## Executive Summary

The 2014 Fish and Wildlife Program (hereafter Program) calls for the Northwest Power and Conservation Council to review ongoing research and revise the Program's Research Plan. The current Research Plan (Council Document 2006-3) lists 44 critical uncertainties, defined as "important knowledge gaps about resources and the functional relationships that determine fish and wildlife productivity in the Columbia River ecosystem." To help update the Research Plan, the Council asked the Independent Scientific Advisory Board (ISAB) and Independent Scientific Review Panel (ISRP) to reexamine these uncertainties and to recommend revisions after reviewing progress achieved by current research, monitoring, and evaluation projects within the Program.

## Organization of the Full Report

Our full response to this request is organized in two parts. Part 1 presents 50 critical uncertainties organized under 14 themes. A rationale is provided for each uncertainty to explain its importance to the Program. Some of these critical uncertainties were revised from those in the 2006 Research Plan, and others are new. Part 2 presents an evaluation of the extent to which 187 ongoing Program projects (those with a research, monitoring, or evaluation component) have addressed, or could potentially address, the 44 critical uncertainties in the 2006 Research Plan. Appendix D to Part 2 provides a synopsis for each reviewed project. The synopsis indicates which of the 2006 uncertainties were directly or indirectly addressed by the project and includes brief comments about methods and results.

## Overview of Current Projects

Within each theme, most projects addressed uncertainties only indirectly rather than directly (Fig. 1).


Figure 1. The number of Program projects that directly and indirectly examined uncertainties in the 2006 Research Plan by theme.

Thus, additional progress in addressing some uncertainties may be achieved by compiling, analyzing, and synthesizing information obtained from indirect studies. Other uncertainties, however, can only be resolved by focused funding to support more cohesive, controlled studies. In any case, the Council could improve communication and coordination among project teams by funding projects designed to synthesize information from diverse sources. The Council could also help convene workshops or symposia so that researchers working on similar uncertainties could share results, foster new approaches to research, and form broader partnerships. The Council could also require annual project reports to identify the uncertainties being addressed and document progress in resolving the uncertainties.

The distribution of projects across themes reflects the Program's past and current emphasis on habitat restoration and the use of artificial propagation to conserve and supplement natural populations, and to support fisheries. More projects directly addressed the tributary habitat and fish propagation themes than all other themes combined. A substantial number of Program projects also addressed uncertainties in the hydrosystem and population structure and diversity themes. The surprising number of projects associated with the population structure and diversity theme is largely attributable to the widespread application of genetic methods across a variety of species and locations and offers a special opportunity for integration and synthesis.

Other entities are leading research efforts in the Basin related to the themes of contaminants, climate change, and estuary habitat. Consequently, communication, coordination, and collaboration with these groups will be essential to incorporate their findings into the Program. Research to address uncertainties in the estuary and hydrosystem themes is largely supported by the U.S. Army Corps of Engineers through its Anadromous Fish Evaluation Program (AFEP), as well as fish passage research conducted at dams in the Willamette Subbasin. Although these projects are not directly funded by the Program, they are reviewed and implemented as part of Bonneville's reimbursable program and help to address Program uncertainties.

Only two Program projects were associated with uncertainties in the ocean theme. Understanding how conditions in the ocean affect growth and survival can help to guide and evaluate the effectiveness of efforts to restore anadromous species including eulachon, white sturgeon, and Pacific lamprey, as well as Pacific salmon and steelhead. No projects were directly associated with the human development theme; more research could strengthen projections of human impacts on fish and wildlife populations in the Basin.

## Identification of New Uncertainties

The Council's draft uncertainties database contains nearly 700 questions that Council staff gleaned from over 130 regional reports and plans including relevant questions submitted during the 2014 Program amendment process. The ISAB and ISRP used this database to identify new uncertainties that should be included in a revised Research Plan. The complete list of uncertainties and judgments about their priority can be viewed in the online uncertainties database. Part 1 of the main report describes the 50
uncertainties judged to be of highest priority (i.e., critical). These critical uncertainties are grouped into 14 revised themes roughly corresponding to strategies listed in the 2014 Program; their order in our report does not reflect priority.

A key finding is that many of the questions listed in the Council's database are too broad for one or even a small set of research projects to address. Typically, research projects in the Basin are focused at or below the subbasin level and are conducted by scientists with expertise limited to one or two disciplines. What is often needed, however, are studies lasting for a decade or more that involve multiple subbasins and are conducted by integrated teams of professionals representing a diverse array of disciplines, such as fisheries, ecology, hydrology, modeling, and social sciences. Creating and supporting such teams will provide opportunities to make substantial progress in resolving many of the uncertainties described below. Strong and visionary leadership will be key to their success.

## Critical Uncertainties ${ }^{1}$ by Theme

Theme 1. Public engagement: The amended 2014 Program acknowledges public engagement as both a guiding scientific principle and a strategy for achieving the vision. Public engagement can improve the flow of information between the Program, its participants, and the general public through communication, consultation, and participation. The ISAB previously identified public engagement as one of four essential elements of a landscape approach (ISAB 2011-4). The other elements are (1) a scientific foundation based on principles from landscape ecology and the concept of resilience, (2) governance that allows for collaboration and integration, and (3) a capacity for learning and adaptation.

In this review, the ISAB and ISRP identified five uncertainties relevant to the landscape approach. The 2006 Research Plan did not include uncertainties specifically related to the landscape approach, so progress was not explicitly assessed in Part 2 of this review. However, the 2014 Program acknowledges the need for greater public engagement and set the stage for progress. Next steps in addressing this theme are to (1) support organizations that show promise for assisting with coordination, integration, and leadership toward achieving Program objectives and (2) engage the public in the development and evaluation of projections of future landscape change and other human impacts.

Theme 2. Human development: Fish and wildlife habitats will be affected by changes in society's use of land and other resources. However, most projections of fish and wildlife populations ignore future change in human population growth, fish and wildlife resource utilization, land development, and technological innovation that will influence the effectiveness of restoration efforts in the Basin. Federal and regional demographic projections provide a degree of confidence about population growth over the coming decades (doubling by 2100), but impacts will vary among locations, and it is difficult to predict changes in institutions and social preferences (e.g., willingness to pay for environmental protection). This uncertainty was identified as critical in the 2006 Research Plan and remains so. None of the projects reviewed in Part 2 directly addressed this uncertainty.

[^0]Theme 3. Tributary habitat: A key assumption of the Program is that improvements in tributary habitats will mitigate for reduced survival and growth caused by hydrosystem operations and passage through multiple dams and reservoirs. Three uncertainties related to tributary habitat were identified (only slightly modified from the 2006 Research Plan). Briefly, these uncertainties are whether restoring or reconnecting tributary habitat to expand productive capacity can (1) mitigate for the loss of habitat capacity farther downstream or in the estuary or ocean, (2) provide benefits for wild populations in the face of high densities of hatchery and non-native fishes, and (3) increase resilience to buffer populations against extreme climate events and toxic contaminants.

More has been learned about the effectiveness of tributary restoration at the reach scale than about its aggregate effects on fish and wildlife populations at the watershed scale. Few projects have been conducted at the spatial scale required to resolve these uncertainties, and none has proceeded long enough to measure the full effects of restoration in the context of multiple stressors. Indeed, current methods may be inadequate to measure effects at the basin scale. The Integrated Status and Effectiveness Monitoring Program (ISEMP) and Columbia Habitat Monitoring Program (CHaMP) projects are exploring these issues, but many challenges remain. A key issue to be resolved is the extent to which population responses are determined by interactions between conditions in tributary habitat and conditions in mainstem, estuary or ocean habitat, fish passage through the hydrosystem, or other stressors such as non-native species and toxic contaminants. Another important issue is the degree to which the protection or restoration of upslope habitat (much of which is in National Forests) can improve downstream water quality and aquatic habitat conditions in tributaries.

Theme 4. Hydrosystem and passage operations: The four uncertainties identified in the 2006 Research Plan remain relevant and were restated with minor revisions. Much progress has been made, but there is a continuing need for information about the impacts of hydrosystem flow and passage operations on all focal species (e.g., salmonids, white sturgeon, Pacific lamprey, and eulachon) to assess project compliance with BiOp-mandated targets and prioritize potential corrective actions. Of particular concern regarding salmonids are uncertainties about impacts on life history diversity due to variations in exposure to hydrosystem operations, the benefits of smolt transportation, and the effects of changing climate on fish passage through mainstem dams and reservoirs. Hydrosystem impacts on juvenile lamprey remain uncertain largely because of the lack of suitable tags.

A new (fifth) uncertainty concerns the feasibility of re-introducing anadromous runs of salmonids to areas that are now inaccessible due to dams. The key question is whether self-sustaining populations can be established above a high-head dam. Studies are planned above Chief Joseph Dam and in some tributaries to the Willamette and lower Columbia rivers. Successful re-introduction would likely require highly productive spawning and early rearing habitat to compensate for juvenile and adult mortality during passage through multiple dams and reservoirs, in addition to potentially unfavorable conditions in the ocean.

Theme 5. Mainstem habitat: The role of mainstem habitat in sustaining fish populations remains poorly understood. For example, fall Chinook and steelhead were once thought to rear exclusively in tributaries but have been reported migrating downstream to overwinter or rear in mainstem habitats. Generally,
more research has been directed at understanding the impacts of habitat degradation in tributaries than the impacts of hydrosystem operations on mainstem habitat for salmonids and other focal species, such as Pacific lamprey, white sturgeon, and eulachon. Only one Program project has directly addressed the role of mainstem habitat, and progress has been slow.

Four uncertainties related to mainstem habitat were identified (including the single uncertainty about mainstem habitat identified in the 2006 Research Plan). These uncertainties emphasize the importance of understanding (1) the locations of thermal refuges in the mainstem that will be increasingly important as temperatures increase with climate change; (2) the extent to which the carrying capacity of mainstem habitats affects density-dependent responses, and hence, the assessment and management of focal species; (3) how carrying capacity in mainstem habitats might be maintained or improved by changing hydrosystem operations; and (4) how the availability of spawning and rearing habitat in the mainstem, especially above Bonneville Dam, affects the viability of white sturgeon.

Theme 6. Estuary, plume and ocean: Three uncertainties were identified for the estuary and ocean. The first uncertainty concerns specific factors that impact the growth, migration, maturation, and survival of focal fish species in the estuary, plume, and ocean. Some factors (e.g., avian predation on Chinook and steelhead smolts in the estuary) have been studied more than others (e.g., climate change, contaminants, hypoxia, acidification, fish propagation, disease, and invasive species). Survival rates during the early marine life-stage have been particularly difficult to measure. A second uncertainty concerns how focal species and population diversity would respond to alternative restoration actions in the estuary versus in mainstem and tributary locations. The scale of data collection throughout the Basin is presently insufficient to estimate relative benefits of restoration by life stage and habitat. A third uncertainty concerns the current capacity of estuarine habitat to support focal species, its adequacy to achieve Program goals, and ways to increase that capacity. At present, it is generally assumed that habitat restoration efforts in the Columbia River estuary are increasing carrying capacity for salmonids, but additional research is needed to test this assumption and to quantify any increase in capacity.

Theme 7. Contaminants: Fish, wildlife, and human populations in the Basin and elsewhere in the United States are exposed to an ever-growing variety of pollutants as a result of increasing urbanization, industrialization, and agricultural development. The two uncertainties identified in the 2006 Research Plan are repeated here. The first concerns the proliferation of contaminants and the need to measure and map the spatial and temporal patterns of their use, transfer, accumulation and persistence. For example, a new interactive mapping tool developed by the National Water-Quality Assessment (NAWQA) Program shows predicted concentrations for 108 pesticides in streams and rivers across the United States and identifies which streams are most likely to exceed water-quality guidelines for human health or aquatic life. The second uncertainty concerns how contaminants affect fish production and survival. Aquatic communities in the estuary and coastal ocean are considered especially vulnerable to the accumulation of contaminants because of their spatial positions in the watershed. Studies of contaminants in invertebrate species, many of which are the first components of the food web to accumulate contaminants, are extremely rare in the Basin. Both uncertainties demand greater attention within the Program given the potential for contaminants to negate restoration efforts. However,
addressing them will require a high level of integration and collaboration with state, tribal, and federal agencies.

Theme 8. Climate change: The three climate change uncertainties listed in the 2006 Research Plan are still relevant, but were restated as two uncertainties. The first uncertainty focuses on how long-term climate trends will affect fish and wildlife. Progress has been moderate for predicting changes in temperature and flow, but low for predicting changes in ecosystems. Predictions of increased temperatures and reduced snow packs and summer stream flows suggest that fish kills, such as observed in 2015, are likely to increase in frequency, extent, and severity. The second uncertainty concerns actions that could ameliorate the undesirable impacts of climate change. Special attention is needed to secure thermal refuges and sufficient high quality water under predicted landscape-scale changes in hydrology. Other water security issues that could affect the success of the Program include tradeoffs between water availability and energy production; and governance issues among countries, states, tribes, and other stakeholders. Two Program projects have directly addressed climate change, but more collaboration is needed with universities, other researchers, and policy makers. Future research will be a continuing process of fine-tuning climate models to understand and manage the impacts of climate change on hydrology, habitat phenology, and biota.

Theme 9. Non-native species: The 2006 Research Plan identified three uncertainties to guide ecological studies of threats posed by non-native species, and management actions to improve outcomes. Little progress has been made, and non-native species continue to arrive and spread to many parts of the Basin. Current Program projects are more focused on the impacts of piscivorous native species (e.g., northern pikeminnow, birds, and pinnipeds) than the impacts of non-native species. However, nonnatives such as smallmouth and largemouth bass, walleye, northern pike, and lake trout have become more widely established as predators on salmonid juveniles, especially in reservoirs. Accordingly, the 2006 uncertainties still apply, but they were consolidated and restated as two revised uncertainties.

The first uncertainty concerns the extent to which non-native species now jeopardize the viability of native fish and wildlife. Non-native species change biotic interactions, create novel ecosystems, and have the potential to undermine otherwise successful habitat restoration efforts. Effects of non-natives on native fauna are seldom well understood, often involve complex interactions with other species and habitat types, are difficult to predict accurately, and may be recognized only after the native species are in steep and sometimes irreversible decline. Most non-native species are not fishes, and include invasive molluscs, lower trophic level taxa, aquatic vegetation, and pathogenic organisms that are unrecognized or unstudied by current projects. Studies to predict how non-natives will fare relative to native species under climate changes are lacking and will undoubtedly prove difficult to design and implement.

The second uncertainty concerns management actions that could limit the abundance and spread of non-native species, and mitigate their impacts. Once non-native species are established, efforts to remove them are typically unsuccessful. Management and policy decisions must consider both ecological issues and sometimes conflicting preferences of stakeholders and the public. Efforts to reestablish salmonids into blocked areas will require a greater understanding of the fish communities
present in those areas, as non-native species are now often major components of those communities and habitats.

Theme 10. Predation: Predation was not specifically listed as an uncertainty in the 2006 Research Plan. However, new or expanded proposals to cull predators of salmon in the Columbia River estuary (e.g., double-crested cormorants and sea lions) have renewed controversy about the merits of such management approaches. The role of predators in maintaining community structure is often poorly appreciated, and controlling predator populations to reduce predation on threatened or endangered species may not be feasible. Accordingly, the ISAB and ISRP identified two new uncertainties related to predation.

The first uncertainty concerns the extent to which predators now jeopardize the viability of native fish and wildlife populations. Predicting the impact of predation on prey populations is complicated, especially if other factors are expected to change beyond historical norms. Predation on adult salmonids during upstream migration (e.g., by pinnipeds, especially sea lions) is of particular concern because it may reduce the potential spawning population more than an equivalent rate of predation at earlier life stages. Losses to predators early in life might be mitigated by compensatory mortality during later life stages, especially if predators selectively remove the least fit individuals.

The second uncertainty concerns the effectiveness of management actions to ameliorate undesirable impacts of predation. Past experience indicates that predator control is best used to solve a local and temporary problem and is generally not practical over a wide geographic area for biological and economic reasons. Removal of predators can also have counter-intuitive and unintended consequences for both the target populations and other predator and prey species. Thus, predator management requires a long-term strategy with careful treatment-control comparisons and monitoring.

Theme 11. Fish propagation: Hatcheries are widespread in the Basin, and consequently, it is critical to understand their effects on natural populations, both positive and negative. Despite significant progress by recent projects, the uncertainties related to fish propagation identified in the 2006 Research Plan are still relevant. To reduce overlap and redundancy, the seven uncertainties listed in the Research Plan have been recast into five uncertainties.

The first uncertainty concerns the cumulative effects of basinwide hatchery production on natural populations given the various ways that hatchery fish can interact, both directly and indirectly, with natural origin fish. For example, it is unclear whether or not the cumulative impact of hatchery releases on density-dependent responses in natural populations is adequately considered in planning supplementation efforts.

The second uncertainty concerns the extent to which production by natural populations can be improved by supplementation. Evaluation of this uncertainty requires pre- and post-project reference streams, infrastructure to sample juveniles and adults, and genetic analyses to ascertain the pedigree of natural origin fish. In several subbasins, hatcheries are also being used to reintroduce salmonids into areas where the original populations were extirpated. Monitoring and evaluation of supplemented and
reintroduced populations are needed to track abundance, local adaptation, and straying rates, as well as impacts on other species.

The third and fourth uncertainties relate to the potential roles and impacts of artificial propagation and translocation to restore the abundance and distribution of Pacific lamprey and white sturgeon, respectively.

The last uncertainty is about the genetic or epigenetic changes that occur in cultured populations, and the impacts of such changes on the fitness of natural populations. A component of this uncertainty is the efficacy of management guidelines that regulate the percentage of hatchery origin spawners (pHOS) in nature, and the proportion of natural origin fish used as broodstock (pNOB). Although these management guidelines are well supported by scientific theory, additional empirical assessments are needed to verify their adequacy for protecting the fitness of natural populations.

Theme 12. Harvest: Despite some progress, three uncertainties related to harvest proposed in the 2006 Research Plan were only slightly modified. The first uncertainty concerns how to define biological escapement goals that balance the tradeoffs among fishery harvests, potential ecosystem benefits of increased spawning abundances, and pHOS guidelines to protect fitness in (i.e. genetic adaptations to) the natural environment. Some biological escapement goals already exist within the Basin, but more are needed, as acknowledged in the 2014 Program.

The other two uncertainties emphasize the need to develop: (1) new strategies to improve harvest opportunities within the Basin that minimize negative impacts on natural populations of concern (e.g., by selectively harvesting hatchery origin fish); and (2) better ways to manage coastal mixed-stock fisheries to protect natural populations of concern. Managing and evaluating harvest impacts on natural-origin populations requires reliable information on the stock composition of fish in mixed-stock fisheries both within and outside the Basin. Newly emerging tools could improve the accuracy and the cost effectiveness of stock identification.

Theme 13. Population structure and diversity: Human activities have reduced the range of life history strategies and genetic diversity in many native fish populations. Loss of genetic diversity is expected to compromise the long-term productivity and adaptability of individual populations, as well as the aggregate production and resilience of collections of populations. Understanding population structure (i.e., how diversity is distributed among populations of a species) is also essential for evaluating the viability of a species.

Only limited progress was achieved on the four uncertainties listed in the 2006 Research Plan. Many additional questions broadly related to this theme were also listed in the uncertainties database, reflecting the diversity of life histories and habitats for focal species in the Basin, and the inherent focus of population studies on individual species. Consequently, five more uncertainties (nine in total) related to this theme were identified. Three of the uncertainties reflect a lack of knowledge about (1) factors affecting demographic status of fish and wildlife populations in the Basin, (2) the existing range of biological diversity among geographic areas in the Basin, and (3) alternative life history strategies in fishes and how they affect growth and survival in different habitats. Co-occurring life-history types (e.g.,
resident versus anadromous rainbow trout, ocean versus reservoir type fall Chinook) that differ in their habitat requirements or productivity can pose special challenges for habitat restoration or harvest management.

Two other uncertainties reflect a lack of knowledge about (1) the dominant processes influencing the distribution and interconnection of populations and (2) the long-term consequences of losing connectivity and populations. The sixth uncertainty concerns the effectiveness of genetic assessment tools for determining trends in population status and population diversity.

The last group of uncertainties involves management approaches for protecting the population structure and viability of species groups of particular interest. The seventh uncertainty is how the abundance and diversity of salmonid populations in the Columbia River can be increased and sustained over the long term given the multitude of biological, physical, and human constraints. The eighth and ninth uncertainties are concerned with threats to the abundance, distribution, and diversity of Pacific lamprey and white sturgeon, respectively. It will be important to identify and protect diversity in Pacific lamprey in tandem with artificial propagation efforts. Habitat connectivity is likely a critical issue for the long-term viability of white sturgeon.

Theme 14. Monitoring and evaluation: Monitoring and evaluation of projects has improved substantially since the 2006 Research Plan because of technological progress (e.g., geographic information systems and remote sensing tools, better tagging methods including genetic methods for stock identification and parentage-based tagging, and superior analytical methods); standardization of protocols (e.g., Columbia River Habitat Monitoring Program); and a stronger focus on the need for monitoring and evaluation during project reviews at various levels. Sound statistical planning for monitoring is essential to ensure proper evaluation of project effectiveness and to identify how monitoring data can be integrated and synthesized across projects to maximize the scope for inference.

Accordingly, four new uncertainties related to monitoring and evaluation were identified. These uncertainties focus on the need to improve (1) the precision and accuracy of methods used for estimating fish survival, (2) methods for "fish-in and fish-out monitoring" to evaluate density dependence and the benefits of habitat restoration, (3) approaches to measuring the cumulative effects of habitat restoration on fish populations at a large spatial scale, and (4) evaluation of impacts of habitat restoration on wildlife, recognizing that changes to habitat that benefit fish might not benefit other species.

## Dissemination of Information

After reviewing annual reports from 187 Program projects with research, monitoring, and evaluation components, the ISAB and ISRP came to more fully appreciate the range of topics currently being addressed in the Basin. Excellent research and monitoring are occurring, innovative approaches are being tried, and research teams are using a variety of methods to address problems. However, we believe benefits to the Program could be increased by greater communication among the project proponents and other practitioners. For example, annual reports should routinely include syntheses of results from previous years, including lessons learned about approaches and methods. Better
dissemination of these findings will improve the collective rate of learning about successful approaches and methods.

Substantial progress could be realized by better communicating the focus, results, and findings of projects within the Program. To improve accessibility, this information needs to be summarized carefully and placed consistently into a single location that can be searched easily. To this end, abstracts produced by project teams should be compiled as a comprehensive annual report for the Program that could, for example, be linked to the Council's web page.

Stronger linkages between project reporting and critical uncertainties in the Research Plan are also needed to track annual progress in resolving uncertainties. Without being burdensome, the annual reporting process should require project teams to explicitly identify which uncertainties are being addressed, and how. These statements could be incorporated into the annual report for the Program (as proposed above) or into a separate, searchable document.

## Moving Forward

The following recommendations are provided to help revise the Research Plan and improve research within the Program during the next five years.

- Improve communication on research issues and results among project proponents, the public, governmental entities, the Tribes, and others involved with the Basin's water, land, and fish and wildlife resources. Communication leads to partnerships, pooling of resources, spreading of innovations, public support, and solutions that would be difficult for one or a few organizations to achieve alone.
- Foster efforts to synthesize information generated by independent studies by improving the rigor, consistency and availability of annual reports, convening workshops or symposia, and funding special projects as needed to compile, analyze, and review progress in addressing uncertainties.
- Recognize that research on the expected impacts of climate change and human development in the Basin should be taken into account when setting future Program objectives.
- Support research to identify thermal refuges and ways to secure the availability and quality of water essential to achieving Program objectives.
- Recognize that toxic contaminants are pervasive in the Basin and support research to determine threats to fish, wildlife, and people because of their persistence and bioaccumulation in food webs.
- Support research to guide the management of non-native species. As conditions change, environments may increasingly favor non-native species, some of which are valued and can be managed.
- Continue supporting research on artificial propagation that will help to measure the benefits and risks to natural populations. Encourage research to help develop biological escapement goals for the Basin's salmonid populations and refine approaches for harvesting surplus hatchery fish.
- Expand research to identify and track changes in population structure and genetic diversity of focal species. Loss of genetic diversity may compromise the long-term production and resilience of fish and wildlife in the Basin.
- Continue to support and demand rigorous monitoring and evaluation programs that have well established objectives and potential for basinwide synthesis. Such evaluation is needed to understand the benefits and risks of Program actions and to manage adaptively.
- Recognize that evaluating the effectiveness of conservation actions is complicated by natural variability and statistical sampling error. Many years of careful monitoring are typically required to confirm small but meaningful changes in ecological outcomes from habitat restoration or supplementation projects.
- Support research on ecological interactions in mainstem, lower Columbia River, estuary, ocean plume, and ocean habitats. Understanding the factors in each habitat that limit population growth will improve management of all four H's (habitat, harvest, hatcheries and hydrosystem).


[^0]:    ${ }^{1}$ Within this section only, critical uncertainties are called "uncertainties" to simplify the text.

