A Review of Predation Impacts and Management Effectiveness for the Columbia River Basin

INDEPENDENT SCIENTIFIC ADVISORY BOARD

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Independent Scientific Advisory Board
for the Northwest Power and Conservation Council,
Columbia River Basin Indian Tribes,
and National Marine Fisheries Service
851 SW 6th Avenue, Suite 1100
Portland, Oregon 97204

Kurt D. Fausch, Ph.D., (ISAB Vice-chair) Professor Emeritus of Fisheries and Aquatic Sciences, Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado

Stanley Gregory, Ph.D., Professor Emeritus, Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon

William Jaeger, Ph.D., Professor of Applied Economics, Oregon State University, Corvallis, Oregon

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Thomas P. Quinn, Ph.D., Professor, School of Aquatic and Fishery Sciences, University of Washington, Seattle

Steve Schroder, Ph.D., Fisheries Consultant and Fisheries Research Scientist (Retired), Washington Department of Fish and Wildlife, Olympia, Washington

Carl J. Schwarz, Ph.D., Professor of Statistics and Actuarial Science at Simon Fraser University, Burnaby, British Columbia, Canada

Thomas Turner, Ph.D., Professor of Biology and Associate Dean for Research at the University of New Mexico, Albuquerque, New Mexico

ISAB Ad Hoc Member

James N. Sanchirico, Ph.D., Professor, Department of Environmental Science and Policy, University of California, Davis

ISAB Ex Officios and Manager

Michael Ford, Ph.D., Director of the Conservation Biology Program, Northwest Fisheries Science Center, Seattle, Washington

Nancy Leonard, Ph.D., Program Performance Manager, Northwest Power and Conservation Council, Portland, Oregon

Zach Penney, Ph.D., Fisheries Science Manager, Columbia River Inter-Tribal Fish Commission, Portland, Oregon

Erik Merrill, J.D., Independent Science Manager, Northwest Power and Conservation Council, Portland, Oregon

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(ISAB Predation Management Report)

LIST OF TABLES AND FIGURES

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EXECUTIVE SUMMARY

The Northwest Power and Conservation Council (Council) requested the Independent Scientific Advisory Board (ISAB) to provide a review of the biological and economic impacts of native and nonnative predators, the effectiveness of predator management control efforts currently implemented, and the potential impacts on the Columbia River Basin (Basin) from the introduction and spread of northern pike. The request included six science questions and two initial economic questions. This report addresses the science questions. The Council obtained the assistance of economists, who will address the economic questions in a separate companion report.

Review approach. The ISAB's answers to the Council questions, conclusions, and recommendations are based on a targeted but not exhaustive literature review and a series of scientific briefings by experts working in the Basin and elsewhere. The ISAB considered native and nonnative fish predators and native avian and pinniped predators in the Basin (page 7). In past reports, the ISAB, Independent Scientific Review Panel (ISRP), and Independent Economic Analysis Board (IEAB) have highlighted important assumptions and observations about the biological and economic impacts of native and nonnative predators and the effectiveness of predator control efforts in the Basin. These assumptions and observations were considered in this report (page 12). The ISAB offers summary answers to the Council's six science questions early in this report (page 15). These summary answers are followed by detailed explanations for a subset of predator species in the Basin.

Brief answers to the Council's questions

1. *What information is needed to develop a common metric of impact across all predator species*? To measure the impact of predation, we need to know (1) the total predation by a predator at each point in time or space where predation occurs; (2) the subsequent predation by all other predators at each point in time or space; and (3) the cumulative survival probability over the full life cycle of the fish or to a consistent point of reference (e.g., Bonneville Dam). An ecosystem-wide, multi-predator, multi-prey approach must be taken to fully understand predation impacts.
2. *What type and level of effort are needed?* A system-wide, ecosystem-based approach for assessing and managing fish, avian, and pinniped predators collectively will create a more effective and consistent framework for developing and implementing control actions. Assessing impacts of all potential predators throughout the Basin will require integrated analytical tools, such as life-cycle models for salmon and steelhead, measurement of SARs, and density dependence analysis. This type of analysis would allow managers and policymakers to identify (a) locations where life stages of prey species are most susceptible to different predators and (b) the relative benefits of decreasing salmonid mortality at different life stages, making control efforts more biologically and economically effective.

3. *Would additional predator management be effective in improving focal species survival?* The ISAB cannot simply answer this question as a “yes/no” option without better information on predation in the Basin. Even with more rigorous information on predation, a portfolio approach (including hydrosystem management, habitat restoration, as well as predator control) for reducing mortalities of salmon and steelhead will likely provide the most biologically and cost-effective management alternatives.

4. *Can we rank predator impacts and then rank which current management activities would be most effective in reducing impacts?* Accurately ranking the impacts of the predators on focal species cannot be accomplished across all combinations of predators and their salmonid prey without synthesis of available Basin-wide information and analysis of salmonid survival throughout their life cycles. Research and monitoring have tended to examine subsets of juvenile and adult salmonids, and a subset of predators, resulting in very uneven coverage and a dearth of information on certain combinations of species and life histories. The ISAB compiled tables (page 31) of the major predators and categorical values of vulnerability of salmonid prey. The tables illustrate some important points, such as effects of seasonal timing of adult returns and differences in body size on differences in vulnerability. Biological effectiveness and cost-effectiveness of management activities vary by predator and prey species, life cycle, and location. However, recent work on avian and pinniped predators is heading in a direction that may lead to a better evaluation of the efficacy of management actions.

5. *Do we know what level of suppression (exploitation) is needed to reduce the northern pike population in Lake Roosevelt to a level sufficient to reduce risk of emigration?* Based on the inexorable invasion by northern pike downstream over the past 65 years, it is likely that even with the best efforts in public education, early detection, and control or eradication, pike will eventually invade the anadromous zone. There is no simple estimable relationship between abundance and the probability of emigration from Lake Roosevelt because, for example, each individual female pike produces tens of thousands of eggs so emigration by even one male and one female pike could produce thousands of juveniles. Moreover, evidence indicates that about as many invasions have been caused by illegal stocking, often to distant locations, as by dispersal of pike themselves. It is essential to develop a monitoring program throughout the anadromous zone and a rapid response program to eradicate new invasions at their earliest stages when it may be possible. After populations become established, control efforts will need to be extensive, river-wide, and must continue indefinitely to be successful in reducing mortality of focal salmonids. Suppression in Lake Roosevelt could reduce risks of downstream establishment by reducing the number and (average) body size of downstream dispersers.

6. *What are the likely ecological impacts of northern pike should they enter the Basin’s anadromous waters?* Pike are highly invasive and through predation are likely to drastically reduce salmonid abundance, especially in low-gradient river segments with wide floodplains. Pike prefer soft-rayed salmonids and are capable of driving preferred prey species to very low levels, or extinction, and all

> sizes and ages of pike (yearling and older) can eat salmon fry, parr, and smolts. If salmonids have no refuges from predation (i.e., habitats that are unsuitable for pike), pike are likely to reduce the salmonid numbers and can cause salmonid populations to collapse. Salmonids that migrate in open water near the surface may be less vulnerable than others that forage or overwinter in habitats occupied by pike.

In this review, the ISAB made a number of conclusions regarding predation management and specific predator species in the Basin:

A coupled ecosystem/socioeconomics approach to predation management and metrics. Predation management requires both biological (page 24) and socioeconomic (page 41) information, especially as it pertains to the spread of nonnative fish such as northern pike (page 67). A coupled ecosystem/socioeconomic approach is required to fully understand both the impacts of predation on focal species and the efficacy of predator management. As the ISAB stated in its Predation Metrics Report (ISAB 2016-1), compensatory mortality is the most important uncertainty to address when developing predation metrics or management plans. Compensatory mortality occurs when predation mortality at one life stage is offset to some degree by decreased mortality at the same or subsequent life stages. The costs and benefits of invasive species prevention, control, and eradication are critical to making sound policy decisions—including the ways in which people's behavior can promote or frustrate those efforts. Given these high levels of uncertainty and often novel ecological interactions, quantitative evaluation of alternative management or policy responses is sometimes not possible, but a potential approach will be described in the forthcoming economic report.

Northern pikeminnow. The primary native piscivorous fish in the Basin is the northern pikeminnow (page 44) for which there is a bounty removal program based on predator studies conducted over 30 years ago. The current efficacy of this program is unknown due to potential changes in the relative abundance of pikeminnow and other piscivore predators, and the distribution of prey in their diets since the early studies. These studies need to be updated; the evaluation of the program must do more than count pikeminnow removed; an ecosystem approach is needed.

Northern pike. Invasive northern pike are now distributed throughout Lake Roosevelt and have invaded to within a few miles of Grand Coulee Dam (page 53). It is likely that even with the best efforts in public education, early detection, and control or eradication, pike will eventually invade the anadromous zone, either naturally or by human agents. Pike are likely to drastically reduce salmonid abundance, especially in low-gradient river segments with wide floodplains. Pike are highly adaptable and fecund. Nevertheless, reducing the numbers of fish emigrating from Lake Roosevelt is likely to reduce the chances that pike will establish new populations downstream and hence delay the invasion. Illegal introductions by humans are difficult to control, and more could be invested in efforts to measure, understand, and reduce illegal stocking of pike. A species distribution model could be developed to estimate the habitat in the Basin most likely to be invaded. Genetic tools (eDNA) are cost-effective for rapid early detection of the presence of pike, and releasing fish with "Trojan" sex chromosomes (YY males) may provide a means for their control (page 61) but could require several decades to develop and implement. Early detection and rapid suppression efforts are cost-effective and paramount for eradicating this species or slowing its spread compared to the cost-effectiveness of efforts after the pike are established. Northern pike have been eliminated from individual lakes and reservoirs, and two small watersheds in California (page 88) and Alaska, and could be removed from small ponds and lakes in the Basin, especially those on the floodplain where they are likely to be introduced illegally.

Other nonnative fish. Other nonnative fish in the Basin also prey on focal species and include smallmouth bass (page 69), which have been in the Basin for over 100 years, and walleye (page 77). At this time, neither the abundance of these and other nonnative predators nor their impacts on focal species are accurately known. Nonnative lake trout are also present in several lakes in the Basin (page 83) where they are impacting native species such as kokanee, bull trout and cutthroat trout.

Avian predation. Large numbers of colonial, piscivorous water birds, such as Caspian terns and double-crested cormorants, nest in the Basin and are believed to be one of the greatest sources of mortality—if not the single-greatest source—for emigrating juvenile steelhead and yearling Chinook salmon from the upper Columbia and Snake rivers (page 95). Modeling avian predation of juvenile steelhead has found an inverse relationship between the level of predation and smolt-to-adult-returns (SARs). Current management of avian predators focuses on dissuading the birds from nesting in some areas of the Basin. While this strategy has reduced the numbers of birds on specific colonies, the actual change in predation is unknown as the birds may have established new colonies in the Basin and resumed preying on juvenile salmon (or other focal species). A Basin-wide monitoring plan is needed to evaluate total avian predation and evaluate birds control methods.

Marine mammals. The negative impacts of pinniped (sea lion and seal) predation on adult salmonids and other focal fish species (eulachon, sturgeon, lamprey) are better understood than those occurring at juvenile life stages. Recently, there has been substantial progress in estimating Basin-wide impacts of California sea lions on adult Chinook salmon, but the results are equivocal given recent dramatic annual fluctuations in pinniped and salmonid populations and many other important uncertainties (page 104). Recent authorization for lethal removal of sea lions may provide relief from this predator at Bonneville Dam and Willamette Falls, but its efficacy must be evaluated as part of a Basin-wide ecosystem examination of predator-prey interactions.

Evaluating effectiveness. The ISAB has evaluated and provides recommendations about the statistical methods agencies use to monitor and estimate predation effects by fish (page 91), birds (page 98) and marine mammals (page 110). The ISAB also evaluated the effectiveness of predation management (page 119). Evaluating the effectiveness of predator control programs is a two-step process. First, the magnitude of the predation impact on focal species must be ascertained, and second the effectiveness of control methods must be evaluated. Estimates of total predation and the estimates of the total number of predators gives the marginal gain from reducing a particular predator population by one individual in one particular time and location. However, marginal gains may fail to reflect the benefits of the control program because of compensatory behavior of the prey (e.g., density dependence) and compensatory behavior of this and other predators (e.g., removing one predator species may increase predation by another predator species; predators displaced by hazing, for example, may move elsewhere). Consequently, evaluation of predator control programs must do more than simply count the number of predators removed. The evaluation must monitor responses from other predators to the predator removals and evaluate responses of the salmon over the remainder of its life cycle up to a common point such as Bonneville Dam.

An altered ecosystem. Human alterations have changed the dynamics of both juvenile and adult anadromous salmonids, abundance and distribution of native and nonnative predators, vulnerability of salmonids to predation, and complexity of food webs in the Columbia River Basin. Predator management in the Columbia River Basin currently focuses on individual predator species and survival of the portion of their prey that are salmon and steelhead. Most predation analyses to develop management actions in the Basin are fragmented and ignore other factors (e.g., hydrosystem operations, habitat degradation) that influence survival of focal species. A Basin-wide, ecosystem-based approach for assessing and managing fish, avian, and pinniped predators collectively is needed to create a more effective and consistent approach for developing more biologically and economically effective predator control actions.

I. INTRODUCTION

This report responds to a November 20, 2018 letter from the Northwest Power and Conservation Council requesting the Independent Science Advisory Board's (ISAB) "assistance in a review of the biological and economic impacts of native and nonnative predators, the effectiveness of predator management control efforts currently implemented, and specifically the potential impacts that the introduction and spread of northern pike can have on the Columbia River Basin (Basin)."

The strategy for predator management in the Columbia River Basin under the Northwest Power and Conservation Council's 2014 Fish and Wildlife Program (the Program) is to "improve survival of salmon and steelhead and other native focal fish species by managing and controlling predation rates" (Council Document 2014-12, pages 49-51). The strategy acknowledges the natural, dynamic, and complex process of predation, particularly in the current hybrid ecosystem of the Basin, and the need for best available science to manage predation to improve salmon and steelhead survival. A General Measure of the strategy calls for evaluation of predator-management actions in the Basin:

> *"The federal action agencies, in cooperation with the Council, state and federal fish and wildlife agencies, tribes, and others, should convene a technical work group to: (A) determine the effectiveness of predator-management actions; and (B) develop a common metric to measure the effects of predation on salmonids, such as salmon adult equivalents, to facilitate comparison and evaluation against other limiting factors. Once developed and agreed upon, future predator-management evaluations funded by the action agencies should include a determination of the effectiveness of such actions and the common predation metric in their reports."*

In 2016, the ISAB addressed Part B to develop a set of common predation metrics (ISAB 2016-1) and reviewed and recommended alternative metrics to evaluate the consequences of predation on the Basin's salmonid populations. This current review is a logical follow-up to the predation metrics review and addresses Part A to determine the effectiveness of predator-management actions. For this review, the Council asked the ISAB and Council-selected economists to consider the following questions:

Scientific questions:

1. *Given the Basin's current predation control efforts and the ISAB's predation metrics report (ISAB 2016-1), what information is needed to develop a common metric to assess the impact of predation across all predator species?*
2. *If current predation [control] efforts are not sufficient to contribute toward protecting focal species, what type and level of effort are needed?*
3. *Would concentrating additional efforts on predator management as opposed to hydrosystem actions, habitat enhancement or other management actions be more effective in improving focal species survival?*

4. *Can we rank (from low to high) predator impacts on focal species, and then rank (from low to high) which current management activities would be most effective in reducing the "higher" ranking predation impacts?*
5. *In consideration of* ISRP 2018-3 *regarding Northern Pike, do we know what level of suppression (exploitation) through gill net removal, angler removal or other methods is needed to reduce the population in Lake Roosevelt to a level sufficient to reduce risk of emigration from the lake or risk to other focal management species?*
6. *What are the likely ecological impacts of Northern Pike should they enter the Basin's anadromous waters?*

Economics questions:

Initial review:

1. *What information is needed to assess the economic impacts to natural resources in the Basin should Northern Pike spread throughout the anadromous and non-anadromous zones? If such information exists, can you estimate the economic impacts of the spread of Northern Pike?*
2. *For the related ISAB question regarding level of Northern Pike suppression needed (question 5, above), can you calculate the costs associated with that?*

Subsequent review (optional):[1]

1. *What are the current economic costs for direct expenditures of current predation management efforts in the Columbia Basin and are those costs (and efforts) sufficient for protecting focal species? Please consider all significant funding entities such as the Council Program, Bonneville Power Administration, US Army Corps of Engineers, US Bureau of Reclamation, states, Public Utility Districts, etc.*
2. *If there is not sufficient information to answer these questions, what additional data/information do we need?*

This report addresses the six scientific questions. Economists David Kling and Jim Sanchirico, with the assistance of the ISAB, are addressing the first two "initial review" economic questions in a forthcoming companion report.

Many entities in the Basin are conducting management actions on predatory species, monitoring the effects of those actions, and researching the impacts of both native and nonnative predators on the ecosystem. Major predator management efforts in the Basin currently include:

- lethal removal of northern pikeminnow (*Ptychocheilus oregonensis*), a native fish species in the Basin, by sport-reward and dam-angling fisheries (www.pikeminnow.org) and other mechanical

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[1] These questions are provided should the Council decide that an additional economics review be needed to include other predator species in the Basin.

removal efforts covering most of the mainstem Columbia River accessible to anadromous salmonids from the mouth to Chief Joseph Dam and the Snake River to Hells Canyon Dam.

- lethal removal of northern pike (*Esox lucius*), a nonnative species, in Lake Roosevelt and Box Canyon reservoirs and Lake Coeur D'Alene
- lethal removal of lake trout (*Salvelinus namaycush*) in Flathead Lake, Lake Pend Oreille, Upper Priest Lake and Lake Cle Elum
- hazing, other deterrents, and lethal take of avian predators, primarily ringed-bill gulls (*Larus delawarensis*), California gulls (*Larus californicus*), and double-crested cormorants (*Phalacrocorax auritus*) at lower Snake and Columbia river dams (www.cbbulletin.com/430260.aspx)
- non-lethal and lethal efforts to reduce the number of Caspian terns (*Hydroprogne caspia*) and double-crested cormorants on dredge spoil islands in the lower Columbia River and estuary (See U.S. Army Corps of Engineers [USACE] web documents for cormorants and predation)
- redistribution of Caspian terns from Goose and Crescent Island nesting colonies in the mid-Columbia River to other nesting sites in the western United States (see USACE Inland Avian Predation Management Plan)
- non-lethal and lethal methods to control predation by pinnipeds, primarily California sea lions (*Zalophus californianus*) at Bonneville Dam and Willamette Falls (see NOAA, USACE, CRITFC, ODFW, and WDFW web documents).

Currently, the Bonneville Power Administration, through the Council's Fish and Wildlife Program, contributes significantly to these efforts. Through project 1997-024-00, monitoring and suppression efforts on avian predators occur in the ocean, estuary, and lower river. Funding for project 2008-004-00 currently allows for non-lethal hazing of sea lions in the estuary and lower river, but discussions are underway regarding potential funding of lethal removal. Suppression of northern pikeminnow, a native predatory species, is conducted via a rewards fishery in the lower and mid-Columbia River through project 1990-077-00. In the upper Columbia, a variety of predator management efforts are underway to suppress northern pike (see projects 1990-044-00, 1997-004-00, 2007-149-00, and 2017-004-00) and nonnative trout, primarily lake trout (see projects 1991-019-01, 1991-019-03, 1994-047-00, 1995-004-00, 1997-004-00, and 2008-109-00). Several other projects remove or exclude fish species that compete or hybridize with native focal species, such as trout that are outside of their native range including brook trout (*Salvelinus fontinalis*) and rainbow trout (*Oncorhynchus mykiss*). Although competition, hybridization, and predation have inter-related impacts on the Columbia River ecosystem and food webs, this report focuses on the efforts to reduce predation impacts rather than competition or hybridization. See Appendix A for the list of projects and a map (interactive version) of the geographic distribution of these projects' work sites.

With the exception of suppression efforts for northern pike, lake trout, and a few other species in specific locations in the parts of the Basin inaccessible to anadromous fish, management of nonnative fish predators of salmonids in habitats altered by the Federal Columbia River Power System (FCRPS) is largely limited to daily catch and possession limits, size limits, and transportation and stocking restrictions for a few species that support popular recreational fisheries (i.e., smallmouth bass (*Micropterus dolomieu*), walleye (*Sander vitreus*), and channel catfish (*Ictalurus punctatus*) (see ODFW and WDFW regulations).

The organization and objectives of this ISAB Predation Management Effectiveness Report follow a logical path toward addressing the Council's questions. Chapter II covers the review process. Chapter III includes answers to the Council's questions. Chapter IV contains the bulk of the report and the supporting information for answering the Council's questions. It begins with sections on ecosystem and socioeconomic considerations that provide an integrated perspective through which to view the sections on individual predator types (i.e., fish, birds, and pinnipeds). An emphasis of the report is on northern pike impacts, threats, and suppression, and Chapter IV provides supporting information to answer the Council's pike-specific questions 5 and 6 and discusses innovative potential approaches for detection and suppression. Chapter IV also describes impacts, threats, and suppression for other native and nonnative predators in the Basin. Chapter V describes methods for evaluating predation management effectiveness.

II. REVIEW PROCESS

A. Sources of information

The methods used by the ISAB to provide the requested independent scientific advice and recommendations followed the ISAB's formal review procedures. Materials reviewed by the ISAB primarily included published scientific journal articles and unpublished reports (gray literature) by government agencies and other entities working in the Basin, as shown in citations in the text and list of references. Although an exhaustive review of the scientific literature on predation was beyond the scope of our assignment, the ISAB members were familiar with the foundational scientific literature on predation, and search engines were used to find additional relevant sources of information.

To obtain the most recent and relevant information, the ISAB also requested and received oral briefings by scientific experts involved in predator-control research, monitoring, and evaluation programs occurring both inside and outside the Columbia Basin. The briefings were held during three 1-day ISAB meetings ISAB in Portland, Oregon:

December 7, 2018

- *CRITFC Overview* – Jaime Pinkham, Executive Director – Presentation
- *CRITFC Presentation on Predation in the Columbia River Basin: Using Salmon Equivalents for Effective Management* – Blaine Parker, Bob Lessard (metrics), and Doug Hatch (pinnipeds) – Presentation

January 25, 2019

- *Northern Pike and Other Non-Native Fish Suppression in Pend Oreille Subbasin, Box Canyon Reservoir: Lessons Learned* – Joe Maroney, Kalispel Tribe of Indians – Presentation
- *Northern Pike Suppression in Lake Roosevelt and Walleye and Bass Suppression in the Sanpoil River* – Holly McLellan, Colville Confederated Tribes – Presentation
- *Strategies for Managing Non-native Predatory Fish Species in Washington (with a focus on efforts in anadromous zone)* – Bill Baker, WDFW – Presentation
- *Understanding the Sources of Pike in the Columbia River Basin and eDNA Fundamentals* – Kellie Carim, U.S. Forest Service – Presentation
- *The Intertwined Relationship of Northern Pike and Flowering Rush Observed in Montana* – Peter Rice, University of Montana and Virgil Dupuis, Salish Kootenai College – Presentation
- *Invasive Northern Pike Management in Alaska* – Kristine Dunker, Alaska Department of Fish and Game – Presentation
- *Evaluation of a long-term predator removal program: abundance and population dynamics of invasive northern pike, Yampa River, Colorado* – Kevin Bestgen and Koreen Zelasko, Colorado State University – Presentation

- *Approach for Economic Analysis of Northern Pike Impacts and Control Efforts* – Bill Jaeger, ISAB; David Kling, OSU; James Sanchirico, UC Davis – Presentation

March 1, 2019

- *Overview of Mid-Columbia Public Utility Districts' Predator Control Programs*
  - Grant County PUD – Curt Dotson – Presentation
  - Chelan County PUD – Scott Hopkins – Presentation
- *Cumulative Effects of Avian Predation on the Survival of Upper Columbia River Steelhead: Implications for Predator Management* – Allen Evans and Quinn Payton, Real Time Research – Presentation
- *Predation in the Columbia River and Elsewhere, What We Know* – John Plumb, Quantitative Fisheries Ecology Section, USGS – Presentation
- *An invader in salmonid rearing habitat: current and future distributions of smallmouth bass (Micropterus dolomieu) in the Columbia River Basin* – Julian Olden, University of Washington – Presentation
- *YY not? Use of YY Males for Eradication of Invasive Brook Trout Populations* – Dan Schill, Fisheries Management Solutions – Presentation

This ISAB review has been closely coordinated with the concurrent ISRP Mainstem and Program Support Category Review, which includes the Fish and Wildlife Program's predation management and monitoring projects implemented in the mainstem Columbia River that is accessible to anadromous fish. The ISRP's preliminary report was released April 4 (ISRP 2019-1), and the final report is due May 30, 2019. As part of the review, joint ISAB and ISRP members benefited from briefings and discussions with the project proponents in February and March 2019:

- *Sea Lion Non-Lethal Hazing* – Doug Hatch and John Whiteaker (Columbia River Inter-Tribal Fish Commission
- *Development of Systemwide Predator Control* – Mac Barr (Oregon Department of Fish and Wildlife) and Steve Williams (Pacific States Marine Fisheries Commission)
- *Avian Predation on Juvenile Salmonids* — Dan Roby (Oregon State University) and Ken Collis (Real Time Research)

The briefings provided invaluable information to the ISAB on predator impacts and risks, management effectiveness, and project and species monitoring. The presenters were also invited to share relevant published and gray literature, which improved our report.

B. Key past ISAB findings, assumptions, and observations

Past reviews by the ISAB, ISRP, and Independent Economic Analysis Board (IEAB) have highlighted important assumptions and observations that should be considered when reviewing the biological and economic impacts of native and nonnative predators and the effectiveness of predator control efforts in the Columbia River Basin. Some key assumptions and observations from past reviews were modified from the original. New assumptions and observations relevant to the current review were added.

Biological impacts of predators

- Native predators are fundamental components of aquatic food webs and play critical roles in aquatic and terrestrial ecosystems (ISAB 2008-4, ISAB 2011-1).
- Predators can have a significant impact on the survival of salmonids at all life stages in both pristine and developed watersheds (ISAB 2015-1, ISAB 2016-1).
- Losses to predators early in the salmonid life history (e.g., from bird and fish predation) might be mitigated by lower (i.e., compensatory) mortality during later life stages, especially if predators selectively remove the most vulnerable individuals (ISAB/ISRP 2016-1).
- Predation on adults during upstream migration (e.g., by sea lions) is of particular concern because it may reduce the potential spawning population more than removals of comparable numbers at earlier life stages (ISAB 2015-1, ISAB 2016-1).
- The overall impact of predators on a salmonid population depends on the feeding rate of individual predators (i.e., functional response), number of predators, and length of time the salmonids are vulnerable (ISAB 2011-1, ISAB 2015-1). These factors can be combined with the abundance of the prey to estimate the total mortality for the prey population as a whole (ISAB 2016-1). Such calculations should consider that predator species often, for one reason or another, selectively consume one prey species or size class within a given species more than another.
- Mortality caused by individual predators is typically depensatory; i.e., each predator kills a higher proportion of the prey population as prey abundance decreases. The impact on a prey population from an individual predator decreases when more prey are available because the predators become satiated and reduce their feeding rate (ISAB 2011-1, ISAB 2015-1, ISAB 2016-1).
- The typical depensatory functional response of individual predators can be offset by an increase in the number of predators due to aggregation in the short term or increased predator reproduction and abundance in the long term. Thus, for example, large releases of hatchery fish can affect predation of natural-origin fish indirectly by influencing the behavior and dynamics of predator populations (ISAB 2015-1, ISAB/ISRP 2016-1). This is an example of the “numerical response” of predators to prey density (ISAB 2016-1).

- Numerical responses of predators due to past or contemporary abundance levels of salmonid prey may increase or decrease predation. Life-cycle models need to be developed to integrate the effects of multiple subgroups of fish passing through, occupying, and using resources across multiple habitats (ISAB 2018-3).
- Native and nonnative fish species with life histories that coincide with salmonids could dilute apex predator effectiveness by increasing overall prey densities at particular life stages (ISAB 2016-1).
- The role of predators in maintaining community structure and ecological diversity is often poorly understood (ISAB/ISRP 2016-1).
- 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 long term (ISAB 2011-1). In some cases, this is well understood, as in the case of keystone predators (ISAB 2016-1).
- In the Columbia River system, little is known about the effects of selective predation on phenotypic (e.g., life-history variation) and genetic diversity of salmonids or how to mitigate these effects (ISAB 2018-3, ISAB 2015-1).
- Predicting the impact of predation on prey populations is complicated, especially when it interacts with other factors such as climate change beyond historical norms (ISAB/ISRP 2016-1).

Economic impacts of predators

- Our understanding of linkages and interaction between natural and human systems is important for recognizing and appreciating the causes of and solutions for predation problems. Without modeling the human components, it may not be possible for salmonid life-cycle models to adequately identify or quantify important metrics for policy makers (ISAB 2017-1). The more that economic models and analyses can be integrated into the life-cycle models the more valuable they will be to policy makers and managers. To set priorities, policymakers and managers will need to evaluate tradeoffs based on differences in cost, effectiveness, timeliness, and other criteria.

Effectiveness and benefits of predator management control efforts

- In cases where the introduction and spread of a nonnative species can be prevented or delayed, this can often be a highly effective and cost-effective measure (ISAB 2013-1). Even where such measures are expected only to delay rather than prevent the introduction of a nonnative species, the social and economic value of these efforts can be quite high (e.g., IEAB 2010-1, IEAB 2013-2).
- Novel predator regimes are often linked to human actions, including accidental and intentional introductions, commerce, direct and indirect effects of habitat alterations, and other regulatory interventions. These include, for example, changes to and management of the hydrosystem and shipping channel dredging. Thus, habitat restoration can be an important strategy to reduce predation pressure at various life stages in the salmonid life cycle (ISAB 2018-3).

- The second principle of the 2014 Program's predator management strategy assumes that predator management is necessary to improve the survival of salmon, steelhead, sturgeon, lamprey, and native resident fish species in the basin. However, this assumption has seldom been evaluated quantitatively (ISAB 2018-3).
- The 2014 Program goal to develop a single common metric to evaluate predation is understood to have limitations and should not be viewed as a sufficient metric for management decisions. Management decisions would need to consider, for example, short-term effects of predation on harvest opportunity and spawner abundance, long-term effects on population viability and ecosystem resilience and sustainability (ISAB 2016-1, ISAB 2018-3), as well as costs, effectiveness, and other social, legal and policy factors.
- Compensatory mortality is the most important uncertainty to address when evaluating the effectiveness of predator management actions (ISAB 2016-1). Considerable uncertainty regarding compensatory mortality over the life cycle can change the demographic outcome of predation (ISAB 2018-3). In the case of predatory fishes, ecological interactions among the potential predators, and with alternative prey, are also very important.

III. SUMMARY ANSWERS TO COUNCIL QUESTIONS

Council Question 1. ***Given the Basin's current predation control efforts and the ISAB's predation metrics report (ISAB 2016-1), what information is needed to develop a common metric to assess the impact of predation across all predator species?***

Impact of predation can be measured at several temporal and spatial scales. To measure impact of a predator on a focal prey species, we need to know (1) total predation by a predator at each point in time or space where it occurs, (2) subsequent predation by all other predators at each point in time or space where they occur, and (3) cumulative survival probability for the focal prey species over its full life history or to a consistent point of reference (e.g., Bonneville Dam). Measurement of predation is more difficult for some predators than for others and in certain locations, such as the ocean portion of the life cycle of salmon and steelhead.

1. A better stratified sampling program needs to be implemented to estimate and evaluate Basin-wide predation. Information on Basin-wide predation is less well developed because not all predator groups are measured in each year; not all birds nest in accessible colonies; not all species of birds are monitored; not all reservoirs have programs to measure abundance and predation by fish predators; and, not all pinniped species are monitored in the estuary. Information in the Basin should be collected throughout the system and statistically representative of the system.
2. The biological "value" of a fish to a population is proportional to future survival of that fish from the point or time it is first detected or marked to the arrival of the adult fish on the spawning grounds (or some other consistent reference point such as Bonneville Dam).[2] Fish consumed at different stages in their life cycle have different consequences for the eventual goal of increasing returning adult salmon. Generally, mortality later in the life cycle is more detrimental than mortality earlier in the life cycle. Economic costs of the different interventions could modify decisions about preferred management actions.
3. Information on survival of salmon throughout the life cycle (e.g., the Comparative Survival Studies [CSS], survival estimates by upper Columbia River PUDs, SARs) will be critical for development of a common metric to assess the impact of predation across all predator species. Survival in the ocean can be measured, but our understanding of the causal factors is much more limited. Survival of returning adults upstream of Bonneville and factors related to it are better understood and have been used in life-cycle models to better understand overall impacts of predation.

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[2] This implicitly assumes that all adults are equally valuable, but this may need to be modified to account for a hatchery vs. a wild fish, for example, or contributions to spawning by different ages (e.g., mini-jacks vs. an older adult). This issue is beyond the scope of this report.

4. It is unlikely that the current life-cycle models will have adequate information to accurately model compensation by predators or prey in the near future, with the exception of avian predators for some salmonids. However, it will be possible to model the value of a fish removed by predation assuming a range of biologically relevant levels of subsequent compensation in the life cycle. Most current life-cycle models ignore compensation by both the prey and predators. The amount of compensation is difficult to measure because (a) ocean conditions where the majority of mortality occurs are highly variable and not consistent in effects, (b) there is a lack of contrast in the amount of predation across different years, and (c) there is a lack of information on the abundances and interactions among predators.
5. The life-cycle models should be run using a range of environmental conditions that are currently related to survival or may reflect future environmental conditions (e.g., climate change) to assess both the mean and variability in subsequent survival. These different model runs can be used to assess outcomes such as quasi-extinction (i.e., the probability that the number of returning adults is below some critical threshold).
6. Cost effectiveness of predator control needs to be included when deciding where and what kinds of predator control measures to implement. As a hypothetical example, it might be more expensive to implement a larger predator control program earlier in the prey's life cycle where the value of an individual fish is less than to implement a smaller predator control program later in the life cycle where the total value of "saved" fish is greater. Assessment of cost effectiveness of different predator control programs in the Basin and their collective system-wide survival effectiveness are not consistent throughout the Fish and Wildlife Program.

<u>Council Question 2.</u> If current predation control efforts are not sufficient to contribute toward protecting focal species, what type and level of effort are needed?

At this time, we do not know whether efforts to control predation are adequate. Predator management in the Columbia River Basin currently focuses on individual predator species and survival of the portion of their prey that are salmon and steelhead. Most predation analyses used to develop management actions in the Basin are fragmented and ignore other factors throughout the life cycle of focal species that influence their survival (e.g., other predators, hydrosystem survival, adverse temperatures, hatchery influences, ocean conditions, and harvest).

1. A system-wide, ecosystem-based approach for assessing and managing fish, avian, and pinniped predators collectively is needed to create a more effective and consistent framework for developing and implementing control actions. We need improved life-cycle models that integrate environmental conditions, human behavior, and populations of salmon, steelhead, and other species. Assessing impacts of all potential predators throughout the Columbia River Basin will require integrated analytical tools, such as life-cycle models, measurement of SARs, and density dependence analysis.

This type of analysis would allow policy makers and managers to identify (a) locations where life stages of prey species are most susceptible to different predators and (b) the relative benefits of decreasing salmonid mortality at different life stages, making control efforts more biologically and economically effective.

2. A number of important questions could be answered as part of a system-wide ecosystem approach:
    - Does bird dissuasion reduce total avian predation, or does it shift the location of that predation or result in greater predation by other predators (a compensatory response)?
    - Will bird dissuasion in the Columbia Basin protect focal species at the risk of endangering other focal species in other regions, such as the Klamath Basin or San Francisco Bay?
    - Will lethal removal of a limited number (i.e., 10%) of selected pinnipeds near Bonneville Dam reduce predation on adult salmonids or merely allow other pinnipeds to increase their consumption?
    - Is northern pikeminnow (subsequently referred to as pikeminnow) control leading to increased survival to the adult stage of focal fish species, and is this the most cost-effective way to increase survival?
    - Does the catch-per-unit-effort monitoring approach for pikeminnow, smallmouth bass, and walleye provide an accurate abundance index for estimating predation losses? The control project’s methods have not been recalibrated since research conducted in the 1980s.
    - Can we measure more complicated food web effects, such as those where removing one fish predator allows other fish predators to flourish and cause greater damage?
    - Are there other nonnative, aquatic animals in the Basin that might affect predation on focal species (e.g., American shad, invasive crayfish, channel catfish, largemouth bass, yellow perch)?
    - Can early detection using newer and more cost-effective methods (e.g., environmental DNA [eDNA] or public alert reporting) coupled with a rapid response program for high risk predators be effective in delaying spread of predators and cost effective?
    - How would changes in aquatic vegetation (native and nonnative) and habitat restoration projects influence vulnerability of salmonids to predation, and how do the costs of these efforts compare to the costs of predator control programs?
    - How could we assess predation on species produced below Bonneville Dam, especially species not routinely tagged such as chum salmon?

<u>Council Question 3.</u> Would concentrating additional efforts on predator management as opposed to hydrosystem actions, habitat enhancement or other management actions be more effective in improving focal species survival?

Benefits associated with hydrosystem changes, habitat enhancement, or other management actions likely will be reduced or nullified if predator control does not occur. Substantial changes and additions in predator management in the Fish and Wildlife Program are needed. As described previously, a system-wide, ecosystem-based approach for assessing and managing fish, avian, and pinniped predators collectively is required to develop and implement effective predator control actions. Actions that restore or alter habitat can either benefit or adversely affect both salmonids and their predators (e.g., riparian restoration to minimize stream warming), making it even more important to have a system-wide ecosystem-based approach. Even with more rigorous information on predation throughout the Basin, a portfolio of approaches for reducing mortalities of salmon and steelhead will likely provide the most biologically effective and cost-effective management alternatives.

1. Estimates of population indices and predation indices for pikeminnow, smallmouth bass, and walleye were developed in the late 1980s and should be updated to provide critical data for managing the Northern Pikeminnow Management Program (NPMP). Methods for obtaining necessary data should be verified and calibrated based on thorough population estimation. Tagging data from the Sports Reward Program could be used more effectively to estimate pikeminnow population size, movement behavior, and habitat use, all of which are important for assessing and focusing control efforts.

2. Targeted efforts to remove pikeminnow near areas of greatest pikeminnow predation, such as forebays and tailraces of dams, might more effectively reduce pikeminnow predation. Monitoring by the NPMP consistently indicates that pikeminnow abundances and predation impacts are greatest in these locations, but the Program pays for pikeminnow harvested anywhere from the mouth to Priest Rapids Dam on the Columbia River and Hells Canyon Dam on the Snake River. Focused harvests could be conducted either by fisheries agencies in restricted areas or by sports harvest in safe zones adjacent to areas of higher predation. Incentives could also favor harvest near Bonneville Dam where the value of a juvenile salmon migrant to adult returns is greater.

3. After 28 years of pikeminnow removal, direct estimation of the benefits for salmon and steelhead is needed. The NPMP has focused on reducing numbers of pikeminnow but has not directly measured the benefit of predator control actions on juvenile salmon and steelhead or returning adults. The NPMP should develop its field studies or models to provide more direct measures to evaluate the effectiveness of the control actions

4. Risks of northern pike invading the anadromous reaches of the Columbia River make early detection and rapid response an important addition to the current predator control program. Managers should design a rapid intensive suppression action plan to be triggered when northern pike or other

nonnative predators are first detected in the Basin. Important locations to monitor include floodplain ponds and lakes, where illegal introductions by anglers may be likely.

5. To reduce the impacts of nonnative predators in tributaries of the Columbia River, efforts to minimize stream warming through riparian and hyporheic restoration should be targeted at the current upstream limits of warmwater predators to maintain cooler water for native salmonids and restrict the invasion by nonnative predators, such as smallmouth bass.
6. Colonies of piscivorous birds shift to various locations throughout the Basin, sometimes to areas where management is difficult or restricted (e.g., bridges, dams, refuges). Managers should identify potential locations where large-scale management of avian predators is not possible and implement actions in those areas to discourage colonization. Monitoring the movement of all avian predators is necessary to assess whether these movements have decreased predation or merely moved it to another place in the Basin.
7. Websites and public education programs of state and federal agencies in the Basin should actively disseminate information on the importance of controlling the distribution of nonnative predators. Currently, these websites promote fishing opportunities for these species but do not highlight regulations to prevent the transfer of the fish to other water bodies. Existing boat inspection programs could integrate such information campaigns about nonnative fish and increase detection of nonnative fish transportation. Managers could work with political leaders in all states in the Columbia River Basin to ensure that regulations are enforced and that fines and penalties are major disincentives for illegally transferring nonnative fish between water bodies.

<u>Council Question 4.</u> Can we rank (from low to high) predator impacts on focal species, and then rank (from low to high) which current management activities would be most effective in reducing the "higher" ranking predation impacts?

Ranking predator impacts and the management activities that would be most effective in reducing the high-ranking predator cannot be accomplished across all combinations of predators and their salmonid prey without synthesis of available Basin-wide information and analysis of salmonid survival throughout their life cycles. A Basin-wide approach for the Fish and Wildlife Program should include (a) information on abundances, distributions, and interactions of predators and their prey, (b) measures of effectiveness of management actions in increasing adult survival and population responses, (c) early detection and rapid response plans for new predator invasions, and (d) comparison of cost effectiveness of the range of possible management actions.

Predator impacts on focal species

Impact of pinniped predation varies among salmonid species and run timing. Where species, timing, and pinniped abundance coincide, there is high likelihood of strong negative impact on returns. Pinnipeds likely have the greatest impact on smolt-to-adult returns (SARs) because they consume fish close to the end of their life cycle. Colonial birds in certain locations, such as the predation on steelhead in the upper Columbia River, also may have disproportionate impacts. However, accurately ranking impacts of the predators on focal species cannot be accomplished until we take an ecosystem and life cycle approach. A holistic analysis would determine whether each predator has an additive or compensatory effect on the focal species and assess their system-wide impact (as opposed to a single reach or reservoir). A more targeted sport rewards program for control of northern pikeminnow would require additional monitoring to ensure implementation.

1. When considering the roles that predation may play in recovery of focal species, it is important to recognize that predators and prey display great diversity in life history traits (e.g., body size, timing of life-history stages, habitat use, and behavior during seaward and return migrations). Research and monitoring have tended to examine either juvenile and adult salmonids and single types of predators, resulting in uneven coverage and a dearth of information on combinations of species and life history forms.

2. Seaward migrating salmonids from the Columbia River differ in size, timing, travel rate, habitat use, and other factors that might affect vulnerability to different predators. For example, from smallest to largest size they are pink, chum, sub-yearling Chinook, sockeye, yearling Chinook, coho, and steelhead, and there is substantial variation in size geographically and interannually. Wild and hatchery origin fish typically differ in body size and also in emigration timing, but even wild populations can differ in ways that might affect vulnerability. Many studies of predation do not report all or even most of these species, and patterns reported are often complex.

3. Fish predator species differ in body size, foraging behavior, habitat use, and other attributes that may affect predation on salmonids. These differences in predators influence their interactions with salmonid stocks that vary in size and timing. For example, smaller Chinook salmon are more vulnerable to predation by northern pikeminnow than are larger conspecifics. Additionally, larger yearling smolts that migrate to sea earlier in the season when water temperatures are cooler and flows are higher are less vulnerable to piscivores. Salmonid species differ markedly in the extent to which they migrate along the littoral zone or the offshore waters of the lower Columbia River and estuaries, which influences their risk of encountering different types of predators.

4. Pinnipeds in the lower Columbia River, especially California and Steller sea lions, likely differ their predation on adult salmonids. These two pinniped species have different seasonal abundance patterns, with a much narrower peak in spring by California sea lions compared to the larger-bodied Steller sea lions. Some populations of both predators and prey may spend more time in the estuary and lower river than others, which also is likely to affect vulnerability. Species such as chum salmon and winter steelhead that spawn largely below Bonneville Dam are less well enumerated than upriver runs, thus the impacts of predation on such species also merit consideration.

5. Assessment of predation by marine mammals should consider predation on juvenile as well as adult salmon. Predation by marine mammals, especially harbor seals, on juvenile salmonids has not received adequate attention. A recent analysis of predation in the Puget Sound concluded that harbor seal predation on smolts may have larger impacts than commercial and recreational fisheries or predation by killer whales.

6. The ISAB compiled tables of the major predators and categorical values of high, intermediate, and low vulnerability of salmonid prey to them (Tables 1 and 2). The tables illustrate that seasonal timing of adult returns and differences in body size affect vulnerability of salmonid species and runs. This synthesis could be expanded by regional scientists to improve general understanding of relative impacts and risks of combinations of predators and prey and to identify locations that are most in need of further study.

Management activities

1. Effectiveness of management activities to control predators varies by predator and prey species, life cycle, and location of predators and prey. However, recent work on avian and pinniped predators may lead to a better evaluation of the efficacy of management actions. Evans et al. (2018a) and Payton et al. (2019) concluded that Caspian tern predation causes greater mortality of upper Columbia River and Snake River juvenile steelhead than all other sources of mortality combined and found an inverse relation between tern predation and steelhead SARs. The Fish and Wildlife Program should determine if approaches developed for avian predators can be adapted for other predator species in an ecosystem context.

2. An important area for additional study is pinniped control alternatives. Pinnipeds annually consume between 51,000 to 224,000 adult spring Chinook in the Columbia River below Bonneville early in spring. Hazing pinnipeds has been ineffective, and lethal removal of pinnipeds has been authorized. Lethal removal of pinnipeds at Willamette Falls coincided with a significant increase in winter steelhead passing over the falls in 2018 as compared to the previous two years, but these adult counts are by no means proof of an effect on overall survival. More thorough evaluation of the biological and social outcomes of lethal removal will better inform future decisions.

3. The NPMP is based on studies completed over 30 years ago, and we do not know if the relative abundance and relationships between multiple predators and prey have changed. Those studies need to be repeated using tools that were not available earlier (e.g., eDNA, PIT tags and detectors) and as part of a system-wide, ecosystem-based approach for assessing and managing predators collectively.

<u>Council Question 5.</u> In consideration of [ISRP 2018-3] regarding Northern Pike, do we know what level of suppression (exploitation) through gill net removal, angler removal or other methods is needed to reduce the population in Lake Roosevelt to a level sufficient to reduce risk of emigration from the lake or risk to other focal management species?

Based on the inexorable invasion by northern pike downstream throughout tributaries of the upper Columbia River Basin above Grand Coulee Dam over the past 65 years, it is likely that even with the best efforts in public education, early detection, and control or eradication, pike will eventually invade the anadromous zone, either naturally or by human agents. Given this, the ISAB was able to reach the following conclusions:

1. It is not possible to estimate the level of suppression necessary to eliminate the risk of emigration of pike downstream from Lake Roosevelt because there is no simple relationship between abundance and the probability of emigration or establishing a population downstream.
2. Each individual female pike produces tens of thousands of eggs, so given the right conditions emigration by even one male and one female pike could produce thousands of juveniles. Nevertheless, evidence from other organisms indicates that reducing the numbers of fish emigrating from Lake Roosevelt will delay the establishment of new populations downstream. Reducing establishment also reduces new source populations that enhance further spread, either naturally or by humans.
3. Evidence from invasions of other organisms indicates that eradication is often possible only at the earliest stages, so once detected, rapid eradication of newly established populations is paramount.
4. Pike can be suppressed with great effort and expense, especially in reaches without much suitable habitat, but likely will not be eradicated from a large river like the Columbia or its major tributaries, especially if there are source populations within about 12 miles (20 km) by river that supply immigrants. Eradication has been successful only in individual lakes, reservoirs, or small watersheds, and so might be successful in isolated ponds and lakes that become invaded.
5. Evidence from past introductions indicates that about as many invasions of new waters were caused by illegal stocking as by dispersal of pike themselves, similar to the pathways of illegal introductions of nonnative fishes in another western state. This indicates development of additional efforts to discourage illegal stocking of pike by humans and analysis of their cost effectiveness are warranted.
6. It is essential to develop a monitoring program capable of accurately detecting newly established pike populations throughout the anadromous zone, not just near the current invasions. Evidence from the Colorado River Basin indicates that illegal introductions of pike into lakes and ponds, including those in the floodplain, are especially likely.
7. Shallow, vegetated floodplain sloughs, like those in the lower Columbia River, will likely provide ideal habitat for pike spawning, rearing, and growth. A species distribution model could be developed to estimate the habitat in the Basin most likely to be invaded and how it could change with a changing

climate. Such information will be valuable in designing more cost-effective targeted monitoring activities.

8. To be successful in reducing mortality of focal salmonids, control efforts will need to be extensive, occurring river-wide where habitat is suitable for pike, and ongoing to be most effective for protecting salmon populations.

<u>Council Question 6.</u> What are the likely ecological impacts of northern pike should they enter the Basin's anadromous waters?

Pike are highly invasive, and through predation are likely to drastically reduce salmonid abundance, especially in low-gradient river segments with wide floodplains. The evidence from other research supports the following conclusions:

1. Pike are highly piscivorous and prefer salmonids but can subsist on other prey including invertebrates. As a result, they are capable of driving preferred prey species to very low levels or extinction.
2. All sizes and ages of pike (yearling and older) can eat salmon fry, parr, and smolts and reduce their abundance to low levels in habitats where they overlap.
3. If salmonids have no refuges from predation (i.e., habitats that are unsuitable for pike), pike are likely to reduce salmonid numbers and can cause salmonid populations to collapse. Varying levels of coexistence may occur where habitats are less suitable for pike.
4. Pike typically occupy relatively shallow, vegetated floodplains and shoreline habitat from which they ambush prey. Consequently, salmonid species and life stages that migrate in open water near the surface, such as smolts, may be less vulnerable than others, such as pre-smolts, that forage or overwinter in habitats occupied by pike.

IV. IMPACTS OF PREDATORS AND EFFECTIVENESS OF PREDATOR CONTROL

A. Ecosystem perspectives

Knowledge of the structure and function of ecosystems provides an essential context for understanding the interactions of native and nonnative predators with salmon, steelhead, and other aquatic organisms in the Columbia River Basin. This framework provides the fundamental basis for developing potential control measures and identifying locations and seasonal periods for implementing actions more effectively. All too often, predator control actions are designed for single predators and selected focal species that comprise only a portion of their prey, which never encompass the array of interactions that determine ecological outcomes for the predator or their prey. Suppression efforts on one location may result in increases in other predators (e.g., pikeminnow and smallmouth bass) or dispersal to other locations where the impacts of predation are even greater (e.g., movement of cormorants and terns to islands in the upper Columbia River).

Previous ISAB reports thoroughly described the importance of understanding food webs and ecosystem processes for managing fish and wildlife in the Columbia River Basin (ISAB 2008-4, ISAB 2011-1, ISAB 2011-4, ISAB/ISRP 2016-1). The ISAB report on Columbia River Food Webs (ISAB 2011-4) called for a broader framework for managing predation:

> *"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."*

Fish communities in the Columbia River Basin contain 53 species of native freshwater and marine fishes (ISAB 2011-1; Appendix B). These species occur in different subbasins of the river network, and most provinces contain approximately 30 species. Though salmon, steelhead, other trout, and sturgeon receive the most attention in this region, fish communities commonly include sculpins, lamprey, suckers, and cyprinids (pikeminnow, chubs, dace, and other minnows) that play major trophic roles as herbivores, detritivores, insectivores, and piscivores and provide prey for both aquatic and terrestrial predators. A substantial portion (47%) of these native species are predators during some phase of their life. The average trophic level of the native freshwater fish species in the Columbia River Basin is 3.4, ranging from 2.3 to 4.5 (plants or detritus =

1, primary consumers [invertebrates or herbivorous fish] = 2, secondary consumer [carnivores or omnivores] = 3, tertiary consumer [predators] = 4, predators of tertiary consumers = 5).

Fish communities in the Columbia River Basin also contain approximately 47 species of nonnative fishes, with about 24 nonnative species in each province (ISAB 2011-1; Appendix B). This number included two recently detected species, oriental weatherfish (*Misgurnus anguillicaudatus*) and Amur goby (*Rhinogobius brunneus*), which were not known during the ISAB review in 2011. Nonnative species account for almost half of the number of fish species known to occur in the Basin. In most rivers and lakes of the Columbia River Basin, the abundance of nonnatives typically is lower than the abundance of native fish, but there are locations where nonnatives are numerically abundant. For example, walleye and yellow perch are numerically dominant in Lake Roosevelt above Grand Coulee Dam (Harper et al. 1981). Nonnative fishes include centrarchids (bass, crappie, other sunfish), cyprinids (carp), percids (yellow perch and walleye), catfishes, clupeids (shad), salmonids, and unusual species associated with the aquarium trade or transported in ship ballast water. Most of these species are sport fish native to other regions of the United States, and state agencies maintain stocking programs for some of these species in all states of the Columbia River Basin. Many of these species are tolerant of warm water and are more likely to extend their distributions when regional warming occurs, though some species, such as brook trout and brown trout, are cold or cool water species.

Predation control actions in the Columbia River Basin over the last several decades have focused on reduction of northern pikeminnow, interference or reduction of Caspian tern, double-crested cormorants, California and Steller sea lions, and harbor seals, and recent suppression of northern pike in Lake Roosevelt above Grand Coulee Dam. With the exception of northern pike, all of these actions are intended to decrease the abundance of native species. Long-term concern for major declines in the abundance and potential extirpations of salmon and steelhead in the Columbia River Basin tends to focus the attention of the public and river managers on species they prefer to control, and we often lose sight of the human role in fish predation. In many ways, we too are predators competing for common prey. The ISAB Food Web Report (ISAB 2011-1) noted:

> *"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 nonnative shad population. In comparison, total predation mortality on anadromous salmonids by avian and mammal predators is unlikely to exceed 20% (see Chapter C.2)."*

FOOD WEBS

Predators are fundamental components of aquatic food webs (ISAB 2011-1). Similarly, the majority of nonnative fish introduced into the Columbia River Basin are predators. Most attention in the Fish and Wildlife Program has focused on potential predation by pikeminnow, smallmouth bass, walleye, channel catfish and recently northern pike. However, many other native species (e.g., bull trout, cutthroat trout, rainbow trout, brook trout, sculpins) and nonnative species (e.g., largemouth bass, yellow perch, crappie) consume juvenile salmonids (Hillman et al. 1989, Hillman and Miller 2002, Monzyk et al. 2013).

Predation often is viewed simply as the consumption of a particular prey of interest, but the process of predation and diversity of predators are fundamental attributes of food webs and ecosystem processes. Native species of both predators and prey have evolved within a complex landscape and intricate food web. Even a simplified food web for the Columbia River prior to hydrosystem development illustrates the numerous interactions and important flows of energy for the native fish community (Figure 1).

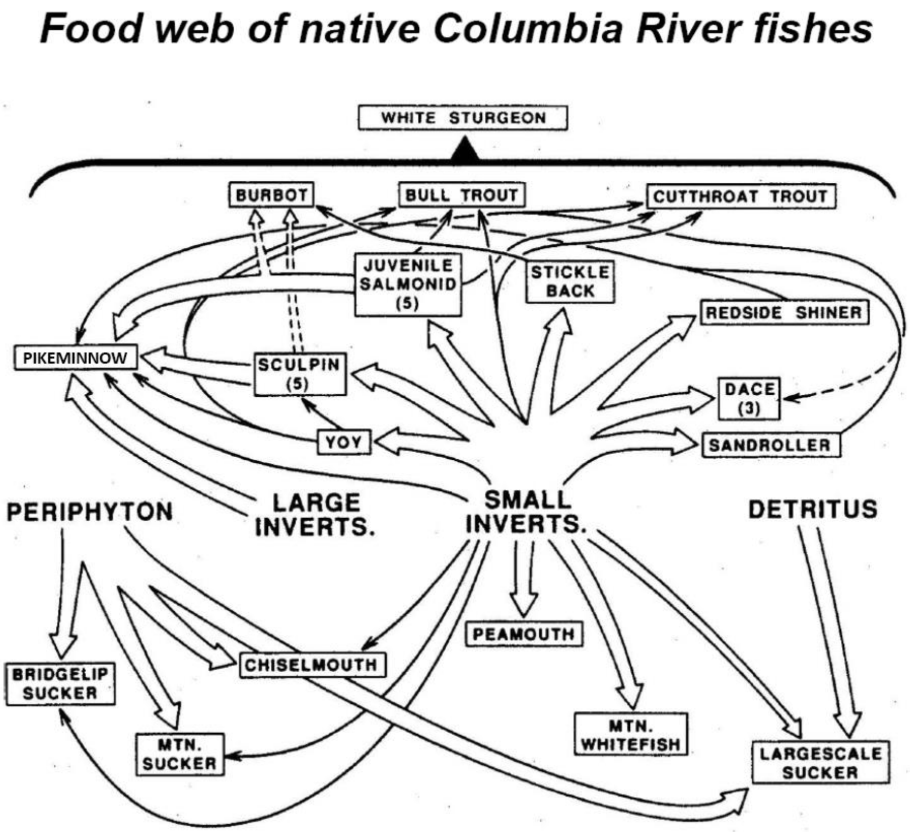

Figure 1. Hypothetical food web of the lower and middle Columbia River before 1800. The width of the trophic link represents the relative importance of the prey to its predator. Dashed arrows denote the assumption that burbot prey mostly in deep lakes in the Basin. Sturgeon are capable of eating a variety of prey. Modified from Li et al. (1987) as illustrated in ISAB 2011-1.

Predator control must be considered in a food web context because of complex and unanticipated response to single-predator suppression. Prey not only transfer energy to a predator, they modify the food base of the aquatic ecosystem, influence nutrient cycling, move matter and energy between different habitats and reaches of the river, and alter behavior of other species. Depending on the complexity of the food web and the types of predators, the abundance of different trophic levels can be determined by the flow of energy from the base of the food web in which the abundance of each successive trophic level increases (bottom up control) or by predation of secondary and tertiary consumers in which the predator diminishes abundance of a prey, which in turn increases the food of that trophic level (top down control). Changing the abundance of a particular predator can influence not only the abundance of its prey but also the abundance of the food resources of the prey and nutrients available within the ecosystem. For example, in top down control the addition of a piscivore can increase the clarity of a lake (Carpenter et al. 1985). The piscivore reduces the abundance of fish that consume herbivorous zooplankton, which in turn becomes more abundant, causing a decrease in phytoplankton leading to an increase in water transparency. Predator control often ignores linkages in the food web that determine these key ecosystem processes. Introduction of nonnative predators can change food web structure and energy flow, even if they heavily consume a focal prey such as juvenile salmonids, because they add additional predatory interactions and may change the food web connectivity and abundance of other species that compete for habitat and food resources (Baxter et al. 2004, Eby et al. 2006).

Native predators presumably are adapted to the Columbia River Basin’s suite of pathogens, competitors, and predators (except nonnatives) and may retain predominant status as predators of salmonids, even in the face of uncertain future food webs. Introductions of nonnative fish species often are not successful initially, but the probability of establishment increases with repeated introductions or colonization events (Moyle and Marchetti 2006). A conceptual model of aquatic invasions based on empirical evidence and theoretical assembly rules provides a context for understanding the outcomes of nonnative fish species introductions (Figure 2; Moyle and Light 1996, Moyle and Marchetti 2006). Nonnative species disperse into or are transported into an existing species pool of native and nonnative organisms. They must physiologically and behaviorally adapt to the environmental conditions in their new habitat, and some will not be able to tolerate these conditions. If their population becomes established, they will experience biological resistance (e.g., prey availability, competition, diseases, parasites) and demographic resistance (e.g., numbers introduced, ability to increase populations at low numbers). These factors will determine whether the nonnative species will become integrated into the aquatic community or will fail to become established. Upon establishment of the nonnative population, the abundances, trophic levels, functional traits, and behaviors of different species in the food web will shift, creating an altered aquatic community. Moyle and Light (1996) concluded that piscivorous predators are more likely to alter the fish assemblages of the recipient aquatic systems and that invasions are more likely to be successful in highly altered or disturbed ecosystems.

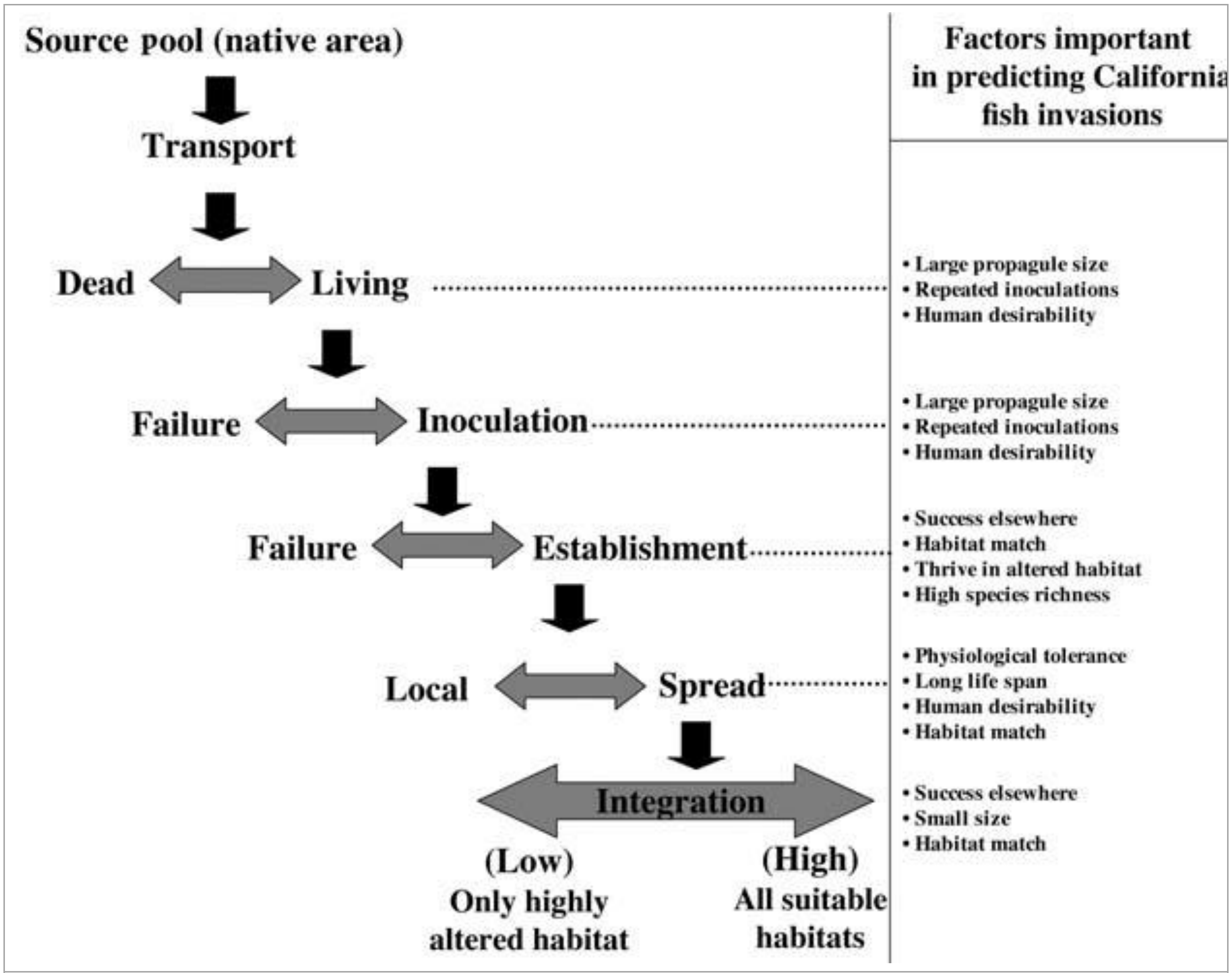

Figure 2. Stages in the invasion process for nonnative fish and biological and socioeconomic factors that influence success at each stage (Moyle and Marchetti 2006).

RELATIVE VULNERABILITY OF SALMONIDS TO DIFFERENT PREDATORS

Background

The ISAB recognizes that predation is a natural occurrence in the Columbia River, as in all systems, and results from complex interactions between predator and prey, including the behavior, size, morphology, and seasonal timing of both predators and prey. Moreover, neither salmonids nor their predators are by any means homogeneous; salmonid species and populations differ markedly, as do the different species of birds, fishes, and marine mammals that prey on them. These patterns result in marked differences in vulnerability. Specifically, predators often eat a non-random selection of the available prey with respect to body size. In some cases, the selection is for larger prey, perhaps because they are easier to see, easier to catch, or more profitable to consume than smaller prey (i.e., they provide more calories taken in than calories expended). However, in other cases smaller prey are more often consumed, perhaps they are easier to swallow by small predators, they inhabit areas more desirable for the predator, or other attributes. The complex community of Columbia River salmonids and their predators has two other important aspects. First, the timing of migration downstream by smolts and the return migration by adults are seasonally defined. Species and populations differ in the peak timing of migration, and they also differ in the duration of the migration—both factors can strongly affect vulnerability to predators. Second, some predators (birds and fishes) only affect juvenile salmonids but marine mammals also consume adults, and it can be difficult to compare predation on different life history stages in a consistent manner.

Methodological considerations

Predation is determined in different ways, and with different sources of error and bias, for different species. Fish predators are typically either killed and the stomach contents preserved and examined, or the contents are pumped from the live predator if it is to be released. Bird predation can be estimated from visual observations of prey in the bird's possession "bill load observations" for species that carry the prey whole in their bill, from chicks that regurgitate their meal, and from lethal samples (Collis et al. 2002). In addition, scans of bird colonies for PIT tags are an important source of data, but the proportion of the Columbia River runs that are tagged is not even by any means. Moreover, the ability to recover predator-consumed tags may vary significantly between predator species (e.g., Caspian terns vs. California gulls, Hostetter et al. 2015) Marine mammals are typically observed with prey, but diets can also be inferred from stable isotope analysis, from samples of the killed prey such as scales, and from fecal DNA.

Temporal and spatial considerations

In addition to sampling issues related to the determination of the prey, there are several other important things to consider when examining reports on predation. First, studies are not all contemporaneous. That is, some excellent work was done decades ago, and conditions in the river or the community of prey or predators may have changed, so the results must be examined carefully. Species that once were scarce may now be more abundant, for example. Second, studies are not all conducted in the same place. Some emphasize the estuary, others the vicinity of a dam or set of dams, or a reservoir, and so forth. Consequently, clear results in one study may be contradicted in another.

Considerations related to the reporting of predation

The reporting of predation is much more complicated than it might first appear. In some cases, a given number of predators are examined and the numbers of different prey salmonids reported. This is essentially per capita predation and provides information on predator differences. However, the numbers of predators are needed before such information can be scaled to estimate effects on the prey. For example, a species of predator might prey heavily or even exclusively on a type of prey, but the predation might be inconsequential to the prey if the predator is rare. Estimates of predator abundance are often much more difficult to accurately obtain than per capita consumption, and abundance can change markedly from year to year from natural processes and as a result of directed control efforts. In addition to the distinction between the number of prey consumed per predator and the number consumed in total, the consequence of the number eaten for the prey populations depends greatly on prey abundance. Even apparently heavy predation might be trivial to the population if the prey are numerous enough. As with predators, the absolute and relative abundance of salmonids as prey varies markedly from year to year and from place to place in the system.

Relative vulnerability of salmonids to predators: "straw dog" tables

Notwithstanding the issues raised here, and others that might also be raised, there is a need to obtain some sense of the relative importance of different species of predators for the different salmonid species and populations, and for other fishes of interest as well (e.g., white sturgeon, Pacific lamprey, etc.). As a first step in the process, we built two "straw dog" tables that list the major predators and the different salmonids, and we propagated the table with categorical values of high, medium, and low vulnerability. We call these tables "straw dog" because they are designed to be criticized, modified, and perhaps even discarded. We do not intend, under any circumstance, for them to be used as the basis of policy. All the above considerations and more apply to them. Regardless of these weaknesses, the tables may serve to illustrate some important points. For example, seasonal timing of adult returns and body size differences result in marked differences in vulnerability of the different salmonid species and runs. Steelhead smolts are typically most vulnerable to bird predation but less vulnerable to fish predation than are sub-yearling Chinook salmon, and so forth. It is not our intent that the tables will be anything more than a framework that can be filled in by experts who have done the primary scientific work on this topic, and a basis for determining which combinations of predators and prey and locations are most in need of further study.

Table 1. Relative vulnerability of juvenile salmonids to avian and fish predators

Predator Species	Prey Species—Juvenile Salmonids						
	Chum Salmon	Pink Salmon	Sockeye Salmon	Coho Salmon	0+ Chinook Salmon	1+ Chinook Salmon	Steelhead
Avian Predators							
Double Crested Cormorants[a]	Low?	Low?	Medium	Medium	Low	Low/Medium	Medium
Caspian Terns[b]	Low?	Low?	Low	Medium	Low	Medium	High
American White Pelican[c]	Low	Low	Low	Low	Low	Low	Low
California Gull*[d]	Low	Low	Low	Low	Low	Low	Medium
Ring-Billed Gull*[e]	Low	Low	Low	Low	Low	Low	Medium
Glaucous-Winged Gull*[f]	Low	Low	Low	Low	Low	Low	Medium
Fish Predators							
Walleye[g]	Low?	Low?	Low?	Low?	Low?	Low?	Low?
Smallmouth Bass[h]	Low?	Low?	Low	Low	Medium	Low	Low
Channel Catfish[i]	Low?	Low?	Low	Low	Low	Low	Low
Northern Pikeminnow[j]	Low?	Low?	Medium	Medium	High	Medium	Low
Northern Pike (future—best guess)	Medium?	Low?	Low?	Low?	High?	Low?	Low?

Notes: Avian Predators

[a] Collis et al. (2001); Ryan et al. (2003)

[b] Antolos et al. (2005); Roby et al. (2003) Collis et al. (2001); Evans et al. (2012)

[c] Evans et al. (2012); Evans et al. (2016)

*Gull species are often grouped and simply regarded as gulls

[d] Evans et al. (2012); Evans et al. (2016); Hostetter et al. (2015)

[e] Evans et al. (2012); Evans et al. (2016); Hostetter et al. (2015)

[f] Collis et al. (2002)

Notes: Fish Predators

[g] Poe et al. (1991); Vigg et al. (1991); Wydowski and Whitney (2003); Sanderson et al. (2009). Walleye were ranked low due to their low abundance

[h] Poe et al. (1991); Rieman et al. (1991); Vigg et al. (1991); Fritts and Pearsons (2006); Sanderson et al. (2009)

[i] Poe et al. (1991); Vigg et al. (1991); Sanderson et al. (2009)

[j] Poe et al. (1991); Vigg et al. (1991); Beamesderfer and Rieman (1991); Rieman et al. (1991); Beamesderfer et al. (1996)

See the "straw dog" caveats in the text above.

Table 2. Relative vulnerability of adult and juvenile salmonids and eulachon, white sturgeon, and Pacific lamprey to marine mammals

Predator Species	Prey Species and Period of Vulnerability at Adult Life Stage for Salmonids											
	Mar-May[b]	Apr-Sep[c]	Jun-Jul[d]	Jun- Jul[e]	Jul[f]	Aug-Nov[g]	Aug-Nov[h]	Oct-Nov[i]	Nov-Mar[j]	Dec-Jun[k]	[l]	May-Sep[m]
	Spring Chinook	Summer Steelhead	Summer Chinook	Sockeye Salmon	Pink Salmon	Fall Chinook	Coho Salmon	Chum Salmon	Winter Steelhead	Eulachon	White Sturgeon	Pacific Lamprey
California Sea Lions												
Adult Prey	High	Medium	Low	Low	Low	Medium	Low	Low	High	Low	Low	High
Juvenile Prey	Low	Low	Low	Low	Low	Low	Low	Low	Low			
Steller Sea Lions												
Adult Prey	High	Medium	High	Medium	Low	Medium	Medium	Medium	High	Low	High	High
Juvenile Prey	Low	Low	Low	Low	Low	Low	Low	Low	Low			
Harbor Seals												
Adult Prey	Low	Medium	Low	Low	Low	High	Medium	Low	Medium	Low	Low	High
Juvenile Prey	High	Medium	High	Low	Low	High	Medium	Low	Medium			
Killer Whales[a]												
Adult Prey	High	Medium	High	Low	Low	High	Medium	Medium	Medium	Low	Low	High
Juvenile Prey	Low	Low	Low	Low	Low	Low	Low	Low	Low			

Notes

[a] Killer Whale Sources

Ford et al. (1998, 2016); Ford and Ellis (2006); Hanson et al. (2010); O'Neill et al. (2014)

Month at Adult Life Stage for Salmonids and Prey Species Vulnerability Sources

[b] Chasco et al. (2017); Wright and Murtagh (2018); Wargo Rub et al. (2019); Scordino (2010); Keefer et al. (2004)

[c] Wright and Murtagh (2018); Robards and Quinn (2002)

[d] Scordino (2010); Tidwell et al. (2018); Tidwell et al. (2019); NMFS BiOp (2019); Keefer et al. (2004)

[e] Scordino (2010); Peven (1987)

[f] Scordino (2010)

[g] Scordino (2010)

[h] Scordino (2010); Tidwell et al. 2018

[i] Scordino (2010); Tidwell et al. (2018); Tidwell et al. (2019); NMFS BiOp (2019)

[j] Scordino (2010); Wright and Murtagh (2018)

[k] Wargo Rub et al. (2019); Gustafson et al. (2010); NMFS Recovery Plan (2017); NMFS BiOp (2019); impacts to eulachon will vary inversely with adult eulachon abundance

[l] Wright and Murtagh (2018); NMFS BiOp (2019)

[M] Scordino (2010); Wright and Murtagh (2018); Tidwell et al. (2018)

See the "straw dog" caveats in the text above.

MULTIPLE SPECIES AND COMPLEX INTERACTIONS

When designing predation control programs, it is important to recognize that aquatic and terrestrial communities in the Columbia River Basin always include multiple predators and prey species. The ISAB and ISRP (ISAB/ISRP 2016-1) identified complex interactions of predators and prey as a Critical Uncertainty:

> *"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."*

Changes in the abundance and distribution of one predator may cause behavioral changes in either the prey species or other predators, leading to non-linear changes in predation on the focal prey (Sih et al. 1988). Because multiple predators may interfere with each other, the risk of prey mortality per capita of predators potentially decreases with multiple predator effects (Vance-Chalcraft and Soluk 2005). On the other hand, multiple predators may facilitate each other and increase predation risk. In a study of two streams in Michigan, predation of stream fishes by smallmouth bass was greater in the presence of herons (Steinmetz et al. 2008).

Effects of the abundance of predators may not be simply additive or multiplicative (ISAB/ISRP 2016-1). First, the life-history stage and location within the geographic range at which predation on salmon and steelhead occurs determine the relative impact on the populations (ISAB 2016-1). Mortality of a returning adult salmonid reduces the spawning population much more than mortality of a juvenile salmonid beginning its migration to the ocean. While decreases in the abundance of a predator may increase the survival of the prey in the short term, greater survival may simply increase prey availability and cause the abundance or efficiency of other predators to increase, resulting in no net benefit to the focal prey. This type of response is referred to as compensatory predation (i.e., a non-targeted predator fills a suppressed predator's role). Even where juvenile salmonid abundances increase in one portion of the river system or life-history stage because of predator control actions, these benefits can be negated in other locations and life history stages by other predators or other mortality-related factors, such as disease. This is an example of compensatory mortality of prey. Predation can disproportionately eliminate fish with lower fitness—those less likely to survive in later life stages, a process that has been observed for steelhead smolts (Hostetter et al. 2011, 2012). Such compensatory responses also may be relevant for evaluation of habitat restoration, fish passage improvements, hatchery supplementation, and estuarine and marine survival, where benefits at one life stage can be negated by factors in later portions of their life cycle. Recent analysis of density dependence in the Columbia River Basin indicates that most populations exhibit compensatory density dependence across the full life cycle of salmon and steelhead (ISAB 2015-1), which determines the overall productivity and resilience of the population.

Complex interactions among multiple predators greatly influence the outcomes of predation control actions. Harvey and Karieva (2005) modelled changes in consumption of juvenile salmonids in the Columbia River in response to removal of northern pikeminnow, smallmouth bass, and walleye. The model projected that removal of pikeminnow and walleye would reduce predation losses, but removal of smallmouth increased predation losses because increases in their prey would cause increases in other predators, including pikeminnow, walleye, and channel catfish, and American shad, an alternate-prey species and predator of small fish. In the San Joaquin River in 2014 and 2015, researchers directly measured the effectiveness of predator removal for reducing consumption of migrating juvenile Chinook salmon and steelhead using Predation Event Recorders and acoustic-tagged salmonid smolts (Michel et al. in review). Predation Event Recorders are GPS-equipped floats that have tethered smolts as bait and underwater cameras to record the predator that consumed the fish. Researchers removed 40 to 70% of 10 potential predators—striped bass (*Morone saxatilis*), largemouth bass (*Micropterus salmoides*), channel catfish (*Ictalurus punctatus*), white catfish (*Ameiurus catus*), smallmouth bass (*Micropterus dolomieu*), spotted bass (*Micropterus punctulatus*), warmouth (*Lepomis gulosus*), green sunfish (*L. cyanellus*), white crappie (*Pomoxis annularis*), and black crappie (*P. nigromaculatus*)—from one reach and moved them to an adjacent site. Removal of these fish predators did not significantly change the observed rate of predation (measured with Predation Event Recorders) or the survival rate of juvenile salmonids (measured with acoustic-tagged salmonids), in part because more predators quickly immigrated into the removal area. The interactions of multiple predators and the array of their prey species make predictions about the effects of the control of a single predator complicated. Managers should be cautious about programs that only determine the numbers of the targeted predators removed and do not measure the response of the focal prey (e.g., salmon and steelhead) or the abundances and distributions of other predators. Such measurements are difficult in a large ecosystem like the Columbia River, but lack of quantitative information weakens management decisions and reduces the certainty of program effectiveness. Essentially, while it may be intuitively obvious that reducing the abundance of a predator species will benefit their prey, this is by no means always the outcome.

LANDSCAPE CONTEXT

River networks and surrounding landscapes of the Columbia River Basin have been changed extensively over the last 150 years (ISAB 2011-4). These human alterations have changed the complexity of food webs, dynamics of juvenile and adult anadromous salmonids, abundance and distribution of native and nonnative predators, and vulnerability of salmonids to predation in the Columbia River Basin. Consequently, a landscape context is essential when assessing the influence of ecosystem conditions and human modifications on anadromous salmon and steelhead. Past reports of the ISAB and ISRP have recommended viewing the Columbia River Basin as a novel or hybrid ecosystem because there is no historical reference (ISAB 2008-4, ISAB 2011-1, ISAB 20011-4, ISAB/ISRP 2016-1). The Non-native Species Report (ISAB 2008-4) identified major modifications that alter predation and influence the impacts of nonnative species:

> *"While intentional and unintentional introductions of non-native species account for initial establishment, habitat change is currently the major factor causing the expanding distribution and*

> *increasing abundance of non-native species in the Pacific Northwest. Many of the free-flowing river (lotic) habitats in the Snake and Columbia rivers have been converted into reservoir (lentic) habitats through dam building, intended for hydroelectric power generation and for flow regulation for irrigation diversion and flood control. The reservoirs have created hotspots of non-native species (Havel et al. 2005), which become source populations of non-natives, facilitating secondary spread of these species throughout the basin. The phenomenon of dams facilitating the spread of non-native aquatic species in altered habitats is well documented in California (Marchetti and Moyle 2001, Marchetti et al. 2004) and the lower Colorado River (Olden et al. 2006). Forestry practices, agricultural development, and urbanization have also significantly impacted CRB aquatic ecosystems in ways sometimes favorable to non-native species."*

Conversion of the free-flowing Columbia River to a series of slower moving reservoirs diminished the range of anadromous salmonids in the Basin and altered adult immigration and spawning and juvenile emigration, rearing, and food resources. These changes in the river network also altered the abundance, distribution, and dispersal of competitors and predators, both native and nonnative. Dams have blocked tributaries, which resulted in reduced productivity of anadromous salmonids and invasion by nonnative fishes. Environmental conditions and water quality have been altered greatly, and the human modifications to the river network will make future environmental changes even more challenging. Major river management structures and practices that influence the impacts of predation on anadromous salmonids include dam infrastructure, flow modification, temperature and water quality, instream habitat, terrestrial habitat, hatchery releases, and estuarine habitat.

DAM INFRASTRUCTURE

For over 150 years, dams, irrigation canals, and diversions have substantially altered riverine habitats within the Columbia Basin. In the mainstem of the Columbia River, this transformation began in 1929 with the construction of the Rock Island Dam. Soon thereafter, Grand Coulee and Bonneville dams were built. From the 1940s to the mid-1970s, The U.S. Army Corps of Engineers (USACE) constructed eight additional dams in the mainstem of the Columbia River and four more in the lower Snake River (see map). These structures, plus hundreds of smaller dams and diversions in the Basin's tributaries fragmented the freshwater habitat, creating barriers and reservoirs with slow-moving and relatively warm waters.

Dams in the Columbia River physically alter the movement of migrating salmon and steelhead and increase effectiveness of some predators. Dams create barriers for upstream and downstream migration of anadromous salmonids, directly causing mortality, turning fish back from their migration route, and reducing numbers that return to their natal streams for spawning. Moreover, the restricted passage concentrates both juvenile and adult salmonids as they try to pass the dams, increasing the potential for predation. Populations of fish, avian, and pinniped predators adapt to these fixed locations of high prey densities and simplified habitat and aggregate in these areas where salmonids are forced to migrate. The turbulence, velocities, artificial structures, and possible passage through turbines create difficult flow conditions that may disorient or stun salmonids, making them more vulnerable to predators. Fisheries managers often consider the cumulative mortality of salmonids attempting to migrate past a series of dams, but the structure of the dams also create areas where fish have to pass through a gauntlet of at least eight native predators—including pikeminnow, terns, cormorants, gulls, sea lions, and seals—and eight nonnative predators, especially in the area of dam tailraces. Predation losses just to nonnative fishes have been estimated to be similar to the mortality caused by passage through the eight dams on the Columbia and Snake rivers, roughly equal to the declines in productivity due to habitat loss, and roughly comparable to harvest related mortality rates for adult salmonids (Sanderson et al. 2009).

FLOW MODIFICATION

Development of the hydrosystem in the Columbia River has altered both the timing and magnitude of river discharge (ISAB 2011-1). In the mainstem Columbia River, peak spring flows have been dampened for water storage and flood control, late summer low flows have been augmented for irrigation, power generation, and navigation, and winter flows increased for power generation (Weitkamp 1994). Thus, the time of year when most smolts would have migrated was characterized with high flows from melting snow, and the dramatic reduction in these flows has slowed smolt migration. In addition to this effect, total annual discharge in the Columbia River is 15% lower than historical natural flows (Naik and Jay 2005). In subbasins with rain- or rain-on-snow-dominated hydrographs, the hydrosystems substantially decrease peak winter discharges and augment summer base flows (Wallick et al. 2013).

Dams and their upstream reservoirs create lake like conditions instead of free-flowing rivers. As a result, velocities decrease and hydrologic residence time increases. This transformation of the hydrology of the river increases the impacts of predation on migrating salmonids. Migration times are longer, exposing juvenile and adult salmon and steelhead to greater predation. The greater storage volume of the reservoirs can support greater abundances of both native and nonnative predators. Equally important, the conversion of the Columbia River to a series of reservoirs creates habitat more favorable for nonnative fishes, such as smallmouth bass, walleye, and channel catfish. A comparison of beach-seine sampling of John Day Reservoir in 1985 and 1995 revealed that nonnative fish species had increased from 1% to 34% of the total catch, providing evidence for increasing relative abundance of nonnative fishes (Barfoot et al. 2002). Researchers also noted that dense macrophyte beds in the backwaters of the Columbia River create favorable habitat for spawning and rearing the warm-water species. These vegetated habitats along the margins of the Columbia River also will create habitat for northern pike if and when they move downstream of Grand Coulee Dam.

TEMPERATURE AND WATER QUALITY

The reservoirs of the Columbia River greatly increase the surface area of water exposed to solar radiation and slow the movement of water allowing it to warm more rapidly. Currently, warming of water in the reservoirs begins earlier in the spring and persists longer into the fall than has historically been the case (Quinn and Adams 1996). Regional climate warming also has contributed to river temperature increases, as revealed by the parallel increases in the Columbia River and the Fraser River, which does not have mainstem dams (Quinn 2018). Thermal increases in the mainstem Columbia River create adverse conditions for juvenile and adult salmonids and create more favorable conditions for nonnative warm water species. Abundances of warm water nonnative species, such as smallmouth bass, walleye, and channel catfish, are likely to increase (Sanderson et al. 2009; Lawrence et al. 2012). Predation rates of native and nonnative fishes also are greater at warmer temperatures (Vigg et al. 1991). Consumption of juvenile salmonids by pikeminnow, smallmouth bass, and walleye is greatest in summer during the period of maximum water temperatures (Poe et al. 1991, Vigg et al. 1991). Juvenile salmonids migrating during this period are exposed to greater predation losses than under historical conditions.

Seasonal warming alters migration rates and exposes migrating salmon to increased predation and mortality due to other factors (Keefer et al. 2008a, 2008b). Elevated temperatures in the Columbia River are likely to increase predation losses. A bioenergetics model was used to examine predation losses under relatively cold periods (1947-58) and warm periods (1933-46, 1978-96) in the Columbia River (Petersen and Kitchell 2001). Predation rates of northern pikeminnow were 68 to 96% greater in the warmest period as compared to the coldest period, and projections of predation by smallmouth bass and walleye revealed similar patterns. These model results illustrate the potential effects of changing the thermal regimes of the Columbia River by damming and possible increases in predation in the future as a result of regional warming.

Conversion of the free-flowing Columbia River to a series of reservoirs also changes other environmental conditions in the river. Reduced flow velocity, longer water residence time, and a greater water volume create conditions more suitable for phytoplankton communities, increase availability of nutrients, and create warmer conditions, all of which increase phytoplankton production. Increased algal abundance decreases water clarity in summer and potentially influence the predation efficiency of visual predators (ISAB 2011-1). On one hand, decreased water clarity can benefit prey, but stalking or ambush predators, such as pikeminnow, bass, or northern pike, may be able to attack and consume prey more effectively. Walleye are physiologically adapted to feeding under low light conditions and may be more effective predators under the turbid conditions of reservoirs (Maule and Horton 1984). Predators that use chemo-reception or tactile detection, such as catfish, can still feed on juvenile salmonids under extremely turbid conditions or deep in the water column of reservoirs.

RIVERINE HABITAT

While development of the hydrosystem may have increased the area and volume of habitat in the mainstem Columbia River, it changed the riverine and floodplain habitat to deeper, slower lake-like habitat with limited floodplain area. The roughness and complexity of the series of pools, riffles, and cascades of the free-flowing Columbia River provided cover and refuge from predation for migrating salmon and steelhead. In addition, access to extensive floodplains provided rearing areas, abundant food resources, flood refuge, and refuge from predators for migrating juvenile salmonids. The loss of these habitats has simplified the life history types of salmon and steelhead (Schroeder et al. 2016), decreasing the long-term population stabilization of the portfolio effect of life history diversity.

HATCHERY RELEASES

In the face of declining abundances of natural-origin salmon and steelhead, hatchery releases have been a widespread method to supplement numbers of harvestable salmon and restore populations that have been extirpated or greatly diminished. More than 140 million hatchery origin salmonids are released into the Columbia River each year (ISAB 2011-1). While the supplementation with hatchery fish may increase numbers of returning adult salmon and steelhead in some basins, release of hatchery smolts provides a food base for native and nonnative predators and may increase their populations and predation on natural origin salmonids (ISAB 2008-4, ISAB 2011-1). The Food Web Report (ISAB 2011-1) concluded that we have created altered food webs in the Columbia River and hatchery releases may create greater predation impacts than in the historical food webs:

> *"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."*

Hatchery releases also modify timing of the co-occurrence of hatchery and natural origin salmonids (ISAB/ISRP 2016-1), which may increase predation on natural origin fish, especially sub yearling juvenile salmonids. Hatchery releases may have additional negative impacts, such as increased competition for food and habitat and genetic effects that alter life history traits related to vulnerability to predators. These effects may alter the fitness of migrating salmonids, and large hatchery releases have been observed to reduce individual size and population abundance of salmonids in the ocean (e.g., effects of chum salmon in Alaska; Ruggerone et al. 2011).

ESTUARINE HABITAT

The Critical Uncertainties Report (ISAB/ISRP 2016-1) concluded that rates of juvenile and adult predation in the estuary are a major question facing managers of the Columbia River. Native birds feed on juvenile salmonids, and native sea lions and seals prey on adult salmon and steelhead. Alteration of estuarine habitat and creation of barriers at Bonneville Dam have increased the potential impacts of predators.

The U.S. Army Corps of Engineers deposited dredge spoils near the mouth of the Columbia River creating Rice Island and East Sand Island. These artificial habitats were colonized by Caspian terns and double-crested cormorants, eventually becoming some of the largest colonies of these native birds in North America. In addition, biologists recently concluded that sea gulls consume more juvenile salmonids than previously recognized. These avian predators are also present in the upper Columbia River and lakes throughout the Basin. A recent analysis of avian predation in the upper Columbia River revealed that these colonial birds account for almost half of the mortality of steelhead between the upper Columbia River and Bonneville Dam

(Evans et al. 2018a). They concluded that avian predation was greater than all other sources of mortality combined in 9 of the 10 study years evaluated.

Marine mammals, including California sea lions, Steller sea lions, and harbor seals, are native predators in the estuary and Columbia River up to Bonneville Dam and Willamette Falls. Though harbor seals consume juvenile salmonids to some degree (see evidence from the Strait of Georgia in Thomas et al. 2017), these pinniped predators feed on adult salmonids to a greater degree than juveniles. As discussed earlier, predation of returning adults has a disproportionate impact on populations of salmon and steelhead. The Food Web Report (ISAB 2011-1) concluded that the simplified habitats of the lower river and estuary, barriers at dams, aggregations of adult salmon at fishways, and manmade structures have increased the impacts of pinniped predators.

Control measures for avian predators have included culling and dissuasion, and managers have attempted to reduce pinniped predation by hazing and non-lethal removal. State and Tribal agencies have recently received authorization to begin the lethal removal of pinnipeds as well. The need for such control measures for reducing mortality of salmon and steelhead is obvious, the effectiveness both biologically and economically is uncertain. The Critical Uncertainties Report (ISAB/ISRP 2016-1) concluded:

> *"Recent 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 predator controls. Lessard et al. (2005) describe the extreme uncertainty associated with any policy aimed at controlling complex interactions that determine extinction risk for focal species and argue that such policies should be treated as management experiments with careful treatment (e.g., control comparisons and monitoring)."*

FUTURE CONCERNS

Regional warming as a result of climate change may substantially increase predation losses for salmon and steelhead in the Columbia River (ISAB 2007-2). Warmer temperatures will likely increase consumption rates by native and nonnative fish predators and increase the abundance of warm water native fishes. Climate change models also project snowpacks will decrease, river discharge will decrease in summer, droughts will be longer, and winter and early spring flows will be greater. While these changes have various consequences for different stocks of salmon and steelhead, most will result in warmer conditions and longer residence time in the reservoirs. The changes in the Columbia River created by the hydrosystem are likely to amplify the effects of future climate change.

While future conditions and outcomes are uncertain, the challenges facing river managers are clear. Current empirical information is not adequate to design effective control actions for the large number of fish, avian, and pinniped predators throughout the Columbia River Basin. Assessment of local predator abundance and consumption of either juvenile or adult salmonids will not answer the questions of predation impacts across the full life history and geographic extent of salmon and steelhead. New approaches for measuring responses to predator control are needed, particularly those that directly measure the response of salmonid prey.

Density dependence analysis and measurement of smolt-to-adult return rates (SAR) provide critical empirical evidence for predation management decisions (ISAB 2015-1, ISAB/ISRP 2016-1). The best available current tool for assessing the systemwide impacts of predation throughout the life cycle of salmonids is life-cycle modeling (ISAB 2013-5), but such models require information that is currently incomplete. Future predation management will be improved by anticipating information needs and incorporating monitoring and evaluation efforts into the future Fish and Wildlife Program. One of the major conclusions of the Food Web Report (ISAB 2011-1) was that anticipatory responses are needed:

> *“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.”*

B. Socioeconomic considerations for control of northern pike and other invasive species

In many ways, the causes of invasive species are socioeconomic and in a broad sense result from human behavior and the incentives that underlie that behavior. As such, they require socioeconomic solutions:

> *"When most people think of the economics of invasive species they think of the damage or control costs of weeds, pests, and pathogens. But economics is much more than just a method for calculating costs. It is a framework for understanding the complex causal interactions between human behavior and natural processes, and for finding institutional and behavioral solutions to seemingly intractable environmental problems. Biological invasions threaten societies in sometimes critical ways; for example, the spread of HIV infection in southern Africa. Economics helps us identify the social causes of such problems, and hence develop institutions and instruments capable of solving them." (Perrings et al. 2002)."*

Some of the reasons for heightened concern about invasive species include concerns that (a) introductions are increasing while mechanisms for excluding, suppressing, or eradicating are non-existent or have been removed or weakened in some cases; (b) societal costs of invasions are rising with human population growth and the intensity of land use for production and other economic activity associated with it (e.g., agriculture, forestry, grazing, industry, residential); (c) a high level of uncertainty owing to novel ecological interactions between invaders and native species, and (d) control or exclusion of invasive species is a public good whose protection is vulnerable to society's "weakest link" (i.e., individuals who ignore the public good; Perrings et al. 2002).

Responding to invasive species involves significant challenges for science, management, policy, and society (Carey et al. 2012). The costs and benefits of invasive species prevention, control, and eradication are critical to making sound policy decisions, but given these high levels of uncertainty and often novel ecological interactions, quantitative evaluation of alternative management or policy responses is sometimes not possible. A framework for such economic evaluations of the northern pike invasion in the Columbia River Basin is developed in a separate report (Kling and Sanchirico, forthcoming).

SOCIAL DIMENSIONS OF HARVEST INCENTIVES TO CONTROL INVASIVE SPECIES

Efforts to control invasive species with harvest incentives include bounty programs, contracts with commercial fishers or public employees to harvest the invaders, developing commercial markets, and relaxed limits on recreational harvests. Examples of species with incentive programs in other ecosystems include Asian carp, lionfish, and Burmese pythons. However, few studies have critically examined the success of such programs (Pasko and Goldberg 2014), which include incentive programs to remove Asian carp, lionfish, and Burmese pythons in other ecosystems. One exception is an unpublished study of effectiveness and economics of the Northern Pikeminnow Management Program in the Columbia River Basin over a 13-year period (Radtke et al. 2004).

The potential for such programs to be successful, and their cost, depends on economic and biological considerations such as damage to non-target species through by-catch, and whether removing a species allows another problematic species to thrive (as described in the Ecosystem Perspectives section above). Incentive programs can also waste resources if the target populations fail to decline relative to levels that would have occurred without the program (Pasko and Goldberg 2014) or if the intended beneficiaries do not gain relative to where they would have been without the program. The effectiveness of recreational eradication programs, for example, may depend on whether anglers are willing to kill the fish they catch as opposed to releasing them, even when killing the invader is mandatory (e.g., the case with lake trout in Yellowstone Lake in the following section).

MANAGEMENT GOALS AND OBJECTIVES

Potential costs and risks need to be evaluated to help determine the goals of a program—whether the goal is suppression or eventual eradication of the invader. Likely risks, potential for success, and the strength of long-term commitment to the program must all be considered (Pasko and Goldberg 2014). In addition, long term control versus eradication requires realistic assessments of the prospects for sustained funding.

INCENTIVE APPROACHES

Differences between various interest groups in society regarding the costs and benefits of invasive species are inevitable, and these differences create conflicts that are often difficult to resolve. In some cases, conflicts can be mediated with the help of a thorough identification of the full costs and benefits, and the allocation of those effects. However, the preferences for an invasive species to different stakeholder groups may change over time, complicating the evaluation of costs and benefits. In addition, the distribution of costs and benefits across different interest groups and stakeholders can often be more important than their absolute aggregate magnitude (McNeely 2001).

For programs that promote harvest of invasive species, one of the greatest challenges is the potential for generating perverse incentives that can cause further spread of the target species. For example, people may come to rely on the income that bounty programs or commercial markets provide and discourage eradication and control. In some cases, bounty programs will "self-regulate" toward an equilibrium population level and suppression effort for a given incentive level because effort may decline as the target species becomes scarce and no longer worth pursuit. However, incentive programs can encourage intentional release into management areas or previously non-invaded habitats (Pasko and Goldberg 2014). In cases where bounties are higher than the cost of breeding, individuals may breed animals to be turned in for the bounty. This was seen with venomous cobras in India and rats in Vietnam (Walker 2013).

Angler habits and preferences may change significantly following the establishment of a charismatic invader like northern pike, and the demand for angling opportunities is likely to increase when such species become fully established in the new range. For example, once established, anglers may consider pike fishing a right, and so not cooperate with agencies that view the species as a risk. This ownership or entitlement effect will alter the balance of benefits and costs associated with control programs (see Ferry Canyon example in walleye in the following section). These changes may also lead anglers to introduce fish illegally in other locations—actions that are extremely difficult to monitor and enforce. Illegal stocking of favorite game fish into nonnative habitats by anglers has been a persistent and widespread problem, threatening native species in many ecosystems (Johnson et al. 2009).

OUTREACH

Programs to eradicate or suppress species often create conflicts when that species is considered an invasive pest by one group, an important source of income or food for another, and a source of recreation for a third. Outreach, information dissemination, and facilitated or mediated discussions can help resolve disputes, especially if initiated prior to the implementation of a program (Pasko and Goldberg 2014). For example, an extensive outreach program helped reverse public opinion and led to support for northern pike eradication from Lake Davis, California (P. Moyle, personal communication). Cultural factors also influence the attitudes and perceptions of different groups about the benefits and costs of invasive species.

Programs aimed at controlling invasive species typically include opportunities to raise awareness and disseminate information to stakeholders. Research has found that stakeholder groups have remarkably different perceptions about the impacts and benefits caused by invasive species and so differ in their willingness to pay for control or eradication programs (García-Llorente et al. 2008). It is important to recognize and consider these differences when developing outreach, public awareness, and management plans.

Engaging the public also may help locate additional populations of invasive species to target for rapid control efforts (Garcia-Llorente et al. 2008). Outreach should include information about the scope, cost, and long-term impacts of the target species on the environment, economy, public health, and other dimensions in order to build program support and encourage participation by multiple stakeholder-groups.

C. Piscivorous fish

NATIVE NORTHERN PIKEMINNOW

As discussed above, dams, irrigation canals, and diversions substantially altered riverine habitats in the Columbia River Basin, creating a fragmented freshwater ecosystem dominated by reservoirs with relatively warm slow-moving waters. Native anadromous and resident fishes that had flourished in the Basin's cold, fast-flowing rivers were confronted with a novel ecosystem, one with physical and biological conditions substantially different from those in which the fish had evolved. These new conditions, however, were favorable to nonnative coolwater and warmwater fishes.

A number of these species, including walleye, smallmouth bass, yellow perch, channel catfish, and largemouth bass, were introduced into the Basin by management agencies or clandestinely by anglers, to provide sport fisheries. Additionally, a native cyprinid, the northern pikeminnow, became more abundant in mainstem reservoirs due to increases in slow-flowing waters. Considerable reductions in the survival of juvenile salmonids in this new environment occurred, resulting from the many physical and biological changes in the basin (Raymond 1979; Sims and Ossiander 1981; Uremovich et al. 1980). Yet, the relative importance of the physical environment, presence of nonnative piscivorous fishes, and increased abundance of northern pikeminnow on salmonid survival remained largely unknown. Observations made at dam tailraces, however, indicated that predation on juvenile salmon by northern pikeminnow and other fish predators could be substantial (Poe et al. 1991).

The uncertainties associated with the potential role that piscivorous fishes have on the survival of migrating juvenile salmonids prompted a suite of investigations in the 1980s and 1990s. It was recognized that diet, consumption rates, distribution, and abundance data would be needed to estimate how predatory fishes were collectively and individually impacting juvenile salmonid survival. Information was gathered on four fish species: northern pikeminnow, smallmouth bass, walleye, and channel catfish. Brief summaries of the key results produced by those studies are provided below.

Poe et al. (1991) examined the diets of these fishes in the John Day reservoir from 1983 to 1986. They found that fish were the dominant prey group by weight for all four species. However, juvenile salmonids were the dominant prey only for northern pikeminnow (34%). Fewer individual walleye and channel catfish (~20%) and smallmouth bass (4%) had eaten salmonids. Insects and crustaceans (e.g., crayfish) were also important dietary items for northern pikeminnow, smallmouth bass, and channel catfish, but walleye fed predominately (96%) on fish (primarily non-salmonids). They also discovered that three factors—sampling location, time of year, and fish size—had substantial effects on fish diets.

Based on the results of their diet study, Poe et al. (1991) concluded that northern pikeminnow were the major fish predator on juvenile salmonids in the John Day reservoir at that time. They regarded channel catfish as another important predator due to their predation on yearling salmonids in the upper reservoir during the spring. Walleye and smallmouth bass were considered less important because these species appeared to select juvenile salmon only when they overlapped with their littoral habitats in August. They concluded that it would be necessary to estimate daily rations (mg of prey/g of predator) and consumption rates (prey/predator/day) for each of the four species to more fully estimate predatory impacts.

Consumption rates, daily rations, and mean prey weights for the four species (northern pikeminnow, walleye, channel catfish and smallmouth bass) were estimated by Vigg et al. (1991). The average daily consumption rate of salmonids by northern pikeminnow in the McNary Dam tailrace was 0.7 salmonids per day, and the maximum consumption rate of two salmonids per day occurred in July. This rate was approximately five times higher than the consumption of juvenile salmonids by northern pikeminnow elsewhere in the reservoir. Similarly, over the season, consumption of juvenile salmonids by channel catfish was 10 times higher in the tailrace than in other reservoir areas. Not enough walleye or smallmouth bass were sampled from the tailrace to examine their consumption rates at this location. However, walleye had the highest seasonal consumption rate (0.19 prey/predator/day) on juvenile salmonids in the John Day pool. Few salmonids were found in smallmouth bass, and they had the lowest seasonal consumption rate (0.04 prey/predator/day) of the four species examined. Based on the results of their detailed consumption studies, Vigg et al. (1991) concluded that northern pikeminnow were “clearly the major predator on juvenile salmonids” in the John Day reservoir.

Before the impacts of predation by northern pikeminnow, walleye, smallmouth bass, and channel catfish on juvenile salmonid survival could be completely understood, estimates of their abundance and distribution in the John Day Reservoir were needed. Hypothetically, a predator species might eat exclusively juvenile salmon, but if it was scarce it would have a negligible effect on salmon, overall. Mark-recapture methods and catch-per-unit-of-effort (CPUE) data were used to estimate abundance and seasonal distribution patterns for three of these species (Beamesderfer and Rieman 1991) because too few channel catfish were recovered to perform comparable analyses. Northern pikeminnow were the most abundant species followed by smallmouth bass and walleye. Given uncertainties in their abundance estimates, Beamesderfer and Rieman (1991) estimated that between 50,000 to 500,000 predators (all species combined) were in the reservoir. Northern pikeminnow were found throughout the reservoir but concentrated in the McNary Dam tailrace. Walleye were mainly located in the upper part of the reservoir, and smallmouth bass occupied lower portions of the John Day pool to a greater degree (Beamesderfer and Rieman 1991). Their results on abundance and distribution led Beamesderfer and Rieman (1991) to hypothesize that northern pikeminnow would have the greatest impacts on juvenile salmon survival. They also postulated that spatial and temporal changes in predator and prey abundance would lead to uneven predation effects throughout the juvenile salmonid migration season.

Losses of juvenile salmon and steelhead to predation were estimated for John Day Reservoir from 1983 to 1986 based on estimates of diet, daily consumption rates, predator abundance, and numbers of juvenile salmonids entering the reservoir (Rieman et al. 1991). Fish predators consumed an average of 2.7 million juvenile salmon annually, which amounted to 14% of the juvenile salmonids that entered the reservoir. Northern pikeminnow were largely responsible (78%), followed by walleye (13%) and smallmouth bass (9%).

Twenty-six percent of the predation by pikeminnow and 21% of all fish predation occurred in a relatively small area immediately below McNary Dam. Predation losses varied seasonally, ranging from 7% of total annual predation in June when salmonid abundance was low to a high of 61% in August when subyearling Chinook were abundant (Rieman et al. 1991). The authors reported that the subyearlings were more vulnerable because they (a) migrate slower than yearling Chinook, (b) are smaller and can be eaten by a wider size range of pikeminnow, and (c) migrate later when the water is warmer and pikeminnow are more efficient predators and consume more prey.

Beamesderfer et al. (1996) estimated the cumulative losses of migrating juvenile salmonids caused by northern pikeminnow predation in the mainstem Columbia and lower Snake rivers to be approximately 16 million or 8% of the Basin's migrating juvenile salmonids. Given what was known about the diet, consumption rates, and distribution of these fish, Beamesderfer et al. (1996) hypothesized that removing 10% to 20% of northern pikeminnow > 250 mm would disproportionately increase juvenile salmon survival.

In summary, the studies briefly described here indicated that predation by resident fishes on migrating juvenile salmonids could be substantial but varied among predators because their relative abundance and per capita consumption were not equal. The predation rates were great enough to suggest a probable solution to a previously suspected source of reservoir mortality. While these studies were taking place, simultaneous efforts to increase salmonid survival via changes in infrastructure and operations at dams were also occurring (e.g., Sims and Ossiander 1981; Raymond 1988). It was understood, however, that improvements in survival at the dams could be at least partly negated by downstream losses due to piscivorous predators. Finally, conditions in the ocean varied from year to year, further complicating the assessment of benefits in terms of adult returns.

Northern Pikeminnow Management Program

Modeling simulations using information from the John Day Reservoir studies indicated that predation on juvenile salmonids could be reduced by as much as 40% if northern pikeminnow $\geq$ 250 mm were exploited at a 10 to 20% rate (Beamesderfer et al. 1996; Williams et al. 2018). Exploitation probabilities of this magnitude appeared to be achievable. It was acknowledged that compensatory responses within the northern pikeminnow population, and among other predatory fishes, might occur. Such responses were thought to be unlikely, however, because only a relatively small fraction of the northern pikeminnow population was targeted for removal (Beamesderfer et al. 1996). To test this idea, a number of fisheries (e.g., tribal long-line, sport-reward, hook-and-line in boat-restricted areas adjacent to dams) were initiated in 1990. Results showed that it was possible to remove northern pikeminnow at desired exploitation rates. This finding led to the establishment of the "Development of Systemwide Predator Control" or Northern Pikeminnow Management Program (NPMP) in 1991.

The NPMP has two overarching goals. One is to reduce northern pikeminnow predation on migrating juvenile salmon by selectively removing older and larger fish. The other goal is to monitor removal or exploitation rates to prevent northern pikeminnow from being extirpated by the program's actions. The project annually conducts sport-reward fisheries, supports fisheries conducted by agency personnel in boat-restricted zones adjacent to dams, evaluates the dam fisheries, examines potential compensatory responses, calculates fishery exploitation rates, and estimates gains in juvenile salmonid survival due to its northern pikeminnow removal efforts.

Three agencies, the Pacific States Marine Fisheries Commission (PSMFC), Washington Department of Fish and Wildlife (WDFW), and the Oregon Department of Fish and Wildlife (ODFW) administer and implement the program. Each has separate responsibilities. The PSMFC provides fiscal and contractual oversight for all parts of the NPMP. It also processes all the reward vouchers sent in by sport-reward anglers (Williams and Miller 2018). WDFW is responsible for implementing the sport-reward fisheries, performing hook and line fisheries at dams, collecting information on harvested northern pikeminnow (sex, length, presence of tags), and documenting fishery statistics (e.g., angler effort, catch by fishery area, bycatch of other species: Winther et al. 2018, Dunlap et al. 2018).

Data collected by WDFW are used by ODFW along with additional fieldwork, laboratory assessments, and data analyses to (a) estimate exploitation probabilities, (b) describe population characteristics of northern pikeminnow, smallmouth bass, and walleye residing in the Bonneville pool and below Bonneville Dam, (c) determine whether intra- and inter-specific compensatory responses have occurred in northern pikeminnow, smallmouth bass, and walleye populations due to the sustained removal of northern pikeminnow from the lower Columbia and Snake rivers, and (d) quantify the potential reduction in juvenile salmon predation due to the program's fisheries (Carpenter et al. 2018, Williams et al. 2018).

Annual exploitation probabilities on northern pikeminnow are estimated using a mark-recapture analysis. ODFW conducts boat electroshocking to sample river transects located from the lower Columbia River to the base of Priest Rapids Dam (river mile 47.2 to river mile 395.8 [rkm 76 – rkm 637]). Similar sampling is performed in the Snake River from the confluence to the base of Hells Canyon Dam (river mile 10 to river mile 156 [rkm 16 to rkm 251]). Northern pikeminnow $\geq$ 200 mm are tagged with uniquely numbered loop tags, injected with PIT tags, and then released. Recoveries of tagged fish are used to estimate exploitation probabilities for specific seasons, locations, and fish sizes.

Boat electroshocking is also used to gather biological information on relative abundance, diets, size (weight), sex, and maturation status of northern pikeminnow. Identical assessments, except for sex and maturation status, are made on smallmouth bass and walleye. Information gathered on fish obtained from electrofishing, caught at dams, or in the sport-reward fishery is used to assess possible compensatory effects in northern pikeminnow, smallmouth bass, and walleye (Carpenter et al. 2018). Length-frequency data, for example, are used in proportional size distribution (PSD) analyses that examine whether there has been a decrease in the occurrence of large northern pikeminnow. PSD analyses are also used to determine whether smallmouth bass and walleye are larger after removal of northern pikeminnow. Relative weight (W_r) values are similarly used to examine possible compensatory responses. In addition, changes in abundance and consumption indices,[3] diet, and the program's predation index are evaluated to examine possible compensatory responses (Carpenter et al. 2018).

A model developed by Friesen and Ward (1999) is used by ODFW to quantify expected reductions in predation on juvenile salmonids caused by the NPMP's sport-reward and tailrace fisheries. The model incorporates (a) area- and size-specific exploitation probabilities, (b) estimates of natural mortality obtained through catch curves, (c) area- and size-specific abundance estimates, (d) location-specific estimates of consumption of juvenile salmon by specific-sized northern pikeminnow, and (e) the size structure of the northern pikeminnow population before removals by fisheries (Carpenter et al. 2018).

Program results and effectiveness

Since its inception in 1991, the NPMP has implemented sport-reward and dam fisheries. Catch, effort, diet, and other biological data have been collected and analyzed for northern pikeminnow as well as on smallmouth bass and walleye. As of 2017, the program's fisheries have removed ~4.9 million northern pikeminnow (Figure 3). Additionally, the objective of reaching a system-wide sport-reward fishery exploitation probability of 10% - 20% on northern pikeminnow $\geq$ 250 mm has been reached 24 out of 28 years. Analyses of a variety of parameters (i.e., PSD, W_r, diet composition, indices of abundance, consumption, and predation) have not revealed evidence of compensatory responses in northern pikeminnow, smallmouth bass, and walleye across the entire length of the mainstem Columbia River. However, evidence of local compensation of smallmouth bass has been reported (Ward and Zimmerman 1999, Zimmerman and Ward 1999, Knutsen and Ward 1999, Carpenter et al. 2018, Williams et al. 2018).

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[3] ODFW uses indices of abundance, consumption, and predation because direct measures of these parameters are difficult to obtain. Season- and location-specific abundance indices are calculated by multiplying mean catch data from the program's electroshocking transects by the surface area of a specific location and dividing by 1000. Consumption indices that incorporate water temperature, mean fish weight, number of salmon per predator, and total gut weight are produced for northern pikeminnow and smallmouth bass. Predation indices for specific seasons and areas are computed by multiplying period- and location-specific abundance indices by period- and location-specific consumption indices (Carpenter et al. 2018)

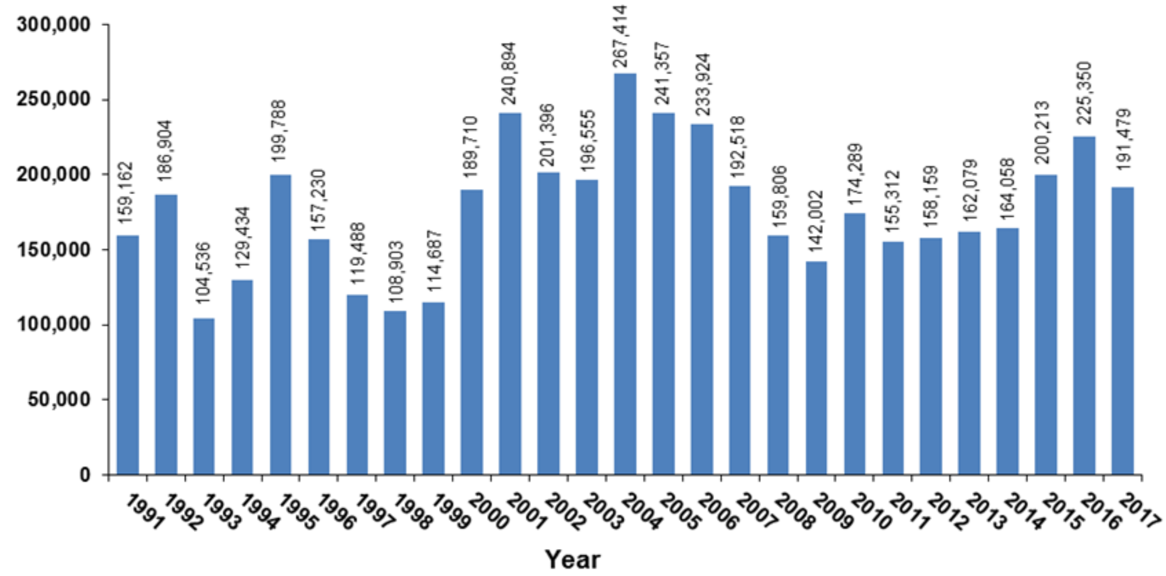

Figure 3. Annual sport-reward harvests of northern pikeminnow from 1991 – 2017. (Figure from Winther et al. 2018)

The principal objective of the program is to improve survival of juvenile salmonids as they migrate through multiple reservoirs and the lower undammed segment of the Columbia River. Northern pikeminnow within discrete size groups are expected to consume a certain number of juvenile salmonids during an entire juvenile salmonid out-migration period. As discussed above, the program keeps track of the number and size of the northern pikeminnow removed annually from specific sites. These data along with other inputs are used in a model to make assessments of how annual removals of northern pikeminnow in year *n* has improved salmonid survival during the following outmigration season or year *n +1*. As it currently exists, river and ocean conditions, number of migrating salmonids, and mortality due to turbines are held constant in the model. Additionally, the model assumes that compensatory responses by northern pikeminnow, smallmouth bass, and walleye have not occurred. Uncertainty exists in some of the input values used in the model, for example, abundances of pikeminnow and other fish predators, distributions and movements of fish, and proportion of dead salmonids in the diets (Friesen and Ward 1999). Consequently, a range of solutions, based on minimal, maximal, and median values for each uncertain parameter are produced (Figure 4). The model projects that the program has reduced potential predation on juvenile salmonids by ~32%.

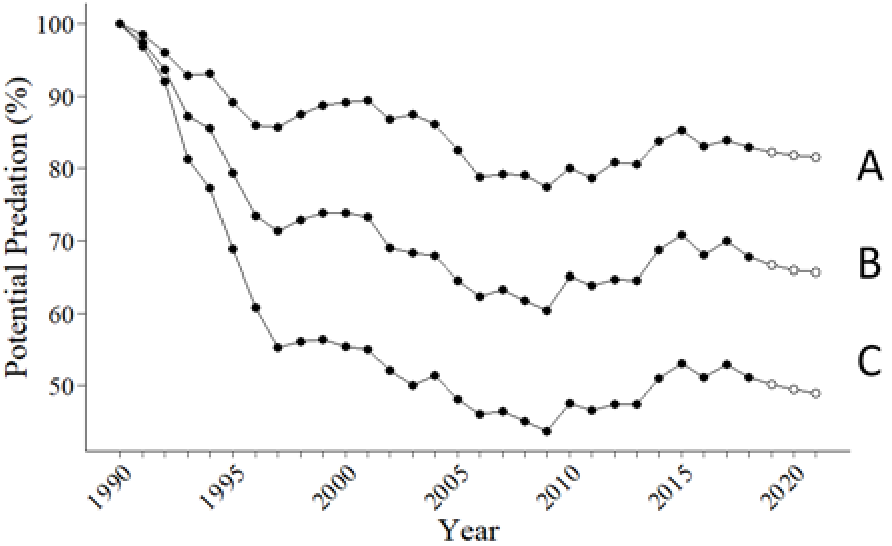

Figure 4. "Estimates of (A) maximum, (B) median, and (C) minimum annual levels of potential predation by Northern Pikeminnow on juvenile salmon relative to predation levels before implementation of the Northern Pikeminnow Management Program. For the years 1991–2018, model estimates (filled circles) are based on exploitation levels from the previous year. Model forecast predictions after 2018 (open circles) are based on average exploitation estimates from years with similar fishery structure (2001, 2004–2017)." Figure and legend taken from Carpenter et al. 2018.

At present, the program's model provides the best measure of how salmonid survival may be benefiting from the selective and limited removal of northern pikeminnow. In a current review, however, the ISRP (ISRP 2019-1) identified a number of new approaches that could be used to refine some of the program's metrics and further investigate the effectiveness of its management actions. These recommendations plus several additional ones are listed below.

- Diet, daily ration, and consumption rate data that have served as important foundations for the NPMP are now over 30 years old. Substantial environmental and biological changes have occurred in mainstem reservoirs and in the river below Bonneville Dam since then. How these changes have altered interactions between juvenile salmonids and their potential predators are not known. Project researchers should be provided with the resources needed to repeat these important assessments.
- Power analyses should be used to help set yearly goals for fish tagging, and collection of diet, PSD, W_r and other biological samples for each of the program's three major geographic sampling areas.
- Improvements in estimates of consumption rates appear to be possible. The program should consider implementing newly developed genetic tools that can identify prey in the gut contents to the species level and also quantify the number of individuals of each species present (Sethi et al. 2018; Krehenwinkel et al. 2019).
- The use of current bioenergetic models to estimate total consumption could also be explored.

- Predation event recorders (PERs) have been used in the San Joaquin Delta to estimate predation rates, identify predator species, and locate areas where predation is likely to occur on migrating juvenile salmonids (Demetras et al. 2016). Use of these devices would help the NPMP validate its assumptions about where predation occurs, predation probabilities, and the importance of predatory species.
- The program should also integrate its data with other ongoing projects (e.g., 1996-020-00 Comparative Survival Study; 1993-029-00 Survival Estimates for Passage Through Snake and Columbia River Dams and Reservoirs) to estimate survival probabilities from one reservoir to the next. Survival probabilities could be correlated with exploitation probabilities and possibly with SAR values.
- The program could also use its abundant mark-recapture data on individual fish to re-evaluate its indices of abundance and predation rates. In 2017, more than 1,400 pikeminnow were tagged with uniquely numbered tags. About 170 were recaptured and used to estimate exploitation probabilities. The Barker model (Barker et al. 2004) for analyzing mark and re-sight data (an extension of the Cormack-Jolly-Seber open-population model) could be used to estimate the survival of pikeminnow by size class and perhaps estimate their abundance (Conner et al. 2015, Bouwes et al. 2016). If these estimates were calculated for different years, they might also provide information about compensatory responses to the project’s consistent removal program.
- Although system-wide compensatory responses were not observed, some may be occurring in individual reservoirs. Increases in abundance are often used as an indicator of a compensatory response. The program’s abundance indices for northern pikeminnow, smallmouth bass, and walleye are based on CPUE data. However, CPUE data have not been calibrated with the program’s mark/recapture data since the early 1990s. Updated abundance estimates based on CPUE data to produce relative abundances in pikeminnow, smallmouth bass, and walleye are critically needed because the accuracy and error associated with the estimates has not been analyzed in 28 years. Since those assessments were made, many changes have occurred in the Columbia River and its fish populations.
- So far, the program’s efforts to evaluate compensatory responses in predators has been restricted to fish species. Program scientists should consider working with avian researchers to determine whether compensatory responses have occurred in populations of gulls, pelicans, terns, and cormorants as a result of northern pikeminnow removal.
- Evans et al. (2018) developed a statistical approach that directly measures the predatory impacts of colonial waterbirds on juvenile salmonids. They discovered that bird predation was additive and varied from one week to the next (see Avian Predation section of this report). The comprehensive data being collected by the NPMP may be suitable for such an analysis.

Currently, the sport-reward fishery harvests the majority of the northern pikeminnow that are annually removed by the NPMP. In 2017, for instance anglers caught and turned in 191,479 northern pikeminnow and the program distributed slightly more than $1.5 million dollars to anglers (Williams and Miller 2018). In its recent review of the NPMP (ISRP 2019-1), the ISRP asked the proponents to evaluate the relative benefits of continuing the program as now it exists with one that would not rely on sport anglers. The alternative suggested would employ agency or contract anglers who would be directed to areas known to harbor concentrations of predators (e.g., dam tailraces and forebays).

Such an approach would be somewhat similar to ones used by PUDs in the upper Columbia River. Contract fishers are employed by the PUDs to remove northern pikeminnow to help meet juvenile salmonid survival objectives mandated in the 2008 BiOp. Their removal programs were established in the mid-1990s and a variety of methods—including hook and line, set lines, electrofishing, seines, and fishing derbies—are used to remove northern pikeminnow and nonnative walleye, smallmouth bass, and channel catfish. A variety of removal tactics are also being implemented. Grant County PUD, for example, removes all life stages of northern pikeminnow. On average, more than 500,000 northern pikeminnow are removed annually by their program. Many of these fish are young-of-the-year or subadults. Possible survival benefits realized by migrating smolts due to Grant County's removal method have not been estimated (Curtis Dotson PPT to the ISAB, 2019). Instead, it was acknowledged that such an estimate would be quite difficult to make. Conversely, the focus of the Chelan County PUD program is to remove large northern pikeminnow, ones that can consume juvenile salmonids. Approximately 83,000 fish of this size are removed each year. Chelan County PUD researchers hypothesize that their removal program saves an estimated 2.6 million smolts per year (Scott Hopkins PPT to the ISAB, 2019). Neither PUD program has formally examined any possible compensatory responses in northern pikeminnow or other fish predators resulting from their removal efforts.

The different removal approaches used by the PUDs and the NPMP, their monetary costs, and estimated benefits provide important comparative information. These data should be considered by the NPMP program when it addresses the ISRP's request to examine the pros and cons of possible northern pikeminnow removal strategies. Does the sport-reward program still provide the best approach for removing northern pikeminnow and assessing possible compensatory responses? Or would more focused fisheries in selected locations be a more strategic and cost-effective method?

INVASIVE NORTHERN PIKE

Distribution and biology

Northern Pike (*Esox lucius*; hereafter, simply pike) are distributed throughout the northern hemisphere in both North America and Eurasia (Scott and Crossman 1973). In North America, they are native to the upper Midwest and Northeast, and to Alaska north and west of the Alaska Range but not to southcentral or southeast Alaska (Dunker et al. 2018; Figure 5).

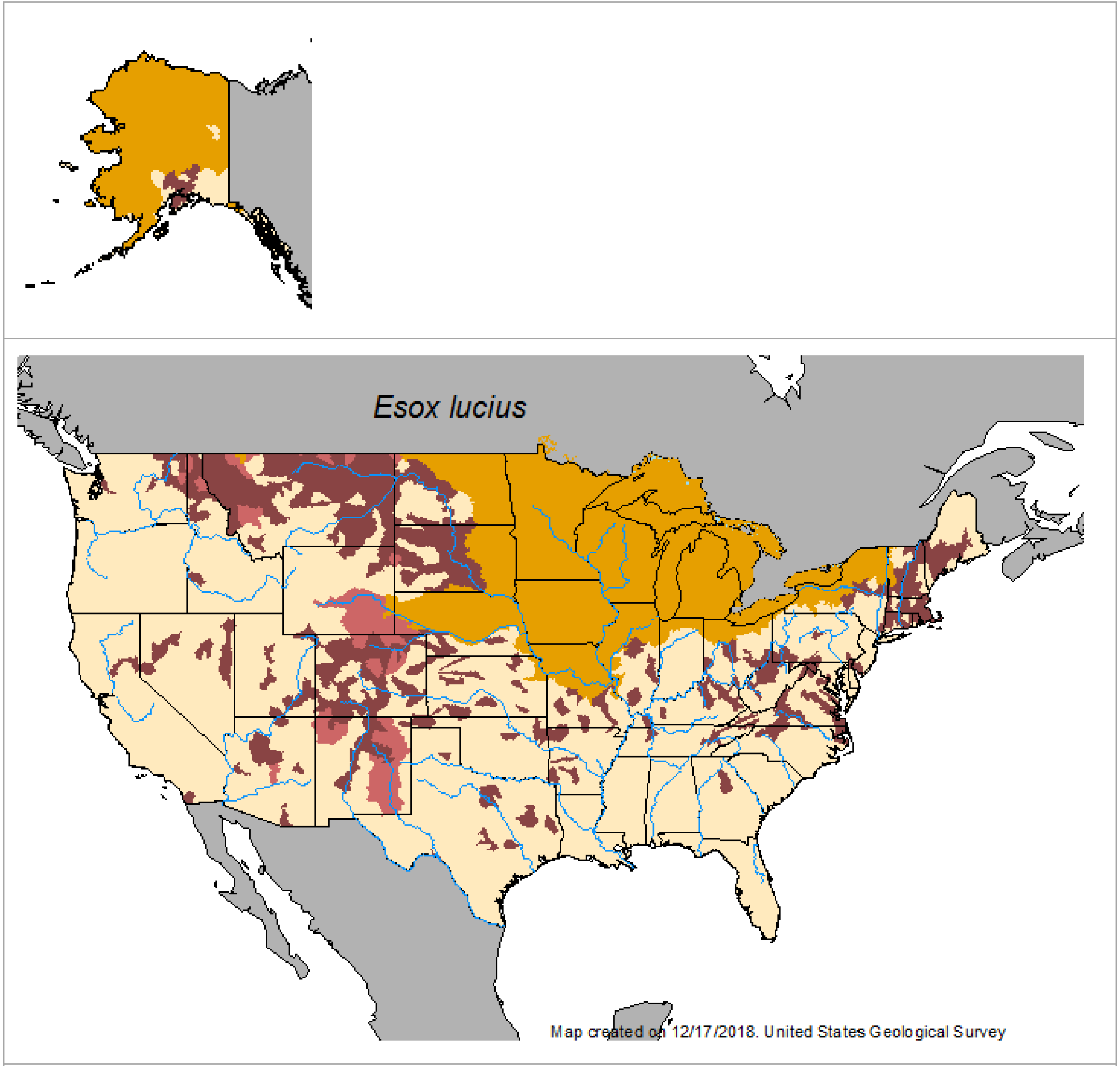

Figure 5. Distribution of Northern Pike in the contiguous United States and Alaska (Fuller et al. 2019; URL https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=676). The acronym HUC means Hydrologic Unit Code, a classification of watersheds by size, with HUC 8 watersheds being smaller than HUC 6.

Pike become highly piscivorous very early in life, although they can also subsist on other prey (Cathcart et al. 2019). They are visual predators, active primarily during the day, and ambush prey from positions in the cover of aquatic plants, logs, or other complex habitat. Pike spawn in early spring, shortly after ice-out or when the water reaches 8-12°C. They spawn over vegetation in shallow calm water, primarily in flooded wetlands or weedy shorelines where the eggs adhere to the vegetation. Eggs are small, so the fecundity of pike is high, ranging about 10,000-100,000 eggs for females of 15-35 inches (38-89 cm; Carbine 1944, Priegel and Krohn 1975).

Risk of invasion downstream

The first documented introduction of pike in the Columbia River Basin occurred in 1953 when an angler apparently transported fish from a native population in Sherburne Lake in the northeast corner of Glacier National Park, Montana to Lone Pine Reservoir near Flathead Lake, in the headwaters of the Clark Fork River basin (Great Falls Tribune, 5 Feb. 1986). During the last 65 years, the invasion has slowly but inexorably expanded downstream. Northern pike now occupy several major upper Columbia River tributaries and most of Lake Roosevelt (Figure 6). They have recently been captured about 6 miles (10 km) upstream from Grand Coulee Dam (J. Maroney presentation to ISAB, 25 Jan 2019).

There is evidence that the expansion of pike has been facilitated by introductions made illegally by humans. For example, pike were illegally placed above Milltown Dam near Missoula, Montana and spread upstream in the Blackfoot River in the 1980s and 1990s. Pike are capable of dispersing throughout river systems (Zelasko et al. 2016) and are probably also able to move downstream over or through dams. For example, it is generally assumed that pike in the Flathead River originated from fish dispersing from the original population established in Lone Pine Reservoir, and those in Lake Pend Oreille washed downstream from the Clark Fork River during spring floods in 1997. Similarly, it is believed that pike in the Coeur d'Alene River drainage naturally expanded from an illegal introduction in the 1970s. The source of the pike that reached the Bitterroot River is unknown.

Genetic techniques provide clues to the history of pike invasions through the Columbia River Basin and current expansion into new waters. Dr. Kellie Carim (National Genomics Center for Wildlife and Fish Conservation, U.S. Forest Service, Missoula) has worked with tribal and state fisheries managers to obtain genetic information from pike populations throughout the upper Columbia River Basin. Her research shows that, unlike the pike in Lake Pend Oreille, those in the recently invaded Pend Oreille River below the lake are most closely related to pike from Medicine and Cave lakes near the Coeur d'Alene River, Idaho rather than to the pike just upstream in the lake. This indicates that the fish were most likely transported by humans rather than having colonized from Lake Pend Oreille and the Clark Fork River upstream.

The genetic data also show that the pike in Lake Roosevelt are most closely related to those just upstream in the lower Pend Oreille River, indicating that they dispersed downstream. Evidence from other fish species suggests that pike will likely move downstream over or through dams. For example, Holly McLellan (fisheries biologist, Confederated Tribes of the Colville Reservation) reported (presentation to ISAB, 25 Jan 2019) that

PIT tags from redband rainbow trout tagged in Lake Roosevelt, upstream from Grand Coulee Dam, were detected on bird colonies at the mouth of the Columbia River. The trout had most likely passed over or through the dam and moved downstream. Therefore, there is no reason to expect that the pike invasion will stop at Lake Roosevelt. They probably will be transported downstream by humans or move on their own.

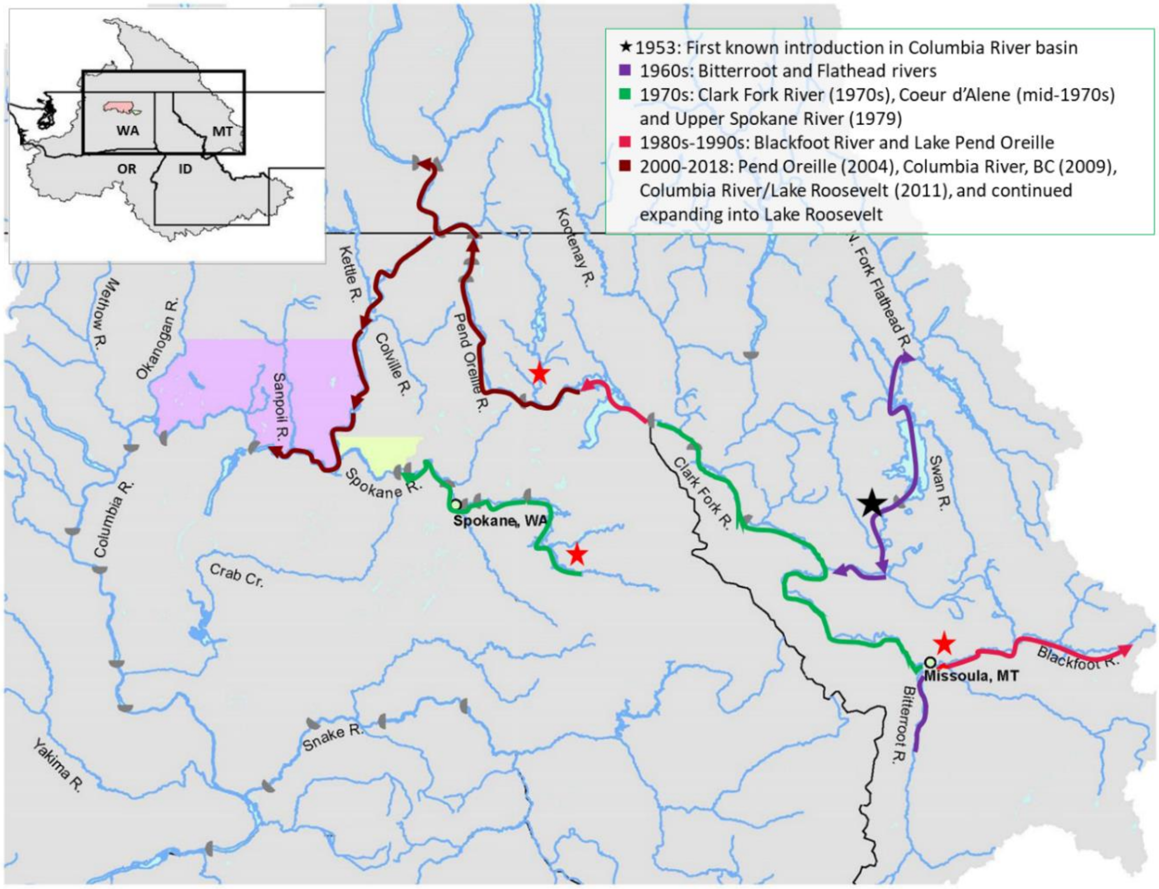

Figure 6. Time course of expansion of Northern Pike in the upper Columbia River Basin (modified from a map courtesy of K. Carim, U.S. Forest Service; H. McLellan, Colville Confederated Tribes; and N. Bean, Kalispel Tribe). The first documented introduction of pike in the Columbia River Basin was into Lone Pine Reservoir, Montana, in 1953 (black star). Circumstantial evidence indicates that they were also illegally moved above Milltown Dam into the Blackfoot River drainage and to the Coeur d'Alene River drainage (red stars). Recent genetic assignment tests indicate that pike in the Pend Oreille River and Lake Roosevelt are more closely related to fish in the Coeur d'Alene River drainage. Therefore, it is unlikely that fish in these recently invaded areas originated from Lake Pend Oreille and the Clark Fork River upstream, and so they are assumed to have been introduced illegally (location of red star is only assumed). The source of pike that appeared in the Bitterroot River in the 1960s is unknown. The small grey half-circles along river courses are locations of dams.

Evidence from other regions also indicates that pike easily invaded downstream from sources upstream.

- In southcentral Alaska, pike stocked in Alexander Lake colonized 40 miles (64 km) downstream into the Susitna River. They then colonized upstream into over 120 lakes and rivers (Dunker et al. 2018).

- Pike were introduced to the upper Colorado River basin in the 1970s and have invaded much of the available habitat. In the Yampa River, Colorado, pike moved, on average, 12 miles (19 km; maximum 241 miles or 388 km), and 90% moved downstream (Zelasko et al. 2016).
- In a study of 1,356 lakes in 26 drainages in northern Sweden where pike are native but were excluded from some waters by natural barriers, Spens et al. (2007) reported that pike were found in every lake downstream from each source population. Pike introduced into headwater lakes that previously lacked pike colonized every lake downstream until they reached the native distribution. Pike also colonized all habitat in an upstream direction with stream gradients less than 6.6-7.0%.

Pike are known to be highly invasive. They have invaded other rivers and lakes in North America beyond their native range and are now established in 38 of 50 states (Dunker et al. 2018). They have also established nonnative populations in Ireland, Spain, Portugal, and parts of Africa.

Illegal stocking has been a major source of pike invasions in other regions. Early stocking of pike and other nonnative fish in North America was often by fisheries management agencies, but after about 1980 almost all introductions of nonnative fishes have been by illegal stocking (Rahel 2004). Illegal stocking is the source of various nonnative pike introductions and invasions in Alaska (Sepulveda et al. 2015; Dunker et al. 2018), California (McMullin and Pert 2010), Montana and Idaho (K. Carim presentation), and Colorado (Zelasko et al. 2016).

Pike are also adaptable. They have colonized and now spawn in Lake Roosevelt, despite a general lack of suitable spawning habitat (McLellan presentation). Invasion by a nonnative plant, the flowering rush (*Butomus umbellatus*), may facilitate pike spawning and the survival of juveniles (Rice and Dupuis, presentation to ISAB). Pike have been captured in Cook Inlet, Alaska in saltwater (K. Dunker, presentation to ISAB), leaving open the possibility that they might be able to colonize nearby coastal rivers via the ocean. In the Baltic Sea, pike not only occupy but also spawn in brackish habitats, for example (Westin and Limburg 2002; Engstedt et al. 2010). Given these reports, it appears likely that they could disperse throughout the entire Columbia River, given enough time and in the absence of control efforts, and find suitable habitat in shallow, vegetated areas, especially in sloughs and floodplains in the lower reaches.

Successful eradication of pike

The literature on biological invasions shows that eradication of a nonnative species is usually successful only at the earliest stages of invasion (Simberloff 2003). Pike have not been eradicated from any major river they invaded, although they apparently have been eliminated with great effort from a few smaller water bodies. This includes eradication from several lakes and reservoirs and from two relatively small drainages in California and Alaska (McMullin and Pert 2010; Dunker et al. 2018) where invasions had expanded to only a relatively restricted area.

- Eradication of pike has apparently been successful in several isolated or relatively isolated reservoirs and lakes in California, Nevada, Colorado, Alaska, and Sweden (Dunker et al. 2018).

- A 20-year program consisting of reservoir drawdown and two rotenone treatments of Lake Davis (the first being unsuccessful), Frenchman Reservoir, and various Sierra Nevada tributaries was required to eradicate pike from the state of California (McMullin and Pert 2010; Dunker et al. 2018).
- Pike were eradicated from the Soldotna Creek watershed, Alaska, a tributary of the Kenai River. Rotenone was used to treat 6 lakes, 22 miles (35 km) of stream, and 143 acres (58 hectares) of connected wetlands, during 2014-2016. No pike were detected afterwards by gill nets or eDNA (Dunker et al. 2016). This and other removals from six isolated lakes eliminated pike from the Kenai Peninsula (Dunker et al. 2018).

Efforts to suppress pike where they cannot be eradicated

At present, no methods are available to eradicate pike from larger watersheds or major rivers, and there are no data available to estimate the level of suppression needed to lessen the likelihood of pike establishing downstream from Grand Coulee Dam. However, there could be value in reducing their numbers (McLellan, presentation to ISAB), especially in the downstream reaches of the reservoir. Reducing the number of pike available to move downstream could lessen the likelihood that they successfully establish new populations that would be difficult and expensive to control, and in turn, provide source populations for other illegal introductions or natural colonization. For example, the ecological literature is clear that across the spectrum of organisms that have been introduced to new locations, increasing the number and sizes of organisms released is one key to successful establishment of nonnative species in new environments (Simberloff 2009). Therefore, reducing the numbers of pike passing downstream from Grand Coulee Dam is an important goal in reducing the probability of a successful invasion in the anadromous zone.

Mechanical removal has been effective at reducing the catches of pike in several major rivers, including upper Columbia River tributaries, but efforts must be sustained indefinitely to be effective. Annual removal efforts are ongoing in several rivers.

- Gill nets set during spawning in spring reduced pike catches to low levels (< 1 fish/net) in the upper Columbia River Basin (Box Canyon and Boundary reservoirs of the Pend Oreille River; Maroney presentation), and reduced pike catch-per-unit-effort (CPUE) in most side-channel sloughs of Alexander Creek, Alaska by 85% (Sepulveda et al. 2015; Dunker 2014; Dunker et al. 2018).
- Three or more passes of boat electrofishing throughout most of the Yampa River, Colorado, during 2004-2010 reduced pike abundance (based on population estimates) to < 20 fish/km (< 12.4 fish/mile) in most years (Zelasko et al. 2016). However, abundance rebounded to near pre-removal levels each year because immigration from headwater reaches that were not electrofished and recruitment of smaller fish increased abundance 4-10 times between annual removal efforts. Removal has been ongoing since 2010 through a combination of gill nets in backwaters where pike spawn, removal of pike from headwater reservoirs, and screening of reservoir outlets (K. Bestgen, presentation to ISAB).

Conclusions: Lake Roosevelt northern pike suppression

The Council asked: *In consideration of ISRP 2018-3 regarding Northern Pike, do we know what level of suppression (exploitation) through gill net removal, angler removal or other methods is needed to reduce the population in Lake Roosevelt to a level sufficient to reduce risk of emigration from the lake or risk to other focal management species?* (question 5). Based on the inexorable invasion by northern pike downstream throughout tributaries of the upper Columbia River Basin above Grand Coulee Dam over the past 65 years, it is likely that even with the best efforts in public education, early detection, and control or eradication pike will eventually invade the anadromous zone, either naturally or by human agents. Given this, the ISAB was able to reach the following conclusions:

1. It is not possible to estimate the level of suppression necessary to reduce the risk of emigration of pike downstream from Lake Roosevelt because there is no simple relationship between abundance and the probability of emigration or establishing a population downstream.
2. Each individual female pike produces tens of thousands of eggs, so given the right conditions emigration by even one male and one female pike could produce thousands of juveniles. Nevertheless, evidence from other organisms indicates that reducing the numbers of fish emigrating from Lake Roosevelt will delay the chances that pike will establish new populations downstream. Reducing establishment also reduces new source populations that enhance further spread, either naturally or by humans.
3. Evidence from past introductions indicates that about as many invasions of new waters were caused by illegal stocking as by dispersal of pike themselves (see Figure 6), similar to the pathways of unauthorized introductions of nonnative fishes in Wyoming (Rahel and Smith 2018). This indicates that more could be invested in efforts to reduce illegal stocking of pike by humans.
4. Given this, it is essential to develop a monitoring program capable of accurately detecting newly established pike populations throughout the anadromous zone, not just near the current invasions. Evidence from the Colorado River basin (K. Bestgen presentation) indicates that illegal introductions of pike into lakes and ponds, including those in the floodplain, are especially likely.
5. Evidence from invasions of other organisms indicates that eradication is often possible only at the earliest stages, so once detected, rapid eradication of newly established populations is paramount.
6. Pike can be suppressed with great effort and expense, especially in reaches without much suitable habitat, but likely will not be eradicated from a large river like the Columbia or its major tributaries, especially if there are source populations within about 12 miles (20 km) by river that supply immigrants. Eradication has been successful only in individual lakes, reservoirs, or small watersheds, and so might be successful in isolated ponds and lakes that become invaded.
7. Shallow, vegetated floodplain sloughs, like those in the lower Columbia River, will likely provide ideal habitat for pike spawning, rearing, and growth. A species distribution model could be developed to

estimate the habitat in the Basin most likely to be invaded, and how it could change with a changing climate (e.g., see Rubens and Olden in review, for a model of smallmouth bass invasion).

8. To be successful in reducing mortality of focal salmonids, control efforts will need to be extensive, occurring river-wide where habitat is suitable for pike, and must continue indefinitely to be most effective for protecting salmon populations.

Ecological impacts of northern pike

Pike are highly invasive. A model of future potential pike invasion in southcentral Alaska predicted that pink, chum, and coho salmon will be highly vulnerable to pike invasion in about 15% of their available habitat, and Chinook in 11% of theirs (Jalbert 2018). Another 15% of habitat for pink, chum, and coho, and 20% for Chinook will be moderately vulnerable to pike invasion, so the five species of salmon will be vulnerable to pike invasion in about 30% of the habitat of each. The model is based on overlap between habitat with high intrinsic potential for salmon based on geomorphic and other physical variables, and low-elevation, low-gradient habitat with wide floodplains that is suitable for pike. Pike are an ambush predator, camouflaged to be inconspicuous in vegetated edge habitat, rather than feeding in open water, so species occupying or moving through such edge habitats will be most vulnerable.

Pike are highly piscivorous, eating small and large fish of all species to more than half their own body length. Soft-rayed fishes like juvenile salmonids are a preferred and vulnerable prey (Sepulveda et al. 2013, Courtenay et al. 2018).

- In an Alaskan tributary where nonnative pike were at relatively low abundance, Pacific salmonids made up about 50-70% of their diets by numbers and biomass (Sepulveda et al. 2013). In a neighboring tributary where salmonids already had been driven to low abundance by abundant pike, the pike continued to eat salmon and other salmonids where they were still present but also switched to lamprey and sculpin when salmonids declined. Hence, pike are capable of driving fish species to rarity or extinction because they can switch to other fish and invertebrates to maintain their populations.
- All sizes of pike (age-1 and older) eat salmonids, but large pike eat more per capita (Courtenay et al. 2018). Contrary to conclusions from an earlier study in Alaska (Sepulveda et al. 2013), a broad range of ages of pike contributed to the total population-level load of predation on salmonids, not just small or large pike (Courtenay et al. 2018). Bioenergetics modeling is a useful tool to estimate biomass of prey consumed by pike in a given waterbody (Sepulveda et al. 2015, Courtney et al. 2018).
- A synthesis of diets of > 2900 pike from 31 waterbodies in Alaska where they are both native and nonnative showed that they specialized on fish when available but subsisted on a generalized diet of larger invertebrates when fish were depleted or unavailable (Cathcart et al. 2019). When salmonids were available, about half of the medium and large pike (>32 cm) had eaten them, and for these pike

salmonids made up about half their diet by weight. Among small pike, about a quarter had eaten salmonids, but they made up about 70% of their diets, on average.

- The effect of different fish predators depends on their preference for fish as well as their abundance. For example, smallmouth bass in the Colorado River included less fish in their diets, but were more abundant than pike, and so were estimated to eat 10 times more fish biomass than the pike population (Johnson et al. 2008). This is consistent with many other studies (e.g., Ricker 1941; Beauchamp et al. 1995) in which the per capita predation differed greatly among predator species. Therefore, relative abundance as well as per capita consumption must be carefully determined at frequent intervals to accurately estimate total predation.

Pike predation can have drastic effects on salmon populations. In one small river in Alaska (Alexander Creek), pike predation was estimated to be sufficient to collapse the Chinook salmon population, by driving smolt production below the level needed for replacement (Sepulveda et al. 2015). Pike had driven Chinook escapement from 3500 adults before 2000, to 1600 adults during 2000-2008, and in 2010 only 177 adult Chinook salmon returned.

Coexistence of pike and salmon will depend on habitats available and likely the co-evolutionary history of the two groups of fish.

- Pike and salmon coexist in their native range in northern Alaska, primarily by using different habitats (Sepulveda et al. 2013, Dunker et al. 2018), whereas in their native range in Sweden pike and Atlantic salmon (*Salmo salar*) rarely occur together in the same lakes or rivers (Spens et al. 2007).
- Pike have driven Chinook salmon to low levels after they invaded one smaller Susitna River tributary with extensive pike habitat and are predicted to collapse the population, whereas in an adjacent river with poor pike habitat they apparently occupy only some habitat and have reduced salmon numbers less (Sepulveda et al. 2015, Dunker et al. 2018).

Conclusions: ecological impacts

The Council asked: *What are the likely ecological impacts of northern pike should they enter the Basin's anadromous waters?* (Question 6). Pike are highly invasive and through predation are likely to drastically reduce salmonid abundance, especially in low-gradient river segments with wide floodplains. The evidence from other research supports the following conclusions:

1. Pike are highly piscivorous and prefer salmonids but can subsist on other prey including invertebrates. As a result, they are capable of driving preferred prey species to very low levels or extinction.
2. All sizes and ages of pike (yearling and older) can eat salmon fry, parr, and smolts and reduce their abundance to low levels in habitats where they overlap.

3. If salmonids have no habitat refuges that are unsuitable for pike, they are likely to reduce their numbers and can cause salmonid populations to collapse. Varying levels of coexistence may occur where habitats are less suitable for pike.
4. Pike typically occupy relatively shallow, vegetated floodplains and shoreline habitat from which they ambush prey. Consequently, salmonid species and life stages that migrate in open water near the surface, such as smolts, may be less vulnerable than others, such as pre-smolts, that forage or overwinter in habitats occupied by pike.

Genetic methods for detection and potential control of invasive northern pike in the Columbia Basin

An important management goal is to slow the spread and establishment of pike in the Columbia River Basin. To accomplish this, management action should focus on early detection and rapid response to pike detected downstream of Grand Coulee Dam. Early detection can be achieved by a well-designed eDNA monitoring protocol implemented on a wide geographic scale and conducted at least each year. Rapid response to detection could include intensive local suppression efforts, and eventually could include longer-term responses of stocking of YY males to eradicate local populations. This section discusses details and uncertainties that underlie eDNA monitoring. It also highlights other genetic approaches that are being used to monitor and predict spread of pike in the Columbia River Basin.

Monitoring and early detection of pike via eDNA

Predator control measures are greatly enhanced when invasion and spread of invasive species can be rapidly and accurately detected and monitored, and intervention measures can be implemented before populations become established. Ideally, sampling for invasive species should occur at large geographic scales and multiple time points to document range expansion. Traditional monitoring and survey work can be logistically difficult and expensive, especially when conducted over large regions and multiple years, and if the target species is scarce.

An alternative is to use environmental DNA (eDNA) to monitor invasive species. Environmental DNA indicates the presence of a species because aquatic organisms shed DNA into the environment through urine, feces, scales, mucus, skin, and carcasses (reviewed by Rees et al. 2014, Barnes and Turner 2016, Dunker et al. 2016). Once released from the organism, DNA molecules become suspended in the water column or attached to other suspended particles, and eDNA is obtained for analysis by filtering water samples. Although eDNA is relatively stable, it begins to degrade through exposure to UV radiation and microbial activity. Accordingly, eDNA concentration in a water sample is a function of the rate of release of DNA from organisms versus rate of decomposition (Dunker et al. 2016), as well as distance from the target species and other conditions (Tillotson et al. 2018). The eDNA methodology is so sensitive that a single target DNA molecule can be detected in a sample.

For fishes, eDNA sampling can be conducted at easily accessible sites with a small crew at relatively low cost. Sampling consists of filtering and retaining particulate matter from a known quantity of water obtained from a lake, stream, or river. Water samples or filtrate are returned to the laboratory and assayed for presence of target DNA using the polymerase chain reaction (PCR) and species-specific PCR primers (Carim et al. 2016). Field sampling and PCR screening must be conducted carefully to avoid contamination with DNA from sources other than the water sampled, such as from humans or residue from other sample collection activities. Experimental protocols in the laboratory use positive and negative control samples to determine the presence and absence of target DNA in the sample. In addition to standard PCR approaches, quantitative PCR (qPCR) can be used to estimate concentration of focal species DNA present in the sample. Environmental DNA technology is used extensively to detect rare and invasive species (Jerde et al. 2011, 2013), estimate biomass and abundance of fish (Doi et al. 2015, Mizomuto et al. 2018, Tillotson et al. 2018), and identify species in gut contents to verify predation (e.g., Ehlo et al. 2017, Sethi et al. 2019). Relative ease of sampling and straightforward laboratory and computational procedures have contributed to widespread use of eDNA monitoring in a variety of aquatic settings.

Like any other monitoring and survey approach, eDNA has limitations and is subject to bias. Several factors can affect detection probabilities, including metabolism and ecology of target species and environmental conditions that affect persistence and transport of eDNA (Barnes et al. 2014, Strickler et al. 2015). Use of eDNA for quantifying abundance or biomass of fishes or other organisms can be complicated by unknown effects of environmental conditions (e.g., water temperature) and collection methods (Lacoursière-Roussel et al. 2016). Other limitations of eDNA include inability to distinguish live from dead animals, inability to distinguish life-history stage, or to provide information about specific habitat use. Because eDNA assays are highly sensitive, it is essential to employ protocols that control for contamination by user error, or by temporary or latent DNA in the environment (Dunker et al. 2016). Thus, eDNA approaches are most informative when used carefully and in concert with traditional surveys that account for life history variation and age structure of populations.

For pike, ***eDNA monitoring should be employed across a broad geographic scale in the basin*** with increasing geographic distance between samples as one moves farther from known source populations. A full set of samples should be obtained at least annually to coincide with reproductive cycles and potential migration of juveniles. Once eDNA is detected in a new waterway, additional eDNA sampling plus traditional sampling approaches should be used to pinpoint the geographic center of the local population and focus sampling on key habitats (e.g., spawning habitat, nursery habitat). These areas may be appropriate targets for mechanical removal or application of a piscicide, or perhaps YY male stocking (see below). Removal projects should be followed by post-treatment eDNA sampling to verify local extirpation.

There has been considerable development of eDNA methodology for monitoring pike in Alaskan waterways (Dunker et al. 2016) and in the Columbia River Basin (Carim et al. 2016). Laboratory protocols, species-specific PCR primers, and optimization of qPCR protocols have been conducted such that assays of field samples are now somewhat routine (Carim et al. 2016). Nevertheless, local field conditions affect detection rates, diffusion and spread, and persistence time of eDNA molecules. Thus, understanding how local environmental factors drive detection probabilities is essential for effective design of an eDNA monitoring program. For example, biologists have deployed caged animals at known densities to evaluate the limits of detection in lakes in Alaska. Similarly, pike carcasses were experimentally placed into waterways to evaluate persistence time and spread of eDNA from dead animals. Empirical data on detection limits and persistence times were used to design eDNA monitoring protocols for that ecosystem. The eDNA survey work in the Columbia River Basin (presented to the ISAB by Carim et al. 2019) provided a preliminary assessment of detection probabilities relative to abundance and distribution of pike based on gill net surveys and other traditional monitoring approaches.

Although eDNA offers tremendous potential for rapid detection and monitoring of pike in the Columbia River Basin, some uncertainties should be addressed before the approach is fully implemented. Future research should answer questions related to sampling density, geographic scale, and frequency of eDNA sample collection and processing. Nonetheless, eDNA monitoring is a powerful tool that can be used to slow the spread of pike in the Columbia River Basin.

Genetic study of pike to predict spread in the Columbia River Basin

There are benefits to characterizing genetic diversity of existing populations of pike in the system. Using genetic methods, it is possible to estimate the source of a particular population, the number of founding individuals in a newly established population, and the probable mechanism (natural dispersal vs. human translocation). Carim et al. (2019) reported on an ongoing genetic study of the sources and spread of pike in the Columbia River Basin. Their strategy is to coordinate genetic sampling and demographic monitoring with the aim of understanding factors that underlie the current distribution of pike. A second goal is to provide a baseline from which the invasion into unoccupied portions of the basin can be understood, including the locations of source populations that potentially drive population expansion.

Carim et al. (2019) builds on considerable genetic information available for pike, including population genetic studies (reviewed in Miller and Senanan 2003) and an annotated genome for the species (Rondeau et al. 2014). Many authors note that pike show low genetic diversity, probably because of genetic bottlenecks over their evolutionary history (Miller and Senanan 2003, Jacobsen et al. 2004). Detailed study of the pike genome indicated that microsatellite DNA regions (short, repeated sequences) harbor more genetic variation than other regions of the genome, such as those characterized by single-nucleotide polymorphisms (SNPs). Because they provide a detailed “fingerprint” for each individual, microsatellites, as used by Carim et al. (2019), are an appropriate marker to study fine-scale changes in allelic frequencies across space and time that give insight into mechanisms of invasion in the Columbia Basin. Somewhat surprisingly, pike exhibit considerable variation in body shape and reproductive behaviors (i.e., phenotypic plasticity and behavioral variation) among individuals and populations (Nielsson et al. 2008, Senay et al. 2017). This is because low levels of genetic variation usually correspond to low levels of variation in physical traits like body shape.

Although Carim et al. (2019) determined that human-mediated translocation is a predominate factor that explains the current distribution of genotypes in the Columbia River Basin, it is also likely that “natural” dispersal from established areas will contribute to the distribution and spread of pike in the system. A potentially powerful application of combined study of genetic and demographic processes ***is the potential to***

predict relative rates of invasion across different river reaches by natural dispersal (sensu Sakai et al. 2001). For example, an extensive landscape genetic study was conducted on pike in the Lake Ontario – St. Lawrence River system that has similar features to the Columbia Basin (Ouellete-Cauchon et al. 2014). Landscape features, like the number of barriers between collection localities and the linear distances between sites, were also characterized.

In the Lake Ontario – St. Lawrence system, genetic differentiation was weak, suggesting large-scale movement of fishes across the landscape. Nonetheless, genetic differentiation and population structure varied considerably over parts of the landscape. Three variables were predictive of levels of population structure. First, ***interannual water level variation was positively associated with pike dispersal*** (as measured by genetic structure). Adult pike spawn in vegetated areas on the periphery of lakes and large river systems and exhibit spawning site fidelity (Minglebier et al. 2008). When water levels fluctuate, access to preferred spawning sites is reduced. Pike dispersal is thus enhanced when water levels fluctuate strongly (as in a hydropeaking scenario). Second, ***pike dispersal was reduced across waterways that differed in water quality and chemistry.*** It is possible that differences in physical and chemical properties of water masses promote retention and inhibit movement of larval and juvenile fishes. This mechanism of population structuring is not well studied in freshwater systems but appears to be important in ocean systems. Perhaps most relevant for comparison to the Columbia River Basin, it is not clear that downstream dispersal of larvae and juveniles would be negatively affected by mixing of waters (i.e., at a tributary confluence) in lotic portions of the range. Nevertheless, areas of distinct water masses that mix in the system may hamper movement of early life history stages of pike and serve as a barrier to dispersal. Third, ***the presence of dams between sampling localities was negatively related to pike dispersal***, although dams do not stop movement of fish entirely.

Relationships of population structure and landscape features can be used to make predictions about dispersal and establishment dynamics in the Columbia Basin. For example, hydropeaking in the Basin is predicted to be negatively associated with population structure and to facilitate dispersal and spread of pike adults seeking suitable spawning habitat (Senay et al. 2017). Reproductive failures associated with fluctuating water levels may lead to lowered recruitment and densities of pike in reaches subject to intense hydropeaking. By studying spatial and temporal patterns of genetic divergence, it is possible to ask questions about local effective population size and turnover (e.g., Miller and Kapuscinski 1997) related to ecological correlates of local abundance. Temporal turnover of allele frequencies could indicate the importance of propagule pressure for sustaining local populations of invasive northern pike. Finally, genetic monitoring could yield insight into mechanisms of recovery of local populations following failed eradication efforts (e.g., Aguliar et al. 2005).

There are at least two uncertainties that affect the use of landscape genetic studies to make predictions about the spatial and temporal dynamics of the spread of pike in the Basin. First is a general caution that demographic (i.e., mark-recapture, otolith microchemistry analysis, etc.) and genetic measures of connectivity (i.e., gene flow) differ in terms of scale and scope (Lowe and Allendorf 2010). It is important to conduct both types of studies in concert to gain accurate insight into processes that occur over years to decades (ecological time) versus longer (evolutionary time).

Perhaps more importantly, extensive variation in body shape is common within and among populations of pike. For example, pike morphology is known to differ between unregulated and regulated (i.e., hydropeaking) river systems (Senay et al. 2017). Extensive phenotypic variation and rapid morphological response to modified flows could confound simplified approaches to predictive and general population- or community-level models of distribution, abundance and ecological effects of pike across aquatic ecosystems (Nilsson et al. 2008, Senay et al. 2017).

Stocking YY males to eradicate Northern Pike

Mechanical removal, attempts at eradication via piscicide treatments, and other suppression efforts have varying levels of success that depend on the life history (e.g., number of juveniles produced) and physiological tolerances of invasive species, and environmental factors such as river and floodplain morphology and barriers to dispersal. For example, a first attempt at piscicide treatment in 1997 failed to remove pike from Lake Davis in California (Aguilar et al. 2005). Pike survived treatment and repopulated Lake Davis quickly because they are capable of prolific breeding and explosive population growth, linked to early age at maturation. Suppression and removal efforts may temporarily reduce abundance of pike but usually cannot remove them entirely.

Another approach to pike eradication involves releasing fish with so-called “Trojan” sex chromosomes that, once mated into local wild-type populations, skew sex ratios such that local populations are reduced and ultimately eliminated (Cotton and Wedekind 2007). Most commonly, the approach involves producing males in a hatchery that have an extra Y chromosome (e.g., have a YY chromosomal genotype). When YY males mate with wild females all of the offspring are male. As the number of females is reduced with subsequent stocking, it becomes more difficult to find suitable mates until the population fails to reproduce entirely.

The YY males are not genetically modified organisms (GMOs) and pose no threat of a “Frankenfish” effect on populations and communities of non-target organisms. Instead, YY males are produced by hormonal treatment in the hatchery without genetic manipulation. Many organisms, including humans, have X and Y chromosomes that determine sex. For example, the female has two X chromosomes (one from her mother, and one from her father) and develops female characteristics and gametes (eggs). The male is called the “heterogametic sex” because he has one X (from his mother) and one Y chromosome (from his father) and develops male characteristics and gametes (sperm). Some fish also have chromosomal sex determination where the male is the heterogametic sex, and it is possible to feminize an XY male fish by hormone treatment early in development. In this case, the XY “female” is genetically male but produces female sexual characteristics and eggs. When XY males and XY “females” are mated together, they produce offspring that are 25% XX females, 50% XY males, and 25% YY males. When YY males are mated to an XY female, they produce all male progeny (50% XY males and 50% YY males). Therefore, when YY males are stocked into a natural population, they produce all male progeny (XY) and progressively skew the sex ratio toward males. In theory, if enough YY males can be produced for an invasive species, they can eradicate that species given sufficient stocking effort and time (Gutierrez and Teem 2006).

Pike appear to have sex chromosomes with males as the heterogametic sex (e.g., XY), and XY males can be feminized by hormone treatment (Schill 2016). Pike are thus good candidates for development of YY males, but none have been produced to date. Assuming that sufficient YY males can be produced to sustain a large-scale stocking effort, the time to extirpation of local population will depend on ecological factors.

There has been some promising work done on brook trout that indicates that YY male stocking could be a valuable tool to control and eradicate invasive species. For example, Schill (2016) and Schill et al. (2017) evaluated stocking rate and YY male survival for nonnative brook trout (*Salvelinus fontinalis*), along with suppression rate of the brook trout in the wild. The time to extirpation was always lower when YY males made up 50% of the total population size and survival of YY males was good. Reducing the local brook trout population by removing individuals also increased the efficacy of YY male stocking. In simulations, rates of suppression and YY stocking that are readily achievable (i.e., 50%) resulted in predicted eradication in 4 to 12 years, regardless of good or poor YY male survival (Kennedy et al. 2018).

For pike, an optimistic estimate is that it could take about 10 to 12 years to produce YY males in the hatchery and an additional 4 to 12 years for stocking to impact invasive populations—or at least 20 years to implement a large-scale YY stocking program. Assuming the YY males can be produced on a scale that can sustain a sufficient stocking effort, the time to extirpation of local population will depend on ecological factors. For example, the mating system and longevity of pike differ significantly from brook trout. Survival and reproductive success of pike YY males should be experimentally determined as was done for brook trout (Kennedy et al. 2018).

Key uncertainties

To consider whether stocking YY males could successfully reduce or eradicate invasive pike populations, several uncertainties need to be addressed by a combination of simulation and experimental studies. These include but are not limited to:

1. How many YY male pike should be stocked and for how long? At what size should YY fish be released to avoid excessive mortality of stocked fishes due to predation?
2. What is the reproductive success of YY males compared to wild-type males? Are older, larger males more successful in reproduction? If so, how does this affect the stocking strategy?
3. Does the release strategy differ between newly invaded populations and established populations?
4. How much, if any, suppression effort is necessary to increase time to extirpation due to YY male stocking?
5. What is the risk of YY male stocking for (temporarily) increased local predation rates on salmonids and other species?

Observations about human behavior that influences invasions of pike and other large piscivores

Humans play a key role in invasions of nonnative species. In an earlier section (page 41), the ISAB presented some of the social and economic research into the topic (e.g., Perrings et al. 2002, Johnson et al. 2008). Fisheries scientists have repeatedly argued that managing fisheries, especially recreational angling, is as much about managing people as managing fish populations (Arlinghaus 2004, Hilborn 2007). Understanding what drives regional-scale problems such as fish invasions will require interdisciplinary research that integrates social and biological sciences (Arlinghaus et al. 2016) and that frames recreational fisheries as strongly coupled social-ecological systems (Arlinghaus et al. 2017). A central tenet of this framework is that managers will need to focus on managing relevant feedbacks between anglers and fish populations and ecosystems, rather than simply fish populations themselves.

Human behavior drives many of these feedbacks, but the behavior that drives the initial illegal introductions of nonnative species like northern pike has received little study by fisheries or social scientists. Here we draw together key points that may be relevant to further study and management of the forces that drive illegal introductions of northern pike by humans. Some information is published in the refereed or non-refereed literature, whereas other information is based on presentations to the ISAB and the combined experience of ISAB members in fisheries ecology and management. Consequently, recommendations presented here should be considered hypotheses to test from both a biological and social perspective and subjected to further study and careful evaluation.

- Evidence from the ongoing invasion of pike in the upper Columbia River Basin (Figure 6), and from fish invasions in another western state (Rahel and Smith 2018) indicates that about half of the nonnative fish introductions result from illegal release of fish by the public.
- Once pike are established, past experience indicates that anglers will want them[4] and will sabotage removal efforts by moving them.
    - For example, in Colorado, pike that were salvaged after removal and translocated to off-channel ponds to create fisheries were detected back in the Yampa River the next year, despite no surface connections, and pike were also moved to new waters in the Colorado and Gunnison river basins (Zelasko et al. 2016; K. Bestgen, presentation to ISAB).
- Consequently, it is most advantageous for managers to mount a rapid response to new pike introductions, not only using biological measures but also developing the means to prevent humans from spreading pike farther, and to keep them from becoming a sport fish with advocacy groups.

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[4] For example, see these three recent 2019 letters to the editor regarding management of northern pike in Lake Coeur D'Alene: *Pike a Political Casualty*, *Pike War against Anglers*, and *Pike a Bassinine Decision*.

  - For example, it seems unwise for management agencies working to prevent pike invasions to post on their websites images of people holding large pike (i.e., so called "hero shots") or to present awards for catching these large nonnative predators. Such images and awards motivate anglers to catch such fish and tacitly encourage illegal translocations.
- The ISAB endorses the idea that if the management agencies make pike illegal when first detected (or better yet, well before they are detected), rather than listing them as a sport fish, this will communicate a clear message that they are a danger rather than an opportunity. This may also deter advocacy groups from developing.
  - Engaging the angling public in controlling nonnative fish through unlimited harvest or mandatory kill regulations (including judicious use of bounty fishing) conveys the message that illegal introductions will not be rewarded by creating a desirable fishery, even though angler harvest may have modest effects in controlling the invader (Rahel and Smith 2018).
  - One option may be a reward for turning in those who transport pike, like the Turning in Poachers (TIP) programs developed by many natural resource management agencies. Johnson et al. (2009) proposed that agencies could pool reward funds and couple this with severe sanctions to deter illegal introductions. The effectiveness of such programs would need to be rigorously evaluated.
- Fisheries conservation groups could be enlisted to help promote the idea of fishing for species where they are uniquely native, which for pike would be in places like northern Saskatchewan and northern Alaska. People travel long distances to fish for iconic species like salmon, and they also do this to catch large pike.
- We caution against creating sport fisheries for other esocids like tiger muskie (a sterile hybrid between pike and muskellunge, *Esox masquinongy*) because they may create demand among anglers to produce these fisheries elsewhere and promote the movement of nonnative pike. Moreover, some anglers may not distinguish between pike and tiger muskies, and may seek more opportunities to develop fisheries for pike or similar species.

OTHER NONNATIVE FISH PREDATORS

Many other fishes that are not native to the Columbia River Basin have become established in the basin, including other salmonids like lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus fontinalis*), various sunfishes (*Lepomis*), crappies (*Pomoxis*), basses (*Micropterus*), walleye (*Sander vitreus*), bullhead catfishes (*Ameiurus*), American shad (*Alosa sapidissima*), and mosquitofish (*Gambusia affinis*). Here we focus on three nonnative fish predators that are considered to be major threats to native listed salmonids or other listed fishes: smallmouth bass, walleye, and lake trout. We discuss their introduction and current range, ecological impacts, control efforts, and potential for further spread.

Smallmouth Bass

Smallmouth bass (*Micropterus dolomieu*) were introduced from their native range into the western United States and the Pacific Northwest by federal and state agencies (Figure 7). In 1874, Livingston Stone of the U.S. Fish Commission transported smallmouth bass from Lake Champlain, Vermont and the St. Joseph River, Michigan to California in a railway "aquarium car" and released them into Napa Creek and Alaitieda Creek (Smith 1896). None of these fish survived, and the Fish Commission concluded that anglers were responsible for their "probable extermination." In subsequent attempts to introduce smallmouth, the fish were acclimated in protected reservoirs and transplanted to other streams in California. In 1923, the master game warden of Oregon, A.E. Burghduff, transported smallmouth bass from Wisconsin to Oregon in his luggage and released them into Lake Oswego in Portland (Lampman 1946). The following year, he captured smallmouth for Oregon state hatcheries from a lake on Blakely Island in the Puget Sound, where a logging company had transplanted them from Michigan. These fish were moved to the McKenzie River Hatchery and 200 fish were released in the upper Willamette River by the Oregon State Game Commission. In the 1920s, smallmouth bass were caught by fishermen in the upper Columbia River and mouth of the Umatilla River, and 5,000 were stocked in the Yakima River in 1925 (Lampman 1946).

In the early 20th century, fisheries professionals and the public were largely in favor of introducing fish species outside their range for both sport opportunities and food production. Though the detrimental consequences were recognized and debated, the overall sentiment of the time was utilitarian and viewed fish introductions as a benefit. In 1904, there was public debate about the introduction of bass into Oregon. The Oregonian newspaper printed a discussion of the issues (Lampman 1946). Judge S.H. Greene contacted two ichthyologists, Drs. James Henshall and David Starr Jordan, to get their opinion and both advocated for introduction. Dr. Henshall was an active proponent for introductions of largemouth and smallmouth bass so his support was not surprising. Dr. Jordan, one of the leading ichthyologists of the time, wrote:

> *"The chances are that the introduction of the bass would not in any way interfere with the abundance of the trout. This would be especially true in Oregon, where the large number of minnows, suckers, and chubs will furnish the bass with plenty of food which will be more to its hand, or rather, to its mouth, than the young trout would be. I think that the introduction of either species of bass would be a gain to the people of Oregon."*

Smallmouth bass have become established outside their native range in 42 states, and Alaska is the only state that does not contain smallmouth populations (Fuller et al. 2016). They are a warm water species and their productivity decreases toward the north and in colder water temperatures (Beamesderfer and North 1995). Smallmouth are a widespread nonnative species in the western United States and were captured in more than 4% of the 113,000 river miles surveyed by E.P.A. in the Environmental Monitoring and Assessment Program (Lomnicky et al. 2007). Smallmouth were the most commonly captured nonnative fish in a survey of seven rivers in the Pacific Northwest (Hughes and Herlihy 2012) and have become established in most of the major rivers of the Columbia River Basin (Figure 7). Smallmouth bass populations have been established in the mainstem Columbia River for more than 100 years. Smallmouth bass were the second most abundant predator in the John Day Reservoir, approximately half the abundance of pikeminnow (Beamesderfer and Rieman 1991). Recent indices of abundance from 1990 to 2017 have been variable from year to year, increasing in some locations but generally relatively consistent across the entire mainstem (Williams et al. 2018).

Ecological impacts of smallmouth bass on focal species

Smallmouth bass readily occupy habitats in both rivers and lakes, whereas largemouth bass primarily occupy lakes or isolated lakes and sloughs along river floodplains. In this sense, smallmouth bass are better adapted for colonizing a greater extent of habitats where they can consume juvenile salmon and steelhead. Smallmouth bass construct nests in the spring and males aggressively defend the nests and young bass, often consuming small fish in the vicinity of the nests. Smallmouth bass consume a wide array of foods, including both invertebrate and vertebrate prey. A literature review of nonnative predators in the Pacific Northwest found that smallmouth bass had the highest diversity of prey items (Sanderson et al. 2009). Crayfish are a common prey item, but fish are also abundant in most diet studies. Individual smallmouth bass ate the most biomass of fish per day in a comparison with pikeminnow and walleye in the mainstem Columbia River (Vigg et al. 1991). Smallmouth have caused local extinctions of fish species in the southwest (Minckley 1973), and introduction of smallmouth and other nonnative predators coincided with decreased numbers of native minnows in a study of 506 small temperate lakes in the Adirondacks (Findlay et al. 2000). Abundance of native fishes decreased precipitously when smallmouth bass distributions expanded in the Yampa River, Colorado, and a bioenergetic model indicated smallmouth were the greatest predation threat to native fishes there (Johnson et al. 2008).

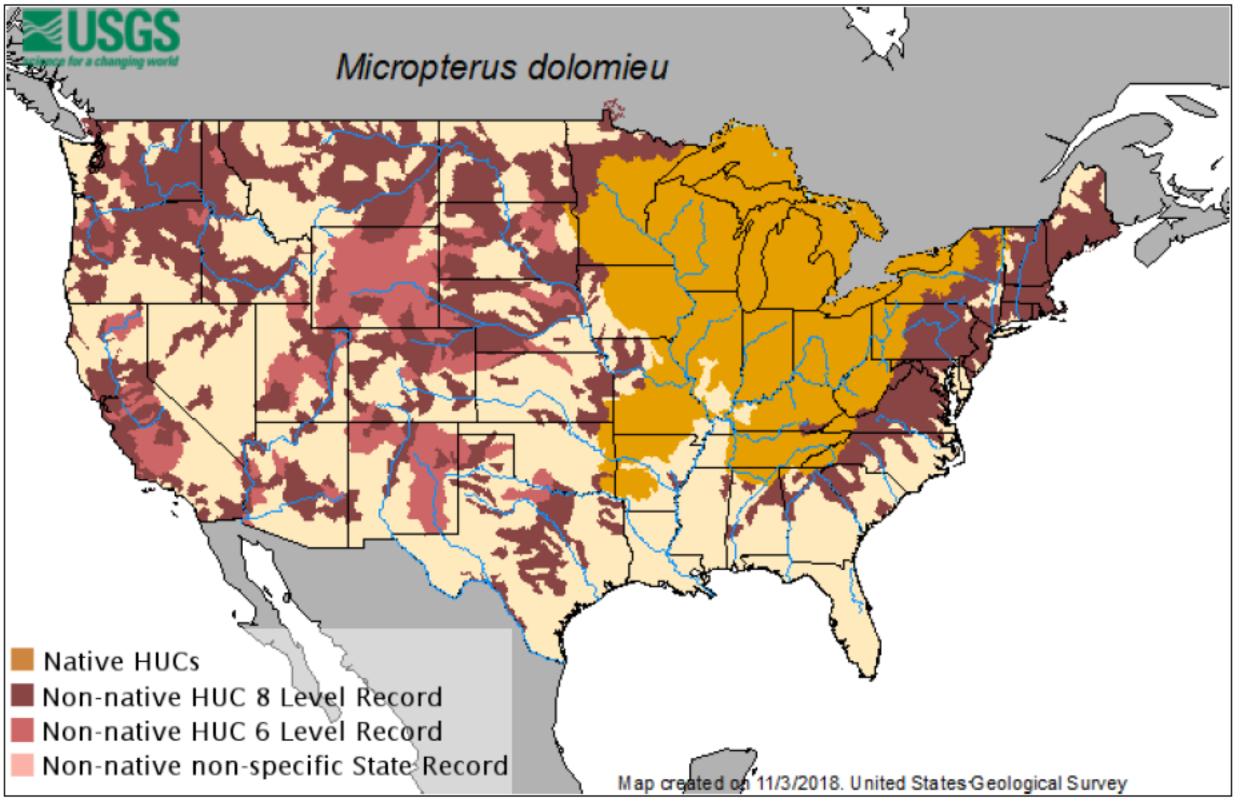

Figure 7. Distribution of smallmouth bass in the contiguous United States (Fuller et al. 2016; URL https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=396). The acronym HUC means Hydrologic Unit Code, a classification of watersheds by size, with HUC 8 watersheds being smaller than HUC 6.

No direct evidence of extirpation or extinction by smallmouth bass has been reported in the Columbia River Basin. A survey of seven rivers in the Pacific Northwest revealed that abundances of native fish species were lower in reaches where abundances of nonnative species were higher (Hughes and Herlihy 2012). However, this relationship could be related to changes in temperature because nonnative species tend to be more tolerant of warm water than native species. In contrast to the Columbia River Basin, one study in the Umpqua River basin in Oregon reported local elimination of a native minnow species by smallmouth bass invasion (Simon and Markle 1999). Between 1987 and 1998, the number of sites where smallmouth bass were sampled expanded from 7 to 19 sites, while those with Umpqua chub (*Oregonichthys kalawatseti*) decreased by half (from 12 to 6 sites). Smallmouth bass abundance had increased in all 6 sites where Umpqua chub were no longer found after 11 years. A similar pattern of fragmentation and isolation of Umpqua chub populations has been reported in the Smith River, Oregon (O'Malley et al. 2013).

The impact of smallmouth bass predation on juvenile salmonids is a major concern in the Basin, though evidence of their impact has been mixed. At most locations and seasons, salmonids make up a small proportion of the diet of smallmouth bass (Poe et al. 1991, Vigg et al. 1991), averaging roughly 20% but varying widely (Figure 8). In a study of the John Day Reservoir from 1983 to 1986, fishes were estimated to have consumed 2.7 million juvenile salmonids, of which smallmouth bass accounted for 9% of the total loss, walleye 13%, and pikeminnow 78% (Rieman et al. 1991). Intermediate sizes of smallmouth (approximately <250 mm or 10 inches) consumed the greatest proportion of salmonids (Vigg et al. 1991, Fritts and Pearsons 2006). Consumption of smaller fish may make natural origin juvenile salmonids more vulnerable than hatchery origin fish, despite maladaptive behavior and inappropriate coloration of hatchery salmonids (Fritts and Pearsons 2006). Larger smallmouth may consume different types of prey, consume larger prey, or occupy habitats where juvenile salmonids are less abundant.

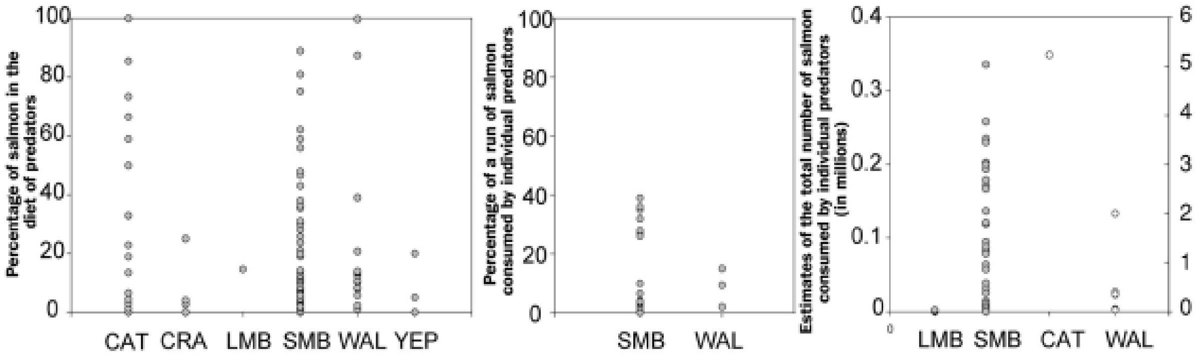

Figure 8. Summary of a literature review of the percentage of salmon in the diet of predators (left panel), percentage of a run of salmon consumed by predator species (middle panel) and estimates of the total number of salmon consumed by predator species annually at specific study sites (right panel; from Sanderson et al. 2009). Species are channel catfish (CAT), black and white crappie (CRA), largemouth and smallmouth bass (LMB and SMB), walleye (WAL) and yellow perch (YEP). For the right panel, data for LMB and SMB (gray filled symbols) correspond to the left axis, and data for CAT and WAL (open symbols) correspond to the right axis.

Estimates of annual consumption of juvenile salmon and steelhead at specific study sites in the Columbia River range 18,000 to 2,000,000 per year (Sanderson et al. 2009; note that study sites differed in size and abundances of predators and prey). Smallmouth bass are abundant in the reservoirs of the lower Snake River (Zimmerman and Parker 1995). Long-term monitoring from 1990 to 2017 has revealed that potential predation impact on juvenile salmonids by smallmouth bass has not increased over the entire mainstem Columbia River following pikeminnow control actions, but predation has increased in several locations, especially the tailraces of dams (Williams et al. 2018). A recent study found Chinook salmon to be the second most abundant fish in the diet of smallmouth in Lower Granite Reservoir and estimates of total predation loss to smallmouth in that reservoir increased 15-fold between the periods of 1996-1997 and 2013-2015 (Erhardt et al. 2017).

Food web interactions can modify the outcomes of predation of salmonids by small mouth and other predators. In recent years since 2005, sand rollers, a native fish species, increased substantially (Tiffan et al. 2017). Analyses of the diets of smallmouth bass revealed that they consumed substantial amounts of both fall Chinook salmon and sand rollers. When diets were compared across years, researchers found that smallmouth bass consumption of fall Chinook salmon decreased (0.11 to 0.05 fall Chinook per day) in years when consumption of sand rollers increased (0.22 to 0.39 sand rollers per day) (Hemingway et al. 2019). Shifts in abundances of different prey species in food webs can alter the feeding behavior of piscivorous fish, such as smallmouth bass, and alter the impacts of predation on juvenile salmonids.

Interestingly, a model of native and nonnative predaceous fish in the John Day Reservoir projected that the total removal of smallmouth bass would ***increase*** the predation losses of juvenile salmon by 9 - 14% (Harvey and Karieva 2005). This counterintuitive response resulted from the increase in fish species that were previously eaten by smallmouth bass, which resulted in increased populations of pikeminnow, walleye, catfish, and American shad. The removal treatment represented in the model has not been implemented in the Columbia River, but the lack of rigorous empirical data on population responses to removing other fish predators makes it difficult to refute or confirm the likelihood of the predicted outcome. Trophic responses and multi-species food-web interactions are likely in a large river ecosystem (ISAB 2011-1), but they are complex and difficult to measure and are rarely considered in managing predators like smallmouth bass or other native and nonnative predators of the Columbia River.

Regional climate warming in the Columbia River Basin potentially increases future impacts of smallmouth bass and other warm water nonnative predators. Peterson and Kitchell (2001) used a bioenergetics model to evaluate the consequences of regional warming based on a comparison of two periods with warmer spring–summer water temperatures (1933–1946, 1978–1996) with a colder period (1947-58). Model projections of predation rates of northern pikeminnow, smallmouth bass and walleye were approximately 26-31% higher for the warm periods than predation rates in the cold period. Under warmer thermal regimes, predators would grow faster, attain larger size-at-age, and consume more salmonid prey than in cooler regimes.

Current smallmouth bass control efforts

Smallmouth bass are considered a desirable sport fish, and few efforts have attempted to suppress or control their abundance and distribution. Beginning in 2016, the states of Washington and Oregon eliminated sport angling creel limits for both smallmouth and walleye in the mainstem Columbia River, and smallmouth are removed by angling at the dams as part of the pikeminnow control program. Other than these measures, there are no programmatic efforts to suppress smallmouth in the Columbia River Basin.

Researchers conducted an experiment to reduce depensatory mortality of natural origin juvenile Chinook salmon in the Yakima River from 1998-2002 by releasing large numbers of hatchery-origin fall Chinook in the spring to see if the predators could be swamped (Fritts and Pearsons 2008). The maximum consumption by smallmouth during those years was estimated at 2.7 million natural origin fall Chinook salmon, but the intentional releases of 2 million hatchery fall Chinook each year reduced the estimated consumption of natural origin fish to 184,000, a 93% decrease in potential predation mortality. Major challenges for this approach included raising small hatchery fish that would be vulnerable to smallmouth predation, releasing hatchery fish over an extended period to match the outmigration of natural origin juveniles, avoiding attracting additional smallmouth by the extended releases of hatchery fish, and negative effects on the objectives of the hatchery program.

Smallmouth bass became established in the Yampa River in Colorado in the early 1990s and moved downstream into the Green River and upper Colorado River. State and federal agencies attempted to suppress their populations by electrofishing (Breton et al. 2014), and more than 185,000 smallmouth bass were removed from the three basins. The electrofishing program successfully reduced abundances of sub-adults and adults by 64% from 2004 to 2011. However, reductions did not persist because sub-adults and adults moved from other reaches and reproduction increased abundance in favorable years.

Intensive electrofishing was repeated for 6 years to suppress nonnative predators (rainbow trout, brown trout, yellow bullhead (*Ameiurus natalis*), smallmouth bass) in a 2.85 mile (4.6 km) reach of the West Fork Gila River in southwest New Mexico (Propst et al. 2015). While some decrease was observed in three of the nonnative fish, smallmouth bass did not change in response to the control efforts. Only one native species responded positively to the reduced predator abundance. Even for species that respond to suppression methods, movement of fish from surrounding areas requires continued control efforts to suppress nonnative predators. Management agencies have attempted to suppress smallmouth bass and other nonnative warm water species in Lake Tahoe using electrofishing, gillnets, and angling (Thayer 2011). More than 12,000 nonnative predators have been removed, but there is no indication of substantial declines in populations of these predators.

Reviews of smallmouth bass control identified different approaches to eradicate or suppress the species but concluded that permanent eradication was unlikely and possible only in small streams and lakes of moderate size (Table 3) (Halfyard 2010, Loppnow et al. 2013, Rytwinski et al. 2019). Loppnow and Venturelli (2014) suggested that control of smallmouth will be most effective when it targets eggs, larvae, and juveniles (e.g., causing nest failure) as part of adaptive and integrated pest management approaches. A recent review of 95 studies of nonnative fish removal with 158 data sets found that 78% of the studies were poorly documented and had inadequate experimental designs (Rytwinski et al. 2019). Successful eradication was possible but required repeated treatments over multiple years and was largely restricted to smaller waterbodies. New approaches and more rigorous study designs are needed in larger, more complex systems.

One of the critical conclusions of the syntheses of methods to control smallmouth bass is that, just as for all nonnative fish in rivers, efforts to prevent smallmouth bass introductions and reintroductions are more effective than attempts at control (Fausch and Garcia-Berthou 2013). Fisheries managers often focus on less effective measures at specific locations while invasive species continue to spread. Angling groups put substantial pressure on state and federal agencies to stock smallmouth and largemouth bass and expand potential fishing locations. Bass anglers comprise 15% of all freshwater anglers in Idaho, Oregon, and Washington and represent an economic value of approximately $66 million annually for the three states combined (Carey et al. 2011). All state agencies in the Columbia River Basin have warm water fisheries programs designed to promote opportunities for nonnative sport angling (Carey et al. 2012, WDFW website, ODFW website, and IDFG website). Potential impacts of smallmouth bass or regulations about transportation and live release are not provided. Other river systems in the western United States face similar political resistance to nonnative fish suppression even when their threats to fish listed under the Endangered Species Act are well documented (Johnson et al. 2008, 2009).

Table 3. Summary of the advantages, limitations, and age class effectiveness for 12 potential methods of suppressing smallmouth bass (modified from Loppnow et al. 2013 and Halfyard 2010).

Method	**Age Class**	**Advantage**	**Limitations**
Electrofishing	3, 4	Conventional gear	Small shallow water bodies, mortality of other species, labor intensive
Netting	3, 4	Conventional gear, can be used in deep water	Small water bodies, size selective, mortality of other species, labor intensive, ineffective
Piscicides	1-4	Can be used in moderate to small waterbodies	Affects other species, moderately labor intensive, expensive, often ineffective
Water level manipulation	1-4	Effective for certain life stages, inexpensive	Limited applications, affects other species, must be repeated
Angling		Conventional gear, public can participate	Affects other species, inefficient, limited effectiveness in large waterbodies and for large populations
Sterilization	1,4	Can be used in moderate to small waterbodies, species-specific	Requires development of genetic or other methods of sterilization
Introduce disease or parasite	1-4	Effective in all habitats	Not well developed, risk to other species, may develop resistance
Introduce predators	1, 2	Potentially effective in all waterbodies	Affects other species, compounds problems if nonnative, unexpected ecological effects
Habitat modification	1-4	Limited to local areas or small waterbodies, labor intensive, expensive	Affects other species, unexpected ecological effects, limited effectiveness
Explosives	2-4	Effective in small waterbodies	Affects other species, destructive
Winterkill	3, 4	Effective in small waterbodies	Affects other species, unexpected ecological effects
Thermal restoration	1-4	May suppress where thermal conditions are marginal, benefits native cold-water species	Not effective in warmer reaches, constrains expansion but may not decrease established populations

Even with the existence of agency policies and state and federal laws to limit their introductions into new locations, intentional illegal introductions continue to spread smallmouth populations throughout North America. Major challenges for enforcement of existing regulations and laws are inadequate funding and political support for the agencies responsible and the establishment of effective penalties to dissuade illegal introductions (e.g., fines, imprisonment; Dentler 1993, Johnson et al. 2009).

Expansion of smallmouth bass nonnative range

Loppnow et al. (2013) concluded that the current expansion of smallmouth bass outside their native range is facilitated primarily by anglers and climate warming. Smallmouth bass readily invade streams and rivers both upstream and downstream from established populations, and humans have repeatedly spread them to isolated locations in lakes or streams outside their current distribution.

As discussed previously, angler pressure on management agencies and local government will continue to encourage the expansion of smallmouth bass throughout the Columbia River Basin. Control of both legal and illegal dispersal of smallmouth bass outside their current distribution will require clear and enforceable regulations and active education and outreach to both the general and angling public. It should be noted that the Washington Department of Fish and Wildlife has had a Warmwater Fish Program since 1997, which began when the state legislature created the “Warm Water Game Fish Enhancement Program” as described on the WDFW website.

Because smallmouth bass are warmwater fish, their invasion upstream is typically limited by cooler water often found in upstream sections of river networks. In the John Day River, smallmouth bass move upstream during summer (the leading edge of invasion), but population establishment is limited by the ability for juveniles to survive the winter (Lawrence et al. 2015, Rubenson and Olden 2017). Additionally, dispersal can be limited by geomorphic and human-constructed barriers (Lawrence et al. 2012). However, these studies have documented recent expansion of the range of smallmouth through upstream dispersal.

Warming of the climate of the Columbia River Basin may reduce the extent of suitable habitat for cold water native fishes but increases the threats of competition and predation with nonnative predators like smallmouth bass, which are expanding. For example, models of smallmouth bass distribution that incorporate warming temperatures predict a nearly 70% increase in the river miles invaded by 2080 (Rubenson and Olden in press; Figure 9). Projections of stream temperatures in 2080 from downscaled climate change models were coupled with fish habitat models for the North Fork and Middle Fork of the John Day River to evaluate the influence of riparian habitat restoration on interactions of bass and juvenile spring Chinook salmon (Lawrence et al. 2014). By 2080 in the model, smallmouth bass occupied the entire upper stream network and thermally suitable juvenile salmonid habitat was almost eliminated; but in the cooler North Fork John Day River with greater existing riparian vegetation, smallmouth could not invade the upper extent of stream network. Overlap between bass and juvenile salmonid habitat increased two- to four-fold in both streams under the projected temperatures of 2080. Riparian restoration was represented in the model as recovery of a proportion of the stream reaches prioritized for vegetation restoration, ranging from zero to 100% restoration. Restoration reduced the abundance of bass in both rivers. Restoration of the top 50% of the riparian restoration priorities in the warmer Middle Fork John Day River restricted smallmouth bass from 19.2 miles (31 km) of the upper river network. Management actions to protect existing riparian shade, restore degraded riparian forests, and minimize water withdrawals can protect natural thermal regimes that benefit anadromous salmonids and other native fish species while limiting the growth and survival of invading smallmouth bass (Lawrence et al. 2014).

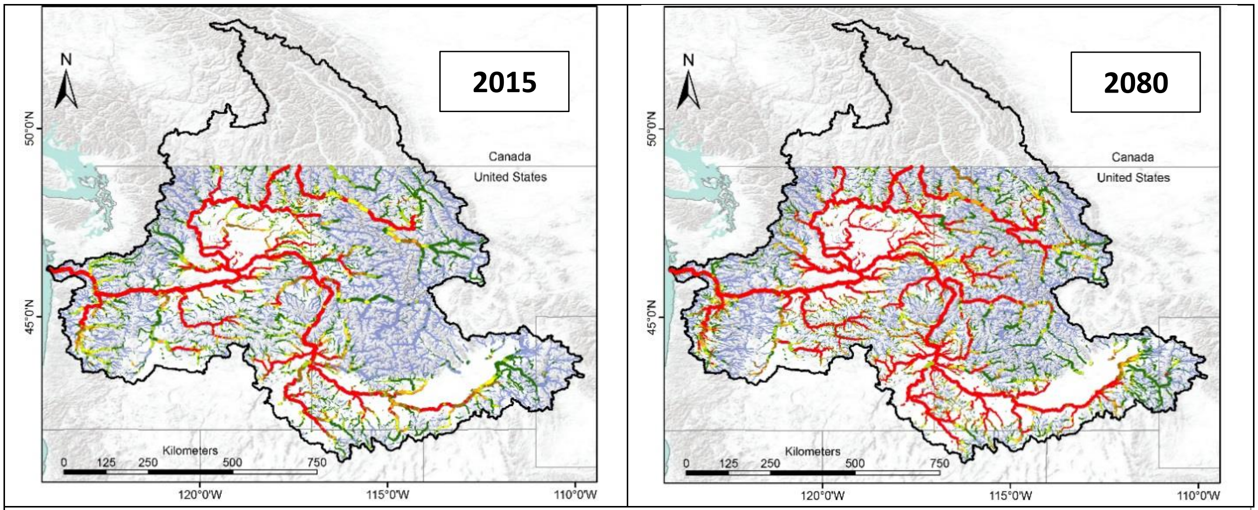

Figure 9. Modeled distributions of smallmouth bass in the United States portion of the Columbia River Basin ca. 2015 and 2080 based on a model of regional warming and dispersal probability (Rubenson and Olden, in press). Current distribution circa 2015 is 17,660 miles, and projected distribution in 2080 is 28,818 miles, an increase of 69%. See interactive map.

Walleye

Unlike most nonnative fish predators in the Columbia River Basin, walleye only recently became established, despite having been introduced into California much earlier. In 1874, Livingston Stone transported 16 adult walleye by railway “aquarium car” from the Missisquoi River in Vermont to the Sacramento River in Sacramento, California (Smith 1896). The Fish Commission of California asked the U.S. Fish Commission to provide large shipments of walleye for stocking in lakes and ponds, and transfers from Lake Erie were planned. In the early 20th century, walleye was highly valued for its excellent taste and potential to reach large size, and sport anglers still value those traits.

Interestingly, there are no records of attempts to transplant walleye into the Columbia River Basin until the middle of the 20th century when they were stocked in reservoirs of the Columbia Irrigation Project and likely dispersed through irrigation canals (Wydoski and Whitney 2003). Though the exact date of introduction is uncertain, walleye were stocked into Banks Lake, Washington near Grand Coulee Dam and moved into Lake Roosevelt by the early 1960s, where they became a widely popular sport fishery (Beamesderfer and Nigro 1989).

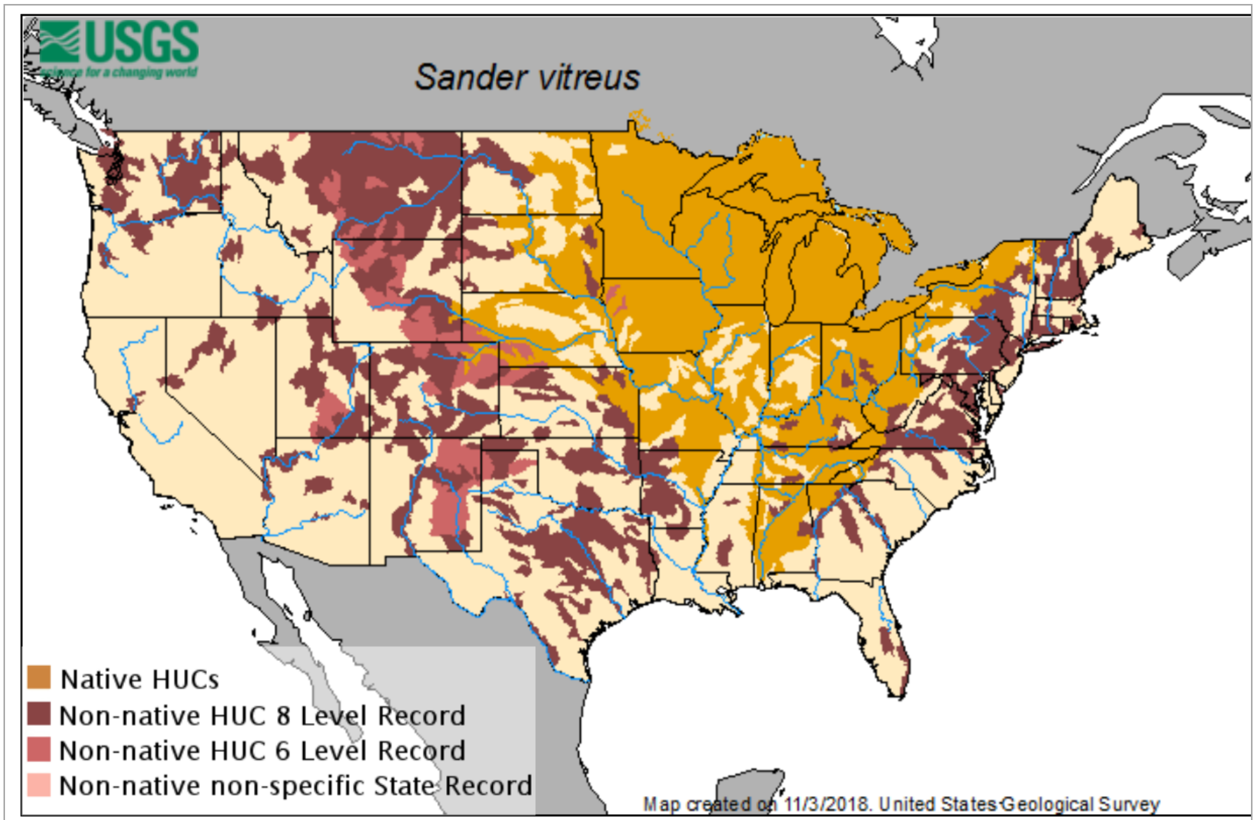

Figure 10. Distribution of walleye in the contiguous United States (Fuller et al. 2019; URL https://nas.er.usgs.gov/queries/factsheet.aspx?SpeciesID=831). Note that walleye do not occur in California currently (Peter Moyle, personal communication), and the occurrence in California in this map is based on unsuccessful introductions. The acronym HUC means Hydrologic Unit Code, a classification of watersheds by size, with HUC 8 watersheds being smaller than HUC 6.

The native range of walleye is the Midwestern United States and Canada. Walleye have become established outside their native range in 43 states of the contiguous United States and occur in all states except for Alaska and Hawaii (Fuller and Neilson 2019). Walleye have spread throughout the Columbia River and major tributaries, but not to the extent of smallmouth bass invasion (Figure 10). Walleye are classified as a cool water species (Eaton et al. 1995) and occur primarily in large rivers, reservoirs, and lakes (Wydoski and Whitney 2003). Unlike smallmouth bass, walleye populations rarely invade streams. Adult walleye move little in summer but can move up to 170 miles during spawning migrations (Wydoski and Whitney 2003). Unlike smallmouth bass, walleye spawn in aggregations in river margins or lakes and do not protect their eggs or young.

By the 1980s, walleye had invaded the entire Columbia River, occurring from Lake Roosevelt down to Tongue Point in the Columbia River and up to Dexter Dam on the Willamette River (Tinus and Beamesderfer 1994). Walleye also have established populations in the Snake River basin, and into the Kettle and Okanogan Rivers (Bradford et al. 2008). The Oregon Department of Fish and Wildlife estimated that anglers caught 128,000 walleye in the Bonneville, The Dalles, and John Day reservoirs in 2017, of which 100,000 were harvested

(Williams et al. 2018). The System-wide Predator Control Program captured the greatest numbers of walleye in the tailrace of Bonneville Dam, whereas abundance indices for walleye were low in the upper and middle reservoir and downstream of Bonneville Dam (Williams et al. 2018). Abundance indices in 2017 were similar to those from 1994-1995. The walleye population in John Day Reservoir in 1984-1986 was estimated to be approximately 15,000, smallmouth were 35,000, pikeminnow were 85,000, and their combined population was approximately 135,000 (Beamesderfer and Rieman 1991). Populations of walleye in the faster flowing reaches of the upper Columbia River, such as near Rocky Reach Dam, are lower than other reaches, both upstream and downstream (BioAnalysts Inc. 2000). Shorter hydrologic residence times potentially limit the populations, and high discharges during periods of larval development and dispersal may reduce recruitment.

Walleye populations can increase rapidly after they are stocked illegally or invade new locations. Walleye were illegally introduced into the Clark Fork River, Montana (Idaho Department of Fish and Game, reported in the Columbia Basin Bulletin 12/5/2014). They moved downstream and were detected in Lake Pend Oreille and the Pend Oreille River in Idaho around 2005. Initial increases were gradual, but captures of walleye in gill net surveys by Idaho Department of Fish and Game nearly doubled between 2011 and 2014.

Ecological impacts of walleye on focal species

Like northern pikeminnow and smallmouth bass, walleye are voracious predators and tend to be even more piscivorous than pikeminnow and smallmouth (McMahon and Bennett 1996, Hartman 2009, Bradford et al. 2008). They are well known for decreasing abundances of their prey (Lyons and Magnuson 1987, Findlay 2000) and can impact stocking programs for salmonids. Walleye predation accounted for 10% loss of hatchery kokanee and 8% loss of rainbow trout within 41 days after stocking in Lake Roosevelt, but the authors concluded that walleye were “swamped” by the large releases of hatchery fish (Baldwin et al. 2003). Because walleye are cannibalistic, they can reduce their own densities when prey become less abundant (Chevalier 1973, McMahon and Bennett 1996), and this can be an important part of natural population regulation.

Of all the native and nonnative predators in the Columbia River system, walleye are the most piscivorous based on proportion of fish in their diet, though salmonids are not the primary fish prey. Proportions of salmon and steelhead in studies of walleye diets vary greatly, ranging from 0 to 100% and averaging approximately 10% (Sanderson et al. 2009; see Figure 8 in smallmouth subsection). In a study of the John Day Reservoir in 1981, walleye diet samples contained 26% prickly sculpins, 13% minnows, 11% suckers, and 4% salmonids by number; by volume the diet contained 34% minnows, 33% suckers, 23% sculpins, and 4% salmonids (Maule and Horton 1984). In a later study of the John Day Reservoir, walleye diets were composed of suckers (27.5%), sand rollers (27%), sculpins (22%), juvenile salmon and steelhead 21%), and minnows (12%); by weight, suckers were (40%), sand rollers (17%), sculpins (16%), juvenile salmon and steelhead (14%), and minnows (11%; Poe et al. 1991). Salmonids consistently accounted for 18-24% of walleye diets. Below Bonneville Dam, walleye diets were composed of redside shiners (25%), sand rollers (25%), pikeminnow (12.5%), sculpins (12.5%), juvenile salmon and steelhead (12.5%), and other minnows (10%; Wydowski and Whitney 2003).

In 2017, captures of walleye (*n* = 30) in the System-wide Predator Control Program were substantially lower than captures of pikeminnow and smallmouth bass, and were inadequate for calculation of predation indices (Williams et al 2018). In Lake Roosevelt, the major fish species in the diet of walleye were minnows, sculpins, perch, suckers, and salmonids in order of proportion (Bradford et al. 2008). Proportions change during the year and are influenced by availability of different prey, flow conditions, water temperature, and other factors. Walleye clearly consume salmonids in the Columbia River, but salmonids tend to be the lowest proportion of fish in their diet.

Seasonality also influences walleye impacts on juvenile salmonids. For example, a sample of 30 walleye was captured from the middle and lower Columbia River in September and November 2010. Ten had food in their stomachs, and these fish consumed only peamouth chub, American shad, and pikeminnow (Rose 2011).

Maule and Horton (1984) noted that the subretinal tapetum lucidum, which causes the “walleyed” appearance of the eyes of walleye, make them efficient predators in low light or high turbidity. They suggested that this visual acuity might be related to the relatively low abundances of salmonids in walleye diets because many of the prey of walleye in the Columbia River are inactive and reside near the bottom at twilight or during the night. In contrast, migrating juvenile salmonids move to the surface and swim actively downstream during those periods. Vigg et al. (1991) reported that feeding by the predators, including walleye, tended to peak after dawn and near midnight.

Studies in the Columbia River differ in the estimates of relative predation by different sizes of walleye. Almost all salmonids in the diet study in John Day Reservoir in 1980-81 were consumed by walleye between 250-350 mm (Maule and Horton 1984). In a subsequent study of John Day Reservoir, walleye between 201-250 mm contained the greatest relative ration of salmonids (42.5 mg/g; Vigg et al. 1991). In contrast, large walleye (300-644 mm) in Lake Roosevelt consumed greater proportions of kokanee and rainbow trout (25-79% by weight) than smaller walleye (275-299 mm), which consumed only 8% by weight (Baldwin et al. 2003).

As reported in the Smallmouth Bass section, regional climate warming in the Columbia River Basin may increase future impacts of walleye and other cool or warm water nonnative predators. Using a bioenergetics model, Peterson and Kitchell (2001) expect that under warmer thermal regimes, predators would grow faster and consume more salmonid prey than under cooler thermal regimes.

Current walleye control efforts

Walleye are similar to smallmouth bass in their reputation as a desirable sport fish. Examples of attempts to suppress or control the distribution of walleye are rare. Beginning in 2016, the states of Washington and Oregon eliminated sport angling creel limits for both smallmouth bass and walleye in the mainstem Columbia River, and smallmouth bass are removed by angling at The Dalles and John Day dams as part of the northern pikeminnow control program. Other than these measures, there are no programmatic efforts to suppress walleye in the Columbia River Basin.

The Colorado River Recovery Program uses long-term intensive electrofishing to remove walleye in the upper Colorado River and its tributaries (Michaud et al. 2019). A review of predator removal programs in the

Colorado River system concluded that removal efforts had not substantially reduced predator populations and native fish communities had not exhibited positive responses in most projects (Mueller 2005).

Managers in the Columbia River have proposed to fluctuate water levels during spawning periods to control walleye and smallmouth bass. Walleye spawn in groups in shallow margins of lakes and rivers, and several males may spawn with a single female. Walleye are broadcast spawners that release adhesive eggs, which fall into cracks and crevices in gravel and adhere to the substrate (Wydowski and Whitney 2003). Abrupt changes in water level could expose those eggs and larvae to desiccation, cause larvae to disperse too early, or cause other adverse conditions. This potential approach is untested.

Unintended declines in walleye populations have been caused by sport angling. Walleye populations in cold, unproductive lakes have collapsed under high angling exploitation rates (> 50%; Baccante and Colby 1996). However, populations of walleye in most lakes reviewed sustained harvest rates of up to 36% without collapse or extreme declines.

Walleye predation can change prey availability and food-web structure, creating complex population responses in the predator. Walleye were stocked in Seminoe Reservoir on the North Platte River, Wyoming in 1961 (McMahon and Bennett 1996). The reservoir was managed primarily as a hatchery-supported fishery for rainbow and brown trout. The newly stocked walleye initially fed on non-salmonid prey, including suckers, minnows, darters, and crayfish. As their prey declined, walleye shifted their diet to stocked salmonids, consuming most of 500,000 recently stocked fingerling trout within two weeks. Attempts to disperse stocking locations were unsuccessful in decreasing walleye predation on stocked fish. Eventually, limited food availability caused walleye growth and abundance to decline and recruitment of new year classes of walleye failed. Fishery managers introduced nonnative gizzard shad and emerald shiners as alternate prey for walleye and began stocking larger rainbow trout, which were less vulnerable to walleye predation. McMahon and Bennett (1996) report similar prey limitation and stocking of larger hatchery trout in five other reservoirs in Wyoming and Idaho.

Suppression may cause unexpected and potentially compensatory responses in predators. For example, increased exploitation can change fecundity in walleye. Populations of walleye were suppressed by trap nets, gill nets, and angling in two Ontario lakes for 6 years (Baccante and Reid 1988). Though populations were reduced by 72% in Henderson Lake and 25% in Savanne Lake, fecundities increased by 27% and 36%, respectively. Therefore, even though predator abundance may be reduced by control efforts, rates of population recruitment may not be reduced by the same amount.

As discussed in the subsection on smallmouth bass, a model of native and nonnative predaceous fish (pikeminnow, smallmouth bass, walleye, catfish and American shad) in John Day Reservoir evaluated the consequences of total removal of specific predators on juvenile Chinook salmon and steelhead (Harvey and Karieva 2005). In the model projections, removal of walleye resulted in the greatest change in annual predation of all nonnative predators evaluated, approximately 10% less annual predation than the baseline condition. The model also projected that predation losses caused by native predators (pikeminnow and avian predators) would decrease with increasing numbers of nonnative predators through direct or indirect food web interactions. As mentioned previously for smallmouth bass, multi-species food-web interactions are likely in a large river ecosystem (ISAB 2011-1), but they are rarely considered in managing predators in the Columbia River.

Efforts to prevent nonnative predator introductions and reintroductions are more effective than attempts at control (Fausch and Garcia-Berthou 2013). Dispersal of walleye and illegal introductions for angling likely exceed the spatial extent and capacity of control programs to reduce them. Moreover, angling groups pressure management agencies to expand potential fishing locations. Political resistance to nonnative fish suppression is common throughout the United States, even when their threats to fish listed under the Endangered Species Act are well understood (Johnson et al. 2009).

Expansion of walleye nonnative range

State agencies have stocked walleye in lakes and rivers of the Columbia River Basin, and walleye are widely established in large reservoirs and rivers. McMahon and Bennett (1996) surveyed fish management agencies throughout North America and found that 86% had tried to establish walleye populations and 65% of these attempts were unsuccessful. Walleye currently are distributed throughout the mainstem Columbia River and major tributaries and do not tend to occupy small streams except for lower reaches near confluences with larger rivers. This distribution is unlikely to change in the future. Walleye populations also become established in lakes and reservoirs where they are introduced. Future expansion of walleye populations in the Columbia River Basin are most likely though illegal introductions into lakes and reservoirs that currently do not contain walleye.

Walleye are promoted as a popular sport fish, and the possible negative impacts of walleye on anadromous salmon and steelhead receive far less attention. Washington, Oregon, and Idaho all promote walleye angling on their websites (WDFW, ODFW, IDFG), and information about the potential risks of walleye to native fish and anadromous salmonids is not provided. Invasive species lists and descriptions on the state agency websites do not include nonnative sport fish.

The State of Idaho is the only state in the Columbia River Basin that continues to stock walleye (IDFG fish stocking), but the State works with citizen groups to discourage illegal introductions and assists a citizen group, Citizens Against Poaching, to maintain a hotline and offer cash rewards for information regarding criminal introductions. In August 2018, a 19-inch illegally stocked walleye was caught in Lake Cascade, Idaho more than 200 miles from the closest walleye fishery. When walleye were proposed for stocking in Ferry Canyon Reservoir, the Montana Department of Fish and Wildlife organized a workshop on potential walleye interactions, conducted a survey of 1,831 anglers, and assessed the risk of introduction. The agency decided not to introduce walleye, but walleye were stocked illegally and the population increased rapidly (McMahon and Bennett 1996). Though support for stocking walleye into new locations is decreasing in state fishery management agencies, future expansion is likely though continued illegal introductions.

Lake trout

Lake trout is a large-bodied, long-lived salmonid native to the northern United States and Canada. They almost exclusively breed and feed in lakes (Eschmeyer 1964) though there is considerable intra-specific phenotypic and genetic diversity, even within some large lakes (Muir et al. 2016). In addition to their native range, they have been introduced by fisheries agencies and also members of the public without authorization into a number of natural lakes and reservoirs. Martinez et al. (2009) reviewed the history of management of nonnative lake trout, including the period of deliberate transplantation, encouragement of large size (i.e., trophies) by protective fishing regulations, followed by the growing concern about their effects on native salmonids, shifts to more liberal fishing regulations, and intensive efforts at reduction.

Efforts to reduce or suppress lake trout have, in some cases, been related to competition and displacement of native bull trout, *S. confluentus*, which has a different distribution but overlaps with lake trout in western North America (Donald and Alger 1993). In other bodies of water, predation by lake trout on native salmonids such as cutthroat trout, *O. clarkia*, and non-anadromous sockeye salmon, *Oncorhynchus nerka*, known as kokanee, are a main concern, although the kokanee are often nonnative.

Martinez et al. (2009) provide details on 18 western United States lakes and reservoirs, including elevation, area and depth, native fish communities, changes in fishing regulations, lake trout life history, control strategies, and the outcomes in each lake. The authors concluded (p. 437):

> *"As we have shown, lake trout management issues across this region—such as public demand for lake trout fisheries and the conflicts that arise when lake trout become an ecological or economic liability for the management of other valued sport or native fish—have much in common. Providing better information to the public about the ecological challenges of managing lake trout might help diffuse criticism focused on agencies or employees embroiled in local management controversies. Information for public distribution should outline concerns about the potential pitfalls of lake trout stocking and protective regulations, encourage anglers to harvest more lake trout, and provide recipes to help anglers prepare their catch for consumption. The emerging understanding of this issue should clarify this message to help address misinformation among anglers, reduce contentiousness, and facilitate management and protection of sport and native fish populations."*

We include information on lake trout and efforts to control them in this report for several reasons. First, this species is now established in the Columbia River Basin. Efforts are underway to suppress them in water bodies such as Flathead Lake (Hansen et al. 2016) that have been assessed (e.g., ISRP 2011-7, ISRP 2012-16). Second, though lake trout are largely confined to upper parts of the basin beyond the range of anadromous salmonids, they overlap in some areas such as Cle Elum Lake, where anadromous sockeye salmon restoration efforts are ongoing (Matala et al. 2019). Third, various case studies show the combinations of efforts that may be devoted to predator suppression (e.g., directed netting, incentivizing anglers, etc.), their benefits and drawbacks, and the kinds of monitoring that may be needed to adequately assess the scope of the problem, plan a course of action, and then assess whether the action had the desired effect. Typically, considerable field sampling and modeling was required to determine whether the suppression had succeeded in the systems reviewed below. Fourth, and perhaps most importantly, they provide lessons in the complexity of freshwater ecosystems and the sometimes-unexpected results of efforts to suppress a top predator in a large body of water. An important part of this last perspective is the lesson, learned in so many systems around the world, that nonnative species can often thrive and strongly affect the environments where they become established, to the detriment of native species and humans reliant on them (for reviews on nonnative freshwater fishes, see Rahel 2002, Casal 2006, Cucherousset and Olden 2011).

Yellowstone Lake

Yellowstone Lake is large (131 square miles or 340 km^2) with 124 tributaries, and the outlet, the Yellowstone River. The native fish fauna was depauperate, consisting of only Yellowstone cutthroat trout (*O. clarkii bouvieri*) and longnose dace (*Rhinichthys cataractae*; Behnke 2002). More recently, longnose sucker (*Catostomus catostomus*), lake chub (*Couesius plumbeus*), and reside shiner (*Richardsonius balteatus*) were introduced. In addition, one top predator, the lake trout, was discovered in 1994 (Kaeding et al. 1996)—the result of an unauthorized introduction apparently from nearby Lewis Lake (Munro et al. 2005). Predation by lake trout on native cutthroat trout became evident and the National Park Service (NPS) initiated control programs to not only protect the native trout but also the complex ecosystem services they provide (Koel et al. 2005). For example, the cutthroat trout spawn in many streams around the lake and were sufficiently large and numerous (Gresswell 2011) that they constituted an important food source for the region's grizzly bears (Mattson and Reinhart 1995) and other elements of the ecosystem (Koel et al. 2019).

Ruzycki et al. (2003) assessed the early stages of the lake trout expansion and reported that in 1996 the lake trout consumed an estimated 129,000 individual cutthroat trout for a biomass of 15 metric tons. The NPS expended considerable effort and removed nearly 15,000 lake trout from 1995 to 1999, and Ruzycki et al. (2003) estimated that those predators would have eaten about 200,000 cutthroat trout in 1999 alone. More recently, Syslo et al. (2011) reviewed the responses of lake trout to the suppression program, which removed nearly 450,000 lake trout from 1995 through 2009. Despite this effort, the lake trout population continued to increase, albeit at a slower rate than would have occurred without removals. Thus, even greater efforts would be needed to cause the population to decline, much less reach levels that might be called full suppression. The authors concluded (p. 2142):

> *"Lake trout suppression in Yellowstone Lake highlights the necessity for baseline data, long-term planning, and a large amount of fishing pressure to substantially reduce a non-native predator from a large, natural water body."*

Flathead Lake

Flathead Lake, Montana, is a large, oligotrophic lake (191 square miles; 496 km^2, mean depth: 50 m, maximum: 113 m) with a native fish community including bull trout, westslope cutthroat trout, northern pikeminnow and several species of whitefish, minnows, suckers and sculpin. Lake trout were introduced in 1905 but were not ecologically dominant (reviewed by Hansen et al. 2016). Nonnative kokanee were introduced and became the focus of a recreational fishery until a combination of reduced zooplankton density (caused by predation from nonnative opossum shrimp, *Mysis relicta*) and lake trout predation reduced kokanee densities (see ISAB 2011-1). Since the late 1990s, the Confederated Salish and Kootenai Tribes have sought to reduce lake trout densities through a combination of fishing contests, a seasonal bounty, and directed gillnet and trapnet fishing (see ISRP 2011-7 and ISRP 2012-16 for information on study plans). Hansen et al. (2016) concluded that the lake trout population could be reduced in density by 75% but a 3-fold increase in total fishing effort would be required.

Swan Lake

Lake trout transplanted into Flathead Lake then colonized other parts of the basin. They were first detected in the Swan River system (tributary to Flathead Lake) in 1998 (Cox 2010; Syslo et al. 2013). Swan Lake is small (5.15 square miles; 13.35 km^2, mean depth: 16 m), and the native bull trout population was threatened by invasive lake trout (Syslo et al. 2013). Consequently, lake trout removal efforts were required to minimize bycatch of bull trout, a federally protected species. Detailed demographic information was collected to produce tables of age-specific natural survival rate, probability of maturity, fecundity, and vulnerability to gear. Simulations allowed estimation of the most efficacious suppression strategy. Syslo et al. (2013) concluded (p. 1079):

> *"We examined the efficacy of targeting life stages (i.e., juveniles or adults) using temporally pulsed fishing effort for reducing abundance and program cost. Exploitation rates were high (0.80 for juveniles and 0.68 for adults) compared with other lakes in the western USA with Lake Trout suppression programs. Harvesting juveniles every year caused the population to decline, whereas harvesting only adults caused the population to increase above carrying capacity. Simultaneous harvest of juveniles and adults was required to cause the population to collapse (i.e., 95% reduction relative to unharvested abundance) with 95% confidence. The population could collapse within 15 years for a total program cost of US $1,578,480 using the most aggressive scenario. Substantial variation in cost existed among harvest scenarios for a given reduction in abundance; however, total program cost was minimized when collapse was rapid. Our approach provides a useful case study for evaluating long-term mechanical removal options for fish populations that are not likely to be eradicated."*

The conclusion that removals of only adults was the least efficacious approach, and only strategies removing adults and juveniles were successful, is noteworthy. The authors further commented that the costs of lake trout suppression may scale with the size of the body of water, exceeding $1 million annually in Yellowstone Lake, and about $0.75 million in Lake Pend Oreille. By comparison, the sum spent in Yellowstone Lake annually would support the suppression operations in Swan Lake for about 15 years (Syslo et al. 2013).

McDonald Lake

McDonald Lake is also in the Flathead Lake drainage and, like Swan Lake, is upstream of Flathead Lake, has federally protected bull trout, and invasive lake trout (first detected in 1959). The lake trout likely colonized volitionally from Flathead Lake, 57.6 miles (93 km) downstream (Dux et al. 2011), which shows the large distances that nonnative predators can move to colonize new water bodies. Gill nets were used to sample the fish for population characteristics and diet, sonic tracking to study movements, and model simulations to predict lake trout responses to suppression (Dux 2005; Dux et al. 2011). The results indicated that the population is long-lived, slow-growing, and that substantial population reduction should be achievable.

Lake Pend Oreille

Lake trout were apparently introduced to Lake Pend Oreille in 1925 (Hansen et al. 2010) but were scarce until the late 1980s. By 1999, the population was estimated to have grown to 1800 fish (Hansen et al. 2008). Despite liberal angling regulations and fishing derbies to encourage retention of lake trout, the population was estimated at 6400 large, mostly mature fish by 2003 and had grown to about 11,000 large fish by 2005 (Hansen et al. 2008). A predator removal program was initiated in 2006 that involved gill nets, trap nets, rewards, and other inducements to encourage anglers to keep them. Given the long lifespan of the species and vulnerability to overfishing in its native range, the rapid rate of increase and resistance to removal efforts was surprising but not unique to this lake.

Management of lake trout and also predatory, nonnative rainbow trout in Lake Pend Oreille is complicated by the presence of a native, valued salmonid, the bull trout, and also kokanee, a valued but nonnative planktivore that is preyed upon by the larger salmonids. Hansen et al. (2010) concluded that bull trout were increasing and that their recovery was compatible with the suppression efforts. A recent summary Dux et al, 2019) indicated that from 2006 through 2016, 194,000 lake trout were removed by a combination of incentivized angling (44%), gill netting (50%), and trapping (6%). These efforts resulted in a decline in adults (age-8+) and recruits (age-3) through annual total mortality of 31%. Importantly, the lake trout did not show a density-dependent compensatory response. The authors concluded that these efforts restored the kokanee population to a level sufficient for a recreational fishery, as well as a trophy fishery for rainbow trout. Bull trout were sustained, despite a reduction in abundance. Thus, the suppression of lake trout was deemed successful.

Lake Chelan

Lake Chelan, Washington is a long (50 miles [81 km]), narrow (<1.86 miles [<3 km]), and exceptionally deep (mean: 144 m, maximum: 453 m) ultra-oligotrophic lake (Schoen et al. 2012). Lake trout were first stocked by the Washington Department of Fish and Wildlife in 1980 but became abundant when stocked heavily over 11 years, from 1990 to 2000, when natural reproduction was observed (Schoen et al. 2012). Concern over lake trout predation on nonnative kokanee motived a cessation of stocking and an examination of the predatory interactions between these species. Bull trout, the native apex predator, were extirpated prior to lake trout stocking. Research indicated that the unusual pattern of stocking (heavy for a specific period, then a cessation) created a pulse of lake trout. Combined with age-specific patterns of piscivory, this created the paradoxical situation of declining abundance of harvestable lake trout but increasing predation.

Conclusions

The case studies above describe only a few of the many systems in which nonnative lake trout were introduced by authorized agencies or surreptitiously by unknown individuals, and then thrived and in some cases colonized nearby waters as well. Each body of water has its idiosyncrasies (e.g., area, depth, native and nonnative fishes) and the results of invasion and suppression efforts depend on the time frame being considered. It is thus difficult to compare them. However, some lessons may be learned from them as a whole, echoing Martinez et al. (2009).

First, suppression is possible, but the feasibility and costs may increase with the size of the lake and its inherent capacity to produce the nonnative species. Even lake trout, a species whose life history makes it vulnerable to over-fishing, has proven difficult and expensive to control in a waterbody as large as Yellowstone Lake. Second, a combination of efforts directed at juveniles and adults may be needed, though the predatory effect of the adults is easier for the public to grasp. Third, public support is important; anglers can be motivated to target the invasive species and their efforts can be a substantial element of control (e.g., Lake Pend Oreille). Thus, for both practical and social reasons, the support of the human community is important. Fourth, none of these examples extirpated the lake trout, and suppression was the goal, not eradication. Consequently, ongoing monitoring and suppression efforts may be needed indefinitely unless some control measure other than direct removal is employed. Thus, it will be important to carefully plan the operation and its costs for not only the initial phase, when predator abundance may be reduced substantially, but also for the subsequent period when it may recover and thus require additional effort.

When evaluating studies that have suppressed a predator such as lake trout to protect species such as cutthroat trout, or suppressed northern pike to protect juvenile salmonids, it is helpful to have units that are comparable. Efforts directed at juvenile predators may remove a large number but smaller biomass compared to efforts on adults, and the size- and age-specific predatory effect and also natural mortality of the predator need to be considered. Conversely, the consequence of predation on prey can be expressed as numbers, biomass, or percent of the population consumed (per predator or as a whole), change in productivity, and other metrics, and they too depend on the size of the prey and other sources of natural mortality. Finally, the predator being targeted may or may not be the primary source of mortality for the prey, and the presence or absence of density dependent responses (compensation or depensation) by predators and prey may strongly affect how the species interactions play out.

CONTROL OF PREDATORY FISHES IN CALIFORNIA: RELEVANCE TO THE COLUMBIA RIVER BASIN

Introduction

Salmon, smelt, and other native fishes are in long-term decline in California, especially in the Sacramento-San Joaquin watershed and the San Francisco Estuary. Some species, such as delta smelt and winter-run Chinook salmon, are on the verge of extinction. It has been easy to blame predation, especially by nonnative fish, as the cause, rather than the massive changes to the rivers and estuaries that have taken place (Grossman 2016). In this way, the Columbia and the Sacramento river systems are similar: predation issues appear most obvious in rivers that have been highly altered by human endeavors, including addition of alien species. However, relevance of the California experience to the Columbia Basin is nevertheless limited for the following reasons:

- The river systems (even the Sacramento River) are small compared to those of the Columbia Basin and are mostly wholly within one political region, California. While every California river of any size has one or more dams on it, most are multi-purpose dams, and hydropower production is a small part of their purpose. This means most California rivers have drastically altered flow regimes and very few dams allow passage over or through them.
- The predators of most concern are nonnative fishes; most have been in California for over 100 years so are naturalized species that are well adapted to the system. Whatever damage they have done to local ecosystems seems to be largely in their past, with a few exceptions. In fact, most have stable ranges and some (e.g., striped bass, American shad) are experiencing long-term declines in rivers below the dams, like the native fishes (Moyle 2002). Increasingly, the concern in California is for "hot spots" where predators can aggregate and feed on small salmon, mostly of hatchery origin.
- The ecosystems have changed dramatically from their historical condition and continue to change. There are many more species of fish (ca. 30-40), for example, in the main California rivers and estuaries than there were historically (ca. 10-15). Aquatic invertebrates are likewise much more diverse than they were historically. The rivers and Delta are true novel ecosystems as a consequence of these multiple alterations (Moyle 2014).
- Birds and mammals do not appear to be major predators on fish in most inland California waters, although killer whales and various birds may have an impact once salmon are in the ocean (especially in the Gulf of the Farallones).

Nevertheless, the search for scapegoats in an ecosystem influenced by many factors has led to a great deal of attention being paid to predation as a cause of fish declines and of endangered species (Grossman 2016). In contrast, the State Water Resources Control Board, which has the power to regulate flows below dams in California, is exploring means by which improved flow regimes, combined with large-scale habitat restoration, can be used to increase populations of Chinook salmon, steelhead and other native fishes (Dahm et al. 2019).

Salmon and smelt as prey

Most juvenile Chinook salmon, delta smelt, and longfin smelt moving through the Sacramento River and the upper San Francisco Estuary (the Delta) presumably are eaten by predators. This predation is assumed to be the ultimate cause of death of 99% of juvenile salmon (e.g., Buchanan et al. 2017) from four runs and of most smelt. The proximate cause, however, is that the small fish are often carried by flows (or lack of them) to places where food, cover, and water quality are poor, increasing vulnerability to predation (Dahm et al. 2019). Presumably most of those not eaten would die of other causes.

Much of this mortality seems to take place in predation "hot spots," where predators can aggregate and small fish moving through have little cover and/or may be concentrated in ways that increase vulnerability. Analyses of stomach contents of large predatory fishes, including use of eDNA, indicate that striped bass, largemouth bass, and channel catfish consume many salmon (Michel et al. 2018), although most of the year these predators subsist on other species of fishes and macroinvertebrates (especially three species of nonnative crayfish). Other adult fishes in the Delta and in the Sacramento–San Joaquin rivers also prey on salmon in small amounts, mainly when naïve hatchery juveniles are passing in large numbers (Grossman 2016). Not surprisingly, hatchery-reared juvenile salmon typically have much higher survival rates to adulthood if they are released downstream of the Delta and rivers. The best attempt to demonstrate the potential impacts of predation through a combination of predator removal and predator addition and use of tethered fish to determine predation intensity (Michel et al. in review) revealed the difficulties in this approach rather than its clear success. The study showed that when multiple species are involved, even in a "hot spot," predation is a complex phenomenon involving behavioral responses of both predators and prey.

Predators

Striped bass. Attempts to reduce predator numbers have typically focused on just one species, striped bass, because their high metabolic rates and tendency to roam long distances allow them to feed on whatever prey are most abundant (Moyle 2002; Lindley and Mohr 2003, Grossman 2016). The California Department of Fish and Wildlife was once sued by water diverters because they were not willing to reduce predator impact by changing angling regulations to allow unlimited striped bass take. The suit was successful, but the attempt to change angling regulations was never fully implemented. In addition, large striped bass are so high in mercury that eating them is not advised, contributing to catch-and-release angling. Reducing striped bass numbers in Clifton Court Forebay (to the State Water Project pumps) may temporarily increase survival rates of salmon moving towards the pumps but "new" bass quickly recolonize and predation rates stay high (annual reports by California Department of Water Resources, e.g., CDWR 2015)

Largemouth bass. Another nonnative species often mentioned as a potential predator on endangered salmon and smelt is largemouth bass. Studies of largemouth bass indicate they are fairly sedentary and mostly feed on nonnative crayfish, but they will consume small salmon and other fishes when they are available and vulnerable (Moyle 2002, Conrad et al. 2016). However, peak out-migrations of salmon are in March through May, when cold temperatures limit largemouth bass activity. There has never really been much enthusiasm for controlling largemouth bass in any case, given their importance as in sport fisheries; bass angling tournaments are an important source of revenue for local communities.

Mississippi silverside. One nonnative piscivore that might be having a significant impact is the Mississippi silverside, which can prey on smelt eggs and larvae. Silversides are small fish which invaded in the 1970s and are now abundant in schools in the shallow edge areas where delta smelt spawn. Recent eDNA studies indicate that the smelt are present in silverside guts (Baerwald et al. 2012). This evidence is circumstantial, but it is logical that egg and larval predation could cause further declines, especially if smelt populations were already low from other causes. This species is an example of the unexpected consequences of introductions of even seemingly small, innocuous species. After it was introduced for aquatic gnat control into a single lake it quickly spread throughout the state, and its effects are still largely unknown.

Sacramento pikeminnow. The pikeminnow, native to California rivers, is the one native species often discussed as a potential predator because large adults are piscivorous and eat juvenile salmon. In the past, major efforts have been made to reduce numbers in the Sacramento River and tributaries, but they have generally failed. Because it *is* a native and is not particularly common in the Delta, there is little current interest in control. However, it has become a major salmon predator in the Eel River, the third largest watershed in California, into which it was introduced in 1979 (Moyle 2004, see below).

Other predators. Grossman (2016) provides a good overview of predation in the Delta, which applies to the state in general. He concludes there is a wide array of possible predators on salmon, smelt, and other native fishes so that attempts to control just one species, even striped bass, are likely to be futile. He also notes that origins of the predator, native or nonnative, makes little difference: a predator does what is does, regardless. It is also worth noting that he finds no evidence of bird or mammal predation being important because such predators are scarce, which fits with observations of regional fish biologists (P. Moyle, personal observation).

In California waters, small fish face a wide array of predators, but little is known about interactions among the predators or possible compensatory effects if one predator is controlled and another is not. Likewise, many complicated food-web interactions are possible. The striped bass, for example, is cannibalistic at times, feeds on Mississippi silversides (a likely egg predator on smelt), and on threadfin shad, a potential competitor with juvenile salmon and smelt for zooplankton.

Conclusions

Grossman (2016) concluded: “Although it has been suggested that a reduction in the Striped Bass ... [and other predator] ... population[s] be implemented to reduce predation mortality of Chinook Salmon, the large number of salmon predators in the Delta make it unlikely that this effort will significantly affect salmon mortality (p. 1).”

In short, the Delta and other California aquatic ecosystems are complex and attempts to fix problems caused by human environmental change by single-species management (to reduce symptoms) will fail unless the fixes also go after root causes. An exception to this “rule” is eradication of potential predators immediately after they have invaded and are still vulnerable to intense eradication efforts. This was demonstrated by the eradication of northern pike from two reservoirs, which took enormous dedication and effort by state agencies. The limited distribution of the pike and the overwhelming perception of experts that pike would be a disaster for salmon populations (already in trouble) made their eradication possible (McMullin and Pert 2010).

Pikeminnow in Eel River

One place where biologists and managers in California should be able learn from predation studies in the Columbia River is management of the invasion of Sacramento pikeminnow into the Eel River. This species was introduced, presumably as bait, from the neighboring Russian River so was perfectly adapted to the Eel, the third largest watershed in the state. The invasion was tracked during a five year-long study in the 1980s (Brown and Moyle 1997). Pikeminnow have now colonized most of the watershed below natural barriers and is regarded as having a major impact on salmon and steelhead populations, especially in drought years. However, the river is recovering from a degraded state (massive landslides from unregulated logging combined with record floods in 1954 and 1962) and the salmon populations are highly variable, so it is difficult to determine whether pikeminnow control would be effective or not. A well-designed study of the effects of pikeminnow control in the Eel River could potentially benefit salmon management in both Eel and Columbia rivers.

STATISTICAL METHODS TO ASSESS PREDATION BY PISCIVORES

A key quantity needed to estimate the total predation on juvenile salmonids is the number eaten by fish predators. This is a most difficult problem to study because predation of juvenile salmon by other fish as the salmon traverse the hydrosystem is “hidden” from any type of direct sampling. In contrast, predation by colonial nesting birds can be assessed by detecting PIT-tags on the colonies, and predation of adult salmon by pinnipeds can be observed because the pinniped usually surfaces after catching an adult salmon to break the fish into more easily eaten chunks and these surface feeding are amenable to observation.

Conceptually, estimates of predation of juvenile salmonids (the prey) by predators can be based on a model of the bioenergetics of the predator population using

$$P_{sta} = N_{sta} \times E_{sta} \times F_{sta}$$

where P_{sta} is the total biomass of predation by a predator species divided by predator population (size or age) stratum *s* who are present in time (e.g., month) stratum *t* and in area (e.g., part of a reservoir) stratum *a*; N_{sta} is the number of predators in (size or age) stratum *s* in time stratum *t* in area stratum *a; E_{sta}*the energy requirements/predator fish; and F_{sta} is the fraction of the diet that is the salmonid of interest. A similar equation can be used if energy requirements are replaced by numbers of fish. Then the total predation is found by summing over the size/age strata of the predator population, over the time intervals of interest, and over the area strata of interest.

The problem must be stratified by predator size/age class because different sizes of predators have different requirements. For example, certain size/age classes of the predators may be too small to consume juvenile salmon. Similarly, the problem must be stratified by time because juvenile salmon are not always present to be consumed and so make up a different proportion of the diet over time. The problem must be stratified by area because fish in different areas may have different energy requirements (e.g., cold vs warm water habitats; reservoirs vs. flowing segments) and/or the diet fraction made up by the target prey species may differ among areas.

In 1982, the Bonneville Power Administration funded a series of studies to quantify the effect of fish predation on out-migrating juvenile salmonids in the John Day Reservoir. The major findings were summarized in four papers published in Transactions of the American Fisheries Society. In these studies, the John Day reservoir was partitioned into different areas and the time intervals were months. Poe et al (1991) reported that fish were sampled monthly. Stomach contents were examined and food items identified directly or through undigested bone fragments. Lengths of prey were estimated directly or through length-weight relationships to body parts. The diet composition was related primarily to predator length. Vigg et al. (1991) determined the rates of consumption of fish. Consumption rates varied by reservoir area, time of day, and predator size/age. A multi-step process was used to estimate energy requirements (in terms of number of fish):

1. Stomach contents of predators were evaluated on a diel schedule over the period of juvenile salmonid migration
2. Original prey weight was computed based on body length and bone measurements.
3. Percent digestion = observed weight/initial weight of prey
4. Evacuation rates were predicted from literature values and regression on time, temperature, fish size, and meal size
5. Duration of digestion period and time of ingestion were determined for each prey fish
6. Mass of prey consumed per diel period per predator was estimated and converted to number of fish based on the average mass of prey items.

Beamesderfer and Rieman (1991) estimated abundance of predators using capture-recapture methods in each month and area of the reservoir. Finally, Rieman et al (1991) combined all the above to estimate total loss of juvenile salmon to predation.

The Pikeminnow Control program (Williams et al. 2018) uses similar methods to estimate the consumption of salmonid juveniles by pikeminnow. Capture-recapture and electrofishing methods are used to estimate predator abundance. Consumption is estimated using the methods of Ward et al. (1995) and Ward and Zimmerman (1999) to estimate the consumption of salmonid juveniles by pikeminnows. McMichael and James (2017) used similar methods to estimate predation by pikeminnow of the upriver Bright Chinook stock. Electrofishing was used to estimate predator abundance (fish/rkm). The stomach contents were examined for a sample of predator fish to estimate the diet fractions of the prey species. Published bioenergetic equations were used to estimate the energy requirements.

Operationalizing the basic equation may require a major effort. Estimating the total abundance and size/age distribution of fish predators will require capture-recapture or catch per unit effort methods, and the statistical methodology is well established. It may be sufficient to measure the predator population at the start of the season and use growth models to model in-season mortality and movement among age/size classes. Energy requirements would seem to be relatively stable across years so once these are established and validated they could be used for several years. The proportion of the diet represented by the prey of interest needs to be established in each time interval because this will vary with the number of prey present, with competition from other predator species, water temperature, breeding season, and other factors. A sampling program to select samples of the predators and examine stomach contents throughout the season using existing methods will need to be established.

Overall, despite this effort, there will be considerable uncertainty in the final estimates. The greatest level of uncertainty likely comes from estimating the abundance of the predators in each size/age stratum. Capture-recapture methods are expensive to implement, and it difficult to eliminate sources of bias in population estimates. For example, Beamesderfer and Rieman (1991) used four types of gear and sampled at 2-week intervals from April to August. They obtained estimates with relative standard errors of around 10% which would require 3-5% of the population of each predator to be captured during each sampling event, a large proportion. McMicheal and James (2017) tagged much fewer predator fish (around 1500) but were able to estimate abundance in only two of nine strata because of inadequate recaptures. The northern pikeminnow control program releases about 1,500 tagged fish to estimate exploitation probabilities by anglers based on tag returns, and then total abundance based on non-tagged fish returned. They also calculated seasonal/area abundance index values for each predator species following the methods of Ward et al. (1995), by computing the mean catch per 900 s of boat electrofishing by season per unit area, then multiplying by the surface area (ha) of specific sampling locations in each river segment. This is used to allocate the total number of predators (estimated from the sport fishery) to each season/area combination prior to estimating consumption.

Sampling for diet composition is much easier and achieving a large enough sample size to reduce uncertainty about diet composition is straightforward. The methods to take the stomach contents and produce diet fractions are well understood.

Finally, the energy requirement equations for predators should be updated to account for impacts of climate change (e.g., increasing water temperatures) that are outside the conditions used to establish the relationships.

Recommendations

The limiting factor in the uncertainty of the estimates is likely to be the uncertainty in the estimates of abundance of fish predators by time/area stratum. A model based solely on mark-recapture methods is unlikely to be successful because modelling of movement and mixing across space and time would require extensive captures and recaptures. It also seems contradictory to replace predator fish back in the reservoir once captured. A hybrid approach as exemplified by the northern pikeminnow program is likely to be more successful. Fish are tagged and released at the start of the season and overall abundance (over all areas and time) are found through removal methods, such as a sport fishery or scientific sampling. Releases cannot be done haphazardly and will require releases of tagged fish to be spread over the areas where the predators exist with releases to be approximately proportional to abundance. Then the removal program can estimate overall abundance (say at the reservoir level) over time. Additional sampling (e.g., electrofishing) will be required to establish the relative abundance of the predators in area/time strata. This assumes that electrofishing is equally efficient in all area/time strata. These relative abundances are used to allocate the total population to the area/time strata. We note that these fish sampled by electrofishing do not have to be returned to the population. Similar methods based on hydroacoustic sampling could be used if the fish in the cone of detection could be identified by species. It is unclear if the quantity of eDNA could also be used to allocate the population in time/space.

Estimates of diet composition are “straight-forward” if not tedious. Again, it is not clear if eDNA methods could be used on a “blended” sample to estimate the relative abundance/biomass of the prey species in the predator fish stomachs (see, e.g., Krehenwinkel et al. 2019).

Estimates of energy requirement do not need to be re-established every year, but some care is needed that the current equations are still applicable in light of climate change and increasing water temperatures.

D. Avian predation on juvenile salmonids

Predation of juvenile salmonids by colonial birds may be easier to estimate than predation by other groups (i.e., fish and mammals). The number of predators can be estimated by visual counts of nests, and the number of fish consumed can be estimated from recovery of PIT tags originally inserted into fish and then deposited in the nest areas after passing through a bird's gastrointestinal tract. There are, however, some issues with the statistical analyses of these data and with the physiology and nesting behavior of some species. Studies of avian predation in the Columbia Basin have focused primarily on predation from colonial waterbirds such as Caspian terns (*Hydroprogne caspia*), double crested cormorants (*Phalacrocorax auratus*), American white pelicans (*Pelecanus erythrorhynchos*), California gulls (*Larus californicus*), and ring-billed gulls (*L. delawarensis*) that nest in large colonies close to the Columbia River and are known to consume salmonids. Recent papers (Payton et al. 2019, Evans et al. 2016, Hostetter et al. 2015) present detailed methodology and results; the Bird Research Northwest website serves as a central repository for research on impacts of colonial nesting birds in the Columbia Basin.

The most successful management actions have been directed toward controlling Caspian tern predation. A large colony of terns developed on Rice Island, which was created by the deposition of dreg spoils from the Columbia River shipping channel. The tern colony on Rice Island was "moved" to East Sand Island, which is closer to the ocean and where it was anticipated that the tern's diet would include fewer salmonids. As a result, Caspian tern diet changed from 90% salmonids to 47% salmonids, with a 62% reduction in consumption of smolts (Collis et al. 2002, Roby et al. 2002). Further management was needed, and beginning in 2006, an effort was made to redistribute half to two-thirds of East Sand Island tern colony to alternative sites in Oregon and California, with a goal of reducing smolt loss another 50% while still maintaining a viable tern population. Eight artificial islands were constructed in Oregon and California as alternative tern nesting habitat with more nesting islands planned as the size of the nesting area on East Sand Island was reduced from 5 to 1.5 acres. Double-crested cormorants on East Sand Island in 2009 consumed an estimated 11.1 million smolts and in 2010 the colony represented 41% of the population in western North America. In 2017, double-crested cormorants apparently relocated from East Sand Island to the Astoria-Megler Bridge, where their predation on smolts will be difficult to assess because PIT tags cannot be easily recovered.

Management actions at these colony sites have been primarily non-lethal (e.g., passive and active nest dissuasion) for Caspian terns and lethal (e.g., culling and oiling eggs) for double-crested cormorants. These actions have reduced the number of tern nests at East Sand Island from 5,000, but the number is still above the target of 3,125 nests set by the U.S. Army Corps of Engineers. In addition, Caspian terns are returning to Rice Island, and terns that were dissuaded from nesting at Crescent and Goose islands in the Columbia Plateau appear to have remained in the region and may be nesting at new sites where predation impacts are unknown. As an example, there has been an increase in the population of terns in the Klamath Basin where nesting areas have been created to draw Columbia Basin birds (Allen Evans, RTR personal communication). The fish species of concern in the Klamath are shortnose and Lost River suckers, populations of which are in serious decline. The USFWS has started a conservation hatchery with the goal of releasing 10,000 age-2 suckers at 200 mm FL. In 2018 they released 3,159 PIT-tagged and 157 radio tagged suckers in Upper Klamath Lake. Subsequently 57 PIT tags were recovered on 5 of the 11 bird colonies (white pelican, cormorant, terns). Release location (i.e., proximity to a bird colony) was a key factor in predation (Nathan Banet, USGS Klamath Station, presentation at Oregon AFS March 7, 2019, Bend OR).

Over the past 10 years, RTR has recovered 42 tags on the colonies, and these tags came from throughout the Columbia Basin, northern California, Nevada, and even Utah. Reportedly the Klamath Basin cormorant and pelican colonies have existed for a long time and have not changed markedly in size. The number of terns, however, has increased since the dissuasion of terns started in the Columbia Basin. PIT tags recovered in the Klamath that originated at long-distances may not have been deposited soon after the fish were consumed nor by Caspian terns. Characteristically terns regurgitate bones and hard parts (e.g., PIT tags) each morning, while pelicans and cormorants may take several days to pass tags in feces (Allen Evans, RTR, personal communication).

Nonetheless, if the Klamath Caspian tern population continues to grow, and the USFWS releases 10,000 200-mm suckers (about the size of a steelhead smolt) each year, tern predation may become an issue. That is, we may shift the problem from terns eating a significant proportion of ESA-listed steelhead in the Columbia River system to terns eating a significant proportion of ESA-listed suckers in the Klamath River system.

Though predation by Caspian terns and double-crested cormorants has been the focus of much attention, predation by gulls has been known for over three decades. Ruggerone (1986) studied ring-billed gull predation at Wanapum Dam and estimated, based on visual observations, that they consumed over 100,000 salmonids or 2% of the estimated spring migration during the 25-day peak migration period. The probability of detecting PIT-tags from smolts consumed by California and ring-billed gulls and subsequently deposited in nesting colonies may be as low as one in seven, and predation on smolts by the gulls may be more serious than that of managed terns and cormorants (Hostetter et al. 2015, Evans et al. 2016a). All dams in the upper Columbia River, and most others in the Basin, have extensive wire arrays crisscrossing the tailraces of the dams to inhibit gull predation of juvenile salmon that have passed the dam via spill or turbine. Additionally, gulls are hazed away from the dams and have been lethally removed. At Wanapum and Priest Rapids dams, 1105 gulls were killed in 2012, but the number has been steadily decreasing to 175 gulls in 2017 (Curt Dotson, Grant PUD, presentation to the ISAB March 1, 2019). The upper Columbia PUDs have also supported research into avian predation in the lower Columbia (Evans et al. 2018a).

Are efforts to reduce avian predation on juvenile salmonids in the Columbia River estuary compensated by seabird predation in the Columbia River plume? Research on seabird predation to date has focused on evaluating relationships between the density and movements of two major seabird predators (common murres and sooty shearwaters) and the size and location of the Columbia River plume (Phillips et al. 2017, 2018, Morgan et al. 2018). Shipboard observations and independent telemetry data indicate that murres and shearwaters can track the location of the Columbia River plume. Investigators found that seabird densities are negatively correlated with plume size (primarily influenced by river flow). Thus, hydrosystem discharge may influence seabird predation and early ocean survival of juvenile Columbia River salmonids. At present, however, investigators lack diet data to directly link seabird predation in the plume to juvenile salmon mortality. Could management of river discharge in the spring be an effective tool for improving the ocean survival of juvenile salmon and steelhead? The ISAB considers this an important information gap that needs to be addressed. As has been noted for other predators, the salmonid prey that are taken are not a random sample but tend to be the individuals in poorer condition. For example, Tucker et al. (2016) compared the fish brought back to nests by rhinoceros auklets (*Cerorhinca monocerata*) to those caught in scientific surveys in the vicinity and found that the salmonids taken by birds were smaller and in poorer condition than the general population. These fish might, therefore, be more likely to later succumb to some other predator had they not been taken by the birds. This reinforces the concept that predation is not random.

A recent, preliminary study (Evans et al. 2018a) considered 10 years (2008-2017) during which some of over 70,000 PIT tags that had been implanted into steelhead from the upper Columbia River (UCR) were recovered from 14 colonial bird colonies in the Columbia River. Birds nesting on the colonies included Caspian terns, California gulls/ring-billed gulls and double-crested cormorants. The authors report that predation from these birds annually accounted for 47% (95% CRI = 37%-61%) to 69% (95% CRI = 54%–88%) of the UCR steelhead smolt mortality during emigration from Rock Island Dam to Bonneville Dam. That is, avian predation was greater than all other sources of mortality combined in 9 of the 10 study years evaluated. Smolt predation by Caspian terns and double-crested cormorants downstream of Bonneville Dam were also substantial and ranged from 14% to 28% of UCR steelhead smolts in the Columbia River estuary. Recently, presenters to the ISAB (Quinn Payton and Allen Evans, RTR, March 1, 2019) demonstrated results from their Joint Mortality and Survival (JMS) model. Using the 10-year dataset and partitioning sources of juvenile mortality, the model (Figure 11) estimated that in the absence of Caspian tern predation, UCR steelhead SARs would have been one (SARs 95% CRI of SARs = 0%-2%) to five percentage points higher (SARs 95% CRI = 3%-8%). That is, Caspian tern predation of UCR steelhead is additive, not compensatory. This is perhaps the only instance in which the effect of a predator on salmonids in the Columbia Basin has been measured using adult equivalents metric (ISAB 2016-1). The same research team reported that in 2014, 31% (95% CRI = 27%-36%) of juvenile steelhead were consumed by avian predators during their outmigration to the ocean, but they have not yet related this predation mortality to SARs (Payton et al. 2019).

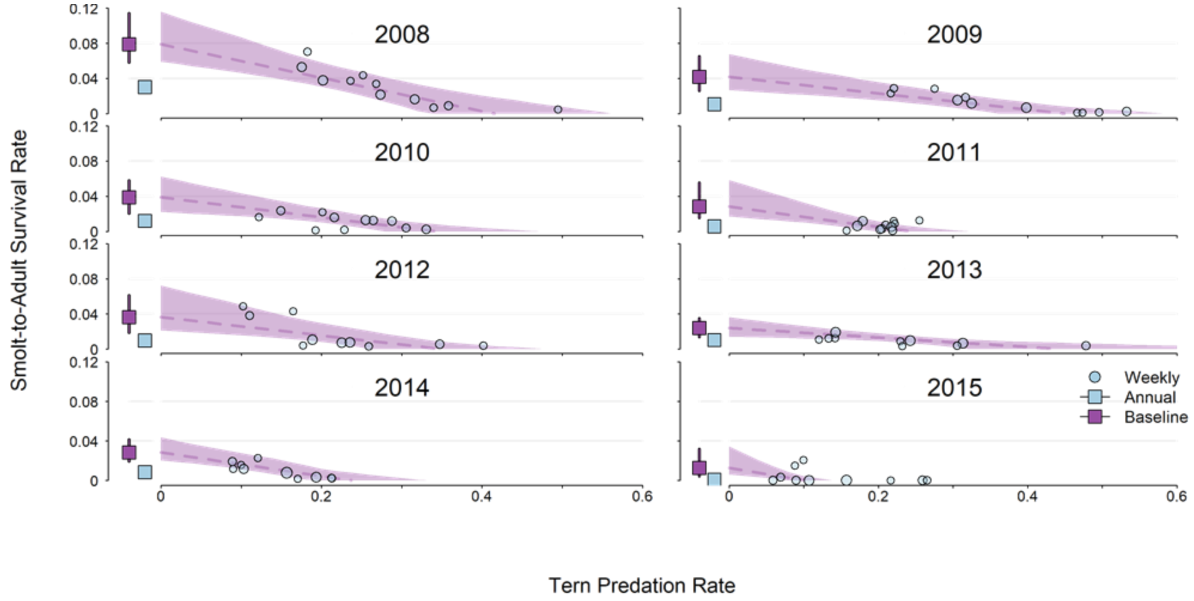

Figure 11. Estimated relationship between smolt-to-adult (SAR) survival for Upper Columbia River (UCR) steelhead from Rock Island Dam (as out-migrating smolts) to Bonneville Dam (as returning adults) and Caspian tern predation rates on out-migrating smolts. The size of blue circles depicts relative numbers of steelhead released each week at Rock Island Dam. Dotted line represents the best fit estimate, shading denotes 95% credible intervals (CRI) around the best fit. Annual estimates of survival with tern predation (blue box) and baseline survival in the absence of tern predation (purple box) are also provided (error bars denote 95% CRI). Figure reproduced with permission from Evans et al. (2018a).

STATISTICAL ANALYSES OF AVIAN PREDATION ON JUVENILE SALMONIDS

Studies of avian predation in the Columbia Basin have focused primarily on predation from colonial birds such as Caspian terns double crested cormorants, American white pelicans, California gulls, and ring-billed gulls that nest in large colonies close to the Columbia River and are known to consume salmonids. Two recent papers (Evans et al. 2016) and Hostetter et al (2015) present detailed methodology and results.

Estimates of avian predation in colonial birds rely heavily on the PIT-tagging programs on the Columbia River. Conceptually (Figure 12), a release group of fish is tagged with PIT-tags. A fraction (θ) of the release group are eaten by birds from a colony; a fraction (φ) of these consumed PIT-tags are deposited in working order on the colony; and searches of the colony, after the birds depart, detect a further fraction (ψ) of the deposited functioning tags. Not all deposited working tags remain on the colony (e.g., wind events may remove some), and this latter probability includes all sources of non-detection after deposition. This provides information on the proportion of the release group that has been eaten by this colony assuming that the latter two proportions can be estimated. A common way to estimate the product of the probability of deposition of a PIT-tag in working order and probability of detection of a functioning PIT-tag is to "feed" a known number of PIT-tagged fish to birds close to the feeding areas and see what fraction of these are eventually detected on the colony. Finally, working PIT-tags are seeded on the colony nesting site during the feeding periods prior to the (multiple searches) to estimate the probability of a deposited working tag being detected. Standard statistical methods (Hostetter et al. 2015) are used to estimate the parameters and finally estimate the fraction of the release group consumed by birds on the colony.

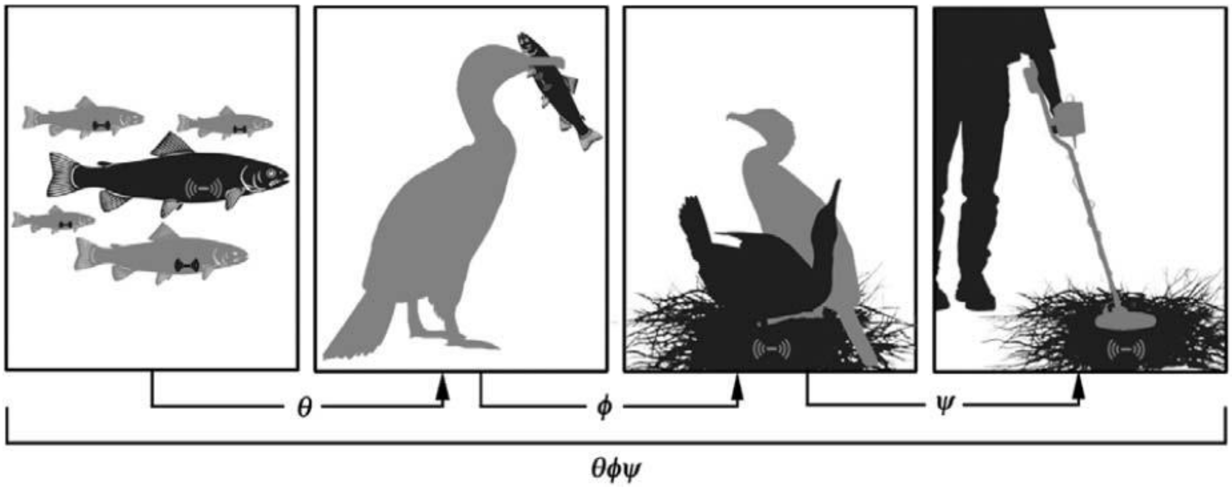

Figure 12. Conceptual model of tag recovery process in capture-recapture studies of avian predation. The probability of recovering a fish tag on a bird colony is the product of three probabilities: the probability that a tagged fish is consumed (predation probability θ), the probability that the tag is deposited on the nesting colony (deposition probability φ), and the probability that the tag is detected by researchers (detection probability ψ). Figure reproduced with permission from Hostetter et al. (2015).

Note, it is not necessary to estimate the size of the colony (e.g., number of nesting pairs) nor the diet composition of the birds for these methods to function. Hostetter et al. (2015) found that the primary cause of uncertainty in the overall estimate of probability of consumption from the release group was caused by uncertainty in the deposition probability.

There are a number of assumptions that need to be satisfied (Evans et al. 2016) notably:

1. Smolt survival, tag deposition, and tag detection are independent events.
2. Mortality due to fish handling and tagging is negligible.
3. After release, tagged fish migrate past the foraging areas in the same proportion as the general population of interest.

There is little to no information to verify the first two assumptions, but they are commonly made for all capture-recapture studies. The third assumption may be problematic if fish residualize (overwinter) in freshwater after tagging and then emigrate in the second year or never emigrate (e.g., steelhead).

There are a number of issues that need to be considered before converting the estimates of fraction consumed from a release group to a fraction consumed of a stock. Foremost is that the release group must match the body size and condition factor, and the temporal and spatial extent of the stock of interest (i.e., be representative of the stock of interest). Representation is ensured by randomly selecting members of the stock to be tagged to ensure that tagged fish are a constant proportion in space and time of the stock of interest and represent the body size and condition factor of the stock. The latter may be problematic if tagged fish tend to be larger and only in good health. This issue has had extensive discussions in the ISAB reviews of the Comparative Survival Study (CSS) (ISAB 2018-4).

Similarly, if a stock of juvenile salmon migrates past the foraging area of the colony over a two-week period, the release group must also migrate past the foraging area over the same two-week period. If the juvenile rearing area comprises a 124-mile (200-km) segment of the Columbia, the release group should also include juveniles from this rearing area. In practice, release groups are formed by capturing juveniles at bypass facilities at a dam downstream of the origin of the stock but upstream of the extent of foraging by the colony. Care must be taken that tagging numbers are proportional to the numbers passing the dam—otherwise weighting factors must be applied to individual release groups before combining. For example, suppose that a stock passes a dam in two pulses of 50,000 and 100,000 juveniles respectively, but only 1,000 fish are tagged and released from each pulse. Then the fraction consumed from the two release groups must be combined with a 1:2 weighting to reflect a tagged juvenile in the first release group represents 50 fish, but a tagged fish in the second group represents 100 fish. This weighting does not appear to have been done (e.g., equation just above the "Implementation Section" in Hostetter et al. 2015) and the overall proportion consumed from several release groups is based on weighting by fish released rather than the population size. The CSS (CSS 2019) does a weighting by population size when combining SARs from several release groups from a single stock, so these weights should be available.

Similarly, to convert the fraction of a stock consumed to numbers of fish consumed, it is necessary to know what fraction of the run has been tagged. The Fish Passage Center provides estimates of the number of juveniles for many stocks that can be used for this expansion.

One issue with the above methodology is that the fraction consumed of a release group is a very coarse measure and provides very little information on the spatial areas where high predation is occurring. It can also be confounded with in-river mortality if release groups are formed substantially upriver of the foraging area, and so the results cannot be directly interpreted as the localized predation probability. For example, consider Figure 13. Suppose that 1,000 fish are tagged and released at point A. Only 1000(0.9)(0.9) = 810 fish are available to be consumed at point C (due to natural mortality) of which about 810(0.2) = 162 fish are consumed by colony 1 for an overall fraction consumed of 0.162 from this release group. But a group of 1,000 fish released at B, now has 900 fish available at C, of which 180 are consumed for a fraction consumed of 0.180 despite colony 1 having the same conditional predation probability on both release groups. The situation for colony 2 is even more distorted because of the additional in-river mortality and the fact that the fraction of the release groups consumed will be lower despite having the same conditional probability of predation. Notice that the fraction of the release group consumed in either case is not a reflection of the conditional probability of consumption by the colony unless the release group is formed directly above the foraging areas (e.g., point C in Figure 13.). Indeed, a comparison of the proportion consumed of a group released at A between colonies 1 and 2 of Figure 13. would show that colony 2 consumes a smaller fraction of the release group because of confounding of proportion consumed with survival, which is correct but may not be a suitable comparison.

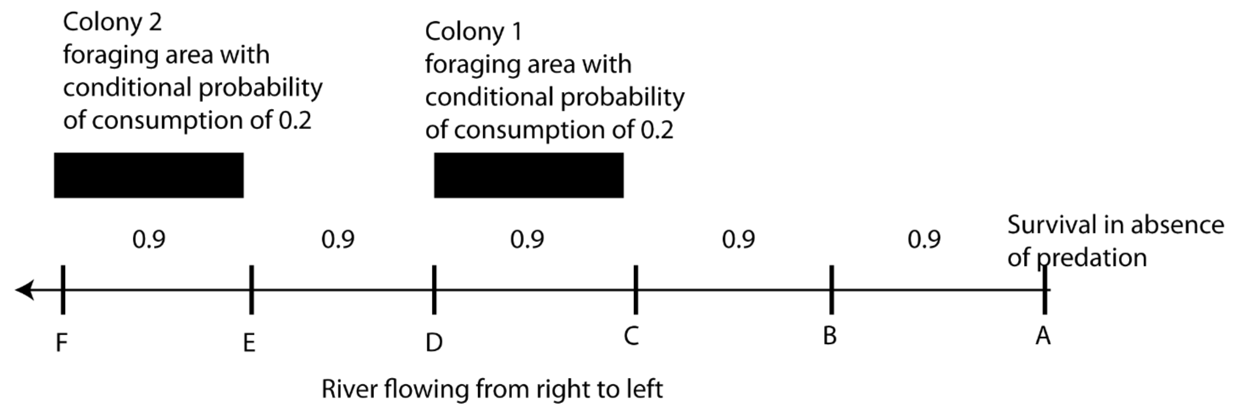

Figure 13. Schematic of potential confounding that occurs in estimating the probability of consuming a fish when fish are released at different points. The natural survival probability (in the absence of foraging) is the same between all potential release points. There are two colonies with the same conditional probability of consuming a fish given that the fish is available immediately upstream of the foraging area (points C and E for colonies 1 and 2 respectively). Natural and feeding mortality are assumed to be additive.

Ideally, one would condition on the number of fish alive at point C in Figure 13 when computing the fraction of the run consumed by colony 1. This may not be possible if studies only use PIT-tagged data because there may not be a detection facility at C to provide a group of fish known to be alive at point C. Hostetter et al. (2015) defined a fish to be available to avian predation at a particular colony if the fish “was detected at the nearest upstream hydrosystem with adequate interrogation capabilities.” Unfortunately, in some cases, this could be point B or even Point A and not point C in Figure 13. Similar issues occur when measuring fish predation.

Evans et al. (2016) reduced the spatial scale at which conditioning took place by double tagging fish with both acoustic tags (e.g., Juvenile Salmonid Acoustic Telemetry System tags; JSATS; McMichael et al. 2010) and PIT tags. JSATS have near 100% detectability at arrays, and it is relatively easy to deploy detector arrays in a dense fashion. By having dense JSATS arrays with high detectability, it is possible to define release groups (i.e., condition on fish availability) at a much finer temporal scale than based on detection facilities at hydrosystem dams only. For example, if JSATS arrays are placed at A, B, C, D, and E (Figure 13) then the number of double tagged fish available to each colony is known and the fraction consumed of each conditional release group matches the conditional probability of consumption. This approach again raises issues about representativeness of the double-tagged fish. Fish must be 95-300 mm FL and in good condition to be double tagged, and mortality is size selective in complex ways, depending on the species of fish and the predator.

Within-year comparisons (e.g., comparing the fraction consumed across stocks or among colonies) must be done with care. Among stock comparisons must ensure that all release groups are comparable (i.e., conditioned at the same release point in Figure 13). If the conditioning takes place well upstream of the bird-foraging area, then the comparisons may also be confounded with differential in-river mortality among stocks between the conditioning points and the foraging areas. Among colony comparisons are best done by conditioning just upstream of the respective foraging area. For example, it would not be sensible to compare the fraction of release group consumed by colony 2 and colony 1 if both condition on the same single release group at point A in Figure 13. Furthermore, as noted earlier in this report, some stocks of salmon are much more vulnerable than others to predation (Sebring et al. 2013), and hatchery and wild fish may also differ (e.g., Ryan et al. 2003).

One final issue raised by the ISAB Predation Metric Report (ISAB 2016-1) is that a fish consumed between E and F in Figure 13 is "not equal" to a fish consumed between C and D in Figure 13. In a simple world, a fish consumed between E and F is worth more adult equivalents than a fish consumed between C and D. Compensatory effects will complicate such comparisons.

Across-year comparisons (e.g., due to the effects of management actions or relationship to other covariates such as flow) must be done with care to ensure that the same conditioning is used for all comparisons (i.e., across-year comparisons should not mix estimates based on release groups at A with estimates based on release groups at B in Figure 13). In all cases, the experimental unit is the "year" and so comparisons can be done using a "statistics on statistics approach" or an integrated analysis that combines data across years.

SUMMARY AND RECOMMENDATIONS

The Evans et al. (2016) and Hostetter et al. (2015) papers are succinct summaries of the state-of-the-art in measuring avian predation by colonial birds.

A successful study will require:

1. Adequate numbers of tagged released fish.
2. A smaller-spatial scale so that predation estimates are not confounded with in-river mortality. Ideally, release groups should be defined just above the foraging area of a colony. This could be done by using more detection arrays and JSATS as done by Evans et al. (2016) or transporting and releasing fish just above a colony foraging area. The latter also identifies problems with the disruption of natural migration timing but may be more cost effective than the current approach. Alternatively, a combined study, e.g., a large number of PIT-tagged fish released at point A in Figure 13. with a smaller study using JSATS to estimate survival to point C in Figure 13 could be used.
3. Effort to estimate working-tag deposition and detection probabilities. As shown in Hostetter et al. (2015), ignoring these effects can lead to (severe) biases in the estimates of the proportion consumed.
4. Many (if not all) major colonies of birds will have to be monitored to estimate the total impact of colonial avian predation as fish pass the hydrosystem. Rather than trying to measure the impact of all colonies in all years, it may be preferable to use a panel design where a subset of colonies is

measured each year and imputation (based on past years' data) is used for colonies when not measured.

Suggested changes to these avian predation studies:

1. These studies typically report the proportion consumed by stock/release group but should also report the number of fish consumed because the same number of fish consumed by a colony on a stock with improved juvenile outmigration survival over time would then appear as a decline in the proportion consumed.
2. Comparison of proportion consumed among colonies must also be expressed in the same equivalents (e.g., adult equivalents) so that the impact of management actions at different colonies can be sensibly compared. These comparisons may be best done using life-cycle models. The impact of compensation is unlikely to be resolved, so a series of comparisons using different sets of compensatory behavior will be needed.
3. These types of studies should be continued for several years so that across-year dynamics can also be studied, e.g., how does predation vary with flow, where many different years at different flow patterns will be needed. An integrated analysis would be preferable so that information can also be shared across years on some parameters (e.g., deposition probabilities)
4. Combined release groups should use weighted averages based on relative population sizes that each release group represents rather than simple averages.
5. Modelling predation patterns on individual fish stocks within years should use an integrated model to share information across stocks on certain parameters.
6. An integrated model should be developed that combines information from JSATS tags (used to obtain survival probabilities at small spatial scales) and the large PIT-tag studies conducted by CSS (and other groups). The JSATS information would allow the model to separate out in-river mortality above the foraging areas from the fraction consumed from each release group.
7. Hostetter et al. (2017) discuss an integration of estimating survival based on PIT-tag detections at the dams and recoveries of PIT-tags on bird colonies based on an integrated recapture and dead-recovery mark-recapture model. This method does not currently provide estimates of avian predation, but as noted above, a further integration with the additional data on tag-deposition and tag-detection probabilities on the colony may be able to separate mortality into in-river and due to bird-colonies. This avenue should be pursued.

E. Marine mammals (Pinnipeds)

INTRODUCTION

Pinnipeds, including California sea lion (*Zalophus californianus*, United States stock), Steller sea lion (*Eumetopias jubatus*, eastern United States stock), and Pacific harbor seal (*Phoca vitulina*, Oregon/Washington coastal stock) are native predators in the lower Columbia River and estuary, where they forage on many of the Council's focal fish species (salmon, steelhead, Pacific lamprey, white sturgeon, and eulachon) as well as many other fish species. Pinniped predators in marine ecosystems are typically opportunistic carnivores, feeding on seasonally and locally abundant species of squid and fish, including juvenile and adult salmonids (e.g., Reimer et al. 2011, Steingass 2017, Robinson et al. 2018). Harbor seals, for example, eat a wide range of demersal and pelagic fishes, and the composition often varies seasonally with the relative availability of the fish species (Olesiuk 1993, Orr et al. 2004, Scordino 2010, Lance et al. 2012, Howard et al. 2013).

In the novel ecosystem formed by the Columbia River hydrosystem (ISAB 2011-1), individual "river type" pinnipeds can become habituated to selective foraging on adult salmon and steelhead, white sturgeon, and lamprey at sites near dams, fishways, and other manmade structures (Wright et al. 2010). Pinniped predator management actions in the Basin are focused largely on reducing impacts on survival of focal fish species at Bonneville Dam and Willamette Falls (Hatch et al. 2018, Tidwell et al. 2018, Wright and Murtagh 2018).

In this report, we present a brief (i.e., not comprehensive) review of recent scientific evidence of the impacts of pinniped predators on salmon, steelhead, eulachon, Pacific lamprey, and white sturgeon in the Columbia River (see *Impacts of pinniped predators*). Because the scope of the Council's request for information on pinniped impacts was limited, the ISAB focuses its review on some of the scientific and statistical methods currently used in the Basin to evaluate pinniped predator impacts (see *Methods used to evaluate pinniped impacts*). To gain a broad perspective of the effectiveness of pinniped predator management, we also briefly review relevant information from both inside and outside the Columbia River Basin (see *Effectiveness of predator control*) on marine mammal control programs and perspectives from other ecosystems. We identify important information gaps and research needs related to pinniped predation impacts and management in the Basin, and recommend areas needing further investigation (see *Information gaps and recommendations*). The following section provides relevant background information on pinniped predator management, monitoring, and evaluation in the Basin, including a brief review of ISAB's recent recommendations on these issues (ISAB 2018-1).

BACKGROUND INFORMATION

In the United States, all marine mammals are protected species, managed under the U.S. Marine Mammal Protection Act (MMPA). The MMPA (Section 120) allows the federal government (Department of Commerce, NOAA Fisheries, West Coast Region) to authorize non-lethal or lethal removal of individual pinnipeds (sea lions) that negatively impact the recovery of U.S. Endangered Species Act (ESA)-listed species or species approaching endangered status. The authorization applies only to pinnipeds that are not ESA listed or designated as a depleted or strategic stock under the MMPA. None of the pinniped species/stocks distributed in the Columbia River are currently ESA-listed or depleted. The eastern population of Steller sea lions, that frequent the lower Columbia River and estuary, were previously listed as threatened under the ESA but have since recovered and were de-listed in 2013. In 2008, the states (Oregon, Washington, and Idaho) were first granted authority under the MMPA to lethally take individually identifiable California sea lions that fed on salmon and steelhead at Bonneville Dam (Federal Register 2008).

In 2018 the MMPA, Section 120, was modified by the Endangered Salmon Predation Prevention Act. This legislation allows the states (Washington, Oregon, and Idaho) and certain Columbia River tribes (for the first time) expanded authority to deter and lethally take California sea lions on the Columbia River (mainstem from river mile 112 to McNary Dam) and its tributaries. Species to be protected include ESA-listed (endangered and threatened) species of salmon, steelhead, and eulachon, and other non-listed fish species of concern (lamprey and sturgeon). The annual take of sea lions cannot exceed 10% of the annual potential biological removal (PBR) level for sea lions. For example, the current PBR for California sea lions is 9,200 animals, and so a total of up to 920 animals could be removed each year.[5] The Secretary of Commerce is tasked with studying and reporting to Congress on the effects of deterrence and the lethal taking of sea lions on the recovery of endangered and threatened salmon and steelhead stocks in the Columbia River and its tributaries.

The ongoing 25-year plan for monitoring pinniped predation in the Columbia River is outlined in the Columbia River Estuary ESA Recovery Plan Module for Salmon and Steelhead (Estuary Module) (NMFS 2011). Because the actions in the estuary module have Basin-wide scope and are expected to benefit all 13 listed salmonid ESUs and DPSs in the Columbia Basin, the Estuary Module is incorporated into all Columbia Basin salmon and steelhead recovery plans. The only high priority management action in the Estuary Module related to marine mammal predation is to “identify and implement actions to reduce salmonid [adult, stream-type] predation by pinnipeds” (CRE-14; NMFS 2011).

The Estuary module lists three monitoring needs and proposed scientific methods to implement CRE-14 (NMFS 2011):

- *Pinniped predation monitoring, including annual monitoring at Bonneville Dam (BON) in spring and summer and one (5-yr) estuary-wide study. Methods include systematic sampling by observers, measuring the number of pinnipeds, deriving weekly average abundance of pinnipeds, and trend analysis.*
- *Action effectiveness monitoring of predator control measures under MMPA Section 120, including monitoring at BON in spring and summer. Methods include before-after-control-impact (BACI)*

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[5] www.westcoast.fisheries.noaa.gov

sampling design, observer sampling, measuring the number of pinnipeds; deriving average abundance, and statistical comparison analysis.

- *Determining the magnitude of pinniped impact, including estuary-wide annual monitoring, stratified random sampling by reach, sampling by observers/scat analysis, measuring the number of pinnipeds, number of salmon and steelhead consumed per predator, and sampling rate, estimating the total number of salmon and steelhead consumed, and analyzing trends.*

The proposed scientific methods outlined in the Estuary Module are expected to evolve through an adaptive management process (NMFS 2011). Many agencies are involved in the implementation of the pinniped monitoring effort, primarily the U.S. Army Corps of Engineers (USACE or "the Corps"), NOAA Fisheries/National Marine Fisheries Service (NMFS), Bonneville Power Administration (BPA), U.S. Department of Agriculture Wildlife Service (USDA WS), Columbia River Inter-Tribal Fish Commission (CRITFC), Oregon Department of Fish and Wildlife (ODFW), and Washington Department of Fish and Wildlife (WDFW).

The Council's Predator Management Sub-strategy is to "improve the survival of salmon and steelhead and other native focal fish species by managing and controlling predation rates" (Fish and Wildlife Program document 2014-12). The plan lists five actions specific to management of predator seals and sea lions:

- *The Corps should take actions to improve the exclusion of sea lions at all main adult fish ladder entrances and navigation locks at Bonneville Dam.*
- *The Corps should continue to support land- and water-based harassment efforts by NOAA Fisheries, the Oregon and Washington departments of fish and wildlife, and tribes to keep sea lions away from the area immediately downstream of Bonneville Dam.*
- *The federal action agencies [BPA, USACE, and the U.S. Bureau of Reclamation (USBR)] should fund federal, tribal, and state agencies to evaluate the extent of seal and sea lion predation on salmonids, sturgeon, and lamprey in the lower Columbia River from below Bonneville Dam to the mouth of the river.*
- *The federal action agencies, in collaboration with the region's state and federal fish and wildlife agencies, tribes, and others, should identify opportunities and implement actions to reduce salmon, sturgeon, and lamprey losses through seal and sea lion management in the lower Columbia River and estuary.*
- *When federal, state, or tribal managers determine that predation by seals and sea lions is causing significant adverse impacts to salmonids or other native fish, state and federal fish agencies employing lethal and non-lethal methods to manage predation shall continue the lethal methods if non-lethal methods are not successful.*

In 2018, the ISAB reviewed the Council's 2014 Predation Management Sub-strategy, finding it "for the most part scientifically sound, justified, and fairly comprehensive" (ISAB 2018-3). However, the ISAB advised the Council that the second principle of this sub-strategy assumes that predator management is necessary to improve the survival of salmon and steelhead, sturgeon, lamprey, and native resident fish species in the Basin. The ISAB previously found that this assumption is seldom evaluated quantitatively (ISAB/ISRP 2016-1). The ISAB/ISRP advised that further research on the efficacy of predator control to protect returning adults (salmonids and other focal species) in the estuary and lower Columbia River is needed (ISAB 2018-3).

In 2018, the ISAB also reviewed recovery actions for spring Chinook salmon in the Upper Columbia River (ISAB 2018-1). To address the review questions: "Are pinnipeds potentially a significant source of mortality for Upper Columbia spring Chinook? Can the effect of pinniped predation of Upper Columbia spring Chinook be quantified?" The ISAB reiterated recommendations from past reviews (see 3.4.2, ISAB 2018-1) and recommended proceeding with the pinniped recommendations listed in NOAA Fisheries 2016 Five-Year Upper Columbia Status Report, as follows:

> *"(1) expand pinniped monitoring efforts to assess interactions between pinnipeds and listed species, (2) maintain predatory pinniped management actions at Bonneville Dam to reduce the loss of upriver listed salmon and steelhead stocks, (3) complete life-cycle/extinction risk modeling to quantify predation rates by predatory pinnipeds on listed salmon and steelhead stocks in the Columbia River and Willamette River, and (4) expand research efforts in the Columbia River estuary on survival and run timing for adult salmonids migrating through the lower Columbia River to Bonneville Dam. The second recommendation is a necessary precautionary measure while better data are collected."*

In addition, the ISAB recommended (ISAB 2018-1):

- *Identifying and investigating other potentially significant sources of mortality of Upper Columbia spring Chinook smolts and adults in the Columbia River plume/ocean shelf habitats, estuary, and lower mainstem and tributaries. New information from NOAA's tagging and modeling efforts revealed important data gaps, including lack of population-specific survival estimates for Upper Columbia spring Chinook.*
- *Use of a variety of approaches to quantify pinniped predation impacts, such as the ongoing tagging studies and coast-wide bioenergetics/life-cycle modeling. Comparison of multiple models could reduce structural uncertainty (e.g., comparing a bioenergetics approach to individual-based models or time series models).*
- *Investigations of the relative effects of pinnipeds and harvest [on spring and summer Chinook] in the lower river and estuary.*

The March 2019 Biological Opinion (Opinion) for the Federal Columbia River Power System summarizes pinniped impacts and predation management actions for the Basin's 13 species of salmon and steelhead and eulachon listed as threatened or endangered under the ESA (NMFS 2019). The Opinion considers increasing pinniped predation to be a serious threat to the recovery of Upper Willamette River (UWR) Chinook salmon and steelhead. Accordingly, NMFS has already issued an authorization to remove sea lions from the vicinity of Willamette Falls and kill them at another location, and these activities have started in winter 2018. At Bonneville Dam, the Corps will continue actions previously implemented under the 2014 Supplemental FCRPS

Biological Opinion, including (1) use of sea-lion excluder gates at all adult fish ladder entrances, (2) support for land- and water-based harassment of sea lions by ODFW, WDFW, and CRITFC, (3) estimation of sea lion abundance, spatial distribution, temporal distribution, predation attempts, and predation rates, and (4) adaptive management to address changing circumstances related to sea lion harassment efforts and predation monitoring. The continuation of these actions is expected "to reduce further, or at least maintain, the ongoing benefits of reduced predation rates. In addition, the Corps will implement a study in coordination with other state and tribal entities that evaluates the effectiveness of Steller sea lion hazing and dissuasion methods and timing."

Impacts of Pinniped Predators

The weight of scientific evidence reviewed by the ISAB indicates that the survivals of many of the Council's focal fish species are potentially impacted by pinniped predators in the Columbia River (Table Appendix C). This is consistent with ISAB's past review findings on the impacts of pinnipeds on Upper Columbia River spring Chinook salmon (ISAB 2018-1). Recent estimates from bioenergetic/life-cycle models and direct estimates of survival from tagging studies indicate that sea lion impacts on adult Chinook salmon survival can approach or exceed removals by fisheries (in the Columbia estuary) in some years (Chasco et al. 2017a; Wargo Rub et al. 2019). The estimated number of Chinook salmon consumed annually by sea lions differs substantially between the two investigations and credible intervals (95% CRI) are wide. For example, Chasco et al. (2017a) estimated that 65,000 (49,000–81,000) adult (ocean age 2 and older) Chinook salmon (all populations) were consumed by California sea lions in the Columbia River during January-August 2015, whereas Wargo Rub et al. (2019) estimated that non-harvest mortality (assumed to be California sea lion predation) from the estuary (Astoria) to Bonneville Dam in 2015 was 224,000 (6,000- 495,000) adult spring-run Chinook salmon (mid- and upper-river populations). Chasco et al. (2017a) ranked their bioenergetic/life-cycle model estimates of in-river impacts on smolt and adult Chinook salmon by pinniped species. For example, in 2015 harbor seals consumed an estimated 312,000 Chinook salmon smolts in the Columbia River, while sea lions were assumed to consume only adult salmonids (Chasco et al. 2017a). In 2015, harbor seals consumed an estimated 1,000 adult (ocean age 2 and older) Chinook salmon, California sea lions consumed 46,000, and Steller sea lions consumed 47,000 (Chasco et al. 2017a).

In the Bonneville Dam tailrace, trend analyses (fall and winter 2007-2017, spring 2002-2018) indicated that California sea lion abundance and fish consumption are decreasing (attributed to successful sea lion removal efforts), while Steller sea lion abundance and fish consumption are increasing (Tidwell et al. 2019). Trends in fall and winter sampling show a rapid annual increase in Steller sea lion abundance and number of days present in the tailrace and corresponding increases in predation on adult Chinook salmon, late-run coho salmon, chum salmon, B-run summer steelhead, and winter-run steelhead (Tidwell et al. 2019). During spring 2018, the estimated average daily abundance of pinnipeds in the dam tailrace was 15 Steller sea lions and 3 California sea lions. The total number of salmonids killed by both species of sea lions was lower in spring 2018 than previous years, but similar to the 10-year average. The estimated percentage of the adult spring/summer Chinook salmon run consumed by sea lions across all three tailraces at Bonneville Dam in spring 2018 was 2.9% of the total run or 2,800 (95% CI 2,600 –3100) fish (Tidwell et al. 2019). The estimated annual consumption of white sturgeon in the tailrace during spring peaked in 2011 (3,000 fish) and has declined since then (148 fish in 2018). This trend may correspond to a decrease in sturgeon population(s) that spawn in the vicinity of the tailrace, but demographics of this sturgeon population are largely unknown (Tidwell et al. 2019). The estimated consumption of adult Pacific lamprey was low at 58 (95% CI 17 –91) fish or 0.04% of the total run in spring 2018; however, underwater feeding by sea lions cannot be observed in the tailrace. The latest fall-winter 2019 update of pinniped abundance and predation impacts in the Bonneville tailrace shows increases (compared to the 10-yr average) in the abundance and predation impacts of Steller sea lions during August-December and decreases in January and February 2019 (K.S. Tidwell, March 2019). The winter 2019 trends correspond to the extremely low passage of winter steelhead over Bonneville Dam.

At Willamette Falls in 2018, the most frequently observed pinniped prey item was adult salmonids (79%), followed by lamprey (12%), sturgeon (8%), and “unknown or other” fish (1%). California sea lions accounted for 89% of total observed predation events, but Steller sea lions accounted for 100% of observed sturgeon kills. Run-specific California sea lion predation (minimum) estimates in 2018 were 1,950 marked spring Chinook salmon (9% of potential escapement above the Falls), 466 unmarked spring Chinook salmon (9% of potential escapement), 516 summer steelhead (6% of potential escapement), and 503 winter steelhead (22% of potential escapement) (Wright and Murtagh 2018). Quasi-extinction probabilities were estimated for four populations of Willamette winter steelhead and two scenarios, "no sea lion" vs highest predation rate (2017): North Santiam: 0.015 vs. 0.644, South Santiam: 0.048 vs. 0.599, Calapooia: 0.993 vs. 0.999, and Molalla: 0.00 vs. 0.209 (Falcy 2017). These extinction probabilities are variable, but typically much higher with sea lion predation than without. However, missing data and incomplete (short) time series of sea lion abundance and predation rates and population-specific data for steelhead necessitated many assumptions about model inputs for this analysis.

While recent progress in evaluating pinniped impacts is substantial, the current results are equivocal to the ISAB given the dramatic annual fluctuations in predator/prey populations and the many important assumptions and unknowns underlying the estimates (Table Appendix C; see *Information Gaps and Recommendations*). The most important information gap is the lack of accurate estimates of the total abundance of pinnipeds (California sea lions, Steller sea lions, harbor seals) in the Columbia River (both intermittent and permanent residents; Wargo Rub et al. 2019). For most focal fish species, life stage- and population-specific data on abundance and length of time prey are vulnerable to predation are also needed to quantify or improve estimates of overall predator impacts. With the exception of Chasco et al. (2017a), we found little or no data concerning the impacts of pinniped predators on juvenile life stages of salmonids and other focal species in the Columbia River, estuary, and plume. However, Thomas et al. (2017) presented such information on harbor seal predation in the Strait of Georgia, Canada, and concluded that predation on both adults and juveniles was substantial. Bioenergetic/life cycle modeling approaches such as Chasco et al. (2017a) currently lack accurate information on in-river pinniped diets and prey consumption at the appropriate spatial and temporal scales. For most focal fish species, estimates of survival, fishing mortality, and pinniped-fishery interactions in the lower mainstem and estuary are lacking.

Methods used to evaluate pinniped impacts

The ISAB previously recommended the use of a variety of approaches to quantify pinniped predation impacts (see Predation Metrics Report, ISAB 2016-1). Several methods have been used to estimate the impacts of pinniped predation (particularly California sea lions) on Chinook salmon from the mouth of the Columbia to Bonneville Dam. These methods fall into three classes: (1) direct observation of predator numbers and predation events, (2) modelling the relationship between predator numbers and survival of salmon to infer their impact, and (3) bioenergetic/diet/food web modelling. We did not evaluate bioenergetic methods in this report because although the number of calories per kg of fish can be derived and the caloric intakes and conversion efficiencies of the predators are known (e.g., Winship et al. 2002), diet estimates cannot readily be apportioned among different focal species without capturing the pinnipeds and assessing their diets. Without this information, guesses must be made about how many salmon are being eaten. However, we note that in forecasting the relationship between marine mammals and prey such as salmon, energetics modelers need to consider that as prey become more abundant, the predators often consume only parts of them. Thus, while the salmon might weigh 5 kg each and one might be tempted to determine that if each predator eats 10 kg per day (made up numbers, of course) then it would eat two salmon, the predator might actually consume a small and variable fraction from a larger number of prey fish. This "partial consumption" is well-known in bears (Lincoln and Quinn 2019) and also marine mammals such as harbor seals (Hauser et al. 2008). In the latter case, predation on female sockeye salmon often (64%) resulted in consumption of only the belly region containing eggs, whereas the entire body was typically consumed in male salmon and only the head was left uneaten.

Direct observations of predation. For many years, the USACE has directly monitored pinniped numbers and observed predation in the tailrace at Bonneville (Tidwell et al. 2018), and ODFW has done similar monitoring at Willamette Falls (Wright et al. 2018). Standard sampling designs (e.g., stratified, systematic, multi-stage, etc.) are used to select areas and times to monitor to estimate the number of predators and observable predation.

Estimates of daily or weekly pinniped abundance are based on the highest point count of the species for each day or week regardless of the time of day. However, some of the pinnipeds have been branded or are individually identifiable through scars and other physical characteristics, so mark-resight methods (McClintock et al. 2019) should be investigated. In these methods, the brand number of a sighted pinniped is recorded. If the average branded pinniped is seen two times, then counts of unbranded pinnipeds are divided by two to account for double counting and estimate the number of individuals. The mark-resight methods will also provide an estimate of uncertainty about the abundance. Similarly, yearly maximum counts are used to represent the total number of animals that forage at Bonneville Dam and Willamette Falls. Again, mark-resight methods should be investigated to better estimate the total abundance.

Estimates of residence time at the dam are based on minimum and maximum time of sighting of branded/identifiable pinnipeds. Mark-recapture methods have also been developed for this situation (e.g., Pledger et al. 2009).

Estimates of consumption are based on observation at the surface. Pinnipeds can consume small prey underwater, but they usually must surface to manipulate and consume larger prey such as an adult salmonid (Roffe and Mate 1984). Sub-surface predation and consumption has been documented previously, particularly with the larger Steller sea lions and smaller fish, and so estimates of the numbers of fish consumed may be biased low (see p. 9 of Tidwell et al. 2018). In some cases, the species of fish being consumed cannot be readily identified, and a simple proportional allocation of unidentified prey into the various species is used—these adjustments are typically minor.

Hatch et al. (2018) use the Tidwell et al. (2018) estimates of predation at Bonneville Dam for individual pinnipeds to fit a functional response model for predation as a function of prey density and predator abundance. Preliminary results are interesting, but it is unclear how this model would be used outside of the Bonneville tailrace to estimate predation.

Capture-recapture estimates of abundance and predation. Hatch et al. (2018) describe a method that used capture-recapture and sampling designs to estimate abundance and predation over the lower areas of the Columbia River outside the area of direct observations by the USACE at Bonneville. The method uses two boats which travel the navigation channel of the Columbia River and independently note the presence of a sea lion and a predation event. These events may be seen by one of the boats or both boats, and these data are used in capture-recapture models (e.g., Lincoln-Petersen estimator) to estimate the number of pinnipeds or predation events missed by both boats during the traverse. This estimate could be expanded to estimate the total predation events using standard sampling theory, but this does not appear to have been done.

Measuring predation by individual pinnipeds. Hatch et al. (2018) also describe the use of accelerometer VHF radio tags applied to sea lions that could be used to measure the thrashing of the head when a pinniped surfaces to consume prey. The methodology appears to be still under development but would allow an estimate of predation to be based on (randomly) sampling pinnipeds, applying the radio tags, extracting the data, and obtaining estimates of predation for the tagged animals which could be expanded to the population if the population sizes were known.

Modeling the relationship between prey survival and pinniped abundance. The objective is to estimate the relationship between survival probabilities of prey and the number of pinnipeds and assume that this is a causal relationship. At the most basic level, one could calculate the relationship between estimates of smolt-to-adult survivals (SARs) and pinniped abundance, but the use of SARs is unlikely to provide much information because so many other factors affect survival early in the life cycle (e.g., hydrosystem, ocean, etc.) that any link to pinnipeds would be difficult to detect. The ISAB is not aware of any primary publications that have modeled this relationship for the Columbia River.

Wargo Rub et al. (2019) designed a six-year study to estimate survival of Middle and Interior Columbia River spring-run Chinook salmon after they entered the lower Columbia River and measured its relationship to pinniped abundance (and other variables). Tangle nets were used to capture returning adult Chinook salmon after they entered the Columbia River from April to late May. Stock origin was determined using genetic methods, and fish were tagged with PIT tags and released. Surviving fish were detected at Bonneville Dam or farther upstream in the PIT-tag detection systems. There is nearly a 100% detection probability of a surviving adult salmon at Bonneville or farther upstream, so non-detection of a surviving fish is not an issue. PIT-tag detections at Bonneville Dam or farther upstream were used to estimate salmon mortality and then to assess the relative effects of different factors.

A generalized linear mixed-effects model was used to evaluate the relationship between survival and fixed effects of the body length of the released fish, an index of the abundance of California sea lions at their primary haul-out location in the estuary (East Mooring Basin at Astoria), adipose fin clip status (indicating natural or hatchery origin), water temperature below Bonneville Dam and spill at the dam, travel time, total angler and commercial harvest in the estuary estimated by creel and harvest surveys, and an index of alternate prey abundance (American shad) based on counts of returning adults at Bonneville Dam. Random effects were used to model the effects of year and when fish were released in each year and to allow an autoregressive correlation structure. The resulting model seems to perform reasonably well (area under the receiver operating character curve (ROC) of 0.71). The odds of salmon survival decreased with California sea lion abundance but increased with American shad abundance, perhaps because of a buffering effect by these alternate prey (Wargo Rub et al. 2019). Although not used as a variable in the model, eulachon abundance was also highly (positively) correlated with sea lion abundance (Wargo Rub et al. 2019). Interestingly, Thomas et al. (2017) noted a reduction in harbor seal predation on Chinook salmon in the odd-numbered years when pink salmon were highly abundant in the Strait of Georgia, also suggesting a buffering effect because many pink salmon were consumed.

After fitting the model, the total adult interior spring Chinook salmon returns at Bonneville Dam was "back casted" to represent the initial number of salmon required to be alive at the time of tagging to result in the number being detected at Bonneville for each year of the study (Wargo Rub et al. 2019). For example, suppose that 1,000 fish were detected at Bonneville Dam in week 10 and the travel time from the tagging site to Bonneville is two weeks. These 1,000 fish would have been subject to the survival processes starting in week 8 at the tagging site. If the model predicted a survival probability of 0.4 over the two weeks for fish released in week 8, this implies that 1,000/0.4 = 2500 salmon would need to alive at the release point in that week to enable 1,000 fish to be detected at Bonneville in week 10. So (2,500-1,000) = 1,500 fish must have died from this release group due all sources of mortality. If the harvest in that two-week interval was 500 fish, then 1,500-500 = 1,000 fish are imputed to have died owing to non-harvest effects, presumably from predation by pinnipeds. This estimate was summed over the entire season. Travel time is not a fixed value, and so the above example was extended by allowing for a distribution of travel times. Based on this model of mortality, an estimated 52,000 – 255,000 adult spring Chinook salmon died annually in the reach between Astoria and Bonneville Dam that could not be accounted for by fishing mortality.

The analyses used in the paper seem to be implemented well and employ appropriate statistical tools. However, there is one important statistical issue that may affect this study. This is the "error in variables" problem where the predictors (e.g., total harvest, sea Lion abundance, shad abundance) are measured with uncertainty. For example, the daily adult counts at Bonneville of adult shad are hindcast by two weeks to represent an index of shad abundance when the Chinook are actively migrating through the lower Columbia River. Sea lion abundance is based on an index of abundance at Astoria and may not represent the actual number of sea lions present in the lower Columbia River. Harvest is estimated using creel and catch survey methods and has substantial uncertainty. The "error in variables" can cause substantial bias in estimates of effects (Stefanki and Carroll 1985). In many cases, estimates are attenuated (i.e., pulled towards zero), but this is not always true particularly when multiple predictors are subject to error and correlated among themselves. In the classical "error-in-variables" models, the uncertainty in the predictor values is unknown—in this case there is good information on the uncertainty of each of the predictors, and it is not difficult to include this in the Bayesian model used in this paper. This should be done.

The success of the Wargo Rub et al. (2019) study also depends on sufficient contrast in the numbers of predators across years. If the number of predators remains constant over the study, then the impact of the predator cannot be estimated. It is also difficult to use this method to estimate in-season predation during a particular year—the model would only predict the "average" change in survival at the values of the covariates for a given in-season point in time.

The only index of predator abundance used was the index for California sea lions (Wargo Rub et al. 2019), and so this index represents all sources of predation that vary with sea lion numbers. It will be difficult to separate the impact of different predators unless their numbers vary orthogonally to those of sea lions.

Finally, the estimated benefit of removing a predator is valid only for small changes in the predictor because the regression coefficients are marginal, i.e., assuming that all other covariates remain fixed. The model should not be used to predict the impact, for example, of reducing the sea lion index to zero.

Approaches to estimating total pinniped predation. The ISAB encourages the use of sampling approaches to estimate total pinniped predation. A key feature of pinniped predation that makes sampling approaches feasible is that larger prey sources such as adult salmonids are difficult for seals and sea lions to consume whole. The behavioral solution for these animals is to surface with prey in their mouth, and with thrashing head motions, break the fish into consumable pieces. Hence, the total of predation events on the surface may be quite close to total predation for predation events at the surface and events that do not take place on the surface. Consequently, estimating total predation requires (1) a suitable sampling design (e.g., stratification by area and/or time) and (2) selection of location-time combinations using simple, systematic, or probability-proportional-to-size methods to determine where and when to monitor.

During the selected monitoring location times, several methodological options are available, but a variant of a dual-observer line-transect distance sampling used for whales (e.g., Buckland et al. 2001, Burt et al. 2014, Borchers and Langrock 2015) seems appropriate. As in Hatch et al. (2018), a transect line is chosen (e.g., down the navigation channel of the Columbia River). In line-transect sampling, the perpendicular distance to the transect line of the predation event is measured. In many cases, this probability of detection declines with distance from the observer; i.e., it is easier to detect a predation event that is 10 m away than a predation event that is 100 m away. The dual-observer method is similar to the tandem-boat method and is used to adjust for predation events that are missed by an observer in the field of interest. This gives an estimate of the number of predation events for that sampled location time. The collection of estimates from the sampled location time are then expanded using standard statistical methods. Williamson and Hillemeir (2001) used a sampling approach to estimate pinniped predation in the Klamath River. This river is much smaller than the Columbia, but a similar sampling design would seem to be feasible. Wright et al. (2007) also used a comparable sampling approach at the Alsea River (Oregon) estuary. Care should be taken, however, to avoid bias, as might occur if the predators were distributed unevenly among habitats that were or were not surveyed.

Methods used to estimate pinniped numbers that we reviewed in the Columbia River rely on peak counts and similar methods and do not seem to consider the use of branded and individually identifiable animals to conduct mark-resight estimates of pinniped numbers. Mark-resight methods (McClintock et al. 2019) would not require a large change to the protocol—the distribution of the number of sightings of marked-animals is used to correct the total sightings of unmarked animals to arrive at an estimate of abundance with measures of uncertainty.

Effectiveness of predator control

The local problem of pinniped predator control in the Columbia River can and should draw from work elsewhere, especially with respect to the complexities of controlling marine mammals, ecological links, and ecosystem management. Many studies have considered the roles of marine mammals and other top predators in ecosystems, emphasizing the fact that humans and such animals can be seen as direct competitors for prey or indirect competitors through trophic links. For example, a review indicated that 84 species of marine mammals in the Pacific Ocean were consuming about three times as much food as humans catch (Trites et al. 1997). However, much of the prey were deep sea squids and other species not routinely consumed by humans, so the extent of direct competition was less than this estimate might suggest. A global review found comparatively little direct competition between humans and marine mammals, hence no broad-scale justification for culling (Morissette et al. 2012). On the other hand, the authors noted that the primary production needed to sustain marine mammals is considerable, and to some extent they do compete with humans in this regard. In another example, penguins and, to a lesser extent, fur seals consumed an estimated $8.3 * 10^8$ tons of krill compared to $1.0 * 10^8$ tons removed by fisheries in the South Shetland Islands (Croll and Tershy 1998).

Some scientific reviews explicitly consider the possible effects of marine mammal reduction in these systems (Bowen 1997). It is generally understood that the ecosystem management approach must consider a multitude of values as well as ecosystem processes and inevitably must balance different sets of values. For example, Crespo and Hall (2002) concluded (p. 484-485):

> *"As it is very difficult to conceive an ecosystem approach to management that completely protects some components of the ecosystem, the ecological approach suggests that the harvesting policies for all the components of the system be set following basic ecological principles, so as to retain the structure and function of the system. These policies may require that the harvests be spread in a balanced way over the whole food web… Policies addressed to the protection of a single species or a group of species could be necessary when the threat of extinction is clear, but they should be avoided otherwise, and replaced with more holistic approaches."*

A review of marine mammal control (i.e., culling) programs indicated that the results are often not convincing and that they are often not scientifically designed or evaluated (Bowen and Lidgard 2013). Quoted from the Abstract (p. 207):

> *"Marine mammal culling programs rarely have measurable objectives with respect to prey populations, and their success has not been evaluated. Culling marine mammals is controversial because of the following: (i) they are high profile charismatic megafauna; (ii) many populations are recovering from a period of over-exploitation while others remain threatened or endangered; and (iii) the scientific evidence needed to justify a cull is usually highly uncertain. Marine mammal culling programs should be based on scientific analysis with stated and measurable objectives to be evaluated during planned follow-up monitoring."*

This dim view may be influenced to some extent by the fact that many control programs involve large-scale ecosystems with many complex processes operating, rather than narrow ones such as the lower Columbia River. For example, Cape fur seal culling in the Benguela ecosystem may have actually reduced total fish yields (Yodzis 1998). A perspective piece by the same author on the difficulties of predator control in complex systems (Yodzis 2001) generated further discussion and debate (Boyd 2001).

Indeed, reviews of predator control programs in general (i.e., including terrestrial predators) tend to reveal a great deal of variation in the outcome. In many cases, the prey abundance increased (1.6-fold on average), but the effect sizes may vary greatly as result of different factors (Holt et al. 2008).

In Puget Sound, heavy predation on winter-run steelhead by members of a rapidly growing number of seasonal California sea lions (i.e., a non-breeding population) began to occur at a set of navigational locks linking Puget Sound with the Lake Washington watershed (Gearin et al. 1988). Deterrence efforts were initially successful, but effectiveness decreased over time due to habituation of individual sea lions. Later efforts came to include displacement and some lethal removal under the authority of the Marine Mammal Protection Act (Section 120).

At present, pinniped control measures in the Columbia River Basin are largely focused on deterrence or removal of individual sea lions feeding on adult salmon, steelhead, lamprey, and sturgeon at Bonneville Dam and Willamette Falls. Non-lethal hazing of sea lions is largely ineffective in reducing pinniped predation impacts (e.g., ISRP 2009-21, Scordino 2010). The CRITFC Sea Lion Monitoring and Non-lethal Hazing project (2008-004-00) reports annual observations of predation by sea lions at Bonneville Dam. However, due to sampling biases the data cannot be used to estimate salmon or sturgeon take (Hatch et al. 2018). Non-lethal removal of sea lions from the river to coastal marine habitats has also proven ineffective. Excluder devices at fishways and navigation locks and lethal removal may be the most effective methods for sea lion control. Recent declines in the abundance of California Sea lions at Bonneville Dam are considered a measure of successful predator management (Tidwell et al. 2018). However, there is uncertainty about how other factors affecting sea lion abundance and distribution, such as changes in the California Current ecosystem, may have influenced this result (NMFS 2019).

Social network-based diffusion analysis and epidemiological models indicate that current levels of lethal removal are successful at reducing predation but not at reducing overall sea lion recruitment at Bonneville Dam (Schakner et al. 2016, 2017). Lethal removal of Individual predators at upriver sites appears to be most effective when used immediately at first detection (Schakner et al. 2016). Accordingly, the new (2018) Endangered Salmon Predation Prevention Act streamlines MMPA permitting processes and criteria required for lethal removal of sea lions in the Columbia River.

Methods to evaluate pinniped control measures

The Council's pinniped predator control program will be easier to evaluate than avian and fish programs because adult salmon have little opportunity for compensatory responses after they reach Bonneville Dam (other than on the spawning grounds, if the populations are dense enough for such effects). If there is no compensation, marginal benefits may not be attenuated. Nevertheless, if salmon are relatively "rare," then removing a predator simply gives another predator another opportunity to feed on it, and so the net benefit is zero.

Two methods would seem suitable for evaluation. First, methods similar to Wargo Rub et al. (2019) seem ideal for evaluating the effectiveness of a predator control program. Briefly, returning adult salmon are intercepted and PIT-tagged before they enter the Columbia River estuary and are detected at Bonneville. This gives an estimate of survival of returning adults from the point of tagging to the Bonneville detectors. Back-calculation provides estimates of the number of adult salmon that died from causes other than harvest—presumably mostly from predation by pinnipeds. Then, the effectiveness of hazing of pinnipeds in the Bonneville tailrace can truly be evaluated—hazing may reduce observed predation events in the tailrace, but pinnipeds may simply move their predation activities slightly downstream out of range of the hazing and may result in no reduction in predator impact. This type of program could be strengthened if the location of mortalities could be determined at a finer resolution. For example, if acoustic tags were added to fish with suitable detection arrays, then the mortality events could be tracked to see if a control program at the dam simply moved predation from the dam to a downstream location in the estuary. Note that simply monitoring survival of the incoming fish is insufficient. For example, if the number of returning adults doubled but survival remained the same, then the remaining pinnipeds could have eaten more fish and the survival of adults through the estuary would be unaffected.

Second, because most direct predation by pinnipeds is observable (pinnipeds surface to eat a captured adult salmon), an estuary-wide monitoring program could estimate the total number of feeding events to see if this has declined after a control program is implemented. While this would give a direct estimate of the total predation by pinnipeds, it assumes that other compensatory events do not occur. For example, suppose that a sea lion program reduces the number of sea lions but not other predators. This monitoring could measure a reduction in sea lion predation, but unless it is properly designed, it may not measure an increase in harbor seal predation.

Predation event recorders (Demetras et al. 2016) would also seem to be suitable for this problem. While developed for juvenile salmon, suitable modifications should make these suitable for adult salmon. Then given a sample of adult fish released with these recorders similar to the Wargo Rub et al (2019) study, it may be possible to obtain a direct estimate of predation by pinnipeds (assuming that the pinnipeds do not also eat the recorder), rather than working backwards from harvest.

INFORMATION GAPS

This ISAB review of pinniped impacts was not comprehensive, but we identified important gaps in information about the system-wide and site-specific impacts of pinniped predators on most of the Council's focal fish species (see Information Gaps, Table Appendix C). To date, system-wide quantitative assessments have focused on the impact of California sea lions on adult Chinook salmon and steelhead. Much less is known about the impacts of Steller sea lions (though they seem to be present over a larger fraction of the year) and harbor seals, which are the more important marine mammal predator in Puget Sound (Chasco et al. 2017b). The impacts of pinnipeds on juvenile life stages of salmonids and other focal species are generally unknown. New research, monitoring, and evaluation will be needed to address the effectiveness of intensified lethal culling of sea lions in the geographic area now used as a criterion for sea lion removal under the Marine Mammal Protection Act. A deeper review by the ISAB of these and other information gaps may be needed.

RECOMMENDATIONS

The ISAB reiterates its past recommendations to fill important gaps in our current understanding of the impacts of pinniped predators in the Columbia River (see *Background information*; ISAB 2018-1) and new gaps identified in Table Appendix C.

The ISAB recommends continued investigations of (1) the system-wide impacts of pinnipeds on adult salmonids and other focal fish species, (2) impacts of pinnipeds on juvenile life stages of salmonids and other species, and (3) the effectiveness of intensified lethal culling of sea lions in the geographic area designated for sea lion removal under the Marine Mammal Protection Act.

The ISAB reviewed some of the methods used to measure pinniped impacts. We recommend the investigation of mark-resight sampling methods to estimate total abundance of pinniped predators. Mark-resight estimates will also provide estimates of uncertainty about the abundance. Methods similar to Wargo

Rub et al. (2019) seem ideal for evaluating the pinniped predator control program, particularly if strengthened by a finer resolution of the location of mortalities.

The ISAB recommends continued investigation of new sampling technologies such as the use of accelerometer VHF radio tags (Hatch et al. 2018) to measure predation by individual pinnipeds, predation event recorders (Demetras et al. 2016), and acoustic tags in combination with PIT tags to evaluate predator control programs.

When comparing the relative impacts of pinnipeds and in-river harvest, there is considerable uncertainty in harvest estimates based on creel and catch surveys, and the ISAB recommends further investigation of this issue.

V. EVALUATING PREDATION MANAGEMENT EFFECTIVENESS

Evaluating the effectiveness of predator control programs is a two-step process. First, the magnitude of the problem must be ascertained; second, the effectiveness of control methods must be evaluated.

Methods to estimate the amount of predation (e.g., juvenile salmonids by predatory fish and/or colonial sea birds; adult salmon in the Columbia estuary by pinnipeds) are reviewed elsewhere in this document. Estimates of total predation and the estimates of the total number of predators gives the marginal gain from reducing the population of a particular predator by one individual in one particular time and location. However, marginal gains may fail to reflect the benefits of the control program because of compensatory behavior of the prey (e.g. density dependence) and compensatory behavior of this and other predators (e.g., removing one predator species may increase predation by another; predators displaced by hazing, for example, may move elsewhere but still prey of focal fish species).

Evaluating effectiveness of programs in different geographical regions and/or different life stages of salmon will require the development of "equivalents." For example, one juvenile saved from predation is "worth less" than one adult saved from predation. This issue was discussed in a recent report (ISAB 2016-1).

There are unique features of this system that distinguish it from other predator-control programs. First, juvenile salmon spend only relatively small amounts of time exposed to the set of predators that are of interest compared to their lifespan. Second, predators of interest vary in their spatial distributions and mobility. Some fish are concentrated into specific geographical areas (e.g. reservoirs) through which the salmon are exposed to predation *en* route to the ocean. On the other hand, birds are much more mobile and can rapidly adjust their foraging to take advantage of shifting prey concentrations. Marine mammals primarily forage below Bonneville Dam. A third issue is that many predators are relatively long-lived and respond relatively slowly to control measures.

A. Levels of evaluation of a predator control program

A predator control program can be evaluated at several levels and time frames. At the simplest level and over the shortest term, the number of predators removed or displaced is relatively easy to estimate either by sampling or direct counts. The **marginal** benefit from removal/displacement is also relatively easy to estimate being the product of the number of animals removed/displaced and the average consumption of the predator adjusted for normal survival of the predator. This is the most common approach taken. For example, the northern pikeminnow program estimates the benefit of removals by computing the number of fish "saved" from predation in the next year after removals based on the time of capture of the pikeminnow. A similar estimate could be made of fish "saved" from predation in the year of removal. The number of adult salmon "saved" after removing pinnipeds is also relatively easy to estimate. These marginal benefits may be suitable assuming that predator responses to the control measures operate at much slower time frames and spatial scales (i.e., predators cannot instantaneously reproduce or move from one location to another) and that immediate compensatory responses by salmonids (e.g., responses to changes in salmonid density by reducing predation from a single predator) is also small. At the start of a predator control program, for example, there may be a "standing crop" of large fish that is removed; it takes time for smaller fish to grow into larger fish; smaller fish consume fewer salmonids; so control efforts may immediately reduce total salmon predation at this point in space and time. The northern pikeminnow control program has now been running for almost 30 years, and so the initial marginal effectiveness may no longer be a suitable measure.

The reason why the marginal benefits may not translate into longer term benefits is compensation. There are numerous forms of compensation. In many cases removing predators simply allows other members of the same predator species to fill the empty habitat. In addition, removal of predators may simply allow other individuals to eat more fish because of the reduction in competition among predators, resulting in little or no net benefit of predator control. If predator control efforts are ongoing, the population of predators will move to a new equilibrium. An estimate of total predation by the predator is needed on an ongoing basis to know if predation control effective.

Indirect methods (e.g., measuring whether predator control has shifted the size/age distribution to smaller predators) are often used to evaluate predator control, but unless the total predator population is estimated, it is not possible to know whether a decrease in predator size is not simply offset by an increase in total abundance, so that the overall predation is unchanged. Similarly, an indirect measure of survival may be misleading. For example, an increase in total number of salmon could temporarily swamp predators so the same number of salmon are consumed before or after predator control measures, but the number of surviving salmon is larger due to efforts elsewhere in the Basin.

This problem is particularly true when non-lethal forms of predator control are used. Hazing pinnipeds or removal of bird colonies may simply shift predation from these predators to elsewhere in the system, reducing or eliminating the benefit of control.

Compensation can also occur among predator species. By removing predators, one may create opportunities for their competitors. For example, perhaps removing northern pikeminnow allows smallmouth bass predation to expand in the year of removal (immediate response) and smallmouth bass numbers also to increase over the long term. Marginal estimates of the benefit of predator control will not reflect this shift in predation. Direct evaluation of total predation is more difficult because estimates need to account not only for the controlled species but also for species that occupy similar ecological niches. Fortunately, methods to estimate total predation by a single predator can often be modified to estimate total predation by a suite of predators without major difficulty, although at greater cost. The indirect measure of survival through the area where control measures are taking place will reflect the total impact of the suite of predators but may also reflect the impacts of other sources of mortality and management actions, as noted earlier.

Lastly, compensation can also occur in salmon populations. This is a major problem for estimating the effects of control measures on predators of juvenile salmonids, because much of their life history and mortality is yet to occur. It is a minor problem for estimating the effects of predators of adult salmon just below Bonneville Dam. Accurate estimation of the effects of multiple predators will require measuring responses over larger units of time/space. Accurate estimates of the total number of smolts and their survival through the hydrosystem to Bonneville Dam are needed to measure the impact of predation of all forms and compensation by the juvenile salmon downstream to Bonneville Dam. Estimates of SARs would also include the effect of ocean conditions in addition to predation and other forms of mortality such as from dams. Unfortunately, as noted below, the longer the area/time over which the indirect response variable integrates, the higher the level of noise in the response variable making it harder to detect effects of single mortality factors like predation.

B. Methods to evaluate a control program

SHORT TERM MEASUREMENT OF MARGINAL BENEFIT

As noted previously, marginal benefit may be a suitable way to evaluate a program at the start of the control measures, but the expected marginal benefit may not materialize over the long run.

To evaluate the effectiveness of a management action by measuring its marginal benefit, a type of Before/After/Control/Impact (BACI) statistical design would be used under ideal circumstances (e.g., Michel et al. submitted). Although such designs are unlikely to be suitable for Basin-wide programs (e.g., northern pikeminnow control), they could be useful when predation control is possible on a small part of the system, such as a reservoir where the system is closed with respect to immigration of new predators. As an illustrative example, two side-by-side reservoirs could be used. In one reservoir a predation control program takes place, while it does not in the paired reservoir. Measurements of survival are made in both reservoirs before and after the control program is initiated to evaluate effectiveness. This type of design is most useful for evaluating the effects of local predator control, assuming that predators cannot quickly immigrate to replace removed predators. This design assumes that measurements are available before predation control takes place. However, in many cases such data are outdated or unavailable.

If a control program can be implemented at the scale of a whole reservoir, a paired design with treatment switching could also be used. In this design, a pair of similar reservoirs both containing northern pikeminnow are selected. The control program is implemented in one reservoir but not in the other, which is a control, and the treatments are switched between reservoirs each year. Alternatively, the experiment could be conducted in a single reservoir and the treatment switched within each year. For example, if you could limit the pikeminnow control program to a short period within a year, then a paired-in-time design could be used with salmonid survival as the response variable. In the first period (A, no predator removal), salmon survival is measured across the reservoir. Then, in period B the predator control program starts and removes many pikeminnow, during which salmon survival is measured again. In the next year, you reverse the order. Alternating periods of predator-control and no-predator-control over several years is necessary to account for uncontrolled environmental and biological variables. After a few years, managers will be able to detect if pikeminnow control really increases smolt survival through the reservoir.

Unfortunately, this is not a practical design. Hundreds of anglers catching X number of pikeminnow over 4 months cannot suddenly concentrate their effort and catch the same number of pikeminnow over 2 months for the "impact" period, and then catch no northern pikeminnow over the "control" period. Another problem is that northern pikeminnow may change their predation rate during the two periods. The mean number of salmon eaten per northern pikeminnow before and after the control is implemented could also be measured using a diet composition study similar to the baseline studies (Poe et al. 1991, Vigg et al. 1991), but this again requires a paired design.

LONG TERM MEASURES OF EFFECTIVENESS

All long-term evaluations of effectiveness of predator control will likely use a form of intervention analysis (https://newonlinecourses.science.psu.edu/stat510/node/76/, Larsen et al. in press) , where one of several response variables, such as the number of salmonids consumed by a predator, is monitored before and after implementation of the control program. This would require an extensive sampling program. Indirect measures can also be used, such as for example, survival through a reach, survival through the hydrosystem, or SARs. The problem with indirect measures is that many other variables influence them, so supplementary information is also needed such as the number of smolts that survive to Bonneville Dam and the number of adults that reach the head of the estuary (to separate out pinniped predation). Survival or smolt numbers will reflect the marginal impact of the predator control measures and all forms of compensation. Similarly, survival and the number of adults present at the mouth of the Columbia (see the paper by Wargo Rub [2019]) will evaluate the marginal impact of predator control and compensatory responses.

A response variable that is "local" will have a higher power to detect a local effect of predator control at the expense of being insensitive to compensation elsewhere in the system. For example, removing a large colony of colonial seabirds may increase reach survival where the colony was located, but if birds simply move upstream and change the location of predation, the overall impact on survival is minimal.

The combined danger and strength of intervention analyses is that the response is confounded with other factors that also may change after the control program begins. Because compensation everywhere in the system is measured, it provides a "net" return on investment. However, other events unrelated to the control program may hide the signal. For example, suppose that at the same time as predator control measures are undertaken, the hydrosystem operations change and begin degrading survival. In this case, there may be no net change in survival even though predation control measures are effective because the improvement in survival by controlling predators is masked by degradation in survival from other changes. Or, ocean survival may be lower due to climate conditions, and no-net benefit is seen.

Intervention analysis can be strengthened if suitable covariates are available (e.g., measures of ocean conditions known to be related to ocean survival) and response measures are partitioned into small parts (e.g., survival to Bonneville, survival from Bonneville to estuary, survival through estuary), but this approach will require many years of data from PIT-tagged salmon measured on small spatial scales to be effective.

Intervention analysis assumes the existence of "pre-intervention" values to evaluate against, but these values may not always exist. Weins and Parker (1995) examined different study designs to evaluate environmental impacts from accidents where no pre-accident data are available. They recommended designs where trends over time in impacted (e.g., subject to predator control measures) and control (not subjected to predator control measures) sites are used to evaluate if the trends differ between the two. Larsen et al. (in press) also discuss other ways to evaluate control-impact designs. For example, if a good model exists for the system, then the outcomes from the intervention can be compared to the potential outcomes as predicted by the model.

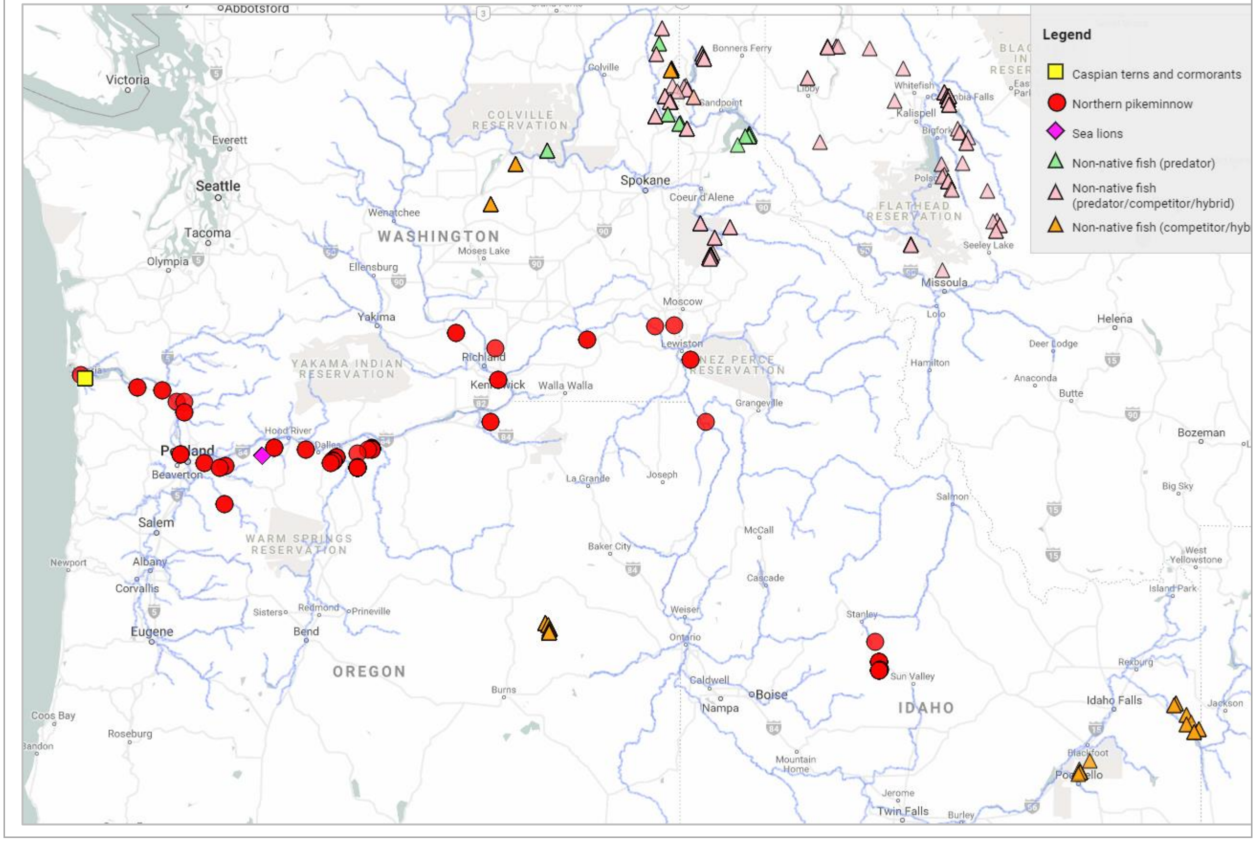
C. Recommendations

Many of the options proposed for experimental design may be difficult, if not impossible to implement. The ISAB believes that the following actions will move the region forward in understanding and, perhaps, controlling predator-prey relationships in the Basin.

- Develop an ecosystem approach to model the effects of compensatory or additive predation. That is, how do all (or major) predators relate to the various life-history stages of focal species and alternate prey?
- As part of the ecosystem approach, redo and expand the work done in the 1980s (e.g., Poe et al. 1991) that is the basis for the northern pikeminnow control and the insufficient monitoring and evaluation of northern pikeminnow, smallmouth bass, and walleye.
- Support the full development of life-cycle models for all focal species.
- Investigate the use of eDNA to more closely estimate numbers of prey consumed by predatory fish and birds.
- Investigate the use of eDNA as a tool for detecting the movement of aquatic predators into and around the Basin.

APPENDIX A. MAP AND TABLE OF PREDATOR AND COMPETITIOR MANAGEMENT AND MONITORING PROJECTS FOR THE FISH AND WILDLIFE PROGRAM

Figure A.1 and Table A.1. Map and list of Columbia River Basin Fish and Wildlife Program projects that between 2006 and 2019 included a work element to remove/exclude predators or competitors as identified in Bonneville Power Administration's CBfish.org project database. Some projects manage nonnative fish to reduce (1) predation and (2) competition and hybridization, and thus are listed twice in the table below. An interactive map is available that shows project information for each icon.



List of Projects

Anadromous zone

Project #	**Title**	**Proponent**	***Primary predator***
2008-004-00	Sea Lion Non-Lethal Hazing	Columbia River Inter-Tribal Fish Commission (CRITFC)	Sea lions
1997-024-00	Avian Predation on Juvenile Salmonids	Oregon State University	Caspian terns and cormorants

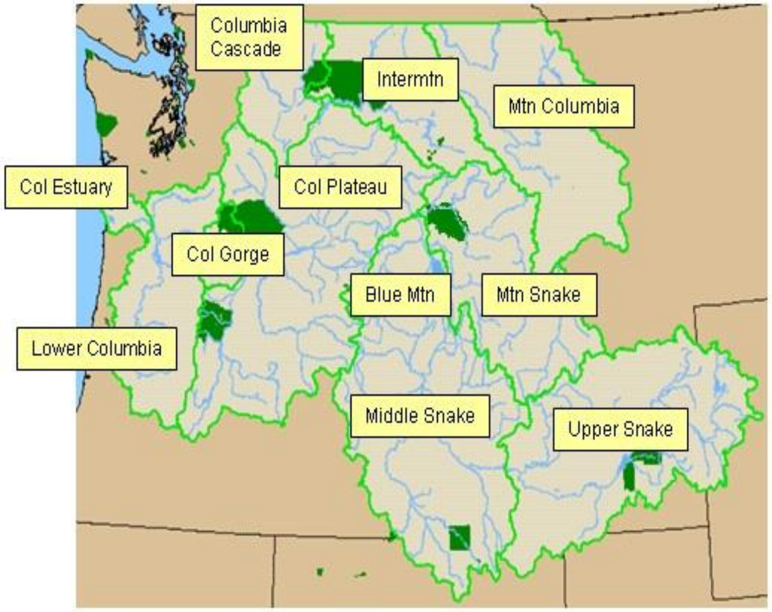
1990-077-00	Development of Systemwide Predator Control	Pacific States Marine Fisheries Commission	Northern pikeminnow
2007-402-00	Snake River Sockeye Captive Propagation	Shoshone-Bannock Tribes	Northern pikeminnow (kokanee - competitor)
Non-anadromous zone (resident fish) - predation			***Primary predator***
1990-044-00	Coeur D'Alene Reservation Fisheries Habitat	Coeur D'Alene Tribe	Nonnative fish (northern pike, etc.)
1991-019-01	Hungry Horse Mitigation/Flathead Lake Restoration and Research, Monitoring and Evaluation (RM&E)	Salish and Kootenai Confederated Tribes	Nonnative fish (lake trout, etc.)
1991-019-03	Hungry Horse Mitigation Habitat Restoration and Research, Monitoring and Evaluation (RM&E)	Montana Fish, Wildlife and Parks (MFWP)	Nonnative fish (lake trout, etc.)
1994-047-00	Lake Pend Oreille Kokanee Mitigation	Idaho Department of Fish and Game (IDFG)	Nonnative fish (lake trout, etc.)
1995-004-00	Libby Reservoir Mitigation Restoration and Research, Monitoring and Evaluation (RM&E)	Montana Fish, Wildlife and Parks (MFWP)	Nonnative fish (northern pike, etc.)
1997-004-00	Resident Fish above Chief Joseph and Grand Coulee Dams	Kalispel Tribe	Nonnative fish (northern pike, etc.)
2007-149-00	Nonnative fish Suppression	Kalispel Tribe	Nonnative fish (northern pike, etc.)
2008-109-00	Resident Fish Research, Monitoring and Evaluation (RM&E)	Colville Confederated Tribes	Nonnative fish (northern pike, etc.)
2017-004-00	Northern Pike Suppression and Monitoring	Colville Confederated Tribes, Spokane Tribe, Washington Department of Fish and Wildlife (WDFW)	Nonnative fish (northern pike, etc.)
Non-anadromous zone - competition and hybridization			***Primary competitor***
1990-044-00	Coeur D'Alene Reservation Fisheries Habitat	Coeur D'Alene Tribe	Nonnative fish (brook trout)
1991-019-01	Hungry Horse Mitigation/Flathead Lake Restoration and Research, Monitoring and Evaluation (RM&E)	Salish and Kootenai Confederated Tribes	Nonnative fish (trout)

1991-019-03	Hungry Horse Mitigation Habitat Restoration and Research, Monitoring and Evaluation (RM&E)	Montana Fish, Wildlife and Parks (MFWP)	Nonnative fish (trout)
1992-010-00	Fort Hall Habitat Restoration	Shoshone-Bannock Tribes	Nonnative fish
1995-001-00	Kalispel Tribe Resident Fish Program	Kalispel Tribe	Nonnative fish (brook trout)
1995-004-00	Libby Reservoir Mitigation Restoration and Research, Monitoring and Evaluation (RM&E)	Montana Fish, Wildlife and Parks (MFWP)	Nonnative fish
1997-019-00	Evaluate Life History of Native Salmonids in Malheur River Subbasin	Burns-Paiute Tribe	Nonnative fish (brook trout)
2001-028-00	Banks Lake Fishery Evaluation	Washington Department of Fish and Wildlife (WDFW)	Nonnative fish (lake whitefish)
2007-149-00	Nonnative fish Suppression	Kalispel Tribe	Nonnative fish (brook trout)
2007-170-00	South Fork Snake River Yellowstone Cutthroat Trout Recruitment and Survival Improvement	Idaho Department of Fish and Game (IDFG)	Nonnative fish (trout)

APPENDIX B. TABLES OF COLUMBIA BASIN NATIVE AND NONNATIVE FISH (ISAB 2011-1)

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	Pisci-vory	Ana-dromy	Hatch-ery		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	+	++		+								

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
	Torrent sculpin	*Cottus rhotheus*	3.4	+	-	-	ABCDEF	+	++		+	+	++	+	+	+	+		+
	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	+	+	+	+		+			+	+		+

Family	**Common Name**	**Scientific Name**	**Special Features**				**Typical Habitat**	**Distribution in Columbia Basin (by province)**											
			trophic level	**Pisci-vory**	**Ana-dromy**	**Hatch-ery**		**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**
Petromyzontidae	River lamprey	*Lampetra ayresi*	4.5	+	+	-	ABG	+	+		+								
	Western brook lamprey	*Lampetra richardsoni*	4.0	-	-	-	AB	+	+		+	+							
	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	+											

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	Pisci-vory	Ana-dromy	Hatch-ery		1	2	3	4	5	6	7	8	9	10	11	12
	Cabezon	*Scorpaenichthys marmoratus*	3.6	++	-	-	G	+											
	C-O sole	*Pleuronichthys coenosus*	3.2	-	-	-	G	+											
	English sole	*Parophrys vetulus*	3.4	-	-	-	G	+											
	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*	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	+											

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
	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	+											
	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	**Pisci-vory**	**Ana-dromy**	**Hatch-ery**		**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	+	+										

Family	Common Name	Scientific Name	Special Features: trophic level	Special Features: Pisci-vory	Special Features: Ana-dromy	Special Features: Hatch-ery	Typical Habitat	Distribution in Columbia Basin (by province): 1	2	3	4	5	6	7	8	9	10	11	12
	Spottail shiner	*Notropis hudsonius*	2.5	-	-	-	D							+	+				
	Fathead minnows	*Pimephales promelas*	2.1	-	-	-	DEF	+	+					+	+			+	+
	Tench	*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						+		+			+	+

Family	Common Name	Scientific Name	Special Features				Typical Habitat	Distribution in Columbia Basin (by province)											
			trophic level	Pisci-vory	Ana-dromy	Hatch-ery		1	2	3	4	5	6	7	8	9	10	11	12
	Atlantic salmon	*Salmo salar*	4.4	+	-	-	AB				+				+	+			
	Brown trout	*Salmo trutta*	3.6	+	-	+	ABCDEF	+	+	+	+			+	+	+	++	+	+
	Brook trout	*Salvelinus fontinalis*	3.1	+	-	+	ABCDEF	+	+	+	+	+	+	+	+	++	++	+	+
	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											+	+

APPENDIX C. TABLE OF ESTIMATES OF PINNIPED PREDATOR IMPACTS ON SALMON, STEELHEAD, AND OTHER SPECIES, AND INFORMATION GAPS.

HS = harbor seals, CSL = California sea lions, SSL = Steller sea lions. CR = Columbia River, UCR = upper Columbia River.

Predator/prey	Scale	Study period	Methods	Results	Information Gaps	Source
CSL/smolt & jack & adult Chinook salmon	Broad scale: West coast of North America; medium scale: regions of west coast; fine scale: Columbia River, System-wide	1975-2015	Bio-energetic, diet, & food web modelling	CSL predation impacts on Chinook in the CR have "increased strongly" over time and exceeded harvest in recent years. Chinook consumed in 2015: HS--14 metric tons (t), 1000 adults (>= ocean age 2), 312,000 smolts; CSL: 219 t, 46,000 adults, SSL: 227t, 47,000 adults.	Need better estimates of abundance of HS, CSL, and SSl in the Columbia River; functional response between salmon and CSL, SSL, and HS unknown; need fine scale estimates by region/season on proportion of Chinook in pinniped diets, and trends in mean length, weight, or energetic content of Chinook; need estimates of competitive interactions between the marine mammals and fishing; need estimates of temporal and spatial availability of Chinook to pinnipeds; need detailed estimates of the escapement and smolt production for wild Chinook stocks; effects of hatchery/wild salmon interactions unknown.	Chasco et al. 2017a
CSL/adult spring Chinook (interior pops.), eulachon, American shad	System-wide: Astoria to Bonneville Dam	2010-2015	Modeling relationship between CSL numbers and salmon survival to infer impact; PIT tags to estimate salmon survival to Bonneville Dam	Estimated 51,751 – 224,705 Chinook died annually in reach between Astoria and Bonneville Dam that could not be accounted for by fisheries (2014: 98,498 (57,200 - 158,520) Chinook; 2015: 224,705 (85,742 – 497,896) Chinook; compared to average annual returns (2010-2015) of wild spawners: 4,450 Chinook for UCR and 33,133 for SR. Fish tagged earlier in spring had lower survival than those tagged later. Non-harvest (pinniped) related mortality of adult Chinook ranged from 20 - 44 % annually. Annual abundance of eulachon and American shad was highly correlated with the annual abundance of CSL in the CR estuary.	Need estimates of number of pinnipeds by species in Columbia River (both intermittent and permanent residents); unknown impacts of other factors (e.g., disease, straying, delayed handling effects); uncertainty in lower river harvest mortality estimates for fin clipped/unclipped fish; pinniped-salmon-fishing gear interactions unknown; need estimates of impact by individual pinniped predator species; harbor seal impacts on jack/adult Chinook salmon unknown.	Wargo-Rub et al. 2019

Predator/prey	Scale	Study period	Methods	Results	Information Gaps	Source
CSL, SSL/adult spring Chinook & steelhead	Systemwide: Astoria to Bonneville Dam for boat surveys; Site-specific: Bonneville Dam for testing accelerometer tags & observing predation events	2012-2017	Functional response analysis to estimate average consumption of salmonids per day; single and tandem boat surveys to estimate CSL abundance; accelerometer tags for remotely estimating predation events	Results are preliminary. Estimated average consumption by CSL below Bonneville Dam is 3.5 to 5.5 salmonids/day; 2017 boat survey data insufficient to estimate pinniped abundance because of sinking of 1 survey boat.	Need to refine methods for estimating sea lion predation on salmonids from boat surveys; total abundance of CSL and SSL outside of Bonneville tailrace unknown.	Hatch et al. 2018
CSL, SSL, HS/adult spring Chinook, summer and winter (s/w) steelhead, Pacific lamprey; white sturgeon	Site-specific, 1/4-mile reach below Bonneville	2002-2017 (two observation periods: Jan-June; fall-winter)	Direct observation of predator numbers and predation events; method for predation estimates changed from stratified random sampling design used in previous years to systematic sampling design in 2017. [1]	2017 (Jan-May): average of 15.4 ± S.E. 1.3 SSLs per day observed; average of 5.1 ± S.E. 0.6 CSLs per day observed; estimated 5,384 (4,671 – 6,042) adult salmonids consumed by pinnipeds (4.7% of all salmonids passing the dam during the season; 4,951 (CI 4,276 – 5,585) spring Chinook (4.5% of the run during January-May.; 322 (144 – 454) s/w steelhead (9.0% of the run during January-May. Range of CSL & SSL impact on interior spring Chinook: 0.3% of run (2002) - 5.9% (2016). s/w steelhead (2017): SSLs consumed 269 (124 – 374) equates to 7.6% of the run; CSLs consumed 53 (20 – 81) or 1.5% of s/w steelhead. No HS predation on focal species observed. White sturgeon (2017): Combined SSL & CSL consumed estimated 24 (24 – 38) sturgeon. Of these, SSLs consumed 20 (20 – 35), and CSLs consumed 4 (4 – 8). Pacific lamprey (2017: estimated consumption by combined CSL & SSL 191 (126 – 256) lamprey. Of these, SSLs consumed 46 (46 – 82), and CSLs consumed 145 (145 – 210).	Not all CSLs are branded, and very few SSLs are branded; no data on subsurface feeding by pinnipeds; prey species consumed sometimes not identified; estimates of predation on lamprey considered minimal due to lack of nighttime observations; need better information on consumption of steelhead kelts by SSL in winter; new NOAA directive is to monitor predation on steelhead in the fall and winter. Mechanisms of dietary shift of SSL from sturgeon to salmonids unknown; stock-specific estimates needed for ESA-listed runs.	Tidwell et al. 2018

Predator/prey	Scale	Study period	Methods	Results	Information Gaps	Source
CSL, SSL, HS/adult spring Chinook, summer and winter (s/w) steelhead, Pacific lamprey; white sturgeon	Site-specific, ¼ mile reach below Bonneville	2002-2018 (two observation periods: Jan-June; fall-winter)	Direct observation of predator numbers and predation events; method for predation estimates changed from stratified random sampling design used in previous years to systematic sampling design in 2017.	2017 Fall & Winter (Aug-Dec): average of 14.5 ± S.E. 1.3 SSLs per day observed; average of 0.2 ± S.E. 0.1 CSLs per day observed; estimated 892 (95%CI 737 – 1,046) adult salmonids consumed by pinnipeds (1.2% of run at the dam during the season; 401 (281-506) Chinook, 0.7% of run; 368 (296-432) coho, 3.1% of run; 123 (63-172) summer/winter steelhead, 1.5% of run; 238 (183-281) white sturgeon; 2018 Spring (Jan-Jun): average of 14.6 ± S.E. 1.3 SSLs and 2.6 ± S.E. 0.3 CSLs per day; estimated 3,112 (2855 – 3,373) adult salmonids consumed by pinnipeds, (3% of run); 2,813 (2,554 – 3067) Chinook (2.9% of run); 295 (227 – 356) Steelhead - Jan. – May (7.2% of run); 159 (140 – 178) Winter steelhead - Nov. – Mar. (6.8% of run); 58 (17 – 91) Pacific lamprey (0.04% of run); 148 (105 – 185) white sturgeon. Increasing impact of SSLs during a year w/near record low runs of ESA-listed winter and summer steelhead and small run of ESA-listed spring Chinook Salmon. Increasing trends in White Sturgeon predation are a concern.	See also above (Tidwell et al. 2018). Mechanism(s) causing increase in recurrence of habitual CSLs at the dam are unknown (increased by 5.3% relative to previous year and number of individuals returning for three or more years increased by 22.8%, even though overall abundance declined 27.1%). Recurrence of SSLs is difficult to monitor given the low numbers of branded SSLs. The value of hazing relative to other predator control methods is questionable; effective alternatives are needed. Potential impact to ESA listed Chum downstream of the dam needs investigation.	Tidwell et al. 2019
CSL, SSL/winter & summer steelhead; marked and unmarked spring Chinook, Pacific lamprey, white sturgeon	Site-specific: Willamette Falls	2014-2018	Direct observation of predator numbers and predation events; randomized spatio-temporal sampling design to estimate total number of adult salmonids consumed by sea lions; predation relative to potential escapement calculated.	Salmonids were most frequently observed prey item (79%), followed by lamprey (12%), sturgeon (8%), and unknown or other fish (1%). CSL accounted for 89% of total observed predation events, but SSL accounted for 100% of observed sturgeon kills. Run-specific CSL predation (minimum) estimates in 2018: 1,950 marked spring Chinook salmon (9% of potential escapement above falls), 466 unmarked spring Chinook salmon (9% of potential escapement), 516 summer steelhead (6% of potential escapement), and 503 winter steelhead (22% of potential escapement).	Need unbiased estimates of local pinniped population size; incomplete spatial and temporal coverage of the target prey populations; fishery-sea lion interactions both above and below Falls, e.g., is sport fishing below the Falls the initial attractant for sea lions? What is the incidental sport catch mortality or illegal catch mortality above the Falls?	Wright & Murtagh 2018

Predator/prey	Scale	Study period	Methods	Results	Information Gaps	Source
CSL, SSL/adult winter steelhead (Willamette populations: N. Santiam, S, Santiam, Calipooia, Molalla)	Site-specific: Willamette falls	2014-2017 data used for 100-yr model	Population viability analysis	Modeling results indicate pinnipeds have a "strong negative impact" on steelhead viability, particularly at the highest (2017) predation rates. Final steelhead mortality estimates are 2014: 521 steelhead, 15% of run, 2015: 395 fish, 14% of run, 2016: 1016, 24% of run. Quasi-extinction probabilities (100-yr period) for "no sea lion" vs highest predation rate (2017): N. Santiam: 0.015 vs. 0.644, S. Santiam: 0.048 vs. 0.599, Calapooia: 0.993 vs. 0.999, Molalla: 0.00 vs. 0.209.	Missing data and incomplete (short) time series of sea lion abundance and predation rates and population-specific data for steelhead necessitate many assumptions about model inputs. Need information on catch and release fishery impacts above Willamette Falls.	Falcy 2017, Data and Code

[1] Tidwell et al. (2018, p. 11) describe a bootstrap procedure to find confidence intervals that requires formal justification. Rather than simply using the 2.5th and 97.5th percentile of the bootstrap distribution, they find the 2.5th and 97.5th percentile of the differences from the observed mean and apply these. Consequently, some of the bootstrap intervals are below 0 – this should never happen in a bootstrap sample.

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