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Ecological Interactions Between Non-Native American Shad and Pacific Salmon: The Columbia River Case Study

Thomas P. Quinn[a] (iD), John Epifanio[b], Peter B. Moyle[c], Stan Gregory[d], Daniel J. Hasselman[e], Erik Merrill[f], Kenneth Rose[g], Thomas F. Turner[h] and Thomas C. Wainwright[i]

[a]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA; [b]Portland, Oregon, USA; [c]Center for Watershed Sciences, University of California, Davis, California, USA; [d]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA; [e]Fundy Ocean Research Center for Energy, Dartmouth, Nova Scotia, Canada; [f]Northwest Power and Conservation Council, Portland, Oregon, USA; [g]Horn Point Laboratory, University of Maryland Center for Environmental Science, Cambridge, Maryland, USA; [h]Department of Biology and Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA; [i]Bend, Oregon, USA

ABSTRACT

Many ecosystems have been dramatically affected by non-native species, but not all such species have strong deleterious effects. American shad, *Alosa sapidissima*, a fish species native to the Atlantic coast of North America, was transplanted to the Pacific coast in the late nineteenth century and quickly colonized many US rivers. Their increased abundance in the Columbia River coincided with declines in native anadromous Pacific salmon and trout, and adult American shad now greatly outnumber returning salmonids. This paper reviews evidence for possible ecological interactions between salmon and American shad across their life histories and habitats. Despite the great abundance of American shad and their apparent overlap in use of Columbia River mainstem habitats, harmful effects on salmon are neither clear from empirical studies nor from ecological principles. Rather, the life histories and habitat use patterns tend to separate spawning adult salmon and their offspring from American shad in space and time. Currently available evidence indicates that this separation results in weak, neutral, uncertain, or offsetting effects on salmon (i.e., a mix of positive and negative interactions). Given the limited research on shad in Pacific ecosystems, several lines of investigation are warranted to advance understanding of their ecology and scope for interactions with native fishes and to support a clearer scientific basis for management decisions regarding American shad.

Introduction

World biodiversity has been greatly affected by the translocation or releases of non-native organisms at all taxonomic levels, including many fishes (Casal 2006). The problems caused by non-native fishes, especially in freshwater habitats, are widespread, acute, and well-documented (Gozlan et al. 2010; Cucherousset and Olden 2011; Toussaint et al. 2018). Allendorf (1991) concluded, for example, that, "… intentional and unintentional introductions usually have been harmful to native fishes and other taxa through predation, competition, hybridization, and the introduction of diseases." (p. 178). The deleterious effects of introduced species on native species are clear in many cases (Britton 2023), and the default position is that such introductions should not be allowed. In some

aquatic ecosystems, co-occurring modifications and complex ecological interactions make it difficult to determine causal relationships between non-native species and declines of local taxa (McDowall 2006; Pascual et al. 2007). These complications do not contradict the large effects in some cases. Rather, as Britton et al. (2011) noted, "Risk management of non-native fishes should ensure that actions taken are commensurate with the level of risk posed by that species…" (p. 256). Indeed, despite a clear bias toward publications on negative effects in recent years, some non-native species can have effects regarded as beneficial for humans, although larger ecosystem effects remain overlooked (Sax et al. 2022). It is therefore important to ascertain the nature and magnitude of the effects non-native species may have so that
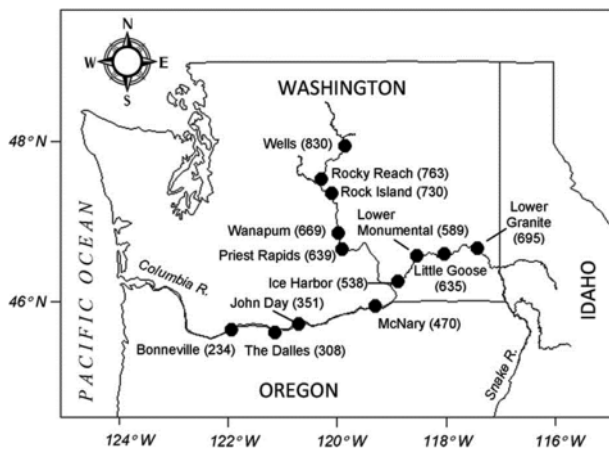
Figure 1. Locations of passable dams on the mainstem Columbia and Snake rivers, with the distance (in parentheses) from each dam to the river mouth in km (from Hinrichsen et al. 2013, with permission). Contiguous parts of the basin in the U.S. and Canada, and significant tributaries, are omitted for simplicity.

resources can be prioritized (e.g., for suppression) and management adjusted (e.g., regulated fisheries) accordingly.

The transport of American shad (*Alosa sapidissima* – henceforth "shad" for brevity) from the Hudson River, New York, across the country to the Sacramento River, California in 1871 was among America's most successful fish introductions. Shad supported important Indigenous fisheries on the East Coast and gained popularity as a food and sport fish with European colonists, who brought them to the West Coast. Shad quickly colonized rivers to the north (Dill and Cordone 1997; Hasselman et al. 2012a) and were captured in the Columbia River as early as 1876 or 1877 (Smith 1896). Shad were also directly introduced into the Columbia and Willamette rivers in 1885 and 1886, but neither additional introductions nor supportive husbandry occurred. By 1894, a few adults
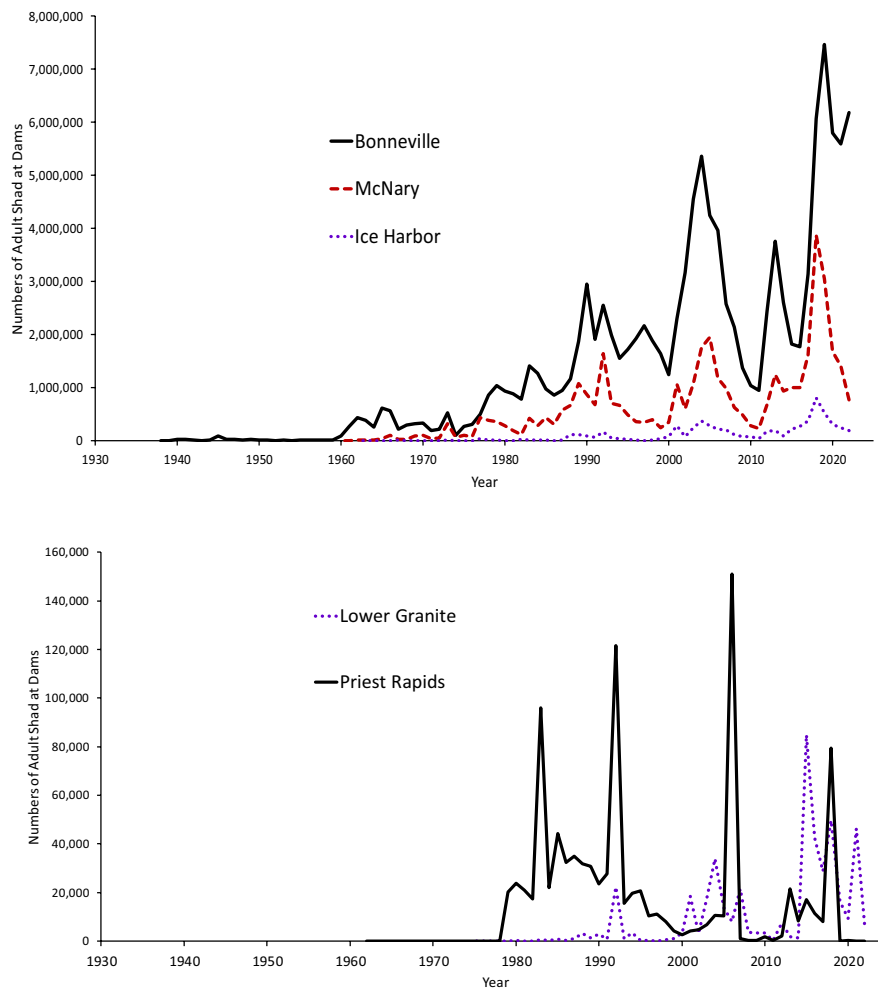

Figure 2. Top panel: estimated counts of American shad at Bonneville Dam (from 1938–2022) and McNary Dam (from 1960) on the Columbia River below its confluence with the Snake River, and Ice Harbor Dam, the lowermost Snake River dam (from 1962). Lower panel: counts of American shad at Priest Rapids Dam, the first dam on the Columbia River they encounter above the confluence with the Snake River (from 1962), and Lower Granite Dam, farther up the Snake River from Ice Harbor Dam (from 1975). Note the difference in Y-axis values. Data from Columbia River DART (2023).
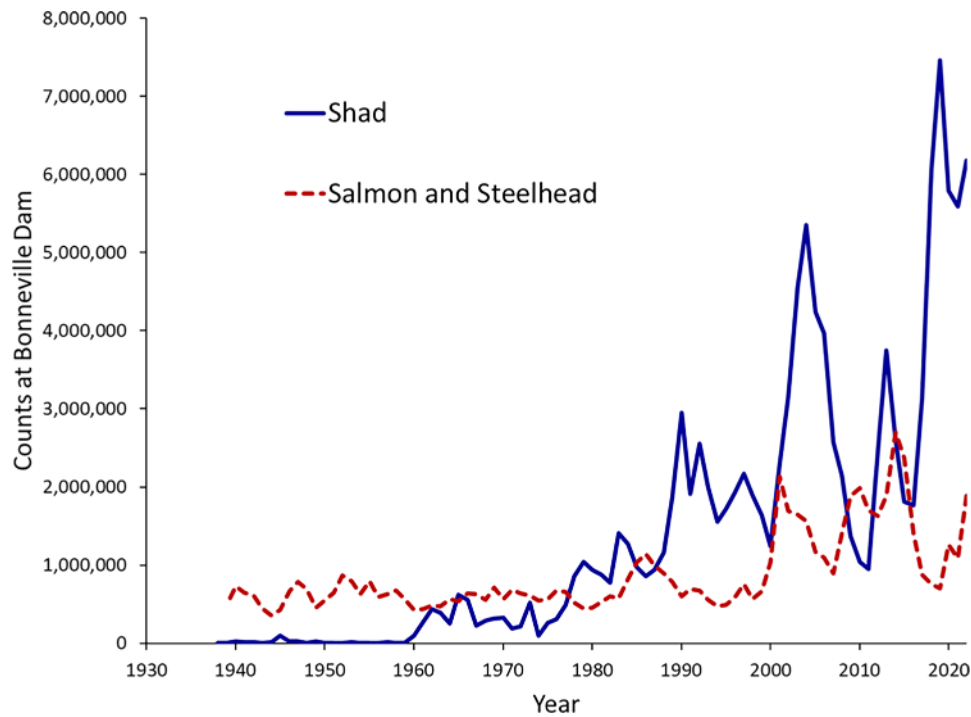
Figure 3. Estimated counts at Bonneville Dam from 1938–2022 of American shad (solid blue line) and all adult salmon and steelhead combined (dashed red line). Data from Columbia River DART (2023).

Table 1. Average estimated counts of American shad, adult Pacific salmon, and steelhead ("salmonids"), and shad as a percent of shad and salmonids combined at Columbia River and Snake River dams from 1992–2003, retrieved from Data Access in Real Time (DART) in March 2021. Lower and Upper Columbia River refer to sections below and above the confluence with the Snake River, respectively, and the dams are ordered from downstream to upstream. This period was chosen because counts were not recorded at one or more dams in subsequent years. 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 River) 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
The Dalles	Lower Columbia	308	2,485,492	612,691	80.2
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	29.0
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	3.0

were captured above The Dalles, 310 km upstream from the Columbia River mouth (Smith 1896). Shad are now abundant in the lower- and mid-Columbia River below its confluence with the Snake River, up to Priest Rapids Dam on the upper Columbia River, and Lower Granite Dam on the Snake River (Figures 1 and 2).

In addition to the spatial expansion, shad have become the most numerous anadromous species in the Columbia River system – comprising over 90% of the upstream migrants counted at lower river dams in some years (Figure 3, Table 1). Recent returns of shad past Bonneville Dam have averaged 4,415,525 over the last decade (2013–2022) and exceeded 7 million fish in 2019. The increasing abundance and associated biomass of shad coincided with declines of native anadromous salmonid populations and a causal connection has been proposed. For example, the Snake River Salmon Recovery Team called for "reducing [the] shad population" to limit interactions with sockeye salmon, *Oncorhynchus nerka* (Bevan et al. 1994). Similarly, 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), and the Lower Columbia River Fish Recovery Board (2004) called for reducing shad to a range of 700,000 to 1,000,000 adults (ca. 15–25% of their current level). The rationale for such actions was largely speculative and concerted reduction efforts were not pursued.

As Hasselman et al. (2012b) pointed out, shad could play many possible roles in the Columbia River ecosystem, including ones that are beneficial, deleterious, or neutral for salmonids (henceforth, for convenience, referred to simply as "salmon"), but their net effect "remains equivocal" (p. 119). In December 2020, because of the uncertain role of shad in the Columbia River ecosystem and their potential interactions with salmonids and other native anadromous fishes were 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. The ISAB is a committee of scientists reporting to the Northwest Power and Conservation Council, National Oceanic and Atmospheric Administration, and Columbia Basin Tribes to inform efforts of the Columbia River Fish and Wildlife Program to protect, mitigate, and enhance fish and wildlife and their habitats affected by hydrosystem development. This review (1) summarizes and builds upon those findings (ISAB (Independent Scientific Advisory Board) 2021b), (2) examines the evidence for potential ecological effects of shad using a decade of work since Hasselman et al. (2012b) considered it, and (3) highlights knowledge gaps regarding shad life history and ecology that still preclude a definitive understanding of the role of shad in this ecosystem.

Life history of American shad in their native and non-native ranges

American shad is a typically anadromous, iteroparous species, native to rivers from Atlantic Canada southward to the St. Johns River, Florida. Adults migrate upriver and spawn in the spring as flows and water temperatures increase; timing variation among rivers and among years within rivers is closely linked to temperature (Leggett and Whitney 1972). Shad spawn pelagic eggs that hatch in a few weeks, depending on temperature (Limburg et al. 2003), and in large rivers the spawning may occur earlier in upstream areas and then later in the season farther downstream (Maltais et al. 2010). Growth and survival benefit from seasonally decreasing river flows, increasing temperatures, and high concentrations of zooplankton (Crecco and Savoy 1985). Typically, young-of-the-year remain in their natal river during the summer, enter marine waters in the fall (Limburg 1996), and spend several years at sea (Leggett 1977; Limburg et al. 2003). The tendency to return and spawn in their natal river (e.g., Hendricks et al. 2002) produces population-specific gene pools (Waters et al. 2000; Hasselman et al. 2013), though some fish spawn in non-natal rivers. Shad are largely iteroparous in the northern part of their native range but semelparity is increasingly common farther south (Leggett and Carscadden 1978).

Shad initially occupied the lower reaches of the Columbia River Basin but expanded upriver after completion of Bonneville Dam in 1938 at river km 234 (Hinrichsen et al. 2013), likely because its fish ladders, constructed for salmon, aided them as well (Figure 1). Completion of The Dalles Dam (river km 308) in 1957 flooded Celilo Falls, eliminating a substantial natural barrier to shad migration and facilitating further numerical and spatial expansion. Through 1959, about 5,000–20,000 shad were counted annually at Bonneville Dam, but from 1960 they dramatically increased, soon exceeded 100,000 annually, and from 1979 onward, nearly every annual count exceeded 1 million fish. Several other dams with fish ladders, completed farther upriver before The Dalles Dam was built, apparently facilitated further upriver migration once shad could ascend past the Celilo Falls site. The upriver ladders allowed shad migration despite being designed to pass salmon and not shad (Monk et al. 1989; Haro and Castro-Santos 2012). In addition, the warmer water and lower velocities in reservoirs associated with the dams benefited the pelagic embryonic and juvenile shad. As a result, the shad population expanded upriver.

The long-term trend in shad abundance throughout the system is difficult to determine because Columbia River dams were not constructed simultaneously, and shad are no longer counted at some (The Dalles, John Day, Lower Monumental, Little Goose). However, taking the 1992–2003 period as "contemporary," shad counts averaged 2,225,797 at Bonneville Dam (Table 1). There is no published record of shad spawning directly below Bonneville Dam, but adults are often caught in spring/summer recreational fisheries there as well as downriver of Bonneville Dam below Willamette Falls and at the mouth of the Clackamas River. Thus, adults may be spawning at these locations

and go uncounted. The average counts at The Dalles Dam exceeded those at Bonneville Dam during this period, indicating some problems with counting, but presumably little or no spawning takes place between these dams. 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.

The Snake River enters the Columbia River upstream of McNary Dam; counts at the next dam shad would encounter in each river (Priest Rapids on the Columbia River and Ice Harbor on the Snake River) are far below the counts at McNary Dam, though some shad migrate up the Snake River past Lower Granite Dam at river km 695. It should be noted that shad counts at Priest Rapids represent fish entering the ladder, but very few ascend into the reservoir above the dam (Curtis Dotson, Grant County Public Utility District, personal communication, 2 April 2021). Specifically, the uppermost three weirs of the ladder require the fish to go through deep openings rather than through spilling water, which shad more readily use (Monk et al. 1989). The sequentially lower counts may reflect some mortality during upriver migration, but likely almost all shad spawn near the confluence of the Snake and Columbia rivers (ca. 25% of the Bonneville Dam count), or in the reservoirs below McNary and John Day dams (Table 1). Consequently, analysis of ecological interactions between salmon and shad must consider the fact that shad occur primarily in the mainstem Columbia River up to or near the confluence with the Snake River, rather than in the many smaller tributaries or upper Columbia River.

Adult shad migrate upriver in spring (primarily in May and June in the Columbia River, at present), coinciding with rising water temperatures and decreasing flows. Shad migrate and spawn earlier in warmer rivers than cooler rivers, and earlier in warmer years than cooler years in a given river, including the Columbia River system (Leggett and Whitney 1972; Quinn and Adams 1996; Nack et al. 2019). Because larval production of shad follows shortly after migration and spawning it is possible to estimate the spatial and temporal patterns of adult, larval, and juvenile shad abundance in the river, and thus possible effects on salmon.

Juvenile shad feed in reservoirs during the summer and enter the Columbia River estuary throughout the year. Smaller, age-0 shad are most abundant in estuary margins and in autumn. In contrast, older, larger juveniles are most abundant in the pelagic zone and in spring and summer (Hamman 1981; Bottom and Jones 1990). In addition to the typical anadromous life history pattern, West Coast shad display a life history variant locally known as "mini-shad." These juveniles spend an additional year in fresh or brackish water before going to sea, or do not migrate. Such fish are routinely sampled at downstream traps in the lower Columbia River Basin (Parsley et al. 2011). Mini-shad may be either males or females, and ages-1 or −2 (Quinn et al. 2024). 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 earlier in life (Quinn et al. 2024).

The marine ecology (e.g., diet, vertical and horizontal and movements, predators, etc.) of shad in the Pacific Ocean is poorly understood. Pelagic and demersal research and monitoring surveys, and bycatch data from coastal fisheries indicate that shad are distributed along the coast from central California north to Vancouver Island (the northern limit of the data), mainly over the shallow (50 to 150 m) continental shelf (Pearcy and Fisher 2011). The highest concentrations were from the central and northern California coast, and from central Oregon to Vancouver Island, likely representing the two largest sources: the Sacramento – San Joaquin and Columbia – Snake rivers, respectively. Shad were caught in salmonid sampling programs at sea over a range of temperatures, but the largest catches were 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. Two indices of shad abundance at sea were positively correlated with adult counts at Bonneville Dam in that year, and analyses indicated that shad populations are favored by warmer ocean conditions (ISAB (Independent Scientific Advisory Board) 2021b).

Mechanisms by which American shad might affect pacific salmonids

Adult shad are far more numerous than adult salmon in the Columbia River (Table 1, Figure 3), and the coincidence of their rise with declines in salmon led to speculation that shad contributed in some way to the declines (Bevan et al. 1994; Parsley et al. 2011). This suspicion is bolstered by the overlap in migration timing and occupancy of the river and estuary,
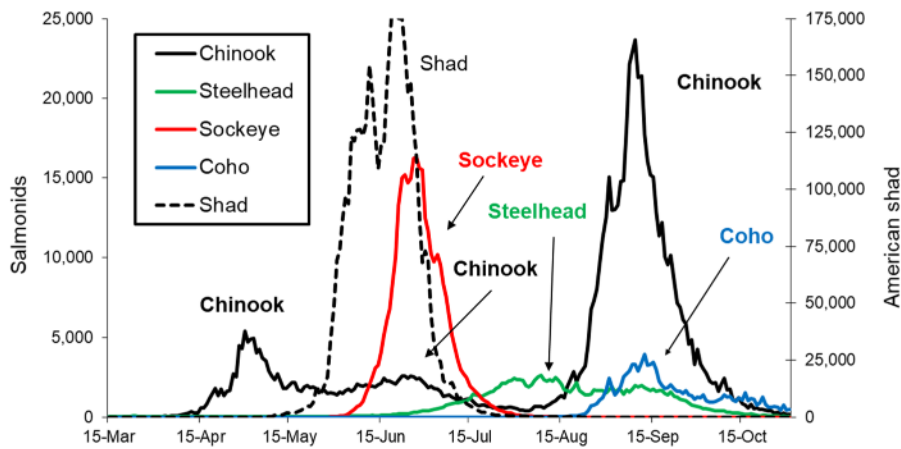
Figure 4. Seasonal timing of upstream migrations of Chinook (black line), sockeye (red line), and coho salmon (blue line) and steelhead (green line, all on the left Y-axis) and American shad (dashed black line on the right Y-axis) in the Columbia River. Note the difference in Y-axis scales. Data are averages of the daily counts at Bonneville Dam from 2013–2022, provided by Geoffrey Whisler (Oregon Dept. of Fish and Wildlife); the graph is modified from JCRMS (Joint Columbia River Management Staff) (2023). Two other much less abundant Pacific salmon species, chum and pink, are not shown.
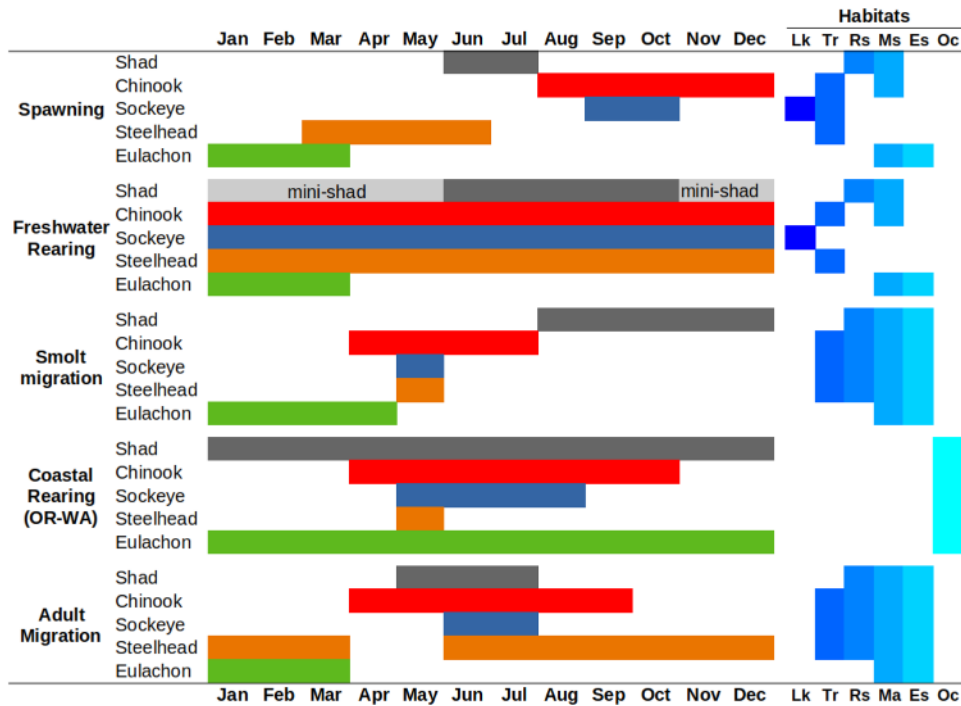

Figure 5. Comparison of generalized monthly habitat use patterns of selected anadromous fishes in the Columbia River Basin. The left side lists the key life history stages and species, and the right side indicates graphically the primary habitats used by each species and life history stage: Lk = lakes, Tr = tributary streams, Rs = mainstem reservoirs, Ms = mainstem river, Es = estuary, Oc = coastal ocean off Oregon and Washington. For example, adult American shad spawn primarily in June and July in mainstem reservoir and river habitats. Data are from multiple sources, including but not limited to Busby et al. (1996), Gustafson et al. (1997, 2010), McCabe et al. (1983), Myers et al. (1998), Beamish (2018).

although there is more overlap for some salmon species and stocks than others (Figures 4 and 5). There are many mechanisms by which invasive fishes can adversely affect native species (Britton 2023) and it is important to identify the most plausible ones. Shad might also have beneficial effects on salmon, in which case the salmon declines would have occurred despite shad abundance rather than because of it. Alternatively, shad may exert little ecological pressure on salmon. This review examines four types of ecological

interactions that are most likely to apply and considers whether the evidence indicates strong effects: (1) competition for breeding space, (2) competition for food in the river, estuary, and marine waters, (3) predator-prey interactions including both direct predation and indirect effects *via* predator buffering, and (4) nutrient cycling. Of these, the second (competition for food) is the most plausible on its face, and the relevant literature is best developed, and this is emphasized here.

Competition for breeding space

Competition for breeding space is a common intra- and inter-specific interaction in salmonids (e.g., Essington et al. 1998, 2000; Quinn 2018), but the markedly different breeding systems of shad and salmon reduce the scope for competition for space among adults for two reasons. First, shad spawn in late spring and early summer whereas most Columbia River basin salmonids (other than steelhead, *O. mykiss*, and cutthroat trout, *O. clarkii*) spawn from late summer to late fall. Second, shad are broadcast spawners in the Columbia River's water column and, to a much lesser extent, that of the Snake River, whereas salmon spawn on gravel substrates in shallow, medium velocity water, primarily in tributaries, and eggs are buried rather than broadcast (Quinn 2018). This combination of temporal and spatial segregation essentially eliminates the scope for competition among breeding adult shad and salmon. Consequently, interactions between shad and salmon are most likely to occur in the juvenile life history stages in the river, estuary, and at sea.

Competition for food in riverine, estuarine, and marine waters

In their native range juvenile shad feed in freshwater in the pelagic zone, primarily on zooplankton and insects (Limburg et al. 2003 and references therein), as do juvenile salmon in reservoirs (McCabe et al. 1983; Haskell et al. 2006; Sauter 2011). Post-larval shad and juvenile salmon overlap in time, because several salmon species feed in their first spring and summer prior to seaward migration (primarily ocean-type Chinook *O. tshawytscha*) or spend a year or more in fresh water (stream-type Chinook, sockeye, and coho salmon *O kisutch*, steelhead, *O. mykiss*, and coastal cutthroat trout, *O. clarkii clarkii*). Thus, competition could occur (Figure 5) and there is scientific literature relevant to this possibility, but spatial separation for some species or life history types reduces opportunities for trophic competition. Prior to their seaward migration, juvenile sockeye salmon feed in upper basin lakes, where shad are absent. Sockeye, coho, and yearling (stream-type) Chinook salmon and steelhead smolts use the river primarily as a migratory corridor to move quickly downriver (Giorgi et al. 1997) and through the estuary (Dawley et al. 1986), rather than feeding extensively while migrating to the ocean. Moreover, these smolts have left for the ocean before post-larval shad might compete with them (Bottom et al. 1984; McCabe et al. 1986; Table 2).

The Columbia River system's Chinook salmon vary considerably in juvenile life history, rearing habitat, and migration timing (Connor et al. 2003, 2005; Copeland et al. 2014; Schroeder et al. 2016). Sub-yearling (i.e., ocean-type) juveniles feed during their seaward migration in river, reservoir, and estuary habitats, and might be affected by shad more than yearlings, which migrate earlier in the year. After the transition to exogenous feeding, juvenile shad ate significant quantities of cladocerans (*Daphnia* spp. and *Bosmina* spp.) in reservoirs, and Haskell et al. (2006) called this consumption "of concern for the management of outmigrating salmonids and other Columbia River fishes" (p. 47). Likewise, Haskell et al. (2013) estimated that juvenile shad consumed over 20% of

Table 2. Mean catches of juvenile Chinook salmon, the most abundant salmonid, and selected other fish species likely to compete with them for food in the Columbia River estuary including American shad, as reported by Bottom et al. (1984).

Species	Age	Winter	Spring	Summer	Fall
Chinook salmon	0+	63	930.5	1062.5	39
	1+	14.2	178.2	0.8	10.7
American shad	0+	0	0.2	112.8	1503.3
	1+	266	150	410.8	19
	2+	3.4	25	28	2.7
Pacific herring	0+	0	12.2	2492.5	320.7
	1+ and 2+	7.8	750.7	700.3	46.7
Shiner perch	0+	0	2.2	2174.8	358.7
	1+ and 2+	3	234.2	1419.3	165
Longfin smelt	0+	0.2	0	1075.5	428.3
	1+ and 2+	934.2	337.7	1273.5	518.3
Northern anchovy	1+ and 2+	224.4	56.7	1130	5.3
Whitebait smelt	Not specified	12.6	2.7	724.8	44

the zooplankton production in John Day Reservoir. Sauter et al. (2011) also indicated that the diet of age-0 shad in reservoirs was dominated by copepods and cladocerans, but the shad also ate insects and bivalve mollusks of the genus *Corbicula*. However, Haskell et al. (2017) found that as juvenile Chinook salmon in the river grew larger, juvenile shad became their prey rather than their competitor for cladocerans, thus the salmon "… likely derive an energetic benefit from juvenile American Shad presence in the Columbia River" (p. 297).

The lower Columbia River and its estuary is a large, complex, and variable ecosystem (Simenstad et al. 1990), with freshwater, euryhaline, migratory, and marine fishes that vary greatly in abundance, depending on year, season, and location (McCabe et al. 1983; Bottom et al. 1984; Weitkamp et al. 2012; Sol et al. 2021). The estuary's littoral and pelagic habitats offer opportunities for trophic competition between shad and salmon. Almost all (97%) the stomachs sampled from age-1 shad in the estuary contained prey (Bottom and Jones 1990), indicating active feeding and abundant prey. They had some of the highest growth rates of any fish species in the estuary, especially in spring (Bottom et al. 1984). Age-1 and age-2 shad consumed calanoid, cyclopoid, and harpacticoid copepods, *Daphnia* spp., *Americorophium* spp. (amphipods), and *Neomysis* spp. (mysid shrimps; Bottom and Jones 1990). Age-0 shad consumed copepods and *Daphnia* spp. but did not consume larger organisms, consistent with the finding that three age classes of shad fed more on zooplankton than did most other fish species in the estuary (Bottom et al. 1984). Similarly, Sauter (2011) found that juvenile shad diets in the estuary were dominated by copepods, amphipods, and cladocerans. Juvenile Chinook salmon, the primary salmon species using the estuary as juveniles, also ate zooplankton, and especially *Daphnia* spp. The scope for competition between shad and salmon in the estuary is mitigated because their peaks of abundance are offset; salmon are more abundant in the spring and summer whereas shad are more abundant in the fall (Bottom et al. 1984; McCabe et al. 1986; Table 2). Moreover, Chinook salmon feed primarily in littoral habitats, transitioning to pelagic habitats as they become larger. Such offsets in phenology, habitat use, and body size might reduce feeding competition between salmon and shad. Regardless of the extent of diet overlap, shad were only 8.7% of the fish embryos and larvae in plankton tows in the reservoirs associated with The Dalles and John Day dams (Gadomski and Barfoot 1998), and also a minor part of the estuary's fish community (Bottom et al. 1984;

Table 2). Emmett et al. (2004) reported that in the Columbia River plume in June shad were orders of magnitude less numerous than other planktivores including Pacific herring (*Clupea pallasi*), whitebait smelt (*Allosmerus elongatus*), eulachon (*Thaleichthys pacificus*), and salmon. Weitkamp et al. (2012) reported that shad were more numerous than juvenile salmon in open waters (i.e., sampled with purse seines) of the estuary from 2007–2010, but shad and salmon were much less numerous than Pacific herring, northern anchovy (*Engraulis mordax*), and especially threespine stickleback (*Gasterosteus aculeatus*), although catches varied greatly with date and location. More recent sampling (2008–2016) yielded similar conclusions; shad were only 0.5% of the total catch from all sites and years combined, compared to 2.3% Chinook salmon (by far the most numerous salmonid) and 78.3% three-spine stickleback (Sol et al. 2021). Thus, even during the recent years of high shad abundance in the Columbia River, they are by no means numerically dominant in the estuary ecosystem.

While concerns over competition for food in the Columbia River system are primarily associated with juvenile shad, returning adults (less numerous but much larger) are also a possible source of competition. Limited research on the Atlantic coast indicated that shad feed during upstream migration (Harris and McBride 2009) as do adult alewife (*Alosa pseudoharengus*), a smaller but similar congeneric species (Stewart et al. 2021). Feeding by adults in rivers (primarily zooplankton, insects, some benthic invertebrates, and even shad eggs) is opportunistic, much less than that at sea, and not nearly sufficient to balance the energy demands of migration (Harris and McBride 2009). In the Columbia River, Sauter et al. (2011) found that 74% of 407 adult shad stomachs had prey, but only in small amounts (primarily amphipods). The most common prey of post-spawning adults were gastropods. Overall, while there are many uncertainties regarding shad feeding ecology in the Columbia River system, the available data indicate that competition with them is unlikely to strongly affect salmon populations.

The food habits of juvenile coho and Chinook, the primary salmonids along the Washington and Oregon coastal marine waters in the summer (Orsi et al. 2007), are dominated by invertebrates (euphausiids, larval crabs, and amphipods) and larval fishes. Chinook salmon rely more on fishes than do coho salmon and both species are increasingly piscivorous as they grow (Brodeur 1989; Brodeur and Pearcy 1990; Daly et al. 2009). The lack of diet data on shad at

sea prevents direct comparisons with salmon, but stable isotopes of nitrogen and carbon provide a tool to assess trophic position. Stable isotope data on salmon from the coastal waters from northern California, Oregon and Washington are consistent with an increase in trophic position with size (Miller et al. 2010; Hertz et al. 2015). By way of comparison, stable isotope values for adult shad from the Columbia River (mean $\delta^{15}N = 13.2‰$; $\delta^{13}C = -18.9‰$: Quinn and Hasselman, unpublished data) overlapped more strongly with post-smolt than with adult Chinook and coho salmon, and were consistent with foraging in coastal rather than offshore waters (Johnson and Schindler 2009). This inference is consistent with sampling summarized by Pearcy and Fisher (2011). Thus, there is the potential for trophic competition at sea, but the prey base is shared with other fishes that are much more numerous than shad. Orsi et al. (2007) reviewed extensive coastal and offshore sampling from 2000–2004 and the California Current region (Vancouver Island southward to California, the apparent range of shad) was dominated by non-salmonids. Pacific herring, northern anchovy, and Pacific sardine each had higher estimated densities than any salmonid, and shad were not listed among the important species in frequency of occurrence or density.

Predator-prey interactions

One possible indirect ecological interaction between shad and salmon might be reduced predation on salmon if shad provide an alternative food source or distract predators that would otherwise consume salmon. However, despite the abundance of shad, the dominant piscivorous fishes (northern pikeminnow, *Ptychocheilus oregonensis*, and non-native walleye, *Sander vitreus* and smallmouth bass, *Micropterus dolomieu*), apparently do not prey heavily on them. Shad were not even mentioned in studies of the food habits of these fishes (Tabor et al. 1993; Zimmerman 1999) or were only a very minor item (Poe et al. 1991). In contrast, these species and especially northern pikeminnow consume many juvenile salmonids (depending on the predator and on salmonid species, size, location, and time of year). None of these studies of native and non-native predatory fishes mentioned the possibility that shad might buffer predation on salmonids. The studies were designed to examine the direct effects of predation on salmonids and, regrettably, often did not detail which non-salmonids were consumed, though they were important dietary items (Vigg et al. 1991; Beamesderfer et al. 1996). Conversely, it is possible that predation on juvenile shad maintains larger

predator populations than would otherwise exist, but evidence for this effect would depend on finding many juvenile shad in the stomachs of predators.

Birds are another group of piscivores in the Columbia River Basin, whose direct effects on salmonids are well-studied (reviewed by ISAB (Independent Scientific Advisory Board) 2021a), but their consumption of shad is not. Petersen et al. (2003) reported that double-crested cormorants and gulls consumed shad in the basin, but the data were collected in spring and summer with a focus on salmon, so the extent of predation on shad is unknown. A recent study of avian predation in the estuary (Good et al. 2022) included shad as a part of "marine forage fish" prey group and found that increasing abundance of this group reduced predation rates on salmonids by Caspian terns, but not by double-crested cormorants. Thus, shad may have a buffering effect, but the evidence is currently inconclusive.

Finally, adult shad might affect predation on adult salmon by supporting larger pinniped populations (either year-round or when at-risk salmon are present) than would otherwise occur, thereby indirectly increasing predation on salmon. Alternatively, shad might satiate or distract predatory pinnipeds, thereby reducing losses of adult salmon. Wargo Rub et al. (2019) reported that adult spring Chinook salmon survival was negatively associated with pinniped abundance, and positively associated with adult shad abundance, consistent with the idea that shad buffer pinniped predation. Shad were a major dietary item for Steller sea lions along the coast of Washington (Lewis 2022), so this possibility merits further investigation.

Nutrient cycling

The transport of marine nutrients into freshwater habitats by adult Pacific salmon and the effects of these nutrients in aquatic and riparian communities have been documented for decades (e.g., Willson et al. 1998). The millions of salmon that once spawned and died in the Columbia Basin imported great quantities of marine-derived nitrogen and phosphorus into the ecosystem. Declines of their populations have reduced nutrient inputs (Haskell 2018), likely affecting many components of terrestrial and aquatic communities. Other anadromous fishes contribute nutrients in Atlantic rivers including alosines (MacAvoy et al. 2009; Walters et al. 2009) and lampreys (Weaver et al. 2018), so the role of shad in nutrient transfer in Pacific rivers should be considered. 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 fishes. The nutrients brought into the Columbia River by anadromous fishes are small, however, compared to background concentrations in the river and nutrients contributed by humans through point- and non-point-sources. Haskell (2018) estimated that shad only increased phosphorus loading 1.3% over background river levels during their spawning season and accounted for < 0.2% of the annual discharge of phosphorus from McNary Dam.

In addition to the modest contribution of marine-derived nutrients from shad to the Columbia River ecosystem, the possible role of their nutrients is complicated for several reasons (Haskell 2018). First, most shad spawn and juveniles rear in the lower river reservoirs, but nutrient limitation affecting salmonids is more likely to occur farther upriver, in smaller streams where shad are absent. Second, Columbia River Basin shad are iteroparous, so spawning biomass exceeds carcass deposition. 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. Third, shad are more numerous than salmon but smaller. On average, adult Columbia River system shad weigh < 1 kg (Quinn et al. 2024) compared with 8.1 kg for Chinook and 2.2 kg for sockeye (Chapman 1986). Fourth, juvenile shad export nutrients when they migrate to sea, as Moore and Schindler (2004) quantified for sockeye salmon in Alaska. Fifth, shad are water-column spawners, so dead fish and gametes might contribute less to food webs than salmon carcasses would. All things considered, it seems likely that shad contribute nutrients to salmon food webs but mostly in mainstem reservoirs rather than in the tributaries (Figure 5) where nutrients are more limiting. 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 river.

Conclusions and recommendations

American shad colonized and formed a self-sustaining population in the Columbia River in the late nineteenth century, became much more abundant after the mid-twentieth century, and now far outnumber native Pacific salmon. Compared to the amount of information available on Pacific salmon, little is known about shad and its role in the ecosystem. The sheer numbers and biomass suggest they should be ecologically important, but the studies reviewed here do not demonstrate or even imply strong interactions between shad and salmon, or a major role of shad in ecosystem processes. Thus, two decades of subsequent research have not fundamentally altered the conclusion by Bottom et al. (2005, p.135) that "in the absence of scientific evidence of direct competition or resource limitation, we cannot assume a deleterious effect [of shad] on juvenile salmonids." This statement, made with respect to estuaries, could be said of the whole system. Indications of possible deleterious effects of shad on salmon are mixed with possible beneficial ones, yielding no conclusive evidence of a net negative effect, but uncertainties abound given the limited research and monitoring. Future interactions between shad, salmon, and other parts of the Columbia River Basin's ecosystem are likely to change with climate-driven increases in temperature, altered river flow regimes, and adapting aquatic communities. The future of shad now looks bright in the Columbia River, in contrast to widespread decline in its native range (Waldman 2013; Zydlewski et al. 2021). The Columbia River system's chain of reservoirs should continue to provide favorable habitat for shad spawning and rearing and a warmer climate may benefit shad more than salmon. However, the limited knowledge about shad in the basin weakens our ability to assess its current and likely future role. Accordingly, a shad research and monitoring program is needed to address the following topics related to the species' life history, population dynamics, and role in the ecosystems they share with salmon.

Life history and ecology

First, there is a clear need to better monitor adult shad abundance and spatial distribution in the system, and more fully understand the species' ecology and life history. Monitoring will require continuing or resuming counts at dams on the Columbia River and its major tributaries and an assessment of spawning below Bonneville Dam. Second, a sampling program is needed to monitor fundamental life-history patterns of the species in the Columbia River Basin: age-structure and survival rates, and habitat utilization within the Columbia River system in time and space. This investigation of life history traits should examine the possibility that phenotypic plasticity or genetic adaptation is taking place among non-native populations on the Pacific coast as gene pools diverge (Hasselman et al. 2018), and life history variation becomes evident (Quinn et al. 2024). The combination of abundance and life history information would allow the construction of a basic stock assessment and population dynamics model, allowing an improved understanding of factors affecting recruitment. Third, research on shad abundance and distribution in the

eastern Pacific Ocean is needed to understand its role in ocean food webs, though riverine and estuarine processes are likely more consequential for salmon.

Ecosystem interactions

This review highlighted important information gaps on the role of shad in freshwater, estuarine, and marine food webs, and noted areas where interactions are unlikely to occur or be strong (e.g., interior lakes and small tributaries). There are many plausible direct and indirect interactions with native species, especially salmonids, planktivores such as eulachon and Pacific herring, piscivorous birds, and marine mammals. At present, information is most available and most readily obtained in the river system, followed by the estuary, and least available for the marine phase of the shad life history. Interactions with salmon are likely to follow this continuum (i.e., weakest at sea). Nevertheless, the lack of information on marine ecology is conspicuous and even small advances would be informative. Fundamental questions include: What are the main prey and predators of shad? To what extent do shad compete with juvenile salmon, alleviate or magnify predation on salmon, and provide nutrients that benefit aquatic and terrestrial food webs? Basic ecological knowledge would help to answer important questions, such as whether shad are approaching carrying capacity in the basin, and how future changes in climate might affect shad and native organisms. Studies of shad in the Columbia River may also provide insights into why they are declining in their native range.

Management and models

The biological research and monitoring outlined above would inform management decisions, such as whether to develop, intensify, or otherwise modify fisheries for shad, whether to redesign fish ladders to hinder their migration while permitting salmon to migrate, or whether to take other actions to benefit salmon and other native fishes. This will require not only research and monitoring, but also development of predictive life history and ecosystem models, starting with a general conceptual model of shad use of the Columbia River Basin and their interactions with other species. The social and cultural impacts or benefits of increasing shad populations in the basin on fisheries must also be considered. Tribal perspectives should be of central importance in assessing these current or future impacts or benefits.

Incorporating new knowledge of shad into ongoing adaptive management processes will lead to a better understanding of the myriad ecosystem processes involving not only the well-studied salmonids but other native and non-native components of the community. Given the large and increasing population of shad in the Columbia River Basin and their potential for altering native food webs, our current lack of knowledge about shad complicates effective management of salmonids and other native species. The costs associated with increased focus on shad might divert funding for salmon studies, but such work should nevertheless be considered. An effective shad research program within a broad, multi-species adaptive management framework should be an important regional goal.

The questions and data to address the uncertainty regarding shad ecology and management options are well suited for MICE (Models of Intermediate Complexity for Ecosystem assessments) type analysis (Plagányi et al. 2014). MICE are question-driven multispecies models; the limited number of species and ecological processes enables the model to be closely tied to empirical information and focused on the interactions of interest. MICE have the same issues as other ecological and food web models – their formulation depends on the developer (the optimal model structure is not known), and parameter estimation and validation are difficult because multi-species and food web models push the limits of available data. MICE offer several key advantages over other food web modeling approaches (Plagányi et al. 2014; Geary et al. 2020). By focusing on relatively few species and interactions, they reduce data needs, enables explicit treatment of uncertainty (1000s of model simulations is possible), and provides the ecological dynamics module for management approaches such as strategy evaluation (Perryman et al. 2021) that can facilitate stakeholder engagement (Feeney et al. 2019).

MICE are especially well-suited to assess competition and predator-prey interactions among shad, salmonids, planktivores, fish and bird piscivores, and marine mammals in the Columbia River. Sauter (2011) initiated the bioenergetics model for shad, and bioenergetics models and diet information are available for salmon (e.g., Haskell et al. 2017). There is also information pertaining to the potential predation pressures on shad and salmon from birds (Good et al. 2022) and pinnipeds (Wargo Rub et al. 2019). Model simulations manipulating shad and salmon abundance and interactions would enable an initial assessment of the potential for ecologically important processes. Such models can be broadened to include human

interactions with the species and habitats represented, helping to explore management alternatives (e.g., Plagányi et al. 2014; Kaplan et al. 2019).

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ORCID

Thomas P. Quinn 🆔 http://orcid.org/0000-0003-3163-579X

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