American Shad in the Columbia River: Past, Present, Future

INDEPENDENT SCIENTIFIC ADVISORY BOARD

ISAB 2021-4   OCTOBER 22, 2021

Cover design by Eric Schrepel, Technical and Web Data Specialist, Northwest Power and Conservation Council. Photos of predominately American shad with a few adult salmon intermingled in the Bonneville Dam fish ladder courtesy of the U.S. Army Corps of Engineers.

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

ISAB Members – Authors and Contributors

Courtney Carothers, Ph.D., Professor, Department of Fisheries, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks

John Epifanio, Ph.D., (ISAB Vice-Chair) Former Principal Scientist with the Illinois Natural History Survey and Research Professor with the University of Illinois; now based in Portland, Oregon

Stanley Gregory, Ph.D., (ISAB Chair) Professor Emeritus, Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon

Dana Infante, Ph.D., Associate Professor and Associate Chair of Research in the Department of Fisheries and Wildlife, Michigan State University

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

Cynthia Jones, Ph.D., Eminent Scholar and Professor of Ocean, Earth, and Atmospheric Sciences; Director of the Center for Quantitative Fisheries Ecology; and A.D. and Annye L. Morgan Professor of Sciences, Old Dominion University, Virginia

Peter B. Moyle, Ph.D., Distinguished Professor Emeritus, Department of Wildlife, Fish and Conservation Biology and associate director of the Center for Watershed Sciences, University of California, Davis

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

Kenneth Rose, Ph.D., France-Merrick Professor in Sustainable Ecosystem Restoration at Horn Point Laboratory of the University of Maryland Center for Environmental Science

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

Thomas Wainwright, Ph.D., Retired Research Fishery Biologist, NOAA Fisheries; now based in Bend, Oregon

ISAB Ex Officios and Manager

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

Leslie Bach, Ph.D., Senior Program 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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Acknowledgements

The ISAB gratefully acknowledges the many individuals who helped us complete this report.

Tami Wilkerson and Maggie Willis of the Columbia River Inter-Tribal Fish Commission's (CRITFC) Columbia Basin Fish and Wildlife Library provided an American Shad Bibliography, which helped us frame and initiate our review and explore primary and grey literature.

At the ISAB's September 10, 2021 meeting, Randy Settler, Yakama Nation Tribal fisher, and Stuart Ellis, CRITFC Harvest Management Biologist, provided invaluable overviews of Tribal treaties and co-management roles in Columbia River fisheries, historical American shad fisheries, and perspectives on shad interactions and impacts on salmon, the ecosystem, and fisheries management.

Tucker Jones, Oregon Department of Fish and Wildlife (ODFW), and Quentin Daugherty, Washington Department of Fish and Wildlife (WDFW), provided information and insights on the current management of Columbia River Basin shad fisheries. Charlene Hurst, Dan Rawding, and Ryan Lothrop (WDFW) helped facilitate the dialogue.

Unpublished life history information on shad in the Columbia River referred to in this report is based on specimens collected by Daniel Hasselman, working as a postdoctoral fellow with Thomas Quinn, and analysis of scale and otolith samples by Lisa Wetzel and Kim Larsen (U.S. Geological Survey, Seattle). Our reporting of the data here should be regarded as preliminary, as more complete analysis is ongoing, and a paper is being prepared for submission to a scientific journal.

Data and information about shad in the Columbia River and Pacific Ocean were generously provided by Bill Pearcy (Oregon State University), Kate Richerson (NOAA NW Fisheries Science Center), and Dan Bottom (Oregon State University). The ISAB obtained data on counts of shad and anadromous salmonids, discharge, and river temperature from Columbia River DART (Data Access in Real Time).

Curtis Dotson and David Duval (Grant County Public Utility District) shared observations regarding shad passage and counting at Priest Rapids Dam fish passage facilities.

The ISAB's manager Erik Merrill and Ex Officio members Zach Penney (CRITFC), Leslie Bach (Council), and Mike Ford (NOAA) helped organize our review, participated in briefings, provided context, and commented on drafts. We especially thank Dr. Penney for arranging the Tribal perspectives briefing by Stuart Ellis and Randy Settler, coordinating with the Columbia Basin Fish and Wildlife Library on developing the bibliography, and providing insights from informal dialogue with Tribal fish managers.

We appreciate Eric Schrepel's assistance in designing the cover and Robert Wertheimer, Patricia Madson, and Richard Piaskowski's (U.S. Army Corps of Engineers) help in providing photos.

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Executive Summary

I. Introduction

The American shad (*Alosa sapidissima* – henceforth "shad" in this document) was introduced into the Sacramento River (California) in 1871 from the Hudson River (New York). From this initial introduction, shad colonized the Columbia River, although direct introductions were also undertaken. This rapid expansion was a consequence of their anadromous life history that allowed them to leave their natal river and then, at maturity, establish breeding populations in rivers elsewhere along the coast. Shad colonized upriver reaches of the Columbia River Basin as the hydropower system expanded, using passage facilities provided for native salmonid species. Today shad occur in the Columbia River and major tributaries from its estuary to Priest Rapids Dam on the upper Columbia River and Lower Granite Dam on the Snake River. Shad are now the most abundant anadromous fish in the river, making up over 90% of the recorded upstream migrants in some years. Despite their abundance, few management or research programs have targeted shad. The possible interactions within the Columbia River ecosystem between shad and native fishes, especially salmonids, and between shad and predatory fish, birds and mammals are many but poorly understood. Ultimately, the extent and impact – on balance – of any interactions have yet to be established with a robust analysis of empirical data.

Not surprisingly, the continued upward trajectory in shad abundance has created potential challenges for managing fishery resources and applying mitigation actions. The extent of these challenges on management of shad, salmon, and other native species is also not well understood. Therefore, improved understanding of the biology of shad and its influences on native species and food webs in the Columbia River Basin is needed to inform management decisions. In this light, the Independent Science Advisory Board (ISAB) was asked to review the current state of knowledge about shad in the Columbia River ecosystem and to make recommendations for improving research and management. The ISAB was asked the following questions:

1. What are the trends in shad abundance in the Columbia River Basin? What are the potential ecological effects of the shad on aquatic communities of the Columbia River and nearshore Pacific Ocean? Answering the second, larger question requires investigation into several more specific questions, including:
    - What is known about the life cycle of shad in the Columbia River Basin in freshwater, estuary, and ocean stages? Are there multiple life history strategies?
    - What risks do shad present to anadromous salmonids and freshwater biotic communities?

    - Do shad magnify predation on juvenile salmon and steelhead by maintaining a larger population of predators, or do they reduce predation by being an alternative food source?
    - Do shad change freshwater and marine food webs through competition, carcass decomposition, or indirect food web effects?
    - Does shad abundance create significant operational problems for the hydropower system of the Columbia River Basin, especially in relation to salmon and steelhead passage?

2. Based on the answers to these questions, should management of shad in the Columbia Basin be changed? If so, what management alternatives should be considered?

We first review the state of knowledge on shad in the Columbia River Basin, present new analyses by the ISAB on the influence of ocean conditions on shad, population dynamics of shad in the Columbia, and the influence of temperature and discharge on timing of adult shad migration, and then use this information to address the questions posed above. This review is followed by recommendations related to the research and management of shad in the basin.

II. History

The success of shad introductions and the rapid expansion of the shad's range along the Pacific Coast can be explained by understanding some basic facts about their biology:

1. The physiology of shad enabled rapid acclimation to the conditions of West Coast rivers. Shad tolerate a wide range of temperature, flow, turbidity, salinity, and other aspects of water quality and quantity.
2. Their anadromy and their low-level propensity to stray among rivers allow them to move from one basin to another, up and down the coast.
3. Their broadcast spawning behavior, high fecundity, and semi-demersal embryos, which float just off the river bottom, allow them to spawn in or above river reaches with high sediment loads. They also engage in serial spawning in which release of gametes takes place in pulses, with each pulse of spawning individuals moving downstream to "fresh" spawning habitat.
4. Their dispersal seems to be facilitated by the often favorable, if complex, set of ocean conditions.
5. The series of hydropower dams and reservoirs in the Columbia River Basin has created near-optimal conditions for shad passage, spawning, and rearing.

III. Shad in their native range

Shad are one of the most studied fish on the Atlantic Coast, research which provides insight into the biology of shad on the Pacific Coast. Paradoxically, while Pacific Coast shad have thrived and increased in abundance in recent years, the Atlantic Coast populations have decreased in abundance. This section, therefore, provides a brief introduction to the biology of shad in the Atlantic Seaboard and compares that information with what is known about Columbia River shad, the main focus of this report.

IV. Shad in the Columbia River Basin

Abundance

Shad were not particularly abundant in the Columbia River until Bonneville Dam (at river km 234) created reservoir habitat that seemed near-optimal for spawning and rearing. However, the biggest boost to shad populations came after completion of The Dalles Dam (river km 308) in 1957, which flooded Celilo Falls, previously a barrier to the upstream migration of shad. Shad are now found upstream of Lower Granite Dam on the Snake River (river km 695) and Priest Rapids Dam (river km 639) on the Columbia. Shad numbers have generally increased over the decades with nearly 8 million adult shad estimated to have moved up the river in 2019, with an average of over 2.2 million shad in 1992-2003. The shad in this period constituted 70-80% of the runs of anadromous fish.

Genetics

Shad in the basin are uncommonly genetically diverse for a population founded with a small number of colonists. They also have diverged from the source populations. Moreover, the presence of genetic differentiation across Pacific Coast populations suggests that some metapopulation structure has developed in the 150 years since founding. This broader structure is attributable to the homing behavior that followed initial colonization.

Physiology and climate change

The range of behaviors and reproductive strategies documented for shad, especially in Atlantic Coast populations, reflects a robust and plastic physiology that allows them to thrive across climate regimes and to migrate through and live in environments from freshwater to marine. Preferred ocean (Atlantic) temperatures are generally observed between 13-18^o C. Warming conditions in ocean, estuary, and river habitats predicted by climate change models for the Pacific Coast will probably favor shad because of their tolerances for warmer water than salmonids. Shad have been recorded living in freshwater at temperatures ranging from 2.2^o C to 35^o C, although preferred temperatures seem to be in the 16-20^o C range when most migration takes place.

Life history patterns

In their native range (and in rivers of the Pacific Coast as well), shad spawn in spring or early summer, influenced by rising water temperatures and flows. The fertilized eggs become embryos that float just off the bottom (semi-demersal), drifting downstream to favorable rearing habitats that include reservoir pools. Following hatching, young-of-the-year remain in the river for up to a year but generally enter marine waters in the fall, spend several years at sea, and then return in spring or early summer to spawn. In the Columbia River Basin, shad have a high proportion of first year spawners, so they are generally younger at maturity and smaller for a given age compared to shad in their native range.

In addition to the typical anadromous life history pattern, West Coast shad display a life history variant that has increased residence time in freshwater and is known locally as “mini-shad.” These fish are larger than expected for young of the year, but also too small to be mature adults. Mini-shad include both males and females and one and two-year-old fish. Some juveniles spend an additional year in freshwater or the estuary before going to sea, while others do not go to sea at all. Mini-shad are routinely sampled downriver. Unlike salmon jacks or other precocial life histories in fishes, a mini-shad is not a terminal life history pattern. Adults in the Columbia River Basin include individuals that have transitioned through a mini-shad stage.

Ocean ecology

Shad are found in marine waters along the West Coast primarily from central California north to Vancouver Island, mainly over the shallow (50 to 150 m depth) continental shelf, consistent with depth distributions in the Atlantic. The highest concentrations of shad are in two areas: from central Oregon to Vancouver Island and along the central and northern California Coast, corresponding to the two largest river populations. There is some evidence of northward migrations in spring and summer, but nothing comparable to the long north-south migrations reported for shad along the Atlantic Coast. Relationships of catch to both sea-surface and bottom temperatures show that shad are caught in salmonid sampling programs at a wide range of temperatures, but that the largest catches occur at surface temperatures of 13° to 17° C (warmer than most areas sampled) and at bottom temperatures of 6.4° to 8.0° C (cooler than most areas sampled). Both surface and bottom temperatures are strongly correlated with latitude, and this inverse surface-bottom pattern is consistent with the largest catches being north of 44° N. Correlations between two marine abundance indices and adult counts at Bonneville Dam also indicate that shad abundance north of 44° N tracks Bonneville Dam counts in the same year. Our analyses suggest that shad populations are favored by warmer ocean conditions.

Ocean diets of juvenile shad have received little attention, but it is highly likely that they are similar to the diets of juvenile coho (*Oncorhynchus kisutch*) and Chinook salmon (*O. tshawytscha*), which feed on epipelagic invertebrates and larval fish. Prey consumed, however, varies with availability. Stable isotope analyses of adult shad show they forage in waters over the continental shelf, rather than the open ocean. Overall, shad feed at a trophic level comparable to post-smolt and sub-adult salmon. Thus, trophic competition at sea is possible, although the prey base is shared with many other fishes such as Pacific herring that are much more numerous than shad.

Adult shad migration

Upriver migration for spawning occurs in spring and is closely linked to rising water temperature and decreasing river discharge. Specifically, shad migrate earlier in warmer years than in cooler years. In papers stretching back 50 years, 60° F (15.5° C) has been used as a convenient index of spring warming on the Columbia River, and the date each year when this temperature is first reached is correlated with shad migration timing (though the peak migration occurs later, at ca. 18° C). After decades of advancing spring warming, temperatures have been reaching that 15.5° C value at a similar time in spring in recent years, so the shad are migrating at about the same time of year (from 2011 to 2020 the median migration date averaged

16 June). This timing is important for considering ecological effects of shad on salmon because larval production follows shortly after migration and spawning, allowing estimates of the spatial and temporal patterns of adult and larval abundance in the river system.

Because water temperature in the Columbia River during spring and summer migration is also significantly related to discharge, the spring upriver migration of shad coincides with peak flows from snowmelt in headwater tributaries along with spring precipitation. The majority of adult shad migrate up the Columbia River from mid-April through the end of August, although adult shad have been observed passing Bonneville Dam from April through early November. River regulation has substantially modified the annual hydrograph, decreasing peak discharges during spring and early summer and increasing flow from November through March during fall and winter seasons. Maximum outflow from Bonneville Dam in the spring decreased from the 1940s to the late 1970s, remaining fairly consistent from 1980 to the present although the day of the year when maximum daily outflow has occurred continues to occur earlier. Peak outflow from Bonneville Dam now occurs approximately 25-30 days earlier than in the mid-20th century which is consistent with the general change in timing of the peak of adult shad returns. In 1950-1970, average adult shad return peaked in early July approximately 25 days after the peak discharge period. In 1980-2020, average adult shad returns peaked in mid-June approximately 20 days after the peak discharge. Flow modification has affected the aquatic communities and anadromous fish species of the Columbia River and obscures the effects of climate change on streamflow below dams. A recent model of climate change effects on Columbia River discharge indicated that the timing of peak flows will shift even earlier, to mid-May, by 2099. Such changes in the hydrology and thermal regimes could influence shad migrations further and have major implications for their interactions with anadromous salmonids and native aquatic communities.

Juvenile shad migration

After spawning below the tailraces of large dams, embryos and larvae experience favorable conditions (specifically in terms of temperature and food supply) in the reservoirs and estuary, especially along the edges and in backwaters. Juveniles likewise find the slowly moving waters of reservoirs favorable for rapid growth and high survival, partly because they move to the bottom during the day, thereby avoiding predation, and then move higher in the water column at night where zooplankton are abundant. They move downstream in September-November and then enter the ocean as large juveniles.

Population dynamics

The adult shad population above Bonneville Dam has increased over the last 60 years from fewer than 100,000 per year in 1960 to a recent (2019) peak of nearly 8 million adults. Prior to 1960, shad counts at Bonneville Dam were below 100,000. To consider population changes in different parts of the basin, we subdivided the destination of returning adults into three sub-basins): mid-Columbia (Bonneville to McNary), upper Columbia (above McNary excluding passage above Ice Harbor), and Snake (above Ice Harbor). Almost all shad spawned in mid-Columbia until the mid-

1970s when an increasing fraction began passing above McNary Dam. The mid-Columbia segment has remained dominant up to the present, although the upper Columbia run has equaled or exceeded the mid-Columbia in a few years (1977, 1982, 2015–2018). Returns to the Snake River remained negligible until the late 1980s when they began to increase, with a peak of about 800,000 adults in 2018. Looked at another way, the proportion of the total run in each sub-population gradually increased from the early 1960s until the mid-1970s. After that the proportions have fluctuated, with the upper Columbia run exceeding the mid-Columbia run in two years. The Snake River run remained very low until about the year 2000, after which it has been an increasing portion of the total.

Overall, we estimate the population growth rate at about 4.7% per year, with no indication that the population has reached an abundance limit. However, there are large fluctuations above and below the average trend line. To explore these variations, we computed an approximate index of recruits per spawner by using the total run size in a given year as spawners (S_t) and computing recruits (R_t) as the average of the run size 4 and 5 years later. The lag in recruits corresponds to the primary return ages of shad in the Columbia River Basin; most returns in the basin are at ages 4 or 5. The R/S index has a geometric mean of 1.49 — a nearly 50% increase in numbers every generation from 1938 to 2020. However, R/S exhibits considerable fluctuation over time, and much of the average R/S is accounted for by the rapid increase in the late 1950s (peak R/S = 47.8 in 1959) shortly after completion of The Dalles Dam. Basic time-series statistics computed for the R/S series suggests similar environmental controls affect both salmon and shad populations, although a positive autocorrelation in R/S will at least partially result from the population age structure (multi-age spawning). However, ocean conditions appear to affect more strongly salmon populations than shad populations.

A major cause of the increases in the Columbia River Basin shad population has been changes to the river's hydrology associated with construction of mainstem hydropower dams. Completion of The Dalles Dam allowed access to substantial upstream habitat and completion of John Day Dam provided a large area of additional reservoir habitat, resulting in a further increase in shad production. The fraction of shad passing upstream of McNary Dam is positively related to river temperature and discharge, which were both affected by the major expansion of reservoir storage volume since the 1950s.

Nutrient addition

The large number of shad spawning in the Columbia River indicates that they are likely an important source of nutrients for the river ecosystem. However, many factors complicate this likelihood, including observations that most shad do not die immediately after spawning and that juveniles could be exporting large quantities of nutrients when they leave the basin. Marine-derived nutrients from shad account for a very small fraction of the available nutrient concentrations in the mainstem river. Background nutrient loading and flux in the Columbia River ecosystem are not well understood, and there is no evidence that nutrients are a major limiting factor for shad populations.

Interactions with other species

The rise to extreme abundance of shad has led to speculation that they adversely affect native fish populations, including salmonids. These impacts are thought to come through competition, predation, increased disease, or some combination of these processes in tandem with effects of habitat loss, dam operations, pollution, other non-native species, and other factors impacting native fishes. The emphasis of studies of juvenile shad has been on their positive and negative effects on juvenile Chinook salmon, usually through competition for invertebrates. However, shad also are abundant prey for birds, fishes, and marine mammals in the river, estuary, and ocean. The questions about these interactions are largely unexplored and include: How important are shad as prey for the array of potential predators? Do shad serve as a buffer, reducing predation on salmon (*Oncorhynchus* spp.*)* and steelhead (*O. mykiss*) when shad are abundant? Does predation on juvenile shad maintain a larger predator population than would otherwise exist? Similarly, do adult shad allow larger populations of pinnipeds to be present year-round than there would be without them, thus indirectly increasing predation on salmon and other species? Does predation on juvenile shad decrease their abundance sufficiently to increase the abundance of zooplankton and insects so growth of juvenile salmon is improved? Predation on shad by resident piscivores (e.g., northern pikeminnow [*Ptychocheilus oregonensis*]) seems to be related mainly to shad abundance, suggesting that predation has little impact on juvenile or adult shad numbers. Despite their potential importance, these interactions of shad are poorly studied and understood.

Other interactions

Parasites and disease organisms are present in shad, but their effects on native species are unknown. Thiamine deficiency has been proposed as a possible problem for predators on shad, including salmon, if they consume too many juveniles, but there is little evidence to support this effect. Shad are part of complex ecosystems with many possible food web interactions that may work collectively to favor shad and cause salmon populations to decline.

V. Fisheries

Overall

Shad were introduced to the West Coast because of their enormous popularity as a food and sport fish on the East Coast. On the West Coast today, they are no longer preferred by consumers to any significant extent given the wide availability and variety of other food fish. As a result, the small commercial fishery that existed in the river in the 1970s has given way to a sport fishery. Among the many reasons a more robust commercial fishery has not developed in the basin is that gillnets and other presently used commercial gear also capture endangered salmonids. Alternative gear types are being explored.

Tribal fisheries

The multiple Tribal perspectives are of central importance in assessment of ecological and social impacts or benefits of shad populations in the Columbia River. They also are important for assessing the current or potential fisheries for shad. To date, no formal presentation of Tribal perspectives has been released. Tribal catches of shad are occasionally sold to wholesalers in small quantities, but in general there is little market for them.

Overall, there seems to be little interest in shad for Tribal fisheries, despite their abundance. This appears to be the result of poor markets for shad, the difficulty of getting them to the markets quickly, and by-catch of salmon in shad fisheries. Moreover, shad do not have a long-standing cultural role among Tribes within the basin.

VI. Shad and the Hydropower System

The chain of hydropower dams and reservoirs is largely responsible for the abundance of shad, an unexpected result of the development. Management is minimal, compared to salmonids, because shad seem to be doing well without it and because there is little interest in them from fisheries, cultural, or ecological perspectives. Aside from shad over-crowding fishways at times, they seem to have little effect on hydropower operations.

VII. Answers to Assigned Questions

1. What are the trends in American shad abundance in the Columbia River?

Before 1957, shad counts were generally below 20,000 adults per year at Bonneville Dam. After The Dalles Dam was built (1957), apparently facilitating upstream access, numbers rose to over 1 million per year, with nearly 7.5 million shad estimated in 2019. Since 1960, shad have increased at an average rate of about 5% per year. Continued monitoring of shad numbers passing the dams in the Columbia River and major tributaries is essential.

2. What are the potential ecological effects of shad on native aquatic communities of the Columbia River and nearshore Pacific Ocean?

There are many plausible ways in which shad might affect salmonids and other fishes. The very large numbers of non-native shad suggest long-term negative effects, but the nature of those effects, if indeed they are present, remains to be discovered.

3. What is known about the life cycle of shad in the Columbia River System freshwater, estuary and ocean habitats?

We have some understanding of the freshwater portions of the life cycle of shad, but our understanding of their use of other habitats by different stages of the life cycle is very limited. As part of this review, the ISAB conducted new analyses of the influence of ocean conditions on shad, the population dynamics of shad in the Columbia over the last 60 years, and the influence of temperature and discharge on timing of adult shad migration from 1938 to 2020. This new information should be useful for fisheries managers in the basin.

4. Are there multiple life history patterns?

Most shad move out to sea in fall of their first year of life, and rear in the ocean for several years before returning to spawn. A distinctive alternative is mini-shad, which spend at least a year in freshwater before going out to sea. Mini-shad can return as fully grown fish. The proportions of repeat spawning individuals of both life history types are poorly known.

5. What risks do shad present for anadromous salmonids and freshwater biotic communities?

The risks (or benefits) of shad to salmonids are largely unknown, and more conclusive analyses are needed to understand these relationships. There is some model-based evidence that adult spring Chinook salmon survival rates increase when shad numbers increase. The reasons are not clear but may involve either shad buffering predation by sea lions or the two species having a common response to changing conditions.

6. **Do shad magnify predation on juvenile salmon and steelhead by increasing the food supply for their predators or do they reduce predation by saturating the predators?**

There are insufficient data to demonstrate either of these possible effects, and few studies collect the kinds of data needed to answer the question.

7. **Do shad populations change the freshwater and marine food webs through competition, carcass decomposition, or indirect food web effects?**

The limited evidence does not support the idea that shad are causing major changes to food webs. However, the lack of information hampers our ability to address this question fully. Importantly, the distribution of spawning by shad is skewed towards the lower portion of the basin, and juveniles feed and migrate later than most juvenile salmonids. Consequently, the likely scope for interactions is uneven among salmonid species, and among regions of the basin.

8. **Does shad abundance create significant problems for the hydropower system of the Columbia?**

We could find no evidence that hydropower managers regard shad as a major problem in terms of interfering with their operations.

9. **Based on the answers to these questions, should management of shad in the Columbia Basin be changed? If so, what management alternatives should be considered?**

Current evidence is inconclusive as to whether shad are having a negative, positive, or mixed net effect on salmon and other biota. Current management is passive because shad continue to be abundant but are of low value in fisheries. There are few restrictions on their harvest. We cannot recommend specific management alternatives based on current information.

VII. Conclusions

American shad are the most numerous anadromous adult fish in the Columbia River, far surpassing the numbers of salmon and steelhead that are so important in fisheries and as endangered species. Given their abundance and biomass, it is surprising how little we know about them. Their sheer numbers suggest there should be interactions with other fishes and with the birds and mammals that prey on them. However, the limited studies available do not identify clear interactions between shad and salmon or the role of shad in major ecosystem processes. A systematic, multi-year research program would be needed to address the questions posed in this document and to improve our understanding of the direct and indirect interactions of all life stages of shad with all life stages of anadromous salmonids, as well as with other organisms.

Future interactions between shad, salmon, and other parts of the Columbia River ecosystem will keep changing as temperatures increase, river flow regimes change, and sea-levels rise – changes that will likely lead to further native species decline while favoring some non-native species, like shad. The future of shad right now looks bright in the Columbia River Basin which should continue to provide near-optimal habitat for shad spawning and rearing in the chain of flow-through reservoirs. A warmer climate will likely favor shad over salmonids, although much depends on the continued productivity of the river and reservoirs, the estuary, and, above all, the ocean. The winds and currents that create this productivity are likely to become even more erratic, so populations of shad and other fishes (and of everything that preys on them) are likely to show wide and unpredictable fluctuations.

IX. Recommendations

Given the current state of knowledge about shad in the Columbia River Basin, a number of critical uncertainties could be addressed by a focused shad research and monitoring program. Continued monitoring of shad numbers passing the dams in the Columbia River and major tributaries is essential. Climate models predict that the basin and near ocean will experience climatic warming, hydrological changes to the basin will continue, and increasing shad abundances show no indication of having reached a plateau. These emerging issues and potential risks warrant increased attention by resource managers in the Columbia River Basin to address uncertainties about possible shad effects on declining native species.

Such a program might benefit from a formal scoping process among management agencies and other stakeholders to identify and prioritize the critical uncertainties to be addressed, recognizing the merits and explicit costs of competing research priorities in the basin. In the interim, we recommend starting with a short-term [ca. five-year] goal of describing fundamental life-history patterns of the species in the Columbia River Basin: age-structure, habitat utilization (in time and space), survival rates, primary predators, and prey.

Longer-term goals should include understanding the role of shad in freshwater, estuarine, and marine food webs as a basis for understanding direct and indirect interaction with native species, especially salmonids, eulachon, piscivorous birds, and marine mammals. A program like this could form the basis of adaptive management decisions, such as developing commercial and Tribal fisheries, building fish ladders that exclude shad, or developing shad removal programs to benefit salmon and other fishes among others. This will require not only data collection but the use/development of predictive life history models, starting with a general conceptual model of shad use of the Columbia River Basin.

Prior to developing extensive field studies or experiments, modeling might be a prudent and cost efficient first phase of analysis. Such modeling could provide the basis to evaluate the potential importance of interactions between shad and anadromous salmonids and other native species. Multispecies models (such as

Models of Intermediate Complexity or MICE) are question-driven and contain a limited number of components and ecological processes. Specifically, the models might address whether shad either increase predation on salmon or act as a buffer that reduces predation. Another promising approach is bioenergetic modeling. Manipulation of the abundances of shad and salmon, and the degree to which they interact, in these or other model simulations could enable an initial assessment of which interactions may be ecologically and economically important.

Though the specific ecological effects of shad are unknown, their potential risks for the ecosystem and anadromous salmonids warrant caution and continued attention. At the very least, managers should continue to monitor shad numbers at the dams, and existing projects that encounter shad should capture information to the extent practicable. Focused studies and modeling, as described in this report, could substantially improve our understanding of the biology of American shad and its potential impacts. The ISAB appreciates that continued counting of shad at dams and new research involve costs at a time when many competing research and management priorities in the basin face critical funding limitations. The Council, BPA, and other managers will need to consider both the potential benefits of efforts to better understand shad as well as the costs of such efforts to balance alternative demands on available resources. Research and monitoring to better understand shad may not be the most important management issue for the Fish and Wildlife Program, but continuing to ignore the role of shad in the Columbia River increases future uncertainties. Strategic assessment and evaluation could provide critical information for decision makers and managers in the future if shad populations continue to increase.

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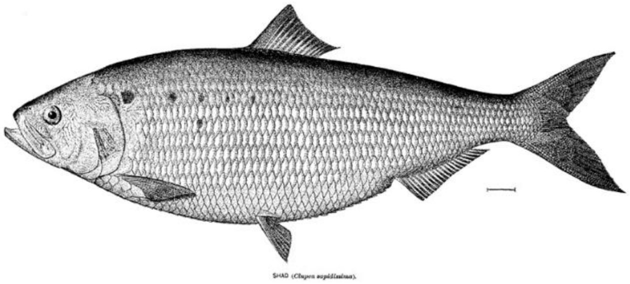

Drawing from H.M. Smith (1896)

I. Introduction

The introduction of American shad (*Alosa sapidissima* – henceforth "shad" in this document) to the United States' West Coast was among the nation's most successful fish introductions in the 19th century. Shad were initially introduced into the Sacramento River (California) in 1871 from a Hudson River (New York) source (Hasselman et al. 2012a, b). From this initial introduction, shad quickly colonized additional rivers and expanded their range coastwide. Shad have been observed from southern California northward and around the Pacific Rim to Russia although the range of self-sustaining populations is more limited. Although most shad home to their natal river, this rapid expansion was a consequence of their anadromous life history that allowed them to leave their natal river and then, at maturity, establish breeding populations in rivers elsewhere along the coast (Waters et al., 2000, Hasselman et al. 2013 and references therein).

The shad's current Pacific Coast range is primarily from the Sacramento River in the south to the Columbia River in the north, with infrequent occurrences farther north along the coast and into the Salish Sea (Welander 1940). In the Columbia River, observational records indicate that shad became established by the mid-1880s, initially from the original Sacramento River founding population but also from later, separate introductions into the Columbia River Basin. Shad colonized upriver reaches as the hydropower system expanded, using passage facilities designed to benefit native salmonid species. While today shad occur primarily in the Columbia River below its confluence with the Snake River, they have been counted at Priest Rapids Dam on the upper Columbia River and Lower Granite Dam on the Snake River. There is evidence that in addition to distance, upriver distribution is limited by the configuration of certain fish ladders because shad avoid submerged entrances, for example at the Priest Rapids Dam fish ladder (e.g., Monk et al. 1989). Regardless of the explanation for their distribution within the basin, shad have become the most numerous anadromous species in the river – comprising over 90% of the upstream migrants counted at lower river dams in some years.

Despite their abundance in the Columbia River Basin, few management programs have targeted shad. In the 1990s, state, Tribal, and federal authorities called for exploring potential control actions to reduce potential interactions between shad and salmonids. Specifically, one of the tasks laid out by the Snake River Salmon Recovery Team under the heading of "predation/competition" was for "reducing [the] shad population" to limit interactions with sockeye (*Oncorhynchus nerka*) (Bevan et al. 1994, Table A-5). Moreover, the 1994 Columbia Basin Fish and Wildlife Program included a measure to "Explore the population ecology of shad to determine effective methods for control and develop programs to eliminate shad from the Columbia River system above Bonneville Dam and reduce the shad population below Bonneville Dam" (Northwest Power and Conservation Council 1994, p. 5-45). Likewise, the 2004 lower Columbia subbasin plan called for reducing shad abundance to a range of 700,000 to 1,000,000 adults (Lower Columbia Fish Recovery Board 2004, p. 3-111). The rationale for such actions appears to be largely speculative, given the paucity of directed research or monitoring data and analyses, and ultimately, concerted reduction efforts have not been pursued.

The web of possible interactions within the Columbia River ecosystem between shad and native salmonids is expansive. Interactions with individual species might be beneficial, deleterious, or neutral, depending on the life history stages of each species, their habitats, and other variables. The net impact of shad presumably depends on the salmon and shad lengths and weights, life-cycle stages, seasons, river locations, and relative abundances. Therefore, determining the net impact to the Columbia River Basin ecosystem has proven challenging. As detailed in this report, for example, planktivorous shad may compete directly with juvenile salmon for food, but they may also be a food source for juvenile and adult salmon, as well as for white sturgeon, birds, and mammals. Moreover, it has been suggested that young shad buffer juvenile salmon and other native fishes from predation in the river, estuary, and ocean, and that adult shad also buffer returning adult salmon from sea lion predation in the lower river. However, in the latter case it would seem unlikely that adult shad weighing 1-2 kg each could easily substitute for adult Chinook salmon that weigh 9-15 kg each, unless they were remarkably easier to catch.

Adult migrants may transport ocean-derived nutrients upriver and release these following their death. Yet, shad may be so abundant that their oxygen consumption in fish ladders may stress upstream migrating salmon. Ultimately, the extent and impact – on balance – of any interactions have yet to be established with a robust analysis of empirical data. Thus, a central, unanswered question relates to the shad's effect on individual native species and the Columbia River ecosystem as a whole: are shad beneficial, deleterious, neutral, or mixed?

In addition to the challenges of understanding the uncertain and complex ecological interactions between shad, salmon and other fishes and wildlife, the recent upward trajectory in shad abundance has created practical challenges for managing fishery resources and mitigation actions. The extent of these challenges and their impacts on management of shad, salmon, and other native species is not well understood or addressed in basinwide reports. Therefore, improved understanding of the biology of shad and its influences on species and food webs native to the Columbia River Basin could help inform management decisions.

Because of the uncertain role of shad in the Columbia River ecosystem and their potential interactions with native anadromous fishes (salmonids, white sturgeon [*Acipenser transmontanus*], Pacific lamprey [*Entosphenus tridentatus*], and eulachon [*Thaleichthys* *pacificus*]) are not well understood, the Independent Science Advisory Board (ISAB) was asked to review the current state of knowledge about American shad in the Columbia River ecosystem.

Specifically, the ISAB was asked to address the following questions:

1. What are the trends in shad abundance in the Columbia River and what are the potential ecological effects of the shad on aquatic communities of the Columbia River and nearshore Pacific Ocean? Answering the second, larger question requires investigation into several other more specific questions, including:

    - How thoroughly do we understand the complete life cycle of shad in the Columbia River: spawning locations, juvenile residence in freshwater, timing of outmigration, ocean residence, freshwater, marine survival rate and life history patterns?

    - What risks do shad present for anadromous salmonids and freshwater biotic communities (e.g., food web effects, predation, disease, habitat utilization)?

    - Do shad magnify predation on juvenile salmon and steelhead by maintaining a larger population of predators, or do they reduce predation by being an alternative food source?

    - Do shad populations change the freshwater and marine food webs through competition, carcass decomposition, or indirect food web effects?

    - Does shad abundance create significant operational problems for the hydropower system of the Columbia (e.g., accurate counting of salmonids)?

2. Based on the answers to these questions, should management of shad in the Columbia Basin be changed? If so, what management alternatives should be considered?

As with other successful species introductions and invasions, some basic examination of a novel species' pathway to success and its general biology in their native range frames the understanding of its biology – and effects – in the expanded range. Therefore, in this report, we first review the state of knowledge on shad in the Columbia River Basin and then use this information to address the questions posed above. During the course of this review, the ISAB conducted new analyses of the influence of ocean conditions on shad, the population dynamics of shad in the Columbia River over the last 60 years, and the influence of temperature and discharge on timing of adult shad migration from 1938 to 2020. This review is followed by recommendations related to management in the basin and identification of research needed to address critical uncertainties.

II. History of Shad on the West Coast of North America

The colonization and western expansion of the United States, especially during the Gold Rush of the 19th century, brought invasions of white settlers to California and then other territories, mostly from the eastern part of the country. Unlike the Indigenous Native American societies for whom these lands were home, these settlers were unfamiliar with the native biota and thus brought familiar eastern species to the West (Moyle 2020). Furthermore, during this era of natural resource exploitation, "acclimatization" societies emerged to bring eastern species west and vice versa. High on the list of species to translocate west was American shad, famous for its culinary qualities and abundance. McPhee (2002) describes the historic importance of shad first to the Indigenous Peoples of the East Coast and then to the European colonists. He notes that George Washington's wealth was based in good part on his control of the Potomac River shad fishery.

The first shipment of shad to California was made possible by the completion of the transcontinental railroad in 1869. In 1871, Seth Green, with considerable difficulty, nursed 8-gallon milk-cans of juvenile shad from a Hudson River hatchery by train to California, where an estimated 10,000 were released into the Sacramento River (Dill and Cordone 1997). In the next 10 years, another half-million shad fry were also imported and released, but that first shipment appears to have been quite successful. Well-curated records are scarce, but an angler caught an adult shad in Monterey Bay in 1873 (Dill and Cordone 1997). Shad had spread to the Columbia River on their own from the Sacramento River within 5 years and were caught there as early as 1876 or 1877 (Smith 1896). In 1880, shad were being captured in the Columbia River by the ichthyologist David Starr Jordan, who sent a specimen to the Smithsonian Institution where it is preserved to this day. There were reports of adult shad spawning in the Columbia in 1885 (Petersen et al. 2003). By 1896, shad were captured above The Dalles, 192 miles upstream from the mouth of the Columbia River (Smith 1896).

Artificial propagation or stocking of shad has been extremely limited in the Columbia River. The first direct shipments of shad from the Atlantic Coast to the Columbia River came in 1885 and 1886 (Smith 1896). The United State Fish Commission attempted to ship 900,000 shad fry to the Puget Sound in 1885, but a railway bridge had washed out, causing most of the shipment to die. Of the 60,000 fry that survived, 50,000 were released into the Willamette River in Portland and 10,000 were released into the Snake River near its confluence with the Columbia River. The following year, the agency shipped shad from Maryland to the Columbia River and released 550,000 fry in the Willamette at Albany, Oregon and 300,000 in the Columbia at Wallula Junction, Washington. As of 1896, no further releases shad into the Columbia River Basin were attempted by agencies or individuals.

Shad runs of varying sizes and permanence were soon established in most of the larger coastal watersheds. In California, runs developed in San Francisco Bay and the Sacramento River and its major tributaries and then in the Russian, Eel, and Klamath rivers; a land-locked population was established in Millerton Reservoir on the San Joaquin River (Moyle 2002). In Oregon, small runs have been recorded from the Tillamook, Salmon, Siuslaw, Smith, Umpqua, Coos, Millicoma, and Sixes rivers (Mullen 1974, Bottom and Jones 1990). Coastal rivers in Washington with shad populations include the Chehalis and Willapa rivers (Wydoski and Whitney 2003). The number and diversity of rivers in which shad have become established demonstrates their adaptability and tolerance for the range of hydrological features and overall environmental conditions of these rivers. Ultimately, shad have been observed in rivers along the Pacific Rim from Todos Santos Bay, Mexico to the Kamchatka Peninsula, Russia (Moyle 2002, Rosales-Casián 2015), but there is little evidence that they have established populations beyond the North American Coast, and their core range seems to be between the Sacramento and Columbia rivers, inclusive.

Remarkably, a summary of shad on the West Coast in 1896 mirrored the observations and uncertainties identified in this ISAB report:

> *"The changes which have been wrought in the habits of the shad as the result of their introduction into new waters are extremely interesting and important from both biological and economic standpoints. In the absence of a special scientific inquiry, no comprehensive remarks on this subject can be ventured, but enough is known, from even casual observation, to prove that certain well-marked habits of the shad on the Atlantic Coast have undergone noteworthy modification in Pacific waters, and the inference is proper that still further changes have occurred as a result of the new physical and thermic conditions, food supply, enemies, etc*." H.M. Smith 1896 [pages 409-410]

By any measure, the successful introduction and rapid secondary expansion of shad to Pacific coast waters are remarkable. There are several hypotheses to explain this success:

- *First*, the basic biology of the shad enabled easy acclimation to the conditions of West Coast rivers. Shad can tolerate a wide range of temperature, flow, turbidity, salinity, and other aspects of water quality and quantity, and have a short life span.
- *Second*, their anadromous migratory behavior, including some straying among rivers, pre-adapted them for colonizing non-natal rivers as well as for developing locally adapted populations.
- *Third*, their broadcast spawning behavior, high fecundity, semi-demersal embryos, and serial spawning behavior allowed them to spawn successfully in large rivers with highly variable conditions, such as sediment load. Serial spawning involves release of gametes in pulses, with each pulse of spawning individuals moving downstream to "fresh" spawning habitat (Maltais et al. 2010, Pess et al. 2014).
- *Fourth*, their dispersal can be facilitated by favorable ocean conditions. Specifically, Hasselman et al. (2012a) hypothesized "that strong El Niño events, possibly within the greater context of favorable Pacific Decadal Oscillation (PDO) conditions and coupled with the Davidson Current and California Undercurrent, may have created ideal conditions for the shad invasion of the Pacific Northwest (p. 109)."

- *Fifth,* Large, but passable, hydropower dams and their associated reservoirs have created near-optimal conditions for shad spawning and rearing.

Some combination of these hypothesized factors seems to have facilitated the shad's early success in the Columbia River (see Section IV.A.) and contributed later to their extreme abundance. Within the river, shad populations appear to have responded positively to warmer temperatures, increased water clarity, and longer water transport times through the reservoirs created by the hydrosystem (Quinn and Adams 1996).

III. Biology and Management on the Atlantic Coast – Shad in their Native Range

American shad were brought over to the Pacific Coast because of their popularity as a food and game fish in their native range and the relative ease with which large numbers could be transported across the country. They are one of the most studied fish on the Atlantic Coast, and that body of research provides insight into the biology of shad on the Pacific Coast. Ironically, while Pacific Coast shad have thrived and increased in abundance in recent years, the Atlantic Coast populations have been decreasing in abundance. This section, therefore, provides a brief introduction to the biology of shad in the Atlantic Ocean, and compares that information with what is known about Columbia River shad, the main focus of this report.

Shad were once among the most abundant diadromous fishes along the Atlantic Coast of North America, surpassing striped bass, American eel, Atlantic salmon and sea lamprey, and supporting large subsistence and commercial fisheries (Limburg et al. 2003). Shad fisheries were important for Indigenous Peoples for centuries before the arrival of Europeans to the East Coast of North America (Gerstell 1998). Algonquin Peoples taught settlers how to catch shad with weirs, traps, and nets and how to prepare them (Cummings 2012). The importance of the fishery to colonial settlers was reflected in an array of community cultural and even political events. For example, New Englanders celebrated spring with a meal of fiddlehead ferns and shad roe, while politicians in Virginia routinely hosted annual shad "planking" (a method of cooking shad with an open fire) celebrations. However, by 2005 the nearshore ocean fishery had been phased out in favor of local in-river fisheries because of precipitous declines caused by overfishing, pollution, habitat loss, and perhaps climate change (Figure 1, ASMFC 2020b). Annual harvest has declined by 99%, from as much as 22,700 metric tons in the late 1800s to 224 metric tons by 2018 (Limburg et al 2003, NOAA Fisheries Statistics). "The trend … suggests that fisheries harvests have created a downward spiral in American shad stocks, with little leeway for recovery (Limburg et al. 2003, p. 134)." In addition, Limburg et al. (2003) estimated that over 4,000 km of stream spawning habitat have been lost throughout their range largely due to construction of dams across rivers. However, shad remain highly sought by recreational anglers, although reliable estimates of recreational harvest are not available.

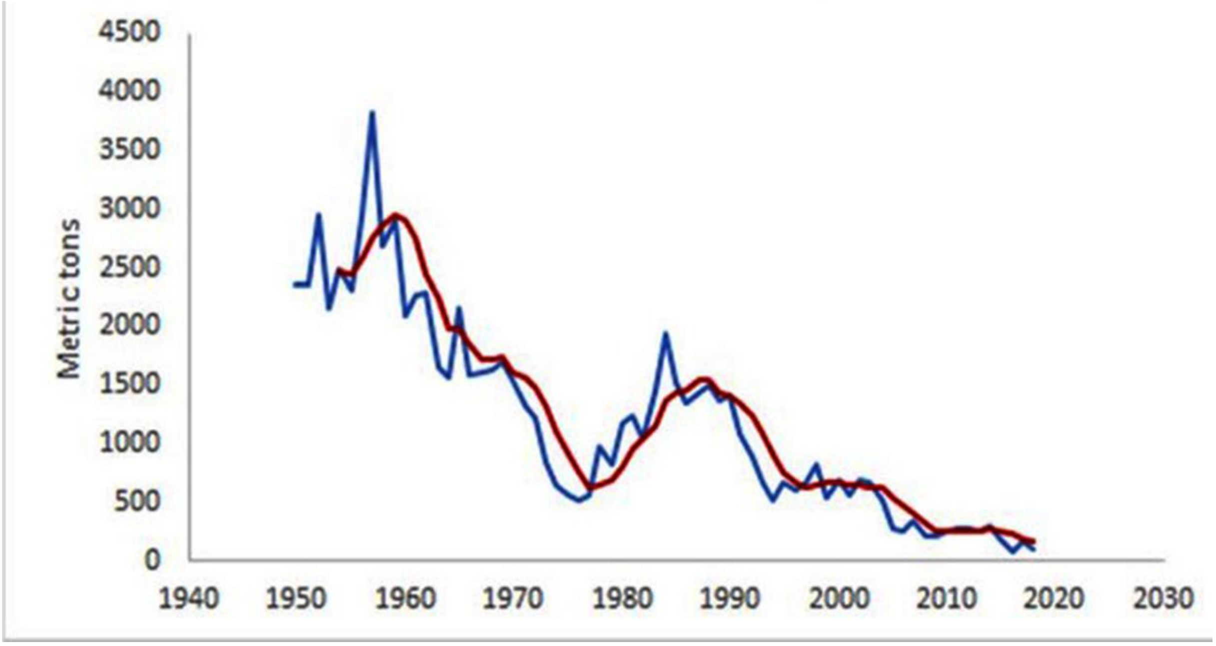

Figure 1. Cumulative commercial landings of American shad on the U.S. Atlantic Coast 1950-2018. Data source: NOAA Fisheries Statistics. Blue line is actual data; red line is five-year smoothed average (ASMFC 2020a). Note that diminishing landings may not solely be an indicator of population decline. Other variables, such as decreased demand, effort, or gear efficiency may also contribute to such a trend.

Shad spawn in rivers that span an enormous range of physical and ecological conditions along the Atlantic Coast from northern Labrador and Newfoundland in Canada, southward to the St. Johns River in Florida. Migrating adults display a considerable level of fidelity to their natal river (Hendricks et al. 2002) or river of previous spawning (Melvin et al. 1986). Shad display a high rate of iteroparity in the northern parts of their range and a gradient of increasing rates of semelparity in the southern range (Leggett and Carscadden 1978 as described in section IVC). At sea, juvenile shad are consumed by predators such as bluefish, striped bass, and Atlantic cod (Bowman et al. 2000), and adults by seals (Scott and Crossman 1973).

One of their key adaptations is flexibility in migration and spawning in response to temperature and river flow. This allows them to vary the timing of their upriver migration and spawning among rivers and among years (Leggett and Whitney 1972, Castro-Santos and Letcher 2010). In this regard they differ markedly from salmon, whose timing of migration and spawning are largely under genetic control (Quinn and Adams 1996). Specifically, shad display a wide range in temperatures that initiate migration (5-23^{o} C) and spawning (8-26^{o} C) across their range (Ross et al. 1993), though the modal temperature for spawning is about 14 – 20° C. Shad can migrate long distances to spawning grounds, for example, 500 miles (805 km) to the upper Susquehanna River (Stevenson 1899).

Because of high, yet imperfect, site fidelity of shad to their natal rivers, each river's population is divergent from those in other rivers. However, there are insufficient data and resources to manage mixed-stock ocean fisheries at such a fine scale. Instead, shad in the United States are grouped into 23 stocks in three coastal management units: (1) south of the Cape Fear River, North Carolina, (2) the Cape Fear River to the Hudson River, New York, and (3) north of the Hudson River (ASMFC 2020a) and managed by individual states under the auspices of the Atlantic States Fisheries Commission (ASMFC). Presently, only the Potomac River (Chesapeake Bay) and the Albemarle Sound (North Carolina) populations have sufficient data to be managed as individual stocks. Nonetheless, extensive data are collected coastwide including ages (largely from scales historically, but recently from otoliths), commercial landings and by-catch discards, fishery-independent adult and juvenile surveys, biological sampling for growth and fecundity, and such. Although there are data on dam passage in some rivers, shad also spawn below dams, making these counts unreliable for estimating total abundance (Beasley and Hightower, 2000). Reliable data from recreational fisheries are scarce.

The most recent benchmark stock assessment was conducted in 2020 (ASMFC 2020a). Because of the long history of data collection on the East Coast, various models have been applied to assess the status of the stocks and the effectiveness of management. Autoregressive Integrated Moving Average (ARIMA) models have been fit to fisheries-dependent and independent abundance survey data (Helser and Hayes, 1995). ARIMA modeling depends on availability of long time series of data. The Thompson-Bell SBPR (Spawning Biomass per Recruit) has been used to estimate biological reference points. SBPR is a production model that relies on the availability of a long series of reliable catch data without requiring constant recruitment (Gabriel et al. 1989). For stocks that have better quality and more extensive data (e.g., Potomac River and Albemarle Sound), stock assessments can use delay-difference models (Carruthers and Hordyk, 2019) and statistical-catch-at-age models. Because knowledge of shad stocks on the East Coast encompasses a wide range of data quality, many of these methods may prove valuable to the assessment of West Coast shad.

Across its native range, population declines in American shad and other alosines such as alewife (*A. pseudoharengu*s) and blueback herring (*A. aestivalis*) are well documented (e.g., Waldman 2013). Shad are the subject of widespread artificial propagation and supplementation stocking by state and federal agencies along the coast as a means to increase population sizes. Nevertheless, shad remain broadly in decline for several reasons. Blockage of upstream migration to spawning sites is a primary cause of decline, and alosines often benefit from dam removal or modification (Burdick and Hightower 2006; Wippelhauser 2021). Once blockages to previously inaccessible reaches of a river are removed, shad readily take advantage of passage opportunities to penetrate farther upriver. However, their behavior at weirs and artificial structures has long been recognized as complicated, and it often precludes their effective use of facilities designed to aid them (reviewed by Haro and Castro-Santos 2012). Specifically, they tend not to use sub-surface openings; this preference has been documented experimentally and noted as an option to enhance their migration on the East Coast and reduce it in the Columbia River Basin (e.g., Monk et al. 1989; Haro and Kynard 1997). See section VI for additional discussion.

IV. Shad in the Columbia River Basin

A. Distribution and Abundance

After their initial colonization of the Columbia River, shad were confined to the mainstem river below Celilo Falls and to larger tributaries, such as the Willamette and John Day rivers that flow into the lower reaches of the Columbia. Hinrichsen et al. (2013) noted that their distribution in mainstem rivers changed with construction of Bonneville Dam (at river km 234), with fish ladders that worked as well for shad as for salmon and steelhead. The ladders allowed access to the newly created, run-of-river reservoir which seemed to provide near-optimal conditions for shad spawning and rearing.

The completion of The Dalles Dam (river km 308) in 1957 and its associated upriver passage facilities also caused (or coincided with) numerical and spatial expansion of shad in the Columbia River Basin. By flooding Celilo Falls, a likely natural barrier to upstream movement of shad, The Dalles Dam and its associated fish passageways allowed access to the upper river and thus enabled upriver expansion. Evidence for this explanation centers on trends and counts at Bonneville Dam. Through 1959, shad counts were on the order of 5,000 – 20,000. By 1960, however, counts dramatically increased and in subsequent years, shad numbers approached or exceeded 100,000. From 1979 onward, nearly every annual count exceeded 1,000,000 fish. Construction of several other upriver dams, each with fish ladders that allowed access to “new” habitat, preceded that of The Dalles Dam (Figure 2). Thus, once shad were able to ascend past the Celilo Falls site, continued passage upriver was facilitated. This habitat was primarily the pools of slow-moving water below each dam that provided conditions suitable for the pelagic embryonic and juvenile shad. Because shad sequentially colonized reaches between each dam, the numbers of returning adults increased dramatically. Thus, Hinrichsen et al. (2013) reported a peak of six million adult spawners in 2005, but this was followed by a peak of nearly 8 million in 2019 (Figure 3). Upstream limits to shad migration are generally considered to be Priest Rapids Dam on the upper Columbia River and Lower Granite Dam on the lower Snake River although some passage of shad over these dams has been observed (Table 1).

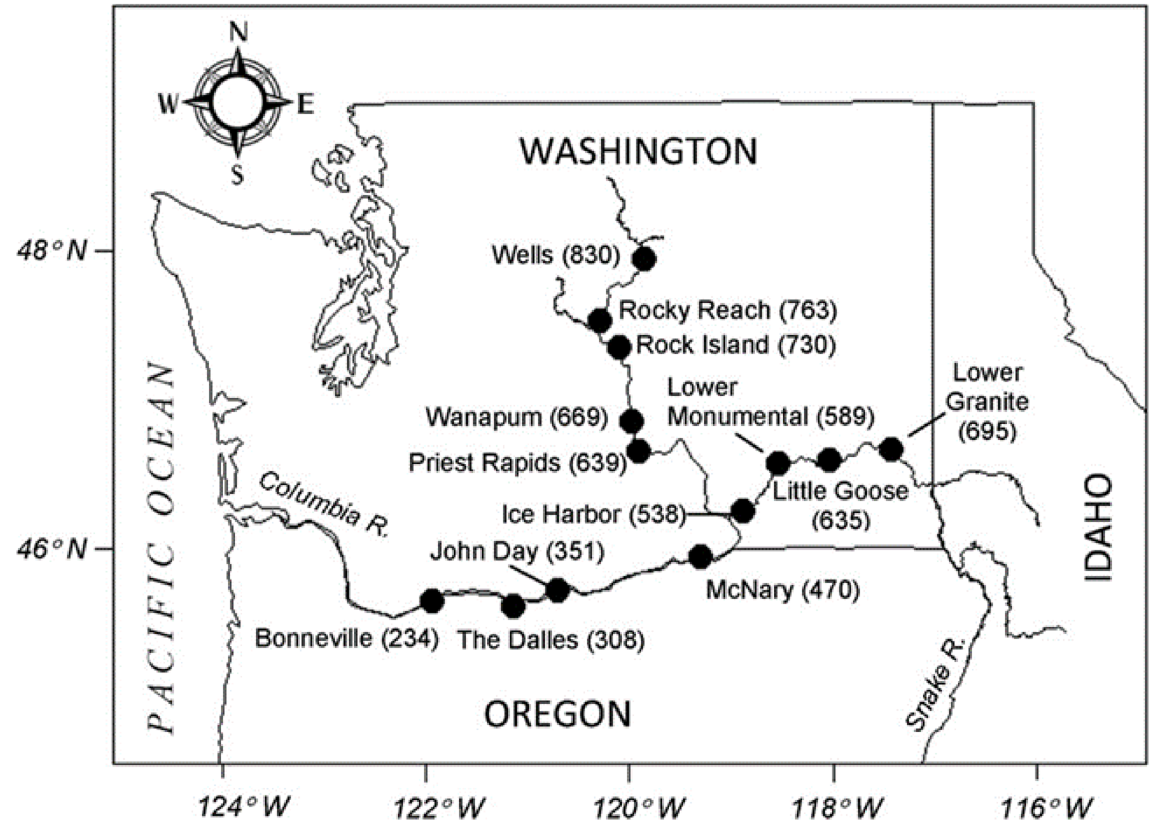

Figure 2. Locations of passable dams on the mainstem Columbia and Snake rivers along the migratory route of American shad. Numbers by each name show distance in river kilometers (km) from the mouth. From Hinrichsen et al. (2013). Contiguous parts of the U.S. and Canada, and significant tributaries, are omitted for simplicity.

Because the dams were not constructed at the same time, and because some no longer maintain shad counts, it is difficult to determine the precise patterns of abundance in different parts of the system. However, if the 1992 – 2003 period is regarded as representing "contemporary" levels, shad counts averaged 2,225,797 at Bonneville Dam (Table 1). There is no information on shad spawning below Bonneville Dam, but by comparing counts at successive dams, we can estimate the distribution of spawning in the reservoirs between the dams. The average count at The Dalles Dam exceeded those at Bonneville Dam, indicating some problems with counting. However, virtually no spawning seems to take place between these dams, because presumably the shad would stop migrating if it did, resulting in lower rather than higher counts at the upriver dam. The John Day Dam average implies that about 928,336 shad (42% of the Bonneville Dam count) spawned between The Dalles and John Day dams, and similar comparisons indicated about 638,116 (29%) spawned between John Day and McNary dams. Above McNary Dam, the river is divided into the Columbia and Snake rivers, and counts at the first dams in each (Priest Rapids and Ice Harbor, respectively) are far below the counts at McNary Dam, indicating that the vast majority of shad spawn below those dams near the confluence of the rivers (ca. 25% of the Bonneville Dam count), or the reservoirs below McNary and John Day dams (Table 1). Thus, while some shad migrate up as far as Lower Granite Dam at river km 695, the majority spawn farther downriver.

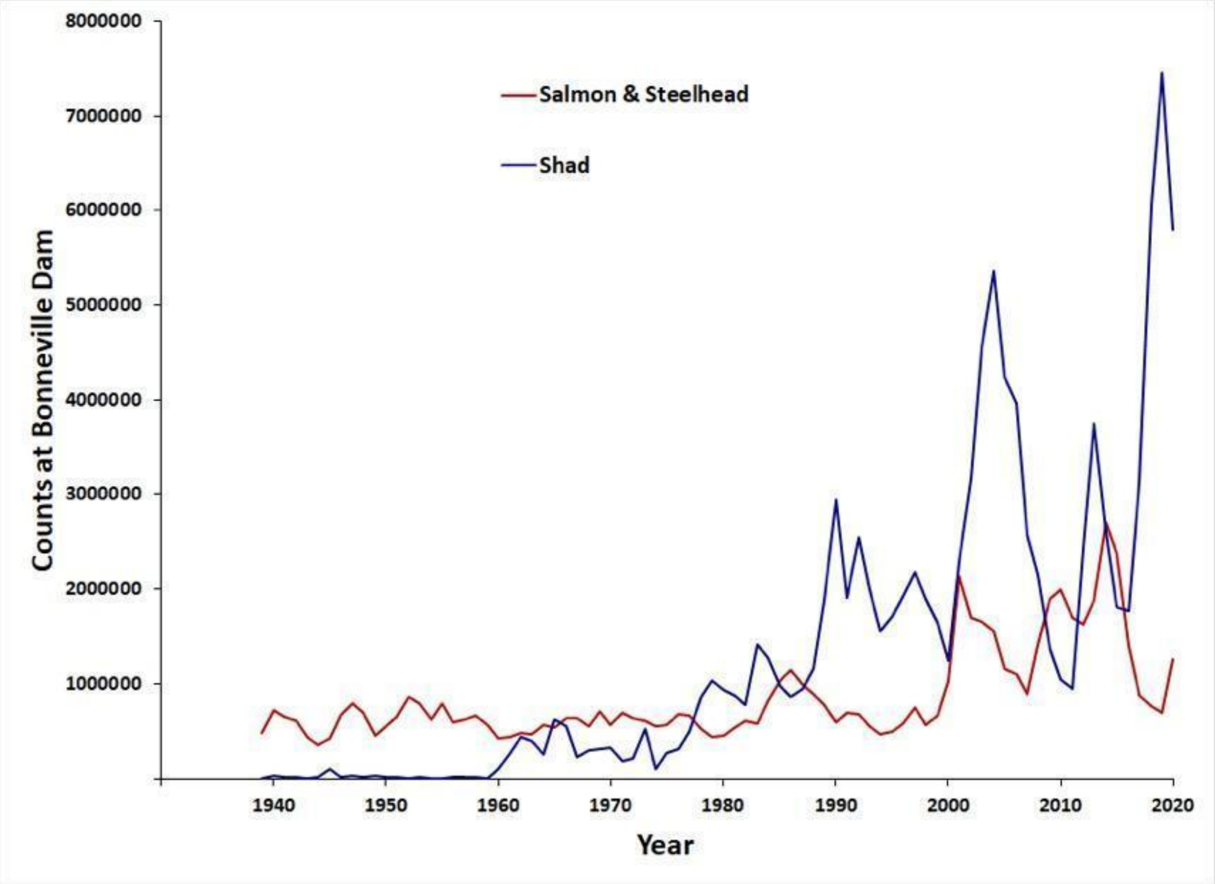

Figure 3. Counts at Bonneville Dam of all adult salmon and steelhead combined (red) compared to counts of shad (blue). Data from Columbia River DART (2021).

For determining the distribution and abundance of shad occupying the lower river and estuary, as either adults or juveniles, no source of information is remotely comparable to the counts available at dams. A glimpse of the difficulty of trying to evaluate this use is provided by Bottom et al. (1984) and Bottom and Jones (1990). In their study, conducted in 1980-81, shad were found in the estuary every month of the year, with age-1 and age-2 shad most abundant in summer and age-0 shad most abundant in autumn. Age-1 and age-2 shad are pelagic, co-occurring with migrating juvenile salmonids in spring and with subyearling Chinook salmon in summer. Yearling and older shad adapt to a wide range of salinities and were found in the pelagic zone throughout the estuary in spring and in the mixing zone and freshwater in winter and summer. Subyearling shad were more associated with the estuary margins so more readily captured in freshwater trawls and beach seines than older size classes.

Table 1. Average counts of shad, adult salmon and steelhead (“salmonids”), and percent of shad of all shad and salmonids combined at mainstem Columbia and Snake river dams from the years 1992 through 2003, retrieved from DART in March 2021. This period was chosen because in subsequent years, counts were not recorded at one or more dams. Locations of dams, in river km from the mouth, were reported by Hinrichsen et al. (2013). Wanapum Dam (river km 669 on the Upper Columbia) was excluded because counts are not available prior to 2006.

Dam	River and Reach	River km	Shad	Salmonids	% shad
Bonneville	Lower Columbia	234	2,225,797	939,242	70.3
John Day	Lower Columbia	351	1,297,460	546,413	70.4
McNary	Lower Columbia	470	659,345	457,086	59.1
Priest Rapids	Upper Columbia	636	19,102	131,167	12.7
Rock Island	Upper Columbia	730	0	110,811	0
Rocky Reach	Upper Columbia	763	0	57,777	0
Wells	Upper Columbia	830	0	54,116	0
Ice Harbor	Snake	538	85,530	209,657	29
Lower Monumental	Snake	589	63,135	198,779	24.1
Little Goose	Snake	635	21,199	182,964	10.4
Lower Granite	Snake	695	5,945	192,534	3

B. Genetics

Introduced species often have low genetic diversity due to founder effects (i.e., a few individuals or lineages serve as initial propagules) and other conditions limiting either acclimation or adaptation. Such effects have not been detected with shad on the West Coast, however. The first introductions into the Sacramento River consisted of 619,000 fry released over a 10-year period beginning in 1871, all propagated from an unreported number of Hudson River adult breeders. These introductions were supplemented by 60,000 Hudson River fry into the Columbia River Basin in 1885, followed by 850,00 eggs and fry from the Susquehanna River in 1886. Fish from both introductions contributed to the rapid spread of the shad, with interesting consequences. At first glance, the number of individuals contributing to the population seems large. However, given the species’ fecundity (upwards of 300,000 eggs per female), the number of parents included in the founding events was likely comparatively small (Waters et al. 2000). Nonetheless, genetic diversity in Pacific Coast shad is now comparable with Atlantic source populations because shad have declined in the native range with concomitant loss of genetic diversity (Hasselman et al. 2018).

The consequences of the shad introduction from a genetic perspective are documented by Hasselman et al. (2018); they examined microsatellite DNA variation from 14 putative populations of shad on the West Coast and compared the genotypes with those from fish from the present-day Hudson and Susquehanna rivers. The following are some of their key findings:

- West Coast shad have diverged genetically from native shad populations on the Atlantic Coast, including the present-day descendants of the source populations. They even possess some unique alleles that appear to have been lost from the source populations or have arisen since founding.
- West Coast populations already show considerable genetic divergence along with an incipient pattern of relatedness (or genetic structure), with each major river population having distinctive arrays of alleles and genotypes. The structure is not as great as found among populations across the shad's native range, but it suggests reduced gene flow as the result of shad homing to natal rivers or river reaches for spawning.
- Shad from the Columbia River are likely the main sources of colonists for rivers to the north of the river's mouth, although these northern populations are currently sparse.
- There are two basic genetic clusters, one is from the Columbia River and adjacent watersheds to the north, and the other is fish from the Sacramento, Russian, and Umpqua rivers. In the Sacramento system, a landlocked population in Millerton Reservoir is genetically distinct, presumably from genetic drift and demographic isolation.
- In their native range, genetic diversity and divergence increases with latitude (Hasselman et al. 2013, Waters et al. 2000). However, a similar latitudinal relationship has not developed on the West Coast.

Ultimately, it is impressive how rapidly shad colonized their new environments, facilitated by their behavioral, life history, and physiological plasticity. Genetically distinguishable groups are now evident among populations in the Columbia Basin, indicating that homing to natal sites for reproduction developed following initial colonization (Hasselman et al. 2018). Observed genetic differentiation between the Sacramento and Columbia river basins may reflect genetic differences between source populations used for initial stocking, but the current shad populations in those two rivers (Hudson and Susquehanna) are quite similar to each other and very different from the West Coast shad. Regardless, genetic differences between West Coast rivers are now reinforced by homing behavior. Interestingly, unlike shad in their native East Coast range, those in the Columbia River have not been subjected to propagation or stocking since limited attempts the late 1880s. As a result, local river environments rather than the hatchery environment has largely shaped their adaptive response and potentially to their expansion and growth.

C. Physiological Adaptations and Climate Change

Within their native range, shad are adapted to a wide range of climatic and ecological conditions in watersheds from Florida to the Canadian Maritime provinces where they spawn, and in the marine waters where they feed. Across this latitudinal gradient, life history variation is also expressed as a gradient. For example, at the southern end of the shad's range in Florida, adults spawn only once and die (semelparity). They also spawn at a smaller mean size and with a lower mean egg production. However, for a given body length, the southern shad populations produce far more eggs than do their northern counterparts (Leggett and Carscadden 1978). Conversely, at the northern end of the range, shad may spawn in multiple years (iteroparity) and at a larger mean size and female mean fecundity. These counter-gradient trade-offs have been hypothesized to optimize spawning success for each of the river populations.

This range of behaviors and reproductive strategies reflects a robust and plastic physiology that allows shad to thrive across climatic regimes. It permits transition from hatching and development in freshwater to having renal and gill functions necessary to survive in saline environments of the estuary and ocean. Fresh water is required only for the egg, larval, and early juvenile stages; thereafter, individuals can adjust quickly to ocean salinity. Likewise, adults can move repeatedly between the ocean and freshwater for spawning. Shad also exhibit a wide range of temperature tolerances. As noted elsewhere in this report, migration timing of mature shad is very sensitive to temperature, showing considerable variation along their geographic range and from year to year (e.g., Leggett and Whitney 1972; Quinn and Adams 1996). Successful development and survival of shad embryos has been observed at temperatures of 13-26^{o}C (Hinrichsen et al. 2013, Klauda et al. 1991). However, shad spawning migrations usually take place at 16-20^{o}C. Juvenile shad can tolerate temporary temperature excursions into water as warm as 35^{o}C (Bayse et al. 2020) and as cold as 2.2^{o}C (Chittenden 1972). Shad can also live in water with dissolved oxygen levels as low as 5 mg/l and briefly tolerate levels of 2-3 mg/l (Chittenden 1973).

The broad physiological tolerances of shad indicate that, at least in freshwater, they will be resistant to, or even favored by, conditions predicted under climate change models for the Columbia River Basin (ISAB 2007). For example, modeling by Ficklin et al. (2014) indicates that stream temperatures in the Columbia Basin will increase 3.5^{o}C during spring, 5.2^{o}C on average during summer, 2.7^{o}C during fall, and 1.6^{o}C during winter. Overall, we might predict, therefore, that higher temperatures should enhance growth and survival of juvenile shad (Crecco and Savoy 1985) and contribute additional stress to salmonid populations. Shad should continue to exploit the Columbia River, modified by dams and reservoirs, as a favorable environment. The ISAB report on climate change in the Columbia Basin (2007) came to a similar conclusion: "Future increases in water temperature will likely continue the expansion of shad in the Columbia River Basin. Research is needed to examine the potential interactions between larval, juvenile and adult shad and juvenile salmonids… (ISAB 2007, p. 45).” However, the ecological factors that might set the carrying capacity of the system for shad and their upper limits of abundance are unknown.

It is unclear how changing ocean conditions will affect shad because there is so little information on their marine ecology in the Pacific Ocean. In the Atlantic, they prefer ocean temperatures of 13° C to 18° C (Leggett and Whitney 1972), somewhat warmer than current coastal temperatures off Washington and Oregon coasts. Presumably, climate-induced warming of the coastal oceans would be beneficial for them and perhaps facilitate a further increase in abundance and northward range expansion. Thus, as conditions become more favorable, shad may colonize additional rivers in Washington and British Columbia. Correlations of shad recruitment with other climate indicators are discussed below (Section IV.D.5).

D. Life History

D.1. Patterns

The life history of shad in their native range has been studied for many decades. They spawn in spring or early summer, influenced by rising water temperatures and flows. The fertilized eggs become embryos that float just off the bottom (semi-demersal), drifting downstream to favorable rearing habitats. Following hatching, young-of-the-year remain in their river of origin during the summer, enter marine waters in the fall, spend several years at sea, and return in spring or early summer to spawn. As discussed in Section IV.C., shad at the southern end of their Atlantic range are mostly semelparous, whereas those at the northern end are mostly iteroparous. This pattern is attributed to northern rivers being more variable in flow and other characteristics than southern rivers, so individual shad have a greater lifetime reproductive success if they spawn more than once. Southern rivers are more predictable (stable) in flow, so greater reproductive success is achieved if shad spawn all their eggs in one event.

Shad from the Columbia, Snake, Umpqua, Russian, and Sacramento rivers (Quinn, Hasselman, and Wetzel, unpublished) have a much higher proportion of first-time spawners (and thus a lower proportion of iteroparous individuals) than the current Hudson River population from which most West Coast shad are derived (but see discussion above about Columbia River receiving a direct release of shad from the Susquehanna River). The West Coast shad were generally younger at maturity and also smaller for a given age compared to shad from their native range.

In addition to the typical anadromous life history pattern, West Coast shad display a life history variant locally known as “mini-shad” that has increased residence time in freshwater. These fish are larger than expected for young of the year, but also too small to be mature adults. Some juveniles spend an additional year in freshwater before going to sea, and others do not go to sea. Such fish are routinely sampled at downstream traps in the Columbia River Basin (Wetzel and Punt 2011, Parsley et al. 2011). Otolith chemistry indicates that mini-shad include both males and females, and ages 1 and 2 (unpublished data, T. Quinn). Being a mini-shad is not, however, a terminal life history pattern. Adults sampled in the Columbia, Snake, Russian, and Sacramento rivers included individuals that had gone through a mini-shad stage. Hasselman et al. (2018) indicated that freshwater resident shad evolved in sympatry with anadromous shad in the Columbia and other rivers, reflecting rapid development of alternate life-history pathways. Such life-history diversity and plasticity are characteristic of American shad in their native range as well as for other alosines. For example, resident alewife, *A. pseudoharengus* are abundant in the Great Lakes, a population that developed from introduced anadromous fish (Miller 1957).

D.2. Ocean Ecology

Distribution. On the Atlantic Coast, once shad enter the ocean, most move long distances over the next 3-7 years, including winter aggregations in a few locations (Leggett 1977; Limburg et al. 2003). As they get ready to spawn, shad move inshore, over the continental shelf, homing to their natal rivers. This is a great over-simplification of complex movement patterns that allow shad to move long distances and to find overwintering grounds even as environmental conditions shift seasonally. In the Pacific Ocean such large-scale movements seem to be lacking or limited.

Pearcy and Fisher (2011) examined incidental shad catch data from a variety of research and monitoring surveys (both bottom and near-surface) and shad bycatch in commercial and recreational ocean fisheries from 1977 to 2008. These data indicated that shad were distributed along the West Coast from central California north to Vancouver Island (the northern limit of their data), mainly over the shallow (50 to 150 m depth) continental shelf, consistent with depth distributions in the Atlantic. They found the highest concentrations of shad in two areas: from central Oregon to Vancouver Island and along the central and northern California Coast, corresponding to the two largest river populations on the coast (Columbia/Snake and Sacramento/San Joaquin). Some evidence was found of northward migrations in spring and summer, but nothing comparable to the long north-south migrations reported for shad along the East Coast. Pearcy and Fisher (2011) speculated that West Coast shad had less need to travel to find preferred temperatures. They examined relationships of catch to both sea-surface and bottom temperatures and found that, while shad were caught at a wide range of temperatures, the largest catches occurred at surface temperatures of 13° to 17° C (warmer than most areas sampled) and at bottom temperatures of 6.4° to 8.0° C (cooler than most areas sampled). Both surface and bottom temperatures are strongly correlated with latitude, and this inverse surface-bottom pattern is consistent with the largest catches being north of 44° N.

Further, Pearcy and Fisher (2011) looked at correlations of two marine abundance indices (catch per unit effort [CPUE] in two groundfish monitoring surveys) and adult counts at Bonneville Dam; they found that abundance north of 44° N correlated positively with Bonneville Dam counts in the same year. However, these correlations included only 6-10 years of marine abundance data. To expand on this, we explored the relationship between shad returns to Bonneville Dam and CPUE from commercial marine fisheries over a longer time span (1981-

2020). In these data, harvest had a moderately positive correlation to shad run size, suggesting a relationship to marine abundance off Oregon.

Pearcy and Fisher (2011) also found that Bonneville Dam counts were negatively correlated with coho salmon marine survival (Oregon Production Index hatchery survival index). This, combined with the positive association between marine distribution and surface temperature, along with other evidence, led them to conclude that shad are favored by warmer ocean conditions.

Diet. There is little information on the diet of shad at sea compared to that available for juvenile coho and Chinook salmon, but the diets are likely to be quite similar. Brodeur (1989) reported the food habits of juvenile coho and Chinook collected on three summer cruises off the Oregon coast. The study indicated that invertebrates (euphausiids, larval crabs, and amphipods) and larval fishes were the primary prey, with the dominant prey changing from month to month. This presumably reflects prey availability. Brodeur and Pearcy (1990) reported similar findings, indicating juvenile coho and Chinook salmon considerably relied on fishes as prey. This is consistent with many other studies (e.g., Daly et al. 2009). While the lack of diet data on shad at sea makes direct comparisons with the diets of juvenile salmon impossible, stable isotopes of carbon and nitrogen provide a tool to assess trophic position, although using isotopes lacks the taxonomic precision of stomach contents. Also, similar isotopic signatures can result from different prey species, and different signatures can even come from different individuals of the same prey. Miller et al. (2010) reported stable isotope N values for coho and Chinook sampled in the summer between Crescent City, California and Newport, Oregon. The June and August values were combined and summarized below (Table 2).

Table 2. Stable isotope values of Chinook and coho salmon caught at sea (Miller et al. 2010). Delta (δ) notation refers to the ratio of heavy (^{15}N) to light isotope (^{14}N) abundance in a sample relative to a standard and is reported in parts per mil (‰).

Species	stage/age	δN (SE)
Coho salmon	yearling	13.5 (0.3)
Coho salmon	adult	13.5 (0.3)
Chinook salmon	subyearling	13.7 (0.3)
Chinook salmon	yearling	14.3 (0.1)
Chinook salmon	adult	14.2 (0.1)
Cutthroat trout	adult	14.6 (0.2)
Steelhead trout	juvenile	13.4 (0.4)

Hertz et al. (2015) reported stable isotope values for Chinook salmon over a range of locations, and data from the Oregon and Washington coasts averaged about 13 for δN and -18 for δC for all but the very smallest fish, whose values might reflect foraging in rivers prior to ocean entry, or a very different diet until they grew to ca. 50 g in size.

By way of comparison with values in Table 2, average δN values (T. Quinn, unpublished data) for adult shad from the Columbia River (mean δN = 13.2) and Sacramento River (mean δN = 13.8) overlap most strongly with post-smolt salmon, indicating that adult shad are slightly lower in trophic position than adult Chinook and coho salmon. Miller et al. (2010) did not report δC values, but they were plotted in Figure 1 of the paper and salmonids were all between -17 and -20, well within the range of adult shad (Columbia River: mean δC = -18.9, Sacramento River, mean δC = -18.5) (T. Quinn, unpublished data). These values are consistent with foraging in the waters along the continental shelf rather than the open ocean, because species that forage further offshore (e.g., sockeye, chum [*Oncorhynchus keta*], and pink salmon [*O. gorbuscha*]) have more negative carbon values, ca. -21 (Johnson and Schindler 2009).

From these studies we infer that shad feed in the Pacific Ocean along the coast rather than in distant offshore waters and that they feed at a trophic level comparable to post-smolt and sub-adult salmon. Thus, there is potential for trophic competition at sea, though the prey base is shared with many other fishes, such as Pacific herring, that are much more numerous than shad.

Marine abundance. One important question is the connection between the abundance of shad in the Columbia River and their numbers in the ocean. Thus, it makes a difference if ocean resident shad off Oregon and Washington primarily Columbia River fish or are a mix from other West Coast populations. While there are no marine abundance estimates for shad on the West Coast, bycatch of shad occurs in commercial fisheries. Because this shad harvest is incidental to other fisheries, effort in these fisheries can be regarded as constant. Therefore, the incidental catch data may provide an index of ocean abundance of sub-adult shad. We examined two different sets of marine harvest data for shad to test this idea.

First, we examined all marine commercial landings of shad for Oregon and Washington using data from the Pacific Fisheries Information Network (PacFIN) "ALL001 WOC All Species" report. These are similar to the landings data used by Pearcy and Fisher (2011). We highlight their caveat that these data are highly variable and only include shad landed at a port and exclude those caught and discarded at sea. The data set extends back to 1980 and shows shad bycatch ranging from near zero around 2010 to in excess of 400 metric tons in 1996 and 2019 (Figure 4; note that this is the same data set referenced in Figure 16.)

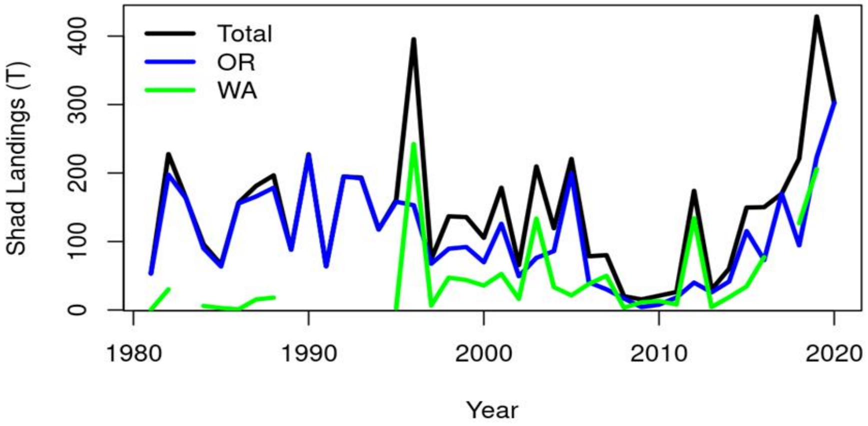

Figure 4. American shad landings in marine commercial fisheries for Oregon and Washington, 1980 to 2000. Data from Pacific Fisheries Information Network (https://reports.psmfc.org/pacfin/f?p=501, accessed June 4, 2021).

Because data for Washington are missing for several years, we only considered Oregon data for comparison with the Columbia River shad run. The two series have a moderate positive correlation of 0.32, suggesting some degree of coherence between marine abundance off Oregon and Columbia River run size, which is particularly apparent in the wide fluctuations in both series since 2000 (Figure 5).

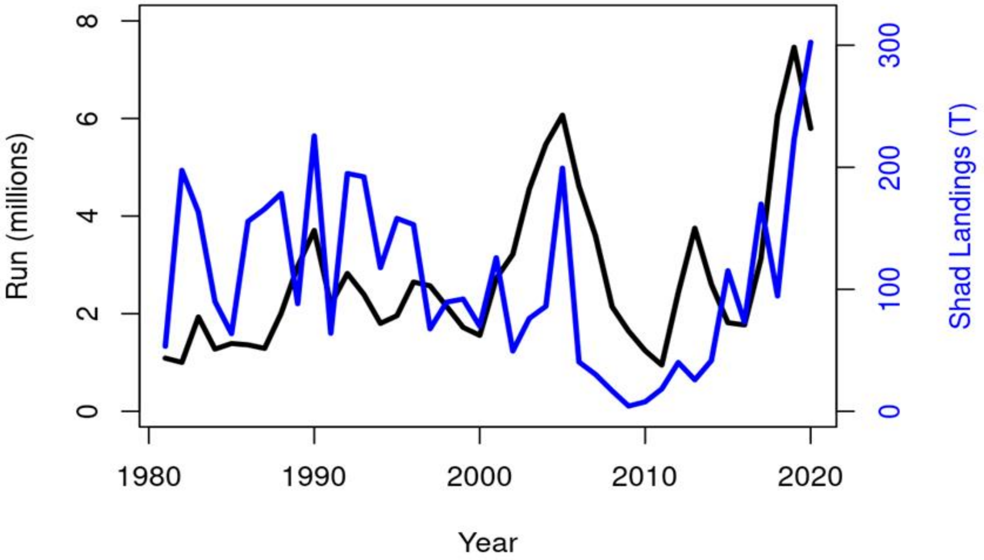

Figure 5. Shad marine landings in Oregon compared with Columbia River run size.

The second data set, provided by Dr. William Pearcy (Oregon State University), consists of observed catch per unit effort (CPUE, catch per hour trawled) of shad in a number of commercial trawl fisheries in a small slice of ocean (46 N to 46.3 N) directly off the mouth of the Columbia River. These data come from two NOAA commercial vessel observer programs: the At-Sea Hake Observer Program (ASHOP) and the West Coast Groundfish Observer Program (WCGOP) representing fisheries using a variety of trawl gear (Figure 6)

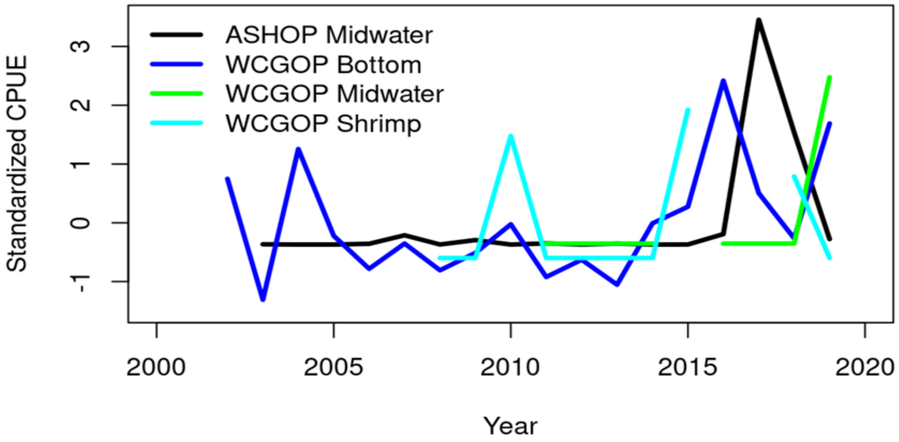

Figure 6. Standardized catch per unit effort (CPUE) of shad for various trawl gear types in the At-Sea Hake Observer Program (ASHOP) and the West Coast Groundfish Observer Program (WCGOP).

Only the WSGOP Bottom Trawl data series is complete and has sufficient variation to compare with the Columbia River run (Figure 7). The two series have a weak positive correlation of 0.17, with little apparent coherence in the trends. This may be due to the short length of the data series or the very small area of the sampling which may not reflect overall ocean abundance.

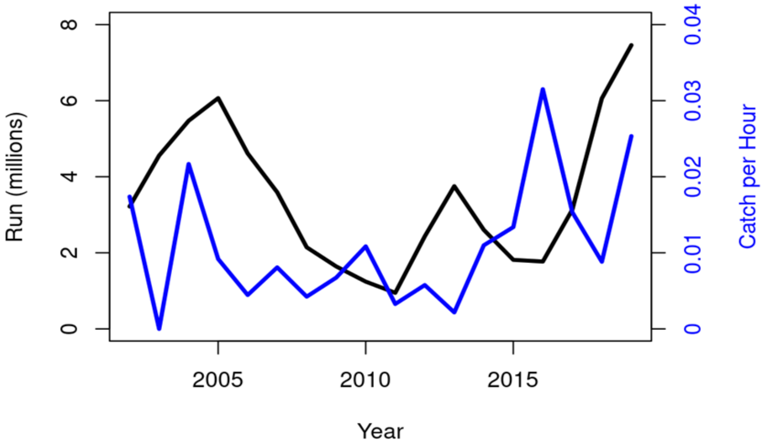

Figure 7. American shad observed catch per trawl-hour in West Coast groundfish bottom trawl fisheries immediately off the mouth of the Columbia River compared with Columbia River run size.

Overall, commercial landings of shad had a moderately positive correlation with Columbia River Basin shad run size, suggesting that favorable conditions in the ocean off Oregon can influence shad numbers in the river. This is also consistent with findings that shad in the coastal ocean off the Pacific Northwest originate from the Columbia River Basin population rather than originating from the Sacramento River and other rivers to the south.

D.3. Migration of Adult Shad

Upriver migration for spawning by shad occurs in spring (primarily in May and June in the Columbia River, at present) and is closely linked to rising water temperature and decreasing discharge. Shad migrate earlier in warmer rivers than they do in cooler rivers, and earlier in warmer years than cooler years in a given river. This was common knowledge nearly a century ago (e.g., Roule 1933), and borne out by subsequent scientific studies including data from their native range and the Columbia River (Leggett and Whitney 1972; Quinn and Adams 1996; Nack et al. 2019). Other alosines in their native range have a similar pattern (e.g., Huntington et al. 2003; Lombardo et al. 2020). Observers have used the first day of the year when water temperatures reach a particular temperature as an index of spring warming. Specifically, Leggett and Whitney (1972) used 60° F (15.5° C) at Bonneville Dam as their index, though they noted “Most of the time the peak [shad migration at Bonneville Dam] occurred at 18.0 C” [p. 661]. Quinn and Adams (1996) also used 15.5° C as an index value for consistency. They reported that the Columbia River was warming earlier in the year than in the past (as well as reaching higher maximum temperatures), and the shad were migrating earlier. A continuation of that analysis, using counts at Bonneville Dam retrieved from DART, revealed that the positive correlation between variables (median shad date and first 15.5° C date) continued ($r^2 = 0.52$). However, temperatures have been reaching that value at a similar time in spring over the most recent years, and shad are migrating at about the same time of year. Specifically, over the past decade (2011 – 2020) the median date has averaged 16 June (Figure 8, T. Quinn, unpublished analysis of Bonneville Dam count data). This timing is important for considering any possible ecological effects of shad on salmon, because larval production follows shortly after migration and spawning, allowing estimates of the spatial and temporal patterns of adult and larval abundance in the river system, from the estuary to the confluence of the Snake and Columbia rivers.

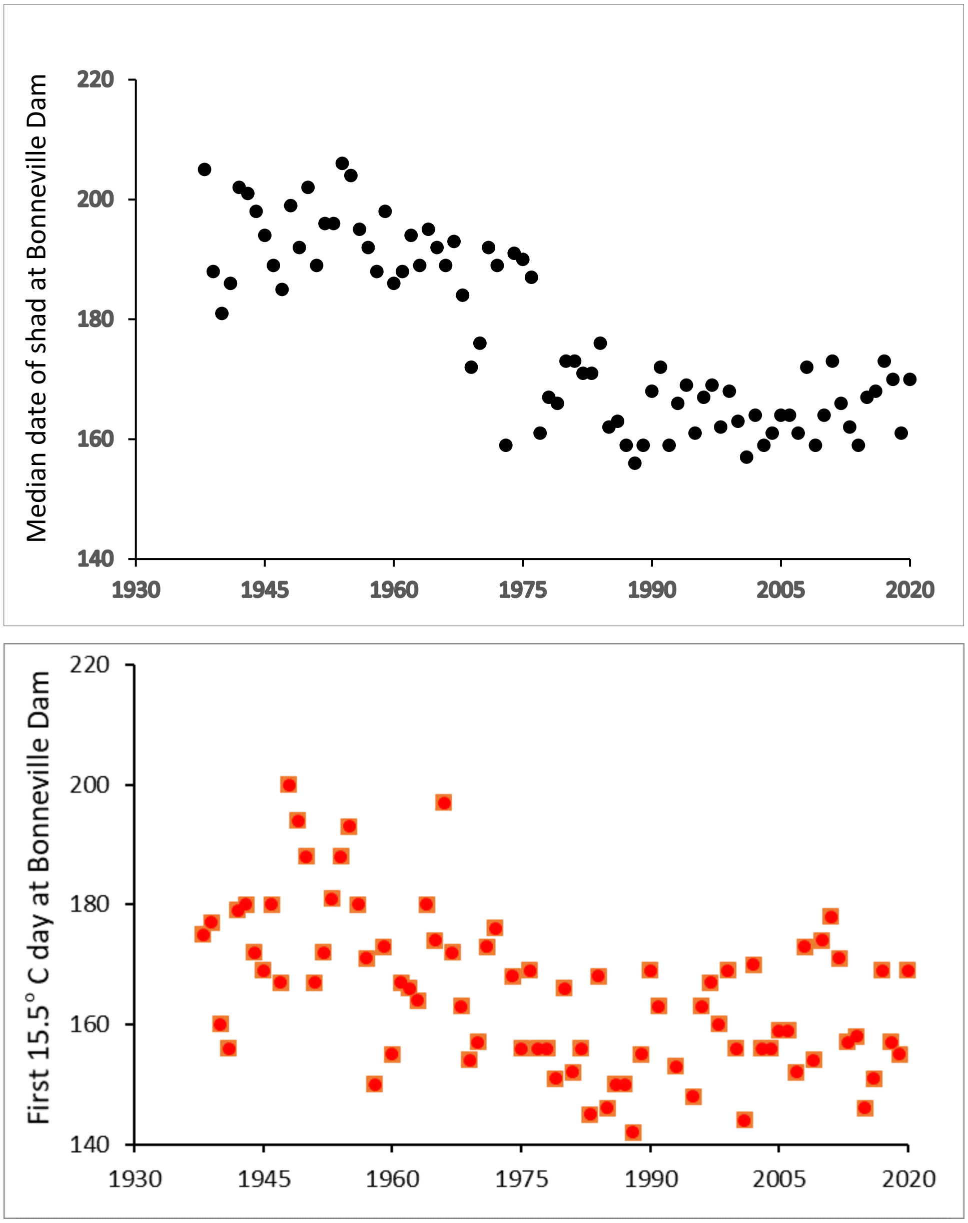

Figure 8. Relationship between temperature and migration date of shad in the Columbia River. 1938-2020. Upper: Median date of shad passage over Bonneville Dam. Lower: First 15° C day at Bonneville Dam. Source: DART data and Talbot 1953.

While temperature is a cue for fish migratory behavior, discharge also plays a role. Quinn and Adams (1996) discussed the influence of temperature and discharge on migration and concluded that migration timing was more highly correlated with temperature than discharge. They also noted that temperature and flow are themselves correlated (see also Keefer et al. 2008), and the spring upriver migration of shad in the Columbia River coincides with peak flows related to snowmelt in headwater tributaries (Hamlet et al. 2013, Queen et al. 2021). Shad migrate up the Columbia River from mid-April through the end of August, but the great majority do so in June and July. River management has substantially modified the annual hydrograph, decreasing peak discharges during spring and early summer and increasing flow from November through March during fall and winter seasons (Figure 9) (ISAB 2011-1, Naik and Jay 2005, Angilletta et al. 2008, Hatcher and Jones 2013, Forbes et al. 2019). Bottom et al. (2011) estimated that water temperatures from May to December in the post-impoundment period (1976-2002) are 2-3˚C higher than temperature in their virgin-flow, cool-temperature scenario (1890-1926), and attributed more than half of the increase to reservoir storage.

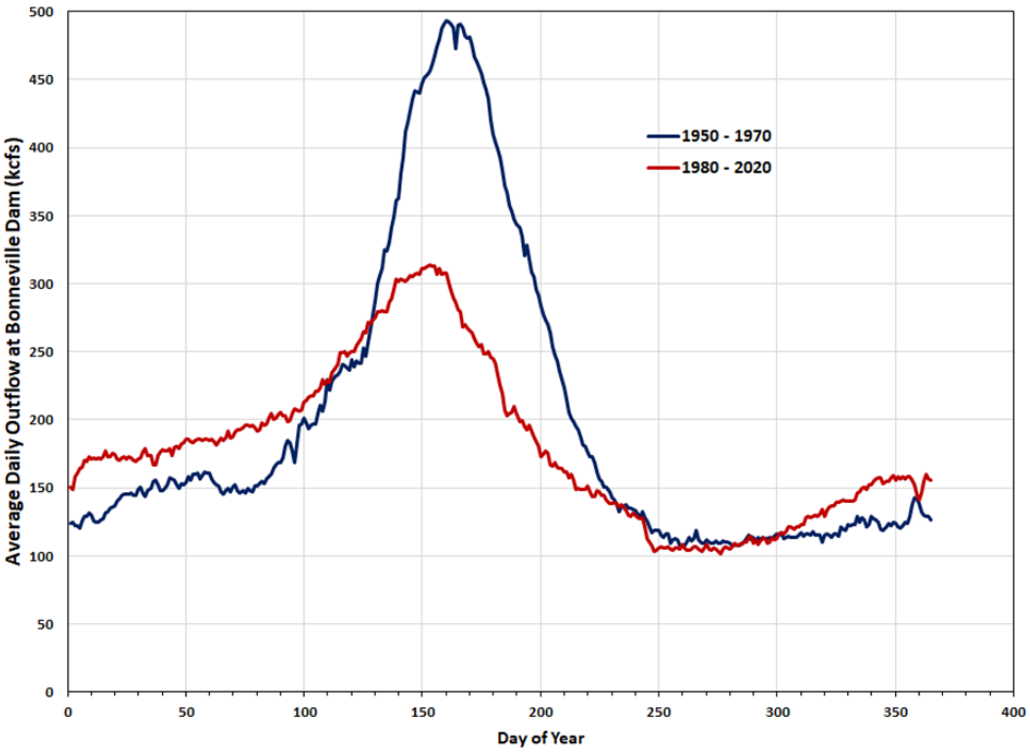

Figure 9. Average daily outflow (in thousands of cubic feet per second; kcfs) at Bonneville Dam during the periods of 1950 to 1970 and 1980 to 2020 (based on data downloaded from DART).

Maximum outflow from Bonneville Dam in the spring decreased from the 1940s to the late 1970s, remaining fairly consistent from 1980 to the present (Figure 10), though the day of the year when maximum daily outflow has occurred continues to occur earlier (Figure 11). The trend in earlier date of maximum flows had been observed since the late 1800s (Bottom et al. 2005, ISAB 2011-1) (Figure 12). Peak outflow from Bonneville Dam now occurs approximately 25-30 days earlier than in the mid-20th century (Figure 13), which is consistent with the general change in timing of the peak of adult shad returns. In the period from 1950-1970, average adult shad return peaked in early July approximately 25 days after the peak discharge (Figure 14). In the period from 1980-2020, average adult shad returns peaked in mid-June approximately 20 days after the peak discharge (Figure 15). Flow modification has significantly affected the aquatic communities and anadromous fish species of the Columbia River (Bottom et al. 2005, Angilletta et al. 2008, Crozier et al. 2011, ISAB 2011-1). Hatcher and Jones (2013) concluded that flow regulation obscures the effects of climate change on streamflow below dams in the

Columbia River Basin. A recent model of climate change effects on Columbia River discharge concluded that the timing of peak flows will shift even earlier to mid-May by 2099 (Queen et al. 2021). Such changes in the hydrology and thermal regimes could influence shad migrations further and have major implications for their interaction with anadromous salmonids and native aquatic communities.

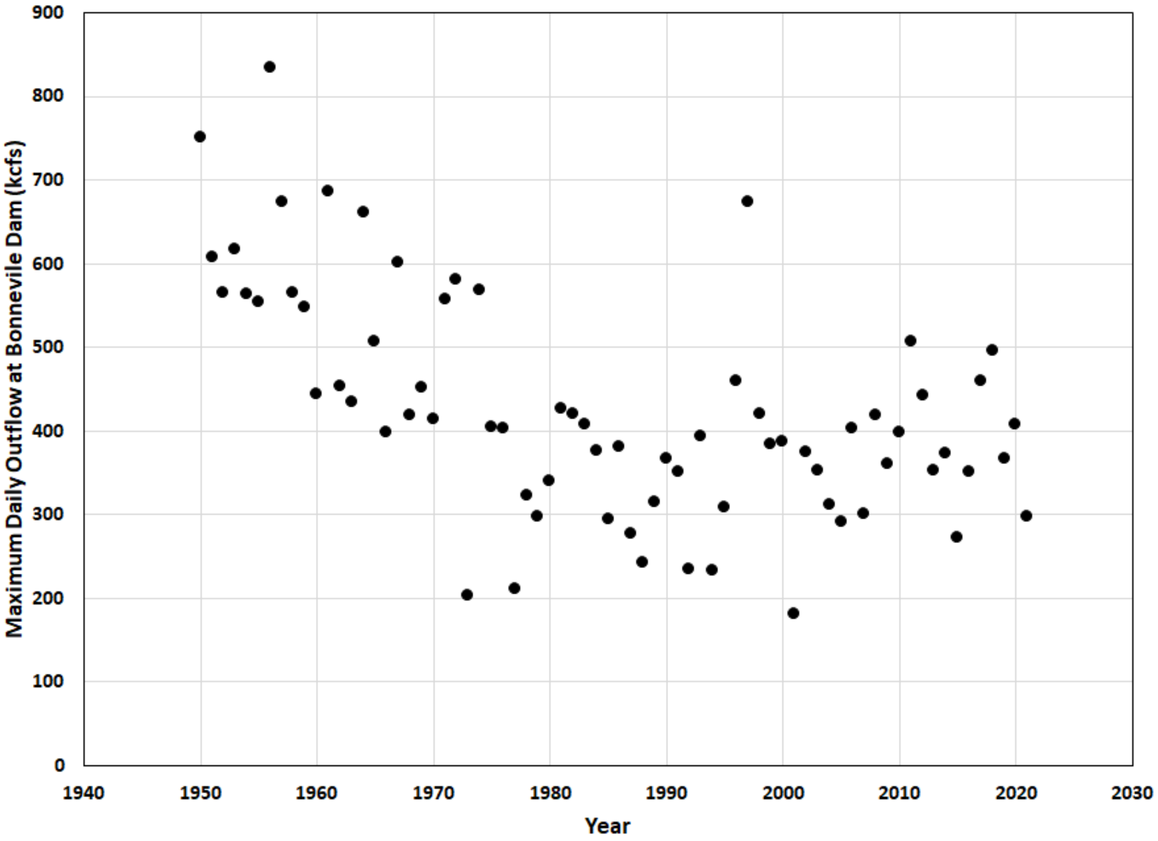

Figure 10. Annual maximum daily outflow (kcfs) at Bonneville Dam from 1950 to 2021 (data downloaded from DART).

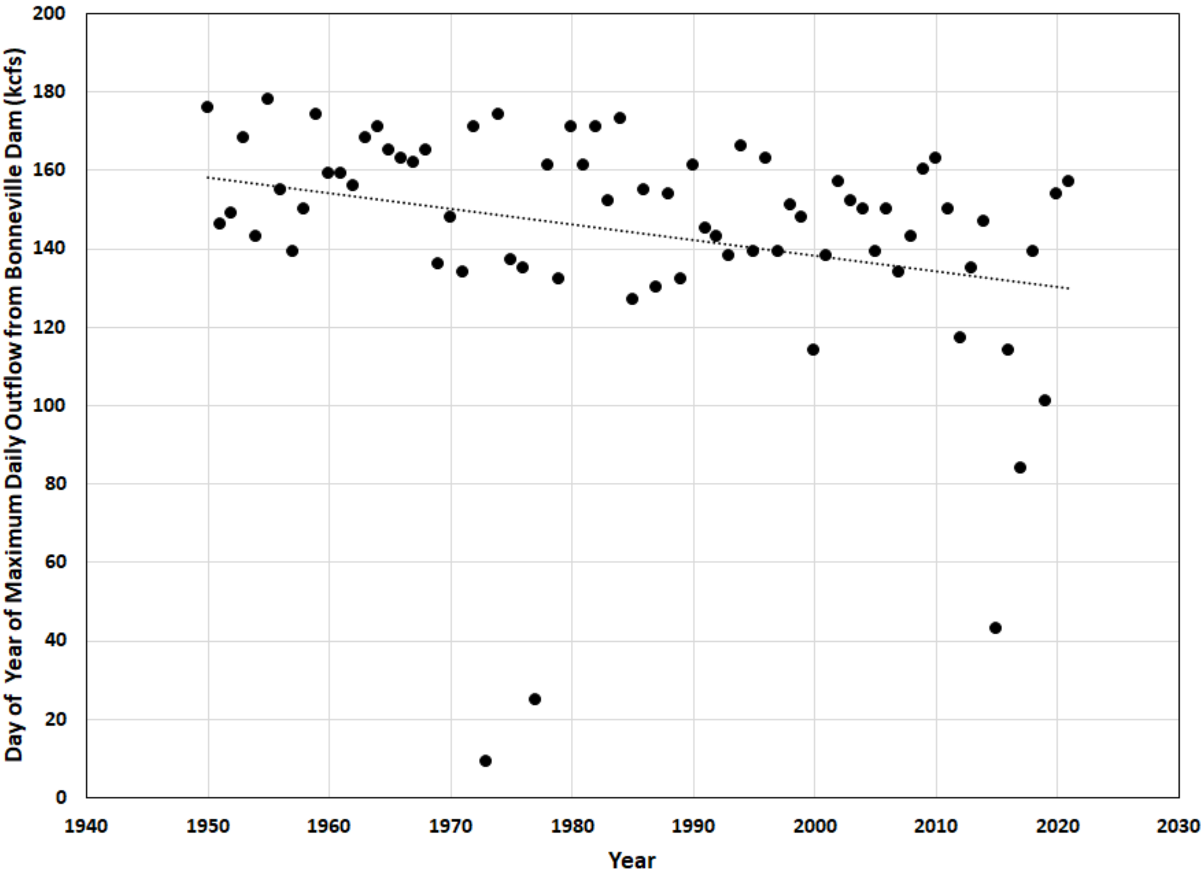

Figure 11. Day of the year when maximum daily outflow (kcfs) occurred at Bonneville Dam from 1950 to 2021 (data downloaded from DART).

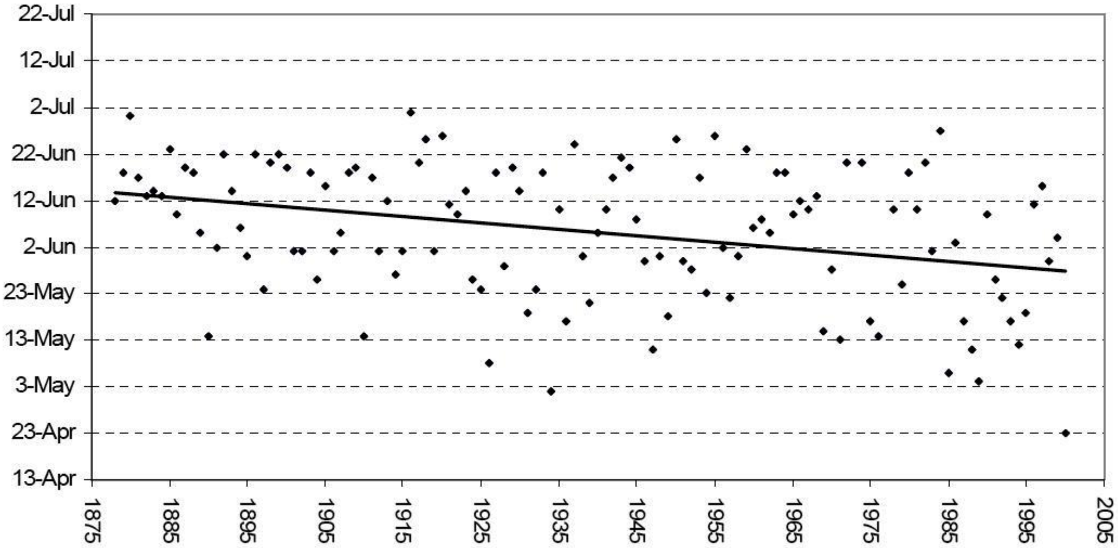

Figure 12. Day of the year when maximum daily outflow (kcfs) in the lower Columbia River from 1878 to 2000 (from Bottom et al. 2005, ISAB 2011-1).

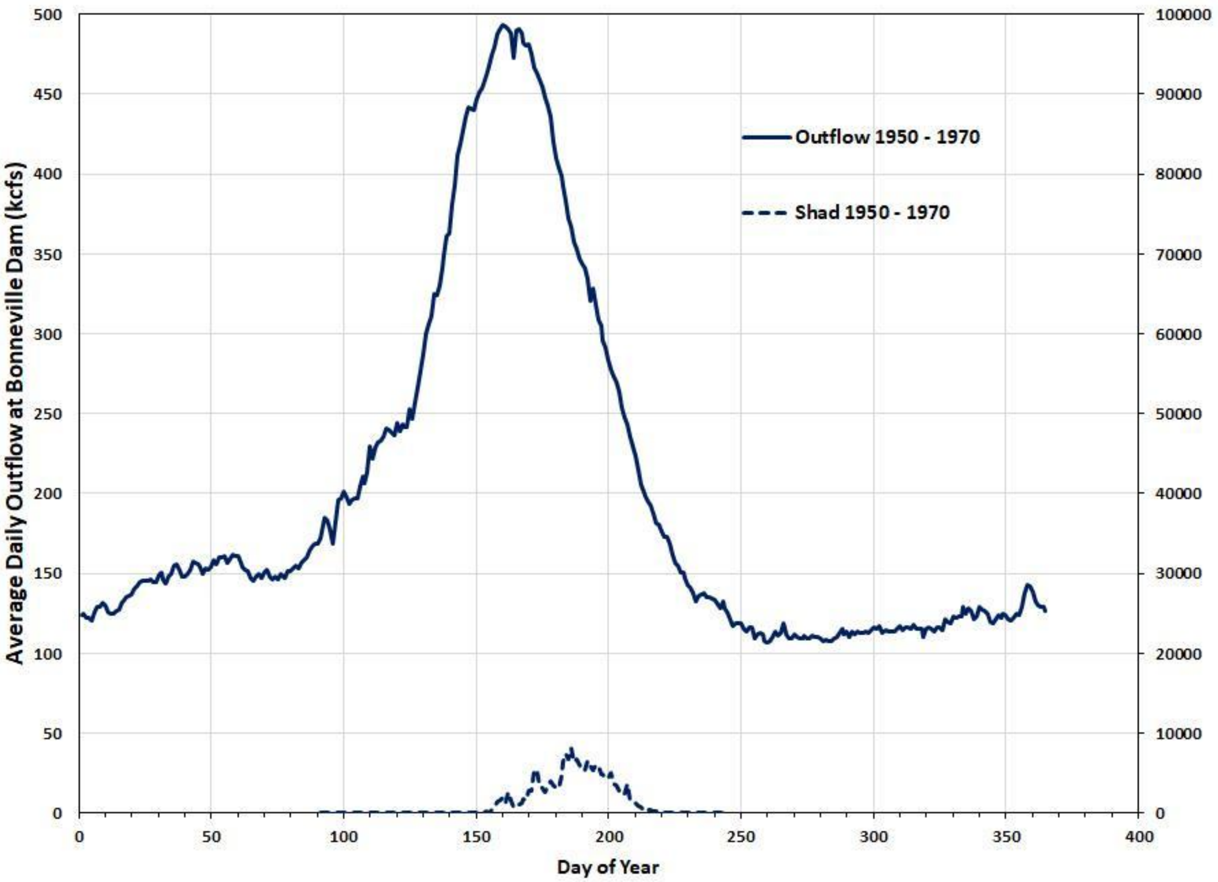

Figure 13. Average maximum daily outflow (kcfs) and average numbers of adult shad at Bonneville Dam for the period from 1950 to 1970 (data downloaded from DART).

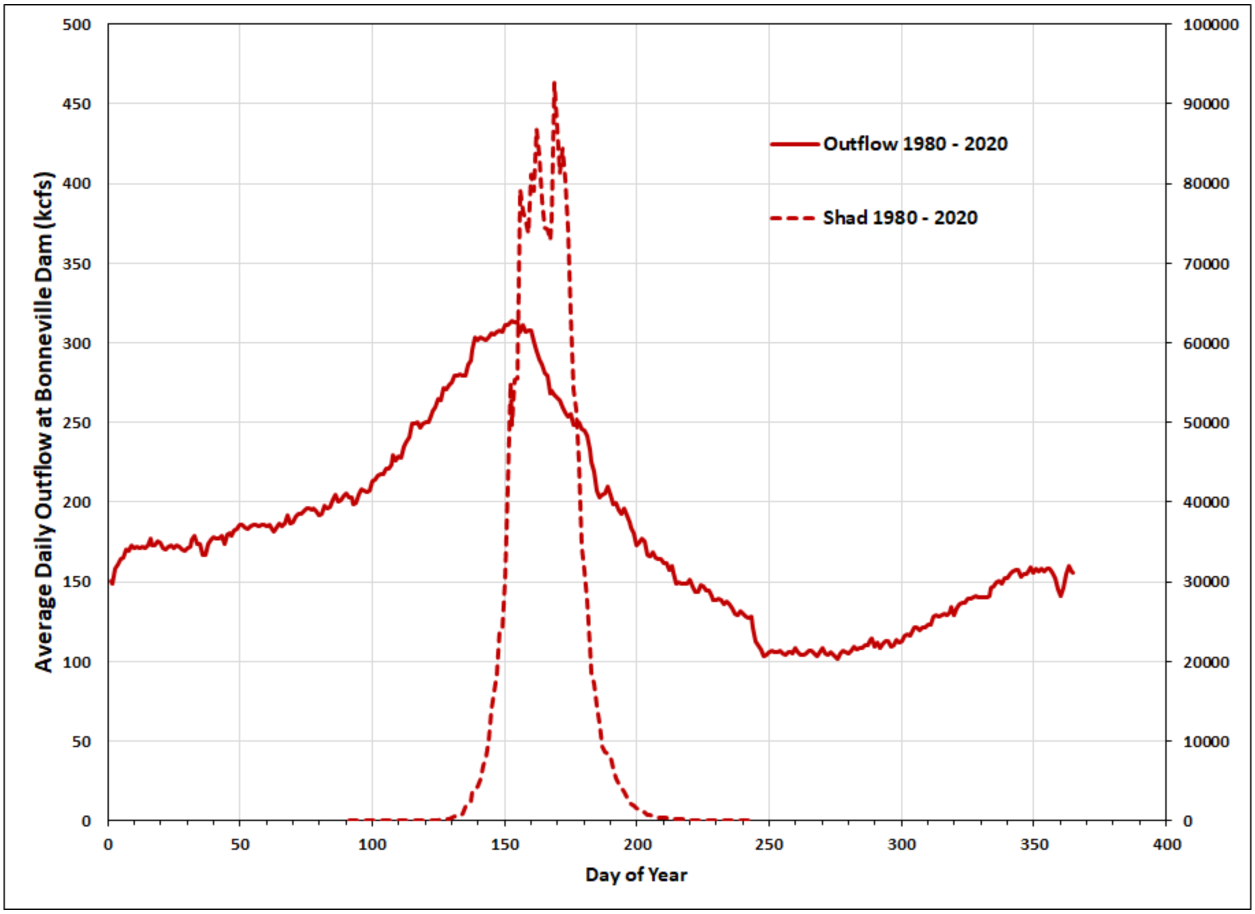

Figure 14. Average maximum daily outflow (kcfs) and average numbers of adult shad at Bonneville Dam for the period from 1980 to 2020 (data downloaded from DART).

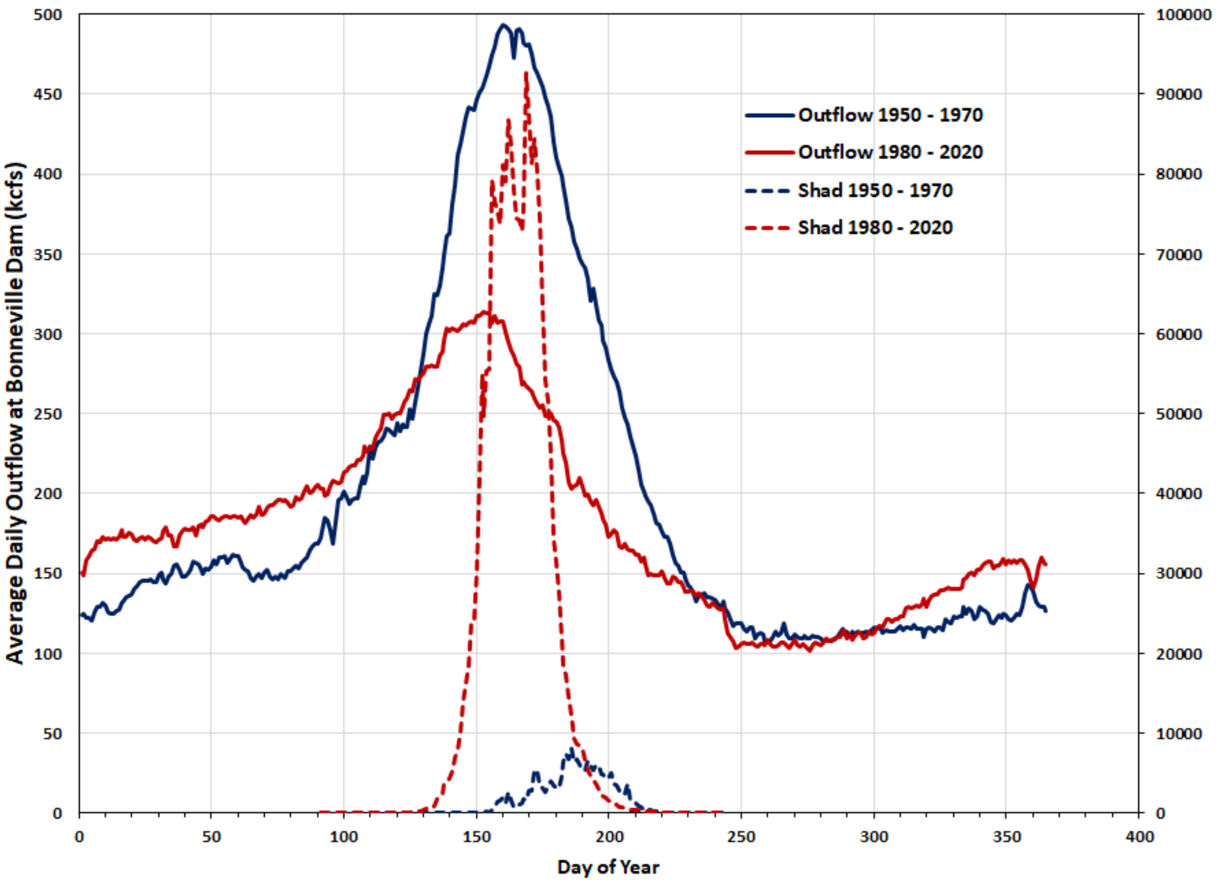

Figure 15. Peak shad numbers versus outflow (kcfs) on at Bonneville Dam, 1950-1970 and 1980-2020 (data downloaded from DART).

D.4. Migration of Juvenile Shad

This summary of juvenile shad movements in their native range is based on Greene et al. (2009). Downstream movement of shad starts when semi-buoyant embryos drift to areas suitable for larval shad to rear – typically slow-moving reaches with eddies and side-channels. The larvae metamorphose into juveniles (ca. 28 mm TL) 3-5 weeks after hatching and start actively moving downstream. They typically spend their first summer in the lower reaches of their natal river, including brackish water, before entering the ocean at 7-15 cm TL. Emigration is in September-November, with juveniles in northern populations emigrating earlier than those in southern populations. The principal cue for outmigration seems to be dropping temperatures when they coincide with the new moon phase, presumably because darkness reduces predation on shad. High flows have also been implicated in emigration at times. There is some evidence that physiological changes that allow rapid adjustment to salt water also trigger emigration.

It is uncertain how much juvenile shad movements in the Columbia River are like those of shad on the Atlantic Coast, but they are likely substantially similar. In the Columbia River, shad spawn below the large dams and embryos and larvae seem to find near-optimal (at times) conditions (temperature, food supply) in the reservoirs, especially along the edges and in backwaters (Petersen et al. 2003). Juveniles likewise find the slowly moving waters of reservoirs favorable for rapid growth and high survival, partly because diel movement puts them on the bottom during the day, thereby avoiding predation, and higher in the water column at night where zooplankton are abundant. They move downstream in September-November. Some then enter the ocean as large juveniles (Petersen et al. 2003), while others remain in the estuary (Bottom et al. 1984).

D.5. Population Dynamics

Numbers. As mentioned above [section IV.A], the adult shad population in the Columbia River above Bonneville Dam has increased over the last 60 years from fewer than 100,000 per year in 1960 to a recent (2019) peak of nearly 7.5 million adults (Figure 16). Prior to 1960, shad counts at Bonneville Dam were low (below 100,000) and relatively flat, with an uptick beginning in the early 1960s. Hinrichsen et al. (2013) attributed this increase to the completion of The Dalles Dam in 1957, which facilitated shad passage upstream and expanded spawning and rearing habitat.

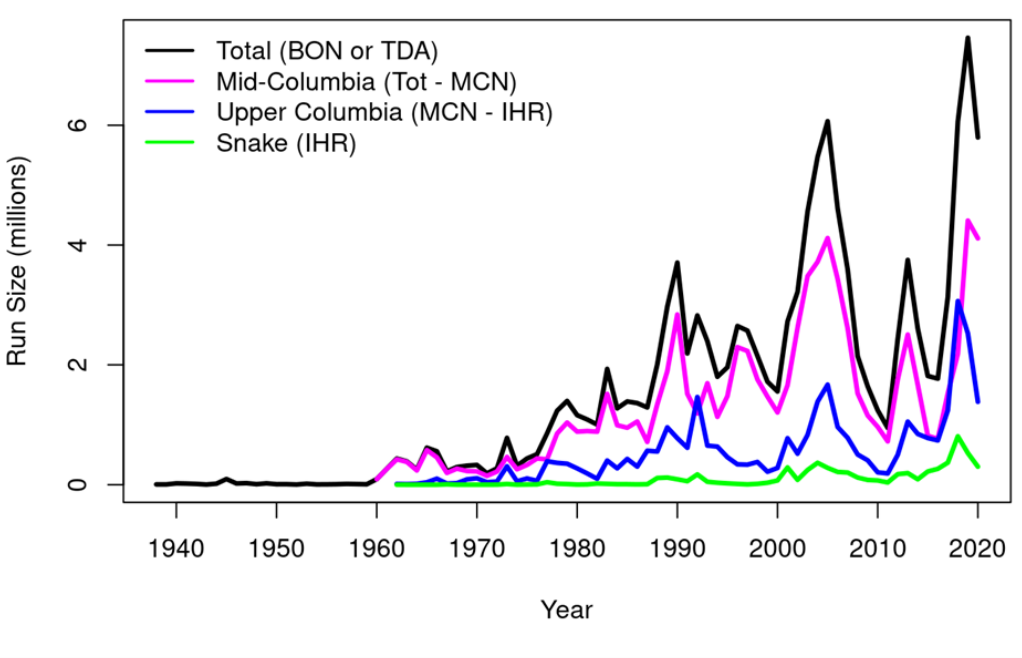

Figure 16. Trends in shad adult counts at Columbia River Basin dams, 1940 to 2020. Adult run size is estimated for river segments as follows: Total -- the greater of yearly counts at Bonneville (BON) or The Dalles (TDA) dams; Mid-Columbia -- the difference between Total and the count at McNary Dam (MCN); Upper Columbia -- the difference between counts at MCN and Ice Harbor (IHR) dam; Snake -- the count at IHR. Data from Columbia River DART (2021) and Talbot (1953).

Spatial structure: To consider changes in usage of different parts of the basin, we subdivided the destination of returning adults into three sub-basins (Figure 17): mid-Columbia (Bonneville to McNary), upper Columbia (above McNary excluding passage above Ice Harbor), and Snake (above Ice Harbor). Almost all shad spawned in mid-Columbia until the mid-1970s when an increasing fraction began passing above McNary. The mid-Columbia segment has remained dominant up to the present, although the upper Columbia run has equaled or exceeded the mid-Columbia in a few years (1977, 1982, 2015–2018). Returns to the Snake River remained negligible until the late 1980s when they began to increase, with a peak of about 800,000 adults in 2018. Looked at another way, the proportion of the total run in each sub-population (Figure 17) shows a gradual increase in the upper Columbia run from the early 1960s until the mid-1970s after which the proportions fluctuate, with the upper Columbia run exceeding the mid-Columbia run in two years. The Snake River run remained very low until about the year 2000, after which it has been an increasing portion of the total.

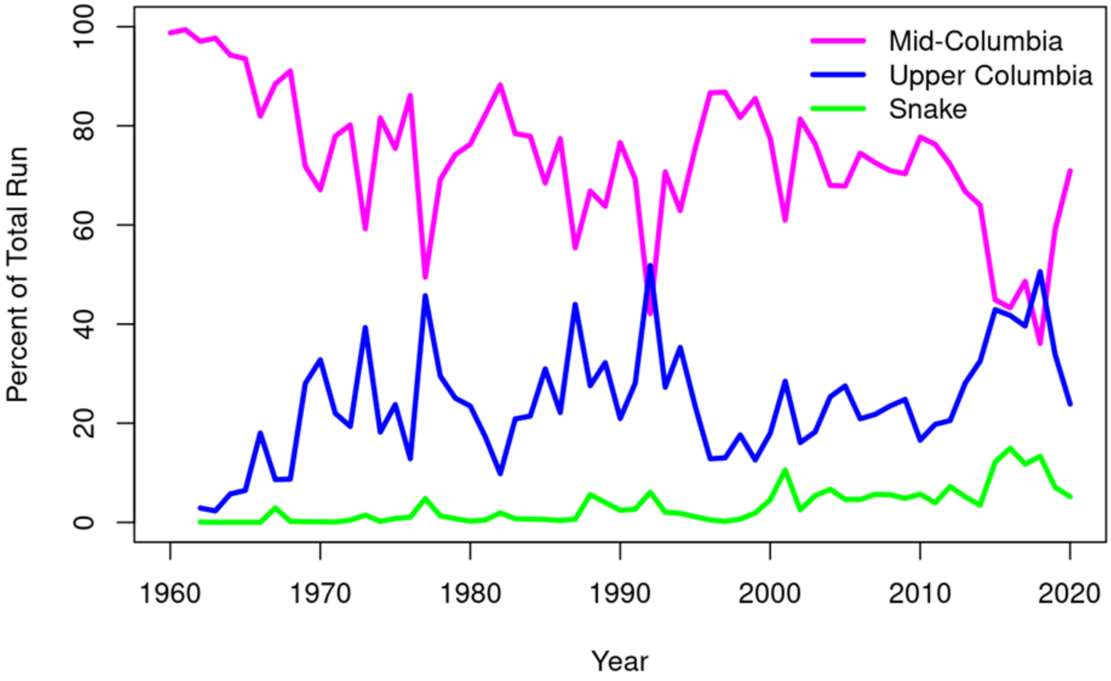

Figure 17. Subpopulation run size as a proportion of the total run of shad in the Columbia River.

Population Growth: By fitting an exponential growth model (log-linear regression) to the abundance time series since 1960 (Figure 18), we estimated an average population growth rate of about 4.7% per year. However, there are large fluctuations above and below the average trend line. To explore these variations, we followed Hinrichsen et al. (2013) in computing an approximate index of recruits per spawner (R/S) by using the total run size in a given year as spawners (S_t) and computing recruits (R_t) as the average of the run size 4 and 5 years later. The lag in recruits corresponds to the primary return ages of shad in the Columbia basin (Wetzel et al. 2011). Hinrichsen et al. (2013) used a 4-year mean of age 3-6 returns, but a recent review has found that 81% of the returns in the Columbia River and 94% of those in the Snake River are at ages 4 or 5, although these data represent only two years (T. Quinn, unpublished). The R/S index (Figure 19) has a geometric mean of 1.49 — a nearly 50% increase every generation on average from 1938 to 2020. However, R/S exhibits considerable fluctuation over time, and much of the average R/S is accounted for by the rapid increase in the late 1950s (peak R/S = 47.8 in 1959) shortly after completion of The Dalles Dam. Ultimately, there must be some upper limit of abundance for shad in the system, but it is not currently known, nor do we know what ecological factors determine it.

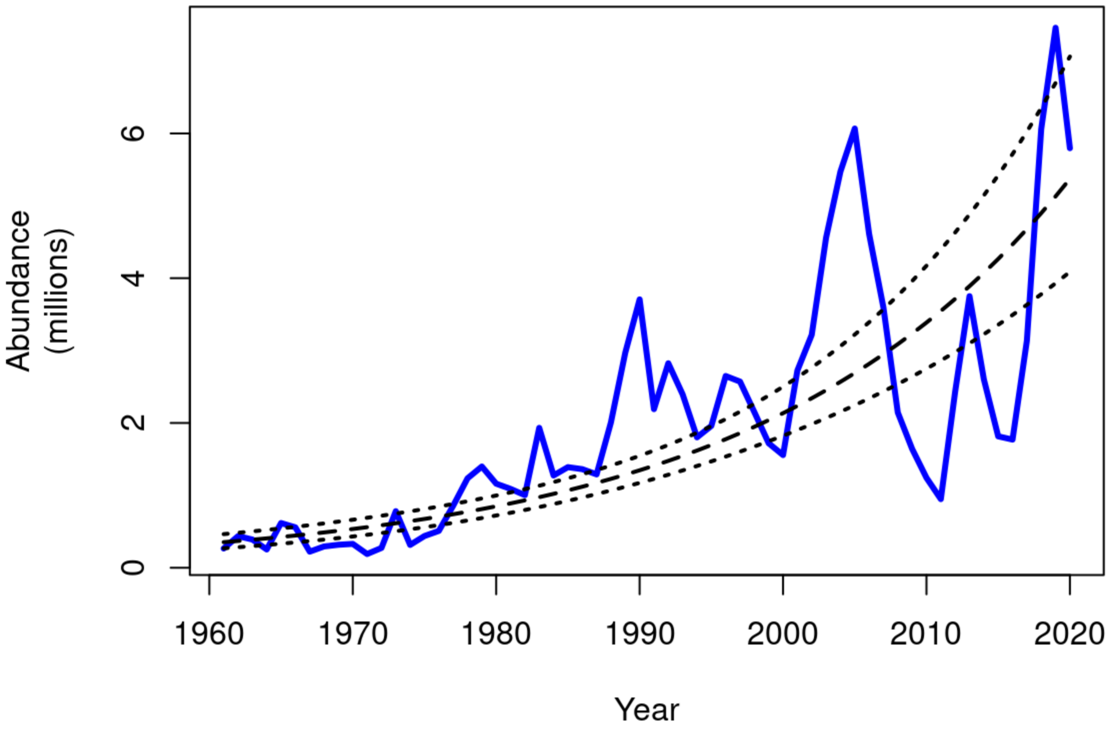

Figure 18. Shad total run size 1961-2020 (solid curve) with fitted exponential growth model (dashed curve) with 95% confidence interval (dotted curves).

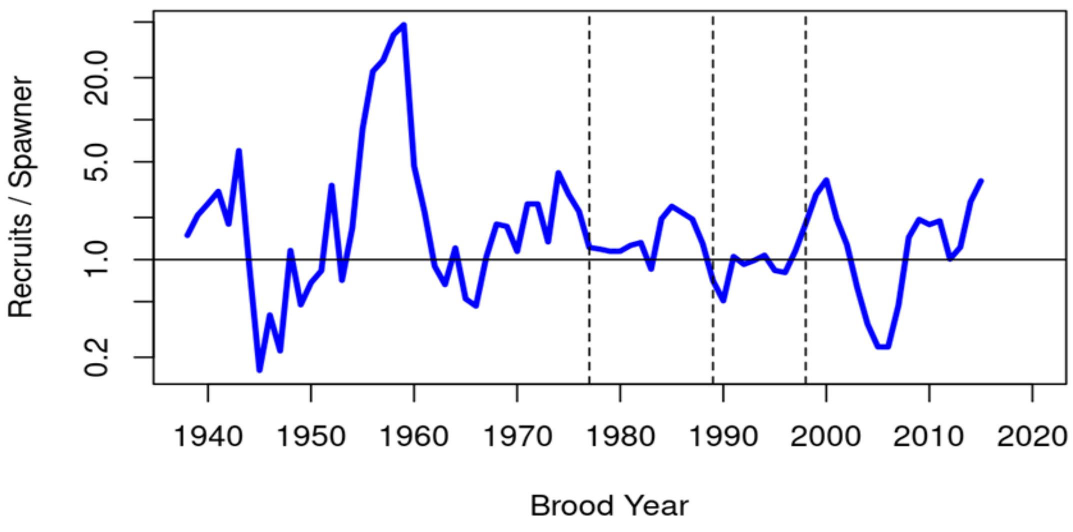

Figure 19. Index of recruits per spawner by brood (parental return) year. Note logarithmic scale on vertical axis. The horizontal line at 1.0 represents the population replacement level; vertical dashed lines correspond to major ocean regime shifts in 1977, 1989, and 1998. The mean R/S is about 1.5 across all years, resulting in rapid population growth.

Environmental controls: Basic time-series statistics computed for the R/S series (Figure 20) show a pattern of declining autocorrelation function (ACF) with a single positive partial autocorrelation function (PACF) at lag 1, which is diagnostic of a lag-1 autoregressive, AR(1), process (Shumway and Stoffer 2006). Fitting an AR(1) model to the data results in an estimated autocorrelation of 0.72, which is similar to time-series patterns for salmon and several common regional climate indices (e.g., Mantua 2004). This suggests similar environmental controls may affect salmon and shad populations, although a positive autocorrelation in R/S will at least partially result from the population age structure (multi-age spawning).

Hinrichsen et al. (2013) assessed total Columbia Basin shad recruitment in relation to the development of reservoirs and assessed the effects of summer (May to August) river temperature and discharge on the upriver distribution (the fraction of the total run that passed above McNary Dam). They concluded that completion of The Dalles Dam allowed access to substantial upstream habitat (a major effect on population abundance) and that completion of John Day Dam provided a large area of additional reservoir habitat, resulting in an additional (but smaller) increase in shad production. They also found that the upriver distribution was related to both river temperature and discharge, and that both temperature and discharge were affected by the major expansion of reservoir storage volume since the 1950s. They concluded that future changes in river temperature and discharge are likely to affect the abundance and distribution of shad in the Columbia Basin.

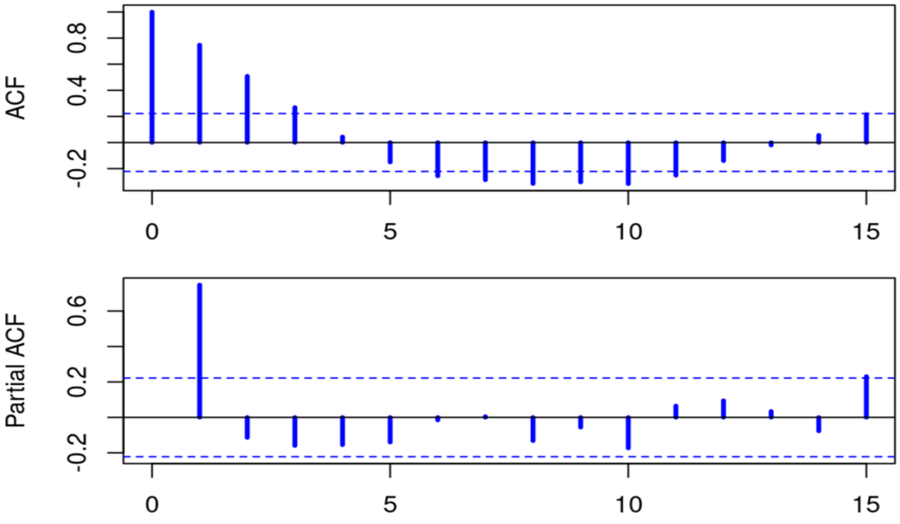

Figure 20. Autocorrelation (ACF) and partial autocorrelation (PACF) functions computed for the recruits-per-spawner time series. Dashed lines are the 95% confidence intervals for a correlation of zero.

Turning to the ocean phase of shad life history, we asked if shad populations have been affected by major ocean regime shifts, which strongly affected Pacific Northwest salmon populations in 1977, 1989, and 1998 (Overland et al. 2008). These regime shifts are marked by dashed vertical lines in Figure 19. The response of the shad R/S index to these regime shifts is not strong, but there appear to be moderate declines in R/S following the 1977 and 1989 shifts, and a brief increase following the 1998 shift.

To examine additional effects of ocean and freshwater conditions on population dynamics, we performed an exploratory analysis of correlations of five local and regional climate indicators with shad recruits per spawner at various time lags. The five indicators were: the Pacific Decadal Oscillation (PDO), the North Pacific Gyre Oscillation (NPGO), the Oceanic Niño Index (ONI), an index of coastal water temperature off Oregon, and Columbia River discharge at the Dalles. At lags within the shad life span (corresponding to possible direct effects), only the NPGO (all seasons) and spring coastal water temperature show strong correlations with shad recruitment. While the NPGO is defined by regional patterns of ocean surface temperature, it is driven by processes of upwelling and horizontal ocean convection, which in turn control lower trophic production (Di Lorenzo et al. 2008). Similarly, the near-shore spring coastal water temperature (CWT) is correlated negatively with the strength of coastal upwelling which drives lower trophic production on the shelf (Bakun et al. 2015). Thus, both NPGO and CWT could reflect effects of temperature and food supply on growth and survival of shad in the ocean.

Climate Indicators of Shad Production. For Columbia River salmonids, regional climate indicators have become an important, if problematic, part of interpreting and predicting population dynamics (e.g., Burke et al. 2013; Litzow et al. 2018; Chasco et al. 2021). To determine if climate indicators are also important for shad production, we conducted an exploratory analysis to see if shad production (recruits per spawner) is correlated with indicators that are commonly used for salmonids.

We examined cross-correlation functions (CCF; Shumway and Stoffer 2006) relating shad recruits per spawner (R/S) to seasonal averages of five climate indicators, including four marine indicators and one river indicator (Table 3). Monthly and daily environmental series were averaged over 4 seasons: winter (January to March), spring (April to June), summer (July to September), and autumn (October to December). The analysis was restricted to 1976 and later, after all dams were in operation. We computed cross-correlations between R\S and each seasonal predictor, including lags up to 10 years before and after the shad birth (age 0) year. RpS is indexed to the birth year with recruits returning 4-5 years later, so a lag of zero would relate predictors to the ocean entry year (spring spawning, fall outmigration) and a lag of +4 or +5 would relate to return year. Correlations within this life span could indicate direct effects of the indicator on shad reproduction or survival, while correlations at lags outside the life span could only represent indirect effects.

Table 3. Climate indicator series used in the analysis.

Indicator	**Abbreviation**	**Source**
Pacific Decadal Oscillation	PDO	NOAA Physical Sciences Laboratory (psl.noaa.gov/pdo)
North Pacific Gyre Oscillation	NPGO	Emanuele Di Lorenzo, Georgia Tech (o3d.org/npgo)
Oceanic Niño Index	ONI	NOAA Climate Prediction Center (www.cpc.ncep.noaa.gov/data/indices)
Coastal Water Temperature	CWT	Computed by T. Wainwright based on multiple NOAA data sets
Columbia River Discharge at The Dalles	DIS	National Water Information System (waterdata.usgs.gov/nwis/)

Results of the analysis are shown in Figures 20 to 25 For the Pacific Decadal Oscillation (PDO), all four seasonal averages have strong negative correlations at lags of -9 and -10 years, which are outside of the shad life span and thus not easily explained. Within the shad life span, only summer (JAS) PDO has a noteworthy positive correlation at lags of +5 and +6 years, approximately the adult return years. This correlation is positive, which is opposite from the typical correlations reported for salmonids and the PDO. The North Pacific Gyre Oscillation (NPGO) in all seasons correlates with shad at lags of 0 to +3 years, corresponding with years of ocean entry and ocean growth. Oceanic Niño Index (ONI) has no strong correlations with shad but has weak negative correlations in (or just before) the birth year, which might suggest ENSO effects on freshwater rearing conditions. Spring (AMJ) coastal water temperature (CWT) exhibits a strong negative correlation at lag 0, and a strong positive correlation at lag +5; that at lag 0 could relate to temperature effects on ocean productivity in the ocean entry year. River discharge (DIS) has no substantial correlations during the shad life span, but several strong correlations at negative lags, suggesting there may be some strong indirect effects.

Exploring correlations among shad populations and climate indicators can contribute to understanding the effects of climate change on population dynamics. At best, correlations can suggest relationships that can be explored using detailed process studies. At worst, they can be overinterpreted and lead to acceptance of unproven hypotheses (von Storch 1999). In particular, the nominal significance levels shown in the figures should not be treated as hypothesis tests – each graph presents numerous correlations, so it would not be surprising to find a few correlations that are significant by chance. In fact, a single significant value invalidates the tests at all other lags (Shumway and Stoffer 2006). Similarly, a lack of significant correlations may suggest a lack of relationship, but in a complex system there are many other factors that could obscure the correlation even if there is a causal relationship. So, results here may be suggestive but are not conclusive.

At lags within the shad life span (corresponding to possible direct effects), only the NPGO (all seasons) and spring coastal water temperature were strongly correlated with shad recruitment. While the NPGO is defined by regional patterns of ocean surface temperature, it is driven by processes of upwelling and horizontal ocean convection, which in turn control lower trophic production (Di Lorenzo et al. 2008). The single season with strong correlations for the near-shore spring coastal water temperature (CWT) is a bit harder to interpret. If this were a direct effect of temperature, we would expect the correlation to hold across all seasons, because shad are in coastal waters for more than a year. However, spring temperature is correlated negatively with the strength of spring coastal upwelling which drives lower trophic production on the shelf (Bakun et al. 2015). Thus, the negative lag-0 correlation between shad and spring CWT could reflect production in the ocean-entry year, although there is a seasonal mismatch between spring upwelling and shad outmigration in the fall. In conclusion, it is plausible, but certainly not conclusive, that both NPGO and CWT could reflect direct effects of temperature and food supply on growth and survival of shad in the ocean.

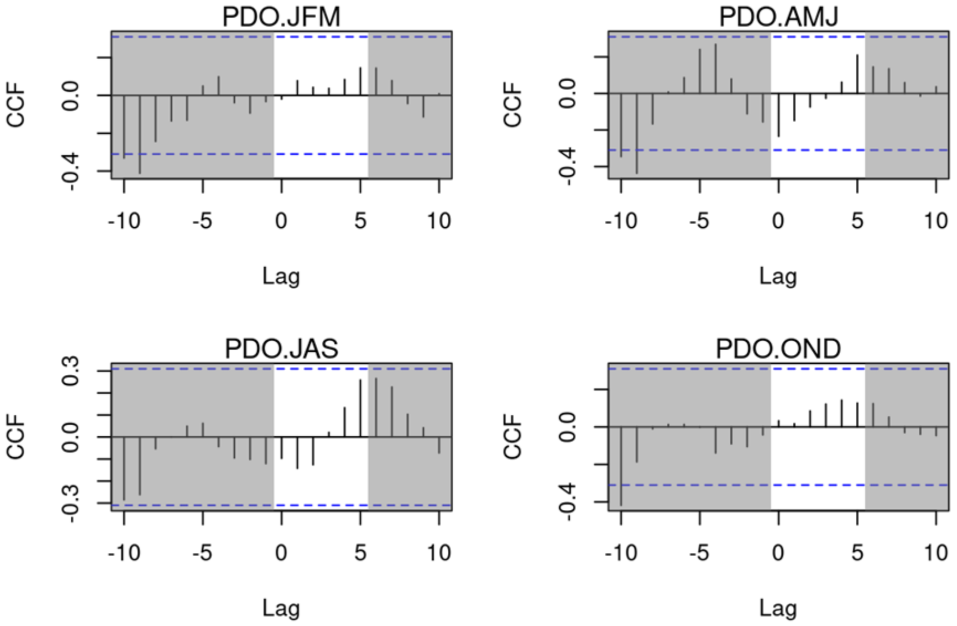

Figure 21. Cross-correlation function (CCF) of seasonal average Pacific Decadal Oscillation (PDO) with lagged shad recruits-per-spawner. Seasons are January to March (JFM), April to June (AMJ), July to September (JAS) and October to December (OND). Dashed blue lines are approximate 95% confidence limits under a no-correlation hypothesis. Grey regions cover lags that are outside the typical shad life span.

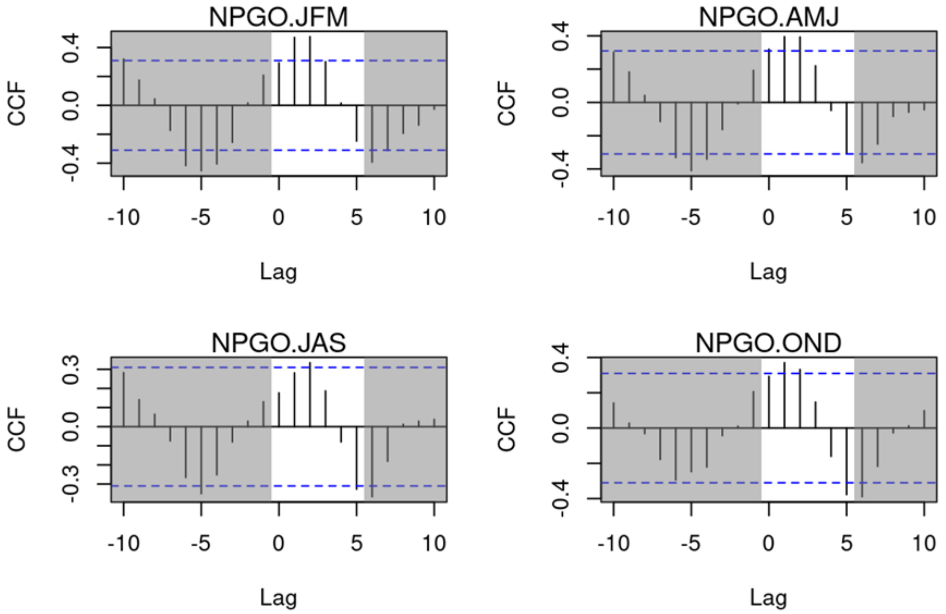

Figure 22. Cross-correlation function (CCF) of seasonal average North Pacific Gyre Oscillation (NPGO) with lagged shad recruits-per-spawner, as in Fig. 21.

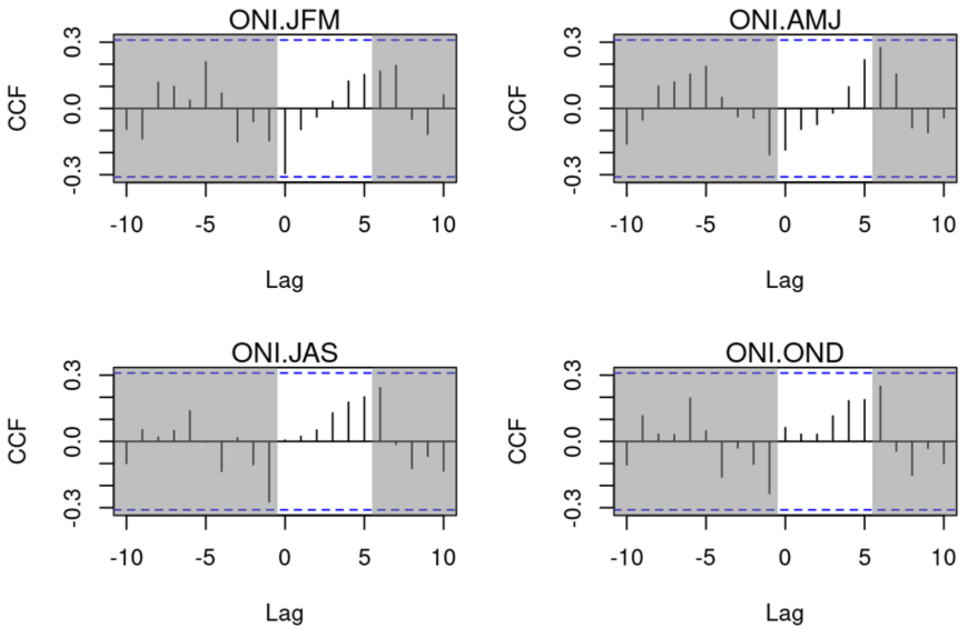

Figure 23. Cross-correlation function (CCF) of seasonal average Oceanic Niño Index (ONI) with lagged shad recruits-per-spawner, as in Fig. 21.

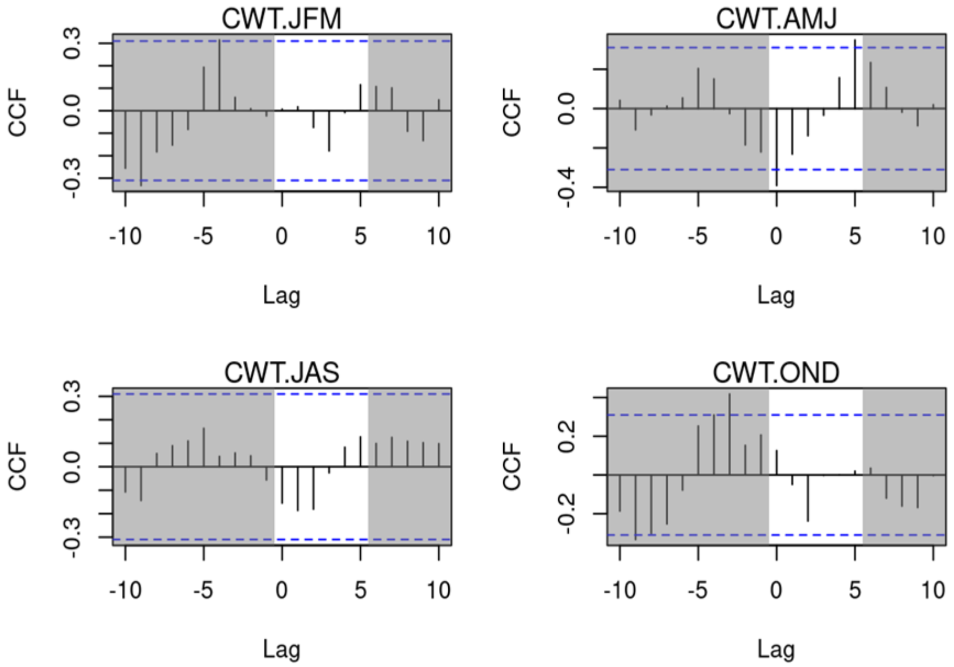

Figure 24. Cross-correlation function (CCF) of seasonal average coastal water temperature (CWT) with lagged shad recruits-per-spawner, as in Fig. 21.

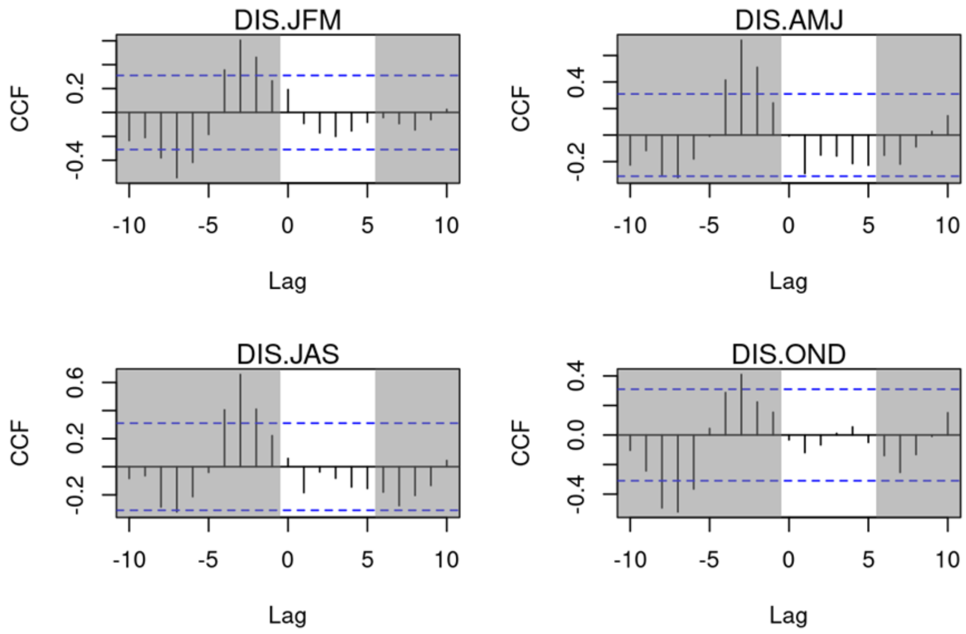

Figure 25. Cross-correlation function (CCF) of seasonal average Columbia River discharge (DIS) with lagged shad recruits-per-spawner, as in Fig. 21.

D.6. Nutrient Addition

Transport of marine nutrients into freshwater habitats by upstream migrating adult Pacific salmon is well documented (Willson et al. 1998). Haskell (2018) notes that “Pacific salmon are large-bodied nutrient vectors that contribute 3.0% of their body mass as nitrogen (N) and 0.36% as phosphorus (P) in the form of excretions, gametes, and carcasses to freshwater areas where they spawn (Brock et al. 2007).” The millions of salmon that once spawned and died in the Columbia Basin no doubt imported huge quantities of marine nitrogen and phosphorus into the ecosystem. Unlike shad, the vast majority of their carcasses were deposited on their spawning grounds in smaller rivers and streams of the basin. Declines of salmon populations have reduced nutrient inputs (Haskell 2018), likely affecting the myriad components of terrestrial and aquatic communities that consume them.

Nutrient subsidies have also been noted for other anadromous fishes, including alosines and lampreys. Walters et al. (2009) documented marine isotopes in all components of the food web of a small stream after its use for spawning by alewives in their native range. Twining et al. (2017) estimated that shad accounted for about half of the marine-derived phosphorus and nitrogen entering the Columbia River ecosystem in anadromous fish, with much of the rest coming from Chinook salmon. The importance of shad was partially due to the decrease in average size and number of Chinook salmon and other anadromous fishes (except shad) while shad numbers increased. Declines in size of all species contributed to about a 6% decline in total phosphorus contributed to the lower river in the form of anadromous fish returning from the Pacific Ocean. The amount of nitrogen and phosphorus coming into the mainstem Columbia River in anadromous fish is relatively small compared to the background concentrations of these dissolved nutrients in the river. Haskell (2018) estimated that the phosphorus contributed by shad only amounted to a 1.3 % increase in phosphorus loading over background river levels during the shad spawning season and would account for less than 0.2% of the annual discharge of phosphorus from McNary Dam.

However, incorporation of marine nutrients from shad into the Columbia River ecosystem is complicated for the following reasons (Haskell 2018):

- Most shad spawn and rear as juveniles in the lower river reservoirs, so the effects of nutrient subsidies are skewed towards the lower parts of the basin.
- Shad in the Columbia are iteroparous, so spawning adults do not necessarily die after spawning. Apparently around 32% of shad are repeat spawners (Petersen et al. 2003), and some presumably survive spawning, return to sea, and die there prior to return and thus also return no nutrients to the river, except those from gametes. Thus, counts of adult shad do not equate to nutrients transferred, as occurs with salmon, especially when the heavier average weights of adult salmon are taken into account (about 8.1 kg for Chinook and 2.2 kg for sockeye, according to Chapman (1986), compared to 1-2 kg for shad).
- Nutrients are exported with the movement of juvenile shad from freshwater, where they grew, to the ocean.
- Retention time of nutrients is low, given the rapid water turnover in the reservoirs.
- Shad are water-column spawners, so dead fish and gametes are less likely to accumulate in shallow water where they would enter food webs and benefit salmon. In contrast, salmon spawn primarily in shallow streams where carcasses are quickly scavenged and decomposed.
- Background nutrient loading and flux in the river ecosystem are not well understood.
- Nutrient transfer is related in part to fish size, and the average size of Columbia River adult shad has declined since the 1970s, when they started becoming abundant (Twining et al. 2017).

When these factors are all considered, shad contribute nutrients but mainly to food webs in mainstem reservoirs. Haskell (2018) concluded that shad “have little effect on underlying nutrient balances in the lower Columbia River” and provide a small fraction of the total supply of nutrients in the mainstem river. Twining et al. (2017) found that the large fluctuations in the numbers of returning shad to the river destabilized nutrient fluxes, making the “new” nutrients less reliable in their availability. Presumably, shad are not a substitute for salmon nutrients because most of the nutrient deficit created by declining salmon runs occurs in the upper watershed where salmon spawn and die. It is possible that more shad spawn below Bonneville Dam than is currently assumed; if so, shad may be important contributors to nutrient dynamics in the estuary where both salmon and shad rear (Haskell 2018). Overall, however, the nutrient dynamics are poorly understood throughout the system, and there is no indication that nutrients are a major factor limiting shad and salmon abundance.

D.7. Interactions with Other Species

Introduction. Adult shad are far more numerous than adults of anadromous salmonids in the Columbia River. Their abundance developed rapidly, tracking the construction of numerous hydropower dams, and coinciding with declines in numbers of salmon, steelhead, and other fishes (Hammann 1981, Bottom and Jones 1990, Weitkamp et al. 2012). Not surprisingly, this rise to extreme abundance has led to speculation that shad adversely affected native fish populations, especially salmonids and other anadromous species (Bevan et al. 1994, Parsley et al. 2011). However, the scope for interactions between shad with other anadromous fishes depends on overlap in the timing and distribution of various life stages. Figure 26 indicates that the greatest potential for overlap in the use of food and space occurs in the early life history stages, in the mainstem river. Interactions between adult shad and sockeye salmon also seem possible, given that biomass of individual adult shad (1-2 kg) is close to the biomass of adult sockeye salmon (2.25 kg, Chapman 1986). The two species have peak run timing that largely coincide (Figure 27).

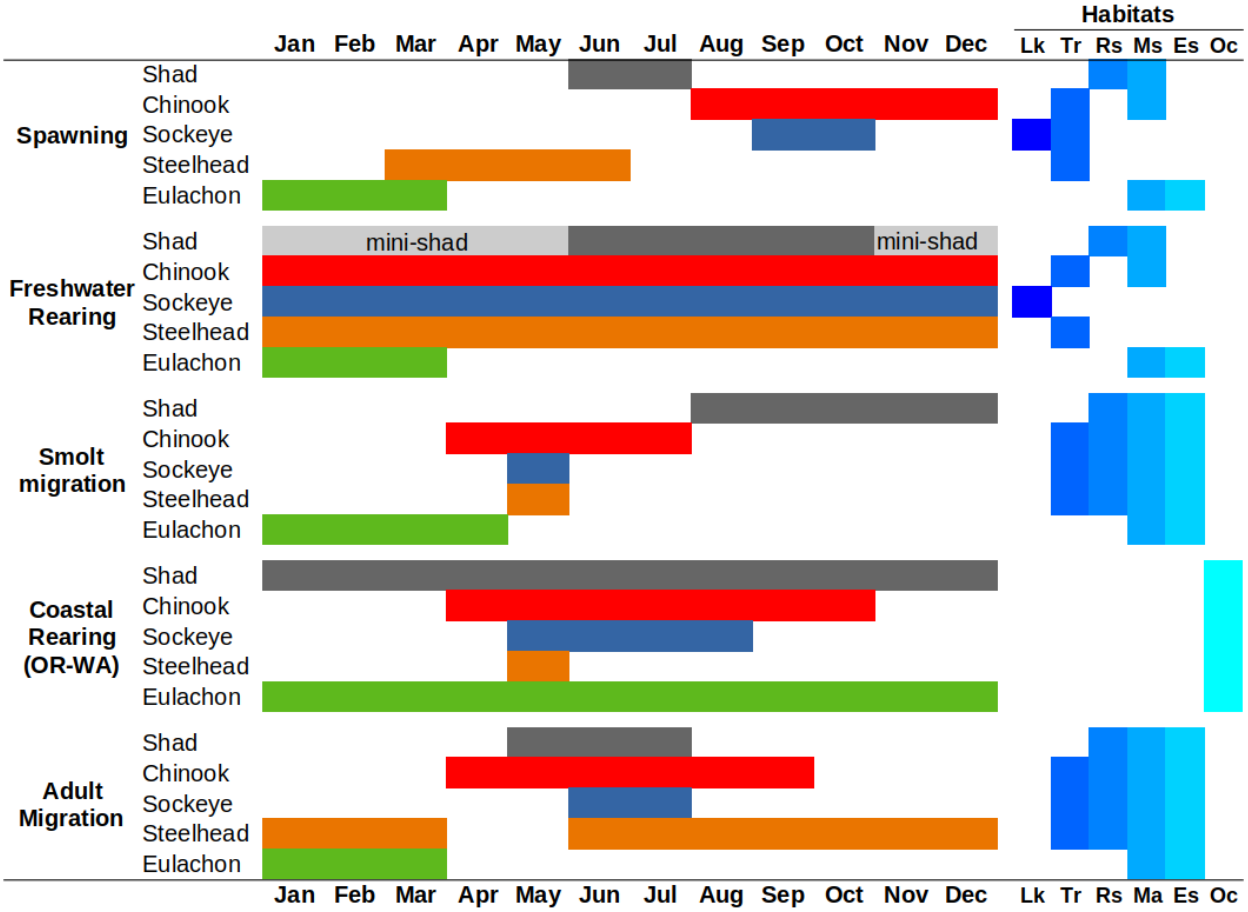

Figure 26. Comparison of seasonal habitat usage by selected anadromous fishes in the Columbia River Basin. On the left are typical seasons for key life history stages. On the right (blue to blue-green) are habitats used: Lk = lakes, Tr = tributary streams, Rs = mainstem reservoirs, Ms = mainstem river, Es = estuary, Oc = coastal ocean off Oregon and Washington. Data from this report, plus Busby et al. (1996), Gustafson et al (1997, 2010), Myers et al. (1998), Beamish (2018).

Impacts predictably come through exploitative competition for food, predation (either direct, or indirect by affecting predator populations), increased disease, or some combination of these processes. However, detection of these effects is complicated by the dearth of research on shad in the basin and the many factors affecting salmonids over the same time period that are unrelated to shad (e.g., habitat degradation and loss, dam operations, pollution, other non-native species, ocean conditions, climate change, etc.). Here we briefly outline the some of the more likely ecological connections between shad and salmonids, emphasizing that not all are negative.

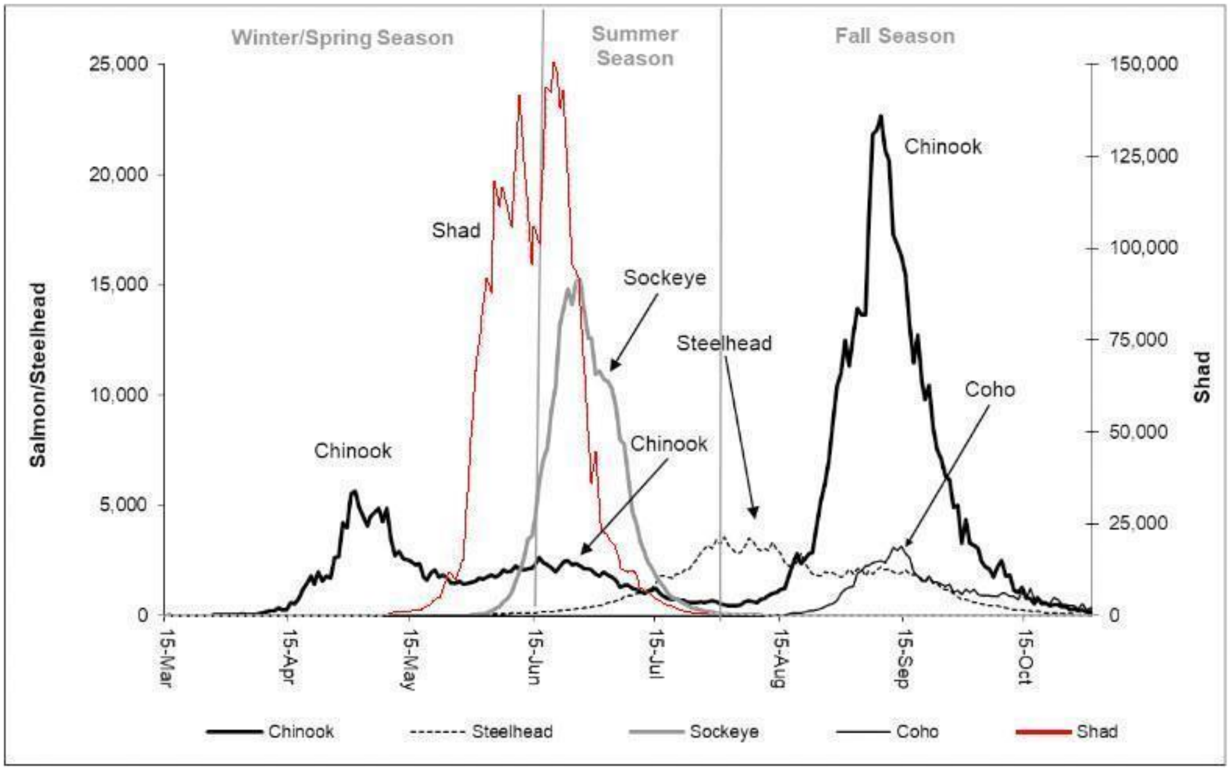

Figure 27. Timing of major runs of salmon and steelhead compared to that of American shad in the Colombia River. Data are average daily counts at Bonneville Dam for 2008 to 2020. Graph modified from JSCRMS (2021).

Diet and Competition. Shad in their native range feed in the pelagic zone, primarily on zooplankton and insects (Limburg et al. 2003 and references therein), similar to juvenile salmon in reservoirs and estuaries. Competition for food, space, or other resources is often inferred if species co-occur and use the same resources, although true competition does not occur unless the shared resources are limiting. Shad do not compete for resources using aggressive behavior (interference competition), but exploitative competition for food is plausible, just because of the large numbers of juvenile shad that must occur at times. Both juvenile salmon and shad consume zooplankton in the reservoirs when ocean-type Chinook salmon are moving downstream (McCabe 1983, Haskell et al. 2006, Sauter 2011). The migrations of other salmonid smolts are largely completed by the time juvenile shad become prominent in the riverine community although in the estuary shad and juvenile salmonids co-occur year around (Bottom et al 1984).

In the estuary, Sauter (2011) found that diets of juvenile shad in one year were dominated by copepods and the amphipod *Americorophium*. In the following year, copepods and cladocerans (*Bosmina*) were the main dietary items but insects were also important. In the estuary in 1980-81, age-1 and age-2 shad consumed copepods (calanoid, cyclopoid, and harpacticoid), *Daphnia*, *Americorophium*, and opossum shrimp *Neomysis* (Bottom and Jones, 1990). Age-0 shad consumed copepods and *Daphnia* but did not consume larger organisms, such as *Americorophium*. The three age classes of shad fed more on zooplankton than most other fish species in the estuary (Bottom et al. 1984). However, juvenile Chinook salmon also ate zooplankton, but more narrowly focused on *Daphnia*. Most other small fishes fed on zooplankton to some degree as well. Shad were a minor share of the fish captured by Bottom et al. (1984). Nevertheless, juvenile shad are apparently voracious feeders on zooplankton. Only 2.8% of the stomachs sampled from age-1 shad in the estuary were empty (Bottom and Jones 1990) indicating active feeding and abundant food. Bottom et al. (1984) found that age-1 shad had some of the highest growth rates of any fish species in the estuary, which was highest in spring (1.76%/d in April-June), intermediate in summer (0.73%/d in July-August), and lowest in winter (0.08%/d in February-March). They estimated that the consumption rates for age-1 shad ranged between 6-9 %/d during spring.

Another factor potentially affecting interactions of shad with other species is development of the hydrosystem, which substantially changed food webs of the lower Columbia River (Bottom et al. 2005, Maier and Simenstad 2009). One of the major changes was the shift from a macrophyte-based detrital system to a food web based on phytoplankton and microdetritus (Sherwood et al. 1990). Reductions of emergent wetlands eliminated more than half the area of tidal swamps and marshes. Emergent plant production has decreased by more than 80%, and microalgal production on tidal flats has been reduced by approximately 15%. Sherwood et al. (1990) estimated that the standing stock of invertebrates that feed on macrodetritus, a major prey for juvenile salmonids, would have been approximately 12 times more abundant than now. Data for pre-hydrosystem phytoplankton abundance are not available, but chlorophyll-a fluorescence in the free-flowing portions of the upper Snake River is four times greater than fluorescence in the reservoir above Bonneville Dam (Bristow et al. 1985). Based on phytoplankton data and carbon budget estimates of Small et al. (1990), the post hydrosystem delivery of phytoplankton to the lower river and estuary is almost seven times greater than it was under historical conditions, and upstream sources provide most of the phytoplankton in the estuary (Sherwood et al. 1990). Overall, the shift from a macro-detritus dominated food web to one dominated by phytoplankton and microdetritus is favorable for filter-feeding predators like shad. The abundance of shad in the Columbia River increased dramatically after 1960, a period that coincides with the development of the current hydrosystem. It is unknown if this change in the food web was a major contributor to recent increases in shad populations, but the feeding behavior of shad is well suited to benefit from this change in their primary food resources.

Overall, there is no direct evidence that zooplankton in reservoirs are a food resource for which shad compete with salmon and thereby limit salmon production or vice versa. However, Haskell et al. (2006, 2013) suggested that the observed reduction in size and abundance of *Daphnia* in reservoirs resulted from shad predation because shad (and juvenile salmon) feed preferentially on larger zooplankters, although they detected no other effects on abundant zooplankton. In addition, Gadomski and Barfoot (1998) found that in reservoirs larval and juvenile shad were most abundant in edge or back waters, where retention time of water is longer, whereas juvenile salmon tended to be in the open waters. Use of edge (littoral) and open water (pelagic) habitat varies among salmon species, and with their progression downriver in the case of subyearling Chinook salmon (McCabe et al. 1986), complicating generalization about habitat and prey overlap with shad. Parsley et al. (2011) noted that when shad are abundant, they can be found in virtually every habitat in the reservoirs, and move readily between habitats (e.g., diel vs. nocturnal movements). Thus, it seems prudent to assume that there is scope for competition for food between juvenile salmon and shad, but there is currently no evidence that it occurs to any significant extent.

Balanced against these possible competitive (hence negative) effects of shad on salmon, Haskell et al. (2017) found that subyearling Chinook salmon fed on juvenile shad as soon as shad became abundant (August). They stated, “By switching from planktivory to piscivory, subyearlings likely derive an energetic benefit from juvenile American shad in the Columbia River” (p 297). Such a benefit is predicated, however, on the assumption that shad provide suitable net nutritional value. While few studies have been conducted on juvenile shad in freshwater even less is known about their lives and interactions with other species in the estuary and ocean. Once in the estuary, juvenile shad face a different set of predators and competitors, although they presumably also continue to share space and food with juvenile salmonids (chiefly ocean-type Chinook) that are emigrating at the same time. Diets of juvenile salmon vary with species and habitat (e.g., pelagic and littoral-intertidal) as well as season, complicating analyses. However, there is considerable overlap in the diets of the dominant salmonids and non-salmonids in the estuary, including other native fishes as well as shad (McCabe et al. 1983). In terms of frequency of occurrence, shad were the most common fish species in open waters of the Columbia River estuary from 2007 – 2010 (Weitkamp et al. 2012). Despite their overall abundance, juvenile shad were scarce in fish samples collected by Emmett et al. (2004) in the Columbia River plume in June. Shad were orders of magnitude less numerous than Pacific herring and whitebait smelt, for example. Thus, when most juvenile salmonids go to sea, shad would seem to be a relatively unimportant part of their ocean habitats and thus not be a significant competitor for food.

Overall, possible competition for food is considered to be primarily associated with juvenile shad vs salmon, in part because of the sheer numbers of juvenile shad at times. However, while returning adults are fewer in numbers, they are much larger in size, and thus constitute a possible source of feeding competition. Limited studies on the East Coast indicate some feeding occurs during upstream migrations of shad (Harris and McBride 2009) and also in alewife, a smaller but similar species (Stewart et al. 2021). However, it is much less feeding than occurs at sea. Bottom et al. (2005, p.135) concluded that “in the absence of scientific evidence of direct competition or resource limitation, we cannot assume a deleterious effect [of shad] on juvenile salmonids.”

These confusing results indicate that a bioenergetic model like that of Sauter (2011) could be useful to explore the interactions between shad and juvenile salmonids and other fishes. Sauter (2011) developed a model for age 0 shad but did not apply it; the author simply offered suggestions and preliminary analyses showing how it could be applied, with caveats. The author indicated that empirical data are insufficient to parameterize the model. Instead, the model mostly depends on data from an alewife model developed for the Laurentian Great Lakes, although alewife data seemed to be a good fit when compared to limited information on shad. Sauter (2011) also demonstrated how the model could be useful for looking at the interactive effects on juvenile salmon of water temperature, salmon size and behavior, and shad abundance as prey. Sauter (2011) concluded that more work was needed before her American shad model would be reliable.

Predation. The highly abundant juvenile shad provide abundant prey for birds and fishes in the river. The questions about these interactions include: How important are shad as prey for the array of potential predators on juvenile salmon? Do shad serve as a buffer, reducing predation on salmon and steelhead when shad are abundant, or by shifting the spatial distribution of predators to benefit salmon? Alternatively, does predation on juvenile shad maintain a larger predator population than would otherwise exist?

Diets of adult shad in freshwater are not well known, but they may consume small salmon both before and after spawning. Sauter et al. (2011) found that 74% of 407 adult stomachs they examined had prey, but not in large amounts. The amphipod *Americorophium* was the most common item consumed, followed by snails. Curiously, these are benthic organisms. Only a few unidentifiable fish parts were noted. A study of Atlantic shad, in the southern end of their native range, found that adults fed opportunistically during their upriver migration (Harris and McBride 2009). Prey included zooplankton, insects, some benthic invertebrates, and even shad eggs, but their food intake was not nearly sufficient to balance the energy demands of migration. These examples suggest that sampling the diets of adult Columbia River shad would be useful to address uncertainties about their possible predation on juvenile salmon.

Another largely unexplored ecological interaction is predation on adult shad by sea lions and other marine mammals in the lower river and estuary. The same questions posed for predation on juvenile shad by birds and piscivorous fishes can be posed here. How important are salmon as prey to pinnipeds in the estuary and lower river? Do adult shad buffer and thus reduce pinniped predation on adult salmon? Do shad allow larger populations of pinnipeds (either year-round or during seasons when at-risk salmonids are present) than would otherwise occur, thus indirectly increasing predation on salmon and other species? Wargo Rub et al. (2019) explored these questions after tagging data indicated that mortality of adult spring Chinook salmon that was not caused by fisheries, largely resulted from predation. Their model indicated a positive association between adult shad abundance and adult salmon survival (Figure 28, below). This correlation might occur if shad buffer pinniped predation, or the relationship may be coincidental if abundances of salmon, shad, and pinnipeds are driven by ocean conditions, to which they respond in ways that are independent but coincidental.

The complexity of predation effects is supported by the observations on eulachon (*Thaleichthys pacificus*) by Wargo Rub et al. (2019; also see Figure 26 above):

> *"Coincident with the warm surface waters and the lack of prey off central and southern California, an unusually large fraction of adult, subadult, and even some*

> *juvenile male California sea lions moved north into Oregon and Washington waters in search of prey. Many of those found their way into the CR in the winter months of January, February, and March. This increase in sea lion abundance within the lower CR also corresponded to an increase in the biomass of eulachon in the river. Thus, we suspect that eulachon attracted predators into the CR. It may be that the future status and trends in the eulachon population will drive abundance of sea lions in the river in coming years. However, we may also observe that the increased pinniped presence will persist due to an abundance of animals having "discovered" there is salmon available to them at this location (p. 1870)."*

It is possible that shad play a similar role as that hypothesized for eulachon.

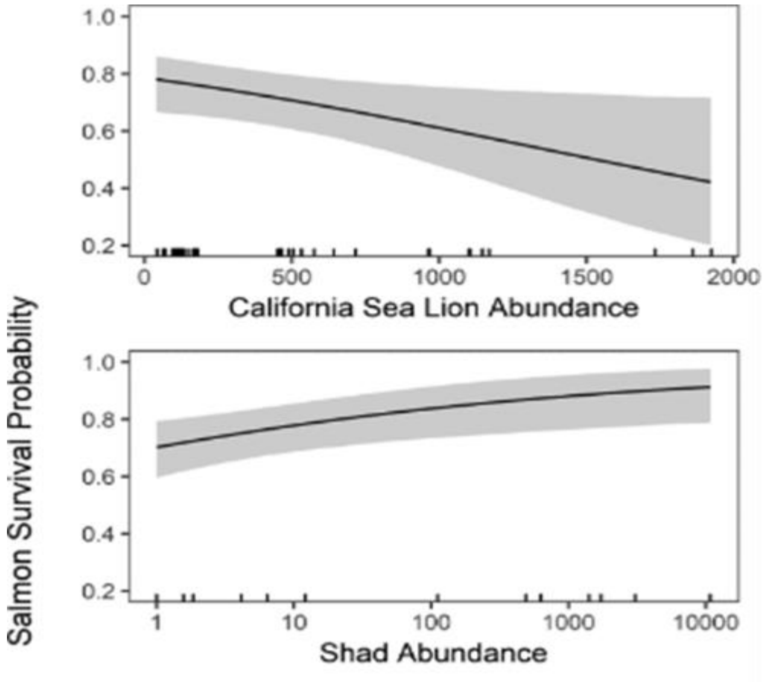

Figure 28. "Model response curves illustrating the relationship between salmon survival and California sea lion (*Zalophus californianus*) abundance (top) and American shad (*Alosa sapidissima*) abundance (bottom). The y axis for each graph represents survival probability, and the x axis is the range of observed values for each covariate. Vertical lines on the x axes represent covariate values observed and do not reflect the frequency of occurrence." From Wargo Rub et al. (2019).

Parasites and disease. Shad, like all fishes, support an array of parasites and micro-organisms that cause disease. Hershberger et al. (2010) found that up to 72% of adult shad carried *Ichthyophonus*, a parasite of marine fish. This parasite may cause a problem for salmonids, but its effects on shad are uncertain. Likewise, Shields et al. (2002) found a marine nematode in adult shad in the Willamette and Umpqua rivers. The nematode can cause ulceration of the guts in mammals, so it is mainly a human health concern.

Thiamine deficiency. Other than the more typical forms of ecological interactions between salmonids and shad (e.g., exploitative competition, predation, etc.), there is a very different possible interaction related to the diets of adult salmonids and thiamine (vitamin B_1) deficiency. This disease can be caused by consumption of prey fish (such as anchovies or herrings) that have high levels of thiaminase, the enzyme that breaks down thiamine, resulting in poor health of the predatory fish and, potentially, premature death. The biochemistry, physiology, and consequences for salmonids and other predators associated with this phenomenon were reviewed by Harder et al. (2018). In the Laurentian Great Lakes, consumption of alewife (an alosine) has been associated with significant health problems for salmonids. Wetzel et al. (2011, Chapter 4 in Parsley et al. 2011) investigated the possibility that consumption of adult and juvenile shad by other fish could result in high dietary thiaminase levels. Thiaminase specific activity assessed from juvenile and adult Columbia River shad was higher than that of alewife, which are an important part of the salmon diet in the Great Lakes. In California, recent studies have attributed some reproductive failure in Chinook salmon to thiamine deficiency, possibly as the result of consuming anchovies (R. Johnson, NMFS, personal communication, 2021). Overall, thiamine deficiency caused by shad consumption is a potential problem (early mortality in young and reproductive failure) for salmonids in the Columbia River, but direct evidence for an effect is so far lacking.

V. Fisheries

A. Overall

Shad were introduced to the Sacramento and Columbia rivers based on their reputation as a food fish, abundance, ease of culture, and appeal to commercial and sport fishers. In 1849, in a book on fish and fishing in North America, Henry William Herbert wrote of American shad, “This delicious and well-known fish, which is by many persons esteemed the queen of all fishes on the table, has been, until very recently, regarded as one that could be taken only with the net, and therefore no avail to the angler. It is, however, now clearly proved that… American shad will take a large gaudy fly freely, and being a strong, powerful and active fish, affords great play to the sportsman... The flesh of the shad is perhaps the most delicate of any existing fish; and, although it lacks the lusciousness...of the Turbot, it is preferred to that fish by many judicious epicures, notwithstanding the drawback occasioned by its innumerable and sharply-pointed bones” (quoted in McPhee 2002, p.227).

Much has changed since the 19th century, including the preference for and the appeal of shad as food. These changes are due to a range of factors involving the supply, demand, and the global expansion of fish markets today. On the supply side, there has been enormous expansion in the availability and variety of fish marketed fresh, canned, and frozen, originating from capture fisheries and aquaculture around the world, available throughout the year. Consequently, consumer choices and expectations have expanded far beyond locally produced and seasonally available fish. Given the description of shad consumption involving "innumerable and sharply-pointed bones," it is not surprising that they are no longer a preferred fish for eating, at least on the Pacific Coast. As a result, the small commercial fishery for shad that existed in the river in the 1970s (Parks 1978) has given way to a sport fishery (Figure 29). The current commercial ocean fishery for shad is almost entirely the result of incidental catch in other fisheries. Commercial ocean landings since 2000 show large swings, with landed weight rising while revenues decline (Figures 30 and 31). These trends seem to represent the influence of shad population increases on incidental catches rather than intentional or targeted harvests. With no commercial market for shad as food, increases in incidental catch would be expected to push prices downward. Indeed, over this period the market price has declined by 90%, and the catch (often in the whiting fishery) is often sold as crab bait or for fishmeal (Mark Lacy, personal communication).

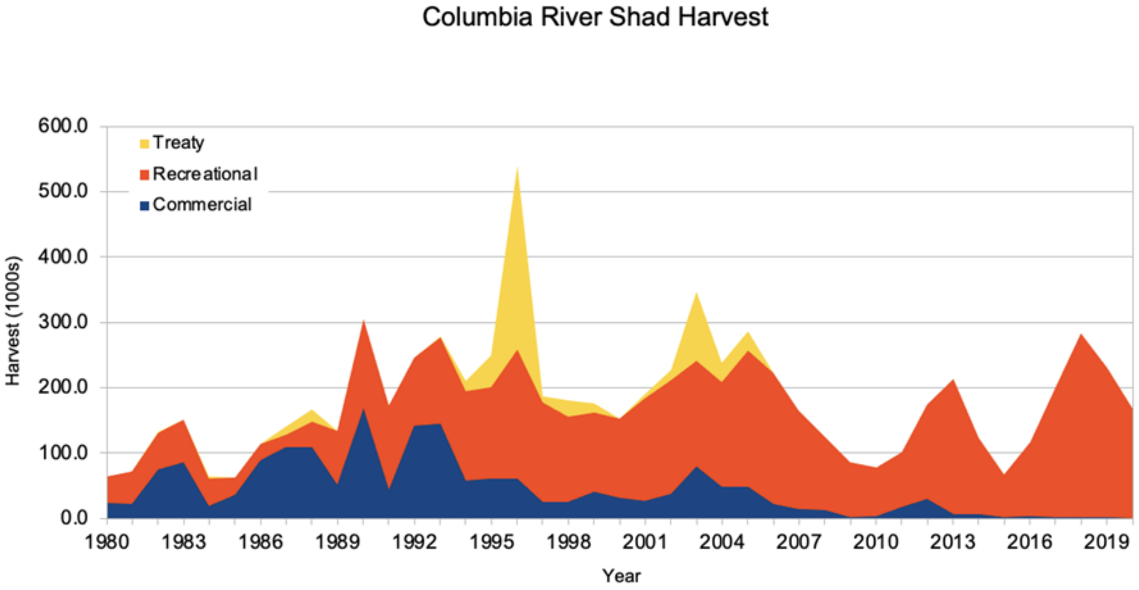

Figure 29. Columbia River shad harvest. Data from: Joint Columbia River Management Staff report (JCRMS 2021). Treaty harvest data are unavailable after 2005.

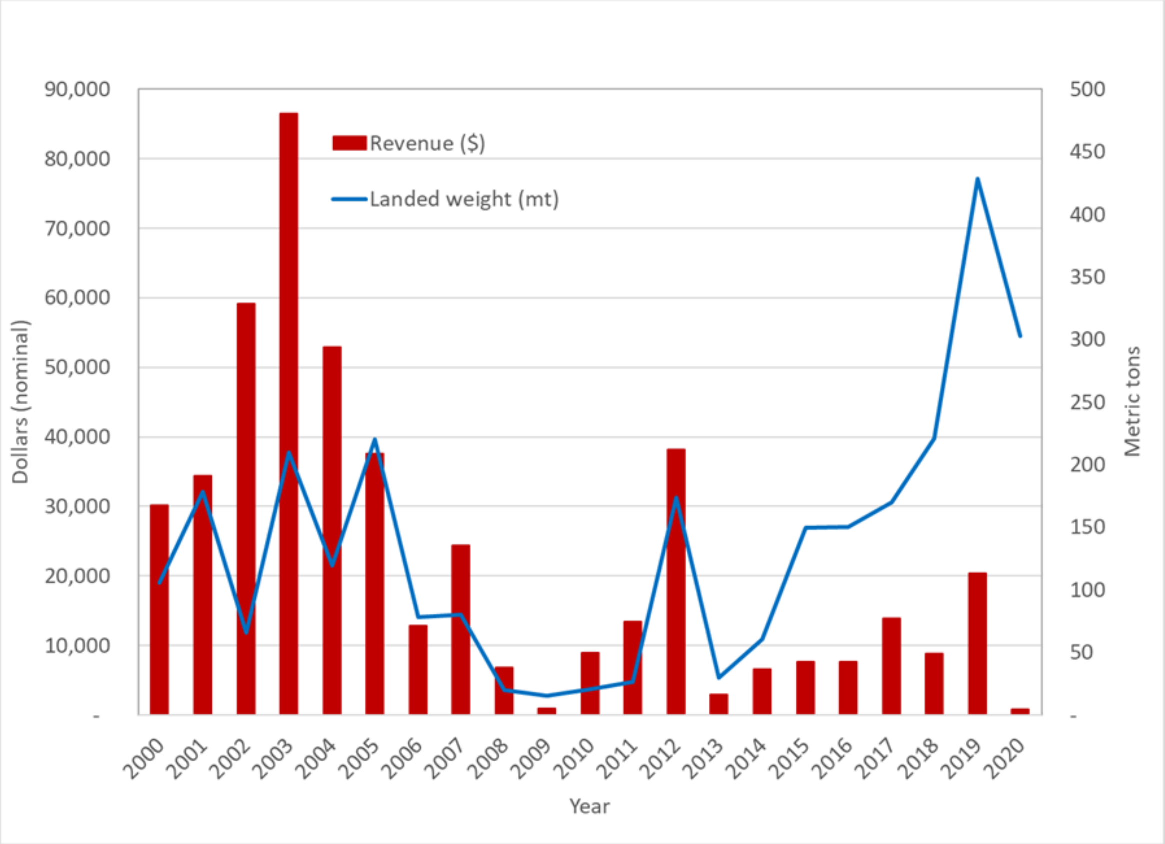

Figure 30. Commercial shad ocean landings and revenues in Washington and Oregon.
Source: Pacific States Marine Fisheries Commission (https://reports.psmfc.org/pacfin/f?p=501:1000).

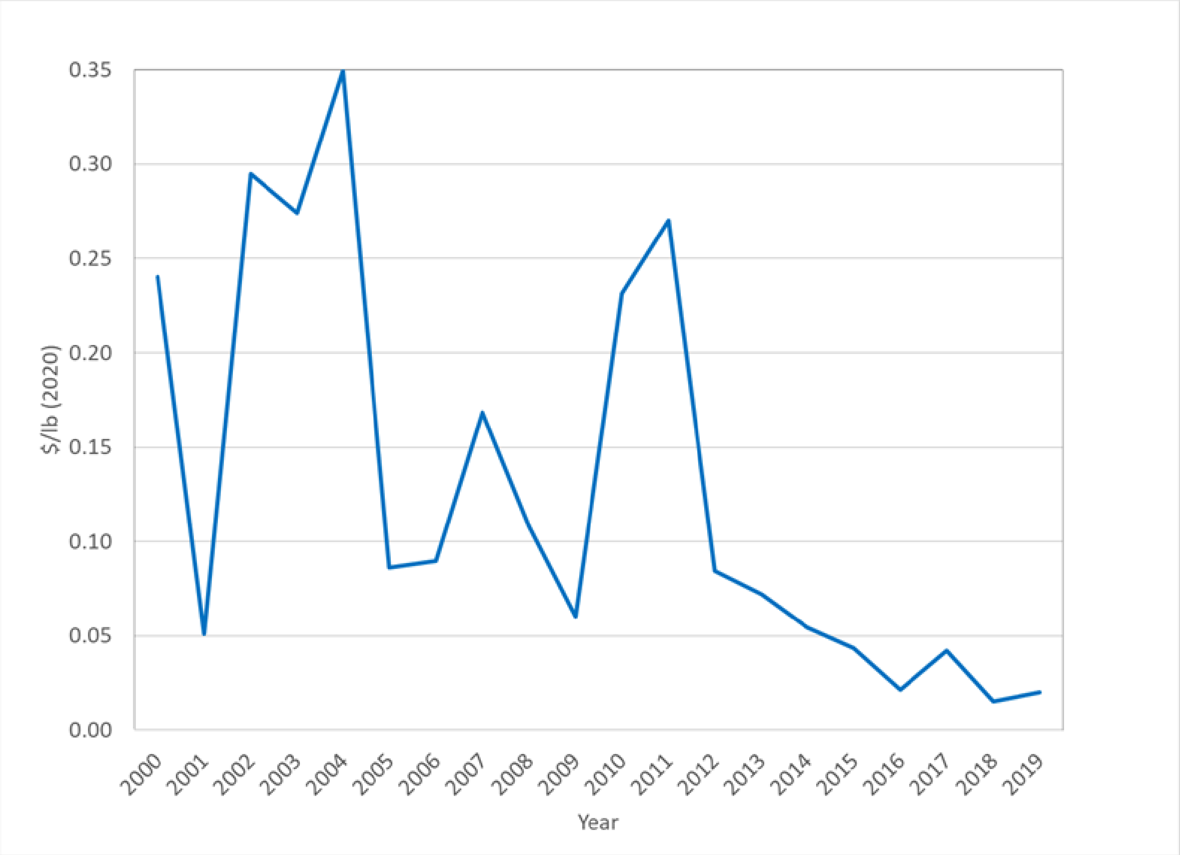

Figure 31. Average price for commercial shad ocean landings in Washington and Oregon. Source: Pacific States Marine Fisheries Commission (https://reports.psmfc.org/pacfin/f?p=501:1000).

Today, shad fisheries in the Columbia River continue, but they are primarily recreational (Figure 29; JCRMS 2021), though data on treaty catches have been unavailable since 2004. Annual total catches of shad ranged from > 500,000 in 1996 to < 100,000 in 2015. Estimates of catch rates ranged from < 5% of the Bonneville run size in 2020 to > 20% in 1996 (Figure 32; JCRMS 2021). Since 2000, on average 180,000 shad have been caught annually in the Columbia River: 85% recreational, 10% commercial (mostly incidental catch in other fisheries), and 5% treaty fisheries (JCRMS 2021).[1] Recreational catches have grown, accounting for most of the total recorded catch in recent years (Figure 32).

According to Tucker Jones, Columbia River and Ocean Salmon Program Manager for the Oregon Department of Fish and Wildlife (ODFW; pers. comm., October 2021) shad can be targeted by “both recreational and commercial fisheries. There are no limits on recreational fisheries and shad are an allowable sale in all treaty (OAR 635-041-0072) and non-treaty (635-042-0105) commercial fisheries. There is also a directed commercial shad fishery downstream of Bonneville Dam (in the vicinity of Gary Island) that is open annually under permanent rule (OAR

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[1] Treaty harvest is estimated for 2004 and 2005, and not included from 2006 onward.

635-042-0110).” But, as indicated above, catches of shad are erratic and “largely driven by economic forces, i.e., lack of markets.”

Because timing of the shad run overlaps with runs of salmonids listed under the U.S. Endangered Species Act (ESA), there have been efforts over the past decade to explore alternative harvesting gear types (purse seines, beach seines, pound nets) to increase shad catch while minimizing impacts to salmonids. “It is expected that harvest opportunity using these alternative gear types would be allowed in future fisheries if demand exists and catch rates warrant their use” (JCRMS 2021: 18). Gill net fisheries are currently permitted in the lower Columbia River, with restrictions on gill net size and mesh, as well as times and days when nets can be fished; these regulations have been in place since 1996 (JCRMS 2021). According to JCRMS 2021, p. 48: “The 2020 fishery produced no shad landings for the first time since at least 1980. The recent trend of low harvest is likely due to a relatively low market value for shad, the fishery being restricted to Area 2S only, and reduced catch rates in recent years.” Other factors that come into play include shutting down the shad fishery in the Bonneville Dam reservoir to eliminate incidental catch of endangered Snake River sockeye salmon (Columbia Basin Bulletin, July 9, 2020).

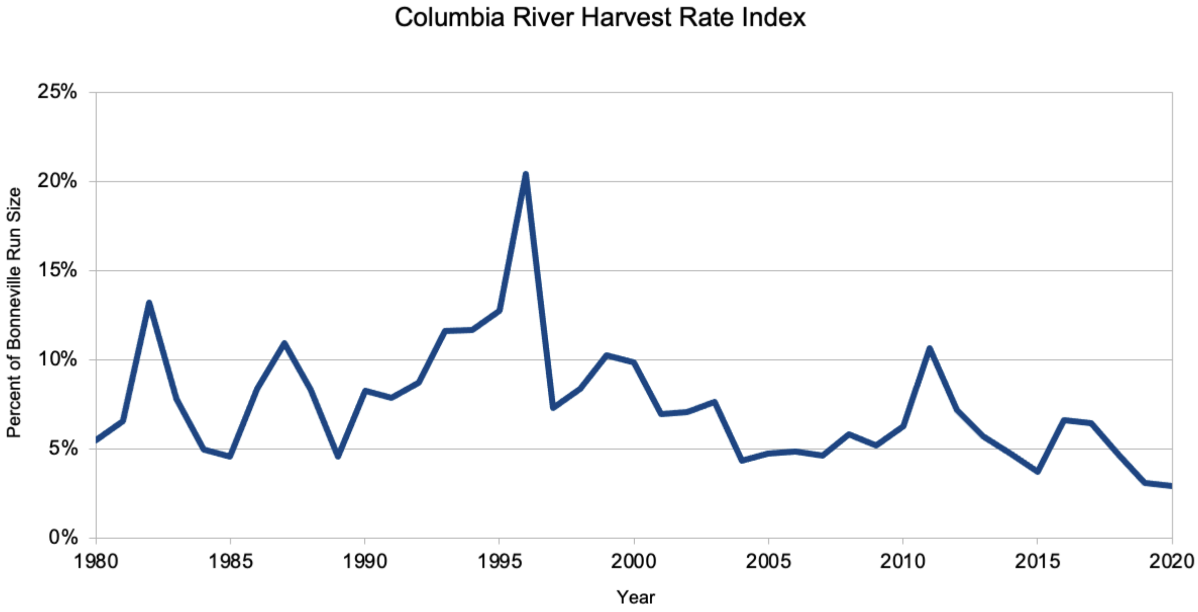

Figure 32. Harvest rate index (% of Bonneville shad count) for shad on the Columbia River. Data from: Joint Columbia River Management Staff report (JCRMS 2021).

B. Tribal Perspectives

Tribal perspectives are of central importance in the assessment of ecological and social impacts or benefits of shad populations as well as for assessing the current or potential fisheries for shad in the Columbia. No formal assessment of Tribal perspectives has been conducted, nor are we aware of any Tribe in the region taking a formal position on shad fisheries or management; such an assessment of Tribal perspectives and Tribal government positions on any shad fisheries development or eradication measures is imperative before any management measures are developed or implemented. We invited Stuart Ellis, CRITFC Harvest Management Biologist and Randy Settler, Yakima Nation Tribal fisherman, to share their perspectives with us during meeting on September 10, 2021.

Mr. Ellis confirmed that CRITFC Tribes have never set a formal policy on shad. He noted that as a non-native fish, shad are not a valued Tribal fishery and their potential disruptions to the restoration of native fishes is a concern. He shared the history of small-scale Tribal shad fisheries that have been pursued in the past, including trap fisheries. He discussed current challenges with limited and lack of market demand for shad as a key barrier for shad fisheries development. He indicated that non-Tribal recreational fisheries for shad are popular, in part because they are comparatively easy to catch, can be fished from shore (i.e., do not require a boat), and because angling gear is simple, often just a shiny hook. Human consumption of shad is variable, but shad are widely used as bait in crab traps. Non-treaty commercial fishing is discouraged in the river because of bycatch of salmon. Tribal fisheries primarily use dip nets and hoop nets from platforms over the river to capture shad. Shad may be caught and sold from any open Tribal fishery.

Shad are caught in spring and summer, but there is little market for them. A few are sold to wholesale dealers, primarily as a way to bring fishers to the dealers who want to buy salmon. These shad are likely used as bait. Foreign buyers have expressed interest in shad but only if available at a low price over an extended period, which is not very compatible with their migration timing and overlap with at-risk salmon. Moreover, development of new harvesting methods, such as fish wheels, would require start-up funding and testing, though the Wild Salmon Conservancy is testing pound nets. Putting traps in fish ladders has been discussed, but there is little enthusiasm for any method that involves modifying the ladders. Mr. Ellis thought that shad populations are large enough so that detrimental effects on salmon seemed possible. Shad could be affecting the entire Columbia River food web even if not overlapping at the same place and at the same time as salmon. Secondarily, he thought shad might be supporting a greater abundance of predators, such as sea lions. Mr. Ellis indicated that research on these issues and others, such as predation, is needed but no funding seems to be available.

Randy Settler, a citizen of the Yakama Nation, has fished the Columbia since he was a child. He shared his deep familial and cultural ties to fishing. His father fished his entire life, as did his grandfather, and ancestors for as long as can be remembered. He also has a long history of serving his Tribe and advising management agencies. He visited with us not in an official capacity, but to share his perspectives as a Tribal fisherman. He expressed his appreciation for this review and report. For Tribes to make decisions about shad, it is helpful to have as much information as possible. He recalled a time in the 1960s when he was young, there were commercial fisheries for shad; he recalled that the government providing canned shad for his Tribe, and he commented that he and his family were thankful for it. He shared his perspective that Tribal people have little interest in shad and Tribal decision makers had no official policy about shad. Mr. Settler noted the "rule" that four shad were the equivalent of one salmon in fisheries but have little value, so are tossed back into the river when taken as a by-catch while salmon fishing. He views shad a threat to salmon in numerous ways, e.g., interference in fish ladders with adult salmon migration passage, predation on migrating juvenile salmon, competition for natural food sources. All of these put additional pressures on salmon. He also noted that in his long time as a fisher, he has seen sea lions capture salmon many times but has never observed one taking a shad. Shad can be a nuisance for him as a fisherman. He said they catch many shad in hoop nets, and it can be chore to throw them back. Overall, he expressed a high level of concern that shad pose a problem for salmon but recognized that removing shad would be difficult and costly, though he indicated that alternate fishing methods, such as fishwheels, could become reliable means to catch shad.

We could find little in the published literature about Tribal shad fisheries. In 2007, the *Chinook Observer* reported that the Columbia River Inter-Tribal Fish Commission Tribes had a small-scale shad fishery of about 50,000 to 60,000 pounds caught and sold per year (Columbia Basin Bulletin 2007). That same year, non-Tribal sport and commercial (by-catch) fishermen caught approximately 130,000 pounds of shad (2007 Joint Staff Report, Oregon and Washington DFW). Columbia Basin Bulletin (2007) reported that the fish trap at The Dalles Dam was a source of fish for the Tribal shad fishery. Shad can be harvested from the trap while salmon and steelhead can be released. This fishery consequently is permitted under the U.S. ESA. In 2012, the Columbia River Compact approved a Tribal request for experimental fishing gear, such as drift gillnets, fish wheels, purse seines, and beach seines, for developing shad fisheries (Columbia Basin Bulletin 2012). As a result, ODFW issued two experimental gear permits in 2011 to evaluate the use of purse seine gear for shad. Although high river flows hampered effort, approximately 6,700 shad were harvested during late May through mid-June. A permit issued in 2012 also resulted in successful harvest, although catch data were not available. Tuohy et al. (2019) indicated that fish traps were being resurrected as a method of harvest that would allow for live release of salmon caught in the salmon fishery.

Overall, there seems to be little interest in shad for Tribal fisheries, despite their abundance. This appears to be the result of poor markets for shad, the difficulty of getting them to the markets, and by-catch of salmon in shad fisheries. Further, as a non-native species with no cultural importance, shad and their potential impacts to salmon and other native fishes remain a large concern for Tribes.

VI. Shad and the Hydropower System

As discussed throughout this report, the construction of hydropower dams and associated reservoirs on the Columbia River is probably a major factor responsible for the millions of shad now migrating up the river to spawn every year. The Dalles Dam inundated Celilo Falls, apparently a barrier to shad migration, and opened up hundreds of kilometers of new spawning and rearing habitat for shad when completed in 1957. This included run-of-river reservoir habitat, which appears to be optimal for rearing of juvenile shad. The unanticipated abundance of adult shad has created a situation in which management is minimal because shad seem to be doing so well without it, and because there is little interest in them from fisheries, cultural, or ecological perspectives.

Other than concerns related to ecological interactions, the sheer abundance and schooling of shad can crowd the fishways created to allow salmon to pass over the dams (Columbia Basin Bulletin 2019). This has created problems for processing fish in collection facilities, depleted dissolved oxygen in fish ladders, and hindered the identification and counting of migrating salmonids. For example, in 2019, about 30 times more shad passed over Bonneville Dam than salmonids (ca. 7.5 million vs 250,000). The reported shad numbers are probably low, both because of the difficulties of counting and the likelihood that some spawn below Bonneville Dam (Hasselman et al. 2012a, b).

Observations indicate that migrating shad prefer to go over, rather than under, a barrier, hence their success in using standard fish ladders on the Columbia. Research in the eastern USA, indicates that they avoid entering ladders with submerged entrances (Haro and Castro-Santos 2012). This behavior presents some options for dam modification to hinder shad migration, though earlier research was used to modify John Day Dam to facilitate, not hinder them (Monk et al. 1989). Even investigating the option of deterring shad seems to be a low priority, however. In the 2020 Biological Opinion by the National Marine Fisheries Service for the "Continued Operation and Maintenance of the Columbia River system" the sole mention of shad in 1,500 pages regards deterrence at Lower Granite Dam:

> *"1.3.7.3 Shad Deterrence. The Corps will investigate the feasibility of deterring adult shad from approaching and entering the Lower Granite Dam adult fish trap, alleviating the need to remove shad from the trap while processing adult salmon and steelhead, and thereby reducing stress and delay for ESA-listed target species. Measures for consideration will be developed in coordination with NMFS and may include acoustic deterrents and operational changes, such as instituting plunging flows or blocking overflow weirs (NMFS 2020 p. 88, also see p. 1423)."*

The overall conclusion of agency reports seems to be that shad are a nuisance when it comes to hydropower operations but not a serious problem.

VII. Discussion: Answers to Questions.

In this section, we provide short answers to questions posed at the start of this report.

1. What are the trends in American shad abundance in the Columbia River?

Before 1957, shad counts were generally below 20,000 adults per year at Bonneville Dam. After The Dalles Dam was built (1957), apparently facilitating upstream access, numbers rose to over 1 million per year, with nearly 7.5 million shad estimated in 2019. Since 1960, shad have increased at an average rate of about 5% per year, with no indication of yet reaching their carrying capacity. Numbers passing a few dams are now uncertain because some counting stopped, but this does not affect estimates of the total numbers passing key dams where counts continue. Continued monitoring of shad numbers passing the dams in the Columbia River and major tributaries is essential.

2. What are the potential ecological effects of shad on native aquatic communities of the Columbia River and nearshore Pacific Ocean?

Studies of shad have largely focused on direct and indirect effects on salmon and steelhead, so effects on the broader biotic communities are not known. There are many plausible ways in which shad might affect salmonids and other fishes. While many assume that the very large abundance of a non-native fish must be having an effect, there is little empirical evidence, if any, to demonstrate the nature or magnitude of an effect.

3. What is known about the life cycle of shad in the Columbia River System freshwater, estuary and ocean habitats?

We have some understanding of the freshwater portions of the life cycle of shad (e.g., migration timing, spatial distribution), but survival rates in different habitats and life stages are largely unknown. Information about shad behavior and movement once they enter estuarine or ocean waters is especially scarce.

4. Are there multiple life history patterns?

Most shad move out to sea in fall of their first year of life, but the Columbia River has a distinctive alternative, mini-shad, which complete their full life cycle in freshwater or spend at least a year in freshwater before going out to sea. Mini-shad can return as fully grown fish, and the factors affecting this life history variant are not known. We also do not know with precision what proportion of the population adopts the mini-shad pattern, nor the ecological implications of year-round resident shad in the basin. Similarly, the proportions of repeat spawning individuals in different reaches of the basin are not known. For example, are shad primarily semelparous in the upper reaches but less so nearer the ocean?

5. **What risks do shad present for anadromous salmonids and freshwater biotic communities?**

The risks (or benefits) of shad to salmonids are largely unknown, and more studies are needed to understand these relationships. There is some model-based evidence that adult spring Chinook salmon survival rates increase when shad numbers increase. The reasons are not clear but may involve buffering predation by sea lions or common response to changing conditions.

6. **Do shad magnify predation on juvenile salmon and steelhead by increasing the food supply for their predators or do they reduce predation by saturating the predators?**

There are insufficient data to demonstrate either of these possible effects, and few studies collect the kinds of data needed to answer the question. Predation impacts need thorough study, and both hypotheses are plausible.

7. **Do shad populations change the freshwater and marine food webs through competition, carcass decomposition, or indirect food web effects?**

The limited evidence does not suggest that shad are causing major changes to food webs. However, the lack of information prior to the arrival of shad, and prior to their becoming very abundant, hampers our ability to address this question fully. Importantly, the distribution of spawning by shad is skewed towards reservoirs in the lower portion of the basin, and juveniles feed and migrate later than most juvenile salmonids. Consequently, the likely scope for interactions is uneven among salmonid species, and among regions of the basin. Moreover, while the proportion of shad spawning multiple times is low, it is not clear whether the others die in the Columbia River Basin after spawning or at sea after returning there. These alternatives present different scenarios for nutrient cycling.

8. **Does shad abundance create significant problems for the hydropower system of the Columbia?**

When shad are numerous, they can crowd fish ladders and make it difficult to count salmonids. Any resulting errors in counting salmonids could create problems for managing endangered species. We could find no evidence, however, that hydropower managers regard shad as a major problem in terms of interfering with their operations.

9. **Based on the answers to these questions, should management of shad in the Columbia Basin be changed? If so, what management alternatives should be considered?**

Current evidence is inconclusive as to whether shad are having a negative, positive, or mixed net effect on salmon and other parts of the Columbia River ecosystem. Current management is passive because shad continue to be abundant but are of low value in fisheries. There are no restrictions on their harvest except when a fishery might also take endangered salmonids. We cannot recommend changes to management or operations based on the state of information at present.

VIII. Conclusions: Future of Shad in the Columbia River System

American shad are the most numerous anadromous fish in the Columbia River, far surpassing salmon and steelhead. Given their abundance, it is perhaps surprising how little we know about this species and its role in the Columbia River Basin ecosystem. Their sheer numbers (many millions of adults) suggest there should be some significant interactions with other fishes, and with the birds and mammals that prey on them. However, the limited studies do not identify clear and strong interactions between shad and salmon, or the role of shad in major ecosystem processes. A systematic, multi-year research program would be needed to address the questions posed in this document and to improve our understanding of the direct and indirect interactions of all life stages of shad with all life stages of anadromous salmonids and other organisms.

Any future interactions between shad, salmon, steelhead, and other parts of the Columbia River Basin's ecosystem will change as the climate changes, sea-level rises, river flow regimes change, and native species disappear while non-native species, like shad, flourish. The future of shad right now looks bright in the Columbia River (in contrast to shad's widespread decline in their native range). The Columbia River hydrosystem should continue to provide near-optimal habitat for shad spawning and rearing in the chain of flow-through reservoirs. A warmer climate should favor shad over salmonids, although much depends on the continued productivity of the river and reservoirs, the estuary, and, above all, the ocean. The winds and currents that create this productivity are likely to become even more erratic, so populations of shad and other fishes (and of everything that preys on them) are likely to show wide and unpredictable fluctuations.

IX. Recommendations

Research aimed at addressing critical uncertainties can help inform decisions by policymakers, fishery managers, and dam operators. Given the current state of knowledge about American shad in the Columbia River, a number of critical uncertainties could be addressed by a focused shad research and monitoring program. Continued monitoring of shad numbers passing the dams in the Columbia River and major tributaries is essential. Climate models predict that the basin and near ocean will experience climatic warming, hydrological changes to the basin from the hydrosystem will continue, and shad abundance shows no indication of reaching a plateau. These emerging issues and potential risks warrant increased attention by resource managers in the Columbia River Basin to address uncertainties about shad impacts to declining native species.

Such a program might benefit from a formal scoping process among management agencies and other stakeholders to identify and prioritize the critical uncertainties to be addressed, recognizing the merits and explicit costs of competing research priorities in the basin. In the interim, we recommend starting with a short-term [ca. five-year] goal of describing fundamental life-history patterns of the species in the Columbia River Basin: age-structure, habitat utilization (in time and space), survival rates, primary predators and prey.

Longer-term goals should include understanding the role of shad in freshwater, estuarine, and marine food webs as a basis for understanding direct and indirect interactions with native species, especially salmonids, eulachon, piscivorous birds, and marine mammals. A program like this could form the basis of adaptive management decisions, such as developing commercial and Tribal fisheries, building fish ladders that exclude shad, or developing shad removal programs to benefit salmon and other fishes among others. This will require not only data collection but the use/development of predictive life history models, starting with a general conceptual model of shad use of the Columbia River Basin.

More specific questions that need continued attention include:

Shad biology

- Have shad reached the furthest spatial extent of their occupation of the Columbia Basin as well as their peak abundance?
- How will climate change affect the distribution and abundance of shad?
- What is the distribution and suitability of spawning and rearing habitat, including spawning and abundance below Bonneville Dam?
- Are ocean-resident shad off Oregon and Washington primarily Columbia River fish or a mix from other West Coast populations?
- What are the principal sources of mortality during migration of adults and juveniles? What are the survival rates?
- How do water temperature and river discharge affect shad abundance?

Ecosystem effects

- How do shad influence other species in river, estuary, and marine ecosystems?
- What is the extent of competition between juvenile and adult shad and juvenile salmon in the Columbia River Basin? More specifically:
    - What is the role of predation as a possible population regulator of shad and salmon?
    - Do shad support elevated predator populations to the detriment of juvenile or adult salmonids, or do they buffer salmonids against such predation?
    - Are nutrients from adult shad important in terrestrial or aquatic food webs?

Modeling

- Should a life history model for shad be developed? If so, what type?
- What would a conceptual model of shad in the Columbia basin look like?
- If a bioenergetics model is deemed desirable, what information is needed to develop it?
- Could models be developed to identify harvest levels likely to have a demographic response?

Management

- What mechanisms are available to manage shad abundance (e.g., targeted harvest, passage modifications, etc.) and what are the associated costs and benefits?
- Can dam operations be modified to reduce shad populations?
- Can fish ladders be modified to exclude shad while still permitting salmon passage?
- How can official policies of management agencies and Tribes be modified to improve shad management?
- What are the perspectives of anglers, Tribal and non-Tribal commercial fishers, and others that should be considered to assess management options?

Recognizing cost/benefit trade-offs with other critical activities in the basin, it might prove prudent to first undertake modeling to evaluate the potential importance of these effects by using analyses, such as Models of Intermediate Complexity (Plaganyi et al. 2014, Kaplan et al. 2019) before developing extensive field studies or experiments. Multispecies models are question-driven and contain a limited number of components and ecological processes. For example, the model (or an alternative) could be used to examine interactions such as how juvenile shad alter the size-structure of zooplankton prey populations and how that interaction affects juvenile salmon feeding, growth, and survival. Other interactions that could be modeled include the role shad play as prey for salmonid predators (other fish, birds, marine mammals); do shad either increase predation on salmonids or act as buffer that reduces predation? Do shad affect the different species of salmonids in different ways? These preliminary analyses could focus future efforts and use limited resources more effectively and efficiently.

Another promising approach is bioenergetic modeling. Sauter (2011) initiated a bioenergetics model for shad, but the work was never completed; so many of the parameters needed to make such models work still need to be developed. Bioenergetics models and diet information are available for salmon (Haskell et al. 2017) that could be modified for use with shad. Manipulation of the abundances of shad and salmon, and the degree to which they interact, in model simulations would enable an initial assessment of the potential interactions that may be ecologically and economically important.

Although the specific ecological effects of shad are unknown, their potential risks for the ecosystem and anadromous salmonids warrant caution and continued attention. At the very least, managers should continue to monitor shad numbers at the dams, and existing projects that encounter shad should capture information to the extent possible. Focused studies and modeling, as described in this report, could substantially improve our understanding of the biology of American shad and its potential impacts. The ISAB appreciates that continued counting of shad at dams and new research involve costs at a time when many competing research and management priorities in the basin face critical funding limitations. The Council, BPA, and other managers in the Columbia River Basin will need to consider both the potential benefits of efforts to better understand shad as well as the costs of such efforts to balance alternative demands on available resources. Research and monitoring to better understand shad may not be the most important management issue for the Fish and Wildlife Program, but continuing to ignore the role of shad in the Columbia River increases future uncertainties.

Strategic assessment and evaluation could provide critical information for decision makers and managers in the future if shad populations continue to increase.

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