Ferrer 2003). The non-native red swamp crayfish also is present in the Basin (Olden et al. 2009). School science programs and golf courses (which may stock crayfish to control pond macrophytes) may be sources of non-native crayfish in Washington (Larson and Olden 2008).

Sidebar C.5.1. The Wide-Ranging Effects of the Introduction of Mysid Shrimp

The introduction of mysid shrimp into Pacific Northwest lakes has been particularly instructive. The initial introduction to Kootenay Lake to stimulate rainbow trout production (Sparrow 1964) was followed by a rapid increase in growth of some kokanee instead (Northcote 1972, 1973). Mysids subsequently have been introduced to cold lakes and reservoirs throughout the western United States in unsuccessful attempts to stimulate kokanee production (Lasenby et al. 1986, Martinez and Bergersen 1991). Where detailed data are available, mysids appear to have radically altered the structure of invertebrate communities, influencing both benthic and pelagic food webs for native fishes and introduced kokanee, while providing a new forage base for introduced lake trout. The result has been a cascade of effects through food webs that has led to the virtual collapse of many kokanee populations, dramatic expansion of lake trout populations, and the decline or displacement of bull trout, bald eagle, and even fishermen seeking kokanee or bull trout (Bowles et al. 1991, Spencer et al. 1991, Martinez et al. 2009).

Introduction to Lake Pend Oreille, Idaho, led to temporal displacement and changing composition of the native macrozooplankton, particularly *Daphnia* and *Bosmina* (Rieman and Falter 1981). Interactions between the cladocerans and mysids are related to their vertical distributions, with cladocerans increasing when the mysids become seasonally isolated from near-surface zones by changes in thermal stratification and transparency, resulting in a reduction in food available for kokanee and other planktivorous fishes. Even further-reaching changes are seen in the biota of the Flathead Lake region due to mysid introduction (Spencer et al. 1991, 1999; Ellis et al. 2011). Although non-native lake trout had been present in Flathead Lake since the early 1900s, the mysid invasion significantly stimulated recruitment of juvenile lake trout, increasing the lake trout population by nearly 20-fold over 10 years. The rapid increase in predation by lake trout extirpated the kokanee population suddenly, 5-6 years after the mysid invasion (see Sidebar C.6.3; Beauchamp et al. 2007, Ellis et al. 2011). Mysids were also implicated in reductions and delayed production cycles of the cladoceran populations, a decline in native copepods, and consequent decline in planktivorous fishes (Stanford and Ellis 2002). The loss of spawning kokanee and their carcasses from upstream tributaries negatively affects birds, particularly bald eagles, California and herring gulls, common mergansers and mallards. Barrow's and common goldeneyes and American dippers, all of which feed on kokanee eggs, declined steadily over the next two decades. The mammalian fauna also changed. Coyote, mink, river otter, even white-tailed deer feed on kokanee, as do grizzly bear, all of which are much reduced in the Flathead Lake region.

Insects

Aquatic invasive insects are notoriously difficult to identify, and surveys to date have not focused on this group (Sytsma et al. 2004). Given their importance in fish food webs, this is a knowledge gap that should be investigated, as we recommend in Chapter E.5.

Microbes, Parasites, and Pathogens

Introduction of non-native microbes, both pathogenic and non-pathogenic, and parasites, both microbial and macrobial, is another potential problem. These taxa are less-well studied and more difficult to observe and identify, so the record of non-natives from these groups remains limited (Pysek et al. 2008, Litchman 2010). There are, however, clear examples where the introduction of non-native parasites and pathogens have had important food-web effects, as well as examples where food-web reorganization provoked by other non-native taxa has been realized through trophic mechanisms involving microbes, parasites, and pathogens. Several examples illustrate the problems that arise from non-native parasites and pathogens, as well as from the effects of other non-native taxa on the transmission and spread of native parasites and pathogens.

- *Myxobolus cerebralis*, a myxozoan parasite that causes Whirling disease in salmonids, was introduced to the United States in the 1950s and has rapidly spread and caused declines in wild trout populations in the western United States (Bartholomew et al. 2007, Gilbert and Granath 2003). The complex and interesting biology *of M. cerebralis* and its infective life cycle involves a suite of food-web interactions that are highly sensitive to ongoing land-use and climate changes, including the nutrient content, temperatures and flow rates of water, and the presence of various alternate hosts (Sidebar C.5.2).
- *Batrachochytridum dendrobatidis* is an emerging fungal pathogen that causes the disease chytridiomycosis, which is now recognized as playing significant roles in the decline of many amphibian species (e.g., Pearl et al. 2004, Hayes et al. 2010). As with many other non-native taxa described in this chapter, the food web effects of this pathogen probably often interact with other identified threats to food webs, such as toxins, other environmental chemicals (Chapter C.7), and changing climate. Infestations by *B. dendrobatidis* not only lead to food web changes through contributing to amphibian decline, but also to food web changes via the non-native bullfrog. The bullfrog is an asymptomatic and frequent carrier of *B. dendrobatidis* (Garner et al. 2006, Pearl et al. 2004) and is implicated in its spread.
- The rock slime diatom "didymo" (*Didymosphenia geminata*), a protist, has been found in the Canadian portions of the Basin. Benthic invertebrate communities in streams dominated by didymo are overwhelmed by stress-tolerant chironomid midges, which results in major changes in the food webs supporting juvenile salmonids (e.g., Atlantic salmon; Gillis and Chalifour 2010). Major reorganization of food webs has followed introduction of didymo into New Zealand streams, where there are increases in periphyton biomass, increases in invertebrate densities and shifts in community composition, particularly shifts to high abundances of oligochaetes, chironomids, cladocerans and nematodes (Kilroy et al. 2009).
- "Parasite spillback" – This refers to an indirect food web interaction in which a non-native species supplies an alternative host for a native parasite, and so increases the abundance and spread of the parasite and thereby its impact on native hosts (Kelly et al. 2009). Over two-thirds of the parasites (including arthropods, parasitoids, protozoa and helminths) of non-native animals are native species, with co-occurring native hosts (Kelly et al. 2009). There is good evidence that the parasites fostered by these non-native hosts increase the infection rates of native species at individual as well as population levels. Such a mechanism appears to be involved in the high infestation of native juvenile salmonids by northern hemisphere endemic sea louse (*Lepeophtheirus salmonis*) that is associated with proximity of native fish to high-density Atlantic salmon farms in the Pacific Northwest (Morton et al. 2005).

Sidebar C.5.2. Food Web Interactions and Invasion by the Non-native Parasite-pathogen *M. cerebralis* (Whirling Disease)

M. cerebralis appears to be of European origin, probably as a parasite of brown trout, which typically do not manifest whirling disease when infected. It emerged as a pathogen when introduced to North America, probably via infected live fish, fish eggs or frozen fish, in the 1950s (Elwell et al. 2009, Gilbert and Granath 2003). It now is present in Idaho, Montana, Oregon and Washington. *M. cerebralis* has a complex life cycle requiring two distinct obligate hosts; one phase infects salmonids, including rainbow trout, which are most susceptible to whirling disease, but also many other salmonids, including sockeye, cutthroat trout, bull trout, Chinook, Atlantic salmon, steelhead, and brown trout. The single known host for the other life phase of the parasite is the worm *Tubifex tubifex*, which is associated with warm, slow, eutrophic waters, but occurs very broadly in aquatic habitats, albeit at lower densities in colder and more rapidly flowing waters (Gilbert and Granath 2003). *T. tubifex* can be abundant in hatchery ponds (Bartholomew et al. 2007), so hatcheries can be sources of whirling disease.

M. cerebralis spreads by many pathways, including illegal importation of fish; hatchery transfers and stocking; use of infected fish as bait; fishing and recreational boating; natural dispersal by piscivorous mammals and birds; and movements of infected fish and parasite spores in waterways (Elwell et al. 2009).The range and dynamics of this non-native species are sure to adjust with continuing environmental changes given the complex of alternative hosts with differing susceptibility to the parasite and to the disease, the environmental sensitivity of the infection process (which increases with water temperature), and the variety of pathways by which *M. cerebralis* and its vertebrate hosts disperse or are spread. Now available is a White Paper summarizing current knowledge of whirling disease in the United States and providing extensive information on the biology and food web-related effects of whirling disease in the Basin.

Non-Native Riparian Vegetation

Riparian vegetation and associated food webs are increasingly compromised by the proliferation of non-native plants (Chapter D.8). These plants can change aquatic habitats by occupying shoreline space, shading, clogging spawning substrates, reducing currents, and creating conditions favored by non-salmonid or non-native fishes. Invasive non-natives comprise about 25-30% of the total species of floodplains associated with coastal rivers, a prevalence that is also typical of alluvial rivers in other parts of the world (Hood and Naiman 2000). Invasive plants are common on recently disturbed surfaces, such as gravel bars, but many tend to disappear as canopy closure (at about 10 years) reduces light levels (DeFerrari and Naiman 1994). However, some riparian non-natives are highly successful invaders and have become widely naturalized in the Basin (e.g., Russian olive, Katz and Shafroth 2003). Non-native riparian plants have been shown to change nutrient dynamics of riparian soils and associated streams. It is also well known that riparian vegetation has large effects on aquatic food webs (Naiman et al. 2005). A few examples will suffice to illustrate the range and extent of ecosystem and food-web effects of non-native plants that have become common in the Basin's riparian areas:

- Russian olive was introduced to the western United States from Eurasia in the early 20th century and is the fourth most common woody species along riparian corridors in the interior of the United States (Friedman et al. 2005). Russian olive is strongly associated with soils having elevated inorganic nitrogen concentrations. This is due to its highly efficient nitrogen-fixing rhizobial symbionts and high concentrations of nitrogen in the leaf litter (Follstad Shah et al. 2010). Altering the chemical composition of riparian soils would be expected to change the soil biota. Recent research shows that stream reaches invaded by Russian olive have altered nitrogen cycling, with higher organic N and higher N demand (Mineau et al. 2011).
- Giant knotweed - This newly invasive plant has profound effects on ecosystem characteristics (Urgenson et al. 2009). The carbon:nitrogen ratio of knotweed litter is 52:1, a value 38–58% higher than that of native red alder and willow. Resorption of foliar N, prior to leaf drop, is 76% in knotweed, compared with only 5–33% among native woody species; this increased resorption by knotweed means that substantially less energy and nutrients are transferred into stream food webs than would have occurred from native vegetation. Where knotweed is abundant (>5 stems m^{-2}), litter mass of native species is reduced by 70%. Richness and abundance of native herbs, shrubs, and juvenile trees are negatively correlated with knotweed density. By displacing native species and reducing nutrient quality of litter inputs, knotweed invasion has the potential to cause long-term changes in the characteristics of riparian forests, their soils, and the food webs of adjacent aquatic habitats. These effects are probably reversible but only with near-complete eradication.

- Purple loosestrife, introduced into the Pacific Northwest in 1929, is found in wetlands that are regularly flooded. It displaces native sedges and cattails and alters detrital-based food webs by shifting local nutrient availability from a winter/spring to a fall flux peak, thereby being detrimental to native fish and wildlife dependent on the winter/spring flux (Grout et al. 1997, Blossey et al. 2001). In the northeastern United States, where purple loosestrife has displaced native cattails from wetlands, the American toad, a native species, has slower development and reduced survival attributable to direct and food-web effects of loosestrife (Brown et al. 2006). It appears that the high tannin concentrations of loosestrife leaves may be directly toxic to developing tadpoles and that a strong indirect effect on the wetland food webs compromises an adequate diet for tadpoles. Thus, non-native plants such as loosestrife threaten not only the plant communities they invade, but also the animals that depend on those communities for habitat and food resources.
- Reed canary grass is a native species that also exists as an invasive European cultivar (Merigliano and Lesica 1998). It is a riparian or wetland plant that out-competes native grasses and other wetland vegetation. This species can be a problem during habitat restoration, as it spreads rapidly into areas of replanted vegetation, thereby disrupting attempts to reestablish native food webs.
- Japanese knotweed is a rhizomatous perennial that grows to 2-3 m high and increases rapidly in disturbed riparian areas. It forms dense thickets, and water flow disperses rhizome fragments, facilitating its spread. Japanese knotweed is an example of a non-native suspected of allelopathy, a process by which plants practice "chemical warfare" on other plants by releasing chemicals that suppress the germination or growth of other species (Vrchotova and Sera 2008).

Submerged Aquatic Vegetation

Submerged aquatic vegetation (SAV)[20] occupies the margins of lakes, rivers and estuaries in the littoral or intertidal zone. As with invasive riparian vegetation, non-native SAVs alter aquatic habitat by occupying shoreline space, shading, clogging spawning substrates, reducing currents and creating conditions favored by non-salmonid or non-native fishes. Increases in primary production from SAVs can also affect rates of many biogeochemical processes. For instance, the nutrient content and physiology of an alien plant may differ greatly from that of native plants being replaced, causing changes in nutrient cycling, rates of herbivory and decomposition, and consumer growth. Additionally, alien SAVs can create beds so dense that they inhibit foraging by predatory fishes, thereby preventing them from taking advantage of the high productivity of these beds (reviewed by Strayer 2010).

- Eurasian water milfoil – Possibly introduced by ballast soils from Europe in the 1800s (Aiken et al. 1979), water milfoil is the most widespread non-native SAV in the Basin's rivers, lakes and reservoirs (Sanderson et al. 2009); it is also found in the brackish part of the estuary (Sytsma et al. 2004). Increases in primary production affects rates of many biogeochemical processes. For instance, this aquatic plant forms dense mats of vegetation that depress dissolved oxygen concentrations (Unmuth et al. 2000, Cronin et al. 2006). Invertebrate abundance on Eurasian milfoil leaves is often as high as that on native plants (Phillips 2008), but detritus from the plant does not seem to enter aquatic food webs in reservoirs (Toetz 1997).
- Japanese eelgrass – Many of the 19 invasive plants in the estuary are of freshwater origin, but this marine non-native species is restricted to the higher-salinity habitats at the mouth of the river (Sytsma et al. 2004). Unlike milfoil, this invasive SAV provides an important food for migratory waterfowl. Brant, American wigeon, mallard, northern pintail, and green-winged teal consume more of the non-native eelgrass than

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[20] Although we refer to these plants as submerged aquatic vegetation because this is common ecological usage, note that certain plants, including milfoil, also float on the water's surface.

native eelgrass (Baldwin and Lovvron 1994). This species' role in food webs supporting juvenile salmonids has not been explored.

Sidebar C.5.3. Non-native Taxa in the Basin's Uplands

While the focus of this report is on the aquatic and riparian food webs, we note that non-native species are also major ecological forces and threats to the food webs of upland habitats. Most importantly, non-native organisms in upland habitats affect the biota and ecosystem dynamics of the aquatic network by changing ecosystem properties, including upland food webs and their interactions with the aquatic/riparian components. This is reflected, for instance, through changes in fire, wind erosion, and run-off/sedimentation regimes caused by these non-native organisms. More than 850 introduced plant species are recorded in the inland Northwest, and the numbers are increasing (Hessburg and Agee 2003).

Non-native Species in the Forest Food Web. Several non-native forest pests have major food web effects on inland forest trees, with significant implications for the aquatic/riparian areas via their effects on tree mortality. For instance, a pathogen, blister rust fungus, *Cronartium ribicola*, which was introduced early in the 20th century from nursery stock, is now widely distributed through the ranges of all native five-needle pines, including western white pine, sugar pine and whitebark pine. It can cause a high mortality (up to 90%; Hessburg and Agee 2003). Although the arrival of non-native forest pests has increased, the eastern interior forests currently have few serious invaders (Hayes and Ragenovich 2001). Among recently recorded non-natives were the western larch casebearer (*Coleophora laricella*), European and Asian gypsy moths, and the balsam wooly adelgid (*Adelges picea*). Healthier native forest stands are less susceptible to infection by such forest pests (Hayes and Ragenovich 2001) but, when established, these pests can greatly reduce the dominant forest trees. A reduction in dominant trees alters and degrades the forest, though perhaps less so than attempts to eradicate pests that are well-established (e.g., Kizlinski et al. 2002).

Non-native Species in the Shrublands-Grasslands. It is widely recognized that non-native plants can jeopardize the shrubland and grassland food webs of the interior Basin. For example, the annual grass Bromus tectorum (cheatgrass) is considered a major threat to the sagebrush-steppe ecosystem and associated food webs (e.g., Dobkin and Sauder 2004, Knick et al. 2003, Bangert and Huntly 2010). Cheatgrass has been responsible for accelerated loss of native steppe and grassland species through promotion of increased fire frequency and intensity (D'Antonio and Vitousek 1992, Eviner et al. 2010). Although cheatgrass and some of the non-native weedy forbs typically have been viewed as aggressive invasives, recent research indicates that diverse native sagebrush communities with intact native ecosystem functions have considerable resistance to invasion by these organisms (e.g., Chambers et al. 2007, Prevey et al. 2010). These findings support the guidance that preventing initial degradation of native ecosystems is an effective way to reduce the spread and impacts of non-native species.

Altered Habitat Conditions Exacerbate the Impact of Non-Native Introductions

The food web impacts of non-native species must be viewed in the context of ongoing changes in habitat conditions. Consider just the fish biota. Over the last two decades impoundments have developed sloughs and backwater habitats, with low water exchange and higher late summer water temperatures than those of nearby main-channel habitats, thereby creating habitats more conducive to warm water species (Gadomski and Barfoot 1998). The native cool water fishes appear to have moved out of backwaters, and resident fish assemblages in shallow nearshore habitats of the reservoirs are changing rapidly. For instance, there has been a dramatic decrease in the native fish biota between 1984-85 (Palmer et al. 1986) and 1995 (Barfoot et al. 2002). In the mid 1980s four native fishes, chiselmouth, northern pikeminnow, suckers and sand rollers, dominated the catch (90%); non-native fishes comprised only 1%. A decade later, the same four natives comprised only 38% of the fish fauna, while the proportion of non-native species (primarily sunfishes and yellow perch) had increased to 34%, with the remaining 28% consisting of sculpin, peamouth, and several species of minnows.

Future increases in temperature, due to ongoing climate change, will favor further expansion of warm-water piscivores, particularly largemouth bass and channel catfish (Poe et al. 1991). Non-native piscivorous fishes such as centrarchids (e.g., bass, bluegill, and crappies) and percids (e.g., walleye and perch) are expanding their distributions and numbers (Poe et al. 1994). Beyond changes in species composition, the non-native fishes change food web dynamics by increasing predation on native fishes, competing for resources, and contributing pathogens and parasites. Other non-native taxa trigger corresponding changes in food webs comprising the rest of the animal and plant biota. The net result is that the Basin's food webs have changed and will continue to change, with consequences that are not entirely predictable. The Basin is entering uncharted territory, with a hybrid collection of organisms never assembled before, and with environmental conditions that have not been encountered before. These are known as novel, hybrid or "no analogue" food webs, for which there is no precedent. While there are actions that can be taken to reverse some of the changes and mitigate the impact of others, it seems clear that we cannot return to the *status quo ante* (Sidebar C.5.4); we can only go forward.

Sidebar C.5.4. Novel, Hybrid, or "No-analogue" Food Webs

The terms "novel, hybrid, and no-analogue" are used synonymously in this report in referring to existing and future food webs. A lesson from paleoecology is that food webs have changed dramatically over time, typically in association with changing climate. These changes presumably reflect the suite of different ecologies and abilities to migrate, tolerate or evolve in response to climate change (Williams and Jackson 2007). The changing food webs, which have been described as hybrid, novel or "no-analogue" food webs because their species composition is unlike any that occurred before them. This is one conceptual model for thinking about the food webs of the Basin's future as climate changes with unprecedented rapidity and both climate and the activities of people result in the introduction and establishment of non-native species.

Guidance is limited for managing hybrid food webs that contain non-natives and the no-analogue environments that lead to hybrid food webs. However, several general guiding principles emerge from recent examinations of the situation. There are four general strategies for coping with a no-analogue future: enhance societal adaptability, increase ecosystem resilience, advocate for actions to reduce human contributions to climate change, and facilitate transitions to more beneficial new ecosystem conditions (Chapin et al. 2006). Thus, it may be prudent to accept and even facilitate new food webs and ecosystems that are beneficial and that work in today's world. Others extend this guidance to give more specific cases, applications and guidelines (e.g., Hobbs and Cramer 2008, Hobbs et al. 2006, Seastedt et al. 2008).

Additionally, one may view the current altered food webs as no more immutable than those that they have replaced. Food webs evolve in response to continuing challenges and opportunities. The ecological capabilities of organisms are not set in stone (Carlsson et al. 2009), nor is the physicochemical template, which will undoubtedly change with climate, population and land-use (ISAB 2007-2, 2007-3). Carlsson et al. (2009) suggest four potential long-term outcomes to predators higher in the food web when exotic prey are introduced: 1) The introduced exotic prey may outcompete native species and become abundant, perhaps even the predominant prey resource, and any predator that cannot effectively consume them will decline to the extent that they are central to its diet; 2) Any predator that can prey upon them effectively, on the other hand, will acquire an adaptive advantage over those that cannot, and these selective pressures will begin to reorganize the predators of food web, perhaps substantially; 3) After a perhaps appreciable time, even non-effective predators may evolve the capability to consume the new prey, so may stage a comeback; 4) It follows that overharvesting of native predators may give an exotic prey an initial ability to invade and slow the natural responses of the food web. This last outcome has relevance to the pikeminnow bounty program. Not only are we removing the native predators of juvenile salmon that compete successfully with non-native predators, we have also made salmon more available to non-native predators by releasing larger than historical numbers of hatchery smolts into modified habitats (reservoirs, spillways) where they are especially vulnerable.

Non-Native Introductions Will Continue

There is every reason to expect that the introduction of exotic species to continue. This is in spite of growing awareness of the problem and efforts to slow the pace of introductions and mitigate problems. A number of potentially serious threats to the native food web are on the near horizon, among them:

- Quagga Mussels –Indigenous to the Dnieper River drainage (Ukraine), Quagga mussels have been reported from Lake Mead and Lake Havasu, Arizona. A recent report indicates this species is moving rapidly northward, and its arrival in the Basin is anticipated soon. The Independent Economic Advisory Board recently completed an economic risk analysis for Quagga mussels and, clearly, this species would have dramatic effects on ecosystems and hydropower operations (IEAB 2010-1).
- *Hydrilla* – The submersed macrophyte *Hydrilla verticillata,* recorded in Florida in 1960, has spread to more than half the states (Langeland 1996). It is a federally-listed noxious weed and local populations have been discovered in Idaho and Washington. It can transform food webs, via many trophic interactions, and is an example of an ecosystem engineer (Sidebar C.5.5).
- Asian toad – In 2009, an unidentified live toad was found in the Port of Portland in a shipping container from China. The toad was killed with a fumigant and its bones sent to China for identification, so the exact species remains in question. The agencies involved created the INVADER ALERT listserv to help coordinate surveillance and eradication in the future, as there was considerable uncertainty among them about how to deal with the issue of a non-native organism that could have threatened the aquatic ecosystem(Anon 2009). This example illustrates that entirely unanticipated organisms can arrive to threaten native Pacific Northwest food webs, and that taxonomic and ecological information must be readily available to respond quickly.
- Parasitic isopod – Recently found in Willapa Bay, Washington, and Yaquina Bay, Oregon, where it reduces the larval output of the ghost shrimp (*Upogebia pugettensis*; Dumbauld et al. 2010). Ghost shrimp are a potential food item for sturgeon (Dumbauld et al. 2008) and other fishes in the Columbia estuary, but it is not yet known if the parasite is affecting ghost shrimp populations there.

A list of non-native species of *particular concern* for the Basin is maintained by Pacific States Marine Fisheries Commission. The list includes many species described above, including zebra mussel, nutria, Asian carp, American bullfrog and New Zealand mud snail, as well as Atlantic salmon, which are considered an escape threat from aquaculture by some states, including Oregon.

Sidebar C.5.5. Food Web Effects of *Hydrilla,* a Non-native Ecosystem Engineer

The submerged aquatic plant *Hydrilla* has major effects on aquatic food webs. It tends to form dense vegetation and can exclude many native species and produce near monocultures, which have a homogeneous and distinct physical habitat structure compared to native aquatic communities (Theel et al. 2008). *Hydrilla* has been linked to reproduction of a non-native fish, the northern snakehead, in the Potomac River of eastern North America. Snakehead were observed in dense *Hydrilla* patches, which appeared to support floating nests and parental care of fry (Gascho Landis and Lapointe 2010). *Hydrilla* also has been linked via food web interactions to wildlife disease: avian vacuolar myelinopathy (AVM; Wilde et al. 2008). It is believed that the cause of the disease is a toxin produced by an epiphytic cyanophyte that lives on *Hydrilla* and that herbivorous waterfowl and the predators that consume them, such as eagles, are exposed through feeding on epiphyte-encrusted *Hydrilla*.

Hydrilla has been deemed an "ecosystem engineer," a species that controls the flow of resources in a habitat, because of its ability to reorganize the habitat template with its structure and physicochemical attributes (Clarke 2002). Some of the major non-native problem species discussed above are recognized as particularly problematic for food webs because of their tendency to be ecosystem engineers. Examples include nutria (extensive burrowing), cheatgrass (increasing fire frequency), and zebra mussels (creating shell bed habitat and filtering water to thoroughly change light availability).

Although *Hydrilla* appears to be an aggressive invader, one recent paper found evidence that two native species of a major aquatic consumer group (crayfish) readily consumed *Hydrilla* and, in fact, consumed it preferentially to a native confamilial species (*Vallisneria*; Parker and Hay 2005).

Strategies to Avoid Undesirable Impacts on Food Webs

Direct removal of well-established non-native species by physical (e.g., netting, electrofishing, mechanical removal) or chemical (e.g., rotenone, antimycin, herbicides, and pesticides) means has yielded limited success wherever attempted. Prevention is the best hope for dealing with non-natives, and certainly the most cost-effective. The ISAB has recommended in its Non-native Species Report (ISAB 2008-4) that the Council and the Fish and Wildlife agencies give the issue of non-native species the same priority as habitat loss and degradation, climate change (ISAB 2007-2) and human population growth (ISAB 2007-3). The Western Governors' Association (Resolution 10-4 on *Combating Invasive Species*) recommends an active stance. Collectively, these reports suggest the following:

- Habitat Protection and Restoration – The most effective way of minimizing the establishment and spread of non-native species (and protecting the native biota) is to maintain healthy habitats and restore degraded habitats. When native species have habitat for which they are best adapted, they have an improved chance of out-competing or persisting with non-native species. Restoring physical features, including natural flow and thermal regimes, may improve persistence of native species in environments now occupied by non-natives.
- Surveillance and Monitoring – Increase surveillance and monitoring of fish, plant, invertebrate and microbial populations to ensure early detection of non-native species and to track their distribution and abundance. Early detection of rare non-natives can be challenging and may require sophisticated sampling and estimation protocols, but the cost is small relative to the cost of control after spread of undesirable species. The Quagga mussel is a case in point.
- Fisheries Management – Smallmouth bass, channel catfish and walleye support significant sport fisheries in the Snake and Columbia rivers. State fisheries agencies in Oregon, Washington and Idaho all have management policies that are tolerant of and conducive to perpetuating (even enhancing) populations of these introduced predators. We recommend that the Council urge the state agencies to increase efforts to eliminate intentional introduction of non-native fishes and other species through enforcement and especially by education of fishing organizations.
- Information Gaps – Information gaps contribute to an ongoing lack of understanding of problems, their locations and possible remedies or preventative measures for them. We need to address gaps and uncertainties in the information base for food webs and the relationships of the still-changing blend of native and non-native biota within these food webs. The research needs are many. We need to: a) map the non-native species of the Basin and improve understanding of their introductions, establishment and spread; b) examine the impacts of non-native species on native salmonids and other native species at the regional scale, taking into account food-web-based effects; c) develop formal models for understanding and predicting the impacts of non-natives on food webs (e.g., as has been done using EcoPath; Harvey and Kareiva 2005); d) improve understanding of species interactions between natives and non-natives; and e) explore the interrelations of climate change, land use, and non-native species. Additional research is particular needed on some groups, especially pathogenic and free-living microbes, parasites, and insects, for which species lists, food webs, and basic ecological information are generally lacking.

Conclusions and Other Recommendations

Non-native species of many major taxonomic groups are now common and widespread in the waterways and riparian habitats of the Basin. Some species are major components of contemporary food webs, and the food web changes they have caused have had major consequences for the Basin's productivity and resilience. Such food web and ecosystem-level transformations, caused by non-native taxa, have been observed generally. Certain types of organisms have been identified as particularly likely to disrupt food webs and have other undesirable effects. These include mollusks that disrupt the base of the food chain, top predators that disrupt the food web from above via strong trophic cascades, omnivorous decapods, aquatic plants that engineer habitat and reset patterns of primary production, and pathogens (Strayer 2010).

Well-established non-native species create hybrid food webs. As the species proliferate, their food web transformations are also promoted by no-analogue physico-chemical conditions, such as those caused by development of the hydrosystem (Williams et al. 2006), by ongoing climate changes (ISAB 2007-2, Rahel et al. 2008, Rahel and Olden 2008), and by changing human population and patterns of land use (ISAB 2007-3). Changed habitats often increase the invasibility of an ecosystem. Propagule pressure (i.e., the number of seeds, larvae or individuals being introduced to a region) is also often directly related to human activity. Increased surveillance of the transport industry (e.g., ship, rail, truck traffic) is required to avoid more complex hybrid food webs. On the other hand, if socio-economic reasons suggest setting up hybrid food webs by stocking of non-native species for food production, we urge a very conservative approach, using the best risk assessment methods available.

Non-natives are inevitably going to be important components of many of the Basin's future food webs, because they are here already and the likelihood of eliminating them is low. Nevertheless, evidence indicates that introduction of non-native taxa generally should be avoided. The effects of non-natives typically have been difficult to anticipate, surprisingly far-ranging, and often destructive to native species, food web functions, and local cultural values. Regardless, the Basin's altered physicochemical template necessitates facing the reality that hybrid food webs will be part of the future; we must learn when and where they should be accepted and managed as persistent ecological components. An inventory of hybrid food webs would be a good first step to scope out future challenges and restoration activities. Additional research is needed to define strategies and actions for effectively managing hybrid ecosystems and food webs, and for deciding when non-natives should be accepted as parts of desirable food webs. The difficulty of the topic and its immediate-term importance suggest that a Basin-wide symposium or workshop would be advisable to gather input to develop better understanding of and strategies for managing the hybrid environments and food webs of the future and to communicate the finding to the general public.

C.6. Food Web Processes – Bioenergetics and Fish Growth

Food demands are set by the abundance and growth of consumers and by the thermal regime. It is the interplay of individual growth, per capita feeding rate, abundance, mortality and temperature-dependent physiological responses that determine temporal dynamics in consumption demand by any species or size of consumer (Beauchamp et al. 2007). However, food demands vary among species and life stages because of differing diets and metabolic responses (Beauchamp 2009). Further, the relationship between the production cycle of common foods and the temporal consumption demand establishes whether the seasonal carrying capacity of a foraging habitat might be exceeded. Even though the biomass and production of prey may appear to be greater than estimated or potential consumption demand, density dependent growth becomes evident as consumption reduces prey densities enough to inhibit individual feeding and growth rates (Ney 1990).

Food demands can be framed by understanding bioenergetics. The term “bioenergetics” refers to physiological processes that regulate food consumption, losses from waste, and use of the resultant energy for basic metabolic requirements such as activity, growth, reproduction or lipid storage (Brett 1983). Since fish and invertebrates are ectotherms, the rates of many physiological processes related to development rates, metabolism and feeding are greatly influenced by water temperature. Fish exhibit indeterminate growth, meaning that individuals within the same species can grow at very different rates and achieve much different sizes in different environments. Consequently, size and growth are useful metrics for determining the overall health and performance of an ecosystem. They represent the integration of an organism’s growth history, which in turn reflects environmental and ecological conditions experienced throughout life.

Bioenergetic models provide an important perspective for understanding the structure and function of aquatic food webs. This is accomplished by quantifying consumption demand while accounting explicitly for temporal changes in body size, temperature and diet of consumers (Hanson et al. 1997). A bioenergetics model estimates how much consumption is required to satisfy the observed growth of consumers over some specified time interval (annual, seasonal, monthly), given temporal changes in diet and thermal experience of the consumer. By estimating temporal consumption rates, the model: 1) quantifies daily, seasonal or annual biomass of different prey consumed by different size classes and species of predators (Figure C.6.1);
2) determines the importance of different prey to the seasonal, annual, or lifetime energy budgets of consumers; and 3) estimates the average daily feeding rate, as a proportion of the consumer’s physiological maximum feeding rate, which can potentially indicate whether the supply or accessibility of food is limiting feeding and growth. Thus, bioenergetics can be used for estimating the magnitude and impact of predation mortality on various species of interest, or for evaluating the impacts of different hatchery release strategies on food competition, individual growth and the carrying capacity of habitats through time (Chapter C.4). Background and details about the bioenergetics modeling approach can be found in Appendix A.

This section briefly describes how bioenergetics models have been applied in the Columbia River Basin to estimate consumption demand and determine the magnitude of predation or potential competition among species; to quantify the impacts of non-native predators, competitors, and prey on a host lake community; and to diagnose factors affecting growth.

Estimating Feeding Rate and Consumption Demand

Bioenergetics modeling has been used in the Basin to estimate consumption demand by juvenile salmon and American shad for zooplankton and benthic invertebrates in run-of-river reservoirs, consumption demand by juvenile coho and Chinook during early marine growth, and the predatory impact by native and non-native piscivores on juvenile salmon, resident salmonids and other prey in reservoir and lake habitats.

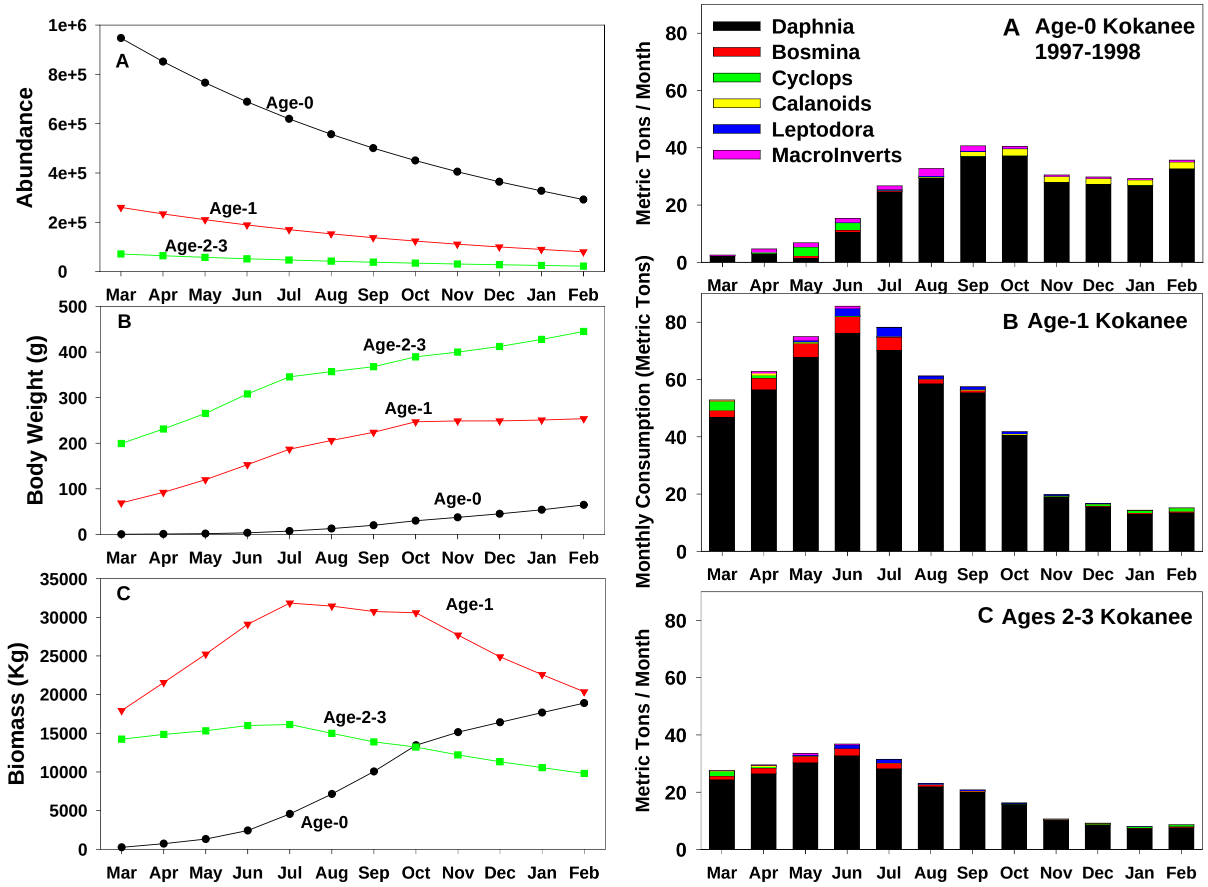

Figure C.6.1. Temporal dynamics in age-specific abundance, growth and biomass of kokanee (left panel) interact with thermal regime to determine timing and magnitude of food demand imposed by each age class (right panel) in Lake Billy Chinook, Oregon (from Beauchamp and Shepard 2008).

Mainstem reservoirs as feeding habitats for migrating yearling Chinook. The importance of run-of-river reservoirs as feeding habitat for juvenile salmon is an important issue. This is because of the link between stage-specific growth and size-selective mortality, as well as the potential for growth depression by competition with hatchery fish and non-native species. For example, during the May 2008 migration of wild yearling spring/summer Chinook from Lower Granite Dam (rkm 695) to Bonneville Dam (rkm 234), the modal transit time was 13-14 days, while the mean weight of migrating smolts increased from 15.0 to 18.2 g.[21] Bioenergetics simulations of the migration indicated that smolts fed at a high rate (78% C_{max}), consuming 23.1 g of food and gaining 3.2 g additional body mass (growth efficiency GE = 14%). The model simulations estimate that for every million yearling smolts, 18.5 metric tons (mt) of food was consumed during the migration (Sidebar C.6.1, Appendix A). Since the population index at Lower Granite Dam in 2008 was 1.3 million wild and 7.8 million hatchery yearling Chinook smolts, (FPC 2008, Tables 16-18), consumption demand during peak smolt migration would have required 166.5 mt of food.

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[21] See Sidebars and Appendix A for data sources.

Sidebar C.6.1. Bioenergetics simulation of food demand and feeding rate by wild spring-summer Chinook smolts

Are mainstem reservoirs important rearing habitats for migrating smolts? We examine this by estimating the growth and feeding rates of wild spring-summer Chinook during peak migration of smolts PIT-tagged at Lower Granite Dam then recovered 461 km downstream at Bonneville Dam during April-July 2008. The objectives are to estimate the intensity of feeding as a percentage of the theoretical maximum consumption rate (%C_{max}), and then determine the consumption demand on the biomass of key prey taxa and the relative contribution of these prey to smolt growth during this period. The bioenergetics modeling simulations are based on empirical inputs for: the average initial and final weights measured over the simulation period, the estimated diet composition, thermal experience, and the energy density of major prey in the diet.

Simulation Results. In order to grow from the observed 15.0 g at Lower Granite Dam on 5 May to 18.2 g at Bonneville Dam on 19 May, bioenergetics model simulations indicated that yearling Chinook needed to feed at 78% of their theoretical physiological maximum consumption rate, given the diet composition and thermal regime experienced during migration. Over that period, individuals consumed an estimated 23.1 g of food, with a growth efficiency GE of 14% (GE = g growth/g food consumed x 100). Assuming 64% survival between Lower Granite and Bonneville dams (e.g., 80% survival from Lower Granite to McNary, and 80% survival from McNary to Bonneville; approximated from Figure 25 and Table 35 in FPC 2008), for every million yearling Chinook passing Lower Granite Dam, 18.5 metric tons (mt) of prey would have been consumed over the 13-d migration. This consumption demand was composed of 3.7 mt of dipterans, 5.8 mt of other insects, 4.3 mt of *Daphnia*, and 4.7 mt of amphipods. Given the population abundance index of 9 million hatchery and wild yearling Chinook at Lower Granite Dam during 2008 (FPC 2008; Tables 16-18), the total consumption demand by yearling Chinook passing Lower Granite Dam would have been 166.5 mt of prey consumed over the 13-14 d migration during mid May. This consumption demand was comprised 33.3 of mt dipterans, 52.1 of mt other insects, 38.8 mt of *Daphnia*, and 42.2 mt of amphipods.

Development and data (Table C.6.A) for model simulations described in Sidebar C.6.1 can be found at the electronic Appendix C.6 under Mainstem reservoirs as feeding habitats for yearling Chinook.

Other potentially important salmonid consumers co-occurring with yearling Chinook during May are age-0 Chinook (Lower Granite Dam population abundance index of 3 million in 2008) and steelhead (Lower Granite Dam population abundance index of 3 million in 2008). However, the importance of trophic interactions among these species and the cumulative consumption demand on common prey resources depend on the degree of spatial-temporal overlap in the reservoirs, growth rates and diet composition. Such data are currently lacking or inaccessible. Nevertheless, it is clear that the total amount of natural food required by the salmon and steelhead smolts (e.g., the biomass of steelhead smolts migrating from the Snake River is nearly 3-fold higher than the biomass of yearling Chinook; see Figure C.4.3) alone during this two week period of peak migration easily exceeds 200 mt.

Consumption demand by juvenile American shad. The potential effects of anadromous American shad on the lower Columbia River reservoir and estuary food webs are a concern. This is because of potential competition between juvenile shad and juvenile fall (ocean-type) Chinook, and also because juvenile shad potentially provide a food subsidy that could increase predator abundance. Millions of adult shad (e.g., 6 million in 2005; UW DART 2005) return to spawn in June-July, primarily in McNary and John Day Reservoirs. Planktivorous larval and juvenile shad feed in these reservoirs from July until peak emigration past Bonneville Dam in early October (Haskell et al. 2006). Bioenergetics simulations of juvenile shad during their July-September feeding period in John Day Reservoir during years of warmer (1994) and cooler (1996) reservoir temperatures show that juvenile shad grow faster and consume more food during warmer conditions than during the cooler conditions (data from Haskell et al. 2006). The shad feed primarily on *Daphnia*, copepods, and *Bosmina*. For every million juvenile shad in the reservoir, an estimated 51.9 mt of food is consumed during reservoir rearing in warm years and 25.2 mt during cool years (Sidebar C.6.2).

Although yearling Chinook salmon have migrated to sea before juvenile shad begin to feed, significant diet overlap occurs between reservoir-rearing age-0 Chinook and juvenile shad. The diet of age-0 Chinook consists of up to 50% *Daphnia* and 50% terrestrial or aquatic insects (Rondorf et al. 1990), whereas shad eat predominantly *Daphnia* and other zooplankton during July (Haskell et al. 2006).

Sidebar C.6.2. Consumption demand by juvenile American shad

Estimated consumption demand by larval and juvenile shad gives insights into potential food competition with juvenile fall Chinook salmon. Adult shad spawn primarily in McNary and John Day Reservoirs. Larval shad begin feeding during July and continue until peak migration past Bonneville Dam and into the estuary in early October. Temperature, growth, and diet data for larval-juveniles in McNary and John Day reservoirs during 1994 (warm year) and 1996 (cooler year) are used as model inputs to simulate monthly growth and consumption (data from Haskell et al. 2006). Reservoir temperatures averaged 1-3° C warmer in 1994 than in 1996 (Table C.6.B, see electronic Appendix C.6). Juvenile shad primarily ate *Daphnia* from July through mid-August, and then shifted to a greater proportion of copepods through September (Table C.6.C, see electronic Appendix C.6).

Simulation Results. Juvenile shad grew faster (6.0 g final body mass) and consumed more food (53 g) during the warmer conditions in 1994 than during cooler conditions in 1996 (1.8 g final body mass, 25.6 g total consumption; Table C.6.E, see electronic Appendix C.6). Both individual and population-level consumption rates were lowest during July and highest in September. Without accounting for mortality, for every million juvenile shad, 51.9 mt of food would have been consumed during July-September 1994 and 25.2 mt in 1996.

July is the period with the greatest potential spatial and dietary overlap with age-0 Chinook, when both species feed primarily on *Daphnia*. For every million larval-juvenile shad present, 2.4 mt of *Daphnia* would have been consumed during July 1994 and 4.0 mt during July 1996 (Table C.6.F, see electronic Appendix C.6). A more thorough evaluation of reservoir rearing capacity and potential competitive effects among wild and hatchery salmon and shad could be accomplished with additional information on juvenile shad abundance (in the reservoirs or passing dams), growth, diet, and abundance of age-0 Chinook, and temporal-spatial patterns in density, biomass and production of key zooplankton species like *Daphnia*, *Bosmina*, calanoid and cyclopoid copepods.

Input data Tables for diet (C.6.C), temperature (C.6.B), prey energy density (C.6.D), and size and growth (C.6.E) used in the model simulations of monthly consumption demand (C.6.F) for American shad in Sidebar C.6.2 can be found in electronic Appendix C.6)

Consumption demand by juvenile coho and Chinook salmon in the ocean. During the first spring and summer of ocean feeding, the combined population-level consumption by juvenile coho and Chinook on the continental shelf along the Oregon and Washington coast increases from 350 mt of fish and invertebrate prey in May to nearly 3,000 mt in September (Brodeur et al. 1992). Consumption varies considerably among areas and months, based on the relative abundance and distribution of consumers. In 1981, monthly consumption by salmon represented a small fraction (1.2–3.0%) of the estimated biomass of macrozooplankton. Salmon potentially ate a much higher fraction of the available monthly forage fish biomass; however, considerable uncertainty is associated with forage fish biomass estimates. The availability of some key prey taxa became limited under El Niño conditions in 1983, although the data on prey availability were incomplete (Brodeur et al. 1992).

Bull trout-kokanee-juvenile salmon-zooplankton in Lake Billy Chinook. A multi-trophic level bioenergetics analysis in Lake Billy Chinook on the Deschutes River indicates that kokanee are not food-limited. Consumption demand (Figure C.6.1) was ≤13% of the *Daphnia* biomass throughout the growing season when kokanee abundance was high during 1997-1998 (Beauchamp and Shepard 2008). However, predation by bull trout imposes an estimated 29-78% mortality on different year classes of kokanee. Previous analyses on the same population conclude that low abundance of kokanee both reduced growth of piscivorous bull trout and increased mortality from cannibalism by larger bull trout on smaller bull trout (Beauchamp and Van Tassell 2001). A new surface and hypolimnetic water withdrawal structure was constructed in 2009 to regulate temperatures both downstream and within the reservoir. Bioenergetics analyses will be useful for determining how the new thermal regime will affect the spatial-temporal overlap of juvenile salmonids with zooplankton and piscivorous bull trout, zooplankton production, feeding and growth by juvenile salmonids, and predation impacts by bull trout.

Quantifying the Impact of Non-native Predators, Competitors and Prey

Walleye predation on hatchery kokanee and rainbow trout in Lake Roosevelt. Acute predation by walleye on hatchery releases removes 7-9% of the stocked kokanee and rainbow trout over the first 41 days after release from the Sherman Creek Hatchery (Baldwin et al. 2003). However, because the proportions of kokanee in the walleye diet remained relatively high at the end of the 41-d study in 1999 and 31-d study period in 2000, the authors warn that longer-term predation could potentially limit kokanee recruitment. If predation rates had declined through the study period, and if the cumulative predation mortality only represented a small fraction of the kokanee hatchery releases, managers could have concluded that predation was a minor source of mortality. This conclusion might have been true for predation on rainbow trout. However, the sustained, significant rate of predation on kokanee by walleye could undermine the hatchery-based efforts to sustain a kokanee fishery. The critical uncertainty here is whether the proportion of kokanee in the diet of different sizes of walleye declines enough during subsequent months or seasons such that predation losses remain within acceptable limits. Predation rates could decline through time due to mortality, dispersal, growth or predator avoidance behavior by kokanee. Regardless of the underlying process, the primary source of uncertainty could be addressed by monitoring the diet of walleye through time.

Lake trout-kokanee-mysid trophic interactions in Flathead Lake. Bioenergetics modeling has been applied to lake and reservoir communities to determine whether salmonid populations are regulated by predation mortality. In Flathead Lake, Montana, bioenergetics modeling demonstrates that predation by lake trout was responsible for the collapse of the kokanee population in the mid-1980s and the failed attempt to re-establish kokanee through a hatchery stocking program in the early 1990s (Beauchamp et al. 2006, 2007; Sidebar C.6.3). The initial rapid expansion of the lake trout population was catalyzed by the invasion of mysid shrimp, which contribute 80–95% of the annual energy budget for juvenile through mid-sized adult lake trout (fork length < 625 mm).

Sidebar C.6.3. Impacts of Non-native Fishes in Flathead Lake, Montana

Bioenergetics simulations revealed important insights concerning the role of non-native species in the food web of Flathead Lake, Montana. The kokanee population in the lake crashed during the mid-1980s, within five years of the establishment of the invasive mysid shrimp, *Mysis relicta* (Beattie and Clancey 1991). During 1993-1997, state, tribal and federal agencies attempted to re-establish kokanee by stocking 800,000 yearling kokanee in the spring each year, but adult returns were much lower than expected.

Simulation results. A bioenergetics analysis of the predatory response to the kokanee restoration program determined that predation by non-native lake trout accounted for 85% of kokanee mortality during their first 12 months in the lake; consequently, the hatchery program was terminated soon thereafter (Beauchamp 1996, Deleray et al. 1999, Beauchamp et al. 2007). A second analysis of the Flathead Lake food web, 10–15 years after the kokanee crashed and the mysid population stabilized (1998-2001), shows that mysids contribute most of the seasonal and annual energy budget for juvenile through adult lake trout, ranging in size up to 625 mm (Figure C.6.2; Beauchamp et al. 2006). These analyses suggest that the mysid invasion supported rapid expansion of the lake trout population, and that increased predation by lake trout was responsible for the extirpation of kokanee, rather than exploitative competition from mysids, as originally hypothesized (Spencer et al. 1991). When examining just the fish-fraction of consumption by lake trout (Figure C.6.2), it is apparent that lake trout become piscivorous at about 200 mm in size. An important forage fish, native pygmy whitefish, are mostly consumed by smaller lake trout during spring-fall, but non-native lake whitefish are eaten extensively by larger lake trout (> 375 mm). There is significant cannibalism by most sizes of lake trout, but it is heaviest in the intermediate size classes (501-625 mm). Non-native yellow perch are important prey for medium and large lake trout during fall and winter, while lake trout also impose significant predation pressure on the depressed populations of native westslope cutthroat trout and bull trout.

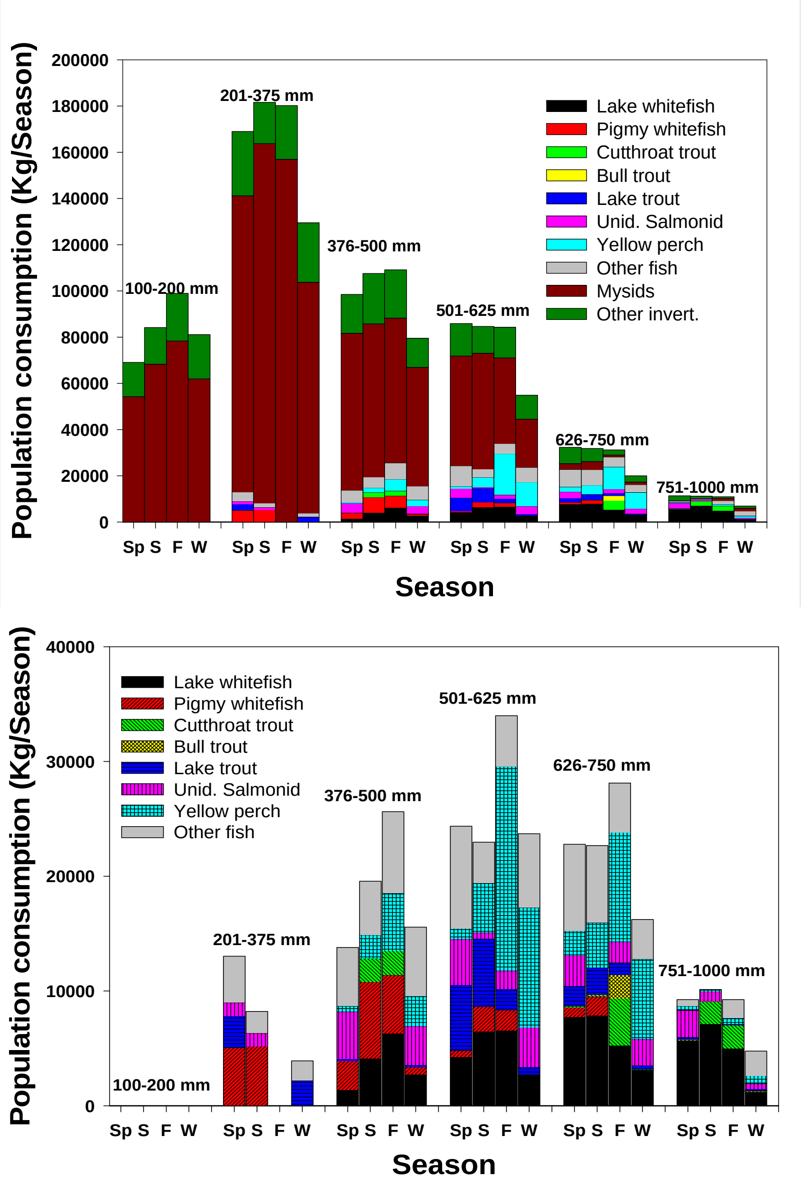


Figure C.6.2. Seasonal, population-level consumption by different size classes of lake trout in Flathead Lake during 1998-2001, > 10 years after the kokanee crash: (A) of all prey, and (B) just the fish fraction of the diet (from Beauchamp et al. 2006).

Diagnosing Factors Affecting Growth

Important insights regarding growth potential – as affected by food demands – can be gained by quantifying basic physiological relationships for body mass, temperature, feeding rate and energetic quality of food. These factors can be placed within the context of environmental variability and the ontogeny of consumers. In nature, fish rarely feed at their maximum physiological rate (C_{max}), because food supply or access to food is often limited. As feeding rates decline, growth rates also decline. There are important consequences to reduced feeding. One is a shift in thermal responses such that both the optimal temperature for growth and thermal tolerance (i.e., the maximum temperature beyond which weight loss occurs) shift to cooler temperatures (Figure C.6.3). Optimal growth temperatures and thermal tolerance also shift to cooler temperatures as the size of consumer increases. Growth rates and thermal tolerance can improve dramatically if a significant portion of the diet shifts to higher-energy prey, such as terrestrial or adult aquatic insects, higher-energy benthic invertebrates (e.g., gammarid amphipods, trichopterans), forage fish, or squid (Figure C.6.3). Therefore, seasonal or ontogenetic diet or habitat shifts and high-energy external food subsidies (e.g., salmon eggs, terrestrial insects) can be important for promoting growth, or at least for maintaining body mass and condition. As historical environmental and habitat conditions change, species adopt different movements, distributions and feeding strategies in order to adapt to changing growth conditions among habitats and through time.

Conclusions and Recommendations for Restoration

The preceding examples of food demands as estimated through bioenergetics modeling demonstrate the need for quantitatively evaluating how trophic interactions and thermal regimes affect growth and survival of focal species at specific times and locations. These few examples from the literature, plus some opportunistic applications of the model to existing data, represent a patchwork of important questions that need examination in restoration efforts. Ideally, concurrent simulations should be conducted on the major planktivores and piscivores inhabiting specific habitats or combination of habitats used during rearing and migration by various life stages of fish. Collective monthly consumption rates, when compared to the temporal biomass or production dynamics of key prey, could inform managers if consumption demand exceeds carrying capacity, or if predation regulates prey population dynamics. In the example of consumption by migrating yearling Chinook (Sidebar C.6.1), concurrent consumption demand by age-0 Chinook (Lower Granite Dam population abundance index of 3 million in 2008) and steelhead (Lower Granite Dam population abundance index of 3 million in 2008) need to be simulated, and linked to prey consumption by American shad as different stocks migrate or rear in the lower reservoirs and estuary. Some of the critical data needed for these analyses are currently lacking or inaccessible. However, food web studies that are designed at the outset to sample growth, thermal experience, and diet of all major species concurrently benefit tremendously from economies of scale.

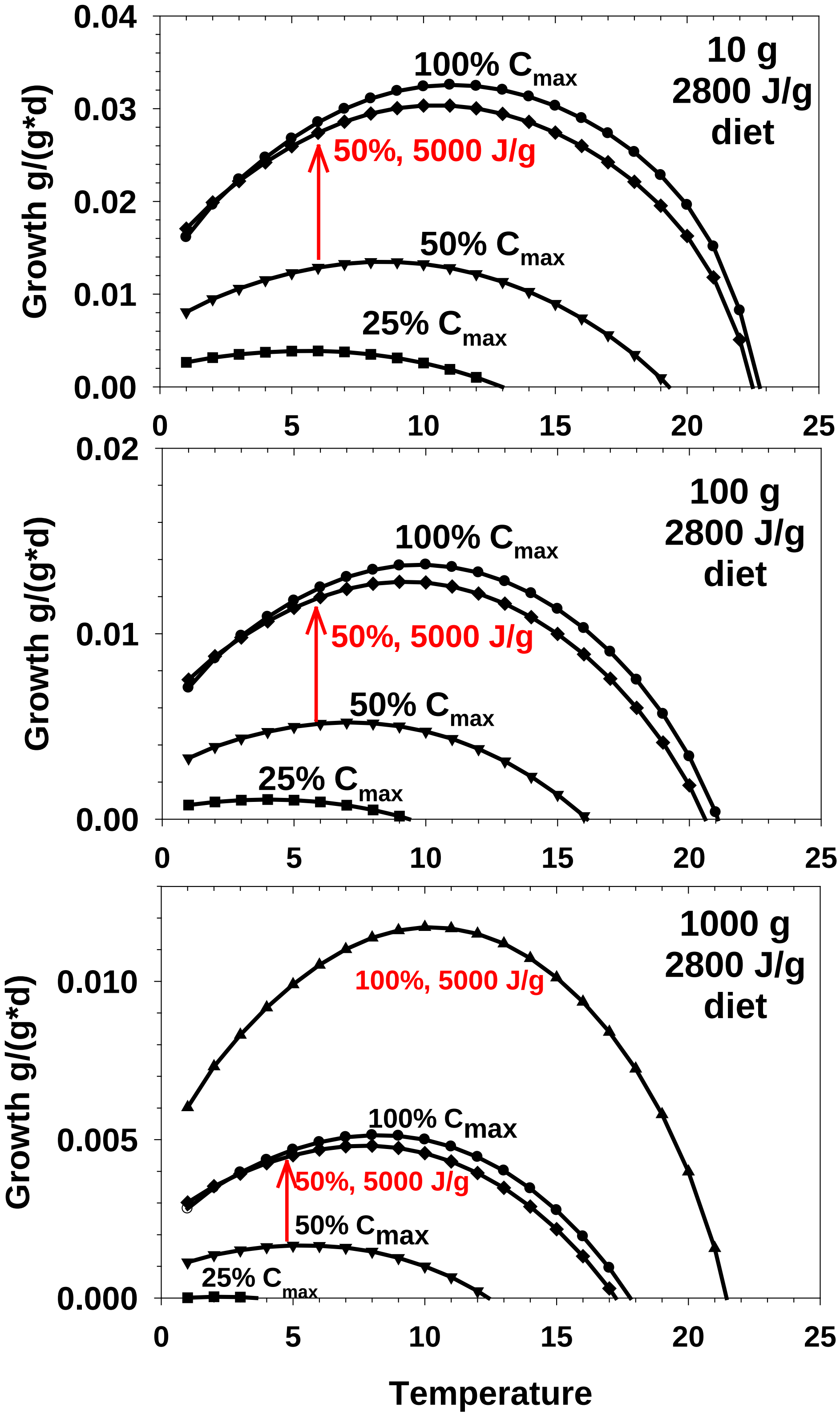
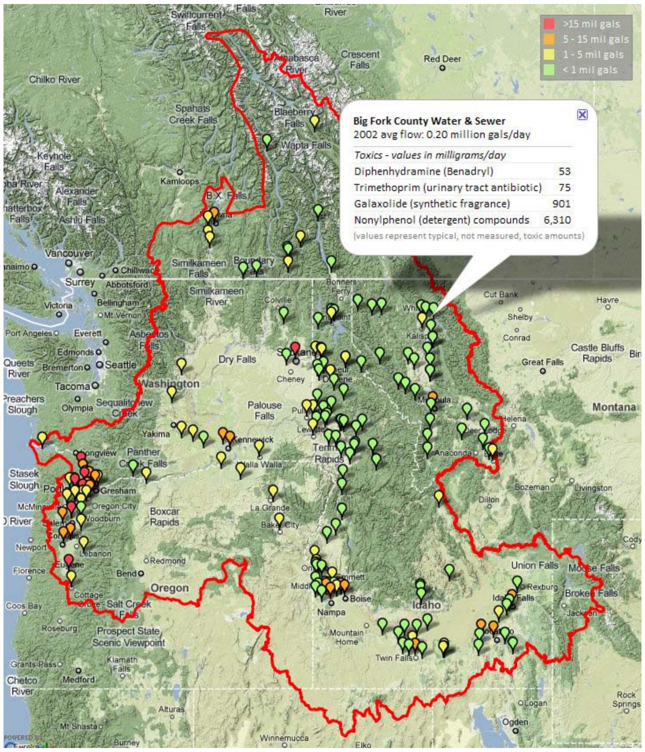


Figure C.6.3. Temperature-dependent daily growth potential for 10-g, 100-g, and 1,000-g sockeye salmon Feeding at 100%, 50% or 25% C_{max} on a composite invertebrate diet averaging 2,800 J/g (composed of zooplankton or benthic invertebrates), or on a higher energy diet averaging 5,000 J/g (composed of adult or terrestrial insects, high-energy invertebrates, fish, or squid). From Beauchamp (2009).

C.7. Toxics and Biomagnification



Big Fork County Water & Sewer
2002 avg flow: 0.20 million gals/day

Toxics - values in milligrams/day	
Diphenhydramine (Benadryl)	53
Trimethoprim (urinary tract antibiotic)	75
Galaxolide (synthetic fragrance)	901
Nonylphenol (detergent) compounds	6,310

(values represent typical, not measured, toxic amounts)

Wastewater treatment plants. See interactive map.

Toxic Pollutants and Food Webs

Stable and resilient food webs, and the persistence of native species over time, are key components of a healthy Columbia River ecosystem. In a sustainable system, food webs are the foundation for many commercial, recreational, human health and aesthetic ecosystem services. The health of species and food webs depends upon habitat conditions, water quality and quantity, and appropriate management (including harvest, prevention and control of disease and control of deleterious exotic species; Puget Sound Partnership 2010). Within this framework toxic pollutants are a "wild card" that can adversely affect water quality as well as significantly alter various components of the ecosystem and its food webs.

Fish, wildlife and human populations in the Columbia River Basin are exposed to an ever-growing variety of pollutants as of result of increasing urbanization, industrialization and agricultural development. It is well documented that the lower Columbia River and its tributaries contain concentrations of toxic pollutants that are harmful to fish and wildlife. Contaminants of concern in the late 1980s and early 1990s included dioxins and furans, heavy metals, polychlorinated biphenyls (PCBs) and organochlorine pesticides such as DDT (Tetra Tech 1996). Today there is continuing and growing concern about persistent pollutants coming from a wide variety of sources, especially those that linger in the environment and have a documented effect on human health, fish and wildlife and the aquatic habitat. There is also concern about emerging contaminants, a group of chemicals where limited information is available. Communities use and dispose of literally thousands of chemicals and many end up in aquatic systems where they persist, affect food webs and, in some cases, accumulate in consumers near the top of the food web.

Despite the massive use of chemicals in the Basin, little attention has been paid to their effects on fish production and survival. This is despite pollutants being a recognized problem in the Columbia River and its tributaries for many years, especially for species positioned higher in the food web (Henny et al. 1981, Buck et al. 2005, Grove 2006, Hinck et al. 2006, Johnson et al. 2007, Henny et al. 2008, Henny et al. 2009a). When fish-eating species experience contaminant-related population declines or reproductive effects, it is obvious that the source of contaminants is the fish they have eaten, which often leads to further investigations of the fish themselves. In the Basin, top fish-eating predators include river otter, mink, bald eagle and osprey, with the latter three nearly eliminated from the lower Basin by the mid-1970s. Bald eagle and osprey populations are recovering, but only after certain persistent pollutants were banned and concentrations in the food web decreased, especially DDT and its metabolites. Unfortunately, contaminant studies with invertebrate species, many of which are the first food web components to accumulate contaminants, are extremely rare in the Columbia River Basin.

This Chapter examines contaminant concentrations at multiple levels of the Columbia River food web (water, sediment, invertebrates, resident fish, salmonids, and fish-eating birds and mammals), contaminant trends over time, possible direct adverse toxic effects on various species, and possible indirect adverse effects on various species (e.g., food shortages).

Several terms are used that require definition: *bioaccumulation* refers to uptake and retention of a chemical from food, water and sediments, as opposed to *bioconcentration,* which considers uptake from water only. *Biomagnification* refers to an increase in the concentration of a chemical at higher trophic levels. *Legacy* refers to a pollutant that remains at detectable levels in sediment and tissue samples even though its use has been banned or restricted for several years.

Background and Approach

Dozens of contaminants have been detected in water, sediments, and non-salmonid fish in the Basin. These include heavy metals, dioxins and furans, DDT and its metabolites and other organochlorine pesticides, as well as industrial chemicals (e.g., PCBs and polycyclic aromatic hydrocarbons; PAHs) (Fuhrer and Rinella 1983, Tetra Tech 1996, Brown et al. 1998, Foster et al. 2001a,b; Sethajintanin et al. 2004, Hinck et al. 2006). The patterns of contaminant concentrations are complex. For example, carp, bass and largescale suckers have higher pesticide concentrations in the lower Basin and higher metal concentrations in the upper Basin (Hinck et al. 2006). These specific patterns reflect land uses. Other patterns may be site specific. For example, the U.S. Department of Energy Hanford Site near Richland, Washington, produced radioactive materials until the early 1990s; high concentrations of PCBs and other organic chemicals have been measured for several decades in fish collected downstream from the facility (USEPA 2002).

As one might expect, contaminant influences on the food web occur at a several levels of biological organization. Usually mixtures of contaminants are present. Effects are strongly determined by the type of contaminant and eventually by interactions of the mixtures.

Research on contaminant mixtures indicates a wide array of possible interactions that fall into four categories: independent, additive, antagonistic and synergistic. The type of response depends on the physiology and developmental stage of the organism, and is influenced by environmental factors such as temperature, salinity, oxygen, and pH (Lawrence and Elliott 2003). Even under natural conditions, chemicals affect vital organs, but even more concerning are the effects on lipid metabolism, growth rate, genetic diversity, reproduction and viability of offspring. For example, juvenile growth is a critical determinant of freshwater and marine survival for Chinook (Higgs et al. 1995), and individual salmon size has been linked to age-specific survival rates, age at reproductive maturity, fecundity and spawning success (Healey 1991, Beamish and Mahnken 2001, Zabel and Achord 2004). Reductions in somatic growth rate of salmon fry and smolts are believed to result in increased size-dependent mortality (West and Larkin 1987, Healey 1982), primarily because they must reach a critical or threshold size to successfully transition from freshwater to saltwater (smoltification; Beamish and Mahnken 2001). Contaminants may also reduce survival through effects on swimming behavior, predator avoidance behavior and foraging behavior, as discussed below. A primary effect of reduction in somatic growth caused by contaminant exposure may be an increase in first-year mortality (Spromberg and Johnson 2008). Unfortunately, information on outmigrant salmonid exposure to contaminants in the Columbia River is greatly limited (Johnson et al. 2007).

The State of Oregon recently published a list of 118 priority toxic pollutants that persist in the environment or accumulate in animals (Mullane et al. 2009). All pollutants on the list have the potential to cause harm to human health or aquatic life and are divided into two categories. One category is *Persistent Pollutants* (69 chemicals), which include PAHs, halogenated flame retardants, pesticides and herbicides, pharmaceuticals and personal care products, perfluorinated surfactants, metals and industrial contaminants. The second category is *Legacy Persistent Pollutants* (49 chemicals), which include pesticides (especially the organochlorines) and herbicides, polychlorinated biphenyls (PCBs), polychlorinated naphthalenes, dioxins and furans. Contaminants reported in Columbia River fish are also summarized for 1996-98 by USEPA (2002).

In this review we use the two general categories (**Legacy and Current Use**) established by Mullane et al. (2009), with a few additional subcategories for chemicals requiring special consideration:

***Legacy pesticides and PCBs*.** These include DDT, dieldrin, chlordane, and heptachlor. Their use has been banned in the United States since the 1970s/1980s due to toxicity; however, they still persist in the Basin. PCBs, used in transformers, paints, and similar products, are included with Legacy Pesticides because they are often analyzed in the same samples.

***Legacy industrial contaminants*.** These include polychlorinated naphthalenes used in insulation of electrical wires, pentachlorophenol used as a wood preservative, rubber and plastic additives; dioxins and furans from chlorine bleaching process for paper; and tributyltin used as an antifouling agent for ships and boats.

Pesticides and herbicides in current use. These include organophosphates such as diazinon, malathion and carbamates such as carbaryl and carbofuran. These are commonly used in agriculture, lawn care, gardening and horticulture, and typically enter waterways through irrigation drainage and storm water runoff.

Industrial contaminants in current use and emerging contaminants. These include polycyclic aromatic hydrocarbons (PAHs) from oil spills and incomplete burning of oil, wood, garbage or coal; perfluorinated surfactants; octochlorostyrene, brominated flame retardants such as polybrominated diphenyl ethers (PBDEs) used in plastic components of computers, televisions, circuit boards, clothing, rugs, and upholstery; and pharmaceuticals and personal care products which typically enter waterways through treated and untreated wastewater. Some mimic hormones and are considered endocrine disruptors by interfering with reproduction, growth and development.

Metals. These include mercury, lead, copper, arsenic and chromium, and are unique among pollutants that cause adverse effects in that they occur naturally and, in many instances, are ubiquitous in the environment. Furthermore, many are biologically essential, but become toxic with increasing dosage. Metals can be introduced into the environment through the atmosphere, soil, ground water or surface water as result of human activities.

Legacy Pesticides and PCBs

Fish-eating predators and resident fish. More information is available for legacy pesticides than any other category of contaminant. Legacy pesticides and PCBs have been evaluated in fish nationwide, including the Willamette and Columbia Rivers, via the National Pesticide Monitoring Program (e.g., Schmitt et al. 1981, 1985, 1990). One of the long-term sampling sites along the Willamette River is at river kilometer (rkm) 42 (Station 45) near Oregon City, and another is along the Columbia River at Cascade Locks (Station 46). Resident largescale sucker composites (whole bodies) at the Willamette River site contained decreasing geometric means of DDE from 1969-70 (380 parts per billion [(ppb]) wet weight [ww]) to 1980 (177 ppb) (Figure C.7.1). Decreases at the same site were also shown for PCBs from 1969-70 (2,336 ppb) to 1980 (300 ppb).

Additional fish residue data are available for comparing largescale sucker and northern pikeminnow from the upper Willamette River (upstream of Newberg) in 1993 and 2001 (Table C.7.1). Legacy pesticides and PCBs evaluated in both species showed continued decreases over time (often in the 50% range). These decreases were also reflected in osprey egg concentrations during the same period (Table C.7.1). Based largely upon sublethal endpoints (growth, reproduction, development, behavior) for DDT and its metabolites, provisional protective whole-body concentrations were 640 ppb ww in juvenile and adult fish, and 700 ppb ww for early life-stage fish (Beckvar et al. 2005). With decreases in Legacy pesticide and PCB concentrations in fish from the Columbia River system over time, it is important to consider the year in which field studies were conducted in evaluating possible adverse effects of these contaminants.

There are considerable histopathological changes in liver, spleen and kidney of fish from long term effects of exposure to PCBs in nature as well as under laboratory conditions (Svobodova et al. 1994). The reported 1.5-fold higher weight loss in the PCB-loaded eels during endurance swimming (to simulate migration) may be the result of PCB effects on the intermediary metabolism (Van den Thillart et al. 2004).

Besides direct effects on the fish, the largescale sucker is an important prey species of osprey, accounting for 84 - 93% (biomass basis) of the osprey diet along the Willamette and lower Columbia rivers (Johnson et al. 2008). The predaceous northern pikeminnow, due to its higher position in the food web, consistently contains higher DDE concentrations than the largescale sucker (Table C.7.1), but accounts for less than 5% of the osprey's diet. Osprey along the lower Columbia and Willamette rivers were formerly common, but by 1976 only 13 pairs were estimated along the Willamette River and perhaps 10 pairs along the lower Columbia River (Henny et al. 1978). Both populations showed DDE-related eggshell thinning (compared to pre-DDT era) and reduced productivity in earlier years, with lowered reproduction continuing for individual pairs into the late 1990s (Henny et al. 2008, 2009a). This continuation of DDE-related reproductive problems along the Columbia system into the late 1990s was unique in North

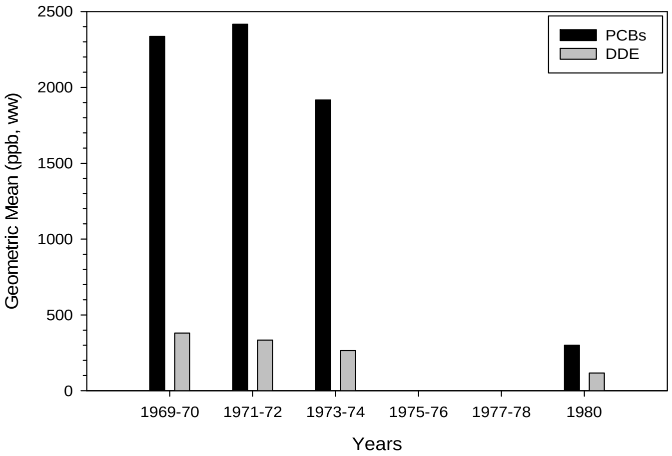


Figure C.7.1. Largescale sucker whole body DDE and PCB residue concentrations (ppb, wet weight basis) at Station 45 near Oregon City on the Willamette River, 1969-1980 (from Schmitt et al. 1981, 1985, 1990).

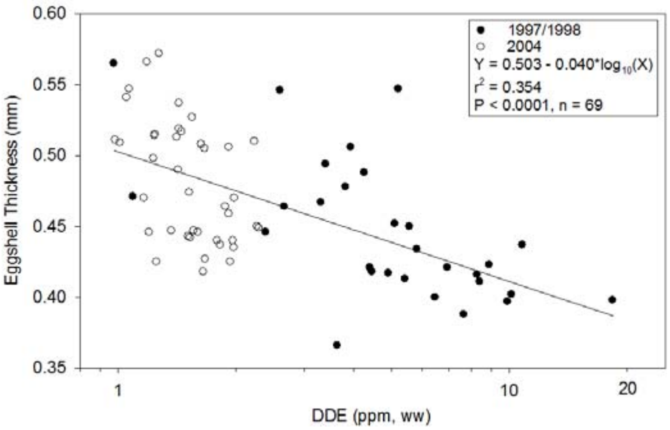


Figure C.7.2. Relationship between DDE concentrations (ppm, wet weight basis) and eggshell thickness (mm) of osprey eggs from the lower Columbia River, 1997/1998 and 2004 (adapted from Henny et al. 2008)

America, and probably occurred because of the large agricultural area, including orchards, drained by the river (Henny et al. 2010). Improvement was evident by 2004 (Figure C.7.2).

By 2001 and 2006, no osprey eggs sampled on the lower Columbia and upper Willamette rivers, respectively, contained DDE concentrations above the critical reproductive effect level (4.2 parts per million [ppm] ww; see Wiemeyer et al. 1988, Henny et al. 2008, 2009a, 2010). In addition, no other Legacy Pesticides or PCBs were found at concentrations in eggs that would reduce reproductive performance. Osprey populations along the lower Columbia River by 2004 and Willamette River by 2008 had increased to 225 and 275 nesting pairs, respectively. It was concluded that DDE was the most serious contaminant for osprey along the Columbia and Willamette rivers, being responsible for a near total population collapse, with a similar DDE-related collapse for bald eagles (Buck et al. 2005).

The mechanism for the population collapse was substantial DDE biomagnification up the food web from tainted fish (weighted by biomass intake) to osprey eggs, resulting in reduced reproductive success. Analyses of osprey eggs revealed a 79 to 87-fold fish to egg increase (ww basis) (Henny et al. 2009a). Other legacy pesticides and total PCBs also biomagnified into osprey eggs, but at much lower rates (e.g., hexachlorobenzene 1.2 -1.5-fold; total chlordanes 2.8-4.3-fold; dieldrin 3.2-6.7-fold; heptachlor epoxide 25-fold; total PCBs 8.4-11-fold).

Table C.7.1. Geometric means for mercury (ppm, dry weight basis), organochlorine insecticides and metabolites and PCBs (ppb, wet weight basis), and dioxins (ppt, wet weight basis) in whole body composite samples of largescale suckers and northern pikeminnows, and in osprey eggs from the Willamette River (Upper River), 1993 vs. 2001, with additional information for osprey eggs in 2006 (adapted from Henny et al. 2009a).

	Largescale Suckers			**Northern Pikeminnows**			**Osprey eggs**		
Contaminant	**1993**	**2001**	**P-value**	**1993**	**2001**	**P-value**	**1993**	**2001**	**2006**
N	10	7		9	7		10	11	10
Mercury	0.29	0.42	0.16	1.12	1.91	0.005	NA	0.33	NA
HCB	3.39	1.33	0.06	2.24	0.96	0.03	3.77A	1.97A	0.70B
DDE	22.4	14.8	0.33	72.7	38.6	0.08	2,347A	1,353A	210B
DDD	4.42	1.42	0.007	4.34	3.9	0.78	98.5A	29.4A	5.43B
DDT	0.56	0.92	0.32	0.22	ND	- -	25.3A	2.08B	1.40B
Mirex	NC(3)	ND	- -	0.35	ND	- -	2.81A	NC(3)	0.87B
Total Chlordanes	3.2	2.67	0.51	10.7	6.78	0.008	16.7A	8.53AB	3.66B
Heptachlor Epoxide	0.16	NC(2)	- -	NC(2)	0.06	- -	3.48A	1.44B	1.21B
Dieldrin	0.55	0.53	0.96	1.15	0.36	0.056	3.96A	1.66A	1.68A
Sum PCBs	57.5	26.7	0.01	103	51.1	0.003	688A	245B	182B
2378 TCDD	NC(2)	NC(1)	- -	0.68	ND	- -	2.28A	0.23B	NA
12378 P_5CDD	ND	ND	- -	ND	ND	- -	6.78	NC(5)	NA
H_6CDD Total	0.47	NC(3)	- -	0.98	NC(1)	- -	63.7A	8.59B	NA
H_7 CDD Total	2.91	NC(3)	- -	0.95	0.23	0.04	287A	41.6B	NA
OCDD	8.47	0.52	<0.0001	2.63	NC(2)	- -	1,299A	252B	NA

NC = Means not calculated when < 50% of samples with detections (number samples detectable concentrations); ND = Not detected; NA = Not analyzed; osprey data for different years that share a letter are not significantly different.

Similar to osprey, the diet of river otter consists primarily of fish (Toweill 1974), and this is the main way by which they accumulate toxics. Major fish families represented in the diet of otters are Cottidae (31%), Salmonidae (24%) and Cyprinidae (24%). Among seven collection localities in the Pacific Northwest in 1994-99, DDE was highest in the livers of adult river otters from the lower Columbia River (Table C.7.2). As with osprey eggs, DDE concentrations in river otter livers from the lower Columbia River in earlier years (1978-79) were much higher (1,650 ppb, ww) (Henny et al. 1981) than in 1994-99 (143 ppb, ww). Total PCBs in livers of adult river otters in 1994-99 were similar for the lower Columbia River (564 ppb, ww) and Puget Sound (585 ppb), with other localities considerable lower. PCBs in livers of adult river otters in 1978-79 on the lower Columbia River contained 6,990 ppb (Henny et al. 1981) compared to 564 ppb in 1994-99. Significant inverse relationships were found between hepatic contaminant concentrations (mainly *ortho*-substituted PCBs and DDE) and juvenile male testes mass, prostate mass and baculum length and mass (Grove 2006).

The same concentration of a contaminant in different species does not necessarily yield the same response because sensitivity among species varies tremendously. Although information on mink from the lower Columbia River is limited to animals obtained in 1978-79, they do provide an interesting example of differential sensitivity when compared with otter (Henny et al. 1981). PCB residues in mink, which have a different diet, were lower in 1978-79 than in river otters. However, laboratory studies indicated that mink are extremely sensitive to PCBs (Platonow and Karstad 1973, Aulerich and Ringer 1977). The PCB problem in mink was first recognized in the late 1960s when coho, taken from Lake Michigan during the spawning run, were fed to ranch mink and caused a precipitous decrease in mink productivity. PCB residues in two-thirds of lower Columbia River mink livers examined were as high as those reported in livers of experimental female mink that experienced total reproductive failure after eating a PCB-contaminated diet of 640 ppb for 160 days. It is obvious (see Willamette River sucker residue data in Figure C.7.1) that PCB concentrations at this level were common in fish during the 1960s and 1970s. Excellent mink habitat (as indicated by the Habitat Suitability Index model) existed in the lower Columbia River in 1994-95, although few mink were present (Henny et al. 1996). Therefore, we believe that fish-eating avian and mammalian predators experienced severe adverse effects when concentrations of Legacy Pesticides and PCBs were much higher in past decades.

***Sediment, invertebrates and juvenile salmon*.** What do we know about legacy pesticides in sediments and in the lower trophic levels of the food web? In sediment samples taken along the lower Columbia River in 1991, total PCBs were not detected and the legacy pesticides DDE and DDD were detected in only a few samples (Buck 2004). Seven of the eight collection sites were below Bonneville Dam, with one site at Umatilla. Similarly, DDE and PCBs were seldom detected from depositional areas in 1991 (Tetra Tech 1993) and backwater areas in 1993 (Tetra Tech 1994). One of the more significant challenges for assessing contaminants associated with sediment, in addition to the high proportion of negative samples (non-detections), is the high level of uncertainty about bioavailability.

Sampling of Asiatic clam *Corbicula* tissues is a reliable indicator of contaminants that may be bioavailable and bioaccumulate in food webs, such as Total PCBs, Total PBDEs and Total PAHs (Sherman et al. 2009). While concentrations cannot be compared directly, the responses can be used to indicate increased relative exposure in specific regions of the river. Spatial trends of PCBs in *Corbicula* and juvenile salmon gut contents were similar although higher levels of PAHs and PBDEs in juvenile salmon gut contents appear to have a downstream lag when compared to the highest levels found in *Corbicula*. This may be due primarily to the downstream migratory behavior of salmon smolts. Water column patterns did not show spatial trends, but appeared uniform over the sampling area in comparison to *Corbicula* and salmon gut content data. Unfortunately, *Corbicula* cannot be used as a surrogate for migrating salmon; doing so would overestimate contaminant exposure (Sherman et al. 2009).

Table C.7.2. Geometric means for mercury (ppm, dry weight basis), organochlorine insecticides and metabolites and PCBs (ppb, wet weight basis), and dioxins (ppt, wet weight basis) in livers of adult river otter males collected in Oregon and Washington, 1994-99.

LCR = Lower Columbia River, CO = Coastal Oregon, OP = Olympic Peninsula, PS = Puget Sound, SW = Southwestern Washington, WB = Willamette River Basin, and WW = Western Washington (adapted from Grove and Henny 2008).

	Location						
Contaminant	**LCR**	**CO**	**OP**	**PS**	**SW**	**WB**	**WW**
N	9	17	18	12	16	17	5
Mercury	**3.46 B**	**9.23 A**	**12.6 A**	**7.89 AB**	**10.0 A**	**9.26 A**	**13.8 A**
HCB	6.27 A	5.39 A	8.59 A	5.17 A	6.61 A	8.00 A	7.24 A
DDE	**143 A**	**16.0 B**	**31.2 AB**	**20.2 B**	**18.8 B**	**85.9 AB**	**78.0 AB**
DDD	**10.3 A**	**0.46 B**	**1.67 AB**	**1.31 AB**	**0.93 AB**	**7.38 A**	**5.95 AB**
DDT	0.07 A	NC (4)	0.09 A	NC (3)	NC (7)	NC (6)	0.15 A
Mirex	**1.23 A**	**0.12 BC**	**0.32 ABC**	**0.06 C**	**0.17 ABC**	NC (8)	**0.67 AB**
Total Chlordanes	**23.5 AB**	**7.75 AB**	**11.2 AB**	**14.2 AB**	**7.36 B**	**25.1 A**	**20.8 AB**
Heptachlor Epoxide	**1.30 AB**	**0.32 C**	**0.56 ABC**	**1.22 AB**	**0.46 BC**	**1.82 A**	**1.23 AB**
Dieldrin	**6.82 AB**	**1.47 C**	**1.96 BC**	**4.58 ABC**	**1.79 BC**	**13.9 A**	**6.28 AB**
Sum PCBs	**564 A**	**96.6 B**	**90.4 B**	**585 A**	**78.9 B**	**219 AB**	**322 A**
2,3,7,8-TCDD	0.83	NC(7)	NC(2)	NC(4)	NC(4)	NC(6)	NC(2)
Total TCDD	0.90 A	0.21 A	NC(7)	0.64 A	0.29 A	0.31 A	0.49 A
Total PCDD	0.23	NC(8)	NC(1)	ND	ND	NC(4)	NC(1)
Total H_6CDD	**12.9 A**	**1.05 AB**	**0.19 B**	**11.1 A**	**0.28 B**	**4.41 AB**	**1.42 AB**
TotalH_7CDD	**59.8 A**	**10.0 AB**	**0.67 C**	**41.4 A**	**2.16 BC**	**30.4 A**	**11.1 AB**
OCDD	**112 AB**	**13.5 ABC**	**3.38 C**	**138 A**	**13.3 BC**	**54.7 AB**	**20.8 ABC**

NC = Means not calculated when <50% of samples with detections (number of samples with detectable concentrations). ND = not detected. Values in row sharing same letter, not significantly different. Rows in bold indicate significant differences.

Outmigrating fall Chinook are exposed to several persistent pollutants (PAHs, PCBs, DDTs and other legacy pesticides) in the lower Columbia River. There is potential for adverse effects on the salmon themselves as well as on the estuarine food web (Johnson et al. 2007). Contaminants measured in whole bodies and stomach contents of subyearling and yearling salmon show average concentrations of PCBs ranging from 1,300 to 14,000 ppb (lipid weight [lw]; data not presented on wet weight basis). In some cases the concentrations exceed the threshold (2,400 ppb; lw) for adverse health effects in juvenile salmonids (Meador et al. 2002). Average DDT concentrations range from 1,800 to 27,000 ppb (lw).

In agreement with the geographic pattern for osprey eggs and river otter livers, DDT and PCB levels in juvenile salmon from the lower Columbia River were among the highest measured from Pacific Northwest estuaries. DDT and PCB concentrations in salmon whole bodies show no spatial gradient from the Willamette/Columbia river confluence to the mouth of the Columbia, but tend to be higher in larger and older fish. This suggests a correlation with residence time. PCBs, DDTs and PAHs are all found in salmon stomach contents, indicating that prey are a source of exposure, with both PCBs and DDTs generally higher at the Willamette/Columbia confluence than at sites further downstream. However, contaminant body burdens are poorly correlated with concentrations previously measured in local sediments, suggesting that pelagic as well as benthic sources are important in determining exposure. PCBs and DDTs are generally lower in salmon bodies than in stomach contents, with average ratios of 0.31 and 0.64 (Johnson et al. 2007). This is probably reflective of relatively short residence times of outmigrant salmon (i.e., there is inadequate time for the body to equilibrate) in the lower Columbia River and estuary (Bottom et al. 2005). Other studies also suggest limited uptake of contaminants by outmigrant juvenile salmon in comparison with resident fish species (see Johnson et al. 2007). Understanding contaminant bioaccumulation or biomagnification, and especially effects, when the fish is migrating (a moving target) is a difficult research challenge. Furthermore, limited information is available regarding contaminant concentrations at lower trophic levels.

Legacy Industrial Contaminants

The most dramatic decreases over time of all legacy contaminants monitored, often exceeding 80%, are for dioxins and furans (Table C.7.1). The decreases result from changes to the bleaching process at pulp mills in the early 1990s. For example, at the Castlegar pulp mill on the Columbia River in British Columbia, no significant temporal change in dioxins or furans in osprey eggs was reported downstream between 1991 and 1994, despite changes in the bleaching technology; however, by 1997 concentrations decreased significantly from previous years (Elliott et al. 1998). Dioxins and furans also decreased in osprey eggs from the Columbia River in the United States from 1997-98 to 2004 (Henny et al. 2008); however, concentrations were consistently higher at two upper reaches (Umatilla to Bonneville Dam and Bonneville Dam to Sandy River) compared to two lower reaches (Sandy River to St. Helens, Oregon and St. Helens to rkm 47). In this case, biomagnification factors (fish to osprey eggs) varied among congeners (similar chemical forms in the same chemical group), ranging from 10 to 174-fold (ww basis) for dioxins and from 0.42 to 15-fold (ww basis) for furans. Additionally, pentachlorophenol (PCP) is correlated with hepta- and octa-dioxins in osprey eggs from the Fraser River in Canada, which is consistent with PCP (wood preservative) sources (Elliott et al. 1998).

It is noteworthy that studies in the late 1980s indicated that wild and hatchery coho smolts emigrating through the lower Chehalis River, which received effluent from two pulp mills and two wastewater treatment plants, consistently survived at lower rates than coho originating from other coastal watersheds (Schroder and Fresh 1992). Coho juveniles from the Chehalis River and estuary were compared with fish collected from the Humptulips River and North Bay, where survival was considered normal. Mixed-function oxidase tests revealed that EROD activities (liver enzymes involved in the metabolism of toxicants and other foreign compounds) increased in fish exposed to the effluents in the Chehalis estuary. Data from Grays Harbor, at the mouth of the Chehalis, showed elevated levels of dioxins and furans in *Corophium*, an epibenthic amphipod that feeds on particulate matter and is itself an important salmon food. It was concluded that degraded water quality and high parasite (*Nanophyetus salmoncola*) loading rates worked in concert to cause exceptionally high mortalities in Chehalis River coho (Schroder and Fresh 1992). Modification to pulp mill procedures took place soon after the study was completed, but apparently salmon mortality rates from later years have not been evaluated or reported.

Another common legacy industrial contaminant of importance is tributyltin (TBT). TBT was used for about 30 years as an antifouling agent in marine paint formulations to prevent accumulation of barnacles and slime on boat hulls. Based upon numerous laboratory studies documenting sublethal and lethal effects of TBT on a variety of marine organisms, many countries (including the United States) passed legislation limiting (but not totally banning) the use of TBT-based antifouling paints in the late 1980s. Growth and reproduction in the most sensitive species – notably stenoglossan gastropods and oysters – can be impaired by TBT at water concentrations of only a few parts per trillion (ppt, ng/L; Bryan et al. 1986). Total butyltins (mono-, di- and tributyltin) were present in bivalve mollusks collected from the Columbia River in 1989-90 (94 ppb ww; Uhler et al. 1993); but mollusk concentrations cannot be directly compared to water concentrations.

Butyltin compounds were also found consistently in the livers of river otter from Oregon and Washington in 1996-97, with otters inhabiting areas near boating activity showing elevated concentrations (Kannon et al. 1999). Otters from the upper Willamette River 100-230 km upstream of navigable waters were found to have been exposed to mono- and dibutyltin, possibly derived from the leaching of polyvinylchloride (PVC) pipes, where these compounds are used as stabilizers (Kannon et al. 1999). More recent evaluations have not been made.

Pesticides and Herbicides in Current Use

Agricultural pesticide use intensity (averaged 1999-2004 data for 246 compounds, in kg/km^2 per year) in various parts of the Basin is shown in Figure C.7.3 and the amounts used are summarized in Appendix C. The more persistent organochlorine pesticides widely used in previous years were largely replaced in the 1970s by less persistent, but often more toxic organophosphates (OP), carbamates (CB) and pyrethroids. The OPs and CBs are anticholinesterase inhibitors which affect the central nervous system and have been shown to alter salmon swimming behavior (Sandahl et al. 2005, Brewer et al. 2001), predator avoidance behavior (Scholz et al. 2000), and foraging behavior (Morgan and Kiceniuk 1990). The net effect on salmon appears to be increased mortality and probably reduced somatic growth. Because these chemicals are relatively short-lived in the environment (compared to organochlorines), the design and duration of field studies may be critical for quantifying short-term and long-term effects on food webs. Pyrethroid insecticides have been used more in recent years, with concentrations acutely toxic to some benthic invertebrates reported in sediments of agricultural water bodies (Weston et al. 2008) and urban stream sediments in several states (Holmes et al. 2008, Hintzen et al. 2009, Ding et al. 2010). A recent comprehensive review of currently used pesticides, aquatic food webs and Pacific salmon highlights information gaps and future research approaches and needs (see Macneale et al. 2010).

Herbicides and fungicides have been seldom investigated in the Basin. Fortunately, the eggs of fish-eating osprey have been analyzed from Puget Sound for 12 chlorophenoxy herbicides, the metabolite of pyrethroids, and the fungicide chlorothalonil (Chu et al. 2007). Only the herbicide dimethyl tetrachloroterephthalate (DCPA or dacthal) could be quantified (2 to 10.3 ppt ww), although the fungicide chlorothalonil was also present. These findings indicate that these compounds can accumulate in the osprey food web and be transferred *in ovo* to eggs, and thus may be of concern to the health of developing chicks as well as species lower in the food web.

The herbicide DCPA was reported in fish sampled via the National Contaminant Biomonitoring Program in which composite fish samples were analyzed from 112 stations in major United States rivers and the Great Lakes. The percentage of samples with detections ranged from 28 to 46% between 1978 and 1984 (Schmitt et al. 1990), with fish from Cascade Locks on the Columbia River having the third highest concentration nationwide in 1984. More recent information is not available and detailed studies are needed. Another commonly used herbicide, atrazine, had significant effects on reproductive output of fathead minnows exposed to environmentally-relevant concentrations (Tillitt et al. 2010). The authors noted that the atrazine threshold concentration in water (0.5 µg/L), at which reductions in egg production occurred, was well within surface water concentrations in agricultural areas.

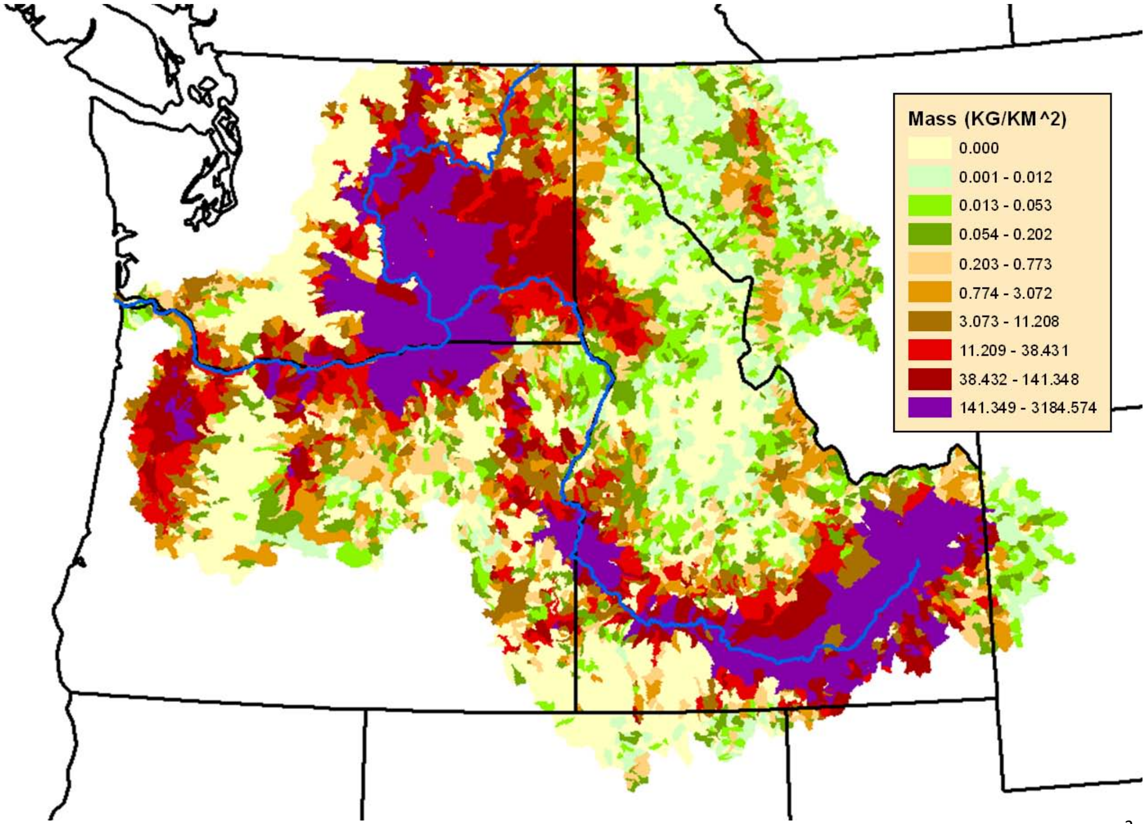


Figure C.7.3. Modern pesticide use in the U.S. portion of the Columbia Basin normalized to area (kg/km^2) for 246 compounds (average 1999-2004). Data were obtained from the U.S. Geological Survey, National Water-Quality Assessment Program, National Synthesis Project.

Current and Emerging Industrial Contaminants

Although many contaminants belong in this category, PAHs, PBDEs, pharmaceuticals and personal care products are the contaminants of greatest concern.

PAHs. Whereas PAHs from crude and refined oils and coal originate from a concentrated hydrocarbon source, PAHs produced by high temperature (combustion or industrial processes) are dispersed in the air, scattered on the ground, or included as a component of liquid waste and municipal sewage discharges (Albers 2003). Juvenile Chinook exposed to PAHs experience both somatic growth reduction and a reduction in biomass and lipid stores. These responses have the potential to cause increased mortality of juvenile salmon during their first winter (Meador et al. 2006). PAHs in tissues of *Corbicula* from the lower Columbia and Willamette rivers in 2005 displayed the same geographic pattern as PCBs and PBDEs, with the highest tissue-associated contaminants in or near the Portland-Vancouver metropolitan area (Sherman et al. 2009). The highest PAH concentration was found on the lower Willamette River. Higher PAH and PBDE concentrations in gut contents of migrating juvenile Chinook salmon appeared to have a downstream lag when compared to the highest levels found in the sedentary *Corbicula*, probably due to the downstream movement of salmonids from the exposure source. In another series of juvenile Chinook samples taken in 2001 and 2002, the highest PAH concentrations in gut contents were fish taken at the Columbia/Willamette confluence, compared to those sampled farther downstream in the vicinity of Longview and West Sand Island (Johnson et al. 2007).

PBDEs. These persist in the environment as well as bioaccumulate and biomagnify in predatory fish, mammals and birds (de Wit 2002). In contrast to organochlorine pesticides and PCBs, which have decreased over time, PBDEs have increased in biota since the 1970s (de Wit 2002). The European Union has banned the use of penta- and octa-PBDEs, and the only U.S. manufacturer voluntarily stopped production in 2004 (Manugian 2004). The only PBDE mixture currently used in the United States is the technical deca-BDE product. The State of Washington banned certain uses of deca-PBDE in 2007.

Between 2002 and 2007, all osprey eggs collected in Oregon and Washington contained PBDEs (Henny et al. 2009b). Concentrations in eggs from the Columbia River progressively increased downstream from Umatilla (rkm460) to Skamokawa (rkm47) which indicated additive PBDE sources along the river. The various congeners increased (not always significant) in eggs at the two locations where temporal patterns could be evaluated (Seattle, 2003 vs. 2006/07 and Columbia River, rkm 47-135, 2004 vs. 2007). Only in 2006 and 2007 (Willamette River, RK 98-253 and Columbia River, rkm 47-135) did total PBDE concentrations in osprey eggs exceed 1,000 ppb ww. Significant negative relationships between productivity (young fledged per nesting attempt) and PBDE concentrations in an egg sampled from each nest were found at both locations. This was the first report of PBDEs showing a negative effect on productivity in a wild bird population.

The Washington Department of Ecology analyzed freshwater fish and water samples collected statewide in 2005-06 to determine the spatial distribution of PBDE contamination (Johnson et al. 2006). PBDE concentrations varied depending upon the fish species and tissues analyzed. Species with high lipid content and larger/older individuals tended to have higher concentrations. Of special concern were the high PBDE concentrations measured in fish from the Spokane River. The situation on the Spokane River may be related to the large human population in the Spokane area and its associated high volume of wastewater discharge into the river, combined with relatively low flows. One of the major sources of PBDEs, in addition to pharmaceuticals and personal care products, appears to be releases from wastewater treatment plants (see interactive map of wastewater treatment plants).

Concentrations of PBDEs measured in gutted bodies and gut contents of outmigrant juvenile Chinook indicate that they are primarily exposed through their invertebrate diet (Sloan et al. 2010). Other potential exposure routes include intake of contaminated sediment and suspended particles during feeding and, to a lesser degree, contaminated water (de Boer et al. 2003). Juvenile salmon from the upper Willamette River contained high PBDE concentrations (3,400 ppb lw; Sloan et al. 2010) in 2005, which is in agreement with high concentrations in osprey eggs from the same area (887 ppb ww; Henny et al. 2009b). Although the health effects of PBDEs in fish are not well understood, juvenile Chinook fed an experimental diet that replicated the diet of Chinook from the Willamette River were more susceptible to the bacterial pathogen *Listonella anguillarum* than controls (Arkoosh et al. 2010). Other studies on effects of PBDEs in fish species revealed changes in hematocrit and blood glucose, as well as reduced spawning success (see deWit 2002 and references therein).

PBDEs in the lower trophic levels of Great Lakes food web show concentrations in fish increasing exponentially from 1979 to 2005, with fish from Lake Michigan exhibiting the highest concentrations (Zhu and Hites 2004, Batterman et al. 2007). Bioaccumulation and biomagnification of PBDEs, especially BDE-47 and BDE-100, are taking place in the food web since invertebrates had much lower concentrations than fish (Kuo et al. 2009). However, BDE-209 (deca-) concentrations decreased at higher trophic levels, suggesting partial uptake and/or biotransformation of BDE-209 in the Lake Michigan food web.

Pharmaceuticals and Personal Care Products (PPCPs). Only recently have human pharmaceuticals accumulating in fish liver, brain and muscle tissues been examined (Brooks et al. 2005). A national pilot study of pharmaceuticals and personal care products in fish from effluent dominated rivers indicated that detection was dependent on the degree of wastewater treatment employed. In other words, more exposure and tissue accumulation are expected in organisms residing in water receiving discharge from wastewater treatment plants employing less advanced versus more advanced treatment (Ramirez et al. 2009). Unfortunately, none of the fish sampled was from the Pacific Northwest. Concentrations in fish livers and fillets were generally in parts per billion. The underlying assumption is that accumulation of detectable concentrations depends primarily upon bioconcentration across biological membranes. PPCPs can adopt a pseudopersistent exposure nature given their continuous introduction from wastewater treatment effluent (Daughton and Ternes 1999).

To illustrate the potential for wastewater treatment plants to contribute personal care products, pharmaceuticals and related chemicals to the Columbia River, Jennifer Morace (USGS, unpublished data, 2010) provided estimates for four compounds. In December

2008, effluent was sampled at seven wastewater treatment plants in the Basin. Concentrations (micrograms/liter) were determined for two pharmaceuticals and two wastewater-indicator compounds (both endocrine disruptors), including a musk and a detergent metabolite. These compounds were generally found at each of the seven plants sampled. Mean concentrations representing these seven plants were used with specific discharge rates for 169 U.S. facilities contributing effluent within the Basin (but not including all wastewater treatment plants in the Basin) to project total grams/day released at each U.S. site. The estimated grams/day released from plants into various U.S. portions of the Basin are summarized in Table C.7.3 for diphenhydramine (an over the counter ingredient used in Benadryl and Unison), trimethoprim (common prescription used as an antibiotic), galaxolide (synthetic fragrance used in cosmetics) and nonylphenol compounds (sum of four different variants: NP1EO, NP2EO, OP1EO, OP2EO) used in cleaners, and a breakdown product from surfactants and detergents. Although wastewater treatment plant discharge rates for Canada are available, it would be questionable to use PPCP concentration data collected in the United States to project/quantify PPCP releases into rivers from a different country. Additional understanding of PPCP accumulation in aquatic life at a broad scale is necessary to support future efforts characterizing ecological and human health risks.

Varied chemical stressors have the ability to cause primary or secondary effects on the endocrine system of vertebrate animals and are collectively referred to as endocrine active compounds (EACs). EACs include pharmaceuticals and surfactants, as well as organochlorine insecticides, PCBs, and heavy metals, (Hinck et al. 2009). The intersex condition (presence of both male and female characteristics in an individual fish) has been suggested as an indicator of exposure to EACs. A large study of nine river basins in the United States reported that 3% of 3,110 fish collected between 1995 and 2004 had intersex characteristics; intersex smallmouth bass were reported from the Snake River at Lewiston, Idaho and the Columbia River at Warrendale, Oregon (Hinck et al. 2006).

Metals

Mercury significantly increased in northern pikeminnow (whole carcasses) in the upper Willamette River from 1993 (1.12 ppm dry weight [dw]) to 2001 (1.91 ppm), and increased, though not significantly, in largescale sucker (0.29 to 0.42 ppm dw) (Table C.7.1). Mercury in osprey eggs from the lower Columbia River also increased significantly from 1997-98 to 2004 (0.29 to 0.45 ppm dw) (Henny et al. 2008). Adverse effects of mercury in bird eggs occur at higher concentrations, but the increasing trend is of concern. Mercury concentrations are elevated throughout the Basin (1997-98) but were greatest in predatory fish from the Salmon River, Yakima River and Columbia River at Warrendale (Hinck et al. 2006).

In field studies, an inverse relation between mercury in tissue and condition factor (an index of fish weight relative to length) has been reported for walleye from the upper Columbia River (Munn and Short 1997) and for white sturgeon from the lower Columbia River (Webb et al. 2006). The literature suggests that changes in biochemical processes, damage to cells and tissues, and reduced reproduction occur in fish at methylmercury concentrations of about 0.3 to 0.7 ppm ww in the whole body (Sandheinrich and Wiener, in press).

Lead concentrations in fish from the upper Basin at Northport and Grand Coulee, Washington exceed fish and wildlife toxicity thresholds. Mining activities in the upper Basin have contaminated portions of the Clark Fork River in Montana and the Coeur d'Alene River in Idaho and resulted in metal bioaccumulation to hazardous levels in fish and birds (Farag et al. 1995, 1998; Henny et al. 1994, 2000).

Table C.7.3. Potential contribution of diphenhydramine, trimethoprim, galaxolide and nonylphenol compounds from wastewater treatment plants by drainage area contributing to the Columbia River, 2008a.

Tributary Drainage	Diphenhydramine	Trimethoprim	Galaxolide	Nonylphenol Compounds
Kootenai	<1	<1	2	16
Pend Oreille	6	8	100	700
Spokane	13	19	230	1,600
Yakima	2	2	26	180
Upper Snake	12	17	210	1,500
Mid Snake-Boise-Powder	14	21	250	1,700
Salmon	<1	<1	7	48
Clearwater	2	3	31	210
Lower Snake	2	3	33	230
Upper Columbia	4	6	67	470
Middle Columbia	3	4	51	360
Willamette	55	78	930	6,500
Lower Columbia	36	51	610	4,300
Basin Totals	150	210	2,500	18,000

[a] Contributions are reported in grams per day; concentrations for these values are from Jennifer Morace, USGS, unpublished data, March 2010; discharge for these values are based on wastewater-treatment plant mean discharges for water year 2002.

Oceanic Contaminants: An Emerging Issue?

Earlier in Chapter C.1 the importance of marine-derived nutrients to freshwater and riparian systems was discussed. However, it was also pointed out that adult salmon not only transport nutrients to freshwater systems, but also persistent pollutants. It is possible that the positive feedback of nutrient cycling between spawning adults and their progeny may be partially counterbalanced by a negative feedback of pollution. Pacific salmon gain more than 99% of their adult mass in marine waters (Quinn 2005), and a comparison of PCB body burdens between subyearling smolts and returning adult Chinook revealed that almost all of the PCBs (>96%) were accumulated in marine habitats (O'Neill and West 2009). The average PCB concentration measured in skinless muscle tissue samples of subadult and maturing Chinook collected from Puget Sound were 3-5 times higher than those measured in six other populations (including the Columbia River) of Chinook on the West Coast of North America (O'Neill and West 2009). PCB concentrations in Puget Sound fish exceeded an experimentally determined effects threshold for salmonid fishes of 2,400 ppb (lw) in 22% of maturing and subadult Chinook samples. Estimation of the effects threshold included endpoints such as reduced growth, altered enzyme and hormone levels, and increased mortality (Meador et al. 2002). It was hypothesized that residency in the contaminated Puget Sound was a major factor contributing to the high and variable PCB concentrations in these fish.

Bioaccumulation of contaminants by salmon is strongly influenced by the feeding ecology of each species. Overall, Chinook and coho have a more coastal distribution along the continental shelf than do sockeye, pink and chum (Quinn 2005), and therefore can be more readily exposed to contaminants in coastal waters. Chinook and coho also feed at higher trophic levels (considerably more piscivorous) than the other salmon. Contaminant concentrations in rainbow trout were related positively and significantly to sockeye spawner density; in this case, the accumulation of contaminants by rainbow trout appeared to rely heavily on direct consumption of sockeye tissue (Gregory-Eaves et al. 2007).

Elevated contaminant concentrations in salmon and other fish have implications for human health. The high PCB levels in Puget Sound Chinook resulted in human consumption advisories by the Washington Department of Health (2006). Human consumption rates for adult salmon from the Columbia River are currently being evaluated by tribes, state regulatory agencies and the Environmental Protection Agency. Finally, it is important to note that PCB levels for Puget Sound Chinook and coho were probably higher in the 1970s and 1980s than at present (West and O'Neill 2007), which is in agreement with the findings reported earlier for bird eggs, mammals and fish from the Columbia River Basin.

Conclusions

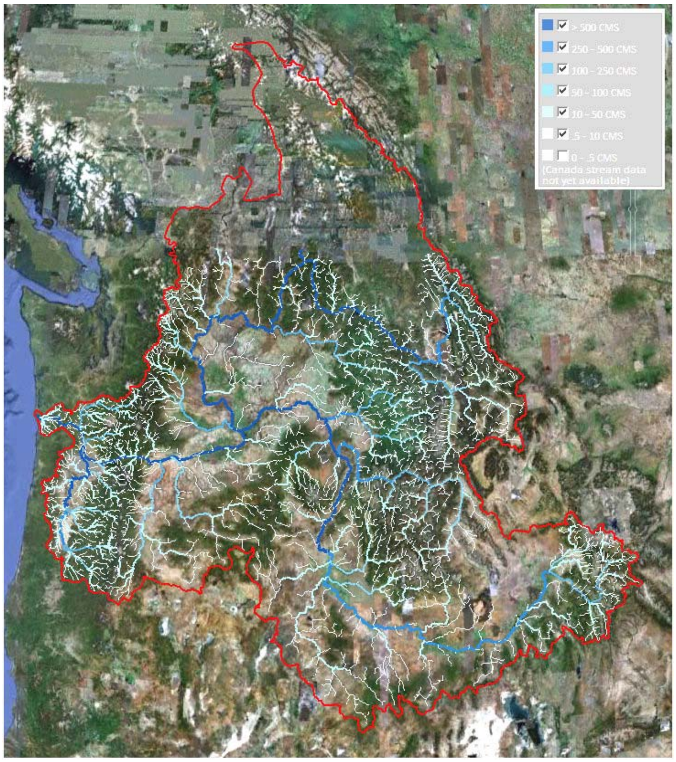
In past years, legacy contaminants adversely affected fish-eating birds and mammals in the Columbia River system; however, residue concentrations have decreased dramatically in the last several decades, and many affected populations have recovered. Certainly, legacy contaminant hotspots remain in the Basin, with residues still present throughout the food web. Some especially sensitive species, such as the mink, or especially vulnerable life stages of other species still may be affected. Pacific lamprey are especially prone to bioaccumulating contaminants, particularly those that are lipophilic.

Impaired olfaction (imprinting, homing, predator detection) and reduced somatic growth rates contribute to lower survival and reduced adult returns (from both mortality and straying). Some impacts will be harder to quantify than others, but if growth reductions could be quantified, they could be tied more directly to size-dependent survival during subsequent life stages discussed in other sections of this report. This ultimately might provide an opportunity to demonstrate how incremental reductions of contaminants could translate into measurable increases in production and survival of salmon.

Further, and of special concern, are the emerging contaminants, many of which seem related to the distribution of human populations, industrial activity and wastewater treatment plants. Concentrations of emerging contaminants will be more diluted at locations with higher river flows. Therefore, when point sources are similar, higher concentrations may be expected in tributaries with lower flows. Other sources of pesticides include agriculture, which is widespread in the Basin. As evidenced by some of the highest concentrations of legacy agricultural pesticides reported in the past, exposure of the aquatic food web to current-use pesticides may be high. The data provided for application of agricultural pesticides and for the location and size of wastewater treatment plants provides basic information for designing studies to more fully evaluate effects of emerging contaminants on aquatic food webs (Appendix C). Understanding adverse effects of contaminants on migrating juvenile salmon under field conditions may be especially difficult when effects are delayed, and perhaps occur at great distances from the source of contaminant exposure. Contaminants can be considered a “wild card” when attempting to understand food web and wildlife-habitat relationships, and as such can cause much confusion. Furthermore, contaminants as mixtures (and mixtures are present at most, if not all, locations in the Columbia River Basin) can act in independent, additive, antagonistic and synergistic ways. Nevertheless, the available information strongly suggests that a better understanding of contaminants and their effects on the Basin's food webs are urgently needed.

D. Food Webs in Typical Habitats

D.1. **Small Tributaries**



Small tributaries. See interactive map.

The Food Webs of Small Streams

Most small tributaries are headwater streams located at the upper reaches of a drainage network. As such, many tend to be steep, narrowly confined, and underlain by coarse substrates (boulders and cobbles). However, a few small tributaries originate on valley floors near rivers and flow relatively short distances before entering larger channels. Often such small streams are groundwater fed, surfacing as springs or as sites of hyporheic upwelling; they typically possess low gradients and fine-grained substrates. Still other headwater streams exist as low gradient, meandering channels in perched alluvial meadows, and it is not uncommon for small tributaries to pass through alternating steep canyons and alluvial flats as they descend from higher elevations. Thus, small tributaries can exist in remarkably diverse and complex geomorphic settings, and the varied structure of their food webs reflects this diversity.

Small tributaries make up the majority of the linear stream length in a drainage system. In arid environments small streams (2^{nd} order and smaller) typically comprise one half to two thirds of the total length of network, while in areas of high precipitation small streams often make up three quarters to >80% of the network (Meyer et al. 2007). The majority of small streams do not contain fish; they are either too steep for colonization, lie above natural barriers such as waterfalls, or are seasonally dry. Many of these channels provide temporary habitat for fish, especially during periods of high precipitation when they can use headwater streams as a refuge from extreme flow events. Although they do not support large fish populations, headwater streams deliver organic matter, nutrients or cool surface water to streams which do contain fish (Richardson et al. 2005, Kiffney et al. 2006). For example, studies have shown that fishless streams provide food organisms to the fish-bearing streams into which they flow (Wipfli and Gregovich 2002). Small stream processes also strongly influence the quantity and quality of water entering fish-bearing channels (Naiman 1983a,b). Therefore, headwater streams are ecologically important in terms of the overall watershed's capacity to produce salmon, trout, and aquatic resources of recreational, commercial and cultural value (Wipfli et al. 2007).

This chapter characterizes the food webs of small tributaries and the importance of these food webs to fish communities in downstream rivers (Figure D.1.1). Because small stream food webs tend to be more dynamic, both seasonally and annually, than food webs of larger channels, we examine temporal changes and discuss the impacts of both natural and anthropogenic disturbances to food web processes. The chapter concludes with a short discussion of factors contributing to food web resilience in the face of changing environments.

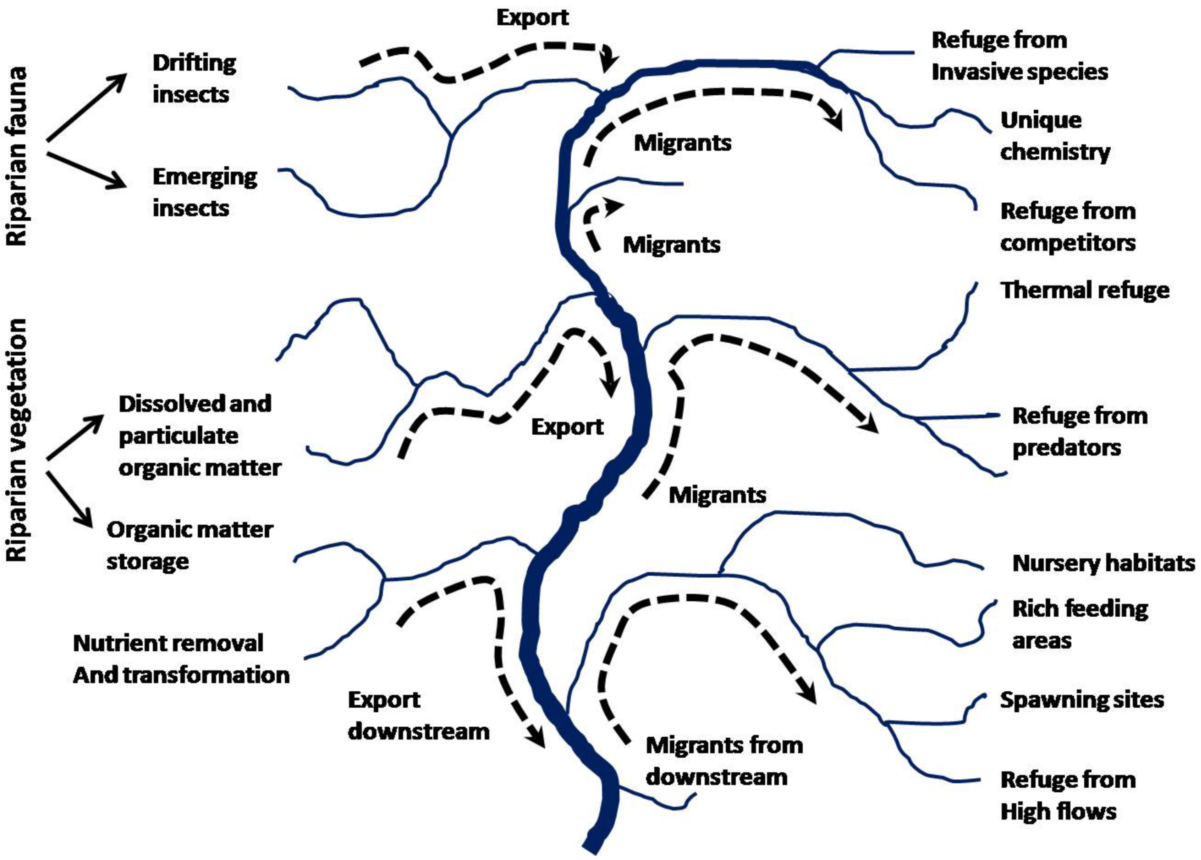


Figure D.1.1. Ecological properties of small tributaries that control food webs and other important factors affecting fish. Redrawn from Meyer et al. (2007).

Vertebrate Communities in Small Streams

Steep headwater streams in the Columbia River Basin, if they contain fish at all, typically have few species (Wydoski and Whitney 2003). Nevertheless, fishes, amphibians and birds can occupy the apex of the aquatic food web when they are present. In general, resident trout and char occur high in drainage networks and can ascend streams with steep gradients, sometimes greater than 10% (Latterell et al. 2003), because salmonids possess swimming and leaping abilities that surpass bottom-dwelling species such as sculpin. At lower channel gradients (<10%), resident trout and char are joined by other headwater fishes that include sculpin, dace, small suckers, shiners, and resident lamprey. Many headwater-dwelling species are generalized invertivores, i.e., they feed on a mixed diet of benthic (aquatic origin) and drifting macroinvertebrates (terrestrial and aquatic origin), while a few are food specialists (Moyle 2002). For example, the bridgelip sucker, found in some large rivers as well as small streams, is an herbivore that possesses mouthparts specialized for scraping periphyton (algae) from hard surfaces. In addition, larvae (ammocoetes) of the western brook lamprey, which do not feed as adults, live in sand and silt substrates where they consume organic detritus. In general, the upstream limit of a given species' distribution is bounded by either a physical barrier to movement or by some attribute of the aquatic environment that prevents the species from successfully completing its life cycle (Wydoski and Whitney 2003).

Anadromous fishes – salmon and steelhead, Pacific lamprey, smelt, sturgeon, and non-native migratory species such as American shad – are almost never found in steep headwater streams. Salmon, steelhead, and Pacific lamprey may enter small streams if not prevented from doing so by a migratory blockage, but their abundance in headwater streams in most instances is low. In low gradient (usually <2%) valley floor streams, however, juvenile anadromous salmonids can be very abundant because it is often much easier to access small tributaries that empty directly into large rivers. In many low gradient systems, juvenile anadromous salmonids constitute a significant component of the fish community (Stanford et al. 2006).

Importance of Small Fishless Streams

In the Basin, as elsewhere, small streams without fish comprise a significant portion of the drainage network (Quigley and Arbelbeide 1997). The exact percentage is generally not known because hydrographic maps often are at a scale excluding the majority of perennial headwater streams and do not show ephemeral (seasonally dry) or intermittent (alternating surface and subsurface flowing) channels. Nevertheless, small fishless streams (Figure D.1.1) can be very important to fish-bearing streams into which they flow (Rice et al. 2001, Kiffney et al. 2006). One of the most important contributions of small fishless streams to larger channels is high quality water (e.g., temperature, chemistry, suspended sediment) which strongly influences food web structure downstream (e.g., Mulholland et al. 2008). Headwater streams are typically well shaded, and because they originate high in the watershed, contain cool water. The confluence of a small stream and a larger fish-bearing channel can provide a cool, well oxygenated thermal refuge during hot summer months when ambient water temperatures rise to stressful or occasionally lethal levels (Torgerson et al. 1999). The lowermost reaches of normally fishless small streams may themselves be temporarily used as thermal refugia in summer (Ebersole et al. 2003). During periods of high flow, seasonally flowing (intermittent) streams that do not possess fish for most of the year can provide temporary rearing sites where water velocity and clarity are more suitable for growth. Anadromous salmonids and some resident fish species are known to use the lower reaches of otherwise uninhabited small tributaries when conditions in the parent stream become unfavorable (Wigington et al. 2006). Likewise, small wetlands, springs, and riverine ponds with seasonal connections to fish bearing streams may be too warm or too dry to support fish in summer, but often provide a productive feeding environment for both anadromous and resident fishes during cooler seasons (e.g., coho; Peterson 1982, Brown and Hartman 1988).

Because they comprise such a large fraction of the drainage network, small headwater streams capture much of the terrestrial organic matter that falls into channels. This externally-derived organic matter, termed *allochthonous* organic material, becomes part of a large organic matter pool that also includes *autochthonous* organic material, which originates from primary production within the streams themselves. Combined terrestrial and aquatically derived organic matter is processed by aquatic organisms (primarily macroinvertebrates such as midges, mayflies, stoneflies, and caddisflies) and by microbial decomposers (fungi and bacteria), and is rendered into finer and finer organic particles as it passes downstream. The transport of organic material from small streams is an essential component of the food webs of larger streams in which most fish production occurs (Morin and Naiman 1990).

Small fishless streams can also export food organisms – aquatic invertebrates and floating terrestrial invertebrates – directly to fish bearing streams. Approximately half of the 1st-order channels in a watershed feed directly into 3rd-order or larger channels (Meyer et al. 2007), and the confluence of small streams with larger channels often creates localized food rich pockets along the drainage network. One study in southeastern Alaska (Wipfli and Gregovich 2002) found that fishless headwater streams contributed enough food organisms to support approximately half of the fish production in the larger streams into which they flowed. This study took place in very unproductive watersheds in Alaska. It is unlikely that the direct export of food organisms from fishless streams is as important to fish in the Columbia River Basin; however, the work underscores the significance of small streams to the food webs of larger channels, both in terms of organic matter export and direct food subsidies to fish.

Seasonal Changes in Small Stream Food Webs

If riparian trees that border small headwater streams are primarily broadleaf deciduous species, production by attached algae and aquatic vascular plants may be low due to light limitation (Hill et al. 1995). During these periods (usually mid-summer to late autumn) an important source of organic matter for small streams is derived from allochthonous (e.g., terrestrial) sources (Figure D.1.2 – top). Small streams can also receive considerable amounts of carbon from phreatic inputs (dissolved organic compounds in springs and seeps feeding headwater streams). This pathway is seldom quantified; however, phreatic inputs to Quebec streams exceed direct terrestrial inputs (e.g., leaf fall), and much of that organic material is available to stream microbial communities (Naiman et al. 1987). This organic matter is processed in the small streams and forms an important contribution to downstream food webs.

After leaf fall in autumn and before leaves are fully developed in summer, however, more sunlight can reach the stream surface and the organic matter base of the food web in small streams can shift to algae and macrophytes (Hill et al. 2001; Figure D.1.2 – bottom). The seasonal shifts in the trophic base of small stream food webs result in changes in the invertebrates that are available to bottom- and drift-feeding fishes (Bisson and Bilby 1998). When allochthonous organic matter sources predominate, benthic invertebrate communities tend to be dominated by shredder and collector-gatherer feeding guilds, including caddisflies (Trichoptera), stoneflies (Plecoptera), and certain midges (Chironomidae). When autochthonous (i.e., within stream) organic matter sources predominate, macroinvertebrate communities tend to be dominated by grazers and algal-based collector gatherers such as baetid mayflies (Ephemeroptera), caddisflies, and small bodied midges. During spring and summer terrestrial invertebrates falling into streams from riparian vegetation can also serve as important components of the food web supporting fishes (Chapman and Bjorn 1969, Nakano et al. 1999). If riparian trees that border these small streams are primarily coniferous, seasonal changes in the relative importance of autochthonous versus allochthonous organic matter is less pronounced. In these locations, food webs are primarily dependent on allochthonous sources.

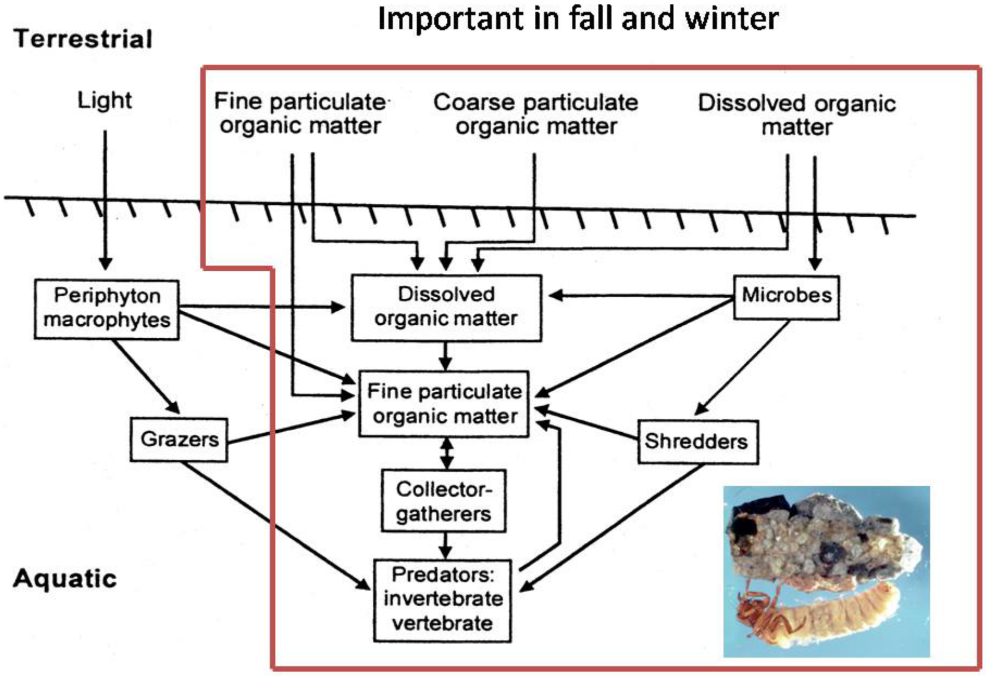
Natural Disturbances and Small Stream Food Webs

More than large rivers, small streams tend to be extensively altered by watershed-scale disturbances such as flooding and debris flows, wildfires and prolonged droughts (e.g., Kiffney et al. 2004). Although the recurrence interval of a large natural disturbance affecting a given headwater stream is usually low, when catastrophic events do occur they often result in significant changes to the stream channel and/or its associated riparian zone (Naiman et al. 1992). With the exception of droughts, most large disturbances result in an opening of the channel to additional solar radiation, often accompanied by elevated soluble nutrients, and commonly, a significant loss of riparian vegetation (Lamberti et al. 1991, Kiffney et al. 2004). This has two major consequences for food webs: (1) the trophic base of the aquatic community usually shifts to an autochthonous-dominated system (see Figure D.1.2 – bottom), and (2) there is a temporary reduction in the input of terrestrial organic matter until understory and overstory vegetation recovers. When such changes occur, the macroinvertebrate community often becomes dominated by small-bodied herbivores and collector-gatherers such as midge and mayfly larvae. Mellon et al. (2008) found that macroinvertebrate abundance in post-wildfire streams in eastern Washington was elevated relative to streams in unburned watersheds, with the increase due primarily to more abundant midge larvae. However, they also found that aquatic biodiversity was reduced in disturbed streams, a finding consistent with studies of disturbed aquatic communities elsewhere (Karr and Chu 1998).

Since natural disturbances and their legacies are an integral part of the landscape, food webs in small headwater streams typically exist in various stages of recovery from the last major disturbance event. In watersheds where large disturbances are very infrequent, small streams possess well-shaded channels with food webs dominated by allochthonous inputs. Where disturbances such as fires and floods are more frequent, a greater percentage of streams have food webs reflecting increased sunlight and aquatic primary production. The relative proportion of streams in the early stages of recovery from disturbance has important consequences for fish populations. Fish production in Pacific Northwest streams dominated by autochthonous processes is often greater than in streams dominated by terrestrial organic matter inputs (Bilby and Bisson 1992), but if many headwater channels are exposed to high solar radiation levels the consequences for downstream rivers could include higher temperatures throughout the drainage network, loss of seasonal refugia, and changes in the type and quantity of organic matter delivered to larger channels (Elliott et al. 2004).

Allochthonous organic matter pathways

Important in fall and winter



Autochthonous organic matter pathways

Important in spring and summer

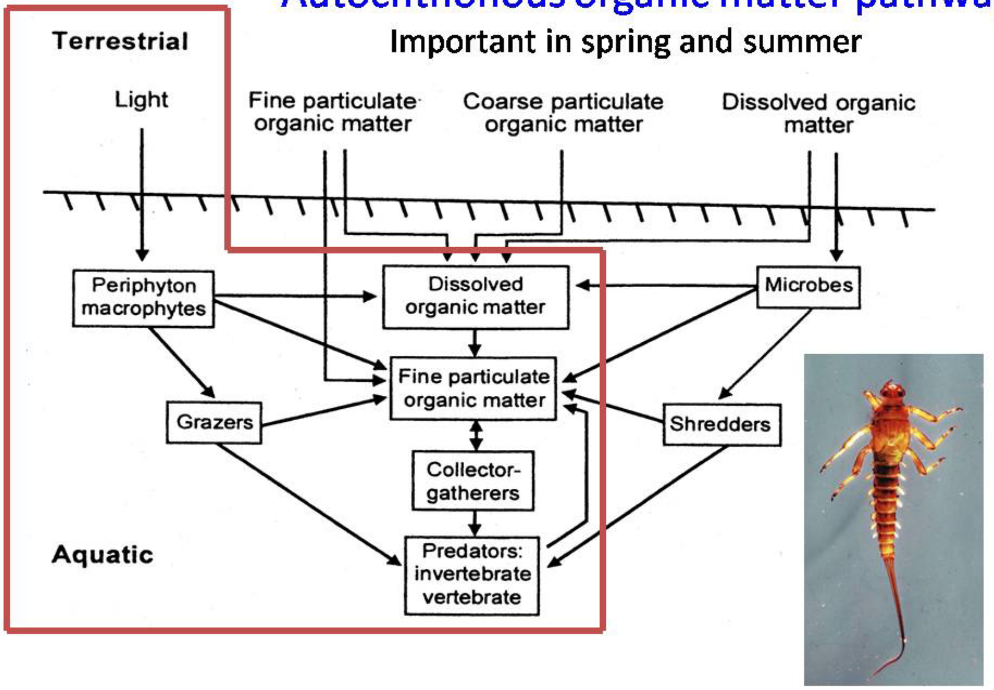


Figure D.1.2. Seasonal changes in the dominant food web pathways in small tributaries.
Top: allochthonous inputs (e.g., terrestrial origin) tend to dominate in fall and winter.
Bottom: autochthonous (i.e., within stream) pathways dominate in spring and summer. After Bisson and Bilby

Anthropogenic Disturbances and Small Stream Food Webs

Some anthropogenic disturbances emulate natural disturbance effects on small stream food webs; however, the number and severity of anthropogenic disturbances may exceed the frequency of the natural events that alter food web structure and productivity (Bisson et al. 1992). Streams in watersheds heavily influenced by human activities, even those well away from channels and their associated riparian areas, tend to possess different food webs than those in pristine watersheds. There are important environmental consequences of different anthropogenic disturbances to food webs in small tributaries (Table D.1.1). Generally, human activities lead to a simplification of aquatic trophic pathways as habitat complexity is lost, channel substrate characteristics are altered, and organic matter inputs are either restricted or overwhelmed by a single source (Allan and Castillo 2007). Simplified food webs often favor non-salmonid fishes (e.g., shiners, dace, and suckers) and certain macroinvertebrates (e.g., snails), many of which are tolerant of higher temperatures and prefer small-bodied prey or algae and organic detritus (Schmid-Araya et al. 2002). Although the overall level of productivity may be elevated in such streams, the consumers benefiting from these increases are not cool water species such as salmon and trout but instead are species of less desirability from a human standpoint.

Table D.1.1. Some common environmental effects of different types of anthropogenic disturbances that are likely to alter various aspects of small streams food webs, including species diversity, feeding guild structure, and productivity

	Environmental Consequences						
Type of disturbance	Dewatering	Shade loss	Increased nutrients	Increased sediments	Increased debris flows	Toxic substances	Increased competition & predation
Water withdrawals	X						
Agricultural chemicals			X			X	
Grazing		X	X	X			
Sedimentation from other sources (e.g., roads)				X		X	
Chemical pollution			X			X	
Loss of riparian vegetation from sources other than grazing (e.g., timber harvest)		X		X	X		
Non-native aquatic species introductions (e.g., brook trout)							X
Climate change	X	X[1]	X[1]	X[1]	X[1]		

[1] Climate change models for the interior Columbia River Basin predict conditions that will favor an increase in the frequency of severe wildfires, which will contribute to shade loss, nutrient and sediment delivery to streams, and increased mass erosion events (see Hessburg and Agee 2003).

Food Web Resilience in Small Tributaries

Natural watershed processes produce highly variable environmental conditions. Collectively these create a mosaic of food webs with linkages between the processes and patterns seldom considered in restoration (Beechie et al. 2010). For example, as mentioned previously, natural disturbances in small headwater streams occur across a watershed at varying frequencies and intensities contributing to a diversity of food web configurations (Kiffney et al. 2004). Habitat-oriented projects will be more likely to foster food web resilience and diversity when landscape dynamics that promote resilience and diversity are explicitly incorporated into environmental planning. Three important focal areas for managing streams based on natural variability are: 1) improving the capacity of aquatic habitats to recover from disturbances such as floods and wildfires, 2) maintaining a natural range of habitat types distributed across stream networks through time, and 3) increasing ecological connectivity among different habitat types (Bisson et al. 2009). The same factors that fragment and isolate fish populations in headwater streams also threaten the resiliency of food webs of these small streams.

It is commonly believed that food web productivity can be improved by nutrient additions, based on the assumption that trophic enrichment from lower to higher consumer levels is important for maintaining healthy food webs (e.g., through addition of marine-derived nutrients, a method of “bottom-up” restoration). This assumption may hold true in some cases, but it ignores the natural variability in watershed processes that affect energy flow (e.g., not all streams received large returns of adult salmon). Within many streams, consumer-regulated (“top-down”) food web dynamics have received inadequate attention (Power and Dietrich 2002) and are usually underappreciated by restoration scientists (e.g., Wootton et al. 1996). In the Basin’s small tributaries the top aquatic predators may be amphibians or large macroinvertebrates, and even terrestrial consumers such as birds or spiders can play an important role in regulating food web dynamics (e.g., Baxter et al. 2005). Thus, a better understanding of processes influencing the food webs of small streams is needed. Food resources, in addition to the presence of competitors and predators other than fish, will exert a strong influence on the ability of focal species to persist in the face of continued environmental change whether natural or anthropogenic. Ultimately, improved understanding of processes controlling energy flow, food web composition and the dynamics of headwater streams will improve our understanding of the importance of small streams to larger fish-bearing channels. This understanding should provide a firm conceptual basis for watershed management as well as for the restoration and conservation of threatened salmonid populations.

D.2. Large Tributaries

Large tributaries. See interactive map.

Introduction

Large tributaries to the Columbia River serve as intermediate links and migratory corridors between small stream habitats and the diverse, highly modified mainstem Columbia River habitats (see map). Their food webs are also critically important for rearing and feeding of native fishes (Stanford et al. 2006).

Large tributaries, as used here, refer to rivers that are typically only one or two river orders below that of the mainstem Columbia River. Most have large complex watersheds (1,370 to 278,400 km^2) drained by streams of several lower orders. They include the Cowlitz, Willamette, Yakima, Deschutes, John Day, Kootenai, Spokane, Snake and several others (Table D.2.1) but exclude smaller streams with smaller watersheds that drain directly into the main river (e.g., Fifteenmile Creek, Oregon).

Large tributaries have historically provided important commercial, recreational and subsistence fisheries. The rivers are large enough to contain harvestable stocks of fish – migratory and resident – yet small enough to be easily accessible to fishers as compared to most mainstem Columbia areas. Examples of large tributary fisheries are the Tribal dipnet fishery at Sherars Falls on the Deschutes River, the historical smelt fishery on the Sandy River, and numerous popular recreational fisheries for salmon and steelhead along all accessible rivers. Numerous fisheries historically have been conducted and continue near waterfalls, other natural obstructions or deep staging areas where fish are concentrated as their movements are impeded.

Large tributaries provide important rearing and feeding areas for young salmonids, including those hatched and reared in smaller (upriver) streams (Chapter D.1; (Schreck et al. 1995). For many salmonids it is not uncommon for juveniles hatched farther upstream to utilize large tributary habitats for extended periods following early rearing in small low-productivity, upper tributaries and before smoltification and migration to the ocean (Myers et al. 1998). This pattern was historically common for many Columbia Basin salmonid stocks and probably for many other fishes as well. In all cases, the food webs of the large tributaries are important for early survival and exert strong effects on year class strength.

In the past century, habitat degradation (including dams, water withdrawals, bank stabilization, channelization, loss of riparian habitat, warming, and introduction of non-native predators such as smallmouth bass) has disrupted the important role of large tributary food webs in sustaining salmonids and other species. These habitat changes, changes in abundance of native fishes from selective harvest and introductions of non-native species have had major impacts on the original ecological functioning of the Basin's large tributaries, their carrying capacity for native fishes and their food webs (Wootton et al. 1996, Stanford 2006, Olden et al. 2009). In the Basin as elsewhere, relatively few un-impacted rivers remain as ideal models to guide restoration (Winemiller 2004). Despite major changes in habitat conditions along large tributaries, however, most large tributaries retain more of their historical river function and food web characteristics than does the mainstem Columbia River (Table D.2.1, column 3; Chapter D.3)

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Table D.2.1. Average discharge, drainage basin area and dominant characteristics of selected major Columbia River tributaries[22]

Tributary	Average discharge (m^3/s)	Drainage basin (km^2)	Watershed and land use characteristics
Snake River	1,610	278,400	
Willamette River	1,060	29,680	Wide, flat floodplain; Tectonic origins modified by (Missoula) flood deposits of sediment; heavily agriculturalized; no mainstem dams except Willamette Falls; river channel stabilized and diked. Most major tributaries impounded with large flood-control, storage and power generating dams.
Kootenay River (Kootenai)	868	50,300	Forested watershed; Mining; diking, flow regulation (Libby Dam, Montana) heavy agricultural (crop) use in lowermost (U.S) portion (Idaho)
Pend Oreille River	748	66,800	
Cowlitz River	259	6,700	Three mainstem dams; forested watershed. Influenced by Mt. St. eruption Helens
Spokane River	224	17,300	Drains mountainous and plain areas; timber and agricultural production. Superfund site on Coeur d'Alene River; affected by water withdrawals Spokane-Rathdrum Aquifer. Seven mainstem dams.
Lewis River	173	2,710	Drains Cascade Range; forested watershed; three mainstem dams produce hydroelectric power.
Deschutes River	166	27,700	Plains/prairie landscape; Heavy agricultural use (irrigation) in upper basin; recreational rafting use
Yakima River	100	15,900	Irrigation agriculture; 5 major water diversion/ storage reservoirs
Wenatchee River	87	3,500	Forested headwaters; heavily irrigation use downriver; Two mainstem dams
Okanogan River	86	21,600	Transboundary river; main uses in U.S are forestry, Irrigation agriculture; urban development in headwaters (Canada); channelization issues
Kettle River	83	10,880	Agriculture, rural homesteading, ranching, forestry, transportation, mining.
Sandy River	64	1,316	Forested watershed; free flowing as of 2008 (mainstem dam removal)
John Day River	58	20,750	Undammed; arid basin; irrigation agriculture and ranching

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[22] See also CBFWA's report on subbasins and rivers

Despite the obvious importance of large tributaries in nurturing and sustaining salmonid fishes, and other fishes and wildlife, relatively few details about the food web structure and processes are available. A major reason is that food web studies in larger tributaries are more difficult and expensive to design and conduct than in smaller tributaries. While some information on effects of predators on migratory salmon is available (Section C.3) and scattered *ad hoc* studies have been conducted, the food webs of most large tributaries can be discussed only in general terms. In some, perhaps most, cases it may be more feasible to understand and manipulate food webs in larger tributaries not by designing a myriad of specialized food web studies there, but by first understanding and manipulating the ecological functions creating and maintaining the food webs. Food web responses can then be understood and monitored based on the responses of keystone species (i.e., species exerting major influences in structuring food webs; Paine 1966, Naiman et al. 1988, Helfield and Naiman 2006), other indicator species and invertebrate communities.

On that assumption, this chapter outlines general aspects of food webs in large tributaries of the Columbia River. We describe nine important conceptual frameworks based on ecological theory that have been used to characterize food webs in rivers and large tributaries. We also examine limitations of past funded studies in answering key questions relevant to food webs, showing how applied research studies of food webs (under the Council's Fish and Wildlife Program and elsewhere) might benefit from being framed in one or more broader conceptual frameworks. This chapter thus leans toward designing better conceptualized studies to yield information on food webs having applications to management and restoration within the Basin. Sustainable management and restoration of fisheries associated with large tributaries requires a strong understanding of ecological mechanisms supporting the food webs than currently exists.

General aspects of Food Webs in Large Tributaries

The foundation of a food web in a large river is determined by a complex combination of physical habitat characteristics starting with the timing and magnitude of extreme flow conditions (i.e., the flood pulse; Junk et al. 1989). In the Columbia River Basin the high water extreme typically occurs in spring but may also occur in winter in milder portions of the Basin such as the Willamette River (Colvin et al. 2009). Higher delivery rates of organic matter and nutrients, whether from upriver or from the floodplain, are usually linked to the timing of this annual flood pulse or other flood events and their magnitudes (Junk et al. 1989, Winemiller 2004). In particular, variations in the magnitude and timing of the flood pulse (and high and low water periods in general) affect connectivity of floodplain habitats (Chapter E.4). Differing degrees of connectivity among habitats and seasons result in variations in nutrient exchange, in abundance and composition of the aquatic community as well as in food web structure and productivity. The flood pulse along with other factors such as water temperature, photoperiod, water clarity and availability of nutrients and organic matter set the stage for primary and secondary production cycles, important foundational aspect of food webs (Winemiller 2004). Although each river is distinctive, in general, higher flood pulses, especially in the spring, result in greater connectivity among habitats, more exchange of nutrients, higher primary and secondary production, more effective fish spawning for many species, and stronger year classes of fish. Typically, fish hatching and emergence are timed to coincide with the annual production cycle resulting from the flood pulse (Junk et al. 1989). Emerging fish are then more likely to immediately find food, thereby resulting in better survival and stronger year classes.

Large tributaries are typically characterized by a deep, persistent main channel receiving large quantities of fine particulate organic matter (FPOM) from the upper watersheds (Naiman and Latterell 2005; Freeman et al. 2007) and floodplains (Junk et al. 1989; see Chapter E.4). Within the floodplain, secondary channels connecting the main channel to backwaters are often seasonally ephemeral, and can change positions over time in response to floods aggradation (building) and degradation (erosion) processes. Water, sediment, organic matter (OM) and nutrients are delivered longitudinally by numerous streams as well as latitudinally from associated floodplains and riparian zones (Naiman et al. 2005, Roach et al. 2009).

Spatially, food webs of large tributaries are also affected by smaller, inflowing streams (Freeman et al. 2007) as well as by larger, downriver processes (Naiman and Latterell 2005) and downstream barriers such as dams (Greathouse et al. 2006). For example, downstream dams and other barriers impact upriver food webs by eliminating or reducing upstream migrating fish, either by loss of their marine derived nutrients (Chapter C.1) or by reducing their effects as top-down consumers limiting organisms positioned under them in the food web (Greathouse et al. 2006).

Large tributaries have distinctive ecological characteristics that shape their food webs. In general, autochthonous (internal or autotrophic) sources of carbon tend to be more important in large tributaries than in smaller tributaries. Delivery of organic matter from upstream tributaries is a significant source of energy and nutrients (Naiman and Sedell 1979, Naiman and Latterell 2005). In the main channel, riparian effects may be less significant in their influences on food webs than in smaller tributaries (Naiman et al. 1987), especially in confined rivers lacking secondary channels. Secondary trophic level consumers such as invertebrates and small fishes rely mainly on phytoplankton, periphyton and suspended FPOM for food. In rivers with larger floodplains, macrophytes are often important but, for the aquatic food web, mostly in the form of detritus after the macrophytes have died. Little of the primary production by macrophytes is typically consumed directly by animals. Many forage species (especially fishes) are detritivores, which transfer energy from plant detritus into forms directly available to piscivorous fishes, the target of most fisheries. Further, in large tributaries most food chains from primary producers to top predators are short (2-3 links and 3-4 levels), based on both diet and stable isotope studies (Winemiller 2004; Chapter C.3). Those tributaries with well-developed floodplains have a wider diversity of habitats, food webs and species diversity than do the headwaters (Dettmers et al. 2001; Chapter D.1). More trophic interactions among fishes are interspecific (as opposed to intraspecific) than in the smaller streams, with species interactions strongly influenced by the annual flood pulse.

Although many species comprise the food webs of large tributaries, most energy transfers are often dominated by a few species (Winemiller 2004). In the Columbia Basin, organisms such as Pacific salmon and beaver act as keystone species, in that they exert disproportionate influence on the ecosystem and on the food web (Paine 1966, Naiman et al. 1988, Helfield and Naiman 2006). Identifying and understanding the role of key species, or cases where keystone interactions of two or more species become important (Helfield and Naiman 2006), are typically the most efficient ways to elucidate the food webs of these large, often complex tributaries.

A worthwhile approach is to *a priori* identify keystone species and use them as access points around which food webs can be understood. Designing applied studies around keystone species and their food web linkages may be the most cost-effective way to understand aquatic community structure, the functioning of the food web, and factors affecting of species of major interest.

Specific Food Web Alterations of Columbia Basin Tributaries

Food web disruptions in Columbia Basin's large tributaries have resulted in major impacts on native species. Two well-documented examples are given here and additional examples are illustrated in Section C of this report.

Food webs for threatened bull trout have been highly altered throughout much of the Basin. In many localities, recovery of potadromous stocks (i.e., spawning in small streams but feeding and growing in large tributaries) has been impeded because of declines in important forage species, including juvenile anadromous salmon. Declines in marine-derived nutrients (Chapter C.1) and anadromous salmon have decreased available food supplies for piscivorous bull trout. In some instances, decreases in forage have been linked to declines in bull trout abundance (Ratliff and Howell 1982). Increased competition with non-native species such as brook trout (Gunckel et al. 2002) and other salmonids (Stewart et al. 2007, Shively et al. 2006) and non-salmonids for forage has also altered food webs. In other locations, however, food webs of adfluvial populations (spawning in streams, rearing in lakes or reservoirs) have been altered by major habitat changes as well as introductions of non-native species. Adfluvial populations in Priest, Pend Oreille, Coeur d'Alene lakes, Idaho, have been negatively affected by predation from introduced lake trout. Bull trout in the Deschutes River, Oregon, became adfluvial with the construction of Lake Billy Chinook, a mainstem reservoir. The resulting food webs involves predation by bull trout on introduced kokanee (Beauchamp and Van Tassel l 2001); available prey supply and cannibalism may limit abundance of the adfluvial bull trout in that location.

A second example of how a food web has been altered to the detriment of an ESA-listed species is from the

Kootenai River. There, recovery of white sturgeon, an endangered ESU, is being impeded by declines in riverine productivity from impoundment (closing of Libby Dam) and loss of floodplain productivity resulting from channel confinement. After impoundment the reservoir became a nutrient sink and greatly reduced the quantities of nutrients and organic transferred downstream (Snyder and Minshall 2005). Specifically, phosphorus limitation downstream of the dam is the probable cause for the decrease in abundance and production of many fish species. As a result, Kootenai River sturgeon grow slowly and do not reach a large size as in lower-basin localities. An overall decline in the productivity of the food web (i.e., food limitation) also negatively affected the abundance and growth of numerous other fish and aquatic organisms (Paragamian et al. 2008).

Limitations of Past Investigations in the Columbia Basin and Beyond

Most studies of food webs in the Basin's large tributaries exhibit major limitations affecting their breadth and applicability. In general, most empirical food web studies and field experiments are highly restricted in space and time – over only one or two seasons and conducted at only the stream reach or segment scale – or they lack an adequate conceptual framework based on ecological principles as a guide.

Spatial and temporal scales are important issues because food webs change along river gradients (Vannote et al. 1980), and they also differ temporally as critical factors such as annual discharge and relative species abundance change (Roach et al. 2009). Landscape level understanding of food webs in large tributaries is not effectively addressed by short-term, site-specific field studies in a given stream. Specific studies often depict ecological mechanisms shaping the food web, but do not adequately depict the structural dynamics of food webs. Food webs at the broad level of large rivers are most easily understood by examining landscape-level outcomes such as species distributions, gene flow and community structure (Woodward and Hildrew 2002). Such a landscape interpretation, however, still requires an adequate understanding of smaller-scale food web processes leading to landscape-level responses and outcomes.

Most investigations of food webs in large tributaries (e.g., the Yakima River; Chapter C.3) have been *ad hoc* studies of predation and consumption rates on migratory salmonids by piscivorous predators such as pikeminnow, walleye and smallmouth bass. Further, site-specific results of food web investigations vary greatly according to the number and size of predators, relative abundance of size classes of predators and prey, presence of alternative predators and prey, and season and location (e.g., Pearsons et al. 1999, 2005; Fritts and Pearsons 2006). Few investigations have been designed to provide results with widespread applicability; instead they focus on a narrow spatial and temporal scope (see examples in Chapters C.3, C.5). Such studies generally have been limited to investigations of two-species interactions such as pikeminnow reducing the numbers and survival of salmon smolts, or occasionally to three-species interactions. Too few studies have directly addressed key ecological questions such as how food webs and resulting food production have been altered for anadromous and resident fishes as altered river alterations have restricted floodplains and their connectivity with the main channels (Stanford et al. 2006; Chapter E.4). Predation studies are not typically integrated with conceptual frameworks of how rivers and their food webs function. In addition, there is little effort to link the food webs of large tributaries with conditions in smaller streams (Chapter D.1) or the mainstem (Chapters D.3, D.5, D.6). Results from the narrowly conceived studies often meet immediate management needs, but are challenging to interpret and apply in the broader context of large tributary food webs.

Only rarely have results of specialized and applied studies, conducted under the Fish and Wildlife Program, been put into theoretical and conceptual frameworks, even in resulting peer reviewed articles. Without an adequate conceptual framework, the broader implications are not easily recognized and the results and applications of food web studies remain site specific. The potential ecological and economic value of this information to the Fish and Wildlife Program is thereby diminished. Future studies should be designed, reviewed, classified and evaluated with a better regard for major theoretical frameworks, ecological concepts and models (Ward et al. 2002), even those with well-defined, immediate, practical sociopolitical and management objectives.

Tributary Food Web Studies in Relation to Conceptual Frameworks for River Ecology

In designing food web studies for the Basin's large tributaries, an adequate and appropriate conceptual framework based on ecological principles is needed to understand, interpret and generalize results. Just as it was effectively argued that an adequate conceptual framework is needed for effective planning and implementation of salmon restoration activities (Williams et al. 2006), it is also needed for understanding food webs and the effects of habitat changes, including restoration.

What is an appropriate conceptual framework for understanding food webs in the Basin's tributaries? There is no ideal framework for all situations since river morphologies and other characteristics affecting food webs are highly diverse. A tributary with a braided channel and broad, forested floodplain has food webs fundamentally different from tributaries with strongly confined channels and narrow, unforested floodplains (Hoeinghaus et al. 2007). Therefore, numerous conceptual frameworks have been proposed based on ecological observations and studies of large tributaries.

There are nine generally accepted lotic (flowing water) conceptual frameworks used to characterize rivers (Table D.2.2; Ward et al. 2002). They include three based on river gradients: the *Stream Zonation Concept* (Illies and Botosaneanu 1963*)*, the *River Continuum Concept* (Vannote et al. 1980), and the *Hyporheic Corridor Concept* (Stanford and Ward 1993). Three more are based on the disturbance framework: the *Flood Pulse Concept* (Junk et al. 1989, Junk and Wantzen 2004), the *Serial Discontinuity Concept* (Ward and Stanford 1995), and the *Telescoping Ecosystem Concept* (Fisher et al. 1998). One is based on the ecotone framework, the *Aquatic-Terrestrial Ecotones Concept* (Naiman and Décamps 1990). Another one is based on the hierarchy framework: the *Catchment Hierarchy Concept* (Frissell et al. 1986). And a ninth one is based on the connectivity framework: the *Hydrologic Connectivity Concept*.

Other concepts have been developed as well. Thorp and DeLong (1994) describe a *Riverine Productivity Model* where significant energy in large rivers is derived from local sources of autochthonous production and coarse particulate matter associated with riparian zones. Power et al. (1995) use a series of hydraulic food chain models linking physical features of rivers with poorly understood aspects of large river food webs. Some of the nine concepts and other concepts were developed mainly for smaller streams (e.g., *Catchment Hierarchy* and *Telescoping Ecosystem Concepts*), and some for large floodplain rivers (e.g., the *Flood Pulse Concept; Hydraulic food web models*), and some for large rivers without large floodplains (e.g., *Riverine Productivity Model*). Each of the lotic ecology concepts is, in a sense, a special case. Nevertheless, all can be understood and linked at a higher landscape level within the concept of hierarchical patch dynamics, which views each river as a "unique, patchy discontinuum, from headwaters to mouth" (Poole 2002; p.641).

In practice, most existing studies relevant to foods funded and completed in the Columbia River's large tributaries have not been designed according to *any* of the broader conceptual frameworks and ecological concepts. They were designed to address more limited objectives related to practical sociopolitical management concerns. The objectives included landscape and land-use changes and practices (including intensive agriculture, land drainage, river channelization, and timber removal), effects of major tributary dams, riverine and reservoir predation by native and non-native species, dietary overlap and potential interspecies competition (both native and non-native species; ISAB 2008-2), and effects of contaminants (Chapters B.2, C.3, C.7, D.5 and D.6).

Collectively, the existing concepts provide meaningful frameworks for understanding food webs in the Basin's large tributaries. However, each concept and its underlying theoretical framework best apply in some form to different tributaries or different segments of tributaries. Morphological differences among the large tributaries present a wide range of floodplain and channel types (Kellerhals and Church 1989), which ultimately affect biotic interactions and food webs. Poole (2002) recognized these differences in applying specific concepts to different rivers as well as to different segments of the same river. Each river is unique, as well as patchy and discontinuous (i.e., non-uniform) in its ecological character.

For rivers with minimal floodplains, food webs may be best understood in the context of the *River Continuum Concept* involving more influences and movements of nutrients and organisms longitudinally. For example, in the lower Willamette River, the bedrock channel is stable and the floodplain is more confined than in upper reaches of the river (Hulse et al. 2002). An even more confined floodplain exists for much of the lower Snake River. In contrast, the upper Willamette River mainstem and the historical Kootenai River in Northern Idaho have more extensive floodplains. Those floodplains have been greatly modified by agricultural development, resulting in loss of seasonal habitats and connectivity. In those situations, food webs may be more effectively interpreted in the context of the *Flood Pulse Concept*, which involves the lateral movement of water, nutrients, organic matter and organisms between the main channel and the floodplains as well as changing sources of nutrients and organic matter over ecological time scales (Naiman et al. 2010). Closely linked to the need for a flood pulse is the need for lateral connectivity between off-channel habitats and the main channel (Roach et al. 2009), an important aspect of natural rivers (i.e., the connectivity concept of Amoros and Roux 1998; Chapter E.4). For example, Roach et al. (2009) report that the food web length in the upper Mississippi River is shorter and therefore more efficient where lateral connectivity is strong because alternative food sources result from connectivity between floodplain habitats and the main channel. Studies evaluating the effects of agricultural development on aquatic food webs would find the *Flood Pulse Concept* and *Connectivity Concept* useful in designing studies and sampling plans. Food webs may thus be best understood by applying one concept in one river and another concept in another river. Similarly, within a river, the best concept for understanding food webs may differ among reaches because of the variable, patchy and discontinuous nature of habitat. For understanding food webs, the question is not “What is an appropriate conceptual framework for large Columbia River tributaries?” but “Which of the concepts is (are) most appropriate in which rivers or river segments?”

Table D.2.2. Nine conceptual frameworks potentially useful in characterizing food web studies in rivers, including a brief description, example, and potential useful application

Concept	Description	Example	Potential useful applications for food webs	References
Stream zonation	Distinct faunal (especially fish) zones from headwaters to river mouth are separated by transition zones.	Coldwater, coolwater and warmwater zones of large tributaries inhabited by salmon or trout, walleye, smallmouth bass or northern pike, and largemouth bass, respectively.	Longitudinal studies of large tributaries with small floodplains. Effects of longitudinal habitat (zonal) changes on species composition and resulting competition/predation interactions.	Illies and Botosaneanu (1963); Huet (1959, 1962); Hynes (1962)
River Continuum	Clinal (longitudinal) rather than zonal changes in resource gradients result in clinal changes in community composition, including functional invertebrates groups and fish.	Fish community structure more heavily dominated by mollusks, other filterers and collectors, and detritivorous fish than in smaller upriver tributaries.	Longitudinal studies of large rivers with small floodplains. Changes in forage composition for native fishes along gradients and effects on community structure.	Vannote et al. (1980); Sedell et al. (1989)
Hyporheic Corridor	" (1)…water, solutes, and organic and inorganic materials, including uniquely adapted biota, move through large-scale interstitial pathways determined largely by the dynamic nature of floodplain morphology, and (2) … the convergence of surface and groundwaters may be the primary determinant of floodplain landscapes and… biodiversity and production" (Stanford and Ward 1993; p. 48).	Distinct biota, including fish, associated with habitats above and below the substrate fed by groundwater and subsurface flow.	Assessment of channel and aquifer interactions with food webs and aquatic community structure, with application to large tributaries having all sizes of floodplains. Links of ground water and subsurface flow and biota with foraging, spawning, and early rearing opportunities for salmonids.	Stanford and Ward (1993)
Serial Discontinuity	Discontinuities in the river continuum and biophysical gradients such as dams are major agents of disturbance; rivers will respond or attempt to reset toward a more natural or unregulated state as distance from the disturbance increases.	Distinct differences in abundance and composition of biota, including fishes, will occur in the forebays and tailraces of dams.	Assessment of dams on blocking and concentrating migratory fishes, with resulting creation of predation traps for upstream and downstream migrating salmon. Predation on lampreys and sturgeon at impassable or nearly impassable barriers.	Stanford and Ward (2001); Ward and Stanford (1995)

Flood Pulse	“The principal driving force for the existence, productivity, and interactions of the major biota in river-floodplain systems is the flood pulse… Fish yields and production are strongly related to the extent of accessible floodplain” (Junk et al. 1989, p. 110).	In the Kootenai River, reduction of the flood pulse from Libby Dam, and disconnection of major portions of the floodplain have negatively affected nutrient delivery longitudinally (from upriver) and latitudinally (from the floodplain, resulting in negative effects on white sturgeon spawning, early survival and growth.	Defining the importance of the flood peak for spawning success of fish. Defining the importance of lateral connectivity among habitat types of large tributaries for survival, year class strength and growth of fishes. Importance of lateral areas off of the main channels along large tributaries as forage sources.	Junk et al. (1989); Junk and Wantzen (2004)
Telescoping Ecosystem	“The whole stream-corridor ecosystem consists of several nested cylindrical elements [including riparian, parafluvial, hyporheic and surface stream, from outside-in] that extend and retract, much as would a telescope.” After a long hiatus in disturbance, the elements are retracted. Minor disturbances may only affect the most central (least resistant) elements of the telescoping ecosystem. Major disturbances will extend all aspects of the telescope.	Disturbance of the riparian zone from timber removal may lead to a long multi-generational recovery period; disturbance from a moderate flood event may be more temporary.	Analysis of expected resiliency and recovery rates of different aspects of large-tributary food webs (e.g., riparian inputs versus instream interactions) to long term habitat changes versus more temporary ecological disturbances and interannual variations in flood pulses.	Fisher et al. (1998)
Aquatic-terrestrial Ecotones	“The productivity of aquatic and riparian habitats is interlinked by reciprocal exchanges of material”; the riparian zone is fish habitat and has strong and direct influences on fishes (Naiman et al. 1988)	Riparian controls on stream processes; roles of keystone species such as beaver; role of marine derived nutrients (salmon) in both fish and riparian/terrestrial production.	Riparian influences on food webs and stream processes; identification of keystone species and how they alter food webs and production at different trophic levels; riparian and nutrient manipulation to increase productivity for fishes.	(Naiman and Décamps 1990; Naiman and Latterell 2005)
Catchment Hierarchy	“By viewing streams as hierarchically organized systems, the approach focuses on a small set of variables at each level that most determine	Potential range of food web interactions at each scale (watershed to microhabitat) is constrained by capacity of river	A range of food web studies of particular species could be evaluated to assess the variations and stability of patterns of food habits across	Frissell et al. (1986)

	system behaviors and capacities within the relevant spatiotemporal frame. Micro-scale patterns are constrained by macro-scale geomorphic patterns. Each unit of the stream remains within the context of the watershed as a whole. Such a classification defines the structure, development, and persistence, and environment of each habitat, features which determine the suitability for different organisms. …stream communities can be viewed as systems organized within this hierarchical habitat template." (Frissell et al. 1986, p. 282).	system at each level.	different spatial scales (microhabitat, pool/riffle, reach, segment, stream/river, basin, and beyond) and different temporal scales.	
Connectivity	"Floodplain water bodies differing in connectivity with surface waters of the main channel exhibit different successional trajectories and contain different biotic communities. The degree of connectivity between ground waters and surface waters is also an important determinant of functional processes in aquatic and riparian systems." (Ward et al. 2002, p. 448)	Fish community structure, colonization, and value of off-channel rearing habitat for anadromous salmonids are influenced by degree of connectivity of backwaters with main channel (Colvin et al. 2009)	Food webs in relation to successional stage of connected versus non-connected backwaters.	Amoros and Roux (1998)

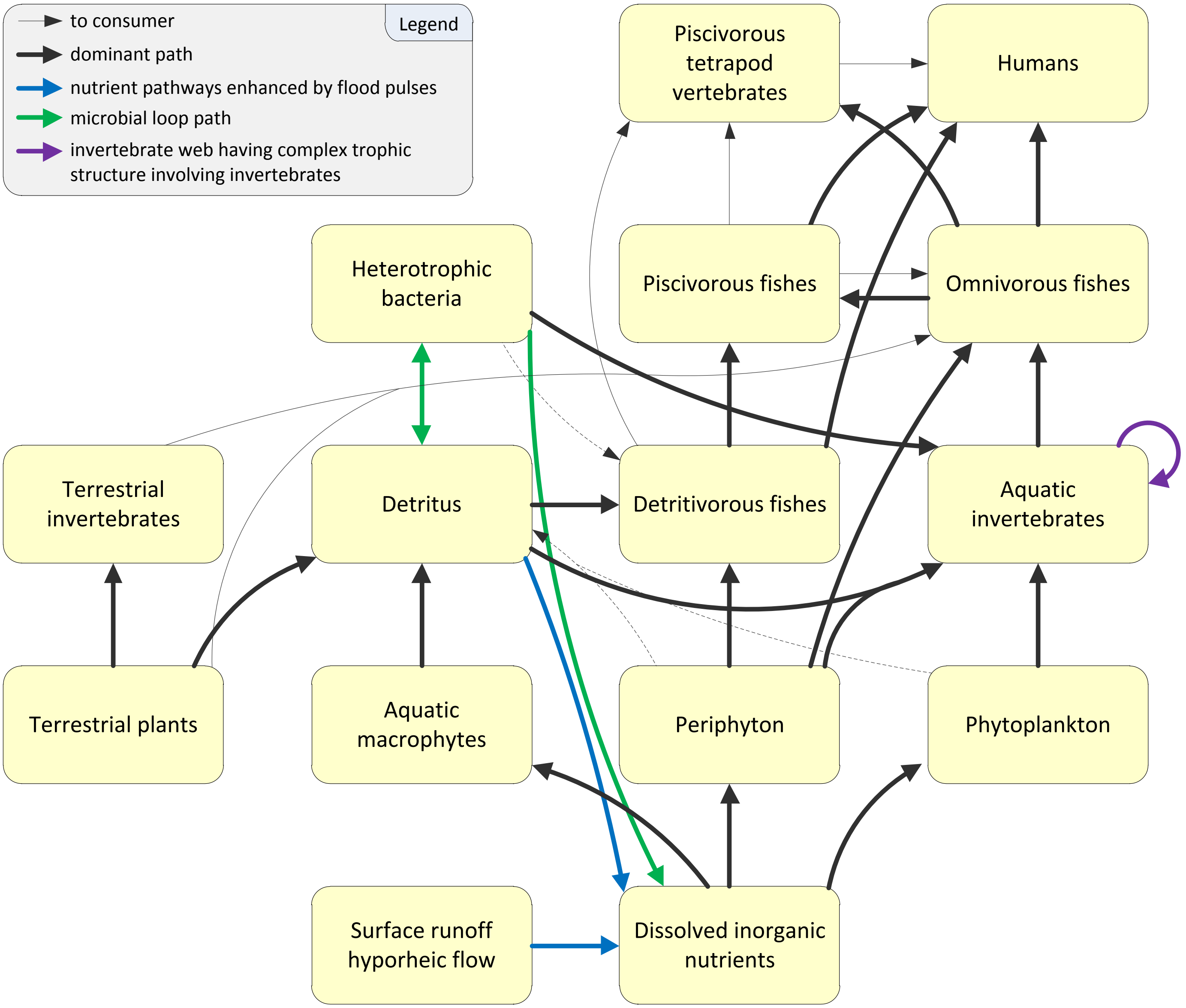


Figure D.2.1. Generalized food web for floodplain-river ecosystems. Boxes are aggregate material pools and vectors represent consumer-resource interactions. See legend for more.

Recommendation: Frame Future Studies involving Tributary Food Webs in Relation to Broader Conceptual Frameworks

Future investigations of food webs in the Basin's large tributaries will benefit by planning investigations in at least one of these major conceptual frameworks. To simplify the issue, and for the purpose of illustration, many investigations can be framed by one of three frameworks: the Flood Pulse Concept, the River Continuum/stream zonation Concept, and the Serial Discontinuity Concept (Table D.2.2). The other six concepts (and others) can be used in conjunction with these concepts to broaden the applicability and meaningfulness of specific studies. Three examples follow:

Food Webs Related to the Flood Pulse Concept*.* The *Flood Pulse Concept* is appropriate for interpreting food webs in most but not all of the Basin's large tributaries and segments (see Figure D.2.1). In general, where the floodplains of large tributaries are modified and agriculture is a dominant land use, the *Flood Pulse Concept* is a powerful aid in designing and interpreting food web studies (Hoeinghaus et al. 2007). In the upper Willamette River, for example, the floodplain has been heavily modified by agriculture for 160 years. In the Willamette mainstem, unlike more interior rivers, a winter (rather than spring) flood pulse is a dominant feature, providing crucial overwintering habitat to a variety of fish (Colvin et al. 2009). Intermittent stream and winter floodplain habitats were more abundant before dams, ditches and revetments impeded seasonal flooding (Sedell and Luchessa 1982; Chapter B.1). In locations where these habitats have been eliminated, strategically planned wetland and floodplain restoration may be beneficial (Colvin et al. 2009), which are consistent with the *Flood Pulse Concept*.

Similarly, in the Idaho portion of the Kootenai River, agricultural development has resulted in significant channelization, bank stabilization and levee construction, greatly limiting river function and reducing connectivity of the main channel with other aquatic habitat on the floodplain. The net result is that natural food webs have been significantly altered. Nutrient trapping by Libby Dam along with floodplain isolation from the main channel has resulted in decreased nutrient inputs (Snyder and Minshall 2005) and altered the carbon balance of the river (Kootenai Tribe of Idaho 2009). This has caused a reduction in abundance, growth and production of many native fishes, including the endangered Kootenai stock of white sturgeon. Maintaining and increasing floodplain connectivity, a key aspect of the *Flood Pulse Concept*, is nearly always a positive outcome for sustaining tributary food webs.

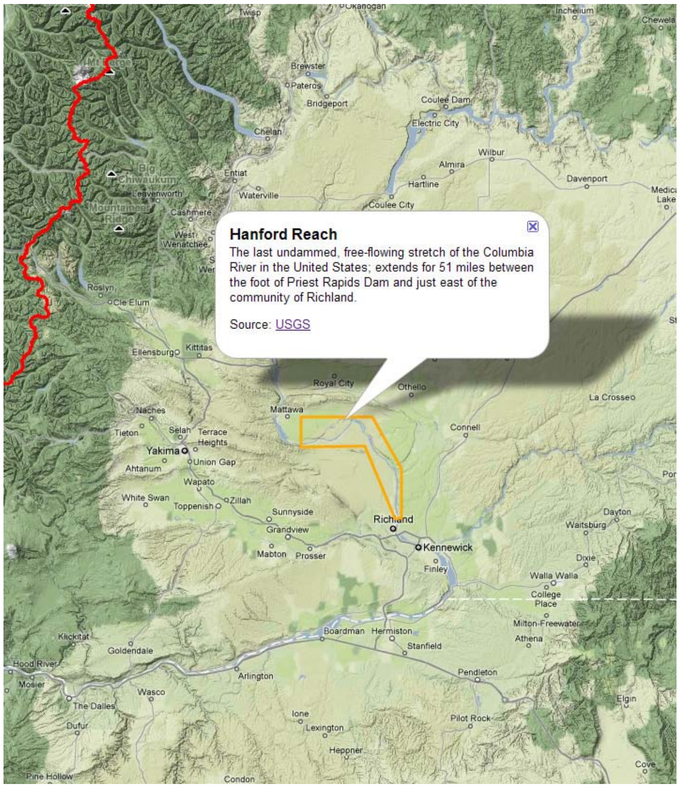
Food Web Related to the River Continuum or Stream Zonation Concepts. Where factors affecting food webs come more directly from upstream or downstream (e.g., longitudinally), the *River Continuum* or *Stream Zonation* concepts are more effective frameworks than the *Flood Pulse Concept*. For example, the lower Willamette River below Willamette Falls contains juvenile Chinook and coho, typically characterized as coldwater species, and several non-native species, especially yellow perch and smallmouth bass, typically characterized as coolwater species. As habitat alterations have warmed waters in larger tributaries, the potential for such coolwater/coldwater fish interactions becomes greater. As salmon move from small streams into large tributaries, issues such as species diversity and presence of non-native species (e.g., perch, walleye, smallmouth bass and shad) become increasingly important (Chapter C.5). Changes to historically cold-water tributaries by warming water in downriver segments can result in a cool or warm water fish fauna (i.e., fish from historically different river zones) expanding, invading, preying upon, competing with, and replacing a cold water fauna (Vile et al. 2004; Friesen et al. 2003). In such situations, the *River Continuum Concept* and the *River Zonation Concept* may be preferable frameworks to the *Flood Pulse Concept* for understanding and interpreting food web interactions.

Food Webs Related to the Serial Discontinuity Concept. Food webs of large impounded tributaries may be better understood in terms of the *Serial Discontinuity Concept* (SDC), as originally formulated (Ward and Stanford 1983), especially if there are limited floodplains. The concept is designed to explain a disruption of longitudinal gradients at dams. For studies on rivers with floodplains, the SDC as modified (Ward and Stanford 1995a,b) may be more appropriate. This concept has not been applied to food web studies so far.

Dams and impoundments, even small impoundments associated with irrigation diversions, typically result in discontinuities in habitat types consistent with the *Serial Discontinuity Concept*. Predators, both native (e.g., pikeminnow) and non-native (walleyes, smallmouth bass, northern pike and marine mammals such as sea lions) can find preferred habitat (slower, clearer water) in impounded waters, resulting in increased effectiveness of predation on native salmon juveniles and other small fishes. Salmon migrations, both downstream and upstream, may be impeded and slowed, resulting in greater vulnerability of salmon to predation at all life stages. Many investigations might benefit from being viewed as how it relates to the *Serial Discontinuity Concept* (as well as the *River Continuum Concept*). Past studies can be viewed in relation to specific expectations and predictions, especially as one moves away from the discontinuity (i.e., the dam; Stanford and Ward 2001).

These examples are intended to show how investigations funded under the Fish and Wildlife Program on food web interactions in large tributaries would benefit from a broader conceptual framework. These conceptual frameworks, including others listed by Ward et al. (2002) and elsewhere, are interrelated and based on ecological theory and field observations (Poole 2002). Once a study is cast in an appropriate conceptual framework, the use of well-designed species interaction studies and models (e.g., Wootton and Power 1993, Wootton et al. 1996) to predict competitive and predatory effects will allow the Program's studies and restoration activities to be broadly applicable. This approach will help fill many existing knowledge gaps associated with large-tributary food webs. It will also add significant value to the Fish and Wildlife Program's funded research activities and ultimately return more useful knowledge per research dollar spent.

D.3. Free-flowing Reaches of the Columbia River



Hanford Reach

The last undammed, free-flowing stretch of the Columbia River in the United States; extends for 51 miles between the foot of Priest Rapids Dam and just east of the community of Richland.

Source: USGS

Free-flowing Columbia (Hanford). See interactive map.

Introduction

It is widely appreciated that the food webs of large free-flowing rivers are substantially different from those of lakes and reservoirs (Wetzel 2001). Historically, the free-flowing reaches of the Columbia River certainly supported productive, diverse and resilient food webs. The importance of these food webs, however, was not broadly valued, as hydroelectric development converted most of the river above Bonneville Dam into a series of reservoirs. Only a short free-flowing reach remains on the Hanford Nuclear Reservation and Hanford Reach National Monument in central Washington. Known as the Hanford Reach, it extends 80 km downstream from Priest Rapids Dam to the city of Richland, yet maintains several ecologically unique populations and significant functions.

Inventories of aquatic biota in the Hanford Reach began with tests for bioaccumulation of radioactive waste products in the late 1940's. Reports on these early sampling efforts (e.g., Davis and Cooper 1951, Coopey 1953) were classified for five decades, and have never been published in the refereed literature. In the 1970's, plans by the Washington Public Power Supply System to build nuclear power plants on the reservation resulted in a new round of ecological surveys of the Hanford Reach (Pacific Northwest National Laboratory 1977, 1984, 1985, 1986), which provides most of the published information on the invertebrate fauna. More recently (2000), designation of the 790 km^2 "buffer zone" surrounding the reservation as the Hanford Reach National Monument instigated an inventory of the area's biological features. The inventory, based on a synthesis of previous surveys and supplemented by limited field work, concludes that the diverse aquatic biota of the Hanford Reach continues to be dominated by native species characteristic of lotic (flowing water) habitats (Nature Conservancy 2003).

This chapter summarizes what is known about changes in Hanford Reach food webs over the past 60+ years. Two upstream dams (Grand Coulee, 1941; Rock Island, 1932) were constructed before sampling of the Hanford Reach biota began in the 1940's, and five additional dams were constructed in the 1960's. As discussed below, these upstream dams have important effects on the Hanford Reach food web.

Flow Regulation and Consequences for Biota

Although the Hanford Reach is free-flowing, the food web characteristics of the reach have been affected by the operation of upstream dams. Water diversion through dam powerhouses can be adjusted to meet changing regional power needs (load-following power production) over short time periods, causing downstream flows and water elevations to vary over a wide range. Changes in discharge from Priest Rapid Dam can result in water elevation changes of 3 m or more within the Hanford Reach on a daily basis (Tiffan et al. 2002). To reduce interference with spawning of fall Chinook and dewatering of redds, agreement was reached between the public utility that operates Priest Rapids Dam and management agencies to limit flow fluctuations during spawning and egg incubation (Volkman 1977). The agreement did not, however, limit flow fluctuations during the late winter and spring juvenile rearing period (Figure D.3.1), and concerns arose over the stranding and death of juveniles in isolated pools during load-following operations (ISAB 1998-5, Wagner et al. 1999). A 2004 agreement specified new operational guidelines for load-following operations at Priest Rapids Dam (Hanford Reach Fall Chinook Protection Program 2004) that limit flow fluctuations during the winter and spring. The effects of fluctuating flows on different food-web components in

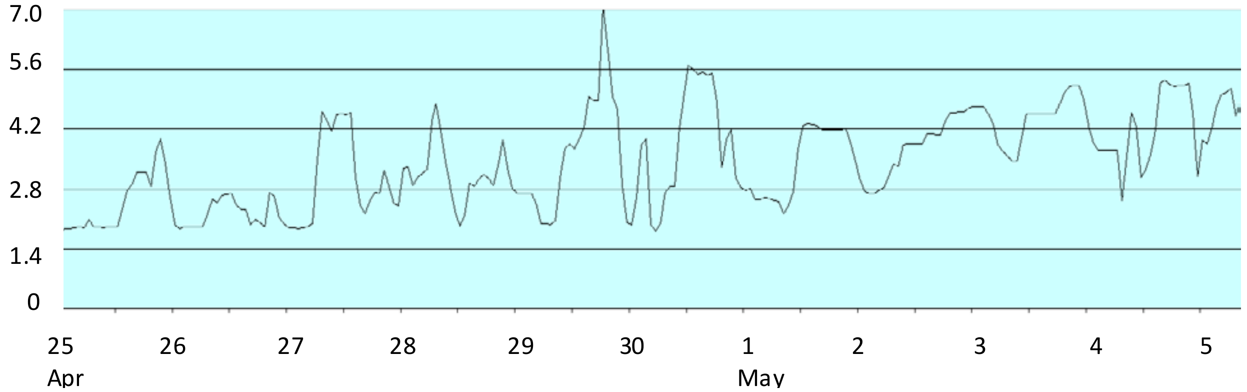


Figure D.3.1. Priest Rapids Dam hourly flow fluctuations ($m^3\ s^{-1}$, in thousands), spring 1998

Hanford Reach littoral areas are discussed below.

Benthic algae and invertebrates are adversely affected by rapidly fluctuating flows. Exposed periphyton (algae) may become desiccated (Blinn et al. 1995), and benthic invertebrate communities show declines in diversity, density and biomass (Cushman 1985, Gislason 1985, Stark 2001). Further, invertebrate taxa differ in resistance to temporary dewatering. Stoneflies are particularly sensitive (Moog 1993), while midges and hydropsychid caddisfly larvae are relatively resistant (Stark 2001). Stoneflies have not been found in the Hanford Reach since the late 1970's (Pacific Northwest National Laboratory 1977, 1984, 1985, 1986), and are presumed to no longer be present in either periodically dewatered or deeper areas (Nature Conservancy 2003). Midge and hydropsychid caddisfly larvae are well represented in the benthic invertebrate community. However, a lack of standardization and continuity in benthic sampling techniques and changes over time in the taxonomy of some groups makes detailed comparison of earlier and more recent survey results problematic (see Sidebar D.3.1).

Although fluctuating flows are clearly deleterious to benthic algae, invertebrates, and fishes in littoral areas, changes in the annual hydrograph brought about by development of the hydropower system and upstream storage reservoirs have additional but uncertain consequences for Hanford Reach biota. Storage reservoirs capture much of the spring runoff and release it throughout the summer and fall months; consequently, peak spring flows have greatly decreased, low late-summer flows have increased, and mean summer and winter flows are now roughly equivalent (Chapter B.2). The annual temperature cycle also has been dampened: releases of deep (hypolimnion) water from Grand Coulee Dam, 321 km upstream, moderate warm summer temperatures downstream at least as far as the Hanford Reach (Chapter B.2). These changes may have created more temporally stable flow and thermal regimes for benthic biota living in sub-littoral areas not directly affected by short-term flow fluctuations. Although the species richness of mayflies is reduced by fluctuating flow regimens, increased richness is associated with flow constancy (Malmquist and Englund 1996), and this may be true for other groups as well. The apparent increased diversity of mayflies and continued high diversity of caddisflies and chironomids in the Hanford Reach since the 1940s (see Sidebar D.3.1) may be related to moderation of annual flow and temperature extremes. Unfortunately, no comparisons are available between pre-development and present-day invertebrate abundances.

Sidebar D.3.1. To what extent has hydropower development altered food webs in the Hanford Reach?

Although the Hanford Reach is undammed, both short-term and annual flow patterns have been significantly altered by upstream dams. Furthermore, numerous non-native invertebrates and fishes have colonized hydropower system reservoirs upstream and downstream (Chapters C.3, C.5, and D.6), and many of these species are also present in the Hanford Reach. To address the possibility that these or other influences may have altered food webs in the Hanford Reach, The Nature Conservancy summarized and compared 11 surveys of benthic invertebrates that took place between 1948 and 2002 (Nature Conservancy 2003). The studies used a variety of sampling methods, ranging from a large barge-mounted suction dredge (Davis and Cooper 1951) to wading along the shoreline in an informal recent study (Nature Conservancy 2003). Survey comparisons were complicated by differing degrees of discrimination between taxa (to the level of species in some studies and to genus in others, or in some instances only to order), and by major revisions in the taxonomy of some groups over time. Voucher specimens were not retained, so uncertainties about species identification cannot be resolved. Despite these difficulties, The Nature Conservancy reached several conclusions: (1) stoneflies have disappeared (three species were reported in the 1940's), (2) the western pearl mussel, present at high densities in earlier years, has almost or totally disappeared (confirmed by Helmstetler and Cowles 2008, who found no pearl mussels in the Hanford Reach), (3) mayfly diversity has increased, and (4) caddisfly and chironomid diversity remains high. Pearl mussels and stoneflies are sensitive species that have declined in altered habitats throughout the western Unites States in recent decades. The decline of these species in the Hanford Reach may be related to hydrosystem-associated changes in short-term or seasonal flows, in temperature regimes or in sediment transport, but the specific causes are obscure. Overall, present-day food webs in the Hanford Reach appear similar to those present in the 1940's. A necessary qualification, however, is that no comprehensive biological surveys have been performed for over 30 years. In the intervening years, some native species may have decreased or increased in abundance, and new, non-native species most likely have become established.

The Contemporary Food Web

The food web in the Hanford Reach, although affected by flow regimes imposed by upstream dams, differs from food webs in mainstem reservoirs, and is typical in many respects of lotic food webs in large free-flowing rivers (Naiman and Bilby 1998). Energy flow from benthic algae, macrophytes, emergent plants and riparian vegetation to benthic invertebrate consumers is of primary importance, in contrast to the dominance of planktonic food webs in mainstem reservoirs. Native fishes, which are well adapted to feeding on aquatic insects, amphipods and other benthic invertebrates, continue to thrive in the Hanford Reach (Figure D.3.2).

Primary production. Being relatively shallow and having clear water, light is able to reach the coarse sediments thereby enabling diatoms to dominate the periphyton community (Neitzel et al. 1982a). Primary production by phytoplankton and macrophytes is secondary relative to periphyton. The importance of periphyton in Hanford Reach food webs is well established by published studies of native fish diets. Periphyton is the major food item (by mass) for largescale suckers and chiselmouth of all age classes (Dauble 1986, Gray and Dauble 2001), and is also important in the diets of redside shiner, peamouth and longnose dace (Gray and Dauble 2001; Table D.3.1). These native fishes are among the most abundant in the Hanford Reach (Gray and Dauble 1977). Periphyton is also a primary food source for grazing benthic invertebrates.

Phytoplankton in the Hanford Reach is derived largely from upstream reservoirs where diatoms dominate even though unicellular flagellates, green algae, and microplankton are present (Shields et al. 2002). Five to seven genera of diatoms constitute 90 to 95% of the phytoplankton (Neitzel et al. 1982a). The phytoplankton appear, on the basis of low chlorophyll *a* content, to include a high proportion of senescent or dead cells, possibly because they are flushed from upstream reservoirs (Neitzel et al. 1982a). Phytoplankton may be an important dietary component for filter-feeding benthic invertebrates (e.g., net-building caddisfly larvae, bivalve molluscs) but the implications of this for system scale processes (e.g., productivity, resilience) remain unknown.

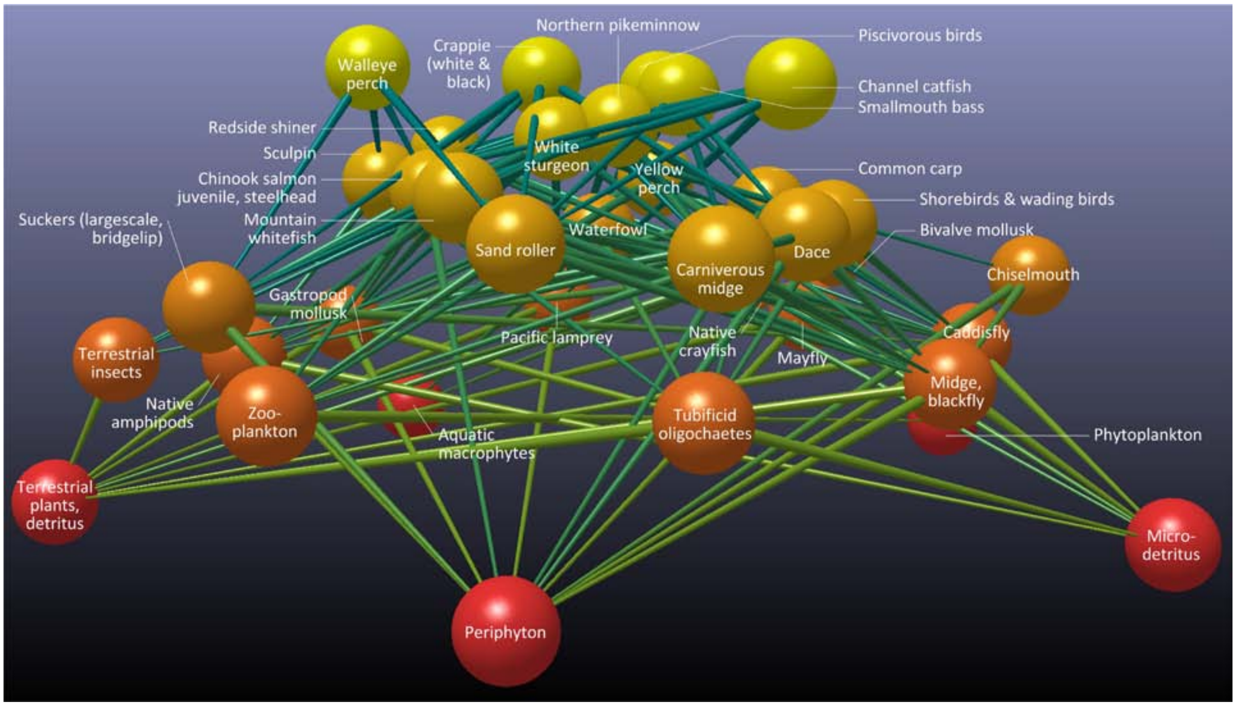


Figure D.3.2. Food-web structure in the Hanford Reach of the Columbia River.
Red = primary producers, orange = primary consumers, yellow = secondary consumers, green = tertiary consumers (created in J. Dunne's *Network3D* software)

Emergent wetland plants and aquatic macrophytes are of some importance as primary producers in the Hanford Reach. Reed canary grass, cattails, and bulrushes are present in backwater areas (Books 1985, Tiffan et al. 2002), and Eurasian milfoil, an invasive non-native species, has become well-established in backwater areas in recent years (D. Dauble, Pacific Northwest National Laboratory, personal communication). Detritus derived from the aquatic plants is likely a source of food for benthic invertebrate species, particularly in the fall and winter months, as it is in the Columbia River estuary (Simenstad et al. 1990, Chapter D.7). Another, possibly more important energy input is organic detritus and terrestrial insects derived from abundant riparian vegetation growing on the banks of sloughs, secondary channels and backwaters scattered along the Hanford Reach (ISAB 2000-12). Several species of willows are widely established in the riparian zone, and it is hypothesized that their presence is facilitated by power-peaking operations at Priest Rapids Dam, which result in daily wetting of a wide horizontal range of shoreline (Books 1985). It is suspected that riparian-derived materials are important contributors to the Hanford Reach food web, just as they are in other Basin habitats (ISAB 2000-12).

Zooplankton. The zooplankton community is presumably derived largely from upstream reservoirs. Production in backwater areas, although important downstream in the John Day reservoir (Haskell et al. 2006), is limited in the Hanford Reach by daily fluctuations in water level. Zooplankton are of low importance in the diets of fishes inhabiting the Hanford Reach (Dauble 1986, Gray and Dauble 2001), including drift-feeding juvenile Chinook (Becker 1970, Rondorf et al. 1990). *Daphnia*, a larger cladoceran preferred over other zooplankton by planktivorous fishes, is relatively uncommon, making up less than 10% of the total zooplankton (Neitzel et al. 1982b). The small cladoceran *Bosmina*, the calanoid copepod *Diaptomus*, and the cyclopoid copepod *Cyclops*, all species less readily eaten by fish, are the most abundant, although in aggregate not exceeding 750 organisms per m^3 at the early-summer peak density in most years (Neitzel et al. 1982b). The diet of juvenile Chinook may include *Daphnia* in mid-summer, but most juvenile salmon have migrated downstream and out of the Hanford Reach by that time (Dauble et al. 1980).

Table D.3.1. Native and non-native fishes reported from the Hanford Reach[a], relative abundance[b] (A, abundant; NA, not abundant; UK, unknown; T, transient in area), and diet[c] (major items in descending order of importance by mass) of abundant species

Family	Scientific name	Common name	Relative Abundance	Diet
Native				
Acipenseridae	*Acipenser transmontanus*	White sturgeon	A	Var
Catostomidae	*Catostomus columbianus*	Bridgelip sucker	A	Per, Tri
	C. macrocheilus	Largescale sucker	A	Per, Tri
	C. platyrhynchus	Mountain sucker	NA	——
Cottidae	*Cottus spp. (five species)*	Sculpin	A	Chi, Tri, Oli, Amp
Cyprinidae	*Acrocheilus alutaceus*	Chiselmouth	A	Per
	Mylocheilus caurinus	Peamouth	A	Per, Gas, Tri, Chi
	Ptychocheilus oregonensis	N. pikeminnow	A	Fish, Cra, Tri,TI
	Rhinichthys cataractae	Longnose dace	A	Zoo, Per, Chi
	Rhinichthys falcatus	Leopard dace	NA	——
	Rhinichthys osculus	Speckled dace	NA	——
	Richardsonius balteatus	Redside shiner	A	Tri, Per,Chi
Gadidae	*Lota lota*	Burbot	UK	——
Gasterosteidae	*Gasterosteus acultatus*	Stickleback	NA	——
Percopsidae	*Percopsis transmontana*	Sand roller	NA	——
Petromyzontidae	*Entosphenus tridentatus*	Pacific lamprey	T	——
	Lampetra ayresi	River lamprey	T	——
Salmonidae	*Corygonus clupeaformis*	Lake whitefish	UK	——
	Oncorhynchus tshawytscha	Chinook salmon	A	Tri, Chi, Eph, TI, Zoo
	O. gairdneri	Steelhead	T	——
	O. kisutch	Coho salmon	T	——
	O. nerka	Sockeye salmon	T	——
	Prosopium williamsoni	Mt. whitefish	A	
	Salvelinus malma	Dolly Varden	NA	——
Non-Native				
Centrarchidae	*Lepomis gibbonsus*	Pumpkinseed	UK	——
	L. macrochirus	Bluegill	UK	——
	Micropterus dolomieui	Smallmouth bass	A	Fish, Cra, Tri
	M. salmoides	Largemouth bass	UK	——
	Pomoxis nigromaculatus	Black crappie	A	——
Clupeidae	*Alosa sapidissima*	American shad	UK	——
Cyprinidae	*Cyprinus carpio*	Common carp	A	Per, Var
	Tinca tinca	Tench	UK	——
Ictaluridae	*Ictalurus melas*	Black bullhead	UK	——
	I. natalis	Yellow bullhead	UK	——
	I. punctatus	Channel catfish	A	Var
Percidae	*Perca flavescens*	Yellow Perch	A	
	Stizostedion vitreum	Walleye	A	Fish

[a] Table adapted from Gray and Dauble (1977, 2001). Some food-preference data added from Scott and Crossman (1973).
[b] Abundance estimates are from surveys performed in 1973-1975 (Gray and Dauble 1977, 2001), and may not accurately represent present abundance.
[c] Abbreviations for food items: Amp, amphipods; Biv, bivalves; Chi, chironomids (midges); Cra, crayfish (native *Pacifastacus leniusiculus*); Eph, Ephemeroptera (mayflies); Fish, fish; Gas, gastropods (snails); Oli, oligochaetes (segmented worms); Per, periphyton (benthic algae); TI, terrestrial insects; Tri, Trichoptera (caddisflies); Var, all categories with the exception of periphyton; Zoo, zooplankton. Food information obtained from Dauble (1986), Dauble et al. (1980), Gray and Dauble (2001), Rondorf et al. (1990).

Benthic invertebrates. The benthic invertebrate community is diverse, with 151 taxa reported (Nature Conservancy 2003). Immature midges (Chironomidae) and black flies (Simuliidae) are abundant and presumably speciose, although not identified to genus or species due to the paucity of distinguishing taxonomic characteristics. Other groups of native invertebrates are also diverse, particularly in comparison with diversity of the same groups in mainstem reservoirs. The Nature Conservancy lists 18 taxa of caddisflies (Trichoptera), 13 taxa of mayflies (Ephemeroptera), and 17 taxa of snails (Gastropoda). The native crayfish *Pacifasticus leniusculus*, an omnivore and an important link in the food web between benthic epifauna and fish, has apparently maintained high population densities (based on informal visual surveys; Nature Conservancy 2003).

Although the Nature Conservancy (2003) reported six species of native bivalves, it also stated that “the only healthy mollusk population is that of the introduced exotic Asiatic clam, which is extremely abundant in the Hanford Reach.” The role of the Asiatic clam in the Basin’s aquatic food webs has not been examined in detail, but Asiatic clams are known to feed non-selectively on phytoplankton and fine organic detritus (Boltovshkoy et al. 1995) and can, even at moderate densities, filter up to 5 m^3 of water per m^2 of bottom area daily (Lauritsen 1986). By producing large quantities of feces and pseudo-feces, nutrient recycling to lower food-web levels is greatly increased (Lauritsen and Mozley 1989). Asiatic clams are eaten by juvenile white sturgeon in the lower Columbia River (Beamesderfer and Nigro 1995) and the veligers are eaten by juvenile American shad (Haskell et al. 2006), and possibly by other fish in Lake Umatilla below the Hanford Reach. On the other hand, dense populations of Asiatic clam can crowd out other benthic invertebrates that are important in the diet of fish, such as chironomids (Brock et al. 1991), and thereby reduce energy flow to higher trophic levels.

Fishes

Native species. A comprehensive mid-1970’s survey of fishes in the Hanford Reach found 37 species (Gray and Dauble 1977). The eight most abundant species were all native cyprinids (northern pikeminnow, peamouth, redside shiner, and chiselmouth; see also Gray and Dauble 2001), native catostomids (largescale sucker and bridgelip sucker), and native salmonids (mountain whitefish and fall Chinook; Table D.3.1). Similarly, the most abundant young-of-year fishes found by beach-seining in the late 1990’s were all native species: northern pikeminnow, peamouth, redside shiner, and unidentified suckers (Gadomski and Wagner 2009). Other relatively common native species are long nose dace and white sturgeon (Gray and Dauble 1977). Less abundant species are the sand roller, threespine stickleback, several species of dace (leopard and speckled) and lamprey (Pacific and river), and six salmonid species other than the two mentioned above. Five species of cottids have been reported from the Hanford Reach (Gray and Dauble 1977) and several are likely to be abundant, but cottids are poorly sampled by the gear types used in the past surveys. Native cyprinid, catostomid, and cottid species (with the exception of one cyprinid, the highly piscivorous northern pikeminnow) feed primarily on benthic invertebrates – particularly immature midges and caddisflies – and periphyton (Table D.3.1).

Non-native species. Only four non-native species, yellow perch, common carp, channel catfish, and black crappie, were among the 16 most abundant species captured in the Hanford Reach in the 1970’s (Gray and Dauble 1977). Ten additional non-native species were captured (Table D.3.1); the abundance of some of these species may have been underestimated because they are not highly vulnerable to the sampling gear used (gill nets, hoop nets, and beach seines, but not electroshocking). Most of the non-native species are piscivorous and could represent a threat to native fish populations (Chapter C.3). Unfortunately, no surveys have been done to determine the occurrence and abundance of non-native fishes in the Hanford Reach for over 30 years. Walleye have become abundant enough to support a sport fishery in recent years, and smallmouth bass have become more abundant (D. Dauble, Pacific Northwest National Laboratory [retired], personal communication).

Subyearling Chinook. The run of wild fall Chinook spawning in the Hanford Reach, the largest in the Columbia River Basin, has remained robust in recent decades and supports important sport and commercial fisheries (Dauble and Watson 1997). From 1979 to 2001, approximately 40,000 fall Chinook, including several thousand strays from a nearby hatchery, spawned in the Hanford Reach. Therefore, rearing conditions – including the supporting food web – for the juvenile fish are of special interest. After emergence, fry remain in the Hanford Reach for up to several months, feeding primarily on midges (largely pupae) and caddisflies (largely adults). Midges make up the bulk of the diet in April and May, when the largest number of juvenile fish are present, and caddisflies become increasingly important in June and July (Becker 1970, Dauble et al. 1980, Rondorf et al. 1990). Mayflies (Ephemeroptera), terrestrial insects (largely Homoptera: cicadas, aphids and leaf-hoppers), and zooplankton (*Daphnia*) are also eaten at times (Dauble et al. 1980, Rondorf et al. 1990), but overall these items make relatively small contributions to total food intake. The dominance of aquatic insects in the diet of juvenile Chinook in the Hanford Reach contrasts with the dominance of zooplankton (primarily *Daphnia*) and terrestrial insects in diets after the juveniles move downstream into Wallula (McNary) Reservoir (Rondorf et al. 1990).

Birds

Aquatic invertebrates and fish are important food items for many species of birds in the Hanford Reach. Hundreds of thousands of migrant waterfowl use shallow backwater and littoral areas for resting and feeding in the fall and winter (Rickard et al. 1982). The riparian zone is used for feeding and nesting by many species, including songbirds (some neotropical migrants), shorebirds, wading birds, woodpeckers, corvids, raptors, and others.[23] Fluctuating water levels associated with power-peaking operations by upstream dams provide a food subsidy for many of the birds. Aquatic invertebrates and juvenile fish stranded on the shore by rapidly dropping water levels are regularly eaten by waterfowl, gulls, shorebirds and wading birds, and even by birds not closely associated with water, such as magpie and killdeer (Books 1985). The Hanford Reach also provides habitat for birds that specialize in feeding on larger juvenile and adult fish, including osprey, bald eagle, double-crested cormorant, American white pelican, grebe (several species), Caspian tern and common merganser. These piscivores feed at the top of the aquatic food web, but are not abundant enough to impose top-down effects on the abundance of aquatic species.

Conclusions

The food web in the free-flowing Hanford Reach is typical of large-river systems and differs in many respects from food webs in the hydropower system reservoirs. Energy input at the primary producer level is primarily by benthic diatoms and other periphyton, rather than from phytoplankton. Periphyton are consumed by benthic grazers, including immature stages of aquatic insects (midges, black flies, caddisflies and mayflies), and directly by some fishes. Aquatic insects and other benthic invertebrates are, for the most part, species typical of riverine rather than lacustrine habitats. Native fishes predominate in the Hanford Reach: the most abundant are native minnows, suckers, sculpin, and salmonids (largely rearing or migrating juveniles). Benthic invertebrates, periphyton, and terrestrial insects are the most important components of the diet for most of these fishes. A number of non-native fishes, including some highly piscivorous species, are also present but were, at the time of the most recent surveys over 30 years ago (1970's), much less abundant than in the hydropower system reservoirs. Birds play a more prominent role in the food web of the Hanford Reach than in run-of-river reservoir food webs.

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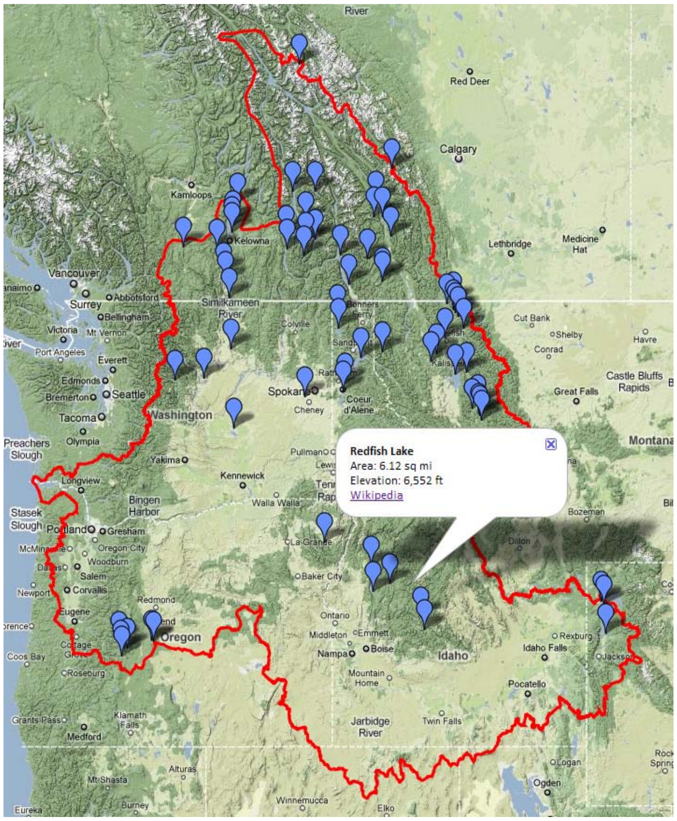
[23] The more abundant bird species in the Hanford Reach are listed on the Fish and Wildlife Service's website. Annual "Christmas" bird counts by Audubon society members in the Richland, WA area, at the downstream limit of the Hanford Reach, may be accessed via the website; data are available for several decades. The most abundant birds in the annual Audubon Society counts have been waterfowl (predominantly Canada geese, mallards, common goldeneye, and ring-necked ducks) and gulls (generally not identified to species).

The Hanford Reach food web is largely supported by organic material and nutrients supplied by upstream tributaries and by irrigation drainage from croplands. Nutrient inputs have been decreased from historical levels by trapping of sediments in upstream storage reservoirs, but these decreases are at least partially offset by the use of large quantities of agricultural fertilizers (Chapter B.2). It is not known if the net effect is an increase or decrease in nutrient supply from historical levels.

Since the Hanford Reach is surrounded by the Hanford Nuclear Reservation, aquatic invertebrates and fish probably have been studied more extensively than in any other location on the mainstem Columbia.

Understanding of food webs and ecological relationships in the Hanford Reach is, nevertheless, quite incomplete. This is in part due to the lack of standardization and continuity in earlier studies, but largely due to the noticeable absence of recent surveys. No thorough biological surveys have been performed in the Hanford Reach for over 30 years. Some populations of native species (stoneflies, western pearl mussels) are known to have declined or disappeared during that time, and others may have declined (or increased) as well. Non-native species are a continuing threat to the integrity of the native food web (Chapters C.3, C.5), but little is known of the current status of non-native species in the Hanford Reach.

D.4. Lakes



Lakes. See interactive map.

Introduction

Four broad factors affect food webs in lakes. They are drivers and changes associated with baseline productivity, seasonal production cycles, individual growth and survival. The productivity of species within lake food webs can be regulated by one or a combination of bottom-up (limited by nutrient or food availability) or top-down (consumer control) forces, and occasionally by regulation from intermediate trophic levels. Bottom-up forces are those limited by nutrient or food availability while top-down forces are driven by consumer processes (Carpenter et al. 1985, Carpenter and Kitchell 1988; Northcote 1988, Hyatt et al. 2004). Regulation from intermediate trophic levels can also be accomplished via direct species-to-species interactions, or indirectly through processes involving a variety of other species at different trophic levels (Stein et al. 1995).

While many potential trophic interactions are possible, under what conditions do certain interactions become important? An understanding of food web dynamics considers how the biophysical environments influence seasonality, distribution, production and energy/nutrient pathways of key species. Quantifying sources of energy and nutrients, and how they flow through the food web are essential for identifying the strong interactions that determine growth and survival of key species, and the relative role(s) of pelagic, littoral and benthic habitats in the interactions. A mechanistic understanding of food web dynamics provides an effective framework for identifying factors limiting production of fishes and other key species at the spatial-temporal-ontogenetic scales relevant for resource decisions.

The surrounding landscape, climate, and hydrologic cycle determine the magnitude, timing and rates of important physical and biological processes in lake food webs (Table D.4.1). They influence availability and connectivity of different habitats and seasonal production cycles for all trophic levels. Basin geology and land use affect nutrient inputs and retention, and primary productivity. Thermal stratification, light and oxygen gradients, and basin morphometry combine to determine seasonal availability of cold and warm benthic and pelagic habitats, their seasonal distribution and the interaction of organisms with different thermal tolerances and adaptations. Daily light cycles influence finer-scale diel vertical or horizontal movement patterns of animals and some plants. Seasonal production cycles, combined with the seasonal and diel distribution patterns of organisms at multiple trophic levels, determine the degree of spatial-temporal overlap and interactions among them.

Reservoirs differ from natural lakes in several important characteristics. Depending on size and location in the Basin, basin morphometry, and water management operations, reservoirs generally exhibit highly altered hydrologic cycles, often with higher flushing rates and modified thermal stratification (Chapters D.5, D.6). The timing and magnitude of water level fluctuations can vary considerably from a natural hydrograph, depending on the primary function of the reservoir (e.g., flood control, hydropower, irrigation). This disrupts production of benthic invertebrates and the contribution of egg banks to the spring recruitment of zooplankton. Timing, magnitude and depth of water withdrawal significantly alter thermal conditions within reservoirs, with important implications for the distribution, feeding and spatial-temporal overlap among prey, predators and competitors.

Table D.4.1. Physical features in lakes and the associated direct or indirect influences on food web processes

Physical Feature	**Influence On:**
Geology	Nutrient inputs, sedimentation
Topography	Basin morphometry, sun exposure, hydrologic cycle
Elevation and aspect	Duration and magnitude of seasonal temperature and precipitation
Basin size	Distinct versus highly overlapping benthic and limnetic habitats, wind fetch
Basin morphometry	
Shape	Circular, elongate, dendritic
Bathymetry	Steep-gradual slopes, mean-max depth Availability of benthic (littoral, profundal) and limnetic habitat
Climate	Hydrologic cycle, thermal regime, wind-driven mixing
Hydrologic cycle	Lake level, nutrient and sediment dynamics, thermal regime
Water residence time	Nutrient loading and dynamics, zooplankton production and retention, thermal regime
Thermal stratification	Nutrient availability, timing and vertical structure for production and distribution of plants and animals
Vertical profiles	
Temperature	Production rates and thermal tolerance, species distribution
Light	Depth constraints on photosynthesis, and visual foraging, species distribution
Dissolved Oxygen	Benthic hypoxia, winterkill, nutrient release from sediments
pH	Species tolerance limits (e.g., crayfish, molluscs)
Clarity-turbidity	Photosynthesis, visual foraging, species distribution

This chapter characterizes the structure and energy pathways of food webs in large natural lakes (> 1000 ha) and the dynamics of these food webs, particularly for fishes. We focus on larger lakes because they are better known, tend to support important populations of native fishes, fisheries and related values, and because they are more consistent in the conditions influencing their food webs. A brief summary of the broad range of lakes in the Basin is in Sidebar D.4.1. The chapter concludes with a short discussion of implications for food web management and restoration of lakes.

Sidebar D.4.1. Summary of Natural Lake Characteristics

There are more than 9,000 natural lakes and ponds in the Columbia River Basin. The precise number is uncertain because most are small and found at the highest elevations. Flathead Lake and Lake Pend Oreille are the largest at about 491,000 and 348,000 ha respectively, although both (and many other lakes) have been modified by outlet dams that control lake level and contribute to variable surface area throughout the year. Water chemistry data for 1,563 lakes in the U.S. portion of the Interior Columbia River Basin are available for chemically classifying the lakes as dilute, moderate, hard, and saline-water (Table D.4.2; Figure D.4.1; Lee et al. 1997). Solute concentrations tend to decrease with increasing elevation and reduced watershed area. Most dilute lakes are found at the highest elevations, moderate lakes are distributed at intermediate to higher elevations within larger watersheds. Hard-water and saline lakes are most common in the lower and drier areas or those areas with geologies that contribute high dissolved loads.

The highest and smallest lakes were often naturally fishless, but many now support a variety of coldwater nonnative salmonids as a result of stocking. Many lakes that were historically, or are currently, important for native salmonids are in the moderate group and range in size from a few hundred hectares to the largest lakes of the Basin. A number of the largest lakes, including Flathead, Pend Oreille, Priest, Coeur d'Alene and Kootenay, still support native populations of lake-rearing bull trout though all populations are now considered threatened or of conservation concern. Sockeye once occurred in multiple lakes in the Snake River and the upper Columbia River where they now persist only as remnant kokanee populations or in the Stanley Basin as remnant endangered populations supported by intensive fish culture efforts. Sockeye persist in several lakes of the mid-Columbia like Lake Wenatchee (WA) and Lake Osoyoos (WA-BC).

Human development has had an important influence on the lakes. Shoreline development, agricultural conversion, population growth, non-native species introductions and atmospheric loading associated with broader industrialization in the region have contributed to declining water quality, altered trophic status and modified food web structure (US EPA 2009). Eutrophication associated with increased nutrient loading appears to be a common problem for smaller, mid or lower elevation lakes where human development has been most pronounced. Nevertheless, even the largest lakes draining expanses of relatively pristine watersheds have shown important effects linked to increased nutrient loading (Stanford and Ellis 2002). Despite these changes approximately half of the lakes in the combined ecological regions encompassing the Basin are considered to be in "good" ecological condition, the highest proportion of any region in the United States (US EPA 2009).

Table D.4.2. Mean or range in chemistry, surface area, mean elevation, and primary factors affecting water chemistry of 1,563 lakes clustered to describe major patterns in lake class across the U.S. portion of the Interior Columbia River Basin Modified from Lee et al. 1997; Appendix A4

Lake Class	**Alkalinity (µeq/L)**	**Conductivity (µS)**	**Total Phosphorus (µg/L)**	**Mean surface area (ha)**	**Mean surface elevation (m)**	**Primary factors affecting water chemistry**
Dilute	≤ 65	≤ 55	3-12	15-30	2000	Atmospheric Deposition
Moderate	420	17-70	20	10-207	1700	Development, water consumption recreation
Hardwater	3000	196-604	200	64-164	560	Grazing, mining, development, water consumption

Saline	8,000-375,000	---	173-2700	39-53	540	Irrigation, agriculture, grazing

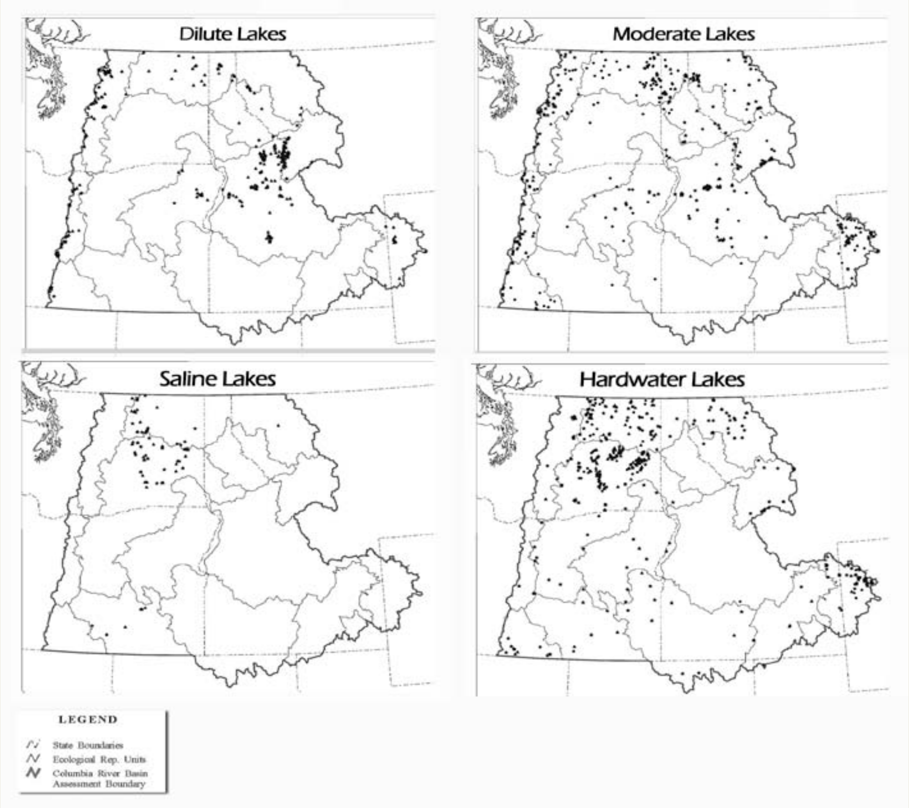


Figure D.4.1. Distribution of 1,563 lakes in the U.S. portion of the interior Columbia River Basin classified as Dilute, Moderate, Hardwater, and Saline (adapted from Lee et al. 1997 Appendix A4).

Energy Pathways and Trophic Levels

Lake food webs are driven by two pathways of primary production (benthic and pelagic). The benthic pathway is largely underpinned by periphyton and macrophyte production while the pelagic pathway is largely based on phytoplankton production (Figure D.4.2). Both contribute to a detrital pathway. The relative importance of each pathway is largely determined by the size, morphometry (mean and maximum depth), trophic state and degree of light penetration (Vadeboncoeur et al. 2008). Benthic primary production declines when light becomes limited, as in deep, steep sided lakes or in eutrophic lakes, thereby shifting dominance to phytoplankton production and detrital processes (Vadeboncoeur et al. 2002). Subsidies of organic carbon and nutrients from upstream, terrestrial, and marine-derived sources can be important to production in some lakes (Polis et al. 1997).

The stable isotope signatures of species and age classes reflect trophic relationships within a food web by identifying the primary energy pathways fueling the community and revealing potential predators, prey and competitors (Figure D.4.3. See also Appendix A: Tools for assessing food webs).

Benthic Energy Pathways are typically based on primary production from periphyton and macrophytes, and by detrital processes which utilize both internal (e.g., dead plankton, macrophytes) and external (e.g., leaf litter) sources. Benthic consumers and detritivores include insects, snails, mysids, amphipods, crayfish, isopods, oligochaetes, ostracods and mussels. Herbivorous fishes (e.g., suckers, adult chiselmouth) feed primarily on epilithic diatoms, and some omnivorous cyprinids (e.g., juvenile redside shiner, speckled dace) eat a mix of algae, periphyton, and invertebrates (Wydoski and Whitney 1979). Many fishes including juvenile salmonids, some minnows, suckers and sculpins, consume benthic invertebrates. Most piscivorous fishes feed on benthic fishes to some degree. Piscivorous birds consume some benthic fishes as well.

Pelagic Energy Pathways are based on phytoplankton (flagellates, diatoms, green, brown and golden algae, as well as cyanobacteria). Herbivorous zooplankton (rotifers, some calanoid copepods, *Daphnia*, *Bosmina* and other cladocerans) and omnivores like mysids eat phytoplankton. Omnivorous and carnivorous invertebrates, including mysids, cyclopoid and larger calanoid copepods, cladocerans (*Leptodora*), and some insect larvae (*Chaoborus*), are important predators on smaller zooplankton. Some larval fishes initially feed on small cladocerans and early stages of copepods before shifting to other foods. Other species may feed extensively on zooplankton throughout their life. Many plantivorous fishes feed selectively on *Daphnia*, but copepods and other small cladocerans become important when *Daphnia* densities are low. Piscivorous fishes (e.g., many salmonids and northern pikeminnow) feed extensively on pelagic fishes in addition to benthic fishes, thereby benefiting from both energy pathways.

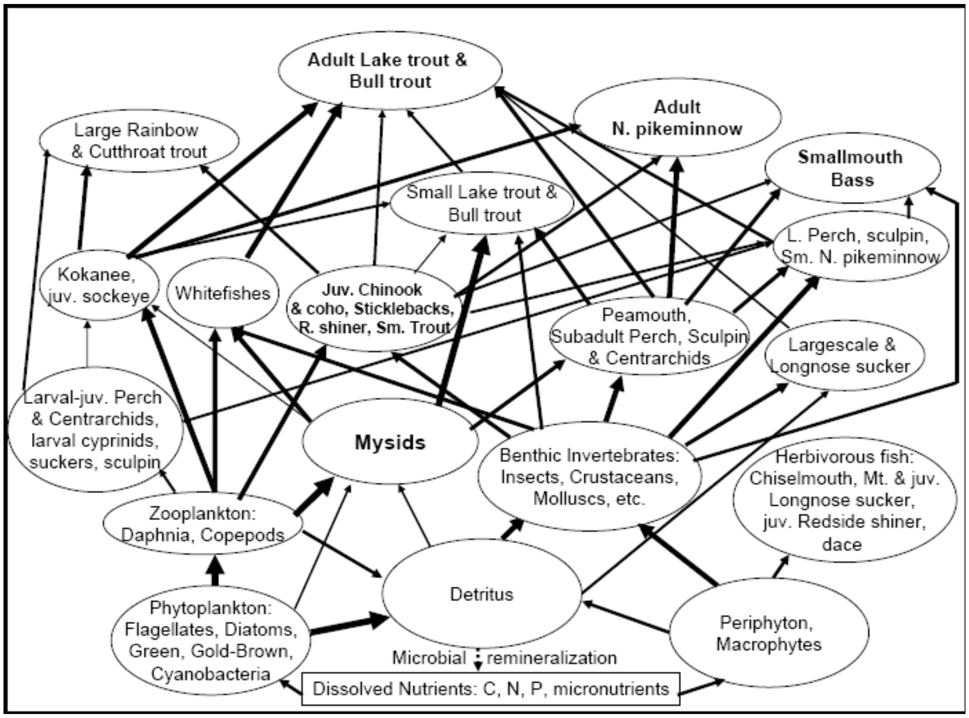


Figure D.4.2. Schematic lake food web. Pelagic energy pathways are shown beginning in the bottom left and benthic pathways beginning in lower right of the figure. The thickness of the arrows reflects the relative strength of the trophic link. All species groups contribute to the detritus pool as dead plant and animal tissue. For simplicity, nutrient recycling from excretion-egestion is not shown, but can be an important source of nutrients for epipelagic algae during summer stratification.

Benthic, Pelagic, and Detrital Pathways are linked through physical mixing, species movements, life history transitions and consumers with diverse food habits (Polis et al. 1997). Gravity, wind, and water flow move nutrients and organic matter between benthic and pelagic environments as well as between terrestrial and aquatic systems (Chapter D.8). Birds and mammals feed and excrete material among terrestrial, benthic and pelagic habitats. Highly mobile fish or invertebrates like mysids feed and move between benthic and pelagic habitats within diel or seasonal time scales, or undergo ontogenetic shifts in diet and habitat (Chipps and Bennett 2000, Vander Zanden and Vadeboncoeur 2002). Some fishes commonly shift from feeding on benthic invertebrates, to pelagic planktivorous fish or a mix of pelagic and benthic fish (Schindler and Scheuerell 2002, McIntyre et al. 2006). Others like juvenile yellow perch and basses may shift from eating zooplankton as juveniles to benthic invertebrates and fish as subadults.

Food Web Dynamics

Lake food webs are not static systems. Lakes shift in structure or importance of different trophic linkages through time. Seasonal cycles in species composition, primary production and biomasses of macrophytes,

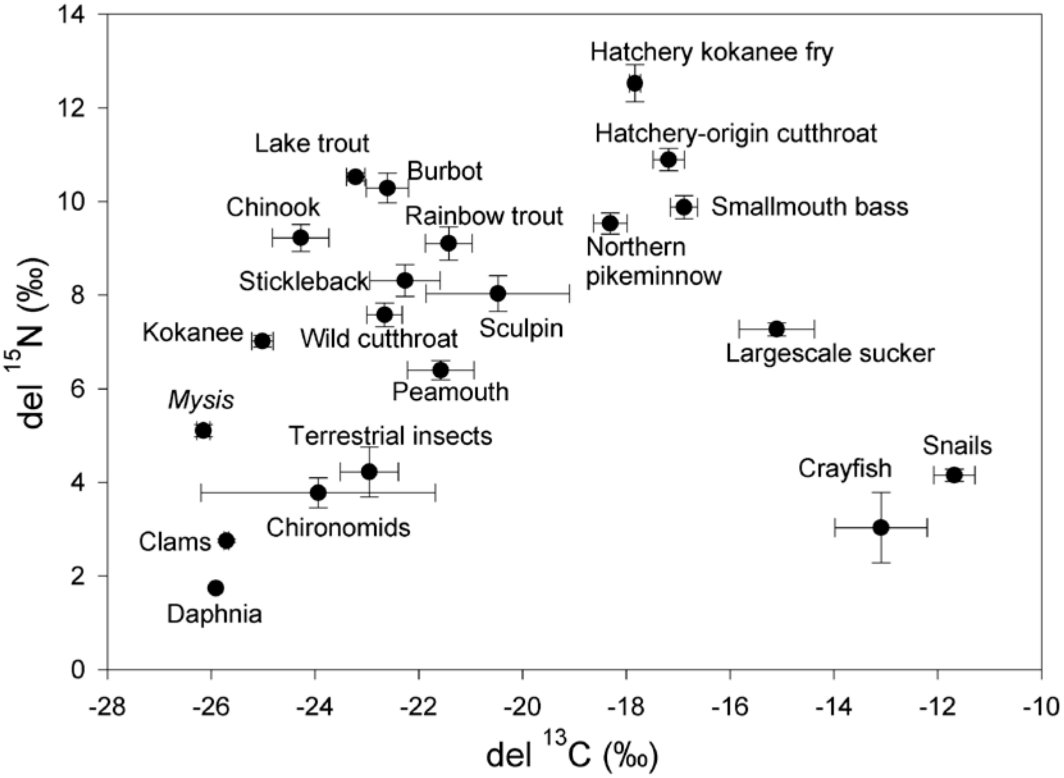


Figure D.4.3. Stable isotope signatures of Lake Chelan organisms.
Means are ± 1 SE; *Daphnia* symbol represents a single sample. δ^{13}C values are corrected to account for variable lipid content among samples. More negative, “depleted” δ^{13}C values indicate a diet primarily based on carbon fixed in the pelagic zone by phytoplankton. Intermediate δ^{13}C derive from detrital food sources (i.e., from dead phytoplankton, zooplankton, and benthic algae), while less negative, “enriched” δ13C values indicate a diet primarily based on carbon fixed in the littoral zone by epiphyton. Nitrogen isotopic values (δ^{15}N) indicate trophic position of consumers within the food web. The position of a consumer on the plot is expected to be near the mean of its aggregate diet on the x-axis and roughly 3.4‰ greater than the mean of its diet on the y-axis. Note the elevated δ^{15}N values for hatchery cutthroat trout and hatchery kokanee fry due to feeding on marine fish meal before release. However, as they grow, the isotopic signature in new body tissue will reflect their feeding on natural prey. From Schoen and Beauchamp (2009).

periphyton and phytoplankton are driven by variability in light, temperature and the availability of nutrients (Tilman et al. 1982, Interlandi and Kilham 2001). The seasonal progression typically begins with low densities of low-light tolerant flagellates in winter; import of a major nutrient pulse during spring runoff and lake mixing fuels spring blooms often dominated by diatoms, followed by green algae as thermal stratification develops (Budy et al. 1995, Gross et al. 1998, Rae and Andrusak 2006). After thermal stratification is established, algal production and biomass tend to decline as nutrients near surface are depleted and algal cells sink or are eaten by zooplankton. During summer, algal biomass in less productive lakes typically remains low, occasionally followed by a second diatom bloom in fall as the lake mixes. In eutrophic lakes, nitrogen-fixing cyanobacteria tend to increase during summer but are less nutritious or even inedible for grazing zooplankton (Infante and Abella 1985). As limiting nutrients become depleted in the epilimnion during summer, excretion by consumers and the microbial loop can support some level of algal production in the euphotic zone by recycling and remineralizing waste and decomposing material into useable forms of nutrients for algae.

Crustacean zooplankton populations exhibit seasonal dynamics in response to primary production, temperature and predation (e.g., Beattie and Clancey 1991, Budy et al. 1995, Steinhart and Wurtsbaugh 1999, 2003; Clarke and Bennett 2007). It is the seasonal dynamics of the crustacean zooplankton which determine their availability to planktivorous fish and predatory invertebrates (Table D.4.3). Some species of cladocerans exhibit dramatic blooms during spring, fluctuate considerably during summer and fall, and often disappear during winter. In contrast, copepods fluctuate less and remain available during winter.

Invertebrate-feeding fishes vary in seasonal diet and distribution in response to food availability, thermal conditions, energy demands and potential threats (Table D.4.4). Zooplanktivorous sockeye, kokanee, and whitefish feed in open water habitats where seasonal and diel vertical distribution and feeding success depend on density of available zooplankton, light levels, risk of predation by other fishes, and vertical temperature and oxygen regimes (Clark and Levy 1988, Luecke and Wurtsbaugh 1993, Beauchamp et al. 1997, Mazur and Beauchamp 2006, Jensen et al. 2006). As thermal stratification develops, cool and warm water fishes (e.g., cyprinids, centrarchids) relocate to feed on benthic invertebrates in the littoral zone or on zooplankton in the limnetic zone above the thermocline. If the temperature near the surface becomes too warm, salmonids are excluded from access to the higher densities of near surface zooplankton and littoral invertebrates and are forced to feed at cooler, less productive depths. When stratification breaks down, salmonids and whitefish are once again able to feed at all depths, whereas some benthic feeding fishes shift to deeper habitats and colder temperatures where they drastically reduce their feeding rate, metabolism and vulnerability to predators.

Feeding preferences of planktivorous fish also respond to seasonal availability of preferred zooplankton (Table D.4.3). When *Daphnia* biomass is low during winter and early spring, copepods become primary prey (Steinhart and Wurtsbaugh 1999, 2003; Clarke and Bennett 2003a,b; Beauchamp et al. 2004). *Daphnia* are commonly the most important zooplankton exploited by salmonids, whitefish, trout, yellow perch, and predatory invertebrates (e.g., mysids) in the late spring, summer and fall. Although the energetic value of *Daphnia* to consumers is no higher than other zooplankton, their relatively large size, high productivity, visibility and weak swimming capability contribute to their high selectivity by planktivores. In addition, salmonids reduce the water content of *Daphnia*, functionally doubling the energy density of prey in the stomach and enabling more prey to be packed into the same gut volume (Luecke and Brandt 1993, Stockwell et al. 1999).

Piscivores also show seasonality in feeding. However, because piscivorous salmonids often share similar thermal requirements with invertebrate feeding salmonids or their own juvenile life stages, they forage on many of the same sources year round (Table D.4.4). Some piscivores like northern pikeminnow, bull trout, lake trout, bass and yellow perch, forage both in benthic-littoral habitats and limnetic waters, but are often thermally segregated during peak summer stratification. Some species like bull trout, Dolly Varden and sculpin show distinct seasonal movements to river mouths or shoreline spawning areas where salmon juveniles or eggs are seasonally abundant (Foote and Brown 1998, Denton et al. 2009) Although predation by northern pikeminnow or other cool or warm water predators might occur during winter, actual predation rates are quite low due to low temperature-dependent limits on consumption and metabolism.

Table D.4.3. Seasonally dominant macro-zooplankton in lakes and the primary species found in the diets (listed in order of importance) of mysids, Chaoborus and Leptodora, and planktivorous fish

Season	**Dominant crustacean zooplankton**	**Mysids**	***Chaoborus*, *Leptodora***	**Planktivorous fish**
Winter-early spring	*Bosmina, Diacyclops* or *Eudiaptomus*	*Diacyclops, Eudiaptomus,* or detritus		*Diacyclops* or *Eudiaptomus*
Late Spring	*Daphnia, Bosmina, Diacyclops, Eudiaptomus*	*Daphnia*	*Daphnia,* other cladocerans and copepods	*Daphnia*
Summer	*Daphnia, Bosmina, Holopedium, Diacyclops, Eudiaptomus*	*Daphnia*	*Daphnia,* other cladocerans and copepods	*Daphnia*
Fall	*Daphnia, Diacyclops, Eudiaptomus*	*Daphnia*	*Daphnia,* other cladocerans and copepods	*Daphnia*

Table D.4.4. Generalized ontogenetic and seasonal diet of benthic and pelagic fishes and mysids in lakes of the Columbia River Basin.

Season	**Winter - Early Spring**	**Late Spring**	**Summer**	**Fall**
Mysids	Bentho-pelagic: *Diacyclops, Eudiaptomus*, or detritus	Bentho-pelagic: *Daphnia* or *Diacyclops, Eudiaptomus,* phytoplankton	Bentho-pelagic: *Daphnia, Diacyclops, Eudiaptomus,* phytoplankton, detritus	Bentho-pelagic: *Daphnia, Diacyclops, Eudiaptomus,* detritus
Kokanee and juvenile sockeye	*Diacyclops* or *Eudiaptomus*	Pelagic: *Daphnia*	Pelagic: *Daphnia*	Pelagic: *Daphnia*
Juvenile Chinook & coho	Littoral: Chironomid pupae	Littoral-Pelagic: *Daphnia*, Chironomid pupae	Pelagic: *Daphnia*	Pelagic: *Daphnia*
Juvenile rainbow and cutthroat trout	Littoral: Chironomid pupae	Littoral-Pelagic: *Daphnia*, Chironomid pupae	Pelagic: *Daphnia*	Pelagic: *Daphnia*
Rainbow trout > 250 mm	Littoral-Pelagic: Benthos, fish	Littoral-Pelagic: Fish, *Daphnia*, Benthos	Littoral-Pelagic: Fish, *Daphnia*, Benthos	Littoral-Pelagic: Fish, *Daphnia*, Benthos
Cutthroat trout > 250 mm	Littoral-Pelagic: Benthos, fish	Littoral-Pelagic: Fish, *Daphnia*, Benthos	Littoral-Pelagic: Fish, *Daphnia*, Benthos	Littoral-Pelagic: Fish, *Daphnia*, Benthos

Season	**Winter - Early Spring**	**Late Spring**	**Summer**	**Fall**
Whitefishes: pygmy, mountain, lake	Benthic: Chironomid pupae, mysids, benthos	Bentho-Pelagic: *Daphnia*, Chironomid pupae, mysids	Bentho-Pelagic: *Daphnia*, Chironomid pupae, mysids, larval fish	Bentho-Pelagic: *Daphnia*, Chironomid pupae, mysids
Small lake trout and bull trout	Mysids, benthic invertebrates, sculpin, small bentho-pelagic fishes, juvenile lake trout	Mysids, benthic invertebrates, sculpin, small bentho-pelagic fishes, juvenile lake trout	Mysids, benthic invertebrates, sculpin, small bentho-pelagic fishes, juvenile lake trout	Mysids, benthic invertebrates, sculpin, small bentho-pelagic fishes, juvenile lake trout
Large lake trout and bull trout	Sculpin, perch, whitefishes, Kokanee/sockeye, trout	Kokanee/sockeye, whitefishes, perch, sculpin, trout	Kokanee/sockeye, whitefishes, perch, sculpin, trout	Sculpin, perch, whitefishes, Kokanee/sockeye, trout
Northern pikeminnow < 200 mm	Benthos, sculpin, cyprinids, other fish, salmonids	Benthos, sculpin, cyprinids, other fish, salmonids	Benthos, sculpin, cyprinids, other fish	Benthos, sculpin, cyprinids, other fish
Northern pikeminnow ≥ 200 mm	Sculpin, salmonids, cyprinids, other fish, benthos	Salmonids, sculpin, cyprinids, other fish, benthos	Sculpin, cyprinids, other fish, salmonids, benthos	Sculpin, salmonids, cyprinids, other fish, benthos
Yellow perch age 0-1	Benthic: Chironomid larvae & pupae	Pelagic: Daphnia, copepods	Pelagic: Daphnia, copepods	Pelagic: Daphnia, copepods
Yellow perch > 100 mm	Benthic: Chironomid pupae, mysids, benthos, perch, sculpin, other fish	Benthic: Chironomid pupae, mysids, benthos, perch, sculpin, other fish	Benthic: Chironomid pupae, mysids, benthos, perch, sculpin, other fish	Benthic: Chironomid pupae, mysids, benthos, perch, sculpin, other fish
Redside shiner		Algae, *Daphnia*	*Daphnia*	Benthos, *Daphnia*
Age-0 suckers and cyprinids		Algae, benthos, zooplankton	Zooplankton, benthos	
Black crappie, bluegill, juv. Bass		*Daphnia*, benthos	*Daphnia*, benthos	Benthos, *Daphnia*
Sculpin < 125 mm	Amphipods, mysids, benthos, sculpin, other fish	Amphipods, mysids, benthos, sculpin, other fish	Amphipods, mysids, benthos, sculpin, other fish	Amphipods, mysids, benthos, sculpin, other fish
Sculpin ≥125 mm	Sculpin, other fish, salmonids, amphipods, mysids, benthos	Salmonids, sculpin, other fish, amphipods, mysids, benthos	Amphipods, mysids, benthos, sculpin, other fish	Sculpin, salmonids, other fish, amphipods, mysids, benthos

Diel and seasonal variability in light, lake clarity or changes in productivity strongly influences the effects of predation on prey fishes. Since piscivorous fish rely primarily on vision to feed, predation rates and predator avoidance behavior are strongly affected by spatial-temporal overlap in prey visibility and vulnerability to predators (Beauchamp et al. 1999, 2007). Planktivorous fishes, mysids, and some zooplankton vertically migrate to minimize vulnerability while feeding at dusk or dawn in the shallower depths on zooplankton (Levy 1990). Alternatively, planktivorous fishes also effectively reduce predation risk by schooling during daylight. Declining lake transparency from turbidity or algal production reduces the threat of predation in pelagic habitats (Beauchamp et al. 1999) without reducing planktivore foraging (Gregory 1994, D. Beauchamp, University of Washington, unpublished data). As lake productivity and associated turbidity increase, piscivorous fishes shift to benthic or littoral habitats, and the piscivore community shifts away from cruising, visually-dependent species (salmonids) to stalking or ambush predators (northern pike, northern pikeminnow, bass). Under extreme eutrophic or turbid conditions, the piscivore community shifts to species like catfish, a nonnative species group in the Basin, that rely on chemo-reception or tactile detection of prey.

Predation, competition and size-selective mortality strongly shape the population dynamics of lake fishes, particularly during the early life history stages. Food availability, feeding and growth are intimately linked to the survival, production and reproductive success of individual species having a variety of life history strategies. Growth declines as constraints on foraging accumulate from predation risk, limited availability or access to prey, thermal stress or poor energetic quality of food. Since piscivorous fish are capable of consuming prey fish up to 40-50% of their own body length (Figure D.4.4), vulnerability to predation depends on the size structure and abundance of the predator population relative to the size distribution and growth rate of prey, and the duration of exposure. Natural perturbations and human manipulations alter the environmental-ecological conditions that historically supported feeding, growth and survival patterns, thereby potentially altering the population dynamics of key species with the effects reverberating throughout the food web.

Human Alteration of Lake Food Webs

An overview of lake food webs reveals a system constantly shifting and adapting to change on daily, seasonal, and longer time scales. Important controls exist from the bottom up through productivity at the base of each trophic pathway, from the top down through predation and composition of the fish communities, and even at intermediate levels through species with diverse or particularly influential linkages. Human activities have important effects on these controls. Interactions between feeding, growth and mortality are influenced by variability in lake productivity, morphometry and habitat availability. Complex patterns in distribution and productivity of culturally or economically important species like salmon or trout can result from changing environmental conditions over diel, seasonal, or inter-annual time scales, and natural or human-induced changes in the population dynamics of various species. Some of the most apparent examples include cultural eutrophication and species introductions (see Chapter C-5), but climate change could have important effects in the future as well (ISAB 2007-2).

Eutrophication. There are more than 9,000 natural lakes in the Basin which span a wide range of watershed conditions, nutrient and sediment loads, morphometry and trophic status (Sidebar D.4.1; Lee et al. 1997). Cultural eutrophication is a common problem associated with increased nutrient loading from land use and human development in individual watersheds. Eutrophication is, or likely will be, most important in relatively small, dilute lakes close to human development, but such effects are evident even for some of the largest and deepest lakes in the Basin (Northcote 1972, Lee et al. 1997, Stanford et al. 1997). There has been little documentation of the food web effects of cultural eutrophication across the Basin, but the transition from oligotrophic to mesotrophic to eutrophic conditions can be anticipated through the effects outlined below.

Oligotrophic lakes offer lower carrying capacity, higher water transparency and deeper light penetration. Visually-feeding piscivores can exert tremendous mortality on prey fishes, especially during predictable periods of high prey fish density such as recruitment pulses, hatchery releases and migration. Mesotrophic lakes offer higher carrying capacity and higher growth rates (within the limits of density dependence), high to moderate water transparency and somewhat shallower light penetration. Visually-feeding piscivores still exert high mortality but predation success is highly sensitive to relatively small increases (e.g., ±1 NTU) in turbidity, either from algal production or sediment transport (Beauchamp et al. 1999). Eutrophic lakes still offer high carrying capacity for some fish species but salmonid production becomes limited as phytoplankton communities shift toward inedible forms of cyanobacteria and herbivorous zooplankton decline. In more eutrophic systems, invertebrate and fish production becomes more reliant on detrital food webs in benthic and littoral habitats. Low oxygen levels in the hypolimnion can limit benthic production and limit access to some hypolimnetic prey. Hypoxia in eutrophic systems, if severe, encroaches into the metalimnion thereby constricting or eliminating access to the deeper, cooler habitat required by coldwater fishes like salmonids. The threat from visually-feeding pelagic predators diminishes as lakes become more eutrophic. However, as food supply or thermal conditions restrict salmonids to benthic or littoral habitats, overlap increases dramatically with benthic or littoral predators and competitors possessing superior adaptations for foraging in these habitats, thus shifting the species composition away from salmonids (e.g., Persson et al. 1991).

Species Introductions. Perhaps the most profound alteration of lake food webs occurs with the intentional and unintentional introductions of non-native fishes and invertebrates. For lake food webs in the Basin, the non-native species that have exerted the greatest impacts have been lake trout, lake whitefish, yellow perch and mysid shrimp (Figures D.4.5 and D.4.6). In addition, a number of fishes that naturally occur in

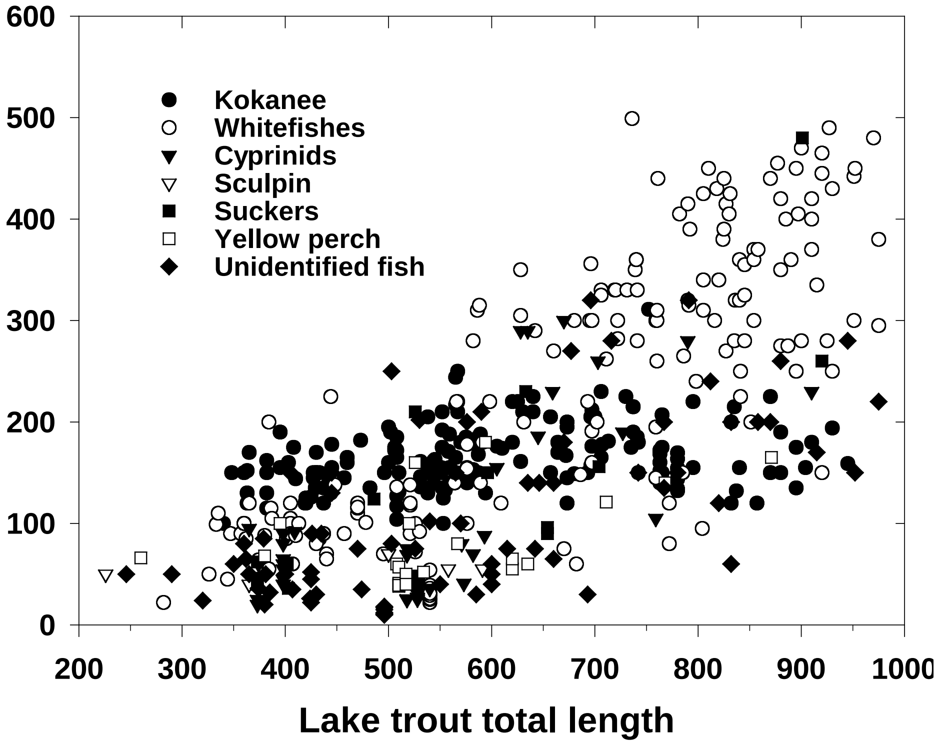


Figure D.4.4. Relationship of lengths of piscivorous lake trout to the lengths of prey fishes by species in Flathead Lake, Montana. The predator-prey length relationship shows a classic "wedge-shaped" distribution for all fish prey collectively, but the pattern varies among prey species. Multiple age classes of whitefish are available year-round over a broad range of sizes, whereas most kokanee are only available for a few months after stocking and thus offer a relatively narrow size range to lake trout (From Beauchamp 1996).

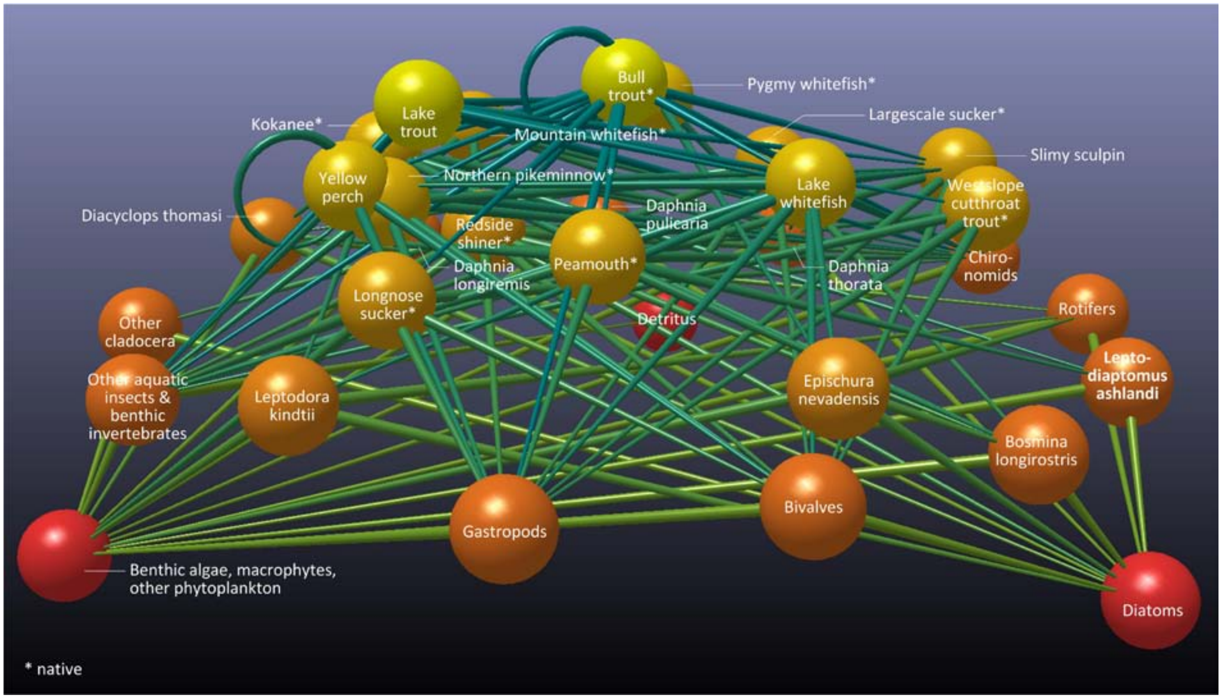


Figure D.4.5. A network visualization of the pre-mysid shrimp food web in Flathead Lake, Montana (created in J. Dunne's *Network3D* software).

other parts of the Basin have been widely distributed to other areas. Kokanee salmon and rainbow trout, for example, have been introduced or invaded virtually every lake or reservoir with the potential to support coldwater species, while cutthroat trout, coho and Chinook have been introduced on a more limited basis. The consequences of these introductions are discussed in more detail in Chapters C.3 and C.5).

Climate Change. Seasonal cycles are common, but not always constant. Interannual variation and trends in climate can have important effects on the structure of lake food webs. Climatic effects on phenology of key species, for example, can disrupt important food web processes by creating temporal mismatches between food availability and consumer demand (Chapter E.4). Over a 40-year warming trend, the earlier onset of spring diatom blooms created an increasing temporal mismatch with the bloom of *Daphnia* and calanoid copepods, resulting in a long-term decline in *Daphnia* in Lake Washington (Winder and Schindler 2004a,b). Warming is also anticipated to lead to longer summers and periods of stratification shifting the balance between introduced warm water predators and native cold water species (Heino et al. 2009). Climate change is anticipated to have important hydrologic effects that also fundamentally alter timing and volume of runoff and lake flushing with implications for lake trophic states and connectivity among life stages for adfluvial salmonids and whitefish. Hydrologic changes coupled with changing patterns in forests, wetlands and riparian communities will likely lead to changes in nutrient supply, cycling and retention, and loading of organic carbon (Schindler 1997, Schindler et al. 1997, Heino et al. 2009). Any one of these could have cascading effects through lake food webs.

Implications for Management and Restoration

The food webs of many lakes have been altered dramatically and, in some cases, irreversibly through human actions. Management and restoration efforts for salmon, steelhead, bull trout and other sensitive species will require an understanding of food web processes in order to identify and remedy factors that limit production of these species. For instance, if depressed populations are food-limited, will nutrient additions help by stimulating food production from the bottom-up, or exacerbate the current limitation by intensifying eutrophication and hypoxia, promoting inedible algae, or reducing spatial-temporal access to food supply? Factors that inhibit accessibility to food will require different remedies than simply attempting to stimulate more food production. Enhancement of fish numbers via hatchery supplementation could undermine growth and survival of lake-rearing species if carrying capacity is exceeded. Moreover, if predation is already severe, then attempts to increase recruitment of target species will likely fail unless predation mortality and the indirect

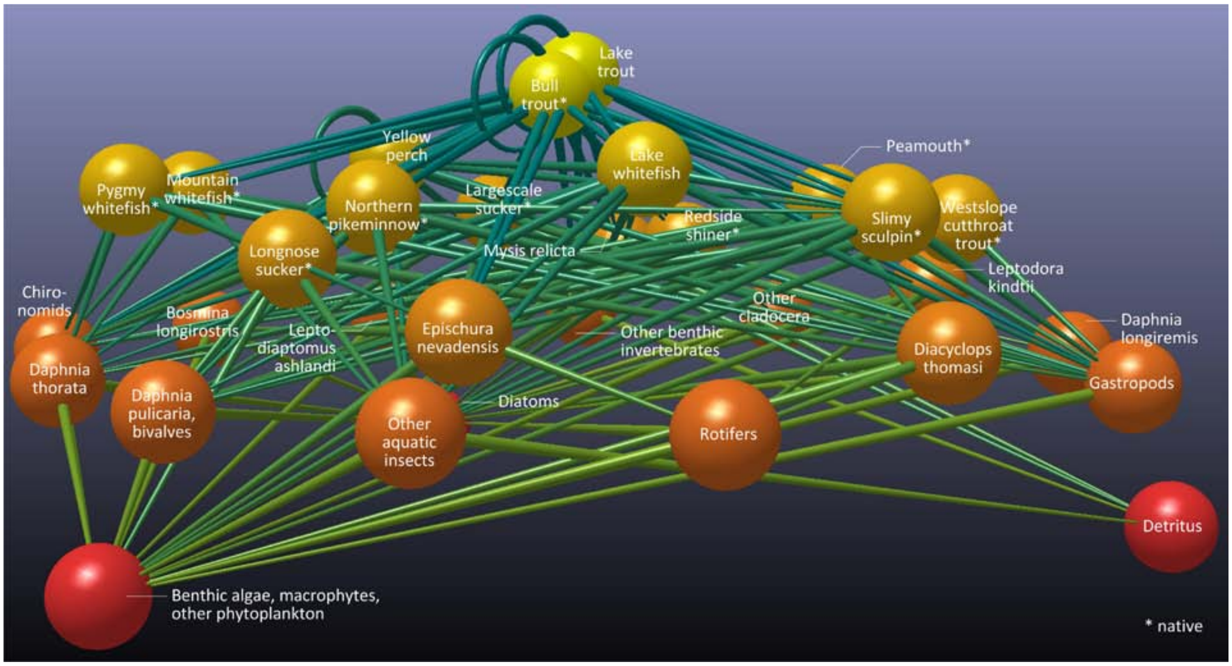
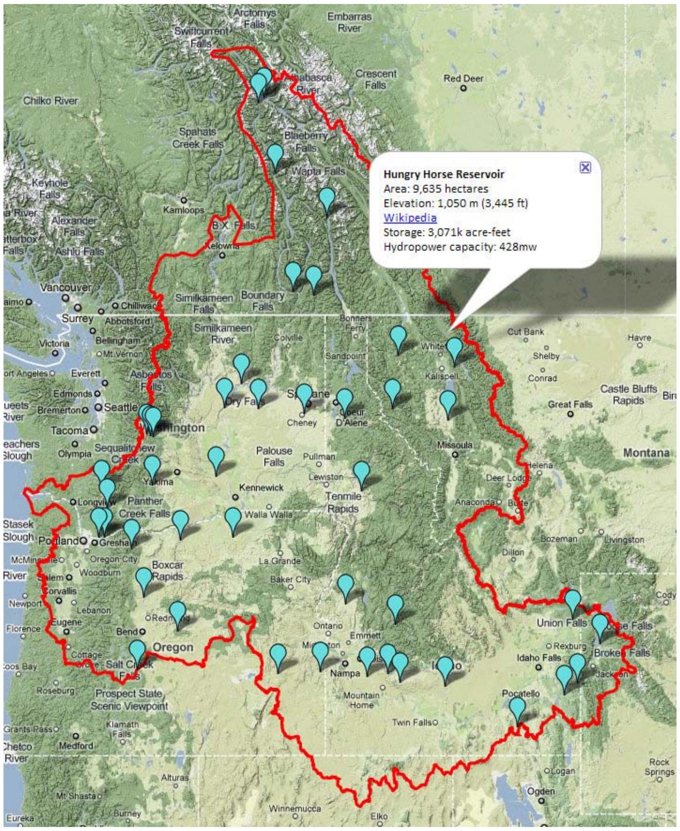


Figure D.4.6. A network visualization of the post-mysid shrimp food web in Flathead Lake, Montana (created in J. Dunne's *Network3D* software).

consequences of predator avoidance are addressed first.

Cultural eutrophication can and has been addressed at some level in many lakes throughout the basin. Active programs to control or eliminate artificial point and non-point nutrient sources are clearly of primary importance. The legal introduction of non-native species has slowed across the Basin in recent years but management of non-native fisheries remains an important tradeoff in the long term management of lake food webs. Recognition of the uncertainty and potential risks associated the establishment or expansion of non-native species continues to be important. It is highly unlikely that non-native fishes and invertebrates can be eradicated with existing technologies whereas control of some species such as lake trout may be possible (Hansen et al. 2008), although at a substantial cost. Mitigation of climate change is beyond the scope of lake management but efforts to maintain or enhance the resilience of lake food webs could be an important response to the threats associated with it. The retention or restoration of natural river flows to minimize alteration of lake flushing rates, drying of wetlands and potential alteration of carbon and nutrient sources and flux will be an important challenge if climate change leads to warming, drying and increased water demand for other uses.

D.5. Water Storage Impoundments



Major water storage reservoirs. See interactive map.

Unique Food Webs: Setting the Stage

There are literally thousands of dams constructed to store water throughout the Columbia River Basin. Water storage reservoirs (WSRs) range from tiny stock ponds in the driest regions to extensive pools behind the largest dams on the Columbia River and its major tributaries. We have classified 35 WSRs as “major” with an active storage capacity > 123.3 M m^3 (see accompanying interactive map for locations and characteristics). Kinbasket Reservoir behind Mica Dam in British Columbia is the largest with an active storage of 14,858.5 M m^3 and a length of 214 km.

This chapter differentiates water storage reservoirs from run-of-the-river reservoirs used primarily for power generation and navigation on the mainstem Columbia and Snake rivers (Chapter D.6). We also differentiate WSRs from natural lakes that now have dams to store water or manage surface elevations (Chapter D.4). This is because management of WSRs creates fundamentally different conditions that change the associated food webs. We focus on the food webs of larger WSRs because they have been relatively well studied (although information is still very limited) and because of their fundamental importance to food webs and ecosystems within, and potentially above and below the impoundments.

An important characteristic of most WSRs is the substantial fluctuation in volume and surface elevation of the storage pool in response to downstream uses. Typically water is stored during spring runoff, filling a pool that is later partially or wholly withdrawn to support irrigation, power generation and other demands. WSRs in Idaho, Montana and British Columbia are also used to mitigate or enhance downstream river temperatures, flow volume, velocity and timing for ecological benefits that include salmon migration and spawning in the Snake and Lower Columbia rivers (ISAB 2004-2).

Creation of WSRs (as well as run-of-the-river reservoirs) dramatically changes the food webs of the streams, rivers and lakes that become inundated. Natural littoral and riparian zones are obliterated and then dried and wetted on time and spatial scales inconsistent with natural water level fluctuation. As water retention time increases, the flora and fauna of running water are replaced with a pelagic and benthic community more characteristic of lentic systems. Due to longer water retention, food webs of WSRs more closely resemble food webs of natural lakes than those of run-of-the-river reservoirs, but important differences exist. Pelagic zone productivity in WSRs is generally reduced by lower water retention time and by instability of water surface area, depth and volume relative to natural lakes. Depending on water year and the vertical location of the withdrawal structure, withdrawal can entrain a significant portion of the pelagic production of phytoplankton, zooplankton and fish, increasing variability and reducing overall production relative to natural lakes. Frequent or extensive dewatering of littoral and benthic zones also substantially alters the relative contribution and composition of benthic, terrestrial and pelagic production sources (Marotz et al. 1996). Water temperature and stratification is generally less stable than in lakes. In summer, temperatures downstream from WSRs may be either increased if warmer surface water is released or decreased if colder deeper water is released; in winter, temperatures downstream tend to be increased if deeper water is released (Sidebar D.5.1).

Food webs in WSRs have been conditioned by efforts to mitigate alterations for native fishes and the management of new fisheries. Impoundment has dramatically altered the character of food webs and connectivity of habitats that were available to native fishes before reservoir establishment. In many cases, however, native salmonids including bull trout and westslope cutthroat trout have persisted and adapted. They exhibit migratory life histories analogous to "adfluvial" forms, moving from natal tributaries to lakes to grow and mature. Hybrid food webs have been created by intentional and accidental introduction of non-native species (Chapter C.5). Introduced salmonids including rainbow trout and kokanee salmon, as well as a host of cool and warm water species, have been introduced to most of the larger WSRs and in many cases support important new recreational fisheries. Most large WSRs in the Basin are now managed both to conserve fish communities and to maintain fisheries within the impoundment itself.

Sidebar D.5.1. Management of Food Webs in Water Storage Reservoirs

Reservoirs are often managed for a range of objectives. These include downstream water uses and ecological conditions, as well as for recreation, fisheries and conservation. Storage and release of water (and other materials, including nutrients and sediment), as well as the introduction of new species to expand local fisheries and the development of recreation or other uses, all directly influence the characteristics of food webs within reservoirs. These can cause deep conflicts and tradeoffs in management (e.g., ISAB 1997-3). Managers must often now consider the social and ecological implications of their actions below, within and above the reservoir pool so tradeoffs considered within and outside the reservoir are increasingly important. Drawdown, for example, alters reservoir surface area, volume and thermal structure thereby fundamentally changing the pool environment for primary and secondary food production. Changing pool volume alters warm, cool and cold water habitats and their relative availability for organisms. Drawdown impacts benthic invertebrate production and reduces influx of terrestrial invertebrates because of the lesser surface area and the greater distance to source habitats. Depending on the depth of the outlet structure and relative volume and timing of withdrawal, drawdown can entrain phytoplankton, zooplankton and fish. Excessive drawdown can remove substantial biomass, which could potentially diminish the productivity and resilience of the WSR aquatic community, and fundamentally alter the downstream environment. Here we provide three examples from WSRs.

***Libby and Hungry Horse Reservoirs*.** Reservoir food webs have been studied to understand and potentially mitigate the impacts of managing reservoir pool volumes, as illustrated by models of westslope cutthroat trout and bull trout populations in the Libby and Hungry Horse reservoirs in Montana (Marotz et al. 1996). These models incorporate a series of empirical and theoretical relationships including those linking the production of phytoplankton and zooplankton with physical characteristics of the reservoir (volume, light and thermal structure); the production and flux of benthic and terrestrial invertebrates with reservoir surface area and shoreline exposure; and fish growth with forage availability and thermal structure (Figure D.5.1). The models indicate that deep and frequent drawdowns dramatically reduce forage production (by 30 to 50% or more) with concomitant effects on fish growth. Models of processes within the WSR have also been coupled with comparable models of conditions downstream to consider how reservoir management affects flow and thermal environments as well as food webs, forage availability and habitats for bull trout and cutthroat trout in the Flathead and Kootenai rivers. Future applications may reveal the implications of water releases for spawning white sturgeon in the Kootenai River. An important result has been the development of rule curves that can help guide drawdown decisions to balance the competing uses of reservoir water as the availability of water varies in response to climate and other demands.

Cle Elum Reservoir. The 40-m maximum annual drawdown in Cle Elum Reservoir has severely compromised the ecological integrity of the littoral zone resulting in a food web primarily based on pelagic productivity. The reservoir is oligotrophic, based on a Carlson's (1977) trophic status index (TSI) of < 29. Nutrient addition to enhance the phytoplankton-zooplankton-sockeye salmon food web has been proposed, but existing models indicate that water retention time may be too short for this mitigation procedure to work. The high flushing rate is likely the most significant cause of poor phosphorus conversion necessary for pelagic productivity. Thus, it may be impossible to enhance pelagic production for local fisheries in reservoirs like Cle Elum without restricting drawdown to increase reservoir storage times (Flagg et al 2000).

Lake Billy Chinook. Round Butte Dam, constructed in 1964 on the Deschutes River, Oregon, below the confluence of the Metolius, Crooked and Deschutes rivers, blocked anadromous fish passage and created Lake Billy Chinook. A wild kokanee population became established, presumably from an existing population of sockeye salmon upstream in Suttle Lake. A previously fluvial population of bull trout from the Metolius River readily adopted an adfluvial life history strategy. Recreational fisheries in the reservoir and the transition zone from the Metolius River now target both kokanee and the ESA-listed bull trout. A precipitous decline in kokanee and large fluctuations in bull trout abundance over the past decade stimulated an analysis of predation, seasonal food supply, and thermal regime as potential limits to the production and population dynamics of kokanee and bull trout. Bioenergetics modeling indicates that the productivity of the pelagic food web is sufficient to support abundant kokanee (Chapter C.6). However, the tight predator-prey linkage between bull trout and kokanee has fluctuated out of balance: at high abundance, bull trout predation can severely depress the kokanee population, resulting in significantly higher rates of cannibalism, reduced body condition (Thiesfeld et al. 1999) and abundance of bull trout (Beauchamp and Van Tassell 2001, Beauchamp and Shepard 2008).

New issues are now emerging as anadromous salmonids are allowed access to the reservoir in an attempt to re-establish spring Chinook, steelhead, and sockeye above the previously impassable dams. In addition, a new surface and hypolimnetic water withdrawal structure regulates temperatures downstream and within the reservoir. The seasonal supply of zooplankton should be sufficient to support the additional feeding demand from juvenile salmon and steelhead rearing in the reservoir. However, a proposed water withdrawal structure will likely alter the thermal regime downstream and may increase spatial and temporal overlap between predatory bull trout and juvenile salmonids. The net effect of increased predator-prey interactions and expanded feeding habitats cannot be predicted and needs to be measured through a directed sampling program.

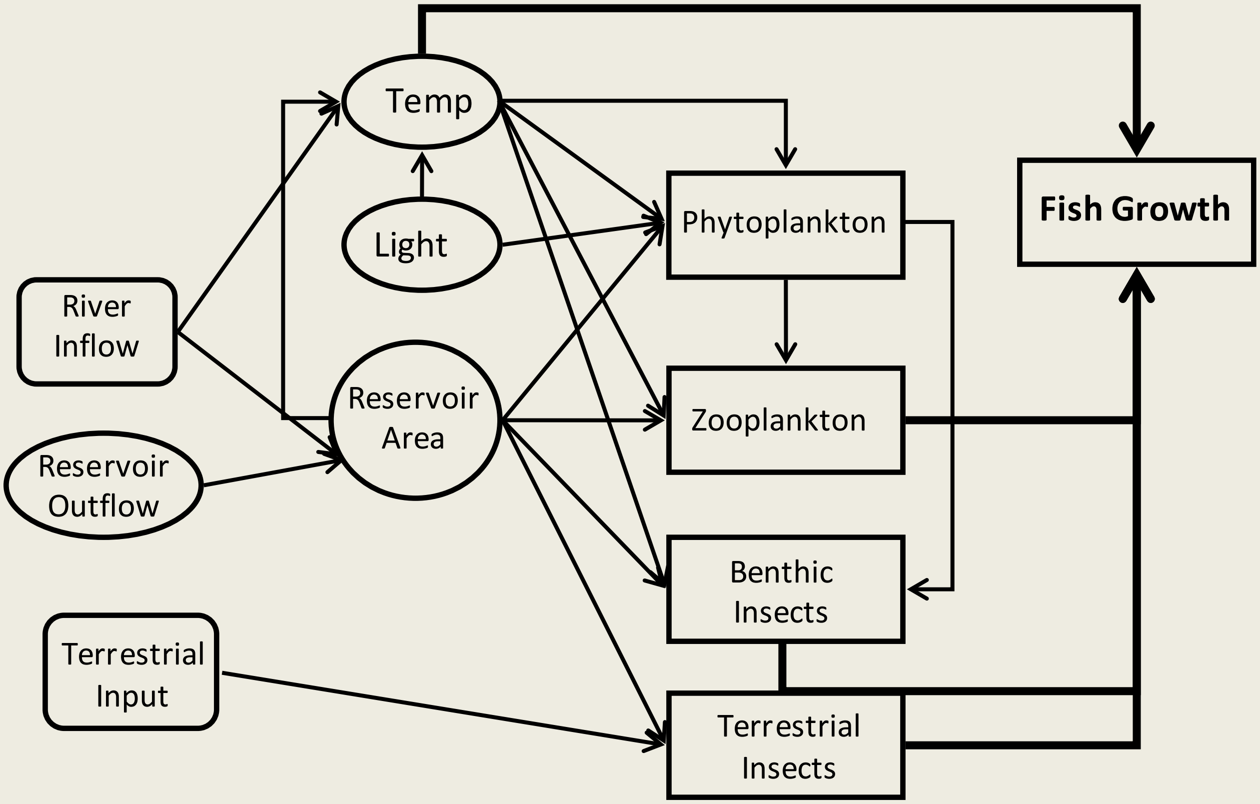


Figure D.5.1. Schematic of compartmentalized food web models developed to evaluate alternative reservoir operations on food availability for native fishes in Hungry Horse and Libby reservoirs in Montana.

Many WSRs influence resident fish populations and fisheries in rivers immediately downstream of the storage reservoirs as well (e.g., Kootenai River sturgeon, Flathead bull trout and westslope cutthroat trout). Water releases strongly influence downstream temperatures (Martoz et al. 1996) and large reservoirs act as sources or sinks for nutrients (Stanford and Ellis 2002). Management of the storage pool has important implications for the productivity of food webs of rivers and lakes further downstream, creating important tradeoffs that must be considered (Marotz et al. 1996; Sidebar D.5.1).

Most of the mechanistic knowledge of WSR food webs in the Basin comes from detailed studies of a few systems including Lake Roosevelt on the Upper Columbia River, Cle Elum Reservoir (875.7 M m^3) on the Yakima River, and Lake Billy Chinook (337.9 M m^3) on the Deschutes River. A food web model based on theoretical and empirical relationships between broad trophic levels also has been constructed to guide management of Libby and Hungry Horse Reservoirs in Montana (Marotz et al. 1996; Sidebar D.5.1). Comprehensive food web data do not exist for most WSRs, large or small, although limnological and fish diet information is commonly available. Food webs in small WSRs could be fundamentally different than in larger systems. For example, small WSRs may be more susceptible to temperature change and eutrophication effects because they are usually shallower and have less capacity to process organic matter coming from surrounding land, especially from farmland (Chapter D.8). The cumulative effect of the many small WSRs on food webs is likely substantial and in need of investigation (ISAB 2004-4; Baldwin and Woller 2006).

An Example Food Web: The Lake Roosevelt Water Storage Reservoir

Formed by Grand Coulee Dam in 1941, Lake Roosevelt illustrates some of the key physical factors affecting aquatic food webs in large WSRs. This reservoir has an active storage capacity of 6395.6 M m^3 and length of 243 km. Flood control protocols at Grand Coulee Dam are designed to annually reduce the water elevation in the WSR by as much as 24 m between January and May (to make room for storage of spring runoff), and to refill of the full pool elevation (393 m) prior to the Fourth of July weekend. Lake Roosevelt then experiences two additional annual drawdowns; one of about 9 m in August and a smaller one earlier in summer of 0.3 to 0.6 m (Figure D.5.2). All three drawdowns facilitate power generation, downriver irrigation, and municipal, industrial, domestic and salmon interests to varying degrees. The dramatic change in water levels dries out shorelines and breaks the connectivity between tributaries and the lake. Streams draining into the reservoir become perched above the shoreline when the reservoir is low, or flooded with back-up water when the reservoir is filled (Scofield et al. 2004 cited in Lake Roosevelt Fisheries Guiding Document, LRFGD, 2009).

Mitigation strategies in Lake Roosevelt have focused on methods to improve productivity of kokanee and rainbow trout, both of which feed on zooplankton. These fishes are reared in hatcheries and released annually into the reservoir. The number released varies from year to year, but average 0.5 M catchable-sized rainbow trout, 0.2 M catchable-sized kokanee, and 2.0 M kokanee fry. The aquatic community in Lake Roosevelt contains a rich pelagic component and the productive phytoplankton and zooplankton base supports much of the food web, which is classified as “meso-oligotrophic” based on nutrient concentrations. The reservoir is well stratified in spring and summer and the relatively long water retention (usually about 40 d) promotes primary and secondary production. Most aquatic organisms in Lake Roosevelt utilize pelagically fixed carbon. Even fishes that are usually considered strictly benthic feeders (cyprinids, catostomids, and cottids) obtain more than 65% of their food energy from pelagic sources. Wild kokanee and whitefish exhibit the largest utilization of pelagic foods and large scale suckers the least (Black et al. 2003). The stable isotope for carbon can be used to differentiate between wild and hatchery-reared fish (both kokanee and rainbow trout) because hatchery fish retain the $\delta^{13}C$ signal of hatchery food that is based on marine fish oils.[24]

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[24] The hatchery reared kokanee and rainbow trout sampled in this study must have been released within a few days of their capture as the hatchery signal would be lessened after the fish shifted to natural food (see Appendix A on stable isotope analysis methods).

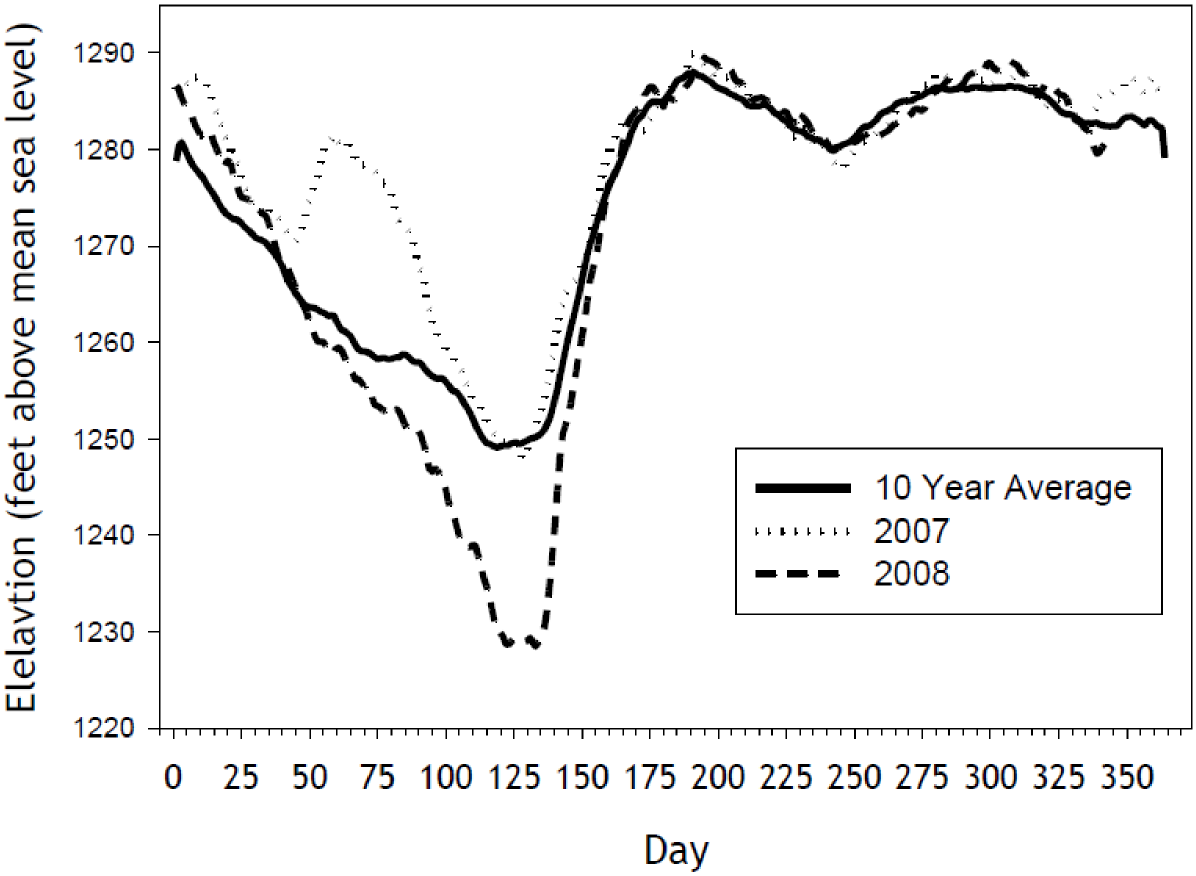


Figure D.5.2. The annual mean water elevation of Lake Roosevelt, Washington for 2007, 2008, and the 10-year average The summer drawn down of 0.3 to 0.6 m referred to the text is not shown on this plot as the release was first implemented in 2009. Source: Columbia River DART

A feeding node consisting of several taxa of cladocerans, copepods, and aquatic insects is clearly important for pelagic feeding fish – stomach content importance values for cladocerans are approximately 75% for kokanee and 47% for rainbow trout. Copepods and aquatic insects are subdominant. Based on relative weight, mean length of spawners, the size and species composition of zooplankton, and monthly ratios of consumption demand to *Daphnia* biomass (C/B) by hatchery trout and kokanee, there is no indication of food limitations for kokanee or rainbow trout in Lake Roosevelt (Baldwin and Polacek 2002). However the ISRP recently cautioned that studies of carrying capacity in the lake, as well as the severely disrupted tributary streams, are required to justify present and proposed stocking densities and release strategies for these species (McLellan et al. 1999, Baldwin and Woller 2006, ISRP 2009, Peone 2003 in McLellan et al. 2008, LRFGD, 2009).

Burbot, a representative native benthic predator in Lake Roosevelt, eats primarily fish and isopods. The low to moderate growth and condition of burbot indicate the relatively poor productivity of benthic invertebrates and forage fishes in Lake Roosevelt. Primary prey species vary with season and habitat. Burbot in the nearshore zones of Lake Roosevelt consume a mixture of fish, insects and crayfish in the spring, but shift to primarily fish (mainly sculpin) in summer and fall. By weight, isopods dominate the diet of burbot in offshore zones during all seasons. Overall, the annual diet of burbot is fish (38%) and isopods (35%), with insects occurring less frequently (11%; Polacek et al. 2006).

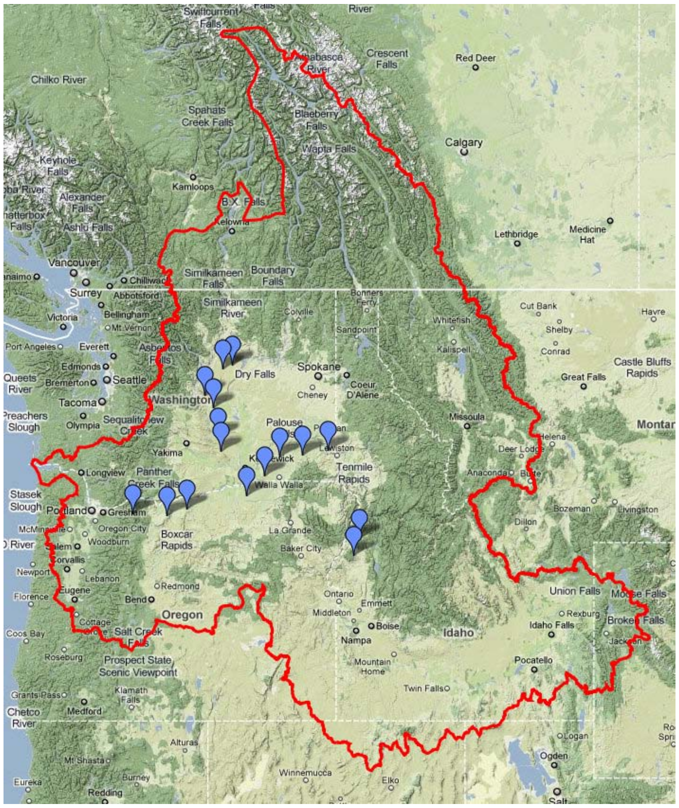
Fifteen species of non-native fishes are now present in Lake Roosevelt (Chapter C.5) exemplifying the formation of a hybrid food web which appears to be typical of many WSRs. The practice of stocking non-native walleye that feed on kokanee and rainbow trout has created a novel food web. Consumption by walleye has been quantified with a bioenergetics model, and estimates of walleye abundance have been used to determine the overall losses of hatchery kokanee and rainbow trout from predation by walleye. Walleye consumed ~ 9% of hatchery kokanee and ~ 7% of the hatchery rainbow trout within 41 d of release in 1999 and 2000 (Chapter C.6). In effect, the walleye population in Lake Roosevelt was ‘‘swamped’’ in the short term by the biomass of salmonids released. Nevertheless, walleye and other fish predators may limit kokanee in the longer term, depending on recruitment success and seasonal variability in the diet of piscivores. Competition with the abundant non-native lake whitefish for common planktonic food resources also may reduce survival of kokanee and rainbow trout (Baldwin et al. 2003, LRFGD 2009).

Conclusions and Recommendations

Water-storage reservoir food webs support important sport fisheries for kokanee and other species and, in some cases, are important for sustaining for ESA-listed adfluvial bull trout. Dam operations and land use affect thermal regime, water retention time, and reservoir levels, which in turn affect seasonal production cycles of algae and zooplankton, accessibility of prey to planktivorous and piscivorous fishes, and connectivity between stream- and lake-rearing phases of adfluvial life cycles. These food-web interactions have important implications for restoration efforts and water management.

Disruption of natural river food webs by the construction of WSRs is possibly the most intensive, and extensive, ecological consequence of the hydrosystem. The thousands of reservoirs in the Basin range widely in surface area, but many are large enough to have important effects on both local and adjacent systems. Some WSRs inundated important habitats with unique food webs, spanning the range from small creeks to the mainstem Columbia and many of the larger tributaries including Snake, Kootenai, South Fork Flathead and other rivers. Water storage reservoirs, generally, are extremely unstable environments with highly varying surface areas, storage volumes, elevations and flushing rates. These operations have dramatic effects on littoral and pelagic components of food webs within the WSR itself as well as on food webs downstream and sometimes even upstream of the WSR. Hybrid food webs are now the norm in most WSRs because of extensive stocking of non-native species. Our knowledge of WSR food webs and how they are evolving is relatively poor and research has focused almost entirely on the larger reservoirs. Several bioenergetic and limnological models have been adapted for use in WSRs (see Sidebar D.5.1), however, and provide important insight to guide restoration or management of downstream food webs through re-establishing environmental water flows. Extension and refinement of modeling approaches like these are needed to forecast the outcomes and tradeoffs associated with reservoir restoration, management and mitigation projects in the Basin.

D.6. Run-of-River Reservoirs



Mainstem Snake and Columbia River run-of-river impoundments. See interactive map.

A Contrast to WSRs and Lakes

Hydroelectric reservoirs on the lower and middle Columbia River and on the lower Snake River have transformed ~ 1,400 km of riverine and associated riparian habitat into reservoirs. These run-of-river (ROR) reservoirs have little water storage capacity, and water retention times are only a few days (Table D.6.1). The short water retention time contrasts with much longer retention times (one to several months) for upstream storage reservoirs (Chapter D.5). As a consequence, ROR reservoirs have some characteristics of both riverine systems (e.g., replacement of water within a short time period, lack of stratification) and lake environments (e.g., relatively deep water, flows slow enough to allow extensive sedimentation, and warming during the summer months). Accordingly, food webs in the reservoirs have become restructured as non-native species adapted to lake conditions displace many native species adapted to flowing water (Chapter C.5). Non-native species have been introduced both fortuitously – by transport in ballast water of ships or barges – and deliberately by management agencies in the 19th and early 20th centuries, as well as by sport fishermen. Reservoirs in the Columbia and Snake rivers also have been colonized by several native crustacean species that did not previously range above the estuary.

This chapter describes changes in ROR reservoir food webs that have accompanied development of the Columbia River hydropower system. We begin with primary producers (phytoplankton and benthic algae), progress to primary consumers (zooplankton and benthic invertebrates) and finally to secondary and tertiary consumers (fishes and birds). Changes in food-web relationships create constantly evolving challenges for fish and wildlife managers, as well as difficult challenges for effective restoration.

Nutrients and Primary Productivity

Phytoplankton constitutes the foundation of aquatic food webs in ROR reservoirs in the Columbia River. Suspended particulate organic matter (POM) in the reservoirs is derived largely from living and detrital phytoplankton. This is reflected by a high ratio of chlorophyll *a* to organic carbon, which indicates the presence of phytoplankton; a low C:N ratio, which is typical of POM derived from phytoplankton rather than from aquatic macrophytes, terrestrial plants or soils; and from isotopic analysis[25] (Prahl et al. 1997, Kendall et al. 2001)[26]. Phytoplankton dominate as the source of organic carbon for several reasons. Primary production by benthic algae (periphyton) and aquatic macrophytes is limited by the scarcity of lotic, backwater, floodplain-pool and other shallow-water habitats, all of which have been reduced or eliminated by impoundment. Conditions in the reservoirs do not favor the establishment of periphyton and macrophytes at most locations. Fluctuating water levels result in desiccation, depths too great to allow adequate light penetration for growth, and fine-sediment substrates unsuitable for periphyton. Organic inputs from terrestrial sources, typically of relatively less importance in larger streams and rivers than in smaller streams (Webster and Meyer 1997), have been further reduced by the loss of

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[25] All plants take up lower-mass isotopes of carbon and nitrogen (^{12}C and ^{14}N) at higher rates than higher-mass isotopes (^{13}C and ^{15}N). Ratios of ^{12}C to ^{13}C and ^{14}N to ^{15}N are higher for phytoplankton than for terrestrial plants and soil-derived organic material, allowing determination of the contribution of phytoplankton to POM.

[26] Additionally, relatively minor inputs of organic matter from terrestrial plant debris and soil erosion are suggested by spikes in the C:N ratio during winter and spring freshets (Kendall et al. 2001).

Table D.6.1. Run-of-river hydroelectric reservoirs on the Columbia and lower Snake rivers

Dam (river km)[a]	Reservoir name	Length (km)	Area (km^2)[b]	Storage (10^6 m^3)[c]	Water transit (d)[d]
Columbia River					
Bonneville (235)	Bonneville Lake	73	82.6	882	1.89
The Dalles (308)	Lake Celilo	39	38.0	407	0.87
John Day (347)	Lake Umatilla	123	210.4	3,113	6.66
McNary (470)	Lake Wallula	99	149.7	1,665	3.56
Priest Rapids (639)	Priest Rapids Lake	30	31.3	292	0.89
Wanapum (669)	Lake Wanapum	61	59.4	856	2.60
Rock Island (730)	Rock Island Pool	32	12.6	140	0.42
Rocky Reach (762)	Lake Entiat	68	36.8	471	1.43
Wells (830)	Lake Pateros	47	39.4	408	1.24
Chief Joseph (877)	Rufus Woods Lake	83	33.9	639	1.94
Snake River					
Ice Harbor (16)	Lake Sacajawea	51	33.9	501	3.60
Lower Monumental (67)	Lake Herbert G. West	46	26.7	465	3.35
Little Goose (113)	Lake Bryan	60	40.6	698	5.02
Lower Granite (173)	Lower Granite Lake	63	36.0	602	4.33
Hells Canyon (397)	Hells C. Reservoir	42	10.0	232	6.04
Oxbow (439)	Oxbow Reservoir	20	4.6	72	1.87

[a] Locations of Columbia River Dams in km from mouth of river; locations of Snake River dams in km from the confluence with the Columbia River (510 km above the mouth of the Columbia River).

[b] Surface area at maximum normal operating level (U.S. Army Corps of Engineers Reservoir Storage Tables, April 1998, unpublished, and Bonneville Dam Water Control Manual, March 1963, unpublished).

[c] Total gross water storage at maximum normal operating level (U.S. Army Corps of Engineers Reservoir Storage Tables, April 1998, unpublished).

[d] Average water transit time estimated by replacement method: Gross water storage (m^3)/ average annual river discharge (m^3/s). Average discharge rates are 5,420 m^3/s for the lower Columbia River at The Dalles (Northwest Power and Conservation Council web site), 1,610 m^3/s for the lower Snake River (Burbank gauging station, USGS web site), 3810 m^3/s for the middle Columbia River above the Snake River confluence (5420 m^3/s – 1610 m^3/s), and 445 m^3/s for the middle Snake River (Hells Canyon and Oxbow dams; Weiser gauging station, Idaho State Department of Environmental Quality).

floodplain and riparian habitat and the associated channel complexity. In addition to phytoplankton production in the reservoirs, phytoplankton is continually flushed to downstream food webs.

Phytoplankton growth is controlled by availability of nitrogen and phosphorus. Silicate is also an essential nutrient for diatoms, a dominant group of phytoplankton (Prahl et al. 1997, Sullivan 1997, Parametrix, Inc. 2001). Unlike natural lakes and water storage reservoirs, which typically act as traps for nutrients (Ward and Stanford 1983, Thornton et al. 1990), ROR reservoirs have little effect on the downstream transport of dissolved nitrogen, phosphorus, silica and other nutrients (Kelly 2001). Although agricultural runoff introduces large quantities of N and P to the river (Wise et al. 2007), dilution and biotic uptake maintain concentrations near levels that potentially limit the growth of phytoplankton (0.1 mg L^{-1} nitrate-nitrogen and 0.01 mg L^{-1} orthophosphate phosphorus; Kelly 2001). Therefore, despite anthropogenic inputs of macronutrients, high water throughputs and uptake prevent nutrient buildup and maintain mesotrophic conditions only moderately favorable for phytoplankton growth. Eutrophication of the middle and lower Columbia River is not likely to occur in the absence of large future decreases in river discharge or increases in nutrient input. Little is known, however, of changes in the species composition of phytoplankton communities in the ROR reservoirs over recent decades, or of changes that may have accrued to the food web foundation. In contrast, food web relationships at higher trophic levels have, as discussed below, changed dramatically since the creation of the reservoirs. Changes at higher trophic levels may have resulted in top-down changes in species composition at lower trophic levels – via predation and herbivory – but no monitoring efforts are currently underway that could detect such changes.

Primary Consumers: Zooplankton and Invertebrate Benthos

Prior to the early 2000s, only native zooplankton species were reported in lower Columbia River reservoirs (Scarola 1968, McNary Reservoir, 1965-66; Prahl et al. 1997, lower 350 km of the Columbia River, 1992; Haskell et al. 2006, McNary and John Day reservoirs, 1994-96). Dominant native species in the reservoirs, presumably derived from populations in natural lakes throughout the Basin, are cyclopoid copepods (*Cyclops* spp.), cladocerans (prominently *Bosmina longirostis, Daphnia galeata, and D. retrocurva*), and calanoid copepods (particularly *Diaptomus* spp.)[27]. These taxa are the same as reported in other major river systems as diverse as the Orinoco, Ohio, and Hudson rivers (references cited by Haskell et al. 2006). Unexpectedly, recent surveys report that the dominant zooplankter in the lower Columbia River is now a previously unreported Asian copepod, *Pseudodiaptomus forbsi* (Sytsma et al. 2004, Cordell et al. 2008). In 2005, this non-native copepod made up 95–98% of the zooplankton in Bonneville Reservoir, 24 to 88% in The Dalles and John Day reservoirs, and 15 to 44% in the upper end of McNary reservoir (Cordell et al. 2008). It was, however, found at only one of eleven stations in the Snake River, where samples were dominated by native cyclopoid copepods and *Daphnia* spp., and was absent from samples taken from the free-flowing Hanford Reach above McNary reservoir. The rapid domination of the lower Columbia reservoirs by an Asian copepod vividly illustrates the vulnerability of ROR reservoirs to invasion by non-native species, in this case with unknown consequences for system productivity or resilience to further perturbations.

The historical benthic invertebrate fauna of the Columbia River – lotic taxa such as caddisflies, mayflies, dipterans, mollusks, and gammarid amphipods (Robeck et al. 1954, cited in Haskell and Stanford 2006) – are quite similar to the benthic fauna existing today in undammed reaches of major tributaries (Chapter D.2) and in the 80-km reach of free-flowing mainstem river between Priest Rapids Dam and Richman, Washington (Hanford Reach, Chapter D.3). Today, soft sediments in ROR reservoirs on the Columbia River (Grant County PUD 2003, cited in Draheim et al. 2007) and Snake River (Dorband 1980, Bennett et al. 1993) support benthic communities dominated by oligochaetes (segmented worms) and immature stages of dipterans (Chironomidae). Similar benthic communities composed of oligochaetes and chironomids are distributed throughout the temperate zone wherever mesotrophic conditions and silty bottoms occur (Dorband 1980). Other abundant benthic invertebrates in ROR reservoirs are the native signal crayfish *Pacifastacus leniusculus* (see Sidebar D.6.1), the estuarine amphipods *Corophium salmonis* and *C. spinicorne,* and the Asian clam *Corbicula fluminea* (Draheim et al. 2007).

Establishment of *Corophium* and *Corbicula* in the Snake River coincides with the completion of the last Snake River dam (Lower Granite) and the initiation of barge traffic between the lower river and the port of Lewiston on the Snake River (Nightingale 1999, Draheim et al. 2007). These taxa are important prey items for juvenile fishes of many species (discussed below). Other non-native benthic invertebrates with the potential to become important components of reservoir food webs in future years are discussed in Chapter C.5

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[27] Rotifers and other tiny microplankton are abundant in the Columbia reservoirs (Haskell et al. 2006; Parametrix, Inc. 2001), but are not retained by sampling gear in routine use. Microplankton are suspected to be important for energy transfer to higher trophic levels.

Sidebar D.6.1. Signal Crayfish: An Important but Neglected Food-web Link

Little is known of changes or trends in the abundance of invertebrate species in ROR reservoirs, even those species that play important roles in food webs. For example, the native signal crayfish *Pacifastacus leniusculus* has received little attention, although it is known to be an important link between primary and secondary/tertiary consumers. Signal crayfish prey on benthic infauna and epifauna such as chironomid larvae, oligochaetes, caddisflies, mayflies and amphipods (Dorband 1980) and are, in turn, major prey items for predacious fish such as smallmouth bass, northern pikeminnow, and channel catfish (Poe et al. 1994, Zimmerman 1999). Signal crayfish populations are large enough to support a small commercial fishery in some Snake River reservoirs (Chris Donley, Washington Department of Fish and Wildlife, personal communication), but abundance is not monitored. The recent introduction of several species of non-indigenous crayfishes into the Columbia River Basin (Adams 2005, Larson et al. 2010, Olden et al. 2009) may, by direct competition or by introduction of exotic crayfish diseases, threaten the signal crayfish and initiate changes in ROR reservoir food webs (Chapter C.5).

Post-impoundment successional changes in the benthic macrofauna of Lower Granite reservoir on the Snake River are well documented (Dorband 1980). Sampling began in 1976, immediately after filling of the reservoir, and continued for 18 months. Sediments accumulated rapidly, and were colonized within the first year by tubificid oligochaetes (>60% benthic invertebrates by number) and two species of chironomids (>30%). These simple new benthic communities were similar to soft-sediment communities in two older reservoirs downstream behind Little Goose and Ice Harbor dams, impounded 6 and 14 years earlier. The development of a stable soft-substrate community in Lower Granite reservoir within the first year is attributed to heavy sedimentation, which rapidly made large areas uninhabitable for riverine species and for less mobile lentic species. Hard-substrate communities remained in a state of flux as riverine species were slowly replaced by lentic species. For the most part, riverine caddisflies (with the exception of *Polycentropus* sp.) and mayflies (with the exception of *Stenonema* sp.) disappeared. The estuarine amphipod *Corophium* sp. was present in the new reservoir, and even more abundant than in the older Little Goose and Ice Harbor reservoirs. In both soft- and hard-substrate habitats, fine-particle detritivore-herbivores and first-level carnivores were the dominant functional groups (Figure D.6.1). Continuing successional changes in the hard-substrate community have been documented (Nightingale 1999).

Fishes

Conversion of riverine habitat in the mainstem Columbia River and the lower Snake River to a novel habitat type, the ROR hydroelectric reservoir, created conditions favorable for colonization by non-native fishes such as centrarchids (smallmouth and largemouth bass, bluegill, and several other sunfishes) and percids (yellow perch and walleye). These fishes, imported from eastern North America (Chapters C.3, C.5), are well adapted to lentic environments. A few studies addressing changes over time in these new mixed assemblages of native and non-native fishes report that non-native species are now among the most abundant fishes in the reservoirs. For example, beach-seine sampling of shoreline habitats in John Day reservoir in 1995 revealed that native species (chiselmouth, northern pikeminnow, sand roller, and several sucker species) that had been numerically dominant 10 years earlier, making up 90% of the catch, had decreased in relative abundance to only 34% of the catch. Over the same period, non-native species increased from 1% to 34% of the catch (Barfoot et al. 2002). Of the native fishes, only sculpins were more abundant in 1995[28] than a decade earlier. Why did this occur? It is thought that shallow, warm backwaters in the upper reaches of the John Day and other ROR reservoirs create favorable conditions for some non-native species, particularly yellow perch and various sunfishes (Gadomski and Barfoot 1998, Barfoot et al. 2002). Dense macrophyte beds in the backwaters, often composed of exotic Eurasian water milfoil, create habitat favorable to spawning and rearing of these species (Poe et al. 1994, Barfoot et al. 2002).

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[28] Since sampling was limited to one season, the authors acknowledge that changes in species composition from the earlier period, although substantial, cannot be unequivocally attributed to long-term change rather than to interannual variations in population sizes.

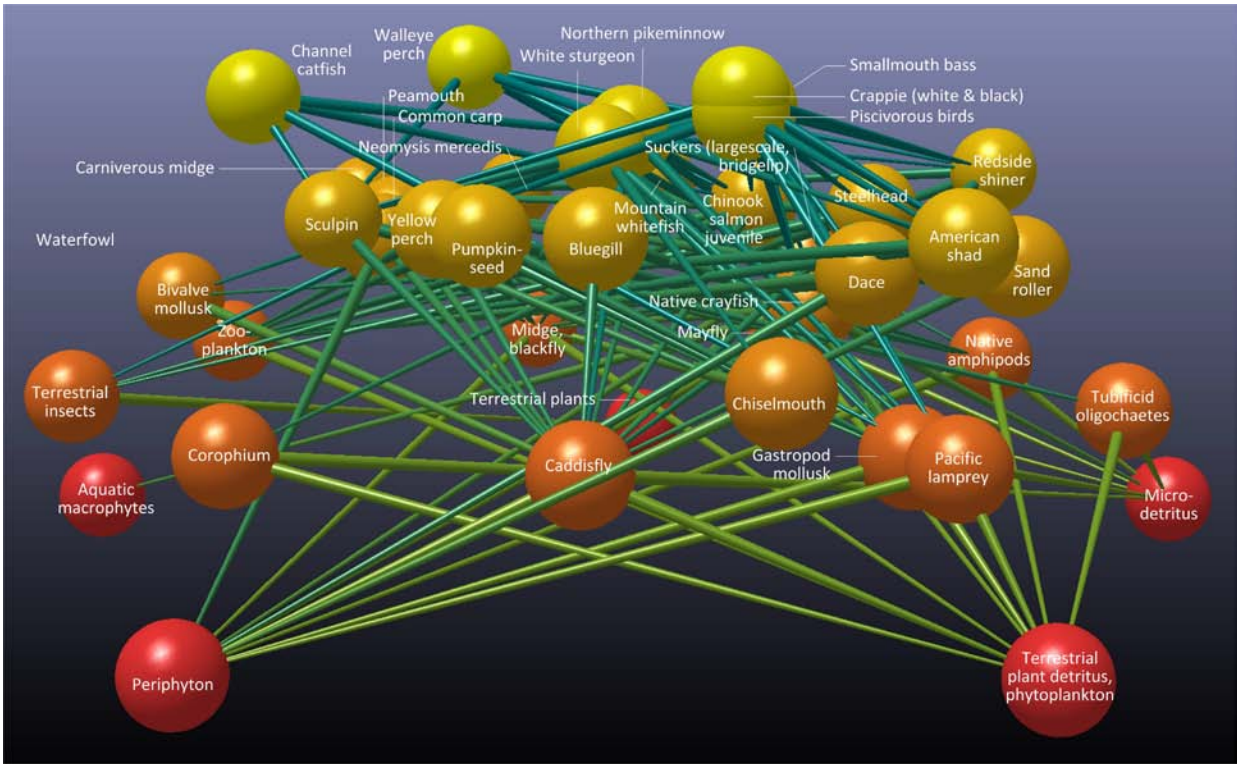

Figure D.6.1. Food-web structure in Columbia River run-of-river reservoirs.
Red = primary producers, orange = primary consumers, yellow = secondary consumers, green = tertiary consumers (created in J. Dunne's *Network3D* software)

Despite the increased importance of non-native fishes in ROR reservoirs, the more abundant native taxa continued to be well represented, and some are eaten by other piscivorous fishes (Poe et al. 1994, Zimmerman 1999). In the John Day reservoir, five of the seven most abundant taxa captured by beach-seining in the main-channel in 1995 were native – sculpins, sand roller, suckers, peamouth, and northern pikeminnow (Barfoot et al. 2002). Native sculpins dominate the diets of smallmouth bass, and the sand roller, a species endemic to the Basin, is an important prey for walleye[29] (Zimmerman 1999). However, the most recent studies of fish assemblages in ROR reservoirs are now 15 to 20 years old, and there are no contemporary sampling programs providing information on the changing status of the fish assemblages or other food web components.

Salmon are of great economic and cultural significance in the Basin. Therefore, the effects of the hydropower system on salmon survival have been extensively investigated. A largely neglected topic, however, has been the potential for interactions between changing environmental factors (e.g., flow velocities and water temperatures) and changing food web characteristics that could affect the energy balance, nutritional condition and survival of juvenile salmon. The energy balance of migrating juveniles is determined by the quantity of pre-migratory energy reserves, duration of migration, rate of energy expenditure (metabolic rate), and rate of energy (food) intake (Chapter C.6). The latter three factors have been substantially altered by impoundments. Migration duration increases with decreasing flow velocity (Chapter B.2), and metabolic rate increases with increasing temperature. Summer and fall water temperatures are now higher than prior to impoundment. The fourth factor, food intake, depends upon the abundance and seasonal availability of benthic and planktonic prey, which are in turn determined by the structure of food webs in ROR reservoirs

Food webs in ROR reservoirs in the Snake River apparently limit the growth of earlier-migrating juvenile salmon. About a third of yearling Chinook arriving at Lower Granite Dam in April and May have empty stomachs, compared with only 3 to 5% at dams on the lower Columbia River (Muir and Coley 1996). Similarly,

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[29] Juvenile salmonids, the majority of hatchery origin, dominate the diet of northern pikeminnow during spring and summer, and are also important prey for smallmouth bass and walleye.

in May food consumption by subyearling Chinook in the two uppermost Snake River reservoirs only slightly exceeds the maintenance ration (Curet 1993). In June and July, food consumption and growth of subyearling Chinook remaining in the reservoirs increases (Curet 1993, Connor et al. 2001), coincident with increased seasonal abundance of benthic invertebrates and other suitable prey (Nightengale 1999). Novel and poorly understood food webs have developed in ROR reservoirs, and they may not support the energetic needs of spring-migrating salmon or other native organisms. Moreover, future changes in ROR food webs can be expected as new non-native species become established, and these additions also may have unanticipated effects on the nutritional condition and fitness of migrating juvenile salmon.

Birds

Birds that feed on aquatic invertebrates and fishes are part of aquatic food webs. Backwaters of ROR reservoirs provide resting and feeding areas for resident and migrating waterfowl, which feed on submerged and floating plants, sedges and grasses. Shorebirds feed on shallow-water benthic infauna and epifauna (molluscs, amphipods, aquatic insects). Piscivorous birds feed on juvenile and adult fishes, and may be important predators on some fish species. Juvenile salmon and steelhead migrating through the McNary and John Day reservoirs are eaten by Caspian terns, double-crested cormorants, American white pelican, and California and ring-billed gulls. These species have established nesting colonies of significant size on several islands in the McNary pool a few kilometers below the Snake-Columbia River, and further downstream in the John Day and The Dalles pools (Chapter C.2). Smaller Caspian tern colonies are located on islands in Potholes Reservoir and Banks Lake; terns may travel over 100 km from these colonies to the Columbia River to forage on juvenile salmon (Antolos et al. 2004). Nesting Caspian terns are highly selective for juvenile salmonids, which make up one-half to two-thirds of the prey biomass consumed (Antolos et al. 2005, Collis et al. 2009). Steelhead smolts are particularly vulnerable. Double-crested cormorants are less selective for salmonids than are Caspian terns, but nevertheless the biomass of Snake River salmonid migrants eaten by nesting cormorants is similar to that eaten by terns (Collis et al. 2009). Bass, sunfish, sucker, and catfish (species unspecified) also contribute to the diet of these piscivorous birds (Antolos et al. 2005, Collis et al. 2009). Juvenile salmonids are much less prominent in the diets of California gull, ring-billed gull, and white pelican than in the diets of Caspian tern and double-crested cormorant.

The abundance of Caspian terns and double-crested cormorants is reduced in ROR reservoirs at considerable distances downstream (reservoirs behind Bonneville and The Dalles dams) or upstream (Priest Rapids to Grand Coulee dam) from the tern and cormorant nesting islands in the McNary and John Day pools. Gulls – predominantly ring-billed and California gulls, but also western and herring gulls at lower-river sites – are the most obvious avian piscivores in these reaches, feeding on juvenile salmonids that have been delayed above the dams and disoriented or injured by dam passage (Ruggerone 1986, York et al. 2000, USDA 2003, Jonas et al. 2008). Less obvious predation in reservoir reaches distant from the dams may be more important than generally recognized. A 2002-2004 study that developed a bioenergetics model for fish consumption by avian piscivores between Wells Dam and Rock Island Dam (Wiese et al. 2008) estimates that common merganser are more important predators on juvenile salmonids than ring-billed and California gulls. Reach-wide, common mergansers are the most abundant piscivorous bird on this section of the Columbia River until mid-July. Wiese et al. (2008) also report that from April through August piscivorous birds consumed more stickleback than salmon or any other prey species.

The avian piscivores currently of greatest concern as predators on juvenile salmonids in ROR reservoirs have only relatively recently established breeding colonies in the region. The first breeding reports for ring-billed and California gulls in Washington State were in the 1930s (Conover et al. 1979), and a single Caspian tern nest was found on an island in Moses Lake in 1929 (Antolos et al. 2004). The great expansion of these species along the Columbia River in the mid- to late 20th century is likely linked to ecological change brought about by human activity. Damming of the river and deposition of dredging spoils has created islands that provide refuges from mammalian predators for nesting birds, and increases in hatchery production of juvenile salmonids have augmented the food supply for piscivorous birds during the nesting season (Chapter C.4). Another factor may be increased agriculture on the Columbia Plateau (Conover et al. 1979); gulls are omnivorous, opportunistic and social, and often feed in flocks on cultivated fields.

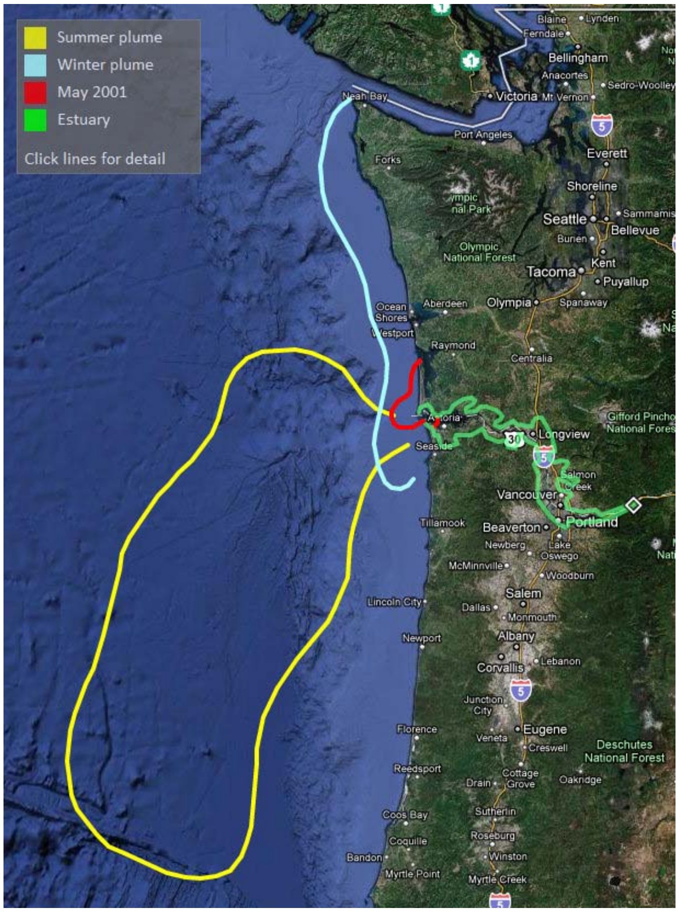
Conclusions

Hydroelectric development of the Columbia River and tributaries has converted the original riverine habitat into a series of reservoirs and resulted in fundamental changes in aquatic food webs at all levels, from primary producers to fishes. Columbia River food webs were originally based on carbon fixation by periphyton and aquatic macrophytes, and on allochthonous input from the terrestrial environment (Chapters D.2, D.3). Periphyton and aquatic macrophytes were largely supplanted by phytoplankton following impoundment. Zooplankton, the primary consumers of phytoplankton, have become prominent as primary consumers. This change in the foundation of food webs has, in concert with physical changes such as slower flows, greater water depths, increased sedimentation and elevated summer temperatures, resulted in extensive changes to the benthic invertebrate fauna. Many native benthic species have decreased in abundance or disappeared (e.g., bivalve mollusks, mayflies and most caddisflies), while small infauna, such as chironomids and oligochaetes, now dominate reservoir sediments. Native fishes have persisted in the reservoirs, despite sweeping changes in food webs and habitat characteristics. In the juvenile phase, most of these species feed successfully on zooplankton, as well as benthic prey. Other species with more specialized food or habitat preferences (e.g., chiselmouth, a periphyton feeder) are likely now more limited in abundance than prior to impoundment. Juvenile salmon are feeding generalists and feed on zooplankton, amphipods and insects in ROR reservoirs. The supply of these food items may be inadequate, however, for the large numbers of juvenile salmonids migrating seaward through ROR reservoirs in April and May.

Non-native species are prominent components of ROR reservoir food webs and are numerically dominant in some habitats. For example, an Asian copepod is now the most abundant zooplankter in lower Columbia River reservoirs, and the Asian clam is the most abundant bivalve mollusk. At higher trophic levels, introduced fishes have become major predators on salmon and other native fishes. Food web structure and function has been evolving rapidly since the formation of the reservoirs and will continue to change as new non-native species arrive. The emergence of such novel, hybrid food webs, with combinations of species that have not previously occurred together, is a world-wide phenomenon (Hobbs et al. 2006), and presents unique challenges for natural resource management (Hobbs and Cramer 2008, Seastedt et al. 2008; see Chapter E.3).

There are no continuing, long-term sampling programs underway to provide up-to-date information on food webs in ROR reservoirs, and the functional roles of exotic species are largely unexamined. Consequently, little understanding has emerged of how food webs in the reservoirs are changing over time, and of the biological interactions, environmental factors and management actions driving these changes. The only certainty is that change will continue, presenting new challenges for resource managers and for protection and restoration of threatened and endangered native species. Ecological monitoring and in-depth studies are needed because attempts to counter or compensate for undesirable changes in food webs are possible only if the changes are detected and the implications for food-web function understood. In addition, food-web linkages are complex and the introduction or loss of a single key species can have cascading effects that affect multiple additional species at several or all trophic levels (Spencer et al. 1991, Chapter E.4). Without understanding of food web structure and function, unanticipated changes in fish and invertebrate populations of special interest may be enigmatic.

D.7. The Estuary and Plume



Plume and estuary. See interactive map.

Contrasts to the River

The Columbia River estuary and plume exhibit food web characteristics in sharp contrast to those in other habitats, and are exceptionally important to sustaining fisheries. Food webs in the river change dramatically below Bonneville Dam at rkm 233; the upper extent of the estuary as defined by Williams (2006) where tidal changes, but not salinity, are obvious (see interactive map). Downstream from here, marine influences increase and currents, water levels, salinity and temperature are structured by tides interacting with river flows. Fish migration rates and requirements for food and growth also change substantially. For example, the migration rates of yearling Chinook smolts accelerate from approximately 23 km d^{-1} (Lower Granite to John Day) to 100 km d^{-1} (Bonneville to Astoria; McMichael et al. 2010, unpublished data). For numerous populations of juvenile salmonids, this is the first exposure to non-reservoir habitat since leaving their natal stream (an exception is the Hanford Reach; Chapter D.3), and their feeding habits change accordingly. Food sources for migrating juvenile salmonids shift from reservoirs, where planktonic production dominates, to a disrupted river channel and wetland areas where insects from riparian habitat and crustacean invertebrates from marshes and mudflats become their major foods. Concomitantly, there are large changes in the fish community and possibly in competition and predation. Flounder, sole, sculpin, white sturgeon and numerous non-native fishes are abundant in the estuary. Some species such as the non-native American shad dominate in pelagic channel habitats; flounder, sculpin, and white sturgeon live in deeper channels; and others such as three-spine stickleback and the non-native killifish reside in tidal channels (Chapter C.5).

Salmonids complete the transition from fresh water to salt water in the lower estuary and plume. This is a time of considerable physiological stress. They require adequate food to complete smoltification and to grow and maintain energy levels to avoid predators. Estuaries are widely regarded as key feeding locations for juvenile salmonids, especially for Chinook and chum which have subyearling or fry life history types that reside and grow there.

The importance of estuaries for salmonids in the northeast Pacific was established with the seminal studies of Reimers (1973) working in Sixes River estuary in southern Oregon. Scale analysis from adults and detailed life history studies on juveniles indicated that estuary residency, growth and feeding confer benefits that increased survival rates for specific life history types of Chinook (Reimers 1973). Further, the percentage of estuaries in pristine condition is significantly positively correlated with survival rates determined from CWT data for hatchery Chinook released into rivers in the region; the same relationship is not significant for coho smolts (Magnusson and Hilborn 2003). The key importance of tidal channels as rearing habitat for juvenile salmonids has been confirmed in the Columbia River estuary and the Oregon Coast's Salmon River estuary using PIT tags (Campbell 2010, Hering et al. 2010). In the Salmon River estuary, juvenile fall Chinook remain within individual channels from 0.4 to 8.9 h and in the marsh channel areas for 48 – 128 days. The longest observed residence times are associated with particularly high tides at night (Hering et al. 2010).

This chapter summarizes the structure and dynamics of food webs in the Columbia River estuary and plume.

The plume is the region further seaward, off the Oregon and Washington coasts where water from the river significantly lowers the ocean salinity. We provide an explanation of how the food webs and habitats of the estuary and river plume overlap, describe the food web relationships in the plume itself as well as their context with offshore fisheries ecology, and comment on how the hydrosystem and other factors have changed estuarine and plume food webs.

Food Web Structure and Spatial Dynamics in the Estuary

Food webs within the estuary respond to multiple physical forces such as currents, depth, salinity and tides. Fish community and food web structures shift dramatically in response to key physical-chemical or habitat factors as the factors change spatially, seasonally and annually.

The first description of the estuarine food web (Haertel and Osterberg 1967) defined four fish assemblages, each comprising a different food web: i) plankton feeders (snake prickleback, smelt, young starry flounders) that feed mainly on the copepods *Cyclops vernalis* in fresh water and *Eurytemora hirundoides* and *Calanus finmarchicus* in brackish and marine waters; ii) bottom feeders (juvenile starry flounders, prickly sculpin, and young white sturgeon) that eat mostly amphipods (*Corophium salmonis*) in fresh water and mysids (*Archaeomysis grebnitzkii*) in brackish and marine waters; iii) piscivores (adult staghorn sculpin and sand sole) that eat longfin smelt (*Spirinchus thaleichthys*) in all salinities; and iv) a group that eats “all types of food”(younger staghorn sculpin, young English sole, and Pacific tomcod). Many of these food linkages were also found in later studies (Figure D.7.1). Prey species for all fish assemblages vary with season and salinity, as these factors determine availability of prey.

Amphipods (especially *Corophium* spp), mysids (*Neomysis mercedis* and *A. grebnitzkii*) and dipteran insects are also important prey of juvenile salmonids including subyearling and yearling Chinook, coho smolts, and steelhead smolts (FigureD.7.1). These species are among the most frequent prey items of salmon in the estuary and hence could be considered key nodes in the food web (Bottom and Jones 1990). These nodes are robust and persistent; studies examining other species of juvenile salmonids, as well as certain non-salmonids, found similar feeding patterns (Figure D.7.1) (chum fry – Durkin et al. 1997; coho fry – Micah Russell; cutthroat trout and sockeye smolts – Russell; Bottom et al. 1984) or habitats (tidal channels – Lott, 2004; freshwater tidal – Kim et al 1986, Sather 2009, N. Sather; Durkin 1982). Although the availability of amphipods and dipteran insects may be reduced relative to the 1980s (Bottom and Jones 1990) because of habitat loss (see below), wetland-dependent prey are still consumed by higher trophic levels (Lott 2004, Maier and Simenstad 2009). Surveys in 2002-2005 consistently ranked adult dipterans as the most important prey for salmonids at all lower estuary beach-seining sites (Bottom et al. 2008). Several food web nodes, primarily zooplankton taxa (calanoid copepods, cyclopoid copepods, cladocerans and harpacticoid copepods), are important for non-salmonids. Eighteen non-salmonids feed on these nodes (McCabe et al. 1983, Bottom and Jones 1990) including American shad, peamouth, three-spine stickleback, Pacific herring, northern anchovy, surf smelt, longfin smelt, shiner perch, starry flounder, eulachon, snake prickleback, English sole, Pacific tomcod, butter sole and whitebait smelt. Interestingly, a key food of American shad is the non-native bivalve *Corbicula fluminea*, presumably eaten at the larval stage because shad are pelagic (McCabe et al. 1983). The estuarine food web is extensive, including many other taxa if moderate or minor constituents are included. Since the estuary encompasses habitats ranging from eelgrass to brackish marsh to classical riparian vegetation, a diverse array of prey species and a large pool of potential prey are available to salmonids. For instance, at Russian Island (rkm 33; see below), insects alone account for 36 potential prey taxa at the family level or above (Lott 2004).

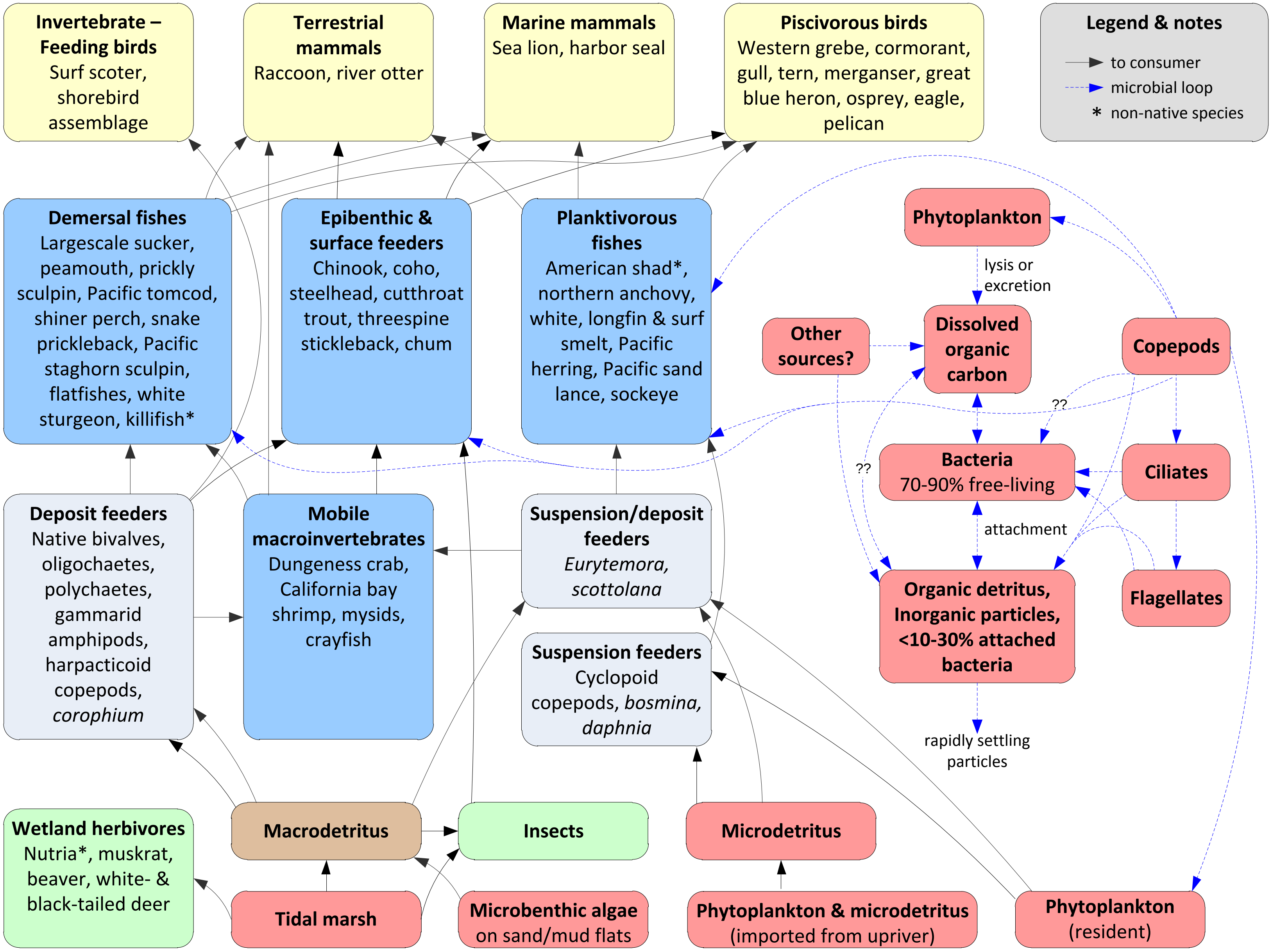


Figure D.7.1. Food web of the Columbia River estuary. Most linkages on the left side are adapted from Johnson et al. (2003) and those on the right side (microbial loop) are adapted from Baross et al. (1994).

In general, less is known about the food webs of non-salmonid fishes in the estuary. Their life history often involves use of multiple habitats and no detailed tagging or migration studies have been done. Bottom-feeding starry flounder, English sole, Pacific tomcod, prickly sculpin, staghorn sculpin and white sturgeon are part of the amphipod-mysid node as described above (Haertel and Osterberg 1967, Bottom and Jones 1990, McCabe et al. 1993; Dumbauld et al 2008; Figure D.7.1). Some species change their diets with ontogeny. For example, the English sole is pelagic in its larval form and bottom-dwelling in its adult form. Other species change habitats with tidal stages. For example, starry flounder move into the intertidal zone to feed at high tide and then retreat to channel bottoms at low tide (Bottom et al. 1984).

The Estuarine Food Web is Detrital Driven

Exploration of the structure and processes at lower trophic levels has been a major research topic for estuaries. The role of detritus as a basal component of the estuarine food web was first discovered in the Nanaimo River estuary in British Columbia (Sibert et al. 1977) and later confirmed in the Fraser River estuary British Columbia (Kistritz et al. 1983) and in Puget Sound (Wissmar and Simenstad 1985).

Detritus is a complex of 1) organic and inorganic matter from decaying plant material mixed with sediment particles, 2) bacteria, fungi and other microbes, and 3) micrograzers such as protozoan ciliates and flagellates. Macrodetritus[30] is consumed by many invertebrates that are eventually fed upon by juvenile salmon in the estuary (Figure D.7.1; Johnson 2003). Based on feeding habits of benthic invertebrates recognized as key nodes in the juvenile salmon food web (e.g., amphipods and mysids), macrodetritus from wetland plants is a key food source compared to microdetritus, which is derived from freshwater phytoplankton produced in the river and upstream reservoirs (Simenstad et al. 1990). Microdetritus supports calanoid copepods and cladocerans important to other estuarine fish such as shad and herring, and some copepods are important in the diet of mysids (Simenstad and Cordell 1985). Nevertheless, the relative mass of carbon in macrodetritus produced *in situ* from estuarine wetlands relative to carbon in microdetritus derived from freshwater (fluvial) phytoplankton shows that microdetritus dominates the contemporary estuary (Simenstad et al. 1990, Sherwood et al. 1990). Before the hydrosystem was constructed, wetland plants annually contributed 19,938 million mt of carbon to the macrodetritus pool as compared to only 3,605 million mt by 1980 (Sherwood et al. 1990). This represents an 82% decrease in macrodetritus mass, providing a strong rationale for restoration of wetland habitat and marshes[2] (see below and Chapter E.3).

The relative importance of the macrodetritus for the estuarine food web has been recently confirmed by stable isotope analysis (SIA, see Appendix A; Maeir and Simenstad 2009). SIA also confirms that marine phytoplankton and benthic macroalgae are significant contributors to the estuarine food web. There are significant taxonomic, spatial and seasonal differences among species, with invertebrates often showing a strong linkage to primary production sources in specific habitats. For example the SIA signature in amphipods sampled from mudflats, where they feed on attached algae, matches the SIA signature for algae, not macrodetritus.

Studies also show microdetritus to be an important food web component in *Corophium salmonis* diets (Maeir and Simenstad 2009). *C. salmonis* has somewhat different linkages to organic matter sources than chironomids, with a much higher contribution of vascular plant detritus across all months and all freshwater tidal sites, with a peak of 90% in July. *C. salmonis* from the middle estuary mostly assimilate macrodetritus whereas those further seaward in the lower estuary assimilate mainly marine phytoplankton and benthic macroalgae.

About 65% of the secondary production may be attributed to suspension feeding crustaceans in the estuary turbidity maxima (ETM; rkm 13 to 32). The secondary production is dominated by two copepods (*Coullana canadensis* and *Eurytemora affinis*; Simenstad et al. 1990). High concentrations of particle-attached bacteria occur in the ETM (Baross et al. 1994, Morgan et al. 1997). Bacteria are an important part of the detrital food base because they are eaten by micro-consumers

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[30] Macro-detritus is detritus based on macrophytes, while micro-detritus is that based on phytoplankton. These are operational definitions (S. Simendstad, University of Washington, personal communication).

[2] Note that the upstream boundary of the estuary in these analyses was 75 km from the mouth and therefore excluded the other 158 km up to Bonneville Dam.

such as rotifers, oligotrichs and flagellates, as well as the crustacean zooplankton. The micro-consumers and the crustacean zooplankton play central roles in the transfer of energy and nutrients up the food chain (Figure D.7.1). The crustacean zooplankton not only graze on particle-attached bacteria, they also consume plant debris, thereby adding another branch to the detrital based food web (Simenstad et al. 1994). The crustacean zooplankton, in turn, are eaten by mysids, a key node in the salmonid food web. Densities of copepods in the ETM vary with depth and tide stages. However, *C. canadensis* densities mirror those of turbidity gradients and are almost always greater at the river bed, while *E. affinis* densities are greater higher in the water column during flood tide and lower in the water column during ebb tide (Morgan et al. 1997).

Subyearling Chinook exploit wetland food webs and grow substantially before entering the ocean (Maeir and Simenstad 2009). Based on otolith chemistry, the mean residency times of subyearling Chinook in the estuary was 30-67 days during 2003-2005, respectively, with smaller earlier migrants residing longer than larger migrants (Campbell 2010). Unmarked hatchery-reared Chinook (subyearlings or smolts), identified using the SIA signature of hatchery feed, shift to natural food within weeks and lose their hatchery food signal. However, hatchery-reared Chinook moving quickly downstream into the lower reaches and the plume are characterized by SIA signatures of marine-origin food as well as a strong signal from hatchery food (S. Simenstad, University of Washington, personal communication). Hatchery food is manufactured mainly from food sources originating outside the Basin (Chapter C.4). Similar to feed for farm animals, it is made from artificial constituents, which include cellulose binders and other plant material, oils from marine pelagic fish (e.g., anchovies), vitamins and other ingredients (Higgs et al. 1995).

Historical Changes in the Estuary – Loss of Wetland Habitat

The loss of wetland from human development (hydrosystem, diking, urban development) has been substantial. However, the extent of change is dependent on estuarine location, survey methods and habitat type. For example, there have been major losses of tidal marsh and swamp habitats, but Cathlamet Bay near the river mouth has been much less disrupted than other peripheral bays near the mouth and the upper estuary (Thomas 1983). Bottom et al. (2008) concluded that the total area of all wetland types in the lower estuary (up to about 75 km upstream) decreased from approximately 155 km^2 historically to 75 km^2 at present. In 2000 it was estimated that 53% of wetlands in the entire estuary are behind dikes (Garono et al. 2003), but this estimate is highly uncertain because of problems with remote sensing methodology (Si Simenstad, University of Washington, personal communication). It should be noted that the estimate of 53% includes forest wetlands and is based on a total area of estuary wetland, from the mouth to Bonneville Dam, of about 703 km^2.

Changes in hydrograph (freshets, flooding, timing relative to food webs). Tidal flows and freshets strongly influence food webs in the estuary. However, the food web structure of the lower Columbia River and estuary has been fundamentally changed by reservoir construction which modified flow, changed seasonal patterns of flooding and thereby altered production processes. At the seaward end of the estuary, the salt wedge penetrates 40 km upstream in spring-early summer, probably further into the river relative to pre-dam conditions because of reduced flows (ISAB 2007-3). The landward head of the salt wedge is characterized by the ETM. Changes in the distribution of the salt wedge influence the location of the ETM and its food web, but it is difficult to forecast ecological effects that might propagate to higher trophic levels such as juvenile salmon.

The hydrosystem and diking have caused major changes in the flooding regime too. Flow regulation has decreased the spring freshets to about 50% of the natural level (Figure B.2.1) and lowered total sediment input to the estuary by approximately 50 to 60% (Bottom et al., 2005; K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data). Further, diking and navigation structures in the lower river and estuary have decreased the tidal prism by about 15% (Sherwood et al. 1990). Overbank flooding from the spring freshet is widely recognized as a mechanism for distributing detritus from vascular plants (e.g., sedges) in the horizontal plane of the estuary, as well as creating new habitat as a platform for the plants to grow on (Macdonald 1984). However, because of hydrosystem operations, modern flows required to generate overbank flooding (24,000 m^{3}s^{-1}) are extremely rare. Overbank flow is rare even during cold wet phases of the Pacific Decadal Oscillation (PDO) and was totally absent during the last PDO warm phase (1977-1995; Bottom et al. 2005). Depending on hydrosystem operations, increased winter freshets owing to climate change (ISAB 2007-2), coupled with sea level rise could increase the occurrence of overbank flow in winter. Overbank flow may become even less frequent during late spring and summer if climate change further reduces natural runoff at this time of year. Overbank flow is not expected to increase even with higher discharge in autumn but if it did, the autumn season is unsuitable for invertebrates to utilize the resulting redistribution of detritus for growth and reproduction (ISAB 2007-2).

Sediment deposition and transport influence food webs in the estuary through effects on benthic substrates and habitat structure and the flux of nutrients and toxic materials. Rivers naturally erode and transport larger quantities of sediment at higher flows. An indirect effect of expanding water storage capacity in the Basin has been to decrease downstream sediment transport. Spring freshets, which carried large quantities of sediments to the estuary in earlier years (Sherwood et al. 1990), have been greatly reduced by flow regulation. Trapping of sediments in storage and hydropower reservoirs has further reduced sediment transport. The net result has been a reduction in average annual sediment transport to the lower river by 50 to 60% (Bottom et al. 2005; K.R. MacGregor, Macalester College, St. Paul, MN, unpublished data). Nevertheless, construction of jetties and pile dikes increased sediment retention in the estuary from the late 1800's through (at least) the late 1900's (Sherwood et al. 1990) and the estuary is now a more effective sediment trap. An analysis of marsh-vegetation change in the lower estuary shows a contemporary shift toward vegetation types consistent with effects of sediment accretion and reduced disturbance from flow regulation (Elliott 2004 cited in Williams, 2006). Also, the eruption of Mt. Saint Helens in 1980 introduced large quantities of sediment to the lower Columbia River (Meade and Parker 1985); these deposits will continue to contribute sediment to the estuary for many years.

The estuarine sediment regime is also affected by dredging and by removal of sediments for landfill and construction use (sand mining). Dredging is necessary to maintain shipping channels; over the past several decades, 4 – 16 million mt of sand has been relocated by dredging each year (if excavated at one location, removal of 16 million mt of sand would leave a one-km square hole 8 m in depth). Because the dredged sand is deposited in various locations, both inside and outside the estuary, the net effect on sediment accumulation is difficult to quantify. The quantities of sand removed from the estuary for landfill and construction in earlier years are also uncertain. In summary, the sediment balance of the estuary is complex, dynamic, and slow to respond to changed inputs and outputs. Currently available data are insufficient to determine if the net accumulation of sediments over much of the past century continues today, or has been reversed (D. Jay, Portland State University, personal communication).

Reductions in the sediment supply have affected the integrity of intertidal habitats in the lower river and estuary. Intertidal habitat accounts for 40% of the estuarine area and the mud and tidal flats in the lower estuary are important detrital producers (Wissmar and Simenstad 1998). For example, Baker, Trestle, Youngs and Cathlamet bays produce 82% of the total benthic algal production in the estuary, some of which enters the microdetritus pool. Net annual primary production by emergent vascular plants in Youngs Bay is highest in the low marshes (~ 1,000 g C m^{-2} y^{-1}; Small et al. 1990). Input of sediment into the estuary is clearly necessary to maintain and build the marsh platforms and mud and tidal flats.

Loss of habitat from diking. In addition to reduced habitat availability from reduced flows, diking has significantly affected fish access to wetland habitat as well detritus production. Nearly 1,300 ha of shallow water habitat area (SWHA) has been lost in the estuary between rkm 50 and rkm 90, due only to changes in hydrology (1974 baseline vs. 1998 observed; 38% of baseline; Kukulka and Jay 2003). However, if flow had not changed, the amount lost to dikes would be 2,300 ha (51% of baseline). At the observed flow (1998), SWHA is reduced to 2,500 ha by dikes. Taking into account flows and diking, 3,200 ha of SWHA needs to be recovered to restore the estuary to "historical" conditions when ~ 4,500 ha were available.

The goal of the Environmental Protection Agency and the Lower Columbia River Estuary Partnership is to restore 5,260 ha (about 5 km^2) of lower estuary habitat (Corbett and Sink 2009). If the above estimates are correct, this will recover only 6% of the 80 km^2 wetland area lost (Bottom et al. 2008) from flow changes and diking. However, this conclusion raises several important caveats or questions: 1. What is the appropriate "currency" that is relevant to food web restoration? Is it simply wetland area, as commonly used by restoration practitioners? Or is it the amount of macrodetritus produced? 2. Will the restored habitat produce macrodetritus that is equivalent in quantity and quality to that produced by the historical ecosystem and its food webs? These questions must be answered by choosing an appropriate year as the baseline target, given that some losses (e.g., dikes protecting human habitation) are probably not recoverable.

The Estuarine-Plume Interface. Just as the plume is caused by the freshwater outflow of the Columbia River, the estuary is the result of the influx of ocean water into the river mouth. These interactions have important consequences for the food webs in both habitats.

Some of the most spatially, temporally, and taxonomically dynamic food webs in the system occur where the plume and estuary communities overlap at the mouth of the river (rkm 1-3). The degree of overlap varies with river discharge, season, upwelling and tidal stages. Marine zooplankton (copepod nauplii, marine copepod species, and larvaceans (*Oikopleura dioica*)) are imported from the ocean at mid depth into the estuary on flood tide, and are an order of magnitude more abundant than freshwater zooplankton at the surface (Simenstad et al. 1994). Zooplankton near the bottom are available as food for demersal and pelagic fishes that migrate into and out of the salt wedge, using multiple estuarine habitats. Both anadromous and marine fishes migrate into and out of the plume or reside in the estuary (see above) on seasonal and tidal time scales. Examples are herring, anchovy, shad, and juvenile salmonids.

Light limitations from turbidity are thought to reduce phytoplankton production in the estuary. Nevertheless, river flow and the relatively rapid flushing time in the estuary (1-5 d depending on river flow) result in large injections of freshwater phytoplankton from upstream reservoirs (Neal 1965; in Haertel et al. 1969). The material is exported to the ocean via the plume, initially in surface layers of freshwater but entering deeper water with mixing. Estuarine detritus derived from phytoplankton, benthic algae, and marsh plants is also injected into the plume. Most is transported in surface and mid-layer waters. An estimated 40,560 mt C of phytoplankton and 159,185 mt C of detritus are exported to the ocean annually (Small et al. 1990), equivalent to the content of about 356 and 1396 railway tank cars, respectively. Some of this carbon must feature in the plume food webs, either through microbial processes in the water column or through benthic systems when detritus settles out on the continental shelf. In addition, the estuary injects important nutrients, such as iron, into the plume that stimulate phytoplankton growth. In contrast, oceanic upwelling is a source of phosphate and nitrate for the estuary during spring and summer. As the plume entrains and is mixed with deeper, nutrient-rich waters are advected into the estuary (Haertel et al. 1969). The low-salinity water of the plume results in a shallow, stable surface layer that warms rapidly in the spring to produce an early phytoplankton bloom.

The Columbia River Plume

The plume is created by the largest point source of freshwater flow into the eastern Pacific Ocean. It forms a dynamic low-salinity region extending seaward from the river mouth for hundreds of kilometers over the continental shelf – with important consequences for fish production via food web dynamics. Its shape, orientation and structure are influenced by winds, tides, sea levels, volume of river flow and coastal upwelling, all which vary daily, seasonally, inter-annually and inter-decadally (see map). For instance, seasonal variability is strongly associated with spring snowmelt and summer drought in the Basin, as well as coastal upwelling. The plume moves north or south depending on the wind forcing and Coriolis effects, usually extending as far south as California in the summer when northwest winds prevail. In contrast, it is usually confined along the coast of Washington during the winter season when southerlies prevail. The plume is often present off Washington shelf from spring to fall, and is frequently bi-directional (Hickey et al. 2005). During low flow years, such as 2001, the plume is small and does not extend far into the coastal ocean.

Maximum mixing of ocean waters and Columbia River water occurs inside the estuary and in the near field of the plume, especially during periods of low flows and spring tides. Upwelling waters are entrained into the plume along with nitrates, iron and other nutrients that enhance primary productivity by pelagic blooms of diatoms. As the plume moves offshore and to the south, nutrients are depleted, grazing by zooplankton increases and phytoplankton productivity decreases.

Similarly, during downwelling events nitrates are not replenished (Whitney et al. 2005, Lohan and Bruland 2006, Bruland et al. 2008, Hickey et al. 2010). Vertical stability of the plume contributes to warm temperatures, a shallow mixed layer and earlier phytoplankton production in the plume than in adjacent waters (Anderson 1964).

The Columbia plume has important influences on the food webs of anadromous fishes migrating into and out of the river as well as on the food webs of coastal communities. The unique vertical and horizontal features, as well as the abrupt frontal boundaries between the buoyant river and ocean water, form density gradients and convergences. These, in turn, cause exchanges of nutrients between the river plume and cold, subsurface shelf waters, including the leading edge of the plume (Orton and Jay 2005). These are locations where productivity and zooplankton are often high, and where predators such as seabirds, fishes and marine mammals tend to aggregate. Elevated concentrations of chlorophyll and zooplankton also have been observed within the pycnocline and thermocline (i.e., regions in the water column with abrupt change in salinity and temperature, respectively) near the base of the plume (Peterson and Peterson 2008).

Juvenile salmonids, mainly smolts emigrating from the Columbia River, are often more abundant in the plume as compared to more marine shelf waters (Pearcy and Fisher 1990). The prey for juvenile salmonids and other fishes often concentrate at associated fronts. However, juvenile salmon do not feed at higher rates at fronts nor do their stomachs contain any prey groups indicative of feeding in the fronts (De Robertis et al. 2005, Morgan et al. 2005). This is possibly because of the ephemeral nature of frontal features. Although juvenile salmonids do not utilize surface fronts along the plume, they may feed along horizontal density gradients below the surface of the plume – a region of high zooplankton abundance (De Robertis et al. 2005). As the plume waters age and increase in salinity, phytoplankton stocks decrease while zooplankton appears to increase (Peterson and Peterson 2008).

Recent changes to flows from the river affect feeding and predation in plume waters. The currently reduced flows in spring reduce sediment discharges, resulting in decreased turbidity in the plume. Annual spring freshet flows are about 50% of pre-dam flows and sediment discharges are about 50 to 60% less than 19th century levels (Bottom et al. 2005; K. R. MacGregor, Macalester College, St. Paul, MN, unpublished data). Turbid environments may be advantageous for planktivorous fishes because they are less vulnerable to predation by larger piscivores while maintaining their ability to capture zooplankton (Boehlert and Morgan 1985, Gregory and Levings 1998, De Robertis et al. 2003). However, decreased turbidity may result in more effective predation by visual predators such as seabirds, large fishes and marine mammals on the planktivores. Juvenile salmonids are distributed mainly near the surface of the plume, and densities of Chinook become higher in more turbid water (Emmett et al. 2004). Conversely, many piscivorous fish predators, such as Pacific hake, are found in less turbid offshore waters (Emmett et al. 2006).

Planktivores, such as Pacific sardine and northern anchovy are often abundant in the vicinity of the plume where phytoplankton and zooplankton may be concentrated. Other forage fishes such as Pacific herring and smelt are also critical links in the food webs along the coast of the northeastern Pacific. These are prey for many species of seabirds, marine mammals and large fishes, including adult salmonids (Emmett et al. 2006).

Juvenile coho and Chinook in the plume and surrounding coastal waters feed selectively on large pigmented prey such as juvenile fishes, crab megalopae, euphausiids, hyperiid amphipods and pteropods. However, their feeding habits vary among years (Schabetsberger et al. 2003) as well as by location. Dungeness crab megalopae comprise larger fraction of the diet of coho in the plume, while hyperiid amphipods and other crab megalopae are more common in the diets of individuals caught in ocean waters (De Robertis et al. 2005).

The diets and trophic relationships of the dominant marine nekton in the northern California Current the plume show five dominant trophic groups (Miller and Brodeur 2007). The trophic groupings are based on the consumption of copepods, euphausiids, brachyuran larvae, larval and juvenile fishes, and adult nekton. Euphausiids are the most commonly consumed prey by most trophic groups. Many fishes consume prey from multiple trophic levels, and diets change depending on upwelling and ocean productivity (Brodeur and Pearcy 1992). This indicates the importance of omnivory in the California Current food web. Food webs in other upwelling coastal regions have been classified as "bottom-up," controlled by productivity of lower trophic levels (Cury et al. 2000), or "wasp-waisted" where only a few species, such as forage fishes, at a mid-trophic levels perform a critical link by transferring production from lower to higher trophic levels (Bakun 1966, Cury et al. 2000). Top-down control via large predators, however, also may be important (Pearcy 1992, Emmett and Sampson 2007).

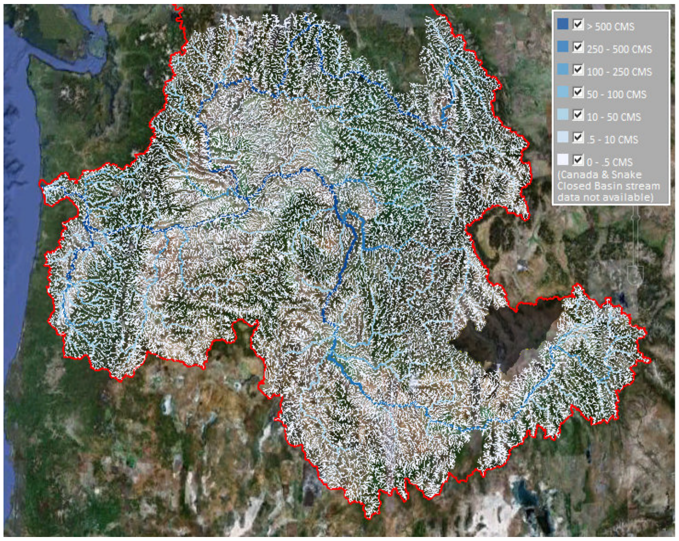
Seabirds and marine mammals are consistently found in plume waters. Common murres (51/km^2) and sooty shearwaters (25/km^2) are often abundant during May through September (Varoujean and Matthews 1983, Zamon 2010, personal communication). Murres feed on northern anchovy and Pacific tomcod and various species of smelt and juvenile salmonids. The foods of shearwaters are unknown. Seabird predators are often concentrated along the leading edge of the plume (Zamon 2010, personal communication). Killer whales as well as California sea lions, Steller sea lions, gray whales and cormorants are also observed in the vicinity of the plume during March (Zamon et al. 2007).

The plume may affect the distribution and survival of juvenile salmonids since it is embedded in the California Current. The California Current is a highly dynamic eastern boundary current with dramatic seasonal, inter-annual and decadal fluctuations in shelf transport, upwelling intensity and timing, and temperature, including El Niños and PDO regime shifts. These fluctuations ripple through all trophic levels (Peterson and Schwing 2003, Brodeur et al. 2005, 2006). For example, during cold years with intrusions of cold subarctic water into the coastal ecosystem, large, lipid-rich copepods dominate the herbivore community (Peterson and Schwing 2003), and thus establish a shorter food chain to secondary consumers.

These prevalent physical changes have major consequences for the distribution and abundances of both forage fishes and piscivorous predators. The "alternative prey" hypothesis predicts that when forage fishes are abundant, predators will consume forage fishes because juvenile salmon of similar sizes would be rarely encountered (Fisher and Pearcy 1988, Pearcy 1992). In warm years, such as after the 1976/77 regime shift, years of El Niños and positive PDOs, large predatory fishes such as Pacific hake, jack mackerel and Pacific mackerel, as well as forage fishes such as Pacific herring and American shad become more abundant off Oregon and Washington. In contrast, in cool years, populations of northern anchovy, eulachon and market squid are more abundant (Emmett and Brodeur 2000). Although Pacific hake and jack mackerel do not often eat juvenile salmon (Emmett and Krutzikowsky 2008), trophic models suggest that the presence of high numbers of Pacific hake could account for low survival of juvenile salmon leaving the estuary, provided forage fish populations are low at the same time (Emmett and Sampson 2007). This mortality would be significantly reduced when forage fishes are abundant. It is clear that river discharge strongly influences predator-prey interactions in the plume, possibly because high flow conditions advect juvenile salmon offshore where predators are less abundant (Pearcy 1992), or because the plume is more turbid during high discharge, limiting predators ability to see and capture prey (Emmett and Sampson 2007). This agrees with the fact that a large surface plume flowing offshore and to the south is correlated with increased survival of juvenile steelhead (but not Chinook) during the ocean entry period (Burla et al., 2010).

The critical importance of early ocean survival on returns of salmonids to the Columbia River argues that research should continue on the ecology of juvenile salmon as they exit fresh water and the estuary into the plume and coastal ocean. We recommend continued research on the availability of food for growth, and the impact of predation on survival, of both in-river and transported smolts in these waters, and on how these factors relate to river flows, plume structure and ocean conditions. This research is vital to understanding and predicting adult returns and SARs. Research should be well integrated and coordinated with similar research in waters to the north where salmonids from the Columbia River migrate. We recommend that that long-term monitoring of the plume and estuary be continued and managed as systems connected to the Columbia River Basin.

D.8. **Riparian Habitats**



Riparian zones (all streams). See interactive map

Food Webs at the Terrestrial-Aquatic Interface

Riparian zones are transitional semi-terrestrial/semi-aquatic areas regularly influenced by fresh water (Naiman et al. 2005, Décamps et al. 2009). They usually extend from the edges of water bodies to the edges of upland vegetation communities. Due to their spatial position, they influence and integrate exchanges between aquatic and terrestrial environments. They are dynamic areas characterized by strong energy regimes, substantial habitat heterogeneity, a diversity of ecological processes, and multidimensional gradients in resources. As a consequence they are often locations of concentrated biological activity. In general, riparian zones may be viewed conceptually as a collection of energy transfer pathways where the type and magnitude of aquatic-terrestrial exchanges vary spatially and temporally. Human activities contribute greatly to this variation, as river valleys have been foci for human settlements and commerce for millennia.

The complexity and distinct ecological functions of riparian zones are maintained through strong spatial and temporal connectivity with adjacent riverine and upland systems (Chapter E.4). Water, sediments, and nutrients enter riparian zones from uplands and streams, mixing and reacting along diverse surface and subsurface flow paths. Under normal flow conditions riparian zones retain a significant portion of these materials and generally return chemically purer water to streams and rivers. At the same time riparian zones are important sources of energy to both upland and aquatic organisms in the form of plants and insects. Many stream food webs depend on these and many upland animals rely on them as important dietary subsidies. At the same time, riparian communities benefit from the enhanced productivity of adjoining ecosystems (especially aquatic systems) through physical and biotic feedbacks that export a portion of their productivity to riparian zones in the form of organic matter (OM) and nutrients. The unique ecological functions of riparian zones are created and maintained by a variety of biophysical processes and exchanges across multiple spatial and temporal scales. Effective management requires maintaining connectivity, both in the timing and extent of energy and material exchanges as well as in the movements and types of animals (Chapter E.4).

Riparian Zones as Sources of Energy and Nutrients for Aquatic Systems

Riparian food webs are connected to those of adjoining aquatic environments and the integrity of each, to differing degrees, depends on the flow of energy and materials between them (Polis et al. 1997). Most organic materials providing the base for stream food webs originate from “outside” the immediate aquatic environment. Likewise, the aquatic environment may be an important source of material (e.g., aquatic insects) for riparian organisms (Baxter et al. 2004). Thus, effective fish management and conservation strategies must consider conditions of the surrounding landscape to ensure connectivity between aquatic and riparian habitats (Wiens 2002). Materials (i.e., carbon, plant-available nutrients, cations, sediments, and woody debris) may originate from upstream, via precipitation, groundwater, and as external inputs from surrounding vegetation, or from the lateral migration of river channels that converts terrestrial to aquatic habitat.

By far the most thoroughly investigated and best understood connection between riparian and stream food webs is the transfer of riparian plant litter to streams (Chapter D.1; Webster and Meyer 1997). Inputs of riparian organic matter represent allochthonous (external) sources of energy as opposed to the autochthonous (internal) organic matter contributed by aquatic primary producers. In low-order streams beneath closed-canopy riparian forests, the influx of carbon from riparian plant sources, both surface and subsurface, may amount to 80-95% of total organic carbon influx to streams (Conners and Naiman 1984, Naiman et al. 1987). Riparian litter fluxes per area of stream surface in the eastern United States range from

40 to 700 g C m^{-2} yr^{-1} (Webster et al. 1995). Inputs are proportionately highest in low-order streams and decrease exponentially as streams widen and the canopy opens (Chapter D.2). In temperate climate zones riparian litter fluxes are strongly seasonal, peaking with the fall of leaves during autumn. Although the proportional inputs of riparian litter to river systems decreases downstream, the total amount of riparian litter input to the river continues to rise and varies as a function of channel morphology and riparian forest structure and composition. Conners and Naiman (1984) calculated that total inputs of allochthonous organic matter increase exponentially with stream order, approaching 500 g C m^{-1} yr^{-1} in fifth- and sixth-order streams. As a dramatic example of downstream effects, leaves of riparian trees were found to be a major source for the more than 36 million mt of carbon carried by the mainstem Amazon River annually (Devol and Hedges 2001). In general, carbon not directly traceable to leaves appears to come from soil organic matter, which for the mainstem Columbia is most likely derived from erosion of riparian and floodplain soils, or delivered to the drainage network by landslides.

Once in the stream, riparian organic matter is decomposed by a variety of specially adapted microbial and invertebrate fauna. When litter (mainly leaves and needles) enters streams there is a brief period (a few days) of rapid leaching in which 25% or more of the initial dry weight can be lost (Giller and Malmqvist 1998). Biotic decomposition is initiated by hyphomycete fungi that break up the litter's structural integrity by secreting enzymes to hydrolyze cellulose, pectin, chitin and other difficult-to-digest compounds (Suberkropp and Klug 1976). Fungal diversity and abundance are closely tied to the riparian forest, and fungal species richness has been positively correlated with riparian tree richness (Fabre 1996). With time fungi give way to bacteria as the dominant microorganism in the decay process. Decomposition rates are driven by substrate quality, stream nutrient concentrations, available oxygen and temperature (Suberkropp and Chauvet 1995). Fungal decomposition alone can fragment leaves into flakes of finer particulate organic matter within weeks (Gessner and Chauvet 1994). This fragmentation process is critical to energy dispersion in streams and rivers because finer fragments tend to be more mobile and therefore fuel metabolism in downstream river sections. Aquatic ecologists classify fragments into coarse (> 1 mm) and fine (< 1 mm but > 0.5 µm) particulate organic matter (CPOM and FPOM) fractions, which tend to vary consistently in quality and abundance along river networks.

Microbially colonized litter is said to be *conditioned*, and generally has higher nutrient concentrations than non-colonized litter. Conditioned litter is therefore the preferred choice of macroinvertebrate consumers that make up the next link in aquatic food webs (Irons et al. 1988, Suberkropp 1998). Benthic macroinvertebrates have evolved a number of strategies to capitalize on the energy of riparian litter, to the extent that species can be generally classified into functional feeding groups (Hershey and Lamberti 1998). The most important groups in transferring riparian-derived energy up to higher consumers are *shredders*, which shred and consume litter material, and *collectors*, which simply consume litter particles they collect in the water column or on the streambed. Shredders include caddisflies (Trichoptera), stoneflies (Plecoptera), non-biting midges (Diptera), and certain families of beetles (Coleoptera). Collectors include these groups plus a wide range of other aquatic animals including shrimp (Malacostraca) and worms (Oligochaeta and Turbellaria). In small streams shredders are by far the dominant group, constituting up to 50% of the entire macroinvertebrate community, whereas collectors become the dominant group in larger rivers (Chapter D.1; Hawkins and Sedell 1981, Hershey and Lamberti 1998).

Sharp changes in the supply of wood and leaf litter to streams (e.g., by removal of riparian forests), or by changing riparian forest composition, may cause significant changes in the abundance and biomass of macroinvertebrate functional feeding groups. Consequent decreases in certain species of aquatic insects may have direct feedbacks to riparian-based food webs (discussed later in this chapter). Wallace et al. (1999) investigated the ecosystem-scale consequences of altering riparian litter fluxes to an experimental stream in the Coweeta catchment of western North Carolina, United States. By suspending a canopy above the stream channel and erecting fences along the stream margin they reduced the combined vertical and lateral inputs of litter to the stream by 94% over a four-year period. In the fourth year they also removed small wood from the stream. Decreasing litter influxes lead to a 50% decrease in organic matter standing crop, from ~ 2,200 g m^{-2} to 1,100 g m^{-2}, in the stream. The invertebrate community responded with an 80% decrease in both abundance (individuals m^{-2}) and biomass (g m^{-2}), and total secondary production declined to only 22% of pretreatment values. Functional feeding groups responded differentially during the experiment; shedders, gatherers, total primary consumers, and predators declined significantly, while scrapers and filterers did not.

Riparian arthropods are also important energy sources to stream consumers such as fish. Arthropods fall into streams from overhanging foliage by accident and the input is proportional to arthropod abundance in the canopy (Figure D.8.1; Nakano and Murakami 2001). Arthropods may also wash into streams and rivers during overland flow events. The normalized input (per square meter of channel area) is higher in smaller streams flowing beneath a closed riparian canopy, but even in larger streams and rivers the flux may remain substantial at the channel margins. Once in the aquatic system, riparian arthropods are consumed by fishes foraging on drift and may constitute a major proportion of their diet. In a detailed study of the annual resource budget of fish in a northern Japanese stream, riparian arthropods accounted for 46% of the diet of rainbow trout, 51% for white-spotted char (*Salvelinus malma*), and 57% for masu salmon (Fausch et al. 2002). Terrestrial arthropods have also been found as a significant component of the stomach contents of redbreast sunfish and bluegill in a Virginia stream (Cloe and Garman 1996). In temperate regions, riparian arthropod fluxes to streams are greater during warm months (Mason and MacDonald 1982, Cloe and Garman 1996). Consumption of terrestrial prey by aquatic consumers is viewed as an energy subsidy to aquatic food webs and the energy derived from riparian arthropods sometimes even exceeds that available from aquatic arthropods (Cloe and Garman 1996, Baxter et al. 2004).

Riparian-derived arthropods are higher quality food than riparian litter and are directly available to top consumers such as fish. Experimental evidence shows that curtailing this energy input from streams has consequences that reverberate through aquatic food webs and ultimately upset the basic composition of the stream community. Nakano et al. (1999) conducted a manipulative experiment in which they partially blocked the input of riparian arthropods to a stream on the northern-most island of Japan by building a 50-m long greenhouse-type enclosure over the stream. There were four experimental treatments: two prey densities (natural versus reduced inputs of riparian arthropods) each replicated with and without the presence of fish predators. Fish were initially removed from the experimental reach, and then Dolly Varden, one of three common fish species inhabiting the stream, were reintroduced to two treatments to assess their impact on macroinvertebrate communities. At 14 and 28 d after initiation of the experiment investigators monitored the biomass of aquatic arthropods, periphyton and the stomach contents of fish. The

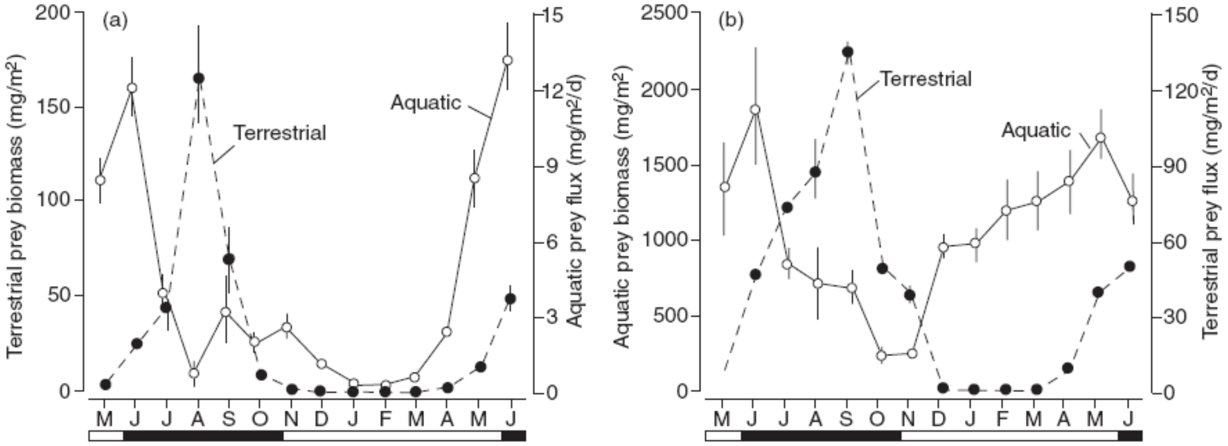


Figure D.8.1. Contrasts in seasonal fluxes of prey invertebrates between a riparian forest and stream in northern Japan demonstrating the exchange of reciprocal energy subsidies: (a) Aquatic prey fluxes to the riparian forest are high in times of low terrestrial prey biomass, while (b) riparian prey fluxes to the stream are higher during periods of low aquatic prey biomass. Both biomass ($P < 0.01$) and flux ($P < 0.01$) differed significantly among months (black and white circles represent mean values for riparian and aquatic prey, respectively. Black and white portions of horizontal bars at bottom of figures indicate leafing and defoliation periods, respectively. From Nakano and Murakami (2001).

consequences of removing riparian arthropods from the diet of Dolly Varden were dramatic. These fish, which primarily had been drift foragers consuming riparian arthropods and drifting aquatic arthropods, shifted to active foraging and significantly reduced the biomass of benthic aquatic herbivorous arthropods. The reduction in benthic herbivorous arthropods led to a concomitant increase in periphyton biomass and thus a fundamental shift in the stream's community structure and composition. Although the loss of riparian arthropods to stream ecosystems is minor compared to the energy flux in leaf litter, the shift in predator dynamics reverberated through the system significantly impacting community-based functions.

Energy flows in both directions across the terrestrial-aquatic interface, and riparian food webs are also subsidized by aquatic resources (Jackson and Fisher 1986, Collier et al. 2002, Sabo and Power 2002b). Aquatic insects are an important energy source to a variety of riparian arthropods, and this energy subsidy is passed to higher trophic levels by the lizards, bats, shrews, and birds that consume riparian arthropods. The reliance of riparian arthropods on aquatic prey is greatest where high productivity gradients exist across the aquatic-riparian interface. Riparian arthropods inhabiting resource-scarce habitats such as exposed gravel bars and desert riparian environments appear to rely almost exclusively on aquatic prey (Jackson and Fisher 1986, Sanzone et al. 2003). For example, aquatic insects compose 80 to 100% of the diet of certain staphylinid and carabid beetles, and about 50% of the diet of lycosid spiders inhabiting gravel bars of an alluvial river in Italy (Paetzold et al. 2005). The more important aquatic insects to riparian food webs are those that emerge on land (like many stoneflies) as opposed to those that emerge from the water surface (e.g., mayflies). Interestingly, detritivorous aquatic insects – those that consume largely leaf litter – made up the largest proportion of the riparian arthropod diet along the Italian river, representing an important energy feedback to riparian food webs. Aquatic insects thereby transform the energy transported to streams as leaf litter into higher quality food that is returned to riparian zones (Paetzold et al. 2005).

Reciprocal energy subsidies such as these are especially important over the course of the year in temperate regions due to strong seasonal variability in the emergence and abundance of different insects. For example, aquatic arthropod abundance peaks following "leaf-out" of riparian forests in spring and after defoliation in autumn (Figure D.8.1) whereas riparian arthropod abundance peaks during the summer when forest productivity is maximal (Nakano and Murakami 2001). Western fence lizards in California rely on the

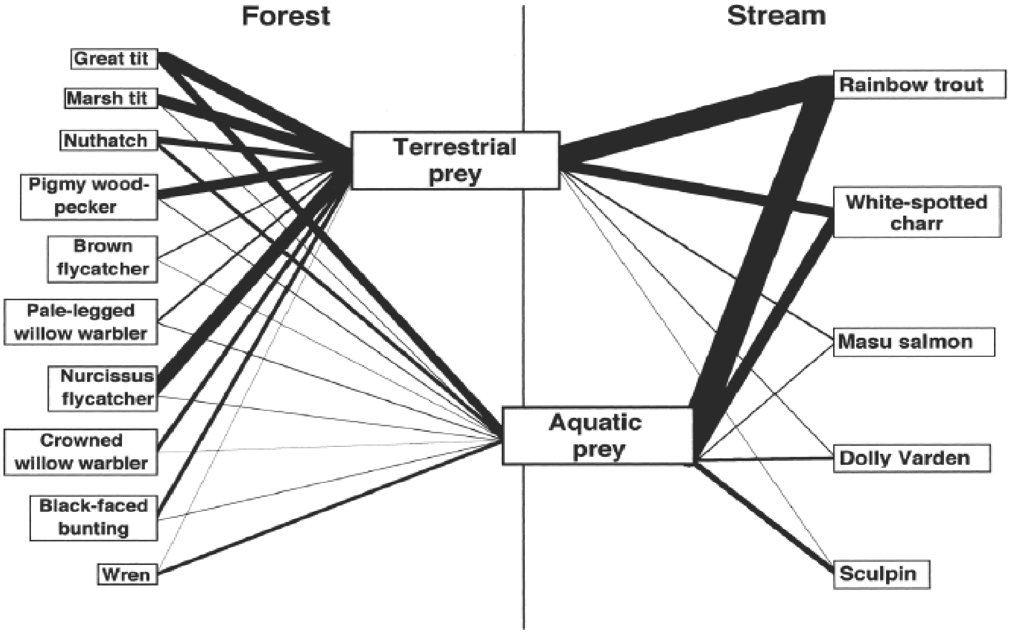


Figure D.8.2. Food web linkages between a riparian forest and a stream in northern Japan. The relative contributions of terrestrial and aquatic prey to the total annual prey consumption of each species are represented by line thickness. From Nakano and Murakami (2001).

energy subsidy provided by aquatic arthropods, and when aquatic arthropod availability is reduced there is a concomitant decrease in lizard abundance and more intense predation of terrestrial arthropods (Sabo and Power 2002a). The reciprocal linkages between terrestrial and aquatic food webs are also well illustrated by the bird community of a northern Japanese stream (Figure D.8.2). Ten species of riparian birds were found to rely on a diet of both riparian and aquatic arthropods.

Migratory riparian birds rely heavily on aquatic arthropods during May and June with aquatic arthropods accounting for nearly 90% of the brown flycatcher diet and nearly 80% of the pale-legged willow warbler diet. Over the course of the entire year, aquatic arthropods account for 39% of the total annual energy budget of the great tit and 32% of that of the nuthatch.

Large Animal Influences on Riparian Processes

Large animals influence nutrient and energy flows by consuming and redistributing energy and nutrients within riparian zones as well as across adjacent system boundaries. More importantly, large animals may alter the hydrologic and geomorphic characteristics of riparian zones, causing fundamental changes in energy and nutrient cycles, and altering plant community composition and structure.

Animals that pond water, dig holes, trample plants or move materials cause fundamental geomorphic changes. For example, beaver profoundly influence the short- and long-term structure and function of riparian zones of drainage networks by cutting wood and building dams. In catchments where beaver are abundant there may be 2 to 16 dams per km of stream length, and each dam may retain between 2,000 and 6,500 m^3 of sediment (Naiman et al. 1988). Ponds are eventually abandoned as they fill with sediment or as local food resources are depleted and, once abandoned, dams fail and ponds drain to produce nutrient-rich wetland meadows.

Animals browsing riparian and aquatic vegetation strongly influence riparian community structure, soil development, and propagule dispersal (Pastor and Naiman 1992). Animals that browse selectively keep preferred plant species from dominating the plant assemblage and thereby provide an advantage to species not browsed. For example, moose prefer willow and poplar, thus giving a competitive advantage to white spruce, which is not browsed.

The reduction of large predators, especially wolves and cougar throughout much of the Pacific Northwest may have equally important effects on riparian vegetation. It has been postulated that the age structure of black cottonwood and bigleaf maple in the western portion of Olympic National Park indicates decreasing recruitment (growth of seedlings/sprouts into tall saplings and trees) as a result of intensive elk browsing following the loss of wolves (Beschta and Ripple 2008). Without this predator and in the absence of human hunting, the structure of the floodplain forests suggests that the recruitment of palatable trees and shrubs has declined. This outcome is consistent with trophic cascades theory (Ray et al. 2005), whereby a loss or reduction of large carnivore predation may initiate changes in herbivore densities and altered foraging behavior that “cascade” to lower trophic levels. We suspect that this phenomenon has occurred throughout the Pacific Northwest wherever the population dynamics of apex predators and their prey have been altered.

Pacific Salmon and Riparian Zones

A remarkable example of the consequences of animal-mediated nutrient and energy flows in riparian zones is the migration of salmon. Pacific salmon transport marine-derived (MD) carbon and nutrients upstream and, upon death after spawning, hydrologic and animal pathways distribute these elements throughout aquatic and riparian systems (summarized in Chapter C.1). In an important biophysical feedback, fertilization of riparian plant communities with MD-nutrients enhances the growth of some riparian plants, positively influencing salmon over the longer term by supplying stream organisms with an increased supply of nutritious litter and by improving salmon habitat via an influx of large diameter riparian-derived wood.

Historically, spawning salmon represented a flux of nearly 7,000 mt of nitrogen and more than 800 mt of phosphorus to river corridors in California, Idaho, Oregon and Washington. Although fluxes have been reduced by >90% during the past century as populations have declined, salmon still are an important source of nutrients to many river and riparian systems of Canada, Alaska, Russia and Japan. There is some indication that in rivers denied MD-nutrients the growth rates of riparian trees have declined (Naiman et al. 2009).

Returning salmon provide seasonal food subsidies for a variety of wildlife that inhabit riparian zones throughout the year or that occupy riparian zones when the runs are occurring. At least 88 wildlife species are associated with spawning Pacific salmon (Cederholm et al. 2001). Of this total, 43 species (6 mammals, 37 birds) congregate at important spawning sites when adult salmon are present. By removing carcasses from the stream and consuming them in riparian areas, a variety of wildlife fertilize riparian plants by leaving partially eaten carcasses or depositing waste, and the leavings or excretory products themselves may attract other wildlife (Willson et al. 2004). Marine-derived nutrients also can be dispersed far from streams in bird droppings and by flies. Thus, the presence of adult salmon facilitates associations between riparian plant communities and wildlife populations that are unique to the spawning season.

The Productivity of Aquatic and Riparian Habitat is Interlinked by Reciprocal Exchanges of Material

Even though it is well established that terrestrial and aquatic systems are strongly linked (see Naiman et al. 2005 for a review), only recently have there been experimental manipulations to elucidate pathways and quantify linkages. For example, sharp changes in the supply of wood and leaf litter to streams (e.g., by removal of riparian forests) causes significant changes in the abundance and biomass of macroinvertebrates (e.g., Wallace et al. 1999). These subsidies may also be reversed – from the aquatic to riparian environment. Further, the magnitude of the subsidy can be dramatically altered by historical fisheries management, such as the introduction of exotic trout. For example, Baxter et al. (2004, 2007) found that the introduction of non-native rainbow trout resulted in a 65% decline in spider populations in the riparian forest (Figure D.8.3). A large portion of the spiders' diet comprised emerging aquatic insects from the stream. Native char (*S. malma*) primarily consumed terrestrial insects falling into the stream from the riparian forest. However, in the presence of non-native trout, the char altered their foraging behavior to consume grazing invertebrates, thereby releasing benthic algae from herbivory. Collectively, the char and trout reduced the amount of emerging invertebrates, and thus, restricted the food supply for riparian spiders.

Implications for Restoration and Key Threats

There are three additional, and relatively recent, human-driven impacts on vegetative succession, and ultimately on floodplain tree production, that require discussion (Naiman et al. 2009). They are seed dispersal and seed banks, the spread of invasive plants, and the eradication of predators that historically controlled herbivory. Seed dispersal via water (hydrochory) is important for maintaining the diversity and genetic continuity of riparian plant communities (Nilsson et al. 1991). Dams, however, may reduce levels of hydrochory to downstream reaches by trapping seeds within their impoundments. Unfortunately, this subject has received little attention in the Pacific Northwest because most trees (e.g., alder, cottonwood, willow, as well as all of the riparian conifers) have tiny, wind-dispersed seeds.

Seeds blanket the landscape and differences in establishment are often due to other factors (such as substrate texture, large wood, light availability, inundation regime, and/or water level). Nevertheless, there has been a 90% reduction in seed abundance and 84% reduction in species richness below Glines Canyon Dam on the Elwha River, Washington, suggesting that hydrochory may be more important than previously thought (Brown and Chenoweth 2008). Further, vegetative succession and soil processes in Pacific Northwest floodplains may be increasingly compromised by the proliferation of invasive plants – as discussed in Chapter C.5.

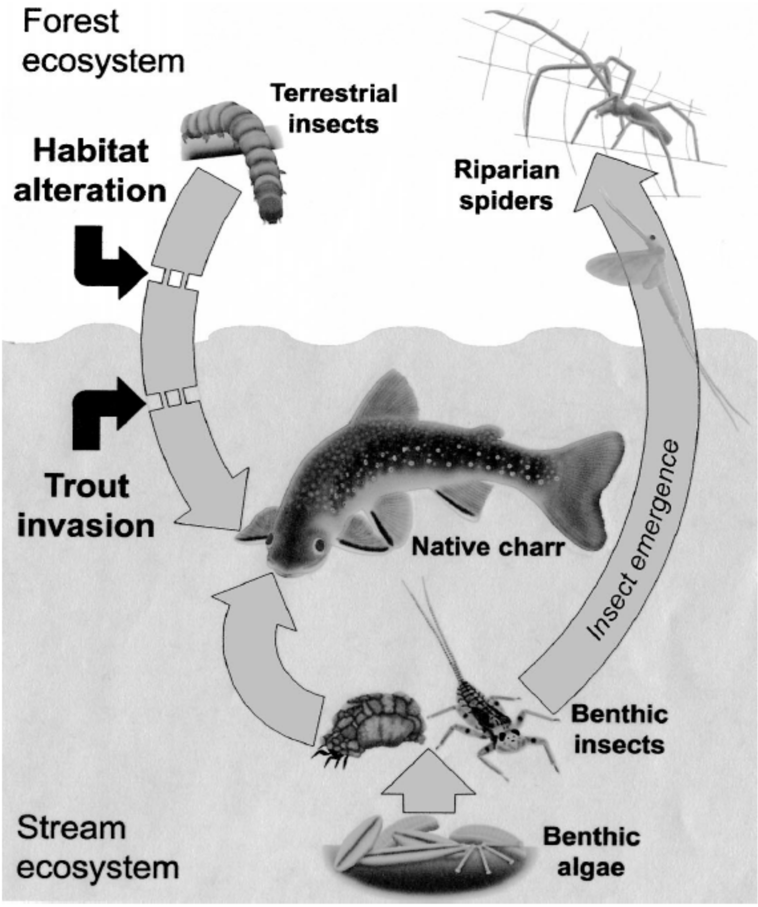


Figure D.8.3. A generalized diagram showing flows of invertebrate prey that drive food web relationships in stream and riparian forest ecosystems in northern Japan. These reciprocal food web subsidies are subject to interruption via habitat alteration or exotic fish species invasion, with consequences that propagate within and between the interconnected ecosystems. From Baxter et al. (2004).

E. A Systems Perspective

"…as we know, there are known knowns; there are things we know we know. We also know there are known unknowns; that is to say we know there are some things we do not know. But there are also unknown unknowns -- the ones we don't know we don't know."

-- Donald Rumsfeld

E.1. Future Vulnerabilities: Climate, Land Use and Population Growth

This prescient remark by a former Secretary of Defense is a useful way to introduce the topic of the future vulnerabilities of aquatic food webs to environmental shifts in the Columbia River Basin. As this report has repeatedly pointed out, we have learned much about food web structure and function and how it has been influenced by changes in environment and species composition in the Basin. However, there is much we do not know about the changes themselves and how they have affected salmon and other species of concern. Furthermore, there is a significant chance that unrecognized future food web vulnerabilities may exist – "the ones we don't know we don't know." For example, continued economic growth in eastern Asia will result in increased atmospheric transport and deposition of a wide variety of substances that may affect Basin food webs, but their impacts are virtually unknown. In this chapter we examine several factors that will likely have an impact on Basin food webs: climate change, human population growth and associated land use shifts. We know what the trends are. The ISAB has examined them individually in previous reports (ISAB 2007-2, -3), and we can speculate about how they might affect food webs in the future, but we must acknowledge that given the speed at which food webs appear to be changing in virtually all parts of the Basin, predicting the future is risky. There surely will be surprises.

Climate Change and Aquatic Food Webs

The ISAB report on climate change (ISAB 2007-2) identified several consequences of climate warming to water temperature and precipitation changes in the Pacific Northwest:

- Warmer temperatures will result in more precipitation falling as rain rather than snow
- Snow pack will diminish, and stream flow timing will be altered
- Peak river flows will likely increase
- Water temperatures will continue to rise

Climate change models vary according to assumptions about future greenhouse gas emissions, but the following Table E.1.1 from the University of Washington Climate Impact Group's *Climate Change Impacts Assessment* (CIG 2009) illustrates the magnitude of change (statewide) predicted by two widely used emission scenarios for Washington.

Projected reductions in summer discharge may be proportionately greater than projected increases in winter discharge (Luce and Holden 2009), although both patterns will have important implications for food webs. Increased cool season runoff, especially in watersheds with rainfall dominated hydrographs, may be accompanied by more severe storms with bed-mobilizing flows. Mobilization of stream substrate at very high flows can cause scour-related mortality of aquatic invertebrates that are not sheltered (e.g., by inhabiting stream substrate below the depth of scour). Lower summer flows will result in less wetted stream area and an overall reduction in habitable substrate. Lower flows may also exacerbate the drying of shallow riffles, resulting in losses of riffle-dwelling taxa.

Table E.1.1. Composite changes in air temperature, precipitation, and runoff across Washington during the cool season (October – March) and warm season (April – September) for the 2020s, 2040s, and 2080s. Based on the Special Report on Emissions Scenarios (SRES) A1B and B1 global greenhouse gas emission scenarios. From CIG (2009), Chapter 3, pages 51-52. Note that the % change in warm season runoff for the A1B scenario in the 2080s is given as +43.2% in CIG (2009) but has been corrected to -43.2% here.

		2020s		**2040s**		**2080s**	
		(2010-2039)		**(2030-2059)**		**(2070-2099)**	
	Changes	**A1B**	**B1**	**A1B**	**B1**	**A1B**	**B1**
Cool Season	Temperature (°C)	+1.05°C	+1.01°C	+1.83°C	+1.42°C	+3.24°C	+2.33°C
	Precipitation (%)	2.30%	3.30%	5.40%	3.90%	9.60%	6.40%
	Runoff (%)	2.30%	3.30%	5.40%	3.90%	9.60%	6.40%
Warm Season	Temperature (°C)	+1.31°C	+1.16°C	+2.26°C	+1.71°C	+3.79°C	+2.66°C
	Precipitation (%)	-4.20%	-0.90%	-5.00%	-1.40%	-4.70%	-2.30%
	Runoff (%)	-19.10%	-15.80%	-28.60%	-22.10%	-43.20%	-33.40%

The forecast changes in runoff are proportionately greater than the predicted increases in stream temperature (Figure E.1.1; also see Kaushal et al. 2010). However, even minor increases in water temperature, accumulated over time, affect the developmental rates of aquatic organisms and have significant consequences (Ward and Stanford 1982). For species with short life cycles, thermal increases can increase the number of generations per year; for species with longer life cycles (e.g., 1-2 years or more), these relatively small temperature increases can mean that metamorphosis to adult can occur in one year instead of two (Allan and Castillo 2007). Elevated stream temperatures tend to shorten the generation times of small-bodied organisms slightly more than those of large-bodied organisms (Gillooly et al. 2001), which could mean that warmer temperatures will enhance the abundance of small-bodied food items such as chironomid midges more than large-bodied invertebrates, such as limnephilid caddisflies. Higher temperatures also will enhance algal production, potentially providing more food for herbivorous invertebrates and fishes, particularly in the absence of scouring flows. However, shifts in thermally-favored algal and herbivorous species abundances may result in added production funneling to a "trophic *cul-de-sac*" – a food web dead-end in which primary and secondary production are concentrated in a few species that are not part of the main food web supporting salmon and trout (Power et al. 2008; also see Wootton et al. 1996). Such a scenario was suggested for streams containing abundant, but inedible, pleurocerid snails in Oregon, where high snail densities sequestered much of the algal production at the expense of food pathways leading to salmonids (Hawkins and Furnish 1987). Similarly, the large-bodied caddisfly *Dicosmoecus*, which constructs stone cases and is generally not consumed by juvenile salmonids, sequesters a substantial fraction of the primary productivity in 3rd-order tributaries of the John Day River (Tait et al. 1994).

Climate change will result in a higher incidence of wildfires in the Basin, as is already the strong trend, and the fires will burn with greater severity (Hessburg et al. 2005). More frequent, widespread and severe wildfires will have important implications for food webs in tributaries. Loss of forest canopy will reduce shading and is likely to exacerbate the water temperature increases caused by climate warming (Dunham et al. 2007). Fires also will introduce sediment and nutrients into stream channels, which could have offsetting effects on macroinvertebrate communities (Minshall 2003, Mellon et al. 2008). While the immediate effects of fire on tributaries are likely to cause short-term (0-3 years) declines in food web productivity, aquatic invertebrate abundance commonly rebounds several years after fires and may exceed normal levels for a few years (Rieman et al. 2006), as primary production remains elevated and terrestrial invertebrates from post-fire herbaceous vegetation fall into streams.

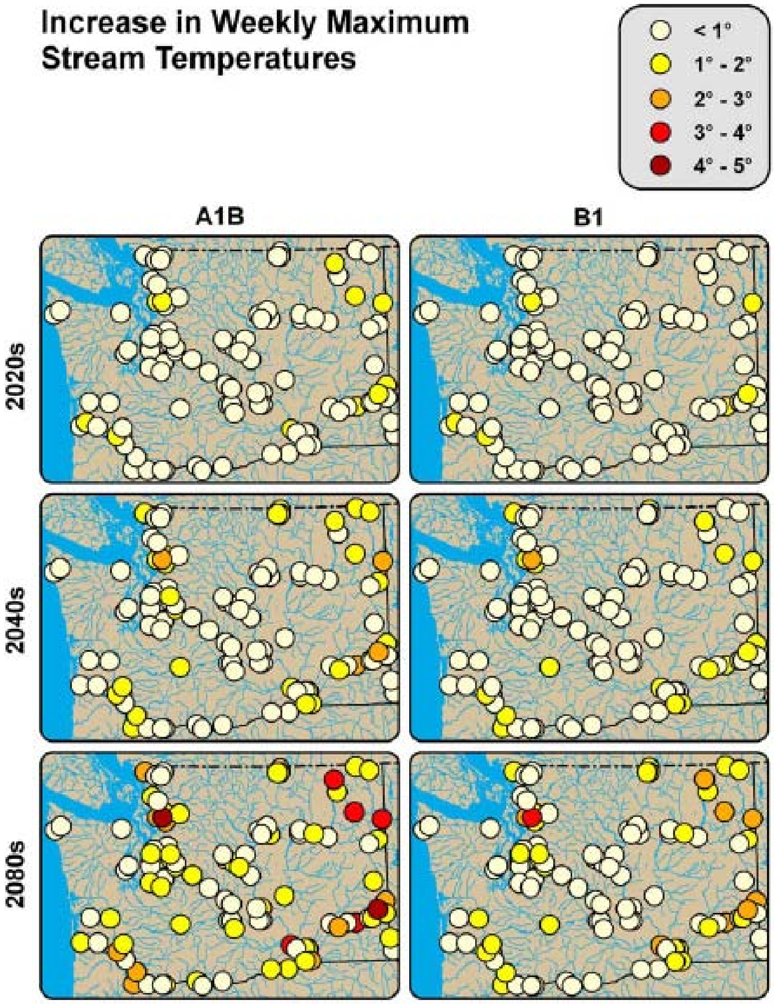


Figure E.1.1. Changes in weekly maximum stream temperatures (oC) in Washington State for the 2020s, 2040s, and 2080s under the SRES A1B and B1 emission scenarios (from CIG 2009, Chapter 6, page 45).

Less well understood are the ways in which climate change will influence the spread of invasive aquatic and riparian species. Certainly, warmer waters will favor introduced fishes better adapted to such conditions (e.g., brown trout, basses and sunfishes, perch and walleye, catfishes and bullheads, some minnows), but there is less certainty about how climate changes and their accompanying indirect effects, such as increased wildfire frequency, will promote, or perhaps inhibit, the proliferation and expansion of undesirable non-native aquatic or riparian plants and animals. Many invasive species thrive in frequently disturbed environments, and it is possible that a combination of elevated water temperatures, erratic streamflows (e.g., from droughts and floods), and accelerated erosion (e.g., from fires and land development) will set the stage for more outbreaks of non-native species that disrupt and transform food webs in unwanted ways. Some invasive non-native species may be pre-adapted to invade relatively pristine habitats if provided access (Fausch 2007). For example, brown trout are penetrating into drainages throughout the Rocky Mountains, where they seem to be able to out-compete native species. Thus, pre-adapted invaders, combined with disturbances that reduce native species and provide “niche opportunities” for newcomers (Shea and Chesson 2002), facilitate changes in the structure of aquatic food webs.

Population Increase and Land Use Changes

The recent ISAB report on human populations in the Columbia River Basin noted that the number of people inhabiting the region is likely to increase until at least 2030 (ISAB 2007-3; Figure E.1.2). More people will require increased drinking water supplies, ecological services (agriculture and hydropower, for example), and water for recreation – all creating competing demands

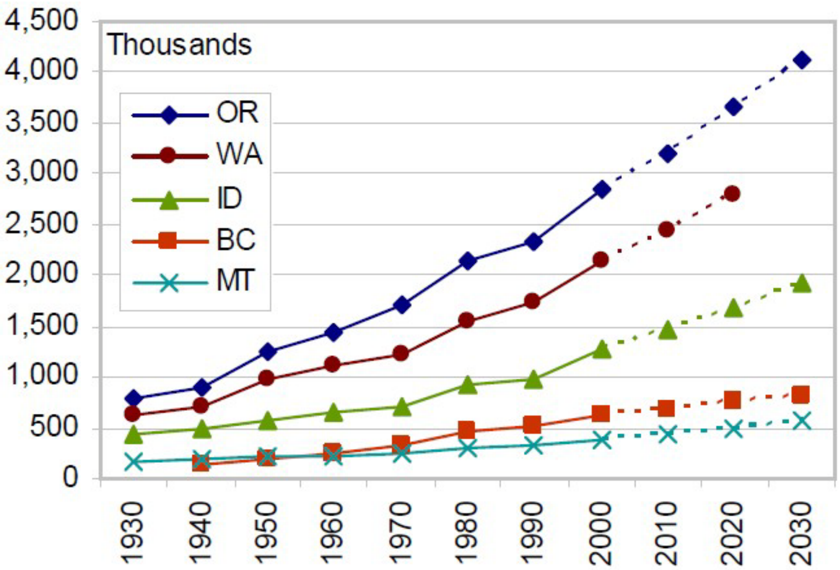


Figure E.1.2. Decadal trends in human population size, by state or province, 1930-2030. From ISAB (2007-3) based on United States and Canada census data (solid lines), plus state and regional projections (dashed lines).

for what is likely to be less water, if future summer climate scenarios are accurate. Water conservation efforts and an aggressive water transactions program to purchase water rights for instream flows could help mitigate the conflicts over uses of water, but it seems inevitable that the combination of reduced winter snowpack and more people will lead to less water for aquatic food webs, at least during the low flow periods.

Although general patterns of land use in the Columbia Basin are likely to persist for the next several decades, some land conversion will take place, especially in urbanizing areas and where "rural sprawl" results in conversion of farmland to nonagricultural uses, and this will impact water quantity and quality. In urbanizing areas, more impervious surfaces will shorten runoff timing and heighten runoff intensity, which scours streambeds and severely reduces macroinvertebrates in the scour zone.

The incorporation of agricultural and industrial chemicals, as well as chemicals associated with urbanization (e.g., flame retardants, antibiotics, hormones and personal care products) into aquatic food webs will continue as the human population grows. The ecological effects of many of these substances on aquatic food webs are poorly known (Chapter C.7); however, many of these compounds are toxic to at least some life forms and a large number are suspected to cause endocrine disruption (Segner et al. 2003) and there is evidence that persistent organic pollutants can be transported upstream in the bodies of spawning salmon, where they enter the food web after the fish die (Ewald et al. 1998).

Conclusions

This chapter has touched briefly on two factors that will continue to alter Columbia Basin food webs in the future – a changing climate and the long-term consequences of human population growth and development. While trends in these two factors are well established, their outcomes for aquatic food webs are far less certain. Their interactions are even less well known. Furthermore, they are only two of a larger and poorly understood suite of factors that threaten healthy, diverse food webs. In particular, the interaction between climate change, human population growth, and the proliferation and spread of non-native aquatic and riparian species is likely to have profound impacts on food webs, yet we tend to study these factors separately, without acknowledging the potential for synergism. Some speculation may be appropriate to consider:

- Future Basin food webs may become increasingly dominated by small-bodied organisms with short life spans. Warmer streams and lakes will have elevated primary productivity, and this may benefit some life stages of some fish species, but the potential loss of large-bodied edible invertebrates with longer life cycles will be harmful to others.

- Invasive aquatic and riparian plants and animals, especially those adapted to frequently disturbed and warmer environments, will continue to displace native species that are better adapted to cooler and more stable environments. Pollution-tolerant species, including those that are non-native, will be favored as well.
- The expanding human population in the Columbia River Basin will create a greater demand for water for direct consumption as well as for agricultural and industrial uses, and there will be increased amounts of a wide variety of anthropogenic chemicals dispersed throughout the drainage network. With more people inhabiting a larger portion of the landscape and increasing societal pressure to control the natural watershed processes that maintain food webs (e.g., flooding), native food webs are likely to become modified and simplified with the addition of non-native species. Although non-native species contribute to food web biodiversity, there is little assurance that they will contribute to the support of native organisms of cultural and economic significance in the Basin, such as salmonids.
- The net result is that food webs will exhibit novel characteristics, as invasive and native species are mixed and as food web related processes are fundamentally altered.

The strong potential for interactions among the above factors and the possibility of unanticipated effects of these interactions on existing restoration efforts suggests that additional studies of food web dynamics in combination with other significant environmental vulnerabilities are needed.

E.2. Comparisons with the Fraser River, British Columbia

Comparisons of food web structure and function in the Fraser River Basin in British Columbia are useful for developing a perspective on what may be possible for restoration of the Columbia River, where few predevelopment data on natural habitats are available. In addition, it is useful to consider what food web restoration activities have been successful on the relatively similar Fraser River and its network of tributaries. Here we provide a *preliminary* overview of the food web data available for the Fraser River Basin.

Although differing markedly in flow volume, the two basins have a number of important characteristics in common, including similarities in topography, climate, native fish communities, a dendritic tributary and lakes configuration, somewhat comparable watershed areas, and an almost common point of origin in the western slopes of the Rocky Mountains. Mean annual discharge of the Columbia River is 6,970 $m^3 \cdot s^{-1}$ (Naik and Jay 2005), 75% larger than that of the Fraser. The pre-development flow pattern of the Columbia River was similar to that of the present-day Fraser, with peak flows in spring from snow melt, a small peak in the autumn from rain runoff in the lower reaches, and low flows in winter (Northcote and Larkin 1989).

A salient feature of this comparison is the striking difference in developed hydropower generation, which is nearly 39,000 megawatts (MW; Jim Ruff, NPCC staff, personal communication) for the Columbia River Basin and only 1,683 MW for the Fraser River Basin (BC Hydro 2010, RioTintoAlcan 2008). A variety of socio-economic and geophysical factors accounts for the lack of power development on the Fraser and the almost complete harnessing of the Columbia for electricity generation. Estimating the total potential hydropower capacity of the Fraser is beyond the scope of this chapter, but even one proposed mainstem dam could generate about 10,000 MW (Ferguson and Healey 2009).

As an out-of-basin comparison, an overview of Fraser River food webs enables a general evaluation of how collective and separate modifications have altered Columbia River food webs. We first provide an overview of the Fraser Basin for general orientation and then give an overview of salient features of fish communities, food webs, stressors and restoration status for comparison with those elements in the Columbia River Basin, using a tabulation of narrative abstracted from our main report and Electronic Appendix E.2.

The Fraser River Basin

Located in southwestern British Columbia, the Fraser Basin (238,000 km^2) has 13 major sub-basins based on the management classification system of the Fraser Basin Council. The river is 1,375 km long, has a mean annual discharge of 3,972 $m^3 \cdot s^{-1}$ and is the largest river without mainstem dams draining into the northeast Pacific Ocean. Chinook spawn in mainstem and tributaries up to Rearguard Falls (Anon 2006), within 30 km of the river's origin, and the Fraser River is one of the largest salmon producers in the world (Northcote and Larkin 1989). Minimum mean flows occur in winter (1,400 $m^3 \cdot s^{-1}$) with maximum flows (>8,000 $m^3 \cdot s^{-1}$) in summer. The hydrograph shows flow patterns typical of rain and glacial-fed, undammed rivers on the northeast Pacific coast.

As in the Columbia River Basin, forested landscapes in the Fraser River Basin have been widely modified by logging, urbanization and agriculture. The percentage of land covered by coniferous forest has declined from 71% in 1827 to 54% in 1990. Concomitantly, by 1990 the amount of wetland declined from 10% to 1% of basin area while the combined urban and agricultural area increased to 26%. Deep sea shipping is restricted to the river's lower 30 km, with wood products (logs, wood chips) and gravel the only commodities moved upstream (Boyle et al. 1997, Macdonald et al. 2003, Reynoldson et al. 2005).

Contrasts in Fish Assemblages, Food Webs, Stressors and Restoration Status

To facilitate a comparison between the Fraser and Columbia basins we divided each into approximately analogous "megareaches." The megareaches for the Fraser Basin are the plume, estuary (within tidal range, up to Mission, British Columbia, rkm 77), lower river estuary to the Fraser Canyon (Hells Gate rapids), rkm 210), and upper river (upstream of Hells Gate; McPhail 1998), and lakes. The megareaches for the Columbia are the plume, estuary (river mouth to Bonneville Dam; rkm 235), lower river[31] (Bonneville to Wishram, Washington;

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[31] We use the former site of Celilo Falls as a reach boundary because the Falls were likely a natural high velocity feature,

rkm 331), and upper river (upstream of Wishram, Washington) and lakes.

Fish Assemblages. There are five major fish assemblages in megareaches (including their tributaries) of the Fraser Basin (Electronic Appendix E.2). The upper river, lower river and estuary assemblages were recognized by McPhail (1998), whereas we arbitrarily selected the lake and plume assemblages to facilitate a succinct comparison. In general, fish assemblages and their feeding ecology differ in each megareach:

- *Upper River*: A total of 36 species, with six anadromous species (chum, pink, Chinook, coho sockeye, steelhead, and Pacific lamprey); others are freshwater residents, including westslope cutthroat trout, bull trout, minnows, suckers, dace, and sculpins. Lotic species dominate. Feeding nodes (Chapter D.5) are mainly connected to insects and basal energy sources from the riparian or littoral zone.

- *Lakes*: Most lakes connected to the Fraser watershed support a fish assemblage similar to the upper river with a few additional lentic species such lake trout, rainbow trout, burbot, and kokanee. Feeding nodes are connected to zooplankton in the pelagic zone and insects in the littoral zone, with basal energy sources from phytoplankton and algae/vascular plant detritus on shorelines.

- *Lower river*: A total of 44 species, with 14 anadromous species (chum, pink, Chinook, coho, sockeye, steelhead, bull trout, sea run cutthroat trout, green sturgeon, white sturgeon, longfin smelt, eulachon, three spine stickleback and Pacific lamprey). Others are freshwater residents including minnows, suckers, dace and sculpins. Feeding nodes are mainly connected to insects and basal energy sources from the algae/vascular plant detritus on shorelines, as the river is generally turbid and there is little phytoplankton production.

- *Estuary*: A total of at least 60 species, with 14 anadromous species (chum, pink, Chinook, coho, sockeye, steelhead, bull trout, sea run cutthroat trout, green sturgeon, white sturgeon, longfin smelt, eulachon, three spine stickleback and Pacific lamprey). Others are marine or brackish water species, such as starry flounder and several other flatfish, as well as a variety of greenlings, gunnels, and sculpins. Freshwater residents include minnows, suckers, and dace. Feeding nodes are mainly connected to insects and crustaceans, such as amphipods, and basal energy sources from the algae/vascular plant detritus on shorelines. In general, the estuary is very turbid and there is little phytoplankton production. Eelgrass is a source of detritus in the outer estuary and some energy from phytoplankton production in the plume moves over the extensive shallow water banks.

- *Plume*: A total of at least 100 pelagic species, including the 14 anadromous species found in the estuary. Additionally, there is a wide variety of pelagic fishes such as pollock, herring, Pacific cod and hake, as well as larval rockfish, greenlings, gunnels and sand lance. Feeding nodes are connected with zooplankton, and phytoplankton as well as bacterioplankton are the basal energy sources. Marine mammals are top predators, including killer whales, harbor seals and sea lions. Sea birds such as grebes and cormorants, also feed on pelagic fish.

Comparison of fish species assemblages between the Fraser and Columbia are not exact because of the ways biologists set up boundaries for species counts in the two basins (subbasins, ecological Provinces in the Columbia River; Chapter C.3). Nevertheless, our analysis of the fish assemblages in the Columbia's plume and estuary (Chapter D.7) shows the species composition to be similar to that of the Fraser's plume and estuary. As well, the basal elements are the same (i.e., phytoplankton and detritus). It is in the lower river, upper river, and the lakes where differences between the Fraser and the Columbia become striking. In contrast to the Fraser, the Columbia's two riverine megareaches are dominated by lotic and non-native species, except for tributaries and isolated parts of the mainstem (e.g., Hanford Reach). Lake assemblages are

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somewhat similar to Hells Gate rapids in the Fraser River. Note that in Chapter C.4 discussing hatcheries and food webs, we define a related megareach as the part of the river from Bonneville Dam to McNary Dam because the data used in C.4 are classified by the dams as boundaries for analyses.

characterized by numerous non-native species that have been stocked or accidentally released (see below). Basal elements of lakes are similar, with a phytoplankton-zooplankton food web supporting pelagic fishes. Where lake water levels fluctuate within normal ranges, insects and benthic invertebrates are important, and the basal energy sources include macrophytes, algae and detritus.

It is notable that the Columbia Basin has twice as many native fish species (97 including marine species, Chapter C.3) as the Fraser Basin (48 including marine species; McPhail 1998). Additionally, the Columbia Basin has four times more non-native fishes (approximately 45 species; 32% of the total including marine species) than the Fraser Basin (13 species; 21% of total). Most non-native species in the Fraser Basin are in the estuary and lower river, but non-natives are widespread throughout the Columbia Basin (Electronic Appendix E.2).

In a relative sense, the Fraser's freshwater habitats are in better condition to support natural food webs than those of the Columbia, thereby providing better opportunities for anadromous fish survival while buffering changes in marine survival. On a broad scale, anadromous salmon from the two systems share the same general regions of the northeast Pacific /Gulf of Alaska. However, the plume of the Fraser River enters an enclosed sea whereas that of the Columbia enters the open ocean, which probably accounts for significant differences between basins in the marine survival of corresponding year-classes for some species (e.g., sockeye); this suggests that food webs supporting salmon in different parts of the northeast Pacific may not be in synchrony (ISAB 2008-5, Peterman et al. 2010).

Food Webs. Relative to the Columbia Basin, food webs in the Fraser Basin are close to natural in all five megareaches (Table E.2.1, Electronic Appendix E.2). Hybrid food webs are more widespread in the Columbia Basin. In the Fraser Basin, accidental and intentional introductions of non-native species have been limited, and most of the latter are in the estuary and lower river. Although the general diets of the non-native species have been described (McPhail 2007), detailed studies to determine if non-native species have fundamentally altered natural food webs have not been conducted. Modeling has shown that the impact of non-native predatory fish could be substantial. Johnson (2009) concluded that even a moderate population of yellow perch (20,000 – 75,000) in Shuswap Lake, a key Fraser River rearing area, could reduce adult sockeye production by 1 – 5%.

Microbenthic algae (periphyton), detritus from riparian vegetation, and littoral insects (especially midges) are key food-web components supporting fish production in the upper and lower Fraser River and larger tributaries. In general, lotic food webs dominate. This is in contrast to the Columbia River where, except for Hanford Reach and some tributaries, lentic food webs with a phytoplankton base are common because previously free-flowing reaches have been converted to reservoirs. Food webs in both the Fraser and Columbia lakes are lentic, with phytoplankton-zooplankton connections leading to fish. Nevertheless, a striking difference in lake food webs is the dominance of hybrid food webs in the Columbia, resulting from intentional and accidental introduction of non-native species to lakes and reservoirs. Good examples are the food webs involving northern pike and walleye, major non-native fish predators, in the Columbia Basin, whereas these hybrid webs are absent from the Fraser. Spread of parasites via these hybrid food webs is also a concern (Bradford et al. 2008).

Fish in the estuaries of the Fraser and Columbia rivers depend on a food web with macro- and microdetritus as their bases, although the importance of the latter is undocumented in the Fraser. Hybrid food webs (e.g., those involving the non-native fish pumpkinseed; McPhail 2007) are less common in the lower Fraser River and estuary where only 11 non-native species have become established, than in the Columbia River estuary, where 35 non-native fishes (Sanderson et al. 2009), as well as 35 non-native invertebrates, are now established (Sytsma et al. 2004). Dense colonies of predatory birds, such as Caspian terns and cormorants, are not present in the Fraser estuary, whereas these colonial birds play a significant role in food webs in the Columbia River estuary (Chapter C.2).

Table E.2.1. Summarized information on food webs, stressors, and restoration of the Fraser and Columbia River basins, contrasted for five megareaches.

	Fraser River Basin	Columbia River Basin
	Food Web Characteristics	
Upper River	Lotic food web[1] in the entire main stem and most tributaries; Lentic food web[1] in water storage reservoirs (WSRs).	Lotic food web in one free flowing reach in the main stem and most tributaries; Lentic food web in reservoirs; Hybrid food webs involving all trophic levels are widespread .
Lakes	Lentic food web; Hybrid food webs mostly involve basal levels (Eurasian milfoil).	Lentic food web; Hybrid food webs involving all trophic levels webs are widespread.
Lower River	Lotic food web in the entire main stem; Lentic food web in WSRs; Hybrid food webs involving all trophic levels in a few off channel habitats.	Lentic food webs; Hybrid food webs involving all trophic levels are widespread.
Estuary	Macrodetritus driven food web with major sand and mudflats as well as eelgrass beds in lower estuary.	Microdetritus driven food web with some sand and mudflats; Minor eelgrass beds; Hybrid food webs involving all trophic levels are widespread.
Plume	Strongly stratified phytoplankton-zooplankton-fish food web; Disperses into an inland sea; Turbidity and wind mixing controls; Driven by primary production.	Strongly stratified phytoplankton-zooplankton-fish food web; Disperses into coastal ocean; Upwelling controls; Driven by primary production.
	Food Web Effects: Stressors	
Upper River	No mainstem dams; Dams on four tributaries with total generating capacity of 1,435 MW; Bioaccumulation of legacy contaminants in white sturgeon; Few non-native species ; Food web effects not well researched.	96 dams[32] for hydropower and multipurpose with hydropower on main stem and tributaries; A few major tributaries and Hanford Reach are the only free flowing segments; 34,220 MW power capacity on main stem plus tributaries and modified lakes; Non-native species widely distributed.
Lakes	Three large lakes and numerous small ones converted to WSRs; Numerous WSRs for irrigation; Mercury bioaccumulation in a major WSR; Non-native milfoil at basal level; Few non-native fish species; Contaminants in some lakes via long range transport.	35 major WSRs documented and many minor WSRs known; Food webs disrupted by drawdowns and water withdrawals; Non-native species widely distributed and numerous.
Lower River	Gravel mining removes basal and secondary food web elements; Riparian habitat disrupted in tributary streams; 11 non-native fish species; Food web effects not well researched.	3 dams for hydropower and multipurpose with hydropower on main stem and tributaries; Lentic food webs in numerous reservoirs; Total hydro-capacity 2,919 MW; Non-native species widely distributed.
Estuary	Estimated 70-90% of wetlands lost from diking and urbanization; 5 non-native fish species; Bioaccumulation of organic contaminants in indicator species; 269 MW generating capacity on	34 dams for hydropower and multipurpose with hydropower on main stem and tributaries; Estimated 48% loss of wetlands; 35 non-native fish species; Water levels and discharge patterns affected by

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[32] Number of dams in the megareaches are from http://www.nwcouncil.org/library/2000/2000-19/TechAppF/losses_part5.pdf (Table 22), corrected for dams removed in recent years.

	tributaries; 3 dams for hydropower.	upstream reservoirs; 1,723 MW capacity; Major replacement of macrodetritus with microdetritus produced in upstream reservoirs.
Plume	Climate change may be affecting oceanic elements in the plume food web.	Climate change may be affecting oceanic elements in the plume food web; Plume characteristics influenced by discharge patterns from upstream reservoirs.
	Food Web Effects: Restoration	
Upper River	Fertilization on Nechako River did not propagate positive effects to higher trophic levels.	Carcass analogue experiments in some tributaries; Riparian and off channel habitat restoration.
Lakes	Lake fertilization implemented experimentally as sockeye enhancement measure but discontinued; however, still being used for kokanee.	Kootenay Lake fertilization improved kokanee survival; Mysid introduction to "improve" food web did not succeed.
Lower River	Riparian and off channel habitat restoration.	Riparian and off channel habitat restoration.
Estuary	Marsh planting; Chum fry feed on invertebrates in restored marshes.	Dike breaching, and culverts; Subyearling Chinook, chum, coho fry and others feed in restored habitat.
Plume	N/A	N/A

Stressors. Physical transformations have been more extensive in the Columbia than in the Fraser Basin, primarily through dam construction and changing land use. Collectively, these actions have converted the original lotic habitat into lentic habitat (i.e., reservoirs) and greatly increased sedimentation and chemical bioaccumulation. The lack of ship and barge traffic well upstream into the watershed, which is a well-known vector for non-native species, also distinguishes the Fraser from the Columbia.

Urbanization and diking in the lower rivers and estuaries have occurred at a comparable scale in both basins, and have substantially reduced wetland area. An estimated 48-90% of estuarine wetlands have been lost in both systems. This is due to concentrated human populations and activities in the estuaries and lower reaches. In both the Fraser and the Columbia, water quality is deteriorating from sewage pollution, modern contaminants, and legacy chemicals in the lower rivers and estuaries, most likely because this is where the byproducts of human activities accumulate.

Food webs in the mainstem Fraser River may give insight into pre-development food webs on the Columbia mainstem. The total lack of mainstem dams on the Fraser strongly suggests that food web alterations from hydrosystem impacts are localized in tributaries, although detailed cumulative effects on the mainstem have not been conducted and are sorely needed (Birtwell et al. 1988).

Restoration. Conditions in the Fraser River suggest that a comparison of the food webs could assist in setting targets for restoration of specific habitats in the Columbia. For example, if a water storage reservoir (WSR) was removed from the Columbia River, the unnatural lentic food web would likely revert to a lotic food web similar to that found in a similar mainstem megareach of the Fraser, which thereby provides a type of “out of basin” reference site. There are also lessons to be learned concerning nutrient additions for salmon enhancement in lakes. This approach was tried experimentally for several years on Fraser River sockeye lakes, but did not become an accepted technique, even though smolt sizes were increased by food web changes resulting from nutrient addition. Fertilization is now being used in a few Fraser Basin lakes to increase kokanee production and also has been applied in the Columbia Basin for kokanee to mitigate for the loss of anadromous salmonids (Schindler et al. 2009).

Management strategies for prevention of hybrid food webs also might be worthwhile to compare (e.g., protocols for prevention of non-native fish dispersal), although stocking of non-natives species is fostered in the Columbia Basin. Wetland and riparian habitat restoration, is used as a recovery strategy in both basins and is presumed to benefit Chinook, coho and other species, but food web benefits have not been empirically assessed. Restoration of riparian habitat has proven to be challenging in the Fraser River drainage and elsewhere in Canada (Quigley and Harper 2006), but is seldom evaluated. Estuarine food webs in the Fraser are severely degraded and an estuary management group (Fraser River Estuary Management Program (FREMP)) is acting as a single clearinghouse for attempts to prevent further habitat loss and encourage restoration. FREMP also provides a common point of contact for scientists and managers, which is fairly effective in maintaining communications. Direct comparisons may be difficult because the Columbia estuary is much larger than the Fraser estuary, and the policy arena is fundamentally different. Nevertheless, there is much to learn in sharing experiences and approaches.

Challenges common to both basins are understanding the cumulative effects of habitat restoration and contaminants on food web structure, productivity and resilience, and quantifying the carrying capacity in current and future climates. In summary, further detailed comparisons of the food webs of the Fraser and Columbia rivers would be instructive for developing restoration strategies for the Columbia. A main benefit would be insights into how Columbia River food webs likely functioned in the past. Because of its size and similar natural fish assemblages, the Fraser provides a convenient “out of basin” reference that is likely a better comparison than, for example, smaller basins in Washington and Oregon. A comparative approach could therefore assist managers by providing illustrations of target food webs for habitat and ecosystem restoration activities in the Columbia Basin.

E.3. **Restoration Strategies**

NPCC Fish and Wildlife Plan Restoration Priorities

The Council's Fish and Wildlife Program (NPCC 2009) represents the largest regional program for restoring fish and wildlife in the United States. Although the plan contains many elements, it places a high priority on habitat restoration. Currently, food web restoration is implied, but not explicitly represented, in the portfolio of actions to the extent that physical habitat improvements are. The 2009 Program states (p. 7): "This is a habitat-based Program. The Program aims to rebuild healthy, naturally producing fish and wildlife populations by protecting, mitigating, and restoring habitats and the biological systems within them. Artificial production and other non-natural interventions should be consistent with this effort and avoid adverse impacts to native fish and wildlife species." The emphasis on habitat restoration is reflected in its dominance in terms of Program expenditures (Figure E.3.1).

The 2009 Fish and Wildlife Program (p. 16) states that the majority of habitat restoration actions will fall into the following categories:

- Removal of passage barriers
- Diversion screening
- Riparian habitat protections and improvements (fencing, vegetation planting, erosion control, best land management practices, easements, and other acquisitions) largely intended to improve water quality, especially with regard to temperature and sediments
- Water transactions and conservation activities to increase the amount, timing, and duration of instream flows
- Floodplain reconnections, passive and active improvements in channel structure and geomorphology and the re-establishment of natural river processes
- Acquisitions of and enhancements to terrestrial uplands for wildlife habitat

While all these actions are undoubtedly beneficial, none explicitly addresses the protection or restoration of the food webs within these habitats, although the food webs directly support, and are essential for, the aquatic species of interest. We suspect the relative scarcity of food web restoration projects in the Fish and Wildlife Program is related to several factors: (1) most aquatic food webs in the Basin have received little study, (2) in general, restoration of instream habitat and riparian vegetation has received the majority of attention from habitat managers, resulting in little experience on which

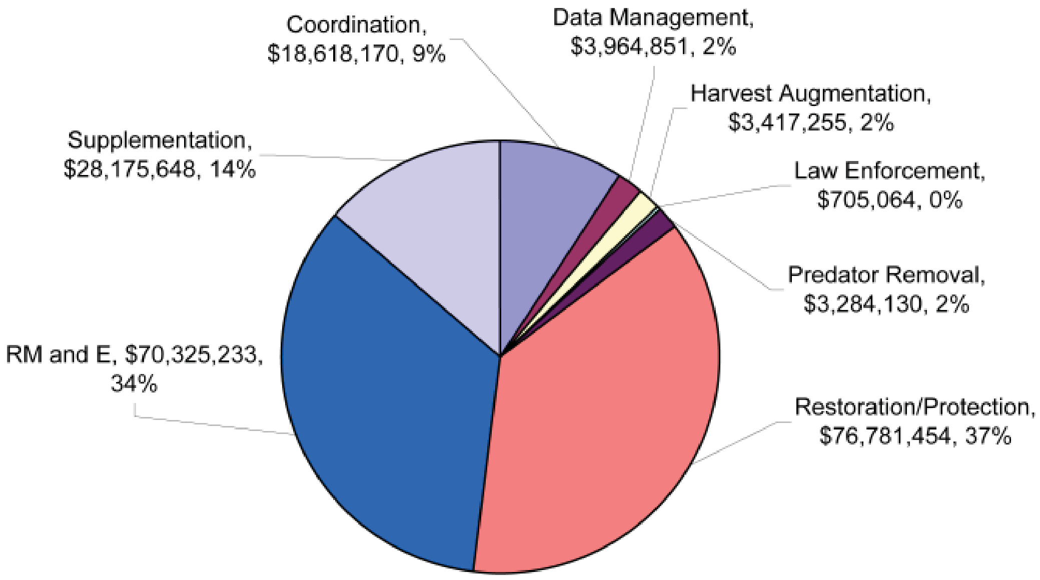

Figure E.3.1. Direct expenditures of the NPCC Fish and Wildlife Program for 2009, total expenditures of $205,271,805 (from Northwest Power and Conservation Council (2010) based on Bonneville Power Administration data).

to base future food web-related actions, and (3) attempts to manipulate freshwater food webs for the benefit of one or two species generally have been unsuccessful. In this chapter, we examine the potential for food web restoration, describe approaches that are currently being used, elaborate major uncertainties in achieving fish and wildlife objectives, and distill a list of factors that threaten food web restoration success.

Food Web Objectives: Enhancement or Restoration?

Apart from predator control, early attempts to manipulate aquatic food webs in the Pacific Northwest for the benefit of salmonids had both enhancement and restoration objectives: (1) increasing salmonid growth and survival above natural or pre-existing levels, and (2) mitigating the loss of adult spawners whose carcasses contributed significant nutrient subsidies to lakes. Both Juday et al. (1932) and Ricker (1937) suggested that nutrients from decomposing salmon were essential to food webs in lakes supporting sockeye and other species and argued that reducing adult escapement would ultimately compromise the growth of their progeny. Warren et al. (1964) demonstrated that cutthroat trout production in a small Willamette River tributary could be increased by adding sucrose, a simple sugar, to stimulate microbially-based pathways. Mundie (1974) summarized the major trophic connections that support salmon in streams (Figure E.3.2) and proposed that food web augmentation might be possible by supplementing heterotrophic food pathways with organic material such as cereal grains – a suggestion that was later implemented in a Vancouver Island stream (Mundie et al. 1983). In 1969 a whole-lake enrichment experiment began in Great Central Lake, British Columbia, for the purpose of enhancing sockeye salmon. Le Brasseur et al. (1978) found that phosphorus additions to the lake increased the growth and subsequent survival of juvenile sockeye, leading to increased adult returns. The success of this effort spurred the Lake Enrichment Program that became a major component of B.C.'s salmonid enhancement effort in the late 1970s and 1980s (Stockner and Shortreed 1985, Stockner and Ashley 2003), a major goal of which was to enhance food webs in lakes of low natural productivity.

Some of the earliest manipulations of aquatic food webs, where anadromous salmonids were not the management focus, involved the addition of non-native fishes. Widespread introductions of non-native salmonids, basses, sunfishes, walleye, perch, catfish, shad and other species were generally intended to expand fishing opportunities without any expressed recognition of food webs effects, but the introductions eventually led to food web-focused efforts. In some cases, high level piscivores such as lake trout, rainbow trout and Chinook salmon were stocked to exploit what were perceived as overly abundant forage species. In others situations, new species have been introduced to provide an expanded forage base for native or introduced predators. The first introduction of the opossum shrimp *Mysis relicta* was made to Kootenay Lake with the intent of inserting a transitional forage species (between small zooplankton and fish), to enhance growth and survival of native rainbow trout (Sparrow et al. 1964). The unanticipated response of rapid growth in native kokanee salmon led to the releases of *Mysis* in lakes and reservoirs supporting introduced (and a few native) kokanee populations throughout western North America (Nessler and Bergersen 1991). In some cases, non-native minnows or other fishes have been considered for introduction where introduced predators have apparently overexploited the existing prey base (e.g., IDFG 1985).

Food web manipulation in streams was not routinely considered an aquatic restoration tool in the 1970s and 1980s. The nutrient enrichment efforts in B.C. lakes targeted sockeye, but aside from this lake-rearing species, restoration programs tended to focus on recovering a variety of stream and river habitat that typically included remediating unstable streambanks, elevated fine sediment levels, damaged riparian vegetation (particularly plants that provided shade for temperature control), and loss of habitat structures in the form of logs and boulders. Passage of water quality protection laws in the 1970s, as well as a variety of state and provincial measures to reduce anthropogenic pollutants in surface waters, kept the focus on preventing dissolved nutrients and other potentially food web-influencing materials from entering streams and lakes. Faced with a perceived choice between food availability and suitable rearing space as the two factors most likely to limit the production of salmon and trout in flowing waters – often based on D. W. Chapman's seminal paper *"Food and space as regulators of salmonid populations in streams"* (Chapman 1966), which was erroneously interpreted to mean that either food resources or available habitat limited production – stream restoration specialists in the 1970s and 1980s usually undertook measures to improve physical habitat

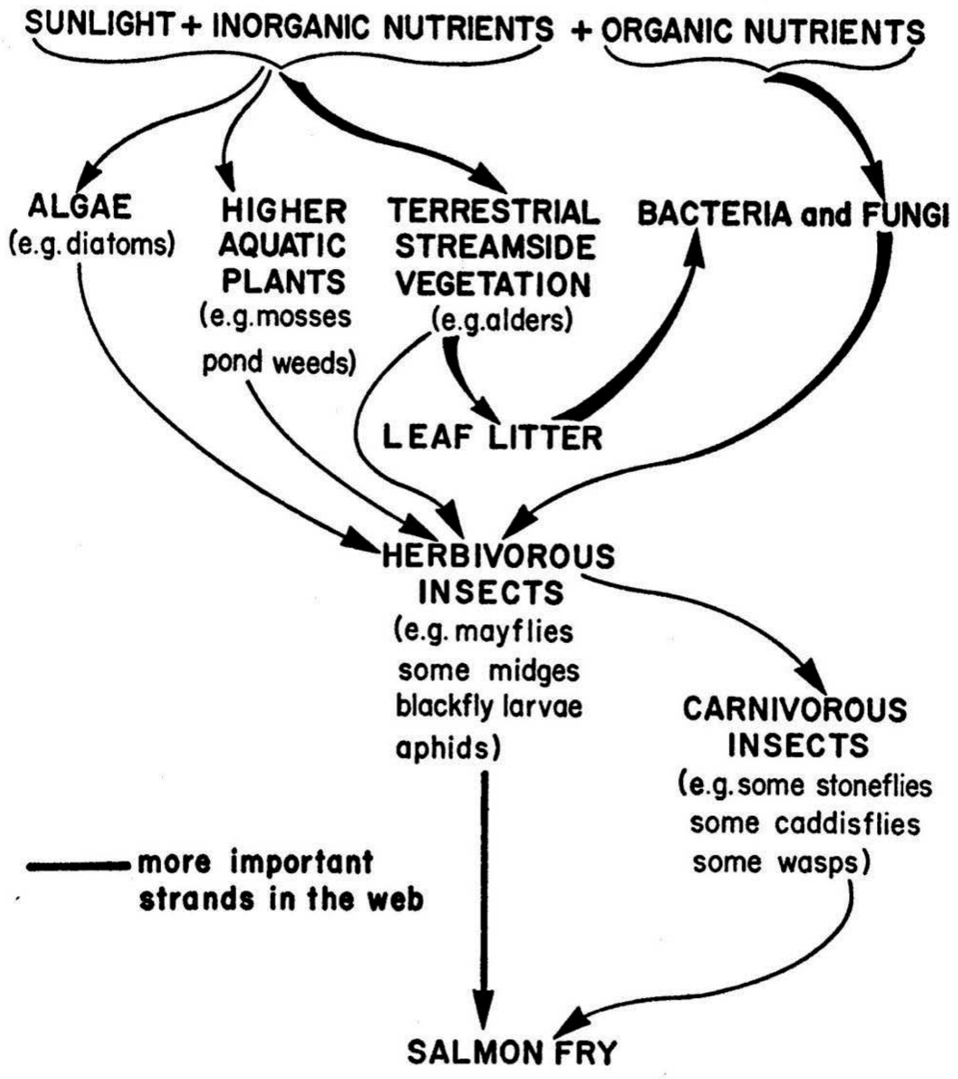

Figure E.3.2. An early representation of the major trophic pathways supporting juvenile salmon rearing in streams in the Pacific Northwest (diagram from Mundie 1974). The thickness of the arrows denotes their relative importance. This food-web diagram reflected a belief that heterotrophic inputs (nutrients and particulate organic matter of terrestrial origin) were primarily responsible for providing food items to young salmon in rivers and streams.

and rarely considered the food web implications of their actions.

Two important advances in scientific understanding that took place in the late 1980s brought about a greater appreciation in the importance of food webs to salmonid production in fresh waters. One was the finding that marine-derived nutrients from spawning salmon played an important role in the rearing ecology of juvenile anadromous and resident salmonids, and that nutrients from the reproductive products and carcasses of adult salmon contributed to the food resources of both their own progeny and those of other species (Kline et al. 1990, Bilby et al. 1996). This scientific advance (Chapter C.1) led to the now widespread practice of placing hatchery salmon carcasses in streams and to the introduction of commercially manufactured briquettes of sterilized carcass tissue (analogs) that are easily transported and decompose at a rate similar to that of natural salmon flesh. The other significant finding related to food webs was that salmon and trout growth exhibited surprising increases lasting from a few months to a few years after large natural disturbances deposited nutrients and opened up forest canopies, allowing more sunlight to reach surface water and stimulate primary productivity. Examples included increased production of cutthroat trout after the large Yellowstone fire in 1988 (Minshall et al. 1989, Minshall 2003) and of coho salmon after the 1980 Mount St. Helens eruption (Bisson et al. 1988, 2005). The positive response of a stream's autotrophic food pathways (i.e., those with autotrophs at the base of the food web, such as algae → herbivorous invertebrates → fishes) to light and nutrients demonstrated the importance of algal-based food webs to rearing salmonids. However, habitat managers have been cautious about applying this finding, because adding too many nutrients (eutrophication) or removing too much riparian canopy (excessively elevated water temperature) can have undesirable consequences.

Current Approaches to Food Web Restoration

Although restoring food webs has received considerably less attention than other types of habitat restoration in the Basin, several categories of restoration projects are designed, at least in part, to benefit trophic pathways or food web interactions: 1) addition of inorganic nutrients to oligotrophic lakes, 2) supplementation of streams with salmon carcasses or carcass products, 3) restoration of native vegetation to improve estuarine food webs, and 4) control or removal of unwanted species.

Inorganic Nutrients. The majority of attempts to increase the productivity of lakes through the addition of inorganic nutrients (chiefly nitrogen and phosphorus) in the Pacific Northwest have focused on sockeye salmon or kokanee. Results from 24 sockeye nursery-lake enrichment experiments, extending from Alaska to Idaho and including Idaho's Redfish Lake, found that "when lakes were fertilized with various mixtures of inorganic nitrogen and phosphorus, pelagic food web bottom-up control was strong enough and predictable enough to ensure that sockeye smolt biomass increased" (Hyatt et al. 2004, p. 133). Additionally the conclusion was that lake fertilization could promote enhancement and conservation of sockeye salmon. There are, however, several potential problems in fertilization (Hyatt et al. 2004). An inappropriate ratio of nitrogen to phosphorus in the fertilizer could, in some lakes, lead to growths of unwanted blue-green algae; the appropriate N:P ratio is specific to each lake. Occasionally, non-target fishes, especially 3-spine stickleback, would respond so strongly to fertilization that the growth of juvenile sockeye was suppressed. Finally, fertilization of lakes where mysid shrimp were abundant would result in most of the food web benefits accruing to the mysids instead of the target species. Nevertheless, the general conclusion of a large number of whole-lake fertilization studies was that this technique does have the potential to increase both survival and growth of sockeye. Further, a cost-benefit study of fertilization in Chilko Lake, British Columbia, found that, despite many uncertainties, the practice appeared to be cost-effective (Maxwell et al. 2006).

Attempts to enhance stream food webs by adding inorganic nutrients have not yielded the more conclusive results that have been observed in lakes. In lakes, the goal of fertilization was to increase the abundance of zooplankton, including large-bodied *Daphnia spp*., but in streams the macroinvertebrates actually enhanced have been benthic species, such as mayflies and midges, commonly consumed by drift-feeding salmonids. Sampling in flowing waters is in many ways more complex and error prone than sampling in standing waters; therefore, it has been difficult to test whether experimental inorganic nutrient additions have enhanced food web connections from benthic algae to macroinvertebrates to fish on a sustainable basis. To circumvent the spatial heterogeneity in stream channels, aquatic ecologists have often used simplified "mesocosms" (usually troughs fed by streamwater into which nutrient solutions are dripped) to test for food web effects. Whether nitrogen or phosphorus is most limiting to primary productivity varies from stream to stream and is generally controlled by watershed geology (Gregory et al. 1987), but for most streams in the Pacific Northwest, the addition of one or the other, and sometimes both, has the potential to increase primary and secondary production, as was demonstrated at several locations in British Columbia (Stockner and Shortreed 1978, Ward and Slaney 1988, Perrin and Richardson 1997, Kiffney and Richardson 2001). However, the spatially limited experimental procedures used in some of these studies have precluded following the growth and survival of young salmon and trout to smolting, and there may be water quality concerns related to the cumulative downstream effects of inorganic nutrient additions (Compton et al. 2006). Therefore, the scientific evidence that inorganic nutrients can be used successfully in streams to restore or enhance salmonids is weaker than it is for lakes. This conclusion may change as more, properly controlled, large-scale experiments are undertaken.

Salmon Carcass Supplementation. Salmon carcasses have been added to streams in the Pacific Northwest for only about 15 years. Although habitat managers acknowledge that many streams are severely under-utilized relative to pre-development spawning salmon densities, relatively little attention has been given to the food web implications of the lack of salmon carcasses and eggs that accompanied higher levels of spawning in the past. Understandably, some of the most influential early investigations of the importance of carcasses were carried out in Alaska, where salmon runs were still abundant. Klein et al. (1990, 1993), using stable isotope analysis to track the flow of marine-derived nutrients through freshwater food webs, found that carcasses contributed significant fractions of nitrogen and carbon to stream nutrient fluxes and, even more importantly, that marine-derived nutrients are progressively magnified through the food webs leading to fish. The Alaskan research triggered considerable interest in examining the importance of salmon carcasses to stream food webs in other areas, using stable isotopes as marine-derived nutrient markers. By the mid- to late-1990s, several investigators had shown that dead salmon not only contributed nutrients of marine origin to their offspring via the food web, but that a number of other species dependent on aquatic food webs benefited from the presence of carcasses as well (Bilby et al. 1996, 1998; Wipfli et al. 1998, Cederholm et al. 2001).

Despite the emerging scientific evidence that marine-derived nutrients from adult salmon and their reproductive products played an important role in stream ecosystems with abundant salmon, there are no controlled, whole-stream, carcass-supplementation experiments that are similar in design to the whole-lake inorganic nutrient enrichment trials that took place in British Columbia. Nevertheless, managers felt the existing evidence was compelling enough to warrant widespread carcass supplementation programs throughout the Pacific Northwest, and, by the year 2000, many such programs were underway, using spawned-out or surplus adults from salmon hatcheries. The unpredictability of carcass availability, coupled with the logistical difficulties of transporting and distributing large dead fish to streams led to the development of carcass analogs, which are sterilized parcels of processed carcass tissue that can be easily deployed in streams. Carcass analogs can substitute for dead spawned-out salmon, but cannot replace the eggs and excreted metabolic byproducts of the spawning process. For example, ammonium and phosphorus concentrations in streams with introduced carcasses or carcass tissue are lower than in streams with spawning salmon, which is attributed to nutrient excretion by live salmon (Janetski et al. 2009).

Carcass analogs have been used to enhance food webs in some Columbia River tributaries (e.g., Zendt and Sharp 2006), but thus far no projects have demonstrated a conclusive increase in salmonid growth or survival attributable to this material. As with salmon carcass supplementation, assessing the effectiveness of carcass analogs awaits further field testing on a broader scale, and many of the same concerns about inorganic nutrient additions, as well as others such as disease transmission, apply to carcass supplementation in streams (Compton et al. 2006). However, there is strong scientific consensus that depriving aquatic ecosystems and their associated riparian zones of the nutrient subsidies provided by salmon carcasses has led to large-scale reductions in productivity and changes in food web structure (e.g., Willson et al. 2004, Drake et al. 2009, Naiman et al. 2009).

Estuarine Food Web Restoration. Development of the Columbia River hydrosystem has resulted in a significant loss of macrodetritus (relatively large detritus particles) which originates from submerged vascular plants and tidally-influenced riparian and marsh vegetation, from the trophic base of the shallow-water estuary food web, as well as a corresponding increase in microdetritus (very small detritus particles), which originates from phytoplankton produced in the reservoirs. Reversing the loss of macrodetritus is an important objective for restoration of estuary marshes in the lower Columbia River, because macrodetritus serves as a principal food resource for many estuarine invertebrates that are consumed by young salmon (Figure E.3.3). Many current estuary restoration projects (Johnson et al. 2003) are incorporating food web considerations, taking a cue from research (e.g., Reimers 1973, Sibert 1979, Sherwood et al. 1990, Simenstad et al. 1992) that suggested macrodetritus-based food availability can limit juvenile salmon growth. Some restoration efforts in the estuary involve reconnecting the floodplain to the main river, because historical diking and tidegates have deprived the main estuary of macrodetritus, and dike breaching and improvement of tidegates and road culverts to restore floodplain connectivity improves detrital flow. Increasing the flooding of tidal marshes is also likely to increase production of wetland plants, ultimately leading to an improvement in the amount of detritus contributed to the estuarine ecosystem.

Control of Unwanted Species. Some of the most visible species control efforts to benefit food webs in the Columbia basin are focused on piscivorous fishes and birds, in efforts to reduce mortality on juvenile salmon (Chapters C.2 and C.3). Although a particular emphasis has been placed on northern pikeminnow, which are native to the Basin, dams in the river may have helped them become more abundant than they might have been in a free flowing environment. Substantial investments also have been made to reduce or remove lake trout from lakes and reservoirs of the Basin that once supported kokanee or native bull trout that have been reduced or even locally extirpated. Idaho Department of Fish and Game has undertaken the most substantial effort, with subsidized commercial and bounty fisheries for predatory fishes in Lake Pend Oreille. Similar, though less intensive efforts are either underway or being considered on a number of other lakes and reservoirs throughout the West (Martinez et al. 2009). Managers have also attempted to control or eradicate some species in smaller tributary streams, lakes and reservoirs. Efforts to eliminate or reduce non-native brook trout from reaches or small streams have been common in the Basin, ostensibly to reduce competition or predation on native salmonids such as cutthroat trout or bull trout (e.g., Shepard 2002, Fausch et al. 2006). Rotenone and other piscicides have been used for decades by fisheries managers to remove problem species, with the intent of benefitting the reintroduction or abundance of select fishes.

Food Web Restoration Caveats

The four categories of food web restoration projects for the Columbia River that are given above illustrate efforts that have been intended to recover food webs that included and support salmon and trout. For one category – inorganic nutrient addition to oligotrophic lakes – the likelihood of success has reasonably strong scientific support, provided that proper limnological studies inform the correct balance of nutrients to use. Addition of salmon carcasses and estuary restoration are logically assumed likely to succeed, but scientifically controlled proof-of-concept demonstrations have not

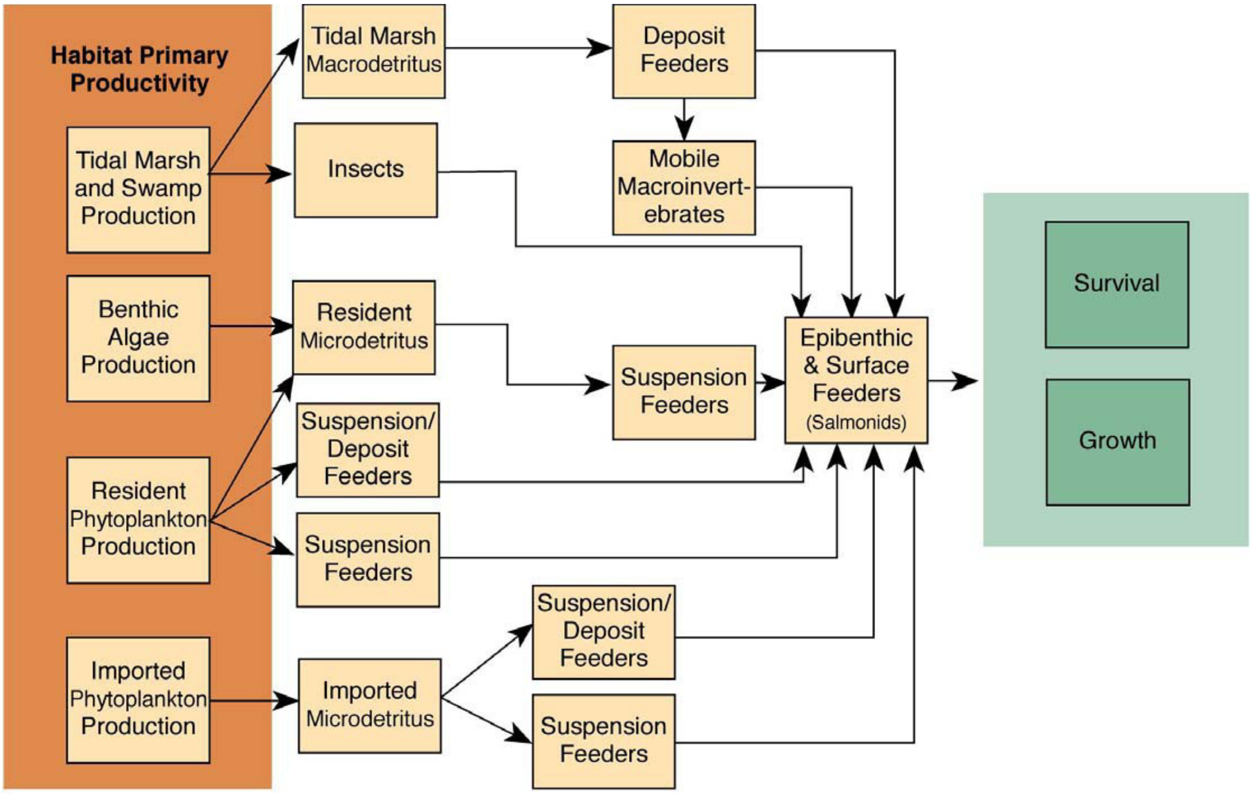

Figure E.3.3. Generalized food pathways in the Columbia River estuary (from Johnson et al. 2003). Many restoration projects are focusing on increasing macrodetritus production from tidal marshes and swamps to recover organic matter that has been lost to diking, channelization, and other development that has isolated the main river from its tidal floodplain.

been completed at spatial scales large enough to demonstrate improvement at the population level. Efforts to control northern pikeminnow in the Columbia River appear to provide some benefit to smolt survival, but the food web effects associated with control of pikeminnow or other species are inadequately understood. There is some evidence that benefits can be limited (Harvey and Kareiva 2004), counterproductive (Wiese et al. 2008), expensive or logistically difficult to maintain (Meyer et al. 2006, Martinez et al. 2009), and controversial (Finlayson et al. 2000), so careful evaluation of costs, benefits, and secondary effects is particularly important.

Food web restoration occupies a very small fraction of the Fish and Wildlife Plan's overall budget relative to channel and riparian restoration, but aquatic food webs are complex and difficult to control and there are many uncertainties and threats associated with food web restoration. Important uncertainties include: (1) the effects of food web restoration on non-target native plants and animals, (2) the water quality impacts of nutrient additions downstream from project sites, and (3) the influence of natural weather variation and other environmental disturbances such as floods, droughts, and wildfires on project outcomes.

Major threats to food web restoration include: (1) the possibility that the benefits of food web restoration will accrue to invasive instead of target species in some places, (2) human development of riparian areas and floodplains that precludes natural ecosystem processes delivering nutrients and organic matter to streams, rivers and lakes, and (3) long-term climate changes that fundamentally alter the recovery potential of food web structure.

These many uncertainties and threats to project success, coupled with the scarcity of long-term monitoring that has accompanied the relatively few attempts to restore aquatic food webs, strongly argues for caution in applying food web improvement techniques widely without requisite experiments and pilot-scale trials needed to learn under what conditions success or failure is likely. There is value in looking to the example of inorganic nutrient addition experiments in British Columbia, where thoughtful monitoring and analyses over a range of sites have demonstrated both the benefits and potential pitfalls of the approach (Hyatt et al. 2004).

Identifying Realistic Restoration Goals – A "No-Analogue" Future with Hybrid Food Webs

Any discussion of restoration strategies would be incomplete without noting what the overall goal of restoration should be. It is clear that we cannot restore the Columbia River and its tributaries to a condition that existed prior to Euroamerican development. Yet many restoration efforts attempt to return aquatic ecosystems to a state that is perceived to be "pristine," assuming that such a state also represents a condition of high productivity for native fish and wildlife. While many ecological attributes of undeveloped watersheds are indeed important for sustaining natural production and are worthy of conservation, the notion that we can restore streams, rivers and lakes to "the way they were" seems unrealistic in light of current restoration science. In a thoughtful essay on restoration, Hobbs and Cramer (2008) make a strong argument that past conditions are inappropriate models for future states – a concept they term the *no-analogue future*. They state (p.54):

> "…Increasing rates of change in climate, land use, pollution, and number of invasive organisms are all leading us into uncharted territory, and the future has no analogues from the past that might guide us. This no-analogue future is where we have to try to manage the environment using new approaches from our revised understanding of how nature works.
>
> This suggests that our knowledge and understanding are always likely to be incomplete and are contingent on both the types of knowledge that have been included and on the values in play at the time. For ecological restoration, which is a very mission-oriented problem-solving activity, this can appear very challenging. The goal is, broadly speaking, to fix damaged ecosystems, and there may be a hint of hubris in assuming that we always know (*a*) what the problem is, (*b*) how to fix it, and (*c*) what the end result should be."

The structure, connectivity and phenology of food webs in the Basin are now sufficiently altered in structure and function to qualify as "no-analog" systems (Chapter E.4). This recognition should be a starting point for restoration and management efforts. Factors that have moved the Basin's freshwater and estuarine ecosystems outside of their historical range of variability are well known: altered water, temperature and disturbance regimes, climate change, nutrient enrichment, proliferation of artificial chemicals, species invasions, local or global extinctions, habitat fragmentation, and others. All impact food web structure, connectivity and phenology, and all are occurring simultaneously throughout the Basin.

Fortunately, considerable thought is going into the management of future ecosystems that have no historical analogues (i.e., novel ecosystems; Hobbs and Cramer 2008). In managing novel ecosystems, the point is not to think outside the box but to recognize that the box itself has moved, and that it will continue to move rapidly in the 21st century (Harris et al. 2006). Past and ongoing environmental changes ensure that many historical restoration targets will be unsustainable in the coming decades. Ecological restoration should aim to conserve and restore historical ecosystems where they will be viable, but also to design and steer novel emerging ecosystems, which have new combinations of species that work where there are new conditions that preclude the success of historical food webs, to ensure the maintenance of important ecological goods and services (Jackson and Hobbs 2009).

While science can often predict the impact of individual factors on local ecosystems, simultaneous changes in many factors across the Basin generate considerable uncertainty. This presents a great conundrum for managers and necessitates an active partnership with researchers now attempting to measure the impacts of complex changes on ecosystem attributes. There is a compelling need to adopt a dynamic framework that explicitly acknowledges and embraces change as a fundamental part of all ecological systems. It is necessary to find a way for the entire Columbia Basin community to work toward sustainable ecosystems for the future. This can be accomplished if scientists work cooperatively with managers and policy makers, given that ecosystems already have been altered in ways that predispose them to further change and potential declines in productivity and resilience. Management should not only anticipate change, but should acknowledge that current systems have been transformed and are in the process of transforming further (Seastedt et al. 2008, Venter et al. 2008).

In the past, managers have attempted to eliminate processes or components that did not fit a general perception of a desirable system. For instance, as indicated by an increasing number of examples, removing unwanted species, or the consequences of unwanted species, will not necessarily restore ecosystems to their historical states and may not move ecosystems to desirable and feasible new states. While climate change may impose limitations on our ability to restore connectivity and phenology in food web dynamics, it often is possible to reverse or negate trends to undesirable states that are caused by other factors. At present, this appears to be best accomplished by implementing environmental water flow regimes that mimic natural conditions (Arthington et al. 2010, and references therein). A logical approach would be to maximize genetic, species, and functional diversity wherever possible, in order to increase the viability of communities and ecosystems under uncertain environmental regimes. Monitoring responses to any action, or lack of action, remains a key activity; without monitoring, one will never determine what can be accomplished (Seastedt et al. 2008).

Advances in our knowledge of ecosystem dynamics and the inevitability of future change suggest that realistic goals of food web restoration will focus on managing watersheds that are resilient to natural and anthropogenic disturbances and that continue to support native plants and animals that society values. This will not be easy, and will require well-designed field experimentation, accompanied by thorough and sustained monitoring.

E.4. A Total System Perspective: Phenology

Attributes of Productivity and Resilience: Connectivity and Timing

Vital resources, including foods, are arranged in space and time. In combination with the changing life history requirements of species during ontogeny, the needs for connectivity and for the timely matching of consumers with available foods become central for successful restoration. Organisms move and change foods during their lifetime, and this demands that restoration activities fully consider the connectivity and timing of movement and food availability within the larger system (Naiman and Latterell 2005). Species have successfully adapted to encounter foods and are able to efficiently exploit the changing food resources, as long as spatial connections are available and the timing is right to allow them to obtain the resources. Additionally, ecosystem connections can permit species to take advantage of unusual food sources when extraordinary opportunities are presented. For instance, when young anadromous fish move from streams to estuaries – if the timing is right – they encounter seasonally discrete foods necessary for adequate growth before entering the ocean (Sibert et al. 1977). Unfortunately, the contemporary Columbia River Basin is beset with many disconnections and mistimings, thereby causing problems that are adversely reflected in productivity and resilience.

Productive and resilient ecological systems show high levels of internal connectivity, as well as environmental coordination of timing in reproduction, movement and feeding by organisms. Connectivity can be thought of as the ability to make and maintain linkages between various spatial points, whereas timing is the synchronization of the various parts of a system – such as arriving at a location when foods are available or the temperatures agreeable. Together, these two attributes are known as phenology – the study of recurring life-cycle events that are initiated and driven by environmental factors (Morisette et al. 2009).

Connectivity and timing are essential ingredients of everyday lives. The expression of connectivity and timing phenology requires that organisms have the ability and the opportunity to adjust so that their actions occur at a desired or favorable time. In the Columbia River Basin these are expressed in several forms. They can be as simple or as complex as:

- Juvenile fishes arriving at new locations as foods become seasonally available
- Floodplains being inundated as fish and other organisms are seeking suitable habitat and size-appropriate foods
- Changes in predator-prey interactions reverberating throughout an ecosystem, with often unexpected consequences: trophic cascades
- Shifts in system properties, such as food supplies and productivity, often create conditions with no analogue in history. These shifts may include alterations to temperature, nutrient and chemical regimes.

There are fundamental interactions between an organism's life-cycle and climate, where climate is expressed by patterns of temperature and flow regimes (Menzel et al. 2005). Phenology describes climate–biota relationships and can be used to document and evaluate the effects of climate change at both the individual species and aggregate levels (Figure E.4.1; Schwartz 2003). Furthermore, observing and documenting changes in the phenologies of various species support efforts to reconstruct historical climates and make predictions about biological responses to alternate future climate scenarios (Cook et al. 2005).

Understanding connectivity and timing in Columbia River food supplies provides insights into vexing resource management and restoration questions, such as:

- Are the preferred foods, or even adequate foods, of migrating juvenile fishes available at the right times, and for all species?
- How have hatchery programs and habitat restoration activities affected the phenology of organisms with their food supplies?
- Will broad-scale changes to temperature, nutrient and chemical regimes indirectly undermine restoration efforts by precluding the ability of organisms to use the environment in space and time so as to effectively complete their life-cycles?

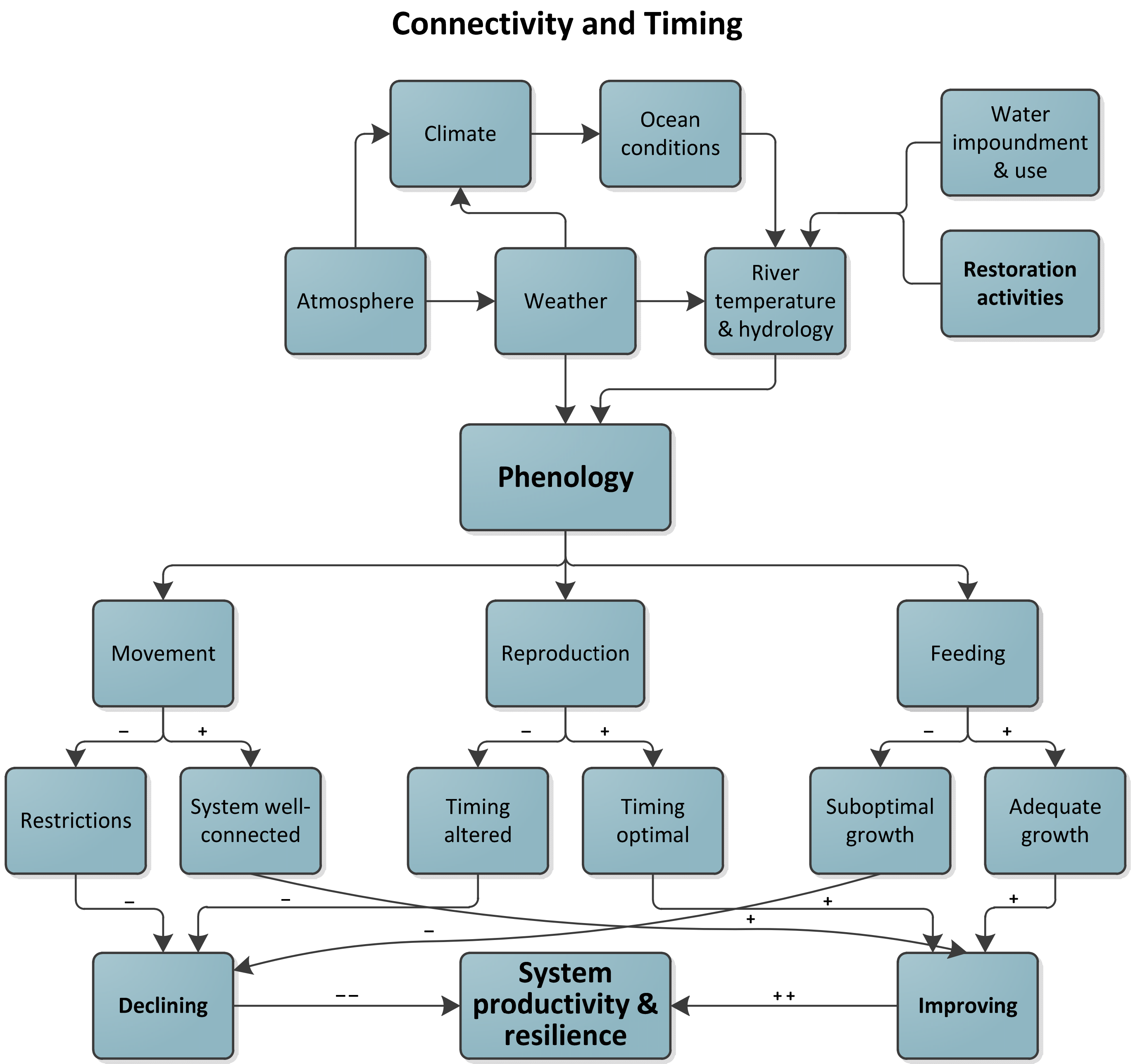

Figure E.4.1. Conceptual model showing some of the ways in which phenology is intricately linked to variations in weather (short term, days to weeks), climate (long term, years to centuries), ocean conditions, water impoundment and uses, and restoration projects. Collectively, the impacts influence phenology and thereby the movement, reproduction and feeding and, ultimately, the productivity and resilience of the ecological system.

This Chapter sheds some light on these and other provocative questions by examining the various forms of connectivity and timing exhibited by productive and resilient ecological systems. These forms of connectivity and timing include floodplain inundation, fish movement and food supplies, trophic cascades, as well as food webs with no historical analogue (basically, a "no analogue" future). We then make several recommendations for better integrating phenology into restoration of the Basin's food webs.

Floodplain Inundation

Rivers and floodplains are connected in all three spatial dimensions (i.e., longitudinal, lateral and vertical), and over time. These linkages are keys to the development of food webs and to their various consumers (Ward 1989, Décamps 1996). Expansion and contraction occur throughout the longitudinal course of a river in response to water supply and geomorphology. Water supply and geomorphology also influence the lateral extent of a floodplain. The vertical dimension is equally complicated. One segment of a channel may be fed largely by upwelling groundwater, while surface runoff at other locations may penetrate into bed sediments (alluvium) accumulated over millennia (Figure E.4.2), thereby affecting food web processes. During flooding, surface flow may recharge groundwater aquifers and spill out over the floodplains, eroding or depositing sediment, in accordance with the energy dynamics of water interacting with geomorphic features. During dry periods, flow and food webs in the channel may be maintained by groundwater draining alluvial aquifers.

It is well established that fish biomass increases with the connectivity of floodplains to a river, and that species use the various floodplain habitat types differently (Amoros and Roux 1988, Grift 2001, Miranda 2005, Vaughan et al. 2009). Although the importance of floodplain inundation has been widely recognized (Junk et al. 1989, Poff et al. 1997, Williams 2006), we are only now beginning to quantify the relationships between river discharge and floodplain inundation as well as food availability, ecological functioning, restoration potential and fisheries productivity (Sommer et al. 2001, Bowen et al. 2003, Bouvier et al. 2009, Vaughan et al. 2009). Yet, it is being put into practice via direct management and manipulation of water regimes that provide "environmental flows" for organisms. "Environmental flows" refer to fluxes of water, sediment, temperature, and physical attributes that mimic (although not exactly the same as) natural patterns (The Brisbane Declaration 2007, Arthington et al. 2010). In Australia, the positive outcomes for native fish recruitment, following intentional delivery of a large environmental flow, have been outstanding (King et al. 2010). In the Colorado River, the results have been less impressive, probably because the simulated floods were too small (Poff et al. 1997). In addition to forming habitat, floodplain inundation is essential for maintaining food web connections between aquatic and terrestrial environments (Chapter D.8).

The preceding investigations and large scale experiments provide important insights into the role of floodplain connectivity in sustaining fish populations. Connectivity via inundation provides needed habitats

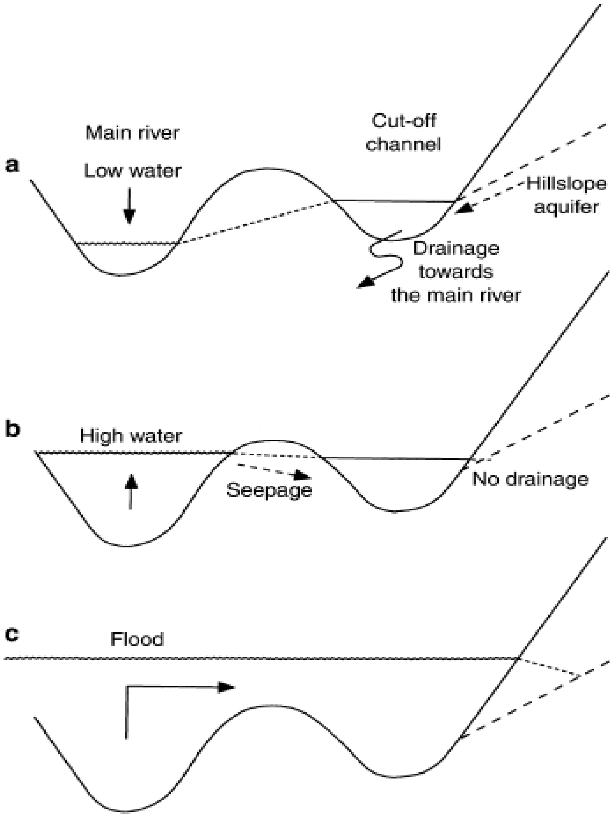

Figure E.4.2. Schematic illustration of the short-term dynamics of hydrological connectivity in relation to river stages (a) (lowwater stage), the floodplain waterbodies may be supplied by a hillslope aquifer; (b) (high-water stage), the floodplain waterbodies are supplied by river infiltration into the alluvial aquifer and possibly by river backflow through a downstream connection; (c) (flood), the floodplain waterbodies are supplied by overbank flow. From Amoros and Bornette (2002).

and foods at critical life stages. Juvenile fishes of virtually all species share the common characteristics of small size, poor swimming capability, and reliance on zooplankton, small insects and detritus as primary food items (Hall et al. 1979, Papoulias and Minckley 1990, 1992; Muir et al. 2000). Zooplankton densities can be two or more orders of magnitude greater in backwaters than in a main channel (Mabey 1993, Ward and Stanford 1995). In addition, shallow water in combination with structural cover, reduces predation risk for small fish (Schlosser 1991, Ward and Stanford 1995).

Therefore, many juveniles need shallow, slow-water refugia between the free-embryo stage and full development of the axial skeleton, internal organs and fins, as well as size-appropriate foods to support development. For instance, in the Missouri River Basin, where more than 20 fish species are listed as rare, threatened or of special concern, the proximate causes for the decline of native fishes include changes in flow regime, sediment transport, habitat availability and foods (Hesse et al. 1989, Bowen et al. 2003). These factors control the structure (species composition and relative abundances) of food webs, as well as their spatial connectivity and phenology.

Fish Movement and Food Supplies

Nearly all organisms require several different habitats and types of foods to complete their life cycles. For instance, a lake may be regarded including a spatial mosaic of habitats and associated foods, connected in vertical, horizontal and temporal dimensions. Most lakes are small, with generally high ratios of edge to volume and perimeter to area. These characteristics result in considerable potential for connectivity and assure that no single habitat type or food web may dominate. Connectivity among lake habitats and food webs supports overall ecosystem structures and functions, as organisms and nutrients move between the benthos and water column, and from near shore to pelagic zones (Lake et al. 2000, Schindler and Scheuerell 2002). At a larger spatial scale, such as the Columbia River Basin, the creation and maintenance of seemingly discontinuous habitats are, in fact, heavily influenced and subsidized by the movements of organisms, materials and nutrients, whether in streams, rivers, lakes, impoundments, estuary or ocean (Polis et al. 1997, 2004). For instance, the transport of phytoplankton and suspended particulate organic matter from reservoirs subsidizes downstream food webs (Chapters D.6, D.7).

Individual fish and fish species follow distinct life history trajectories through space and time. Conceptually, life histories dictate the need for a chain of habitats and associated foods arranged in a favorable spatial-temporal distribution (Thompson 1959, Mobrand et al. 1997). Fishes evolve behaviors and life history characteristics that ensure they will be in the right place at the right time to obtain food and shelter that are needed for completion of their life cycles. Conditions vary among rivers and lakes, and there are concomitant differences in life histories. Conditions also change over time in a given location. As the environment changes, it may cease to provide resources required by a species or life stage, with possibly dire consequences. Irregularities in the temporal distribution of favorable habitats, whether over a day, a season or a year, can have significant consequences for fish productivity. Effective management strategies recognize that species depend not only on the existence of suitable habitat and foods, but on their availability in the right place at the right time.

This is exemplified in the movements of juvenile chum salmon from spawning grounds to the coastal zone. In the Nanaimo River, British Columbia, young chum move quickly to the estuary in the spring, coinciding with the availability of select benthic meiofauna. Entry into the estuary is nearly perfectly timed with availability of principal foods. Approximately 53 million fry migrate from the river between March and the end of May. In March and April, individual fish stay in the shallow mudflats for ~13-18 days (Healey 1979). This period of residence decreases to ~1.5 days in May as preferred foods are exhausted. The biomass of fry reaches a maximum of 2,300 kg (fresh weight) by the end of April and, from March to May the relative increase in weight of these fish averages 4% per day. The amount of food required to support the observed growth of the fry population during their residence in the estuary is estimated to be approximately 3,850 kg (Sibert 1979). Analysis of stomach contents shows their primary food is only a few species of epibenthic and interstitial harpacticoid copepods of the hundreds potentially available. The copepods are feeding on microbes associated with detritus (Sibert et al. 1977), with the production of detritus showing strong seasonal timing (Naiman and Sibert 1979).

Trophic Cascades

Trophic cascades take two forms, top-down and bottom-up. Intense predation creates strong direct and indirect effects that reverberate through food webs (i.e., top-down effects). Bottom-up trophic cascades result from stimulation of microbes and primary producers, with the effects working their way up the food chain. The strength and ubiquity of trophic cascades has been the focus of sustained debate in ecology, and considerable effort has focused on quantifying their strength in aquatic and terrestrial ecosystems (e.g., Nakano and Murakami 2001, Knight et al. 2005). Fish are especially important in this regard as many species indirectly facilitate system productivity through cascading trophic interactions across habitat and ecosystem boundaries.

Top-down trophic cascades are well known. They have been used to restore lakes and fisheries to healthy trophic status (Carpenter et al. 1985, Power 1990). The concept of cascading trophic interactions can explain differences in productivity among ecosystems with similar nutrient supplies but contrasting food webs. The concept of trophic cascades reflects an elaboration of long-standing principles of fishery management based on logistic models (Larkin 1978). Simply put, a rise in piscivore biomass brings decreased planktivore biomass, increased herbivore biomass, and decreased phytoplankton biomass. The concept links the principles of limnology with those of fisheries biology and suggests a biological alternative to the engineering techniques that have dominated lake management. Variation in primary productivity is mechanistically linked to variation in piscivore populations. Piscivore reproduction and mortality control the cascade of trophic interactions that regulate algal dynamics. Through programs of stocking and harvesting, fish populations are managed to regulate algal biomass and productivity.

Negative examples are also seen. A recent example of direct relevance to the Columbia River Basin has been quantified for Flathead Lake, Montana where the introductions of predaceous lake trout and mysids have fundamentally altered the food webs (Ellis et al. 2011). Positive interactions among the non-native invertebrate and vertebrate predators played out over many decades to cause a substantial and abrupt shift in community composition and the attendant food webs resulting in a trophic cascade that extends to primary producers as well as to terrestrial species (bald eagle). Another example is when non-native rainbow trout are stocked into streams. Rainbow trout usurp terrestrial prey that fall into the stream, causing native Dolly Varden charr to shift their foraging to insects that graze algae from the stream bottom (Figure D.8.3; Baxter et al. 2004). This indirectly increases algal biomass, but also decreases biomass of adult aquatic insects emerging from the stream to the forest. In turn, this leads to a significant disconnection in food subsidies to the associated riparian zone.

Bottom-up cascades are equally well known. Often recognized as undesired eutrophication, bottom-up processes are also used to stimulate fish production via controls on nutrient availability in oligotrophic systems (Huntsman 1948). Fertilization has been successfully used in numerous oligotrophic situations – from temperate to arctic regions – to increase fish productivity via improvements in the food supply. For instance, despite some site-specific difficulties, when lakes are fertilized with various mixtures of inorganic nitrogen and phosphorus, bottom-up pelagic food web stimulation is strong enough and predictable enough to ensure that sockeye smolt biomass increases in almost all cases (Hyatt et al. 2004). There have been 24 sockeye salmon nursery lake experiments involving whole-lake fertilization with appropriate treatment and control years, as well as monitoring. Of those experiments, 21 of 21 show that fertilization increased chlorophyll *a* concentrations, 16 of 16 show increased zooplankton biomasses, 16 of 16 demonstrate increased average smolt weights, and 11 of 13 show increased smolt biomasses. Studies involving assessments of egg-to-smolt survival are rare, but all (4 of 4) show increased survival rates. Studies involving increased smolt-to-adult survival (i.e., marine survival) are few, but all (3 of 3) show that lake fertilization and increased smolt size are associated with increased marine survival (Hyatt et al. 2004).

In streams, the initial results are equally impressive. The addition of inorganic nutrients, and even sugar, stimulate microbial and primary production thereby resulting in increased fish production (Warren et al. 1964, Johnston et al. 1990, Degan and Peterson 1992). Like lakes, the ultimate effect of stream fertilization is to increase the abundance of fish food organisms, mainly the immature stages of aquatic insects. Increases in the standing stocks of stream zoobenthos, after organic enrichment, also have been demonstrated in experimental streams and troughs (Warren et al. 1964, Mundie et al. 1983, 1991), suggesting that the manipulation of microbial and primary production is a useful restoration management tool to increase salmonid growth in nutrient poor streams, although caution is often warranted when non-native species are present.

Understanding top-down and bottom-up trophic cascades is confounded by organisms with complex life histories that connect seemingly different habitats (Polis et al. 1997, 2004). This is because food supplies in different habitats are driven differently. Similar processes are also seen in the coupling of aquatic with terrestrial ecosystems (Chapter D.8; Naiman et al. 2005). Species with complex life histories often shift habitats and foods during their life cycles and provide potent conduits coupling ecosystems. Thus, local interactions that affect predator abundance in one ecosystem (for example a larval habitat) may have reverberating effects in another (for example an adult habitat). Ecologists increasingly recognize that fluxes of organisms across habitat and ecosystem boundaries can have major consequences for system productivity. Mutual trophic interactions between contiguous habitats have potential significance for system productivity and resilience (Nakano and Murkami 2001). In temperate regions, aquatic insect emergence often peaks in spring, when terrestrial invertebrate biomass is low. In contrast, terrestrial invertebrate input to the stream occurs primarily during summer, when aquatic invertebrate biomass is nearly at its lowest. As discussed in Chapter D.8, such reciprocal, across-habitat prey flux alternately subsidized both forest birds and stream fishes, accounting for a significant portion of the annual total energy budgets of bird and fish assemblages (Figure D.8.2). Seasonal contrasts between allochthonous prey supply and *in situ* prey biomass determine the importance of reciprocal subsidy. Thus, species invasions can interrupt flows of resources between interconnected habitats and ecosystems and have effects that propagate across their boundaries, effects that may be difficult to anticipate without in-depth understanding of food web relationships. Other examples include fish reducing larval dragonfly abundance in ponds, leading to fewer adult dragonflies nearby. Adult dragonflies consume insect pollinators and alter their foraging behavior. As a result, riparian plants near ponds with fish receive more pollinator visits and are less pollen limited than plants near fish-free ponds – resulting in more robust communities (Knight et al. 2005) and improved food subsidies from the riparian forest.

A “No Analogue” Future

As discussed in Chapters C.5 and E.3, the structure, connectivity and timing of the Basin’s food webs and their associated processes are now sufficiently altered in structure and function to qualify as “novel” systems. In the past, managers and restoration activities have attempted to eliminate processes or components that did not fit the general perception of a desirable system. With these new challenges, managers must re-examine their perceptions and develop management strategies to promote ecosystems that are both feasible and resilient. Where to start? As suggested in Chapter E.3, this is best accomplished by implementing environmental flows (The Brisbane Declaration 2007, Arthington et al. 2010) to maximize genetic, species and functional diversity. Doing this would increase the productivity and resilience of communities and ecosystems, via food web connections and timing, under uncertain environmental regimes. Certainly there is a compelling need to adopt a more dynamic framework that explicitly acknowledges and embraces change as a fundamental process occurring throughout the Basin. This is possible if scientists work cooperatively with managers and policy makers. Given that ecosystems have already been altered in ways that predispose them to easier future change, often with declining productivity and reduced resilience, management activities should not only anticipate change, but should acknowledge that current systems already have been transformed and are being transformed further (Seastedt et al. 2008, Venter et al. 2008). One way to determine which conservation actions foster food web productivity and resilience in a rapidly changing environment would be to implement a coordinated suite of large-scale experiments (focusing on specific management questions) with suitable controls and well-planned monitoring, and with an emphasis on food web connections and timing. This is easy to state but heroically hard to accomplish given the complex patchwork of land ownership and water uses, but large-scale experimentation may be the best way to answer some of the most difficult questions about food web productivity and resilience.

Conclusions and Key Challenges

Answers to the questions raised at the beginning of this Chapter concerning fish community productivity and resilience are fundamentally affected by phenology. Connectivity and timing impact the availability of preferred foods eaten by migrating juvenile fishes while hatchery programs and habitat restoration activities affect the connectivity and timing of organisms with their food supplies and broad-scale changes in temperature, nutrient and chemical regimes undermine restoration efforts via shifts in connectivity and timing. These processes and many others rely on having the ecologically acceptable connectivity and timing for maintaining sustainable relationships between organisms and their food supplies.

Three important observations have been made regarding phenology (Vaughan et al. 2009). First, current scientific understanding of river ecology and hydrologic linkages is generally poor, especially at the quantitative levels required for effective prediction and management. This is despite scientific literature stretching back more than 80 years (e.g., Riley 1921, Percival and Whitehead 1929) and comprising many thousands of peer-reviewed publications. Numerous studies – mainly observational – have described links between biological patterns, ecological processes, river form, and physical processes, yet the underlying mechanisms are often only known in outline and are seldom applied to restoration. Relationships between riparian and floodplain environments are less widely appreciated than those within the wetted channel, highlighting the need to consider whole catchments and river landscapes in restoration programs.

Second, improved understanding of the ecology–hydrology linkage is a pressing challenge if the timetable and goals of restoration actions are to be met. Major challenges arise in distinguishing the influences of hydrologic modifications on food webs from other potentially confounding effects, such as chemical pollution (Chapter C.7). Biological indicators and monitoring of physical modifications are still preliminary, rarely described or poorly founded, while few biological models diagnose how physical effects contribute to biological departures from expected conditions (Davies et al. 2000).

Finally, those expectations are challenging enough for reference food webs, given the inherent variability in both physical habitat and biology. The need to understand food web–hydrologic connections is accentuated by the prospects of climate change, altered flow regimes and increased water consumption (Naiman and Turner 2000, Jackson et al. 2001, ISAB 2007-2). It is vital that such changes are both understood and translated into actual practice, if riverine food webs are to be managed effectively in future. Rivers are highly sensitive to climate and land use effects, but features that mitigate food web impacts or increase their resilience are poorly understood (Durance and Ormerod 2007).

There are three key research challenges in establishing a better understanding of how food web connections and timing can be functionally incorporated into restoration activities:

1. In the short term, use existing literature or data to better identify extant food web patterns (e.g., aquatic insect emergence) and their related ecological responses. Much can be learned from the information already in hand, if it is examined in a thoughtful and comprehensive manner.

2. In the medium term, discover and quantify connections among patterns and processes. For instance, connections between the place-based production of foods and the timing of movements by juvenile salmon during their seaward journey. Basic investigations will advance a mechanistic understanding of phenology within the Columbia River Basin. Similarly, multidisciplinary, large-scale catchment projects can foster collaborative efforts among various scientific disciplines and resource managers. Expertise is currently fragmented across the main contributory disciplines (ecology, hydrology, geomorphology, flood risk management, civil engineering), restricting the effectiveness and potential of restoration activities. This is counter-productive, given the shared vision of effective river management and restoration that is based on good science producing positive social impacts. We need a diverse expertise because a range of approaches is necessary to build a sufficient, integrated capacity that delivers science of real management value.

3. Management and restoration of food webs on river floodplains – for the sustainable productivity and diversity of fish – demands a sound understanding of connections between water regimes and ecological responses. Basically, we have to restore the floodplain component of the food web to restore the fish. It is necessary therefore to understand relationships between river discharge, flood magnitude, floodplain inundation patterns and fish production at scales commensurate with the issues. Even though such analyses are largely in their infancy (e.g., Schramm and Eggleton 2006, K. van de Wolfshaar et al. 2011), they are key parts of an integrated and comprehensive restoration program. Large scale and seasonally appropriate experimental inundation of floodplains is just one example of how to approach this multidisciplinary research challenge.

E.5. Threats, Knowledge Gaps, and a Strategy for Columbia River Food Webs

Charting the Way Forward

Developing a comprehensive understanding of food webs associated with the Columbia River is surely on par with understanding the complexity of life itself. All structures, processes, linkages, behaviors and nuances found in Nature come into play and they are expressed in vitally important ways. We do have considerable information on some species and their life histories, which allows insights into important food web processes, but there are also significant information gaps and a lack of clarity, as patterns and processes change in seemingly unpredictable ways. These seemingly unpredictable aspects, as well as insufficient and/or inaccurate knowledge, lead to fundamental problems in the management and restoration[33] of natural resources. An example is the addition of what some once believed to be "innocuous" non-native species that have fundamentally altered trophic states. A high profile example of an unforeseen problem is currently being played out in the upper Mississippi River system, where the Great Lakes are under imminent threat from invasion by silver and bighead carps, two invasive Asian species that have been shown to alter the food web supporting native fishes (Irons et al. 2007).

Here we identify and prioritize – without apology for the number or complexity – a substantial collection of food web-related research challenges for the coming decade (Table E.5.1). Despite the large number of challenges, the list is not complete. There are many additional knowledge gaps identified in individual chapters. Though much is known about the Columbia Basin, our knowledge of food web structure, productivity and resilience is, on the whole, fragmented and parochial. While the report synthesizes existing knowledge, it also provides initial analyses to illustrate what is needed to deepen our understanding of a complex system.

Overall, there are several critical threats to the productivity and resilience of the Basin's food webs, and we offer a strategy to offset those threats. This chapter identifies major knowledge gaps in understanding the food webs and considers the implications of those deficiencies for successful restoration. Collectively, the basic issues are central to the long-term maintenance of the Columbia Basin as an integrated ecosystem, one that retains many of its valued historical characteristics. This means having effective strategies for reversing degraded conditions while suppressing harmful components. The topic is inherently complicated, primarily because many key threats, knowledge gaps and implications for restoration are site-specific or time-sensitive. The following discussion provides an initial framework for charting the way forward.

Key Threats to Resilience and Productivity

Foods webs of the Columbia River are potentially productive yet fragile. There is a considerable diversity of potential threats but, during the course of this evaluation, three critical and several important threats were consistently identified by the ISAB. The three critical threats are:

Uncertainty about the Aggregate Carrying Capacity of the Columbia River for Salmon and Steelhead. There are 130-150 million hatchery fish added to the system annually. Not only are there substantial volumes of foods imported from outside the Basin to rear the fish, hundreds of metric tons of natural food are required to sustain them subsequent to release (Chapters C.4 and C.6). Hatchery operations, in addition to ongoing habitat changes, have the potential to significantly affect the capacity of the Columbia River to support *wild* native fishes and other wildlife. The consequences of large scale hatchery releases for food webs, as well as for the growth and survival of *wild* juvenile salmonids have not been adequately evaluated in freshwater, the estuary and the ocean. This is especially relevant for those stocks residing and feeding in riverine and estuarine habitats for long periods, such as sub-yearling (ocean-type) Chinook. We need to determine the aggregate capacity of the system, and the temporal and spatial variability in that capacity, to support the production of food for fishes and other organisms. Further, we need to determine the impact of hatchery fish on food web properties in the various habitats, and over a range of abundances for both hatchery and wild fish.

Proliferation of Chemicals and Contaminants. Bioaccumulation and biomagnification of chemical pollutants in the Basin's food webs are occurring and

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[33] Used in the sense of restoring, renewing, reviving or reestablishing ecological properties.

could, if not addressed, undercut restoration efforts. With nearly 200 agricultural chemicals in use, among others, and the approximately 45,000 metric tons added annually, the productivity of many food webs and their resilience are likely affected (Chapter C.7 and Appendix C). The ISAB recognizes that this issue goes beyond the Council's mandate, but there is a strong likelihood that it constrains the effectiveness of the Fish and Wildlife Program. The Council needs to coordinate with other regional agencies in pinpointing and understanding the consequences of chemical use for the Basin's food webs. The region urgently needs a large, well-coordinated collective effort. As well, the Council needs to work with regional agencies to implement the recently completed Columbia River Basin Toxics Reduction Action Plan and update it regularly, so that current and future chemical insults to the system can be dealt with in timely fashion – before the problems becomes further magnified.

Consequences of Non-native Species: Hybrid Food Webs. The introduction and expansion of non-native species will continue, with impacts that are potentially very damaging yet not entirely predictable. The existence of more than 900 (terrestrial and aquatic) non-native species that we know of today, and the prospect of considerably more arriving in future years, is a grave problem (Sanderson et al. 2009, Chapter C.5). There is substantial uncertainty in terms of consequences for the resilience and productivity of habitat-specific food webs, but accumulated experience suggests that the native biota will not benefit. It is also clear that future food webs will have no historical analogue; they will be novel, hybrid food webs. There is a basic need to consider the implications of hybrid food webs as well as to develop a fundamental understanding of characteristics needed to support important ecological functions, especially in view of ongoing climate change. Further, it is necessary to intervene quickly when and where invasive problems first emerge, averting problems wherever possible, or slowing them down when not completely avoidable.

In addition to the three critical threats identified above, there are three other critical threats that should be considered simultaneously:

Altered Nutrient Organic Matter (Energy), Water, and Thermal Sources and Flows. Nutrients and organic matter constitute the fuels for food webs. Water flow and temperature directly control their availability and incorporation into food webs. Continuing losses of marine-derived nutrients and riparian-derived organic matter, in addition to increased land-based leaching of nutrients and organic matter, accelerating eutrophication, ongoing atmospheric deposition of nitrogen and micro-nutrients, as well as water storage, extraction and flow manipulation, collectively threaten to alter the Basin's food webs (Chapters D.4, D.6, D.8). There is an important need to assess these problems and to be able to predict the consequences of such alterations.

Disconnects among Critical Habitats and their Food Webs. Connectivity and timing impact the availability of preferred foods for resident and migrating juvenile fishes (Chapter E.4). Broad-scale changes in temperature, nutrient and chemical regimes, hatchery programs, and habitat access or condition affect the connectivity and timing of organisms with their food supplies. There is a fundamental need to manage for total system productivity, rather than concentrating on optimizing local components. At one extreme, this means reconnecting the river with its floodplain and tributaries as well as providing seasonally-based environmental flows (Chapter E.4; Arthington et al. 2010) that provide adequate food for migrating salmon from tributaries into the ocean. At the other extreme, it means developing comprehensive, system-scale models of interconnected habitat-based food web processes.

Environmental Change and Surprises. One can anticipate continuing changes over the foreseeable future. Management decisions, made in this decade (including the implementation of an FCRPS Biological Opinion), will affect food webs and other resources well into the future (Chapter E.1). Canadian and regional authorities are already planning for large-scale water and power management needs over the first half of the 21st century. There is an important need to insert the region's biota and associated food webs into the list of planning targets from the outset, with strategies for ameliorating those changes we can do something about. Further, the Basin will continue to receive unexpected perturbations. There is need to develop a response system that can absorb short term ecological surprises readily with resilience and capacity to adapt. More specifically, there is an urgent need for forecasting how shifts in environmental conditions could dramatically alter predation impacts or habitat carrying capacity based on shifting distributions or trophic relationships among species as we enter a "novel" future. The ISAB urges the Council to consider setting aside funding for exploratory activities, and to remain alert to impending challenges thereby providing early intervention where needed.

Fill Specific Knowledge Gaps

Even with the knowledge acquired to date, it is clear that our base-level understanding of the Basin's food webs is still rudimentary, especially with the rapid changes taking place. This report has highlighted a collection of vignettes on ecosystem and food web structure, many of which reveal worrisome *information gaps*. The gaps are large in specific areas, but tools are increasingly available to fill them (Appendix A), and they should be addressed over the next decade. Developing a useful and pragmatic understanding of food webs is possible, for example, by focusing on critical linkages and keystone species that most strongly influence those webs. We identify and prioritize a number of major gaps of immediate importance (see Table E.5.1 and below). Additionally, there are numerous gaps in understanding specific habitats and processes, and these are identified in the individual chapters. Timely attention is needed to determine the consequences of hatchery releases on carrying capacity, understand the consequence of chemical use, model the complexities of the ecological network, understand the base of food webs, and identify physical controls of food web structure and processes. Collectively, these include measuring production dynamics, quantifying patterns of abundance of important foods, determining how foods affect growth and survival of juvenile fishes, fully exploring the complexities of marine-derived nutrients, understanding the roles of intermediate as well as apex predators, establishing historical baselines, and quantifying land-water interactions. The challenges fall in four general areas: data gathering and synthesis, modeling, experimental testing of models, and evaluation of alternative policies. Specifically, we need to:

Data Gathering and Synthesis

- Determine the ability of the system to produce foods to support proposed or anticipated numbers of both wild and hatchery reared fishes at a level promoting adequate growth and/or successful migration.
- Fully understand the trophic consequences of adding hatchery fish to the system as well as the imported foods used to grow them and the waste products produced during rearing.
- Quantify incremental improvements in available foods and fish production derived from habitat-specific restoration activities, with special emphasis on floodplains.
- Mount a region-wide monitoring program to quantify the temporal pace and spatial extent of non-native introductions and continuing invasions, and to spot impending problems while still minor and manageable.
- Establish a monitoring strategy to track constituents and sources of contaminants, nutrients and organic matter, spatially and temporally. Further, determine the extent to which marine-derived nutrients are helpful, and, which pollutants and artificial chemicals are helpful and/or harmful.
- Identify the nutrients that enhance the productivity of food webs, and determine whether existing concentrations are limiting productivity. Keep in mind that ratios of nutrients also shape the structure of communities, and an imbalance of essential nutrients hampers productivity.

Modeling

- Quantify critical connections between place-based production of foods and the timing of movements and production or growth by juvenile fishes, thereby establishing a mechanistic understanding of their relationships within the Basin.
- Initiate directed studies and modeling of the impacts of the increasing chemical load on the organisms and thus on the structure, resilience and productivity of the Basin's aquatic food webs.
- Model how to get the fish where they need to be, when they need to be there, with the right blend of available food resources, thermal regimes and interactions with predators and competitors. Incorporate connected system thinking into management planning and coordinate agency efforts to improve total Basin productivity.

- Evaluate a broader application of seasonal environmental flows to connect habitats, mitigate disruption and benefit ecological functions of food webs downstream.

Restoration Actions and Experiments to Test Model Predictions and Assumptions

- Determine where and when fish growth is density dependent as well as when hatchery fish may displace or otherwise cause wild juveniles to move downstream due to food limitations. Experimental manipulation of the number and timing of hatchery releases is a logical method to quantify this.
- Use large-scale experiments to evaluate the relationships between survival (smolt to adult) during years of different ocean productivities and river conditions. Consider the impact of altering hatchery releases or transportation during years of predicted poor ocean or river survival. Survival in the ocean is often food limited, and perhaps density dependent, and may be related to food availability and predation intensity. Survival in the river may be as well. Further, experiments should consider stage-specific size and growth to identify critical life stages and periods that impose important constraints on survival.
- Using a food web perspective, mount multidisciplinary, subbasin-scale catchment projects, including both rural and urban locations, to promote concentrated collaborative efforts among scientific investigators and resource managers. Use the projects to test predictions about the most effective food webs to sustain and enhance species of interest.
- Restore the Basin's river floodplains (including those in the estuary) and floodplain-supported food webs, and reconnect them with the main channel. While doing so, establish the relationships between river discharge, floodplain inundation, food webs and fish production. Experiment with large scale and seasonally appropriate floodplain inundation, and evaluate the food web effects.

Evaluation of Alternative Policies with Models

- Reevaluate stocking practices for native and non-native species, in the context of the regional concern for production, recovery, and conservation of wild stocks and native biota. Some policy changes may be in order. Model scenarios of different policy options with respect to nutrient additions (e.g., direct fertilization, carcasses) or reductions as a guide to future management efforts. The process to date has been guided more by perceptions of benefit than by hard proof of success.
- Establish planning goals for the Basin's biota and food webs for the next 50-100 years, taking into account anticipated climatic and anthropogenic changes impacting the Basin's environment. Mount modeling exercises to project the impact of alternative policy choices on all components.

A Strategy for Protecting the Best and Restoring the Rest

In deciding what habitats and associated food webs are key, we need to establish desirable end-targets to protect the healthy habitats and to restore degraded habitats to healthier states. "Desired end states" was part of the subbasin planning effort (ISRP/ISAB 2004-13) and needs to be expanded to include food web processes.

Conservation is most successful where actions are aimed at protecting ecosystems, before they are degraded. Trying to restore them after the damage is done is expensive, time-consuming and often not fully successful. The realization is growing that a concerted effort to protect the food webs of the Basin's critical environments will be needed, and Congress is considering legislation (H.R. 2055 and S. 817) that would direct federal, state, local and private stakeholders to develop conservation plans that make new investments in the healthiest natural salmonid populations. To accomplish that, we need to preserve the Basin's most functional food webs, even while steering degraded systems to a healthier status.

The continued existence of the critical threats and food web knowledge gaps significantly impact our ability to manage the ever-changing resources effectively. Each gap and threat requires a substantial and sustained effort to understand and resolve it in a pragmatic way. More specifically, acknowledging food webs as an integral component of resource management has a variety of implications for ongoing and emerging restoration activities. To date, restoring food webs has received considerably less attention than other forms of habitat restoration. Nevertheless, there are ongoing restoration projects designed, at least in part, to benefit trophic pathways: nutrient addition to oligotrophic lakes and nutrient control in culturally eutrophied ones; supplementation of streams with salmon carcasses or carcass products; restoration of processes controlling the nature of habitat including flows, native vegetation and connectivity; and control or restoration of food web structure through removal or control of non-native species. Nevertheless, additional actions are required if we are to “protect the best and restore the rest”:

Identify Properties Sustaining Desired Ecosystem States. This is an exercise that every restoration activity would benefit from doing on a regular basis. What would the food web structure look like if the restoration activity was successful? And would the new improved food web permanently increase the carrying capacity, improve salmon survival, or improve the health and resiliency of the local food web of the habitat targeted by the restoration activity? In effect, this exercise provides a blueprint for project activities, and provides targets for measurable outcomes. Further, it aids in guiding selection and acquisition of restoration sites. A better understanding of properties sustaining desired ecosystem states is critical during this period of rapid environmental change and when perturbations of ecological structure are unavoidable.

Suggestions for specific activities include:

- Determine sustainable food web structures for each of the eight habitat types enumerated in Section D. There are myriad variations on each theme, but
- For each type of habitat, execute carefully matched comparisons (healthy versus degraded; restored versus not restored), and develop a blueprint for what to protect and what to restore.
- Develop reasonable targets for measureable outcomes, so as to gauge ongoing success as we move forward with protection and restoration efforts.

Sustaining Resilient Populations. In the Introduction to this report, we posed several basic questions related to food webs and their role in maintaining resilient populations. Addressing these questions would inform ongoing and future restoration efforts and would aid in predicting basinwide responses to many key threats. Developing a working understanding of trophic interactions, seasonal production cycles, system carrying capacity, accumulation and biomagnification of toxic chemicals, changing species competition and predator-prey relations, and other processes is a large challenge but is, at the same time, necessary for maintaining resilient populations.

Existing food webs are undoubtedly resilient to some perturbations and vulnerable to others. The loss of some species and species-specific sensitivity to some abiotic factors might be of little importance, but other species replacements and heightened sensitivities can have drastic effects. In order to better understand system-scale properties imparting resilience, we suggest some specific activities:

- Identify rapidly changing food webs that are matched with trophically stable reference sites, and then examine how much the abiotic parameters and biotic components differ between them. Translate those results into “real time” and “real world” sensitivity analysis by characterizing the changes that occur. For example, this would have been very helpful had it been done prior to the *Mysis* introductions.
- Extrapolate from these empirical comparisons to wider predictions, and from there into policy choices. For that, we need food web modeling under a range of biotic and abiotic challenges.

Hybrid Food Webs as Legitimate Targets, while Maintaining Productivity. A key concern is the emergence of novel or hybrid food webs that contain many non-native elements and that differ fundamentally from food webs composed of native species. The habitat itself has changed drastically and it is not possible to restore original conditions. Since the original conditions and biota cannot be restored, we can only go forward. It is possible to target a healthy food web, defined as one that is resilient and productive, even if some species and conditions have changed, and that can be managed and adjusted from time to time. Whether that food web will ultimately include the region's salmon and other species of concern is unknown, but being proactive in this regard would be prudent.

Additionally, the proliferation of non-native species and the widespread, intense use of artificial chemicals represent serious concerns for the future productivity of the system. Even if protection and restoration actions are initially successful, non-native species and chemicals may undermine the capacity of those sites to be productive for the long-term. The ISAB views non-native species and artificial chemicals as potential threats on par with a significant scarcity of water in the river. Food web protection and restoration is not explicitly envisaged in the Fish and Wildlife Program's scientific principles, and that ought to change. We suggest some specific activities:

- Carry out management experiments at a scale similar to the habitat restoration experiments now being studied in intensively monitored watersheds (IMWs), through the Integrated Status and Effectiveness Monitoring Program (ISEMP). We need to bring diverse expertise to bear; a range of approaches is needed to build sufficient, integrated capacity that will deliver science of real management value.
- Establish meaningful long-term monitoring on all food web-related restoration projects, and evaluate successes and failures. There are many uncertainties and threats to project success, and we need to assess conditions under which success or failure is likely.
- Initiate scientifically controlled proof-of-concept restoration demonstrations, at a scale that is sufficient to provide confidence of benefits, rather than concentrating on "targets of opportunity" for restoration projects.

Restore for a Changing World. Maintaining resilient and productive systems, relatively free of non-native species and harmful chemical contaminants,[34] is the best ecological insurance against ongoing large scale environmental changes and surprises. By definition, one cannot anticipate specific surprises. However, the Columbia River Basin's ecological properties will continue to change in response to an increasing variety of unanticipated perturbations. The management challenge is to shape the system so that it absorbs most ecological surprises or, if it is unable to readily absorb the perturbation, it has the capacity to reorganize quickly to a desirable state. Biophysical complexity underpins that capacity, while the energy and nutrient pathways of food webs fuel the recovery.

If we are to attain healthy food webs as targets, then the following suggestions might be considered:

- Build consideration of changing conditions and their influences on food webs into future habitat restoration projects.
- Insist that restoration proposals explain how the proposed actions will accommodate or otherwise respond to future environmental conditions, especially as these relate to food webs. This question should be incorporated in the Taurus proposal[35] form for habitat and supplementation projects.
- Develop landscape-based strategies that emphasize food web restoration in high impact areas and conservation in low impact areas. The Council should consider a targeted solicitation for proof-of-concept proposals that deal with conserving food webs in a changing environment.
- Extend management to the estuary and plume by considering effects of flow patterns on the near-ocean habitats. If we are to be effective, manage the Basin as a connected ecosystem. Continue and expand current partnerships with NOAA, state agencies, and others to accomplish connectivity.
- Coordinate restoration efforts to simultaneously meet BiOp provisions for recovery of listed stocks and estuarine restoration goals, and review restoration

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[34] The ISAB recognizes that all chemicals are not the same. There have been major improvements in the types of chemicals being used as compared to a few decades ago. Adverse affects on food webs will vary from chemical to chemical, species to species and among life stages. Much remains unknown regarding non-target affects.

[35] Taurus is an initiative led by Bonneville Power Administration (BPA) in collaboration with the Northwest Power and Conservation Council (NPCC) that provides online access to the current portfolio of projects designed to protect and rebuild fish and wildlife populations affected by federal hydropower development in the Columbia River Basin.

targets. For example, the quantity and quality of estuarine macro-detritus may be a more useful "currency" than wetland area restored *per se*.

- Continue monitoring the plume and near ocean to evaluate how changing conditions, upwelling timing and intensity, and abundances of forage fishes and predators affect food web structure and the ocean distribution and survival of juvenile salmonids.

The Case for a Comprehensive Food Web Model. It is critical to connect growth performance in freshwater, estuarine, and marine habitats. If fish have a difficult season in terms of growth during one or more freshwater habitats, can they compensate during later life stages? Throughout this report, the need for better quantitative food web and related bioenergetic models has arisen repeatedly. The need for a major modeling effort to build a "total system model" of the Basin is abundantly clear. The effort would be large and would need to be sustained, but necessary for understanding the Basin as an integrated system. It is unclear how a model can precisely represent a system as large or complex as the Columbia, but that is the size of the challenge facing habitat restoration and management. The model could be developed in parallel with the life-cycle model envisioned by NOAA (Crozier et al. 2008). The goal of the model would be to:

- Synthesize what we know about the biotic and abiotic factors, as well as processes governing food web structure and function – the foundation of the food web modeling platform.
- Challenge the structure and resilience / sensitivity of the resulting food webs, in the face of changing inputs. We envisage an effort on the pattern and scale of the COMPASS effort.
- Ground-truth (benchmark) model predictions against empiric reality for both the example cases used to construct the model and for others that it would mimic.

A Time-Prioritized Action Plan

The ISAB suggests that the Northwest Power and Conservation Council (NPCC) consider a systematic action plan addressing the priority concerns outlined above. We envision a concerted 12-year plan with an estimated *total* cost of at least $20-25 M. This estimate is given only to provide an initial sense of the scope and scale of the food web issues. The food web activities could be nested within the existing Council Fish and Wildlife Program, representing on the order of 1% of the annual budget. Some of the suggested projects fall naturally under the Monitoring section of the Program, as they involve determination of the state of the system, both in advance of intervention and for progressive monitoring as the effort unfolds. Some fall under the Habitat section of the Program, as they involve efforts at habitat manipulation and/or restoration/reclamation. Some fall under the Production section of the Program, as they may involve adjustments to which fish are reared and released, in what numbers, and where. The rest of the suggested projects fall under the Research portion of the Program, particularly those aimed at filling information gaps.

Collectively, these investigations and activities need to be well integrated with accelerating landscape-scale changes taking place within the Basin, as well as being well coordinated with complementary research and management activities by agencies and Tribes. As we know so well, this is not a trivial task. Nevertheless, a focus on food webs provides a strong complement to the ongoing emphases on hydrosystem, habitat, hatcheries and harvest (the four H's).

Table E.5.1. Summary of major knowledge gaps in understanding Columbia River food webs and proposed actions
The rationale and details for each are given in individual chapters and the appendices.

Major Knowledge Gaps	Proposed Actions
Very High Priority	
Impact of Hatchery Releases on Food Webs Massive releases of juvenile fish from hatcheries surely affect natural food webs and wild stocks of fish.[36] Better information on numbers and timings of releases, as well as on demands of juvenile fish on wild food webs is needed. Further, there is a need to determine the bioenergetic demands of hatchery releases and the energetic costs to both hatchery and wild fish. How many fish can the Basin support, relative to the magnitude of releases and ocean conditions? Gauge the density-dependent effects that can be anticipated, including where, when and who will be affected.	Determine how food webs are impacted by the release of hatchery fish as well as how the aggregate carrying capacity of the ecosystem to support wild and hatchery fish changes with alterations to water flow, temperature, non-native competitors and migration processes. Develop a sense of the magnitude of releases that the Basin system “can handle” in good and bad flow years, and under different ocean conditions. Model the consequences for hatchery and wild populations, particularly dealing with bioenergetic requirements, and the “load” on receiving ecosystems. Model alternative release scenarios (numbers of releases, locations, time of release). Assess temporal changes in food supply for juvenile salmon relative to the consumption by potential competitors. Investigate causes of density-dependent growth evident in preliminary analyses for some ongoing supplementation projects. Calculate effects on the food supply and other wild organisms using bioenergetic models, including the abundance of apex predators and their consumption of wild fishes.
Be Proactive on Non-native Species The arrival of non-native species will continue, with impacts that are not entirely predictable and potentially very damaging. There is substantial uncertainty for food webs, but accumulated experience suggests that the native biota will not be entirely beneficial. Clearly, food webs will not have a historical analogue; they will be novel, hybrid food webs.	Mount a region-wide monitoring program documenting the temporal pace and spatial extent of non-native introductions, spotting impending problems while they are still small and manageable. Intervene quickly when non-native invasive problems are likely to emerge, averting problems wherever possible, or slowing them down when not completely avoidable. Reevaluate stocking practices for non-native species, in the context of the regional concern for production and conservation of its native biota. Some policy changes may be in order. Develop a fundamental understanding of the implications of novel food webs and the characteristics that will continue to support important ecological functions.

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[36] The ISAB recognizes that fairly complete records of fish releases are maintained by the Fish Passage center, but these data are not daily release numbers by river location (zone only). Further, The RMIS program at Pacific States Marine Fisheries Commission maintains a detailed anadromous fish release database. All agencies submit daily release data by river reach to this database for all CWT fish and fish releases associated with the CWT releases.

Proliferation of Chemicals and Contaminants

The amount and diversity of artificial chemicals and nutrients in the Basin are stunning and of legitimate concern. Additionally, anadromous fish transport both beneficial nutrients and persistent industrial pollutants acquired at sea back to freshwater systems. The benefits of nutrient additions from spawning adults may be counterbalanced by deleterious effects of pollutant delivery. The net balance is unclear and needs attention.

Mount a coordinated campaign to assess the ever larger array of chemicals applied to land and water, as well as loads derived from pharmaceuticals, personal care products, and industrial manufacturing.

Actively coordinate with EPA and other agencies to quantify amounts of artificial chemicals used, measure transfers and accumulations in the food chain, and identify consequences for food web properties.

Assess the levels of both marine-derived nutrients and marine-derived pollutants in the fresh water ecosystems to which they are delivered, as well as their respective impacts. Assess costs and benefits for future management planning.

Quantifying Food Webs and Ecological Networks

Techniques for description of food web connections are continually improving, but they still do not provide accurate predictions of performance characteristics such as productivity and resilience, particularly under future conditions or alternative environmental scenarios.

Gather the requisite food web data from the Basin’s major habitat types. Integrate genomic, taxonomic, biogeochemical, bioenergetic, environmental and economic data into a single general modeling framework to promote a pragmatic understanding of the ecological networks underlying productivity.

Develop a systemwide quantitative food web model for the Basin, providing perspective on the relative impact of predation by fishes, birds, mammals and humans on fish productivity in fresh water, the estuary and plume, and the significance of competition with non-native fishes and hatchery-released salmonids. Initially this will require the creation of multiple food web models. Currently, many such models operate at annual time steps that are insufficient for capturing critical processes that occur in localized areas over very short time scales, but these processes are often the primary mechanisms regulating production and survival.

Develop modeling and network tools for separate aquatic and riparian systems, as well as joint models and networks dealing explicitly with coupled land-water systems. Use those tools as management aids for forecasting, policy evaluation and comparative analyses. Basically, are current restoration activities in the Basin “improving” food webs?

High Priority

Physical Controls on Structure and Processes

Considerable quantitative information on alterations to water regimes exists but monitoring, using quantitative information on the abundance and diversity of available foods is also needed for systemwide strategic planning purposes. In general, even though physical controls are important to a system-wide understanding, they remain poorly documented.

Augment physical monitoring and quantify relationships between physical variables and their ecological consequences. Knowledge of these relationships is rudimentary for most biota with the exception of a few vertebrate species. Add temperature and sedimentation information to that characterization.

Initiate a modeling project (such as the COMPASS effort) to translate changes in physical variables into impacts on biotic abundance, productivity and resilience, as well as the associated food webs. Use models to produce a dynamic

	physical map of the "state of the system" that shifts over time and space, predicting how the system will respond to particular perturbations in fresh water, the estuary and plume.
Base of the Food Web Information on the basal layers of the Basin's food webs, the small organisms that feed everything else, is woefully inadequate. These organisms have been hard to identify and study with traditional methods, but new technologies can remedy that. Nevertheless, systematic surveys are inadequate to provide an initial understanding of how seasonal production cycles at lower trophic levels support juvenile salmon and other fishes. We need to identify essential pathways, "strong interactions" and productivity bottlenecks to guide more intensive studies to understand specific bottlenecks of productivity.	Mount major systematic surveys of the lower (invertebrate, lower plant, microbial) layers of the aquatic and riparian food webs, using DNA barcoding and other readily available methods (Appendix A). This information is necessary to understand food webs processes in pragmatic ways. Determine how lower trophic organisms interact with fish and wildlife by identifying essential pathways, "strong interactions" and productivity bottlenecks. The few studies indicate that those connections are of prime importance, but current understanding is very limited. Determine how the base of the food web changes when abiotic conditions (temperature, flow, nutrient status) change, as this component will determine what happens in the upper layers of the food web, of primary management interest. Use emerging genetic techniques to develop (i.e., catalog) molecular signatures of all species, including protozoans and parasites. It may not be possible to identify all organisms to species with conventional taxonomy; therefore, the use of molecular signatures may be a practical approach.
Growth of Juvenile Fish Data on the seasonal consumption demand and energetic carrying capacity of major habitat types are currently lacking or inaccessible, and the information is needed for system-wide planning purposes.	Acquire data on the initial and final body masses of juvenile anadromous fish in different habitats, during rearing, overwintering and migration periods. Determine food requirements, using bioenergetic models, and compare those with available food supplies. Conduct investigations to compare the food base, growth and production of juvenile fishes utilizing restored or non-degraded vs. un-restored or degraded tributaries, as well as conduct similar comparisons for estuarine wetlands. Measure body mass of juvenile fishes over time and space (e.g., rearing, seasonal diets, overwintering, and migration periods). Sample scales and/or otoliths at key life stages to track stage-specific growth trajectories (and identify periods or processes related to size-selective mortality.
Productivity Trends A large range of habitat types and ecological conditions exist within the Basin, and production processes are highly connected in space and time. We have only a rudimentary understanding of processes that shape food web structure and determined trends in productivity.	Quantify the productivity of the Basin's food webs, doing so in terms of inherent processes underpinning them. Track food webs over extended periods to separate seasonal trends and episodic fluctuations from longer term trends. Integrate the influences of temporal and spatial variation in climate, channel morphology, rate of escapement, predator density, and local biophysical characteristics on food web

	structure and productivity – as these factors collectively translate into numbers of returning adult salmon.
	Quantify the abundance and availability of important foods in space and time. Understand the system-scale implications of hybrid food webs, especially those impacted by abundant non-natives: shad, lake trout, mysids, smallmouth bass, *Corbicula*.
Plume Dynamics The Columbia River plume supports food web characteristics that are in sharp contrast to those in other habitats. Plume food webs are exceptionally important in sustaining the fisheries.	Monitor and model interactions between river flow, temperature, and ocean conditions to assess plume behavior and its effect on food web characteristics, the productivity and predator abundances within the plume, and the relationship with smolt-to-adult survival.
Land-Water Interactions Riparian conditions impact stream loading and filtration, but information on riparian conditions and trends is still lacking at the Basin scale.	Measure the extent to which vegetative succession, litter deposition and soil processes in the Basin's floodplains are impacted by proliferation of non-native plants. The productivity of adjacent aquatic food webs appears to be reduced, due to the poor quality of the ensuing detritus.
	Determine the influence of changing patterns in forest and rangeland structure, composition and disturbance regimes on the dynamics, heterogeneity, and productivity of food webs in streams.
	Quantify extent, biotic character and the roles of large predators/herbivores and non-native plants in shaping riparian zones, and their collective consequences for mediating land-water interactions. An understanding of how these alterations affect aquatic food webs is needed for long-term sustainable management.
Up-slope and Up-stream Specific understanding of how up-slope and up-stream activities and processes affect aquatic food webs is surprisingly rudimentary. This information is vital for the control and management of nutrient loading and riparian conditions, especially in view of ongoing land use and climate changes.	Assess the sources, spatial dynamics, temporal trends and fates of energy and nutrient resources underpinning food web resilience and productivity, starting in headwater streams and lakes in forested watersheds. Consider the implications of changing patterns in forest structure, composition, pattern and disturbance regimes.
	Use linked physical, food web and bioenergetic models to evaluate tradeoffs of water level and discharge management on the characteristic food webs within, below and above storage reservoirs. Provide opportunities for refined management.
	Initiate studies to evaluate the cumulative effects of the hundreds to thousands of small reservoirs on native food webs and the impacts of hybrid food web development within them on system resilience and productivity. Though individually small, their cumulative volume and their system-wide impact are likely to be large.

Important	
Historical Baselines Reliable information on the (pre-1950) conditions of the biota and ecology are sparse for most of the Basin. Broad brush strokes are available from early commentators, but they are not sufficient to reassemble the history of constituent food webs or system productivity.	Gather accounts of the biota and physical conditions of the river, and extract as much 1800-1950 information as may exist, permitting a broad-brush-stroke historical reconstruction. Mine the literature; good information may be available from archaeological and paleoecological studies and some from published accounts of early explorers and commentators. Capture the more abundant information from the late pre- and post-hydrosystem periods to benchmark changes from hydrosystem construction. Since dams were constructed in sequence, the changes may be temporally/spatially progressive. Develop a spatiotemporal environmental (food web) reconstruction from accumulated reports, covering the last 200 years, for planning purposes. Use the information to project the changing panorama a hundred years into the future.
Apex Predators It is not clear whether apex predation rates on the region's fish resources are an issue in terms of food web dynamics and total ecosystem productivity. The net impact of apex predation should be put into an appropriate regional food web context.	Model how changes in apex predation would ripple through the system, using models to estimate system-scale consequences of increases or decreases in predation rates. Quantify abundance in space and time; use bioenergetic and community process models to estimate system-scale consequences. Further, clarify the extent to which anadromous salmonids and shad, in particular, contribute as nutrition to the food web, as well as extract nutrition from the rest of the web. Determine the impact of predation on salmonids by piscivorous fish, seabirds and mammals and whether this is additive or compensatory. Do this by comparing predation rates as a percent of the juveniles passing Bonneville or PIT tag detectors in the lower estuary with appropriate SARS for these different ESUs and run timings.

Implications for Restoration

Food webs reveal insights into basic properties underpinning productivity and resilience that cannot be obtained from an exclusive focus on the four H's. Understanding food webs demands an understanding of system-scale drivers and processes, thereby greatly improving the execution and value of restoration activities.

Restoration activities have traditionally focused on physical habitat, an approach that assumes local habitat structure and quality dictate fish production. Physical characteristics of riverine habitats, such as large wood abundance, pool geometry and distribution, riparian vegetation cover and surface flow conditions, traditionally have been thought to constrain fish production. More importantly, traditional freshwater food web illustrations have typically conveyed the notion that most fish food is produced within the local aquatic habitat itself. In reality, much of the food comes from external or very distant sources — including subsidies from marine systems borne by adult returns of anadromous fishes, from fishless headwater tributaries that transport prey to downstream fishes, and from adjacent streamside and estuarine vegetation and associated riparian and terrestrial habitats (e.g., Nakano and Murikami 2001, Naiman and Latterell 2005, Maier and Simenstad 2009, Wipfli and Baxter 2010). Key trophic pathways and food sources vary over time and space throughout watersheds. When restoration activities are not successful, it is often because they do not take a sufficiently broad view of watershed drivers (Meffe et al. 2002), including food webs and the processes that regulate food availability. It is well recognized that many fishes use an array of habitat types to complete their life cycles, and thereby encounter a diverse array of important prey resources – and this is fundamental to effective restoration.

The Council has a well-established vision of restoring and maintaining an ecosystem that sustains an abundant, productive and diverse community of fish and wildlife through the Columbia River Fish and Wildlife Program (NPCC 2009-09:6). The ISAB’s assertion here is that sustaining an "abundant, productive, and diverse community" that provides "abundant" harvest can be better achieved through a food web perspective. This idea is not new. In fact, it is being implemented in the Sacramento – San Joaquin Restoration Program (California State Water Resources Control Board 2010). Implementing a food web perspective for the Columbia River would complement other approaches, such as the hatchery program, and thereby enhance our collective ability to meet the Council’s vision.

F. APPENDICES

F.1. Appendix A. Tools for Investigating Food Webs

A.1. Use of Stable Isotopes for Assessing Food Webs

The fate of carbon (C), nitrogen (N), and sulfur (S) may be quantified through analyses of naturally-occurring stable isotopes. Over time, the biogeochemical cycling of elements has resulted in a predictable distribution of heavy and light isotopes in nature. For example, atmospheric C (CO_2) is enriched in the heavier isotope (has a higher $^{13}C/^{12}C$ ratio relative to carbon in the oceans) but marine C is also enriched relative to terrestrial organic matter in plants and soils. Marine SO_4^{2-} is enriched in the heavier isotope (^{34}S), while freshwater SO_4^{2-} is highly variable, encompassing enriched marine values and much more depleted values. The heavier isotope of nitrogen (^{15}N) is present in higher abundance in the oceans and also accumulates as trophic level increases (Schoeninger et al. 1983, Owens 1987, Peterson and Fry 1987, Fry 2008). As a result of these natural distributions and trophic accumulation, C, N and S in aquatic organisms are isotopically distinguishable from most freshwater and riparian organisms (Mathisen et al. 1988, Kline et al. 1990, Scheuerell et al. 2005). N isotopes have been the most widely used natural tracer, because N is often a limiting nutrient, so it is taken up when available. N is also more abundant in biological pools (salmon consumers, soils) than sulfur, facilitating mass spectroscopic analyses. Carbon isotopes are used to determine the importance of organisms in the diets of consumers (invertebrates, fish; Bilby et al. 1996), but are not applicable for primary producers, which derive C from the atmosphere [in deeper lentic systems, much of the ^{13}C comes from respired or detrital carbon sources, which are even more depleted in ^{13}C (Vander Zanden and Rasmussen 1999)]. Sulfur isotopes are not used widely in research, but a few studies have shown promise (e.g., Hesslein et al. 1991, MacAvoy et al. 1998).

Isotopic ratios, typically expressed as δ values, represent the parts per thousand deviation in a given sample from the international isotope standard established from atmospheric N_2, which contains 0.36630% ^{15}N. For example, a common approach is to compare $\delta^{13}C$, $\delta^{15}N$ or $\delta^{34}S$ values observed at sites with spawning salmon to those observed at comparable sites to which anadromous access is blocked (e.g., Helfield and Naiman 2001). δ values closer to those of salmon than reference site values are indicative of salmon-derived nutrients. Observed δ values may be converted to proportions of marine-derived C, N or S through use of linear 2-source mixing models (Kline et al. 1990, Bilby et al. 1996). Fortunately, there is a growing body of work on multi-source models (Phillips and Gregg 2003, Phillips et al. 2005, Moore and Semmens 2008; Maier and Simenstad, 2009) that promise to yield new ecological insights.

The use of stable isotopes to quantify food webs is predicated on the assumption that organisms possess a distinct "signature" of ^{13}C, ^{15}N, and ^{34}S. All inferences are based on differences between the fractions being examined, and subtle environmental influences such as resorption of nutrients from senescing leaves or age of the plant occasionally can result in biases (Fry 2006, 2008). In fact, isotopic fractionation associated with various biogeochemical processes alters isotopic signals and can potentially confound analyses. In freshwater ecosystems, such confounding effects are generally considered insignificant. In terrestrial ecosystems, biogeochemical processes that have high fluxes generally have slight fractionations (N mineralization, nitrification, N_2-fixation), whereas those with potentially large fractionations (ammonia volatilization, denitrification) tend to have relatively small fluxes and are generally confined to specific areas within the landscape (Delwiche and Steyn 1970, Nadelhoffer and Fry 1994). Riparian zones are among those areas within the landscape where processes with high fractionations are most likely to occur. For example, studies of riparian soils adjacent to streams suggest that, under anaerobic conditions with sufficient influx of nitrate (NO_3^-), denitrification could result in some ^{15}N enrichment (e.g., Pinay et al. 2003); however, there is no evidence to date suggesting that enrichments are significantly process-based. Nevertheless, metabolic modifications by scavengers and decomposers in transferring N from fish to riparian ecosystems may result in fractionations that, if not accounted for, can cause errors in mixing model estimates (Morris et al. 2005). Additionally, there are issues with propagation of error in mixing models (Fry 2006, 2008, Moore and Semmens 2008).

Recent technological advances have made stable isotope analyses more affordable and accessible, allowing for an increasing number of investigations using a wide range of organic matter types. This has contributed greatly to our understanding organic matter fluxes, as long as the assumptions of mixing models are acknowledged, but studies in this area are limited to elements for which naturally-occurring stable isotopes exist (e.g., C, N). This is often at the expense of other potentially important elements, for which no such isotopic tracers exist (e.g., P) or, if present, are expensive to analyze (e.g., S). As a result, comparatively few studies have examined the pathways and effects of P, Mg, or Ca in stream and riparian ecosystems. Fortunately, isotopes of Si, Ca, and Fe are starting to be used in ecological studies (Clementz et al. 2003, Varele et al. 2004, Rouxel et al. 2005), and may eventually have applications in better understanding food web structure, cycling processes and rates.

Because of variation in metabolic rates, turnover rates of stable isotopes in soft tissue such as muscle, and variability of the isotopes in food, establishing geographic-specific residence and movement patterns with this method is probably less reliable than methods involving isotopes in hard parts such as otoliths and scales. This may be because the turnover rate of the isotopes is relatively slow (e.g., annual deposition) for the organic matrices of otoliths and scales, relative to that of muscle tissue.

Otoliths conserve the isotopic signals acquired while growing. This property has been used to advantage for determining habitat associations at specific life stages, based on the isotopic composition for a suite of elements (ISAB/ISRP, 2009-1). Muscle and fin tissues provide time-integrated signatures of trophic position that reflect the prior ~ 6-12 months (or shorter periods for smaller, rapidly growing fish). More metabolically-active tissues (liver, blood) integrate isotopic signals over shorter periods (e.g., ~ 1 month for fish slime; Church et al. 2009).

However, the method may have utility for specific problems. For example, stable isotopes of carbon and nitrogen can be used to compare the movements of net-pen reared and wild rainbow trout in a reservoir. Net-pen reared fish acquire the isotopic signatures of their artificial food, which would be different than those of natural food, allowing the fish to be tracked.

A.2. A Bioenergetics Modeling Approach

Bioenergetics modeling provides a framework for identifying and quantifying how environmental or ecological factors limit growth of key species, as well as for estimating the strength of predator-prey interactions in aquatic food webs (Hansen et al. 1993; Hartman and Kitchell 2008). Bioenergetic models for fish and invertebrates incorporate functions that account for how changes in temperature, body size, and diet affect consumption and growth of the consumer through time. The Wisconsin Bioenergetics Model (Hewett and Johnson 1987, 1992; Hanson et al. 1997) is the best known and most frequently used framework (Hansen et al. 1993; Ney 1993; Chipps and Wahl 2008; Hartman and Kitchell 2008). The Wisconsin Model has been parameterized for many of the major species of fishes and at least some aquatic invertebrates (e.g., mysids) that are relevant to the Columbia River Basin (Table F.1.1). In general, such models simulate the dynamic responses of consumers to changes in body mass, thermal regime, feeding rate, and the energetic quality of prey. The actual models are energy balance equations; energy inputs from consumption (C) must equal energy losses due to metabolism (M), specific dynamic action (SDA, the metabolic cost of processing food), and waste (W). The remaining energy surplus or deficit is allocated to growth (G; either a weight gain or loss), where growth could involve somatic tissue, gonadal investment or lipid storage.

The energy balance features of these models are typically used to determine growth, given an estimated or assigned consumption rate, or to solve for consumption, given an observed or assigned growth rate. The simplest form of the energy balance equation is:

$$\text{Growth} = \text{Consumption} - \text{Waste} - \text{Metabolism} - \text{SDA} \quad [1]$$

The model contains weight-dependent functions for maximum daily consumption (C_{max}) and metabolism (basal respiration and activity), temperature-dependent functions for maximum daily consumption and metabolism, and a temperature- and ration-dependent function for waste. SDA is treated as a constant proportion of consumption. The model operates on a daily time step, thus enabling simulations to account for changing body size, temperature, diet composition, and energy content of both consumer and prey at fine temporal scales. When applied to species in the environment, field sampling can provide input data for growth, diet composition (including changes through time and size of consumers), and thermal regime. Based on these input data, model simulations can estimate the feeding rate (g/d) required to achieve the observed growth rate, based on the diet composition and thermal experience during the simulated time interval.

Thermal experience of the consumer can be estimated by coupling their temporal-spatial distribution patterns with the corresponding thermal environment. In homogeneous thermal environments, such as specific river reaches or continuously mixed lakes, ponds and epipelagic marine waters, the thermal experience of the consumer can be determined simply by using mean temperatures recorded at daily or longer intervals by temperature loggers. In thermally heterogeneous environments, the spatial-temporal distribution of the consumers must be combined with the corresponding thermal environments. For example, in stratified lakes where consumers undergo diel vertical migrations,

Table F.1.1. A list of bioenergetics models parameterized for species (or closely related species) in the Columbia River Basin that are available in the Wisconsin bioenergetics model.

Species	**Source**
Chinook salmon	Stewart & Ibarra 1991
Coho salmon	Stewart & Ibarra 1991
Sockeye/kokanee salmon	Beauchamp et al. 1989
Steelhead/rainbow	Rand et al. 1993
Cutthroat trout	Beauchamp et al. 1995
Lake trout	Stewart et al. 1983
Bull trout	(under development, M. Mesa & D. Beauchamp, USGS)
Brook trout	Hartman and Cox 2008
Generalized coregonids	Rudstam et al. 1994
Lake whitefish	Madenjian et al. 2006
Northern pikeminnow	Petersen & Ward 1999
Walleye	Kitchell et al. 1977
Smallmouth bass	Shuter & Post 1990, Whitledge et al. 2003
Largemouth bass	Rice et al. 1983
Burbot	Rudstam et al. 1995, Paakkonen et al. 2003
Northern pike	Bevelhimer et al. 1985
Yellow perch	Kitchell et al. 1977
Clupeids (shad, herring)	Stewart & Binkowski 1986, Rudstam et al. 1994
Smelt	Lantry et al. 1993
Bluegill	Kitchell et al. 1974
Cyprinids	Duffy 1998
Invertebrates	
Mysis relicta	Rudstam 1989, Chipps & Bennett 2002

time- and depth-averaged seasonal and diel distribution patterns can be combined with temporal thermal profile data to estimate thermal experience.

The inputs for diet composition can be obtained from either direct diet analysis, or inferred from more integrative measures of feeding behavior such as stable isotope analysis (Vander Zanden and Rasmussen 1999; Post 2002; McIntyre et al. 2006) or fatty acid analysis (more common for birds and mammals; Budge et al. 2006). However, in complex food webs, the more integrative measures may not discriminate among prey species within similar feeding guilds. Consumption is reported as both a proportion of C_{max} (P-value) and as the daily mass of each prey eaten. Diet analysis provides the most directly relevant inputs for bioenergetics modeling. The inputs are computed as the proportional wet weight contribution of each prey type to the total diet, stratified by ecologically-significant time interval (e.g., month or season), size class of consumer, habitat. Since stomach contents only reflect what was eaten over the previous 12-24 h, diet analysis can sometimes miss evidence of important but elusive processes like piscivory (Beauchamp et al. 2007). The more temporally-integrative measures, stable isotopes and fatty acid analysis, provide a complementary examination of feeding patterns by ensuring that important trophic links were not overlooked by diet analysis. For example, stable isotope data are especially useful for identifying the size at which a species becomes piscivorous, and whether prey are derived primarily from benthic or pelagic sources (Figure F.1.1). Prey energy density inputs can be obtained from literature values (e.g., Parrish et al. 2006; Ciancio et al. 2007; McCarthy et al. 2009) or measured directly using bomb calorimetry.

Diagnosing Which Factors Affect Growth. Important insights regarding growth potential and constraints can be gained by placing basic physiological relationships for body mass, temperature, feeding rate and energetic quality of food within the context of environmental variability and the ontogeny of consumers. Both C_{max} and metabolic rates (rates standardized as % body weight) decline with increasing body mass, whereas waste is a relatively constant fraction of consumption. As consumers grow, C_{max} declines faster than the combined loss rates from metabolism and waste (Figure F.1.2). Consequently, smaller fish can utilize a larger percentage of their energy budget for growth or activity than larger fish. For example, a 1-g sockeye salmon or kokanee, feeding at C_{max} on a diet of zooplankton or aquatic insects (containing an average energy density of 2800 J/g), could allocate 47% of the ingested energy to growth. A 1,000 g sockeye, however, feeding at C_{max} on the same diet, could only allocate 33% to growth.

Temperature affects consumption much differently than it does metabolism, creating nonlinear growth responses to temperature (Figure F.1.3). The temperature-dependence of C_{max} is a dome-shaped curve, whereas metabolic costs increase exponentially with temperature. Since waste (W) is a relatively constant fraction of consumption, the curve for C_{max}-Waste is mirrored below the C_{max} curve, and the remaining energy available for growth is represented by the distance between the Waste and the Respiration + SDA curves (Figure F.1.3a). When extracting just the growth component and plotting for different sizes of consumers (Figure F.1.3b), the combined effects of temperature and body size allometry translate into optimal daily growth rates that are higher for smaller fish (e.g., 7.2% body mass per day for 1-g fish, versus 1.5% per day for 100-g fish), and the optimal temperature for growth shifts to cooler temperatures for larger fish (e.g., 14^{o}C at 1 g, versus 13.0^{o}C at 100 g; Figure F.1.3b).

Estimating Feeding Rate and Consumption Demand. A second and more common application of bioenergetics models is used to estimate prey consumption (Beauchamp et al. 2007). The model uses the same functions as described above for estimating growth, but in this case, the model is used to estimate how much consumption was required to satisfy the growth of consumers observed over some specified time interval (annual, seasonal, monthly), given the temporal changes in diet and thermal experience of the consumer. Consumption over the simulation interval is fit to an initial and final body mass for each age- or size-class of consumer (Hanson et al. 1997). In practice, the initial and final body masses are estimated from either: 1) mark-recapture studies, 2) tracking age-size modes in length frequency histograms, obtained seasonally or annually, 3) back-calculation of size-at-age from scale pattern analysis, or 4) from von Bertallanfy growth curves fit to the consumer population (e.g., Ruzycki et al. 2003). The model produces estimates of daily consumption on each prey (g/d), the average feeding rate (termed *p*-value, or %C_{max}) needed to fit growth to the final observed weight over the simulation period, and the resulting simulated daily growth trajectory of the consumer.

By estimating temporal consumption rates, the model can be used to: 1) quantify daily, seasonal or annual biomass of different prey consumed by different size classes and species of predators; 2) determine the importance of different prey to the seasonal, annual, or lifetime energy budgets of consumers; and 3) estimate the average daily feeding rate, as a proportion of the consumer's physiological maximum feeding rate, which can potentially indicate the supply or accessibility of food.

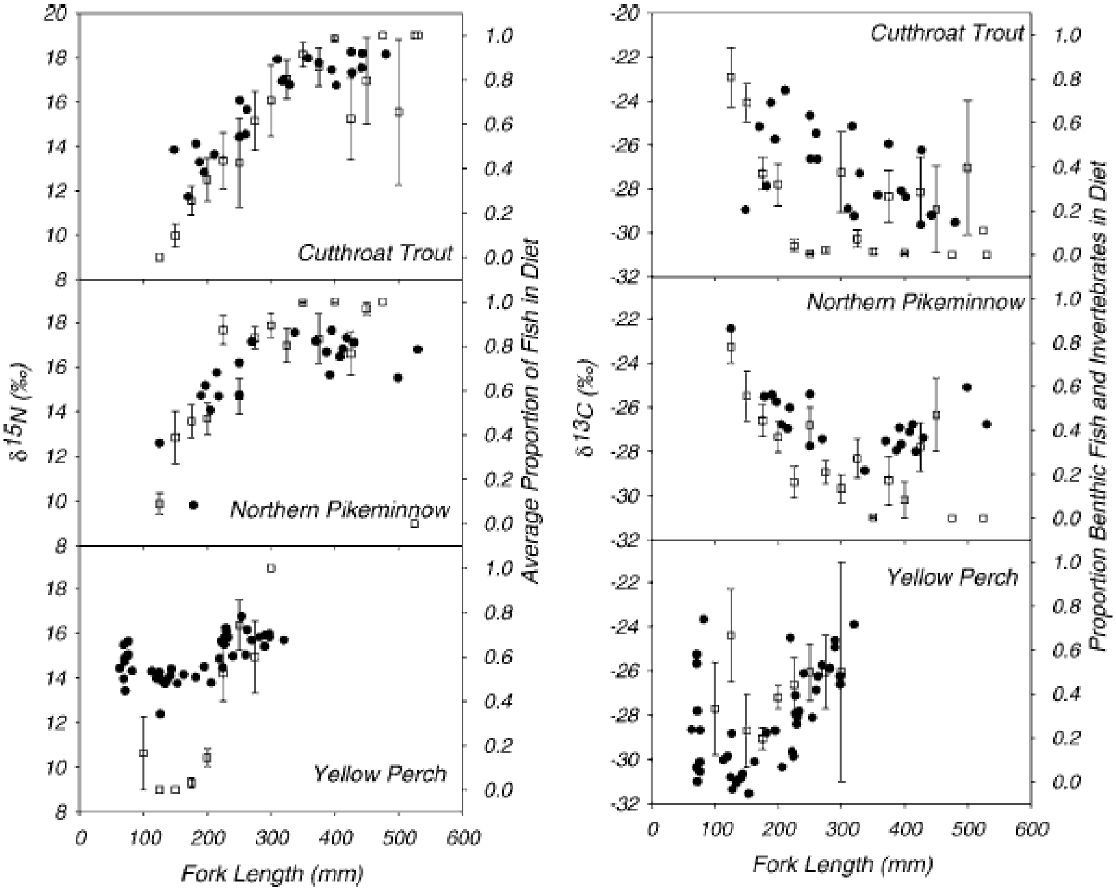

Figure F.1.1. Stable isotope analyses showing the ontogenetic change in trophic interactions by cutthroat trout, northern pikeminnow, and yellow perch in Lake Washington. Both trout and pikeminnow exhibit rapid increases in the degree of piscivory, as indicated by the rise in δ^{15}N over fork lengths of 200-300 mm (left top two panels), and a coincident trend toward increasing reliance on pelagic prey, as indicated by the decline in δ^{13}C (right top two panels). These patterns suggested that both species fed initially on benthic invertebrates, and then shifted to fish prey at larger sizes. Cutthroat trout fed more intensively on pelagic forage fishes (juvenile salmon, smelt and stickleback), whereas pikeminnow fed on a mix of these pelagic fishes and benthic fishes (e.g., sculpin). In contrast, yellow perch showed a more subdued increase in δ^{15}N, but the coincident increase in benthically-derived prey suggests that most perch fed initially on zooplankton before shifting to a more omnivorous trophic position of feeding on a mix of benthic invertebrates and fish (e.g., sculpin). Figure from McIntyre et al. (2006).

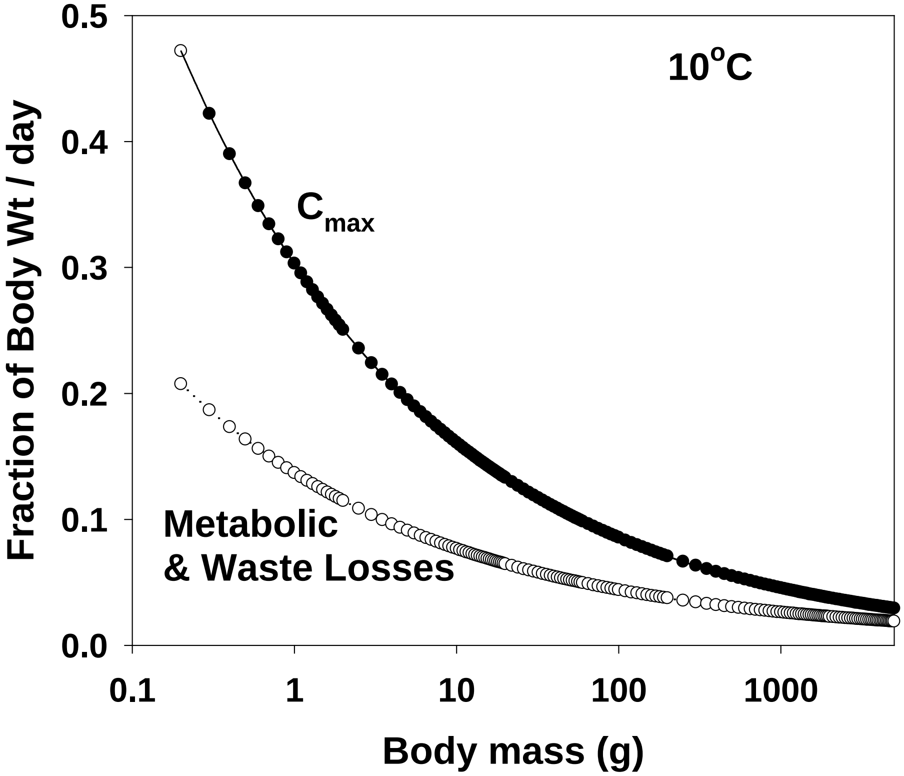

Figure F.1.2. Allometric relationship of body mass to maximum daily consumption Cmax and metabolic and waste losses for sockeye salmon at 10°C. Because the slope of the C_{max} curve declines more rapidly, metabolic and waste losses represent a larger percentage of the energy budget as fish grow (e.g., 53% at 1 g but 67% at 1,000 g). Consequently, smaller fish have a larger potential scope for growth and activity when food is unlimited.

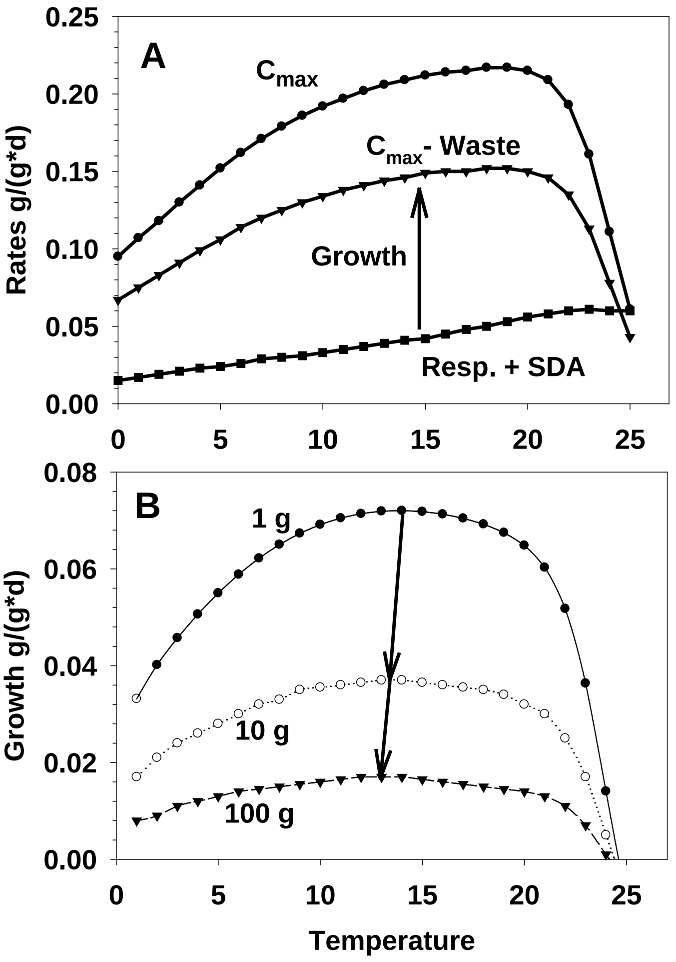

Figure F.1.3. Temperature-dependent relationships: (A) Cmax, Cmax-Waste, and metabolism (respiration + SDA) in terms of g food per g body mass per day. The space between C_{max}-Waste and Respiration + SDA represents the growth potential for a 10-g sockeye salmon, feeding at C_{max} at any temperature; (B) daily growth potential (g growth per g body mass per day) for 1-, 10-, & 100-g consumers at C_{max} & 2800 J/g prey energy density. Arrows indicate optimal growth temperatures for consumers with different body masses.

F.2. Appendix B. The Legal and Policy Foundations for Fish and Wildlife Program Projects and Management Actions that Specifically Address Food Webs

The Legal and Policy Web

Treaties, laws,[37] regulations, policies, plans, and court decisions concerning Columbia River Basin fish and wildlife create a complex web of communications, litigation, and management actions (GAO 2004). This legal/policy web is intricately linked to (or tangled with) the biological food web and helps define what actions can be taken to manage food webs.

The ISAB's Partners

The laws directing the entities that the ISAB serves offer an illustrative, albeit not exhaustive, example of this complex legal/policy web. The interests of NOAA Fisheries relate particularly to anadromous fish conservation and management, while those of the Northwest Power and Conservation Council and the Columbia River Indian Tribes include all fish and wildlife populations affected by operation and development of the Columbia River Basin hydroelectric system. More specifically, NOAA Fisheries is responsible for federal stewardship of the Nation's marine and anadromous fish, and marine mammals. The Council is charged to "protect, mitigate and enhance" fish (anadromous and resident) and wildlife affected by operation and development of the hydroelectric system.[38] The Tribes manage fish and wildlife resources on their respective reservations, are co-managers on ceded lands, and are responsible for ensuring treaty provisions governing natural resources are secured for future generations. These directives charge NOAA Fisheries, the Council, and Tribes with not only restoring and protecting fish and wildlife that interact in complex food webs, preying on each other, but also with providing harvest opportunities for people.

The Endangered Species Act and the Federal Columbia River Power System

Of particular relevance to the Columbia River Basin and the hydroelectric system, the federal Endangered Species Act (ESA[39]) provides for the conservation and recovery of species of plants and animals that NOAA Fisheries or the U.S. Fish and Wildlife Service determines to be in danger of or threatened to become in danger of extinction. Specifically, the ESA restricts the "taking"[40] of endangered species through direct harvest as well as by protecting species' critical habitats[41] which include food webs essential to the conservation of the species.

Many species of fish and wildlife inhabit, migrate through, or use the Columbia River Basin, some of which are listed as threatened or endangered. Thirteen anadromous salmonid runs in the Basin are listed including Chinook, steelhead, sockeye, coho, and chum originating from the headwaters in the Snake River to the lower Columbia near the estuary (Figure F.2.1). ESA-listed Steller sea lions use the lower Columbia for feeding – their diet includes endangered adult salmon and steelhead. Sea lions are also protected by the Marine Mammal Protection Act.[42] Brown pelicans are currently listed but will likely be de-listed. Like the sea lions, the pelicans also feed on salmon, and the pelicans' protection goes beyond the ESA and includes protection under the Migratory Bird Treaty Act.[43] Other ESA-listed species in the Basin include bull trout, white sturgeon, Columbia River smelt (eulachon) and pygmy rabbits, among others.

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[37] See Bonneville Power Administration's legal framework

[38] Pacific Northwest Electric Power Planning and Conservation Act (Northwest Power Act). 16 U.S.C. §§ 839-839h

[39] Endangered Species Act. 16 U.S.C. §§ 1531-1544

[40] ESA §3(19) defines "take" as "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct."

[41] ESA §3(5) defines "critical habitat" for a threatened or endangered species as: "(i) the specific areas within the geographical area occupied by the species, at the time it is listed…on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species at the time it is listed…upon a determination by the Secretary that such areas are essential for the conservation of the species."

[42] Marine Mammal Protection Act. 16 U.S.C. §§ 1361-1421h

[43] Migratory Bird Treaty Act. 16 U.S.C. §§ 703-712

Figure F.2.1. Map of the Columbia River Basin Showing Action Areas, Dams, and Listed Species.
The Columbia River and its tributaries form the dominant water system in the Pacific Northwest and are a heavily used regional resource. From: Federal Columbia River Power System 2008 Progress Report.

These listing have both a regulatory and management effect. ESA regulations restrict the take and harassment of listed species through direct harvest and habitat degradation. Regulations cover federal permitting, funding, project operation, and land management and thus affect operations of all the Columbia River hydrosystem dams and any development project that is on federal land, receives federal funds, requires a federal permit, or is implemented by a federal agency. The management effect is that operations of federal projects and federally funded habitat restoration and protection actions to benefit listed species are designed, prioritized, and driven by ESA mandated biological opinions and guided by recovery plans. Thus, when considering potential food web management approaches, conserving listed species is a federal priority, and food web links should be evaluated in terms of supporting listed species.

Under the ESA, the federal action agencies operating the Federal Columbia River Power System (Bonneville Power Administration, Bureau of Reclamation, and the U.S. Army Corps of Engineers) must develop operational plans that do not jeopardize listed species or adversely impact those species' critical habitat. NOAA Fisheries and the U.S. Fish and Wildlife Service have developed various biological opinions that review the sufficiency of these operational plans for listed salmon, steelhead, bull trout, and Kootenai white sturgeon. For the power system 2008 Biological Opinion,[44] the action agencies determined that without further mitigation, the operations of the power system would jeopardize listed species. Consequently, the action agencies presented NOAA Fisheries with a set of additional measures designed to benefit the listed species. NOAA included these actions and added its own, for a total of 73 actions, to reach a no jeopardy decision on power

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[44] 2008 FCRPS Biological Opinion

system operations. In ESA terminology, these actions constitute the Reasonable and Prudent Alternative (RPA).

The bulk of these actions are habitat focused, directed at offsite mitigation to improve habitat attributes related to spawning, rearing, and migrating conditions for juvenile salmon and steelhead. Although these habitat actions are not described as specifically addressing food webs, these actions do have the potential to affect and improve food sources for salmon and steelhead. In addition to these habitat actions are several actions directed specifically at food web management. Most explicit are actions to control predation, including the northern pikeminnow management program (RPA 43); non-native fish management program development (RPA 44); avian predation management primarily directed at Caspian terns and double-crested cormorants through habitat modification and colony relocation efforts (RPAs 45-48); and marine mammal control actions (RPA 49). Research, monitoring and evaluation are also included for predation management (RPAs 66-70). In the RPA, certain habitat actions such as piling removal in the estuary (RPA 38) are also designed to reduce avian predation. Interestingly, actions are not included that specifically use the term "food web," and primary and secondary production is raised in the research and monitoring actions (e.g., RPA 59) but not specifically under other strategies. Hydro, hatchery, and harvest actions that significantly impact food webs are also included.

The legal sufficiency of the 2008 Federal Columbia River Power System Biological Opinion, like its 2004, 2000, 1995 and earlier predecessors, is being challenged in the U.S. District Court of Oregon. The litigation surrounding these biological opinions has been extensive and complicated. One of the recent outcomes of the litigation is supplemental plans, analyses, and actions have been developed to augment the 2008 Biological Opinion. These supplemental materials include food web related analysis and actions.

Of note, the September 2009 Adaptive Management Implementation Plan (AMIP) for the 2008 Biological Opinion enhances the focus on predation and specifies that shad need to be evaluated in terms of their role in feeding salmon predators, especially northern pikeminnow. The AMIP also raises the option of excluding shad from upper mainstem dams, which is feasible with modifications to adult fish ladders. In addition, the AMIP calls for enhanced life-cycle monitoring, including examination of hatchery and wild fish interactions, density-dependence effects, and potential hatchery release timing strategies. The AMIP also anticipates using a food web or bioenergetics model to evaluate the impact of inter-species interactions.

On May 10, 2010, NOAA Fisheries augmented the 2008 BiOp and the AMIP with the Endangered Species Act Section 7(a)(2) Consultation Supplemental Biological Opinion. In March 2010, the ISAB provided NOAA Fisheries with the references it had collected to draft the Food Web Report. The Supplemental BiOp includes a consideration of these references, and food web issues are prominent in several areas. Specifically, the section on Predation and Other Ecological Actions discusses the impact and management of marine mammals, avian predators, northern pikeminnow, and non-native predators. Some of this work is responsive to the ISAB's Non-Native Species Impact Report (ISAB 2008-4) recommendation to look at opportunities to reduce predation and competition by non-native game fishes through relaxing state harvest regulation that may be enhancing or protecting those non-native game fishes. In addition, the Supplemental BiOp describes an RPA to develop an enhanced life-cycle model that will evaluate "a variety of factors including interactions between salmonids and both native and invasive species that are predators, prey, competitors, etc. If sufficient data exist, potential effects will be evaluated through food web or bioenergetics models."

In addition to the biological opinion for the power system, NOAA issues biological opinions for harvest plans and hatcheries, develops habitat conservation plans (such as for the Mid-Columbia Public Utility Districts' dams) and creates recovery plans. Three biological opinions – the FCRPS, Upper Snake, and United States v. Oregon management plan biological opinions – are analyzed together in one comprehensive, combined jeopardy analysis. Other biological opinions and the recovery plans are coordinated, but combined, they add to the complexity of managing the Basin's salmonid populations and the food webs that support them.

Treaties and Agreements of the Columbia River Indian Tribes

Columbia River Basin fish and wildlife management is inextricably linked to the treaties, agreements, and legal agreements between the United States government and the fifteen federally recognized tribes of the Basin.[45] Five tribes signed treaties in 1855 including the Nez Perce Tribe, the Confederated Tribes of the Umatilla Indian Reservation, the Confederated Tribes of the Warm Springs Reservation of Oregon, the Confederated Tribes and Bands of the Yakama Indian Nation, and Confederated Salish and Kootenai Tribes of the Flathead Reservation, Montana. In these treaties the tribes reserved exclusive rights to harvest fish in streams running through and bordering their respective reservations and also reserved the right to continue to take fish at all other usual and accustomed stations (even if off the reserved lands), in common with United States' citizens. The tribes also reserved the right of hunting, gathering roots, and pasturing stock in unclaimed lands in common with citizens. The Shoshone-Bannock Tribes of the Fort Hall Reservation of Idaho signed a treaty in 1868 which granted the tribes the right to hunt on the unoccupied land of the United States so long as game may be found.[46]

Most of the other tribes in the Basin live within their historic territories on lands recognized as theirs through a variety of other legal mechanisms, including nineteenth century executive orders and twentieth century federal acknowledgments, and all manage or have an interest in particular fish and wildlife resources. For example, the Kootenai Tribe of Idaho has a reservation established in 1894, which consists of allotments on the public domain, but does not have a treaty or executive order establishing tribal lands.

Over the past century, a progression of litigation further defined rights under treaties and agreements including those of certain Columbia River Indian tribes. In the early part of the twentieth century, a set of cases defined access to usual and accustomed sites for fishing and hunting.[47] A second series of cases in the late 1960s and early 1970s recognized the rights of certain Indian Tribes to a treaty-based equal share of the opportunity to harvest salmon and steelhead.[48] Recently, the District Court of Washington further concluded that the treaty-reserved fishing rights also impose a duty on the State of Washington to refrain from building or maintaining road culverts that hinder fish passage and thereby diminish the number of fish returning to usual and accustomed fishing stations.[49] The extent to which the treaty rights impose additional obligations to protect and restore habitat is an open question.

These treaties and court cases firmly establish the tribes' rights and position in the food web as both a consumer and a protector, which reflects a key foundation of tribal culture. This relationship is described on the Columbia River Inter-Tribal Fish Commission (CRITFC) website:

> The people of these tribes have always shared a common understanding—that their very existence depends on the respectful enjoyment of the Columbia River Basin's vast land and water resources. Indeed, their very souls and spirits were and are inextricably tied to the

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[45] The Confederated Tribes of the Warm Springs Indian Reservation, Confederated Tribes and Bands of the Yakama Nation, Confederated Tribes of the Umatilla Indian Reservation, Nez Perce Tribe, Shoshone Bannock Tribes of the Fort Hall Reservation, Shoshone-Paiute Tribes of the Duck Valley Reservation, Burns Paiute Tribe, Confederated Salish and Kootenai Tribes of the Flathead Reservation, Confederated Tribes of the Colville Reservation, Spokane Tribe of Indians, Coeur d'Alene Tribe, Kootenai Tribe of Idaho, Kalispel Tribe of Indians, Confederated Tribes of the Grande Ronde Community of Oregon, and Cowlitz Indian Tribe.

[46] For more information on United States and Columbia River Basin Indian tribes' treaties and agreements see Institute for the Development of Indian Law 1974, GAO 2004, and Northwest Power and Conservation Council 2007. Also see the section "The Legal Context: Rights, Trust Responsibilities and Trust Resources" in Wy-Kan-Ush-Mi Wa-Kish-Wit, Spirit of the Salmon: The Columbia River Anadromous Fish Plan of the Nez Perce, Umatilla, Warm Springs, and Yakama Tribes (CRITFC 1996).

[47] See U.S. v. Winans. 198 U.S. 371 (1905)

[48] See Washington v. Washington State Commercial Passenger Fishing Vessel Ass'n, 443 U. S. 658 (1979) and Sohappy v. Smith. 302 F. Supp. 899 (D. Or. 1969) and United States v. Washington. 384 F. Supp. 312 (W.D. Wash. 1974). The federal courts retain continuing jurisdiction over salmon and steelhead harvest in the Columbia and Puget Sound, U.S. v. Oregon… and U.S. v. Washington… A long-term Columbia River Fish Management Plan executed by these tribes, the states of Oregon, Washington and Idaho, and the federal government under the umbrella of U.S. v. Oregon (and analyzed for ESA consistency) includes both harvest and production agreements.

[49] U.S. v. Washington, No. 9213, Subproceeding 01-1, USDC, WD Wash, Order of August 22, 2007, Docket No. 388. This case is known as the "Culverts" case.

> natural world and its myriad inhabitants. Among those inhabitants, none were more important than the teeming millions of anadromous fish enriching the basin's rivers and streams…Today, perhaps even more than in the past, the Columbia River treaty tribes are brought together by the struggle to save the salmon and by shared spiritual traditions such as the first salmon feast.

Among the Tribes' many efforts and approaches to restore fish and wildlife populations is Wy-Kan-Ush-Mi Wa-Kish-Wit, Spirit of the Salmon: The Columbia River Anadromous Fish Plan of the Nez Perce, Umatilla, Warm Springs, and Yakama Tribes. The Plan recognizes the role of food supply in tributary and estuarine habitats for salmonid production including the role of recovering vegetation to support a trophic base and the threat of pollutants to reduce food availability. The Plan also describes food web relations of species such as the importance of lamprey as a food source for sturgeon in the mainstem.

In 2008 the Confederated Tribes of the Umatilla Indian Reservation (CTUIR), the Confederated Tribes of the Warm Springs Reservation (CTWSRO), the Confederated Tribes and Bands of the Yakama Nation (YN), the Columbia River Inter-Tribal Fish Commission (CRITFC), Confederated Tribes of the Colville Reservation, and the Shoshone-Bannock Tribe have also entered into agreements known as the Columbia River Fish Accords with the federal action agencies. These Accords include commitments to implement a set of projects and actions intended to benefit the region's fish and wildlife. These projects are implemented through the Columbia River Fish and Wildlife Program, which is described below. A number of these projects are directed at food web issues including nutrient enhancement and sea lion predation of salmon, sturgeon, and lamprey. At the same time these Accords were being made, some of these tribes, the federal government, and the states of Idaho, Oregon, and Washington entered into a 2008-2017 Management Agreement under U.S. v. Oregon.

In addition, hatchery production, including some non-native species, is a major tribal strategy to mitigate for decreases in or complete loss of salmon production due to construction and operation of the hydrosystem. As described in this Food Web Report, this production represents a significant input into the Basin's food webs.

Columbia River Basin Fish and Wildlife Program

The Program

As stated above, the Northwest Power Act directs the Council to develop a fish and wildlife program to "protect, mitigate and enhance" fish (anadromous and resident) and wildlife affected by operation and development of the hydroelectric system. In addition, the Council's Columbia River Basin Fish and Wildlife Program, last amended in 2009, is intended to bring together, as closely as possible, Endangered Species Act (ESA) requirements and the policies of the states and Indian tribes into a comprehensive Program based on a solid scientific foundation. Specifically, the Program has built a large mitigation program combining mainstem and off-site mitigation planning and actions. Based on that foundation and approach, the action agencies and NOAA (and the Accords) further emphasized and expanded this mitigation approach, which is in turn recognized in the Program and implemented under the Northwest Power Act and other existing authorities.

Essential to the Program's foundation are eight scientific principles. All actions implemented under the Program must be consistent with these principles. Food web considerations are embedded in each of the principles, especially Principle 5 "Species play key roles in developing and maintaining ecological conditions" and Principle 6 "Biological diversity allows ecosystems to persist in the face of environmental variation." Principle 6 includes the statement, "Maintaining the ability of the ecosystem to express its own species composition and diversity allows the system to remain productive in the face of environmental variation." This statement is tempered with, "It is not simply that more diversity is always good; introduction of non-native species, for example, can increase diversity but disrupt ecological structure." In sum, the Program's Principles anticipate the role of food webs as integral components in forming and defining ecosystems.

In addition to this foundational consideration, food webs are covered in specific sections of the Program. Generally, the Program recognizes the link between habitat restoration and food availability. For example, in the Program's Mainstem Habitat section, actions are called for that create littoral habitat and fish structures on the shores of Lake Roosevelt to diversify food sources and increase rearing habitat. Although the Program's focus is on habitat restoration actions that affect and have the potential to improve food sources for salmon, steelhead, and other species, the Habitat Strategies section only implies the importance of food webs by describing the historical importance of the mainstem in providing feeding habitat and by emphasizing the restoration of ecosystems.

The more explicit coverage of food web issues in the Program is similar to the FCRPS Biological Opinion's areas of focus: predation and non-native species interactions. In the Non-Native Species Strategies section, the Program specifically acknowledges that non-native species invasions can imperil native species through food web disruption. The Mainstem section includes a subsection on the control of predators, specifically piscivores (e.g., northern pikeminnow, small mouth bass, channel catfish, and walleye), birds (e.g., double-crested cormorants and Caspian terns), and pinnipeds (sea lions). The northern pikeminnow bounty reward program is recommended for continuation. Avian management plans are called for, and the Corps is asked to take action to exclude sea lions from the main adult fish ladder entrances at Bonneville Dam. Legal, lethal take of pinnipeds is acknowledged as appropriate if non-lethal means are not successful and adverse impacts on salmonids are significant.

Among the emerging issues identified in the Program, toxic contaminants are described as a threat and suggested actions include long-term monitoring, investigation of how toxics are taken up by different species, and efforts to reduce toxics.

Subbasin Plans

The Subbasin Plans, adopted into the Program in 2005, identify priority restoration and protection strategies for habitat and fish and wildlife populations in the United States portion of the Columbia River Basin. Specifically, the plans guide implementation of the off-site mitigation elements of the Council's Columbia River Basin Fish and Wildlife Program. These Subbasin Plans cover almost all of the 62 subbasins demarcated in the Basin, including the estuary and certain mainstem reaches. A database of limiting factors, also referred to as habitat concerns, identified in the Subbasin Plans includes "food" as a standard limiting factor. A survey of this database indicates that most Subbasin Plans identify "food" as a limiting factor and several common themes emerge. The most common theme is competition for food among focal, native species (those targeted for enhancement) and non-native species. For example, many plans for headwater tributaries describe brook trout competition (and hybridization) with native bull trout. Similarly, the issue of hatchery fish competing with wild juvenile fish for food is raised in many plans.

Another common theme is dams and other barriers have altered primary productivity by blocking nutrient transport, particularly carbon transport and nutrients from salmon carcasses. In general, plans identify that marine derived nutrients are low, but some plans also cite nutrient loading from storm water, feedlots, and agriculture as limiting fish populations. Each subbasin has a unique description of nutrient alteration. Non-native plants and animals are also identified as impacting food webs.

The Columbia River Basin Research Plan

As called for in the Council's 2000 Fish and Wildlife Program, in 2006, the Council completed a Columbia River Basin Research Plan to guide its research program development and foster collaboration with research programs of other resource management entities in the region (NPCC 2006-3). The research plan recognizes the effects of river operations and shoreline modifications (rip-rap, erosion, and such) on food production in littoral habitats.

Under the section on Mainstem and Tributary habitats, the plan notes that "little is known about the food webs in the Columbia Basin, especially in the tributaries (e.g., how have they been altered by land and water use, by the introduction of toxics and of non-native plants and animals, by harvesting, and by climate change). Scientific understanding of the role of nutrients in the growth of juvenile salmon in freshwater and estuarine conditions is also incomplete, but fewer adult salmon returning to spawn in many streams has resulted in decreased import and transport of nutrients such as nitrogen and phosphorus." However, the critical uncertainties following that passage are more general and do not emphasize food web interactions as a critical uncertainty.

The Estuary section of the plan describes changes in biological processes that have altered the food web. The Ocean section states that "there is increasing evidence that ocean fisheries on groundfish (Pacific whiting, pollock, halibut and others) and coastal pelagic species (squid, sardines, anchovies, and others) may affect salmonids through food web interactions." And a critical uncertainty in the ocean section is "4. What are the effects of commercial and sport fishing on ocean food webs?"

The Harvest section recognizes the role of returning adults' contribution to tributary watersheds, and a critical uncertainty includes "4. How can the multiple ecological benefits that salmon provide to the watersheds where they spawn (e.g., provision of a food resource for wildlife and a nutrient source for streams and riparian areas) be incorporated effectively into procedures for establishing escapement goals?"

Consistent with the Program and the Subbasin Plans, invasive species role as predators and competitors in altering food webs and other habitat conditions is described. In terms of critical uncertainties, food web interactions are not specifically mentioned but are implied in questions such as "2. To what extent do (or will) invasive and nonnative species significantly affect the potential recovery of native fish and wildlife species in the Columbia River Basin?"

Collectively, the Program, Subbasin Plans, and the Research Plan provide and describe an ecological framework that food webs are an integral part of. Subbasin plans expressly identify food resources, competition, and predation as limiting factors. The Research Plan indicates research is needed regarding the impact on species' viability from food web alterations caused by non-native species and human actions such as river operations and harvest. However, the role of food webs is often implied as a component of habitat conditions and is not specifically described or emphasized for specific actions or research.

Despite the need for more specific actions and language regarding food webs, the Program has provided a framework and guidance that has resulted in funding and implementing numerous predation control projects, habitat restoration efforts, nutrient supplementation projects, species interactions studies, and fundamental food web research.

F.3. Appendix C. Pesticides Used in the Columbia River Basin

The following data are from the U.S. Geological Survey, National Water-Quality Assessment Program (NAWQA), National Synthesis Project. To better understand the affects pesticides could have on drinking water and aquatic resources the NAWQA National Synthesis Project performed a national assessment of pesticide use. Listed here are the average annual amount of 182 pesticides (active ingredients only in kilograms) used in agriculture in the Columbia River Basin from 1999-2004. Pesticides have been ranked according to their use in the Basin (the highest use ranked Number 1). An additional 64 pesticides were reported at zero kilograms use; hence, no apparent use in the Basin.

Rank	Pesticide Name	KG_Code	Annual Use (kg)
3	1,3-D	KG8008	5,152,885
6	2,4-D	KG1302	969,457
63	2,4-DB	KG1308	20,619
164	ABAMECTIN	KG6001	559
73	ACEPHATE	KG6002	14,166
105	ACETAMIPRID	KG6	5,456
68	ACETOCHLOR	KG3000	17,821
	ACIFLUORFEN	KG1002	0
38	ALACHLOR	KG1863	69,046
15	ALDICARB	KG6003	167,568
	AMETRYN	KG1982	0
152	AMITRAZ	KG6091	1,017
	ASULAM	KG9048	0
29	ATRAZINE	KG1980	99,945
168	AZADIRACHTIN	KG2001	172
17	AZINPHOS-METHYL	KG6004	154,286
75	AZOXYSTROBIN	KG2002	13,200
88	BENEFIN	KG1362	9,809
95	BENOMYL	KG5001	7,694
	BENSULFURON	KG7009	0
	BENSULIDE	KG1098	0
72	BENTAZON	KG1287	14,358
159	BENZYLADENINE	KG2003	703
90	BIFENAZATE	KG25	9,637
150	BIFENTHRIN	KG6063	1,092
	BISPYRIBAC	KG9100	0
	BROMACIL	KG1809	0
21	BROMOXYNIL	KG1116	120,014
	BUPROFEZIN	KG2004	0
155	BUTENOIC ACID	KG2005	876
	BUTRALIN	KG33	0
	CACODYLIC ACID	KG8017	0
65	CAPTAN	KG5014	19,823

18	CARBARYL	KG6006	151,793
25	CARBOFURAN	KG6007	104,861
160	CARFENTRAZONE	KG9101	690
	CHLORETHOXYFOS	KG2006	0
	CHLORIMURON	KG4008	0
37	CHLOROPICRIN	KG8000	69,670
12	CHLOROTHALONIL	KG5007	244,188
13	CHLORPYRIFOS	KG6009	235,920
140	CHLORSULFURON	KG1913	1,577
104	CLETHODIM	KG7010	5,782
172	CLODINAFOP	KG9102	114
147	CLOFENTEZINE	KG7204	1,304
177	CLOMAZONE	KG9001	36
81	CLOPYRALID	KG4002	11,412
	CLORANSULAM	KG9103	0
14	COPPER	KG5011	179,135
179	CRYOLITE	KG6010	22
	CYCLANILIDE	KG2007	0
55	CYCLOATE	KG2069	30,161
148	CYFLUTHRIN	KG6081	1,284
	CYHALOFOP	KG9104	0
124	CYMOXANIL	KG3008	3,220
181	CYPERMETHRIN	KG6011	13
127	CYPRODINIL	KG9105	2,983
	CYROMAZINE	KG6012	0
174	CYTOKININS	KG8015	103
138	DCNA	KG5008	1,679
35	DCPA	KG1872	71,464
	DELTAMETHRIN	KG2008	0
78	DESMEDIPHAM	KG9014	12,871
41	DIAZINON	KG6014	58,153
44	DICAMBA	KG1298	51,981
170	DICHLOBENIL	KG1865	154
66	DICLOFOP	KG1005	19,496
	DICLOSULAM	KG9106	0
120	DICOFOL	KG6016	3,757
	DICROTOPHOS	KG6082	0
94	DIFENZOQUAT	KG1374	7,995
131	DIFLUBENZURON	KG6064	2,301
182	DIFLUFENZOPYR	KG9107	1
56	DIMETHENAMID	KG3001	30,072
	DIMETHIPIN	KG7004	0
52	DIMETHOATE	KG6017	32,475

	DIMETHOMORPH	KG3006	0
67	DIQUAT	KG1950	18,036
87	DISULFOTON	KG6018	10,043
32	DIURON	KG1991	78,093
122	DODINE	KG5033	3,442
	DSMA	KG4001	0
	EMAMECTIN	KG92	0
42	ENDOSULFAN	KG6019	55,530
157	ENDOTHALL	KG1948	785
7	EPTC	KG1414	669,841
97	ESFENVALERATE	KG6020	7,500
50	ETHALFLURALIN	KG9009	36,294
62	ETHEPHON	KG7003	20,961
82	ETHOFUMESATE	KG9012	11,076
23	ETHOPROP	KG6023	109,196
	ETRIDIAZOLE	KG5051	0
161	FENAMIPHOS	KG6025	619
126	FENARIMOL	KG5032	3,125
163	FENBUCONAZOLE	KG2009	616
107	FENBUTATIN OXIDE	KG6026	5,126
102	FENHEXAMID	KG9108	6,295
83	FENOXAPROP	KG9003	10,854
128	FENPROPATHRIN	KG7203	2,812
167	FENPYROXIMATE	KG9109	340
178	FERBAM	KG5017	30
	FIPRONIL	KG114	0
153	FLUAZIFOP	KG9007	951
59	FLUAZINAM	KG9110	26,448
158	FLUDIOXONIL	KG9111	773
	FLUFENACET	KG9112	0
	FLUMETRALIN	KG2010	0
	FLUMETSULAM	KG3003	0
	FLUMICLORAC	KG2011	0
	FLUMIOXAZIN	KG9113	0
	FLUOMETURON	KG1998	0
60	FLUROXYPYR	KG9114	24,504
103	FLUTOLANIL	KG2012	6,165
	FOMESAFEN	KG4010	0
	FORAMSULFURON	KG9115	0
89	FORMETANATE HCL	KG6071	9,688
64	FOSETYL-AL	KG5031	20,461
137	GIBBERELLIC ACID	KG8013	1,735
106	GLUFOSINATE	KG9116	5,452

8	GLYPHOSATE	KG1099	668,353
180	HALOSULFURON	KG2013	20
33	HEXAZINONE	KG2070	74,727
156	HEXYTHIAZOX	KG2014	875
98	IMAZAMETHABENZ	KG7001	7,295
144	IMAZAMOX	KG9117	1,409
176	IMAZAPIC	KG2015	81
	IMAZAPYR	KG9118	0
	IMAZAQUIN	KG4005	0
91	IMAZETHAPYR	KG9000	9,421
86	IMIDACLOPRID	KG3004	10,481
	INDOXACARB	KG144	0
57	IPRODIONE	KG5006	29,680
	ISOXAFLUTOLE	KG9119	0
10	KAOLIN	KG148	520,031
132	KRESOXIM	KG9120	2,280
166	LACTOFEN	KG4009	361
135	LAMBDACYHALOTHRIN	KG6083	2,022
143	LINURON	KG1993	1,420
47	MALATHION	KG6033	43,535
43	MALEIC HYDRAZIDE	KG8010	54,450
9	MANCOZEB	KG5000	552,344
	MANEB	KG5009	0
11	MCPA	KG1305	321,611
119	MCPB	KG1889	3,888
77	MEFENOXAM	KG2016	12,981
	MEPIQUAT CHLORIDE	KG8007	0
	MESOTRIONE	KG9121	0
169	METALDEHYDE	KG6073	156
2	METAM SODIUM	KG8002	9,955,584
36	METHAMIDOPHOS	KG6036	71,102
165	METHIDATHION	KG6037	365
84	METHOMYL	KG6038	10,536
114	METHOXYFENOZIDE	KG172	4,352
	METHYL BROMIDE	KG8001	0
110	METHYL PARATHION	KG6042	4,871
51	METIRAM	KG5029	32,947
16	METRIBUZIN	KG1975	163,418
130	METSULFURON	KG4003	2,428
	MOLINATE	KG1417	0
	MSMA	KG1124	0
71	MYCLOBUTANIL	KG5036	15,037
141	NAA	KG8003	1,504

162	NAD	KG8014	616
	NALED	KG6044	0
112	NAPROPAMIDE	KG1900	4,423
	NAPTALAM	KG1307	0
171	NICOSULFURON	KG7007	114
48	NORFLURAZON	KG1018	41,534
4	OIL	KG6049	4,317,691
53	ORYZALIN	KG1873	31,618
30	OXAMYL	KG6045	91,634
92	OXYDEMETON-METHYL	KG6046	9,292
49	OXYFLUORFEN	KG4000	37,854
101	OXYTETRACYCLINE	KG5038	6,454
20	PARAQUAT	KG1616	144,192
31	PCNB	KG5021	81,146
	PEBULATE	KG1419	0
22	PENDIMETHALIN	KG1629	119,607
111	PERMETHRIN	KG6048	4,468
79	PHENMEDIPHAM	KG2220	12,871
19	PHORATE	KG6050	149,047
26	PHOSMET	KG6051	104,468
74	PICLORAM	KG1051	13,565
	PRIMISULFURON	KG7008	0
	PROFENOFOS	KG6084	0
115	PROHEXADIONE	KG9122	4,218
	PROMETRYN	KG1987	0
54	PRONAMIDE	KG1888	31,122
	PROPAMOCARB	KG3007	0
	PROPANIL	KG1282	0
40	PROPARGITE	KG6055	59,990
96	PROPICONAZOLE	KG5020	7,624
154	PROSULFURON	KG2017	926
121	PYMETROZINE	KG217	3,503
116	PYRACLOSTROBIN	KG9123	4,110
85	PYRAZON	KG2250	10,499
129	PYRIDABEN	KG2018	2,468
93	PYRIDATE	KG7012	8,019
151	PYRIPROXYFEN	KG2019	1,086
	PYRITHIOBAC	KG2020	0
	QUINCLORAC	KG7013	0
117	QUIZALOFOP	KG7006	4,080
149	RIMSULFURON	KG2027	1,177
69	SETHOXYDIM	KG1910	16,635
46	SIMAZINE	KG1981	45,069

24	S-METOLACHLOR	KG9124	107,363
	SODIUM CHLORATE	KG8004	0
100	SPINOSAD	KG2021	6,615
139	STREPTOMYCIN	KG5037	1,669
175	SULFENTRAZONE	KG2022	101
109	SULFOSULFURON	KG9125	4,971
5	SULFUR	KG5004	3,699,667
1	SULFURIC ACID	KG8016	14,290,876
108	TEBUCONAZOLE	KG2023	4,999
134	TEBUFENOZIDE	KG3005	2,041
	TEBUPIRIMPHOS	KG2024	0
	TEBUTHIURON	KG1963	0
	TEFLUTHRIN	KG6066	0
58	TERBACIL	KG1109	29,513
34	TERBUFOS	KG6060	74,085
	TETRACONAZOLE	KG9126	0
146	THIAMETHOXAM	KG248	1,309
	THIDIAZURON	KG8006	0
99	THIFENSULFURON	KG4004	7,181
	THIOBENCARB	KG1903	0
	THIODICARB	KG6061	0
70	THIOPHANATE METHYL	KG5019	15,214
80	THIRAM	KG5022	12,864
76	TRALKOXYDIM	KG9127	13,147
	TRALOMETHRIN	KG6067	0
145	TRIADIMEFON	KG5015	1,326
28	TRIALLATE	KG1790	100,704
142	TRIASULFURON	KG7011	1,445
118	TRIBENURON	KG7002	4,022
	TRIBUFOS	KG8009	0
39	TRICLOPYR	KG1988	67,278
136	TRIFLOXYSTROBIN	KG9128	1,945
61	TRIFLUMIZOLE	KG2025	21,560
27	TRIFLURALIN	KG1361	101,645
123	TRIFLUSULFURON	KG2026	3,225
173	TRIFORINE	KG5003	113
125	TRIPHENYLTIN HYD	KG5012	3,185
113	VINCLOZOLIN	KG5013	4,382
133	Z-CYPERMETHRIN	KG274	2,082
45	ZIRAM	KG5016	50,158
	ZOXAMIDE	KG9129	0
Total Amount Used in the Basin Annually:			**45,939,032 (kg)**

F.4. Appendix D. Species referenced in the Food Web report

The following species information augments the common names of species referred to in the body of the report. Most of the species listed are found in the Columbia River Basin; however, this list is not intended to be exhaustive and does not cover all organisms in the Basin. In some cases many species from one family can be found in the Basin, but not all are listed here. For further information on species found in the Basin, we encourage readers to consult the following sources:

- Species of Idaho
- Aquatic Species of Oregon
- Wildlife Species of Oregon
- Species of Montana
- Species of Washington

For ease of use, the table is sorted alphabetically by common name. However, accessed online the table can also be sorted by scientific or family name by clicking the title of the column that you wish to sort by. When sorting by family name and scientific name be aware that in some cases numerous names are included in each cell.

Common Name	**Scientific Name**	**Family Name**
Alder	*Alnus*	Betulaceae
Alder, red	*Alnus rubra*	Betulaceae
Alewife	*Alosa pseudoharengus*	Clupeidae
Alfalfa	*Medicago sativa*	Fabaceae
Algae, green	*Various species*	Scenedesmaceae
Amphipod	*Various species*	Chalcidoidea, various families In the arthropod family Amphipoda
Anchovy, northern	*Engraulis mordax*	Engraulidae
Aphid	*Various species*	Aphididae
Barnacle	*Various species*	Various families in the arthropod order Cirripedia
Bass, largemouth	*Micropterus salmoides*	Centrarcidae
Bass, rock	*Ambloplites rupestris*	Centrarchidae
Bass, smallmouth	*Micropterus dolomieui*	Centrarcidae
Bat	*Pipistrellus pipistrellus*	Vespertilionidae
Bear, black	*Ursus americanus*	Ursidae

Bear, grizzly	*Ursus arctos*	Ursidae
Beaver, American	*Castor canadensis*	Castoridae
Beetle	*Various species*	Various families of the Arthropod order Coleoptera
Beetle, carabid	*Carabus*	Carabidae, various families of the Insect order Coleoptera
Beetle, carrion	*Various species*	Silphidae
Beetle, mountain pine	*Dendroctonus ponderosae*	Curculionidae
Beetle, rove	*Aleochara bilineata*	Staphylinidae
Bluegill	*Lepomis macrochirus*	Centrarcidae
Broom, scotch	*Cytisus scoparius*	Fabaceae
Bullfrog, American	*Rana catesbiana*	Ranidae
Bullhead, black	*Ictalurus melas*	Ictaluridae
Bullhead, brown	*Ictalurus nebulosus*	Ictaluridae
Bulrush, American	*Schoenoplectus americanus*	Cyperaceae
Bunting, black-faced	*Emberiza spodocephala*	Emberizidae
Burbot	*Lota lota*	Gadidae
Cabezon	*Scorpaenichthys marmoratus*	Cottidae
Caddisfly	*Dicosmoecus*	Hydropsychidae, Limnephilidae and various families in the Insect Order Trichoptera
Carp	*Cyprinus carpio*	Cyprinidae
Carp, grass	*Ctenopharyngodon idella*	Cyprinidae
Catfish, blue	*Ictalurus furcatus*	Ictaluridae
Catfish, bullhead	*Ameiurus melas, Ameiurus nebulosus, Ameiurus natalis*	Ictaluridae
Catfish, channel	*Ictalurus punctatus*	Ictaluridae

Catfish, flathead	*Pylodictis olivaris*	Ictaluridae
Catfish, white	*Ameiurus catus*	Ictaluridae
Catfish, yellow	*Ameiurus natalis*	Ictaluridae
Cattail	*Typha latifolia*	Typhaceae
Cattle	*Bos taurus*	Bovidae
Cedar, western red	*Thuja plicata*	Cupressaceae
Char	*Salvelinus*	Salmonidae
Char, white-spotted	*Salvelinus leucomaenis*	Salmonidae
Chironomid	*Various species*	Various families from the order Diptera
Chiselmouth	*Acrocheilus alutaceus*	Cyprinidae
Chub	*Various species*	Cyprinidae
Chub, lake	*Couesius plumbeus*	Cyprinidae
Chub, leatherside	*Snyderichthys copei*	Cyprinidae
Chub, Oregon	*Oregonichthys crameri*	Cyprinidae
Chub, tui	*Gila bicolor*	Cyprinidae
Chub, Utah	*Gila atraria*	Cyprinidae
Cicada	*Magicicada, Tibicen*	Cicadidae
Cichlid	*Cichlasoma*	Cichlidae
Cladoceran	*Bosmina longirostis, Daphnia galeata, Daphnia retrocurva, Holopedium gibberum*	Bosminidae, Daphniidae, Holopedidae
Clam, Asian	*Corbicula fluminea, Corbicula manilensis*	Corbiculidae
Copepod	*Various species*	Various families of the order Arthropod
Copepod, Asian	*Pseudodiaptomus forbesi*	Pseudodiaptomidae

Copepod, calanoid	*Microdisseta, Epischura spp.*	Heterorhabdidae, Temoridae
Copepod, cyclopoid	*Various species*	Cyclopidae
Copepod, diaptomus	*Diaptomus spp.*	Diaptomidae
Copepod, harpacticoid	*Heteropsyllus nr. nunni*	Heterorhabdidae
Cormorant	*Phalacrocorax*	Phalacrocoracidae
Cormorant, double-crested	*Phalacrocorax auritus*	Phalacrocoracidae
Cottonwood	*Various species of Populus*	Salicaceae
Cottonwood, black	*Populus trichocarpa*	Salicaceae
Cougar	*Puma concolor*	Felidae
Coyote	*Canis latrans*	Canidae
Crab, brachyuran	*Carcinus maenas*	Portunidae
Crab, Dungeness	*Metacarcinus magister*	Cancridae
Crappie	*Pomoxis*	Centrarchidae
Crappie, black	*Pomoxis nigromaculatus*	Centrarcidae
Crappie, white	*Pomoxis annularis*	Centrarcidae
Crayfish	*Various species*	Astacidae, Cambaridae, Parastacidae
Crayfish, northern	*Oronectes virilis*	Cambaridae
Crayfish, red swamp	*Procambarus clarki*	Cambaridae
Crayfish, signal	*Pacifastacus leniusculus*	Astacidae
Crustacean	*Various species*	Various families
Dace	*Leuciscus, Rhinichthys*	Cyprinidae
Dace, leopard	*Rhinichthys falcatus*	Cyprinidae
Dace, longnose	*Rhinichthys cataractae*	Cyprinidae
Dace, speckled	*Rhinichthys osculus*	Cyprinidae

Dace, Umatilla	*Rhinichthys umatilla*	Cyprinidae
Deer, white-tailed	*Odocoileus virginianus*	Cervidae
Dipper, American	*Cinclus mexicanus*	Cinclidae
Dogfish, spiny	*Squalus acanthias*	Squalidae
Dolly Varden	*Salvelinus malma malma*	Salmonidae
Duck, American black	*Anas rubripes*	Anatidae
Duck, mallard	*Anas platyrhynchos*	Anatidae
Eagle, bald	*Haliaeetus leucocephalus*	Accipitridae
Earthworm	*Lumbricus terrestris*	Lumbricidae
Eelgrass, Japanese	*Zostera marina*	Zosteraceae
Elk	*Cervus canadensis*	Cervidae
Eulachon	*Thaleichthys pacificus*	Osmeridae
Flea, water	*Daphnia*	Daphniidae
Flounder, arrowtooth	*Atheresthes stomias*	Pleuronectidae
Flounder, starry	*Platichthys stellatus*	Pleuronectidae
Fly, black	*Simulium*	Simuliidae
Fly, true	*Various species*	Various families of the insect order Diptera
Flycatcher, brown	*Muscicapa dauurica*	Muscicapidae
Flycatcher, narcissus	*Ficedula narcissina*	Muscicapidae
Goby, Amur	*Rhinogobius brunneus*	Gobiidae
Goby, bay	*Lepidogobius lepidus*	Gobiidae
Goldeneye, Barrow’s	*Bucephala islandica*	Anatidae
Goldeneye, common	*Bucephala clangula*	Anatidae

Goldfish	*Carassius auratus*	Cyprinidae
Goose, Canada	*Branta canadensis*	Anatidae
Grass, reed canary	*Phalaris arundinacea*	Poaceae
Grass, tufted hair	*Deschampsia caespitosa*	Poaceae
Grayling, Arctic	*Thymallus arcticus*	Salmonidae
Greenling, kelp	*Hexogrammos decagrammus*	Hexagrammidae
Gull	*Larus spp.*	Laridae
Gull, California	*Larus californicus*	Laridae
Gull, herring	*Larus argentatus*	Laridae
Gunnel, saddleback	*Pholis ornata*	Pholidae
Hake, Pacific	*Merluccius productus*	Merlucciidae
Hemlock, western	*Tsuga heterophylla*	Pinaceae
Heron, great blue	*Ardea herodias*	Ardeidae
Herring, North Sea	*Clupea harengus*	Clupeidae
Herring, Pacific	*Clupea (harengus) pallasi*	Clupeidae
Hog	*Sus domestica*	Suidae
Iris, yellow	*Iris pseudacorus*	Iridaceae
Isopod, parasitic	*Orthione griffenis*	Bopyridae
Kestrel, American	*Falco sparverius*	Falconidae
Killifish	*Fundulus*	Cyprinodontidae
Killifish, banded	*Fundulus diaphanus*	Cyprinodontidae
Knotweed, giant	*Fallopia sachallinense*	Polygonaceae
Knotweed, Japanese	*Fallopia japonica*	Polygonaceae
Kokanee	*Oncorhynchus nerka*	Salmonidae

Krill	*Euphausia*	Euphausiidae
Ladybug	*Harmonia axyridis*	Coccinellidae
Lamprey, Pacific	*Lampetra tridentata*	Petromyzontidae
Lamprey, western brook	*Lampetra richardsoni*	Petromyzontidae
Leafhopper	*Various species*	Cicadellidae
Leech	*Various species*	Erpobdellidae
Lingcod	*Ophiodon elongatus*	Hexagrammidae
Lizard	*Various species names*	Various families in the Suborder Lacertilia
Lizard, western fence	*Sceloporus occidentalis*	Phrynosomatidae
Loosestrife, purple	*Lythrum salicaria*	Lythraceae
Mackerel, jack	*Trachurus symmetricus*	Carangidae
Mackerel, Pacific	*Scomber japonicus*	Scombridae
Madtom, tadpole	*Noturus gyrinus*	Ictaluridae
Maple, bigleaf	*Acer macrophyllum*	Aceraceae
Mayfly	*Various species names*	Various families in the Suborder Lacertilia
Mayfly, baetid	*Ephemeroptera*	Baetidae
Merganser, common	*Mergus merganser*	Anatidae
Midge	*Various species names*	Chiromonidae and Ceratopogonidae and other Dipteran families
Milfoil, Eurasian water	*Myriophyllum spicatum*	Haloragidaceae
Mink, American	*Mustela vison*	Mustelidae
Minnow	*Various species names*	Cyprinidae
Minnow, fathead	*Pimephales promelas*	Cyprinidae

Moose	*Alces alces*	Cervidae
Mosquito fish	*Gambusia affinus*	Poeciliidae
Mudminnow, central	*Umbra limi*	Umbridae
Mudsnail, New Zealand	*Potomopyrgus antipodarum*	Hydrobiidae
Murre	*Uria aalge*	Alcidae
Muskie, tiger	*Esox lucius x Esox masquinongy*	Esocidae
Mussel, freshwater pearl	*Margaritifera margaritifera*	Margaritiferidae
Mussel, quagga	*Dreissena rostriformis bugensis*	Dreissenidae
Mussel, Rocky Mountain ridged	*Gonidea angulata*	Unionidae
Mussel, western pearl	*Margaritinopsis falcata*	Margaritiferidae
Nuthatch, white-breasted	*Sitta carolinensis*	Sittidae
Nutria	*Myocaster coypus*	Myocastoridae
Osprey	*Pandion haliaetus*	Pandionidae
Ostracod	*Various species*	Various families in the class Ostracoda
Otter, North American river	*Lutra canadensis*	Mustelidae
Oyster, Pacific	*Crassostrea gigas*	Ostreidae
Peamouth	*Mylocheilus caurinus*	Cyprinidae
Pelican, American white	*Pelecanus erythrorhynchos*	Pelecanidae
Perch, Nile	*Lates niloticus*	Latidae
Perch, pile	*Rhacochilus vacca*	Embiotocidae
Perch, shiner	*Cymatogaster aggregata*	Embiotocidae

Perch, yellow	*Perca flavescens*	Percidae
Pickerel, grass	*Esox americanus vermiculatus*	Esocidae
Pike, northern	*Esox lucius*	Esocidae
Pikeminnow, northern	*Ptychocheilus oregonensis*	Cyprinidae
Pipefish, bay	*Syngnathus leptorhynchus*	Syngnathidae
Poacher, pricklebreast	*Stellerina xyosterna*	Agonidae
Poacher, tubenose	*Pallasina barbata*	Agonidae
Poacher, warty	*Chesnonia verrucosa*	Agonidae
Pollock, walleye	*Theragra chalcogramma*	Gadidae
Poplar	*Various species names*	Salicaceae
Prickleback, snake	*Lumpenus sagitta*	Stichaeidae
Pumpkinseed	*Lepomis gibbosus*	Centrarcidae
Raccoon	*Procyon lotor*	Procyonidae
Rotifer	*Various species*	Various families in the phylum Rotifera
Roundworm	*Various species*	Various families in the phylum Nematoda
Rush	*Juncus spp*	Juncaceae
Rush, Baltic	*Juncus balticus*	Juncaceae
Rush, common	*Juncus effusus*	Juncaceae
Russian-olive	*Elaeagnus angustifolia*	Elaeagnaceae
Salamander	*Various species names*	Various families in the amphibian Order Urodela
Salmon	*Oncorhynchus spp*	Salmonidae
Salmon, Atlantic	*Salmo salar*	Salmonidae
Salmon, Chinook	*Oncorhynchus tshawytscha*	Salmonidae

Salmon, chum	*Oncorhynchus keta*	Salmonidae
Salmon, coho	*Oncorhynchus kisutch*	Salmonidae
Salmon, masu	*Oncorhynchus masou*	Salmonidae
Salmon, pink	*Oncorhynchus gorbuscha*	Salmonidae
Salmon, sockeye	*Oncorhynchus nerka*	Salmonidae
Sand lance, Pacific	*Ammodytes hexapterus*	Ammodytidae
Sand roller	*Percopsis transmontana*	Percopsidae
Sanddab, Pacific	*Citharichthys sordidus*	Paralichthyidae
Sanddab, speckled	*Citharichthys stigmaeus*	Paralichthyidae
Sandfish, Pacific	*Trichodon trichodon*	Trichodontidae
Sardine, Pacific	*Sardinops sagax*	Clupeidae
Scoter, surf	*Melanitta perspicillata*	Anatidae
Sculpin	*Various species names*	Cottidae
Sculpin, buffalo	*Enophrys bison*	Cottidae
Sculpin, coastrange	*Cottus aleuticus*	Cottidae
Sculpin, mottled	*Cottus bairdii*	Cottidae
Sculpin, Pacific staghorn	*Leptocottus armatus*	Cottidae
Sculpin, padded	*Artedius fenestralis*	Cottidae
Sculpin, Paiute	*Cottus beldingi*	Cottidae
Sculpin, prickly	*Cottus asper*	Cottidae
Sculpin, reticulated	*Cottus perplexus*	Cottidae
Sculpin, riffle	*Cottus gulosus*	Cottidae
Sculpin, shorthead	*Cottus confusus*	Cottidae

Sculpin, Shoshone	*Cottus greenei*	Cottidae
Sculpin, slimy	*Cottus cognatus*	Cottidae
Sculpin, torrent	*Cottus rhotheus*	Cottidae
Sculpin, Wood River	*Cottus leiopomus*	Cottidae
Sea lion, California	*Zalophus californianus*	Otariidae
Sea lion, Steller	*Eumetopias jubata*	Otariidae
Seaperch, striped	*Embiotoca lateralis*	Embiotocidae
Seaperch, white	*Phanerodon furcatus*	Embiotocidae
Sedge	*Various species names*	Cyperaceae
Sedge, Lyngby's	*Carex lyngbyei*	Cyperaceae
Shad, American	*Alosa sapidissima*	Clupeidae
Shearwaters, sooty	*Puffinus griseus*	Procellariidae
Sheep, domestic	*Ovis aries*	Bovidae
Shiner	*Various species names*	Cyprinidae
Shiner, golden	*Notemigonus crysoleucas*	Cyprinidae
Shiner, redside	*Richardsonius balteatus*	Cyprinidae
Shiner, spottail	*Notropis hudsonius*	Cyprinidae
Shrew	*Various species*	Soricidae
Shrimp	*Various species*	Branchinectidae, Chirocephalidae, Cyzicidae, Lynceidae, Triopsidae, Streptocephalidae
Shrimp, mysid	*Mysis relicta*	Mysidae
Shrimp, opossum	*Mysis relicta, Neomysis Americana, Neomysis mercedis*	Mysidae
Skate, big	*Raja binoculata*	Rajidae
Slider, red-eared	*Trachemys scripta elegans*	Emydidae

Slime, rock	*Didymosphenia geminate*	Gomphonemataceae
Smelt	*Various species names*	Osmeridae
Smelt, longfin	*Spirinchus thaleichthys*	Osmeridae
Smelt, night	*Spirinchus starksi*	Osmeridae
Smelt, rainbow	*Osmerus mordax*	Osmeridae
Smelt, surf	*Hypomesus pretiosus*	Osmeridae
Smelt, whitebait	*Allosmerus elongatus*	Osmeridae
Snail	*Various species names*	Various families of freshwater Gastropoda
Snailfish, ringtail	*Liparis rutteri*	Cyclopteridae
Snailfish, showy	*Liparis pulchellus*	Liparidae
Snailfish, slipskin	*Liparis fucencis*	Liparidae
Snakehead, northern	*Channa argus*	Channidae
Sole, American	*Various species names*	Achiridae
Sole, butter	*Isopsetta isolepis*	Pleuronectidae
Sole, c-o	*Pleuronichthys coenosus*	Pleuronectidae
Sole, English	*Parophrys vetulus*	Pleuronectidae
Sole, Pacific sand	*Psettichthys melanostictus*	Pleuronectidae
Spider	*Various species*	Vaejovidae, Triaenonychidae
Spider, wolf	*Rhabidosa rabida*	Lycosidae
Spikerush	*Eleocharis palustris*	Cyperaceae
Spruce, Sitka	*Picea sitchensis*	Pinaceae
Spruce, white	*Picea glauca*	Pinaceae
Squid	*Various species*	Various families in the order Teuthida
Squid, market	*Loligo opalescens*	Loliginidae

Steelhead and rainbow trout	*Oncorhynchus mykiss*	Salmonidae
Stickleback	*Various species*	Gasterosteidae
Stickleback, brook	*Culaea inconstans*	Gasterosteidae
Stickleback, three-spine	*Gasterosteus aculeatus*	Gasterosteidae
Stonefly	*Various species*	Various families of the Order Plecoptera
Stonefly, perlodid	*Various species*	Perlodidae
Stonefly, winter	*Various species*	Capniidae, Nemouridae, Taeniopterygidae
Stoneroller	*Percopsis transmontana*	Cyprinidae
Sturgeon	*Acipenser spp*	Acipenseridae
Sturgeon, green	*Acipenser medirostris*	Acipenseridae
Sturgeon, white	*Acipenser transmontanus*	Acipenseridae
Sucker	*Various species names*	Catostomidae
Sucker, bridgelip	*Catostomus columbianus*	Catostomidae
Sucker, largescale	*Catostomus catastomus*	Catostomidae
Sucker, longnose	*Catostomus macrocheilu*	Catostomidae
Sucker, mountain	*Catostomus platyrhynchus*	Catostomidae
Sucker, Utah	*Catostomus ardens*	Catostomidae
Sucker, white	*Catostomus commersoni*	Catostomidae
Sunfish	*Lepomis spp.*	Centrarchidae
Sunfish, green	*Lepomis cyanellus*	Centrarcidae
Sunfish, redbreast	*Lepomis auritus*	Centrarchidae
Sunfish, redear	*Lepomis microlophus*	Centrarcidae

Surfperch, redtail	*Amphistichus rhodoterus*	Embiotocidae
Surfperch, silver	*Hyperprosopon ellipticum*	Embiotocidae
Surfperch, spotfin	*Hyperprosopon anale*	Embiotocidae
Surfperch, walleye	*Hyperprosopon argenteum*	Embiotocidae
Swan, mute	*Cygnus olor*	Anatidae
Swan, trumpeter	*Cygnus buccinator*	Anatidae
Tench	*Tinca tinca*	Cyprinidae
Terns, Caspian	*Hydroprogne caspia*	Sternidae
Tilapia	*Tilapia sp.*	Cichlidae
Tit, great	*Parus major*	Paridae
Tit, marsh	*Poecile palustris*	Paridae
Toad, American	*Bufo americanus*	Bufonidae
Tomcod, Pacific	*Microgadus proximus*	Gadidae
Trout and salmon	*Various species*	Salmonidae
Trout, brook	*Salvelinus fontinalis*	Salmonidae
Trout, brown	*Salmo trutta*	Salmonidae
Trout, bull	*Salvelinus confluentus*	Salmonidae
Trout, cutthroat	*Oncorhynchus clarki*	Salmonidae
Trout, cutthroat, Lahontan	*Oncorhynchus clarki henshawi*	Salmonidae
Trout, cutthroat, westslope	*Oncorhynchus clarki lewisi*	Salmonidae
Trout, Dolly Varden	*Salvelinus malma malma*	Salmonidae
Trout, golden	*Oncorhynchus aquabonita*	Salmonidae
Trout, lake	*Salvelinus namaycush*	Salmonidae

Trout, rainbow and steelhead	*Oncorhynchus mykiss*	Salmonidae
Trout, redband	*Oncorhynchus mykiss gibbsi*	Salmonidae
Trout, tiger	*S. trutta x S. fontinalus*	Salmonidae
Trout, perch	*Percopsis omiscomaycus*	Percopsidae
Turtle, snapping	*Chelydra serpentina*	Chelydridae
Walleye	*Sander vitreus*	Percidae
Warbler, crowned willow	*Phylloscopus coronatus*	Phylloscopidae
Warbler, pale-legged willow	*Phylloscopus tenellipes*	Sylviidae
Warmouth	*Lepomis gulosus*	Centrarcidae
Water flea, Daphnia	*Various species*	Daphniidae
Weatherfish, oriental	*Misgurnus anguillicaudatus*	Cobitidae
Whale, gray	*Eschrichtius robustus*	Eschrichtiidae
Whale, killer	*Orcinus orca*	Delphinidae
Whitefish, lake	*Coregonus clupeaformis*	Salmonidae
Whitefish, mountain	*Prosopium williamsoni*	Salmonidae
Whitefish, pygmy	*Prosopium coulterii*	Salmonidae
Willow	*Salix spp*	Salicaceae
Woodpecker, pygmy	*Dendrocopos kizuki*	Picidae
Wren	*Various species*	Troglodytidae
Zooplankton	*Various species*	Wide range of invertebrate taxa; in fresh water, predominately the crustacean Orders Cladocera, Calanoidea, and Cyclopodia and the Phylum Rotifera.

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