American Shad of the Pacific Coast: A Harmful Invasive Species or Benign Introduction?

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Available online: 06 Mar 2012

To cite this article: Daniel J. Hasselman, Richard A. Hinrichsen, Barbara A. Shields & Curtis C. Ebbesmeyer (2012): American Shad of the Pacific Coast: A Harmful Invasive Species or Benign Introduction?, Fisheries, 37:3, 115-122

To link to this article: http://dx.doi.org/10.1080/03632415.2012.659941

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American Shad of the Pacific Coast: A Harmful Invasive Species or Benign Introduction?

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ABSTRACT: Research on the ecological effects of aquatic invasive species in North America has largely focused on the Laurentian Great Lakes, with less attention directed to their influence in coastal ecosystems. American shad (Alosa sapidissima) were introduced to the Pacific coast in the late 1800s, rapidly established, dispersed, and became prolific. Despite constituting a remarkable biological invasion, shad in their introduced range have not been the subject of much scientific investigation. The species persists in relative obscurity in the Pacific Northwest and remains ecologically overlooked and evolutionarily underappreciated. In this second of two complementary articles, we consider the potential ecological effects of invasive American shad on Pacific coastal ecosystems and the possible consequences for the persistence of native salmonids. We also reflect on the intrinsic value that this invasion provides to studies of ecology and evolution and highlight several areas of research that require immediate investigation if we are to determine whether nonindigenous shad constitute a harmful invasive species or a benign introduction.

INTRODUCTION

The spread of invasive species has resulted in substantial environmental and economic cost (Pimentel et al. 2000) and constitutes a serious threat to global biodiversity, ecosystem function, and the long-term persistence of indigenous biota. Invasive species can disrupt community trophic structure through interactions with key indigenous taxa, causing a cascade of effects that can alter species compositions of entire ecosystems (Chapin et al. 1997) and cause reductions of biodiversity at local and regional scales (Williamson 1999). Although invasive species have affected biomes worldwide, aquatic ecosystems appear particularly impacted, because exotic species have contributed to alarming extinction rates for North American freshwater fauna, rivaling those of tropical forests (Ricciardi and Rasmussen 1999).

Much of the research on the effects of aquatic invasive species in North America has focused on the Laurentian Great Lakes region; this is a consequence of the number of aquatic invasive species detected there (>182 spp.; Mills et al. 1993; Ricciardi 2006). Comparatively little attention has been afforded to the role of invasive anadromous species in coastal ecosystems, largely because purposeful (and often repeated) attempts at introduction of these species generally fail to produce self-sustaining anadromous runs, although resident populations of salmonids are routinely established outside of their native range (Withler 1982; Harache 1992; Wood 1995; Altukhov et al. 2000; Utter 2001). Although there are notable exceptions, such as Chinook salmon (Oncorhynchus tshawytscha) in New Zealand (McDowall 1994) and the secondary development of anadromy in rainbow trout (O. mykiss) in Argentina (Pascual et al. 2001), among others (Hendry et al. 1996; Burger et al. 2000; Ayllon et al. 2004), these are exceptions to the rule. We do not consider the successful establishment of pink salmon (O. gorbuscha) in the Great Lakes (Gharret and Thomason 1987) in this regard, because these fish exhibit anadfluvial life cycle (“quasi-anadromous”; Huey et al. 2005), migrating between la-
Invasive anadromous fishes. To this end, we (1) discuss the potential effects of invasive shad on native salmonids and highlight areas of research that are needed to understand the consequences of this invasion to future studies of evolutionary processes for anadromous fishes. To this end, we (1) discuss the potential effects of shad on native salmonids and highlight areas of research that require investigation if we are to understand the consequences for native taxa and (2) provide a perspective on the intrinsic research value of invasive shad for future studies of ecology and evolution.

**IMPLICATIONS OF INVASIVE SHAD FOR NATIVE SALMONIDS**

The enthusiasm and dedication with which early U.S. fish commissioners facilitated the spread of valued species beyond their natural distributions (reviewed in Hasselman et al. 2012, this volume) contrasts sharply with the precautionary principles inherent in fisheries management today. When shad were introduced to the Columbia River, it was viewed as a wonderful, even noble, accomplishment. Since then, people have become acutely aware of the consequences of invasive species and their influence on native biota and ecosystems.

Because aquatic invasive species have contributed to alarming extinction rates for North American freshwater fauna (Ricciardi and Rasmussen 1999), the effects of invasive shad are of particular concern, especially where they involve interactions with threatened or endangered species. Shad have been reported from several rivers in the Pacific Northwest that contain multiple evolutionarily significant units (ESUs) or distinct population segments (DPSs) of Chinook (O. tshawytscha), chum (O. keta), coho (O. kisutch), and sockeye (O. nerka) salmon and steelhead (O. mykiss). Some of these rivers constitute critical habitat for the long-term persistence of one or more of these ESUs/DPSs, many of which are federally listed as endangered or threatened.

In fact, it is out of concern specifically for salmon that biologists now seriously contemplate the ecological role of shad in the Columbia River. For some, the “scientific” response has been “guilty until proven innocent” (Simberloff 2007), with calls to eliminate shad above Bonneville Dam (Snake River Salmon Recovery Team [SRSRT] 1994; National Marine Fisheries Service [NMFS] 1995). Though some hypotheses have been advanced to suggest that shad may negatively affect Pacific coastal ecosystems (e.g., Haskell et al. 2001; Harvey and Kareiva 2005; Hershberger et al. 2010), the specific interactions with salmon remain largely untested hypotheses, and the a priori vilification of shad in the absence of supporting data constitutes speculation and opinion, not established fact (J. H. Brown and Sax 2007). The presence of shad in the Columbia River may actually be a mixed blessing.

Although the specific effects of shad on aquatic communities in Pacific coastal ecosystems are uncertain, invasive planktivores (especially clupeids) can cause dramatic changes in zooplankton communities and alterations at several trophic levels in aquatic systems (Crowder 1980). Although adult shad typically do not feed while in freshwater (e.g., during the incubation and larval stages in freshwaters), shad are known to feed on zooplankton and zooplanktonic subcomponents (Odum 1959; Yamasaki et al. 1992). Tidal and estuarine waters with high densities of zooplanktonic components, such as copepods and cladocerans, support high shad larval survival (Yamasaki et al. 1992).
spawning run; Cleaver 1951), larval and juvenile shad occur at relatively high densities in the Columbia River and feed primarily on zooplankton (Petersen et al. 2003), a primary dietary component of sub-yearling Chinook salmon (Rondorf et al. 1990). McCabe et al. (1983) found a significant dietary overlap between shad and juvenile salmonids in the Columbia River estuary. Although cyclopoid copepods are the primary dietary component of juvenile shad (86% by mass in John Day Reservoir; Petersen et al. 2003), the feeding of abundant larval and juvenile shad has been suggested as the cause of declines in abundance and reductions in size of Daphnia spp. in the Columbia River (Haskell et al. 2001, 2006). Although Hammann (1982) observed Daphnia spp. in the diets of yearling shad captured in the Columbia River estuary, other dietary items of importance include calanoid copepods, numerous taxa of cladocerans, dipteran larvae (Petersen et al. 2003), and mysid shrimp (Hammann 1982).

Beyond competition for zooplankton by larvae and juveniles (Petersen et al. 2003), shad may compete with indigenous taxa for space (McCabe et al. 1983) and cause migratory delays for other anadromous fishes. Accumulations of large numbers of adult shad have caused avoidance behaviors or delays among salmon at fish ladder entrances at dams on the Columbia River (Monk et al. 1989), thereby impeding migration. Such accumulations have also blocked sub-yearling Chinook salmon passage at the juvenile bypass system at the McNary Dam, causing mortalities in the collection system (Basham et al. 1982). To circumvent this issue, flow regimes at the Bonneville Dam fish passage facility are modified during the peak upstream migration of shad to facilitate their efficient passage (U.S. Army Corps of Engineers [USACE] 2011). Furthermore, the fish ladder at John Day Dam originally experienced poor shad passage (approximately 18%) and was modified in the early 1970s with overflow slot weirs that improved shad passage to greater than 70% (Monk et al. 1989).

In addition to interspecific competition for resources, shad may indirectly affect native salmon through secondary and tertiary-level ecological interactions. Shad larvae and juveniles may provide abundant seasonal food sources for northern pikeminnow (Ptychocheilus oregonensis), an important predator of juvenile salmon (Beamesderfer et al. 1996; Petersen and Kitchell 2001), inadvertently increasing these predators’ abundance and the overall threat to native salmonids (Petersen et al. 1994). The abundance of smallmouth bass (Micropterus dolomieu), walleye (Sander vitreus), and other nonindigenous fishes that may affect native salmon might also be increased through predation on shad larvae and juveniles (Harvey and Kariova 2005). Shad may also serve as an important food source for double-crested cormorants (Phalacrocorax auritus) in the Columbia and Snake Rivers (Roby et al. 2008), as other alosines do on the Atlantic coast (Dalton et al. 2009), and may be partly responsible for the birds’ increased abundance in the basin and their increased predation on salmon smolts (B. Sanderson, National Oceanic and Atmospheric Administration–Northwest Fisheries Science Center, personal communication).

Shad may also alter parasite–host dynamics or the ecology of native pathogens by serving as an alternate vector for the transport of marine parasites into Pacific coastal ecosystems. In addition to indirectly affecting native salmon, this could have implications for other animals in the freshwater aquatic food web. Hershberger et al. (2010) found that the increased abundance of shad in the Pacific Northwest during the 1980s resulted in amplification of Ichthyophonus sp., a mesomyctezoan parasite of wild marine fishes. Although Ichthyophonus is native to the Pacific Northwest and has always been brought into freshwater systems with native infected salmon, the Ichthyophonus epizootic event in Columbia River shad in 2007 resulted in the mass transport of the parasite into the Columbia River basin.

Shad in the Columbia, Willamette, and Umpqua rivers have also been shown to be heavily infected with the larval form of the nematode Anisakis (Shields et al. 2002). Unlike Ichthyophonus, Anisakis was historically restricted, with its native herring (Clupea harengus) host, to marine environments (Hauck and May 1977). The spread of Anisakis into freshwater systems via shad represents an ecological expansion of this parasite. Furthermore, Anisakis poses a potential health risk for mammalian consumers (including humans) and has been demonstrated to infect shad-eating river otters (Lutra canadensis) in the Pacific Northwest (Hoberg et al. 1997; Shields et al. 2002). Taken together, these events raise concerns that shad may act as a potential vector for parasite “spillback” to native species and for the establishment of wholly freshwater life cycles for these and other parasites in the Columbia River.

Although we have so far highlighted the potential negative consequences of shad to native salmonids, there may be some unrecognized benefits. In 1995 and 1996, shad larvae and juveniles were among the five most abundant taxa sampled by plankton tows and beach seines in main channel and backwater habitats in the John Day Reservoir and below Bonneville Dam (as described in Petersen et al. 2003). As such, abundant shad larvae and juveniles may serve as readily available food sources for salmonids at various life history stages. Although the consumption of alosines is suspected to induce early mortality syndrome for salmonids in the Great Lakes via a thiamine deficiency (S. B. Brown et al. 2005), this effect was largely detected in salmons whose diets were comprised primarily of alewife (A. pseudoharengus; Honeyfield et al. 2005). Although juvenile shad in the Columbia River exhibit elevated levels of thiaminase (L. Wetzel, U.S. Geological Survey, personal communication), no study has been conducted to determine predation rates of salmonids on larval and juvenile shad in the Columbia River or what proportion of their diets are comprised of shad. Early life history stage and adult shad may also occur at sufficiently high densities to partially alleviate the predation pressure applied by avian, piscine, and mammalian (e.g., pinnipeds) predators on salmon smolts and adults (i.e., prey swamping). Furthermore, in their native range, anadromous clupeids serve as a major source of marine-derived nutrients far upstream in riverine habitat and provide an important annual subsidy to the energy and nutrient budgets of these ecosystems (Garman and Macko 1998; MacAvoy et al. 2000). As the number of native salmonids...
has declined, the increase in shad abundance may have offset any nutrient deficits and buffered against whole ecosystem and food web effects from the bottom up.

Considering the rapid dispersal and colonization ability of invasive shad (see Hasselman et al. 2012, this volume), the species’ capacity for dramatic increase in abundance, and their ecological role, the scope for interaction and niche overlap with Pacific salmon is great. Understanding ecological interactions and the degree of niche overlap of shad with salmon species in Pacific coastal ecosystems, particularly the Columbia River basin, represents an area of high research priority for fisheries management. Resolving the spatial and temporal overlap of shad of all life history stages with native species will help address the effect of shad on indigenous taxa. Understanding the magnitude of the threat posed by shad to Pacific coastal ecosystems and specific salmon ESUs/DPSs requires knowledge of the distribution and relative abundance of self-sustaining shad populations in the Pacific Northwest—information that is currently lacking—and efforts to project future shad range expansion under climate change scenarios.

**INTRINSIC VALUE OF INVASIVE SHAD FOR EVOLUTION/ECOLOGY**

Because successful introductions of anadromous species to coastal regions are rare, the establishment of shad in the Pacific Northwest holds inherent value to studies of evolution and ecology. Species introduced to novel environments can exhibit rapid evolutionary changes (Thompson 1998), and the shad invasion provides an opportunity to examine evolutionary responses of an anadromous species to a novel set of selection pressures. Because evolutionary adaptations may contribute to the future establishment and spread of invasive taxa (Allendorf and Lundquist 2003), understanding the life history variation exhibited by shad is an important aid to the effective management of this invasive species.

It was noted soon after their introduction “that certain well-marked habits of the shad on the Atlantic coast have undergone noteworthy modification in Pacific waters … as a result of the new physical and thermic conditions, [prey], [predators], etc.” (Smith 1895). Specifically, Smith (1895) reported the tendency of Sacramento River shad to remain in the San Francisco Bay region throughout the year, with some proportion of the population foregoing the typical marine migration altogether. Smith (1895) also reported San Francisco Bay shad to be in spawning condition from December to August. This is considerably longer than the source stock used for introduction (Hudson River: May–June; see Hasselman et al. 2012, this volume) or any other spawning population along the Atlantic Coast but similar in the commencement of spawning season to stocks from the southern portion of their native range (Georgia, Florida; Limburg et al. 2003). This suggests that certain shad life history attributes may be plastic and readily adaptable to novel environments.

A freshwater landlocked population of shad has become established above Friant Dam on the San Joaquin River, in Millerton Lake, California (Ecological Analysts, Inc. 1982; Ahern 1992). Although other alosines can persist as landlocked populations (Palkovacs et al. 2008), this is the only self-sustaining landlocked population of shad in existence and refutes the notion that shad are an obligate anadromous species, whose juveniles gradually lose the ability to osmoregulate in freshwater (Zydlewski and McCormick 1997; Zydlewski et al. 2003). This suggests the establishment of a local adaptation for freshwater persistence; the underlying physiological changes required for this adaptation have yet to be explored. Although the Millerton Lake shad population has not been the subject of much study, it has been suggested that this population has become piscivorous, feeding primarily on introduced threadfin shad (*Dorosoma petenense*). One might hypothesize predictable modifications to trophic feeding structures (i.e., reduced number and length of gill rakers) in response to possible decreased reliance on zooplankton.

In their native range, shad typically occupy free-flowing rivers during the freshwater portion of their lives. The reservoir dominated habitat of the present-day Columbia River basin is not likely something that shad have experienced during their evolutionary history (Baxter 1977). The lentic condition of the Columbia River basin may have presented the species with altered selection pressures in a novel environment that may become manifest as altered phenotypes (Haas et al. 2010; Franssen 2011), life histories (Hamann 1982; Wetzel et al. 2011), and demography (Rottiers et al. 1992). For example, though shad in their native range shad are believed to emigrate from their natal rivers to sea as juveniles (Walburg and Nichols 1967), a shad life history variant exhibiting extended freshwater residency appears to have become established in the Columbia River (Wetzel et al. 2011). Increasing reports of so-called ‘mini-shad’ (too small to be adults but too large to be young of the year/ juveniles) are consistent with the finding that Columbia River shad exhibit an evolutionary adaptation for increased juvenile growth rate (Rottiers et al. 1992). This life history variant is largely comprised of 1+ and 2+ individuals (Wetzel et al. 2011) and is consistent with Hammann (1982), who documented overwintering of 1+ shad in the Columbia River estuary. These individuals either delay outmigration or return prematurely after seaward migration (L. Wetzel, personal communication), spending a shorter period of time at sea than their larger conspecifics. This notion is consistent with the presence of “yearling” (sensu Limburg 1998) shad from the Hudson River, a source population for the Columbia River introduction. However, it is uncertain whether this represents a truly novel life history variant or one that was transported during the
species’ introduction that is simply more prominent due to the magnitude of the Columbia River spawning population.

Although the spread of shad to Asiatic waters was predicted as early as 1887 (McDonald 1891), reports of shad from Russia (Chereshnev and Zharmikov 1989) and Alaska (Mecklenburg et al. 2002) are sporadic and may constitute early colonization attempts, akin to occasional reports of shad from Labrador in their native range (Hodder 1966; Hare and Murphy 1974; Dempson et al. 1983). These early colonization attempts may become increasingly frequent and ultimately successful under scenarios of climate change. Thus, invasive shad provide an opportunity to empirically examine the process of colonization in a (non-salmonid) anadromous species and to test theoretical predictions of allele frequency distributions under models of mutation surfing (Excoffier and Ray 2008), dispersal (i.e., stepping stone vs. leptokurtic; Ibrahim et al. 1996), population bottlenecks, founder events, and relaxed selection.

A common theme in the empirical analysis of population genetic data is that populations are in a state of drift-migration equilibrium and that gene flow among populations is restricted (Kinnison et al. 2002). However, many natural populations do not exist in this steady state, and this assumption is often violated when equilibrium approximations are used to estimate population genetic parameters—for example, estimation of gene flow \((N_m)\) using Wright’s (1943) \(F_{st}\) approximation (Whitlock and McCauley 1999). The development of population genetic approaches for nonequilibrium situations might be greatly advanced through the examination of biological systems in the early stages of population divergence, such as New Zealand Chinook salmon and other introduced populations (Kinnison et al. 2002). Invasive shad may be inherently valuable in this regard, providing a model system to examine the nonequilibrium patterns that may characterize the early stages of population divergence and aiding the advancement and application of population genetics theory.

**CONCLUDING REMARKS**

Calls for the elimination of shad above Bonneville Dam in the Columbia River (SRSRT 1994; NMFS 1995) are largely based on the supposition that invasive shad must have a negative ecological effect on Pacific coastal ecosystems and native salmon. Although shad are likely to have an ecological influence in their introduced range, the nature of the effect (neutral, beneficial, or detrimental) has not been well characterized but requires immediate investigation to determine whether shad present a risk to the persistence of native salmon ESUs/DPSs. It is uncertain whether the increased abundance of shad in the Columbia River has resulted in active displacement of native salmonids via competition in a “healthy” ecosystem or passive displacement in an already heavily modified environment. Although there is little direct evidence of either process in the Columbia River basin, active displacement may be more likely in the main stem, estuary, and perhaps the ocean, because shad do not typically enter the cooler tributaries where salmon spawn and rear. Alternatively, contrasting trends in shad and salmon abundance may reflect reciprocal periods of high and low marine survival consistent with alternating Pacific Decadal Oscillation conditions on extended temporal scales.

Whether nonindigenous shad constitute a harmful invasive species or a benign introduction remains equivocal. Understanding the nature of the ecological effect of shad in Pacific coastal ecosystems, as well as the scope for niche overlap with salmon, requires knowledge of the extent of spatial and temporal overlap with native taxa in marine and aquatic habitats and the degree to which shad influence the availability of resources. Understanding the magnitude of the potential threat posed by shad to salmon requires knowledge of the species’ current distribution and abundance among Pacific coastal rivers and the ability to project future range expansion under climate change scenarios.

Despite the ecological consequences, invasive shad hold intrinsic value for future evolutionary research of anadromous species, particularly invasion dynamics, adaptation, colonization processes, and range of phenotypic plasticity. The introduction of shad to the Pacific coast has exposed the species to a suite of novel selection pressures that may have become manifest as altered phenotype, demography, and life history attributes that have permitted shad to become prolific and will provide valuable insight into evolutionary processes for invasive species.

At the time of the species’ transfer to the Pacific Coast, fisheries commissioners were so preoccupied with whether shad could be introduced to the West Coast that they never paused to consider whether they should be. Now that shad are firmly established, such a reflective view is required for the management of this invasive species and consideration of whether shad should be eradicated. Regardless of the ecological role that shad play in Pacific coastal ecosystems, it is doubtful that the species could ever be completely eliminated from the region, given the magnitude of the spawning run on the Columbia River. However, if an intensive commercial shad harvest were permitted, perhaps to supply an expanding Asian market (Jia et al. 2007), abundance levels might be anticipated to decline accordingly. Regardless, shad constitute but a single link in a chain of anthropogenic factors—hundreds of invasive species (Sanderson et al. 2009), habitat loss (Waples et al. 2007), climate change (Mantua et al. 2010), salmon hatcheries, and other influences to the ecological dynamics of Pacific coastal rivers—with which indigenous taxa must contend. Biological invasions constitute “experiments in nature” (Gaston and Blackburn 1999), and only through a broad examination of invasive shad ecology and evolutionary biology can we begin to decipher the consequences of this invasive species for the future persistence of native salmon and to critically evaluate our options for management.

**ACKNOWLEDGMENTS**

This article is dedicated to the memory of J. H. Petersen, whose pioneering research with Columbia River American shad paved the way for further investigations. This article was a
product of discussions among the authors regarding the current state of knowledge of shad in the species’ introduced range and the need to raise awareness among fisheries professionals about this invasive species. The authors thank T. P. Quinn, F. Utter, S. Narum, D. Gordon, K. E. Limburg, S. Gilbert-Fox, and an astute anonymous reviewer whose comments on earlier drafts greatly improved the quality of this article. This work was supported by the Cooperative Institute for Limnology and Ecosystems Research at the University of Michigan and a National Oceanic and Atmospheric Administration (Great Lakes Environmental Research Laboratory) Aquatic Invasive Species Program grant (No. NA07OAR4320006) to D.J.H. at the School of Aquatic and Fishery Sciences, University of Washington.

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