

Re-colonization of Atlantic and Pacific rivers by anadromous fishes: linkages between life history and the benefits of barrier removal

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Abstract The last two decades have seen a rapid increase in barrier removals on rivers of the Northern Hemisphere, often for the explicit purpose of expanding the abundance, spatial distribution, and life history diversity of migratory fishes. However, differences in life history such as seasonal timing of migration and reproduction, iteroparity versus semelparity, and the extent of natal homing are likely to affect the capacity for expansion and re-colonization by taxa such as alosines, lamprey, and salmonids. We first review some basic life history traits that may affect re-colonization

by migratory fishes, and then present selected examples from Atlantic and Pacific basins to illustrate these patterns and their implications for the success of barrier removal as a measure to advance the goal of fish conservation. We conclude that diadromous fishes have the capacity to rapidly re-colonize newly available habitats, though the life history patterns of each species, the proximity to source populations in the same or nearby river systems, and the diversity of habitats available may control the patterns and rates of re-colonization.

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Introduction

Re-colonization of freshwater systems by migratory fishes has been an important process in the post-glacial ecology of the Northern Hemisphere, and the distributions of species reflect their pathways and capacities for taking advantage of vacant, suitable habitat (e.g., Lindsey and McPhail 1986; McPhail and Lindsey 1986). Euryhaline and diadromous fishes can move between watersheds via marine routes, facilitating colonization of previously glaciated habitat (though colonization via inland routes also took place). The processes of glacial retreat and colonization are generally viewed as having taken place in past millennia but in parts of Alaska they are contemporary processes (e.g.,

Milner and York 2001; Milner et al. 2000, 2008). In addition, natural and assisted re-colonization efforts have been important components of aquatic ecosystem restoration recently (Duda et al. 2008; Kesler et al. 2011) and in previous decades (Havey 1961; Roos 1991; Pess et al. 2012). Where fish ladders have been installed or culverts removed, streams have experienced natural colonization of upstream habitats, and self-sustaining populations were established within a decade (Bryant et al. 1999; Glen 2002; Anderson and Quinn 2007; Burdick and Hightower 2006; Pess et al. 2012; Anderson et al. 2013).

The rivers draining into the North Atlantic and Pacific oceans include many anadromous species (e.g., alosines, salmonids, lamprey, sturgeons, striped bass, sticklebacks) and a few catadromous species (notably eels but flounder in some cases). In addition, there are many fluvial migrants (Lucas and Baras 2001), including non-anadromous populations of facultatively anadromous species and entirely non-anadromous but migratory fishes such as catfish, cyprinids, and others. The patterns of life history (degree of iteroparity, parental care, size at maturity, seasonal timing of migration and breeding) also vary widely in these species and can influence the capacity for colonization. In addition, the mechanisms of migratory orientation, homing, and population structure vary greatly and likely affect colonization.

Colonization is hypothesized to depend on three factors: (1) Is the habitat accessible? (2) Does the species have the capacity to reach and use the habitat in the context of its life history? (3) Do the species' patterns of juvenile learning (e.g., olfactory imprinting), attraction to odors of conspecifics, or other mechanistic aspects of migration inhibit or encourage colonization of new habitat? Several large-scale restoration actions in river systems draining into the Atlantic and Pacific have occurred over the last several years, allowing scientists and managers to observe how re-colonization by different migratory fishes occurs and apply the lessons to future fish conservation efforts. In this paper we briefly review aspects of the life history of selected anadromous North American fishes, with a focus on species that are most often targeted for restoration. We then examine several case studies of re-colonization, considering the similarities and differences among rivers, species, and life histories. Lastly, we discuss the consequences of factors and how they affect fish conservation and restoration.

Life history of diadromous fishes: implications for colonization

Anadromous fishes are spawned in freshwater, rear as juveniles in freshwater for variable time periods, migrate to sea to grow to their adult size, and return to freshwater to spawn. Conversely, catadromous species are spawned at sea, enter freshwater to feed and grow, and migrate back to sea for reproduction. Fewer than 1 % of all fish species (~320 out of ~32,000) are diadromous, with over half of those being anadromous and approximately 25 % being catadromous; the others are amphidromous, spawned in freshwater, rearing for a period at sea and then returning to freshwater for further growth prior to maturation (McDowall 1988). While these migratory patterns between freshwater and the sea are uncommon among fishes, they are critical in understanding how reconnection of freshwater and marine environments through the removal of blockages to migration such as dams can lead to re-colonization of fish populations. Many of the anadromous fishes are very important in commercial, recreational, ceremonial or subsistence fisheries, yet some populations have been depleted to critical levels, and are protected under the U.S. Endangered Species Act (ESA) or comparable laws in other countries. Many factors caused these declines but habitat loss from impassable barriers was often a contributing factor (e.g., NRC 1996, 2004; McPhee 2002).

Among the diadromous fishes, anadromous species are much more common at higher latitudes than are catadromous species (McDowall 1988; Gross et al. 1988) and our review emphasizes the anadromous species. However, the catadromous eels (*Anguilla rostrata* in North America and *A. anguilla* in Europe; Tesch 2003) show fascinating patterns of migration and ecology (e.g., Helfman et al. 1987) and are of considerable conservation concern (Jonsson et al. 1999). The processes of colonization are likely very different between anadromous and catadromous fishes, as homing to the natal freshwater site for breeding is typical in anadromous fishes (but not universal, e.g., lamprey), whereas catadromous fishes breed at sea, and so their entry into freshwater is directed by other cues rather than detection of imprinted odors. The juvenile glass eels migrating upriver are not homing because they have never been to the river before, nor had their parents (in all

likelihood) been there either. Their migration may be stimulated by the presence of conspecifics (Briand et al. 2002) but flow and other environmental conditions also play a role (Sorensen and Bianchini 1986; Schmidt et al. 2009). Regardless of the mechanism, eels can colonize hundreds of kilometers upstream of former passage barriers and increase population abundance after dam removal (Hitt et al. 2012).

Anadromous mechanisms

The primary mechanism that allows for diadromy is the ability of fish to tolerate the osmotic differences between freshwater to the marine environments, and this is crucial for colonization from one basin to another via marine routes. These processes are best known in salmonids (Clarke and Hirano 1995), particularly the transition of smolts to sea (e.g., (Hoar 1976; McCormick et al. 1998) that characterizes the semelparous species and steelhead trout, *O. mykiss*. Among salmonids, the facultatively anadromous, iteroparous species such as char (*genus Salvelinus*), and cutthroat trout (*O. clarki*) are seldom studied. Movements between basins during the spawning season are known in anadromous Dolly Varden, *S. malma* (Armstrong 1984; Bernard et al. 1995), and bull trout, *S. confluentus*; adults may breed in one river but enter other nearby rivers to feed or over-winter (Brenkman and Corbett 2005). The relatively large size of these fish (more tolerant of varying salinities than smaller fish) may contribute to their capacity to explore, and we expect that similar patterns may be revealed in cutthroat trout as well. This is consistent with the observation that Dolly Varden were the first salmonid in the newly de-glaciated Wolf Point Creek in Glacier Bay, Alaska (Milner et al. 2008). Osmo-regulation studies in non-salmonids such as sturgeon indicate considerable variation from salmonid patterns, and also variation among species (e.g., McEnroe and Cech 1987; Krayushkina 1998; Kuz'michev et al. 2005). It is important to bear in mind these physiological aspects of each species' biology, as they may influence the capacity to colonize basins across a salinity gradient.

The population structure of migratory fishes, notably the anadromous ones, is largely controlled by their strong tendency to home to the natal site or site of first reproduction when mature and ready to breed. As McCleave (1967) pointed out, homing to the natal site

is a subset of the more general phenomenon of homing, including return to the site of previous reproduction (relevant to iteroparous species), and homing after natural or experimental displacement. Homing can be demonstrated directly, by the recovery of fish marked as juveniles in freshwater at the same site when they mature (Quinn 1993). However, persistent phenotypic differences in fish from different rivers convinced early researchers that fish homed (e.g., shad: Milner 1876), and differences in genetic markers provide additional evidence of homing (e.g., Atlantic salmon, *Salmo salar*: Primmer et al. 2006; Dionne et al. 2008; American shad, *Alosa sapidissima*: Hasselman et al. 2013).

Despite the strong homing impulse, dispersal from the natal site, or “straying,” is necessary for post-glacial establishment and modern recovery of the species' range (Westley et al. 2013). Straying is typically defined as returning to spawn outside the river of origin (Westley et al. 2013), though the network structure of river systems can make it difficult to distinguish between straying and movement within rivers. Straying within watersheds and especially the tendency to migrate farther upriver, past the natal site (Keefer et al. 2008a) is especially important to re-colonization after dam removal, though straying from adjacent watersheds (i.e., via marine routes) also occurs. The phenomenon of straying has not been adequately explained on mechanistic or evolutionary grounds (Hendry et al. 2004), so it is difficult to determine how different factors will affect it. Is straying a failure to home, through inadequate learning, retention, or detection of imprinted odors, an alternative life history pattern, or a habitat choice (Quinn 1984)? In any case, straying can be viewed as an “exploratory behavior,” that can contribute to population persistence, colonization, and range expansion (Secor 1999).

Olfactory imprinting for homing is particularly well studied in salmon and trout, and the imprinting has been hypothesized to be sequential, related to a combination of environmental stimuli, developmental and seasonal cues associated with smolt transformation and downstream migration (Hasler and Scholz 1983; Dittman and Quinn 1996). The involvement of imprinted odor memories to which fish return as adults is less often studied in other fishes than salmon but it has been reported in white suckers, *Catstomus commersonii*, (Werner and Lannoo 1994) and is likely a very

general phenomenon. However, the abilities of larval fishes to learn odors may depend on features of the structure and function of the olfactory organs, and the capacity of drifting pre-hatch embryos in the water column or larval fishes to detect and learn odors may not be as great as that of the larger salmon alevins and fry. To the extent that this is the case, homing to the natal stream may be less precise in non-salmonids unless the fish remain in the natal waters long enough to develop sufficient sensory capacity (see Horrall 1981 for a further discussion of this issue, with special reference to homing in salmonids compared to walleye, *Sander vitreus*, and white perch, *Morone americana*).

In addition to the learned odors from the stream's rocks, soil, plants and other chemical constituents, the odors of conspecifics can also play a role in guiding upstream migrants. Attraction to pheromones was hypothesized to influence salmon migrations (Nordeng 1971), and adult salmon are indeed attracted to the odors of juvenile conspecifics (Solomon 1973; Quinn et al. 1983; Groot et al. 1986), though this does not seem to be the primary source of odors leading salmon home (Brannon and Quinn 1990). Upstream-migrating adult sea lamprey, *Petromyzon marinus*, orient to pheromones from juveniles residing in streams rather than odors that they learned themselves earlier (Bjerselius et al. 2000; Vrieze et al. 2010, 2011; Johnson et al. 2012). However, sea lamprey quickly colonized the Great Lakes after they circumvented the Welland Canal (Bryan et al. 2005), and Pacific lamprey colonized the Babine Lake system in British Columbia (Farlinger and Beamish 1984), so pheromones may not be necessary for upstream migration and colonization. Attraction to species-specific odors has been documented in other diadromous species (e.g., the banded kokopu, *Galaxias fasciatus*: Baker and Montgomery 2001, and Atlantic eels: Briand et al. 2002, and references therein), and this is a fruitful area of further research with respect to colonization and migration patterns.

East versus West comparisons

The east and west coasts of North America share two genera of native diadromous fish: *Acipenser*, the sturgeons, and *Salvelinus*, the char. The west coast has four native genera of anadromous fish: *Oncorhynchus*, the Pacific salmon and trout, *Thaleichthys*, smelt,

and *Lampetra* and *Entosphenus*, lamprey. The east coast has six native genera of anadromous fish (*Salmo*, the Atlantic salmon; *Alosa*, the American shad; *Osmerus*, the smelt; *Microgadus*, the tomcod; *Morone*, the striped bass; and *Petromyzon*, the sea lamprey) and the typically catadromous genus of eels (*Anguilla*). Thus, there are some broad similarities (i.e., lamprey and sturgeon are common to both Pacific and Atlantic basins) and some important distinctions (i.e., the prevalence of *Oncorhynchus* spp. compared to prevalence of *Alosa* spp.). We now briefly consider several ecological mechanisms of importance to restoration and re-colonization efforts. Our taxonomic focus is limited to several major genera (*Oncorhynchus*, *Alosa*, and *Salmo*) and our geographic focus is limited to “the salmon-bearing” portions of the Atlantic and Pacific basins but we include some information on other taxa.

West coast: *Oncorhynchus* anadromy;
the importance of straying, and colonization

Straying

Straying is a natural biological process that results in the establishment or re-establishment of populations (Pess 2009). Three generalizations have emerged from homing and straying studies that advance our understanding of how salmonids establish self-sustaining populations with respect to barrier removal. First, regardless of species or origin (wild vs. hatchery), most salmon home but some straying is always detected (Hendry et al. 2004; Quinn 2005). Salmon homing rates average 92 % (SD \pm 9.4 %) and the remaining 8 % stray (Hendry et al. 2004; Keefer et al. 2005; Keefer et al. 2008b). Thus a proportion of any salmon population will likely stray into newly created or accessible habitats once connectivity is restored, though the fraction can vary greatly.

A second generalization is that the amount of straying into a recipient stream is inversely correlated with geographical distance from the source, though other factors also influence the distribution of strays (Quinn 1993). Quinn and Fresh (1984) and Quinn et al. (1991) found that greater than 95 % of all fish that strayed were within 30 km of their home river system or hatchery release site, and other studies also found that most straying occurred to nearby sites (Labelle 1992; Unwin and Quinn 1993; Hard and Heard 1999; Candy and Beacham 2000; Keefer et al. 2008a).

Keefer et al. (2008a) found that two types of straying behavior, overshooting a natal stream and the temporary use of another tributary, declined exponentially with increasing distance from the natal tributary. Because nearby populations are most likely to seed newly available habitats, metapopulation concepts aid our understanding of salmon population dynamics (Cooper and Mangel 1999; Schtickzelle and Quinn 2007).

A third generalization that emerges is that straying rates differ among salmon species (Quinn 1984; Hendry et al. 2004; Quinn 2005). Hard evidence to support this generalization is scarce because there have not been controlled experiments on all species in the same river, and data on wild populations are very limited. Nevertheless, sockeye salmon (*O. nerka*) tend to have very low straying rates (<0.8 %), whereas coho (*O. kisutch*), Chinook (*O. tshawytscha*), steelhead (*O. mykiss*), and Atlantic salmon were reported to have similar and somewhat higher rates (7.8, 6.2, 7.7, and 7.7 %), and chum (*O. keta*) and pink salmon (*O. gorbuscha*) had the highest rates (19.1 and 15.4 %: Hendry et al. 2004). Recent examination of straying rates from the same hatcheries revealed marked differences between species: coho salmon (0.52 %), Chinook salmon (15.3 %), and steelhead (1.2 %: Westley et al. 2013), and also differences among life history types of Chinook salmon. Notwithstanding the difficulties in determining empirical rates of straying among species, why might one expect them to vary? Quinn (1984) hypothesized that there is a dynamic equilibrium between homing and straying in all populations, and that three main factors influence the relative frequency of homing and straying among species: (1) variation in the stability of the habitat, as it affects the certainty of reproductive success (e.g., variation in number of recruits per spawner), (2) the extent of specialization for freshwater habitats, (3) variation in age of maturity, and the extent of iteroparity. Thus if a stream is stable in the recruitment of salmon due to attenuated flow conditions during spawning and incubation, such as a river flowing from a lake, then variation in recruitment would be less and consequently homing would be favored over straying. Conversely, in spawning areas prone to dynamic changes that produce great variation in egg-fry survival (e.g., systems with large variation in flow conditions such as coastal, rain-dominated watersheds), straying might be more prevalent.

An illustration of the role of straying in species' persistence in the face of environmental disruption is provided by the eruption of Mt. St. Helens, Washington on 18 May 1980. When Toutle River origin fish returned (e.g., fall 1980, 1981) they encountered drastically degraded habitat and elevated turbidity from volcanic ash and silt (Leider 1989). Faced with these conditions, Toutle River steelhead straying rates increased from 16 to 45 % after the eruption, and most strays entered watersheds with lower turbidity (Leider 1989). However, within 4 years, or one life cycle of steelhead, straying into nearby rivers decreased to pre-eruption levels and densities of spawning steelhead in two of the major tributaries that returned to pre-eruption streambed elevation had steelhead redd densities that went from 0 to 5.7–21.5 redds km⁻¹ within 7 years of the eruption (Lucas and Pointer 1987; Leider 1989; Bisson et al. 2005). It cannot be determined if the steelhead strayed because they could not identify their natal river because of the ash or because they sensed that the stream was no longer suitable for reproduction. However, experiments indicated that the presence of suspended volcanic ash did not prevent home-stream recognition by Chinook salmon but that they tended to avoid ash-laden water (Whitman et al. 1982). Conversely, as stream conditions changed and sediment concentrations decreased, salmon apparently recognized the change and returned to their natal systems (Bisson et al. 2005).

The second element of Quinn's (1984) hypothesis was that species with less extensive use of freshwater habitats might stray at higher levels than species with extensive specialization for freshwater. For example, the population-level patterns of disease resistance (Buchanan et al. 1983; Bower et al. 1995), migratory orientation (Raleigh 1971; Brannon 1972) and other forms of behavior and morphology (Rosenau and McPhail 1987; Swain and Holtby 1989) that characterize species such as steelhead, Chinook, coho and sockeye salmon may reflect the longer periods of freshwater residence compared to chum and pink salmon. For pink and chum salmon that spawn in the lower portions of coastal streams, conditions are very similar among the streams available to them, and straying to a nearby non-natal stream may not have a large effect on fitness (Quinn 2005). Lower levels of genetic difference between populations as a function of spatial separation in pink and chum salmon compared

to the other species (Hendry et al. 2004) is consistent with this hypothesis but not direct proof of it.

Quinn (1984) also hypothesized that straying is inversely related to variation in age of maturity because parents whose offspring will all spawn in a single year are more at risk of having no grandchildren (owing to some future one-time disaster) than those with offspring spawning in different calendar years. At one end of the spectrum are pink salmon with a fixed 2-year cycle. As Bakshtansky (1980) pointed out, an event occurring in a stream can extirpate an entire year class of this species. It may thus optimize the parents' fitness to have some offspring home and have others stray, to reduce the probability that the entire line will be lost. Chinook salmon are at the other end of the spectrum, varying more in total age than the other Pacific salmon species. Thus, even with the complete loss of one or more year classes and no straying, the parents might still have some surviving grandchildren. Variation in age at maturity is thus a form of straying in time to balance the straying in space. However, recent data challenge the hypothesis that straying is inversely related to variation in age; coho salmon had a lower average straying rate than Chinook salmon in the same river, even though they have less variation in age at spawning (Westley et al. 2013).

Colonization

We hypothesize that the rate of re-colonization is most likely affected by four key factors: the species' presence in the same or nearby watershed(s); productivity of the nearby (donor) population; suitability of newly available habitat for the species; and the presence of life history variants in the donor population to take advantage of the newly opened habitat.

In addition to the studies specifically focused on homing and straying, there have been studies of colonization by salmon to new, naturally created habitats (Leider 1989; Milner and Bailey 1989; Milner and York 2001; Milner et al. 2008) or recently opened/re-opened habitats (Bryant et al. 1999; Young 1999; Burger et al. 2000; Glen 2002; Pess et al. 2003, 2012; Milner et al. 2007; Anderson et al. 2008; Kiffney et al. 2009; Anderson et al. 2013). The time general period for colonization and establishment of self-replacing populations, regardless of whether the new habitats were newly opened or re-opened, was ~5–30 years, and mostly ~10–20 years (Withler 1982; Bryant et al.

1999; Young 1999; Burger et al. 2000; Glen 2002; Pess et al. 2003, 2012; Milner et al. 2008; Kiffney et al. 2009; Anderson 2011) (Fig. 1). Colonizing salmon populations often showed an exponential growth phase ~18–108 % per generation (Table 1).

Pink salmon, coho salmon, sockeye salmon, and Dolly Varden (*Salvelinus malma*) colonized new streams that had recently formed due to de-glaciation in Glacier Bay and established self-sustaining populations within 20 years (Milner et al. 2008). Where fish ladders were installed or culverts removed, natural colonization led to self-sustaining populations in 1–5 years (Bryant et al. 1999; Glen 2002; Pess et al. 2003). Recolonization and establishment of pink salmon in the Fraser River above Hell's Gate landslide required approximately 20 years to establish large spawning populations (Pess et al. 2012).

One of the most important attributes associated with successful salmon colonization in newly opened habitats is the link between compatible life history adaptations and geographic, hydrologic, and ecological characteristics (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). For example, as the Glacier Bay landscape evolved over time, certain habitat features such as lakes became separated from the stream network, resulting in a loss of sockeye salmon populations (Milner et al. 2007). Burger et al. (2000) also found that life history adaptation needed to be compatible with local habitat conditions for sockeye salmon donor populations to successfully colonize a lake system in Alaska after passage facilities allowed them to circumvent a waterfall, underscoring the need to consider life history traits and genetic adaptations in other introduction programs. Further evidence for the link between life history adaptation and environmental and ecological condition again comes from Glacier Bay, Alaska. Milner and Bailey (1989) compared the salmonid spawning density in two recently de-glaciated, geomorphically similar, and adjacent streams. They found that low turbidity, a higher proportion of preferred spawning temperature range (12–15° C), and a more attenuated hydrology were dominant factors associated with higher spawning density. Colonization of these streams over time varied for each species and resulted in more cold water oriented species colonizing first (i.e., Dolly Varden), while pink, coho, and chum salmon appeared 2–10 years later as temperatures warmed (Milner et al. 2008). The sequential

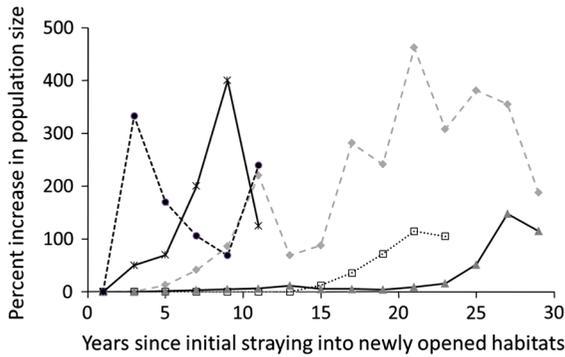


Fig. 1 Percent increase in population size of several salmon populations over time along the Eastern Pacific Rim. *Solid black dots with hashed black line* represent Cedar River, Washington State coho salmon (Kiffney et al. 2009). *Solid black line with stars* represent Cedar River, Washington State Chinook salmon (Kiffney et al. 2009). *Solid grey diamonds with grey hashed line* represent Fraser River, British Columbia pink salmon (Pess et al. 2012). *Open dark squares dark hashed line* represent Glacier Bay, AK pink salmon (Milner et al. 2007). *Solid grey triangles with solid black line* represent percent increase in South Fork Skykomish pink salmon above Sunset falls, Washington State. Population size of the Cedar coho and Chinook salmon is 100 s; 100,000 s for Fraser River pink salmon; 10,000 s for South Fork Skykomish pink salmon, and 1,000 s for Glacier Bay, AK pink salmon

colonization by species over a changing temperature regime also suggests ongoing exploratory behavior by all of these species and a non-random pattern to the colonization.

Another excellent example of the link between life history adaptation and environmental and ecological condition with respect to recolonization is the juvenile coho salmon in the Cedar River watershed of Washington, USA. Juvenile coho salmon typically rear in freshwater habitats for a year prior to seaward migration. Anderson et al. (2013) used a combination of DNA-based parentage analysis and mark–recapture

techniques to document dispersal by juvenile coho salmon in the initial stages of re-colonization following installation of fish passage structures at a dam. Over 25 % of the offspring were outside the area where their parents had spawned, and moved as much as 6.3 km (median = 1.5 km) upstream from the redd locations. Juvenile coho salmon also colonized tributaries where spawning had not taken place, providing a secondary process of spatial expansion following initial colonization by adults (Anderson et al. 2008; Pess et al. 2011; Anderson et al. 2013).

As previously mentioned, most salmonids home to their natal streams to spawn but some (usually <10 %) stray. This entry into recipient streams is inversely correlated to geographic distance from the natal site, and can lead to the establishment of new populations in ~5–30 years, with population growth rates during the initial phase of ~20–100 % per generation. In contrast to the rich literature on salmonids on the west coast, the information on straying and colonization by other anadromous fishes is more limited. There are two sturgeon species on the west coast, the white sturgeon, *Acipenser transmontanus* and the green sturgeon, *A. medirostris*, and the latter is more strongly anadromous in behavior and ecology (Moyle 2002; Wydoski and Whitney 2003). Fish ladders and other passage structures at dams designed for salmonids do not function well for these large-bodied fish, resulting in largely isolated populations (Parsley et al. 2007; Cocherell et al. 2011). Pacific lamprey, *Lampetra tridentata*, also do not use salmon ladders well, though for other reasons, and there is considerable work on the need to modify dams to facilitate their passage (Jackson and Moser 2012; Moser et al. 2002a, b, 2011). Indeed, a recent review indicated that in general salmonids are more successful at using passage facilities than non-salmonids (Noonan et al. 2012).

Table 1 Estimated annual rates of increase based on the exponential growth phase of six colonizing populations (Pess et al. 2012; Milner et al. 2007; Kiffney et al. 2009; Anderson 2011)

| Species | Location | Population growth rate (r) |
|----------------|--|----------------------------|
| Pink salmon | Fraser River (Above Hell’s Gate), British Columbia, Canada | 1.18 |
| Pink salmon | Glacier Bay, Southeast Alaska | 2.01 |
| Pink salmon | South Fork Skykomish, Puget Sound, Washington State | 1.18 |
| Coho salmon | Cedar River, Puget Sound, Washington State | 2.08 |
| Chinook salmon | Cedar River, Puget Sound, Washington State | 1.95 |
| Chinook salmon | South Fork Skykomish, Puget Sound, Washington State | 1.28 |

Colonization opportunities, particularly for salmonids, have been or are being created throughout the Western United States with the removal of both small and large dams. Notable dam removals that have occurred or are occurring in the Western US include Marmot Dam on the Sandy River, Oregon, Condit Dam on the Little White Salmon River, Washington, Savage Rapids Dam on the Rogue River, Oregon, and the Elwha and Glines Canyon dams on the Elwha River in Washington state (http://en.wikipedia.org/wiki/Dam_removal). Passage facilities have recently been implemented in other locations such as the Cedar River in Washington State (Anderson and Quinn 2007), and there are recent on-going efforts to move salmonids above large dams with no passage facilities such as the Cowlitz River, Washington State (<http://cowlitzfish.net/>) and the Willamette River, Oregon (Keefer et al. 2013).

East Coast: Multispecies anadromy dominated by alosines

The life history patterns of the diverse, native anadromous species on the east coast of North America differ in many ways from those on the west coast. Unlike the west coast, the east coast was not dominated by salmonids. Atlantic salmon were never as abundant as the alosines that shared many of the same rivers, particularly in the southern portion of the Atlantic salmon's North American range. In addition, Atlantic salmon are a single species, with brook trout (*Salvelinus fontinalis*) as the other native salmonid other than Arctic char, whereas there are five species of Pacific salmon, plus two anadromous trout species, and three species of anadromous char. We thus focus our east coast review on community interactions, recolonization patterns, and restoration outcomes with a particular emphasis on the southern portion of the Atlantic salmon's North American range. These patterns and observations would likely shift substantially as the geographic focus moves north and Atlantic salmon become one of the very few diadromous species able to tolerate the challenging climate of northern Quebec and Labrador.

Community interactions

Historically, numerous east coast rivers had large runs of sturgeon (*Acipenseridae*), striped bass (*Moronidae*)

and alosines (*Clupeidae*), which dominated most systems from New England to northern Florida (Stevenson 1899; Limburg and Waldman 2009). Within New England, abundant runs of Atlantic salmon, rainbow smelt (*Osmerus mordax*), and sea lamprey (*Petromyzon marinus*) were ubiquitous as well (Moring 2005), although alosines were likely the most abundant species (Foster and Atkins 1869; Limburg and Waldman 2009).

A growing body of evidence suggests that the formerly abundant runs of other diadromous species, alosines, sea lamprey and rainbow smelt in particular, provided demographic security to Atlantic salmon and sustained ecological functions required by Atlantic salmon through a series of interspecific interactions. Saunders et al. (2006) hypothesized that these other species provided demographic benefits to Atlantic salmon through four specific mechanisms: nutrient cycling (i.e., marine-derived nutrient deposition), habitat conditioning, providing alternative prey for predators of salmon (i.e., prey buffer), and serving as prey for juvenile and adult salmon. These hypotheses are difficult to test, given the severely depressed abundance levels of many of the species, but there is evidence of their individual effects. The role of marine-derived nutrient deposition was recently evaluated by Guyette et al. (2013) using carcass analogs to simulate nutrient deposition by sea lamprey carcasses in headwater tributaries of the Penobscot River, Maine. Guyette et al. (2013) provided clear evidence of enhanced growth (e.g., 33–48 % greater mass) experienced by juvenile Atlantic salmon in treatment reaches. Further, evaluations of the potential for sea lamprey to “condition” the freshwater habitat of Atlantic salmon by Hogg (2012) showed that bioturbation was associated with sea lamprey nest construction in sympatric reaches of Atlantic salmon habitat. A suite of abiotic effects such as increased permeability and decreased embeddedness, and biotic effects (e.g., abundance of benthic organisms) were detectable immediately and for several months after lamprey spawning (Hogg 2012). Further research may elucidate the potential role of sea lampreys as ecosystem engineers (sensu Brown 1995) in freshwater habitats important to Atlantic salmon production in similar ways that bioturbation studies from the West Coast (e.g., Montgomery et al. 1996) have provided evidence of intraspecific interactions for Pacific salmon species. Some evaluations of the roles of river herring

as a prey buffer for emigrating Atlantic salmon smolts are currently underway (NMFS unpublished data), and the role of rainbow smelt as an important food source, particularly for re-conditioning kelts, is already well recognized (Saunders et al. 2006).

Although refinement and testing of these hypotheses remain a priority, recovery of the last remnant stocks of Atlantic salmon in the United States are moving forward on the basis of a multi-species approach to Atlantic salmon recovery. For example, the National Marine Fisheries Service specifically identified “freshwater and estuary migration sites with abundant, diverse native fish communities to serve as a protective buffer against predation” as a primary constituent element of Critical Habitat for the endangered Gulf of Maine Distinct Population Segment of Atlantic salmon (USOFR 2009a, b). Thus, understanding the factors limiting restoration of the suite of east coast diadromous fish is important in its own right, but also in the context of recovering Atlantic salmon in the US.

Re-colonization patterns and restoration outcomes

There is a wide range in our understanding of genetic structure, homing rates, and life history variation among native species on the east coast. For Atlantic salmon, the general pattern of philopatry coupled with distinct river-specific adaptation is well studied (Klemetsen et al. 2003; Garcia de Leaniz et al. 2007), as is the importance of life history variation (Saunders and Schom 1985; Vähä et al. 2008). Life-stage specific vital rates are also available for Atlantic salmon, permitting the development of very detailed life history models (e.g., Juanes et al. 2009). Atlantic salmon homing rates are quite high (roughly 98 % reported by Baum and Spencer 1990, in general accord with those reviewed by Stabell 1984). Studying homing rates in the southern portion of the North American portion of the range of Atlantic salmon is complicated by the presence of many dams with inefficient fishways, low post-spawning survival of kelts, and substantial hatchery influence in many cases. In contrast with Pacific salmon, Atlantic salmon are iteroparous and this appears to be an important component of the Atlantic salmon’s “bet hedging” strategy (see Klemetsen et al. 2003). McCleave (1967) stated that iteroparity may increase the rate of homing

due to previous experience, though empirical evidence remains sparse.

While the importance of homing, straying, and life history variation described above for west coast salmonids is likely as significant in non-salmonid anadromous fishes, substantially less information is available for the alosines, sea lamprey, and sturgeon. For example, Hasselman and Limburg (2012) searched Thomson Scientific’s Web of Science and found that the keywords “*Alosa* AND genetic” revealed 34 publications; “*Salmo* AND genetic” revealed 1,721 publications; “*Oncorhynchus* AND genetic” revealed 1,914 publications. This anecdote illustrates the comparative dearth of genetic information of alosines compared to Atlantic and Pacific salmon; this pattern generally holds true for other kinds of information (e.g., life history variation), and other kinds of fishes.

Like other clupeids, the alosines are schooling fish that tend to be broadcast spawners (e.g., Loesch and Lund 1977) with no parental care (Fay et al. 1983). These life history traits contrast sharply with salmonids, and the differences are largely consistent with their respective evolutionary lineages (see McDowall 1993, 1997; Dodson 1997; Dodson et al. 2009). These basic differences in life history are relevant to restoration and re-colonization in at least three major ways. First, schooling behavior (i.e., the desire to pass upstream together), coupled with relatively large body size of American shad creates great difficulty for upstream passage even in state-of-the-art fishways. American shad and other alosines tend not to leap (Larinier and Travade 2002), they avoid submerged orifices (Monk et al. 1989), and they tend to be very sensitive to turbulence and shadows (Haro and Castro-Santos 2012). Large fishways with lower slopes, little air entrainment, and fewer eddies are thought to be more effective for passing American shad (Larinier and Travade 2002), but the current lack of quantitative field evaluations and variation in passage efficiency when such studies are conducted have led to conclusions that high performance of upstream passage for American shad cannot be achieved (Haro and Castro-Santos 2012). Few large fishways that would accommodate the large body size and schooling behavior of American shad have been built on eastern rivers. Evaluations of scaled-down versions of traditional fishways, modeled after Columbia River-style fishways, produced disappointingly low efficiency

estimates (e.g., Rideout et al. 1985) and full size evaluations of these types of fishways have yet to be undertaken broadly (Haro and Castro-Santos 2012). In some instances, fish lifts have successfully passed American shad, but problems with siting, attraction, and peak-run capacity still need to be resolved (Haro and Castro-Santos 2012). Presumably, the presence of relatively large fishways that can accommodate large-bodied, schooling fish is at least partially responsible for the colonization of rivers along the west coast, especially their numerical and spatial expansion in the Columbia River following the construction of The Dalles Dam in 1957 (Quinn and Adams 1996; Hasselman et al. 2012; Hinrichsen et al. 2013). Conversely, the relative absence of such fishways on the east coast has likely inhibited the colonization by shad in rivers (Hinrichsen et al. 2013).

Second, stock-specific adaptations are not well documented in alosines and their importance to restoration and re-colonization is largely unknown. While there is evidence of philopatry among alosines (e.g., Carscadden and Leggett 1975; Hendricks et al. 2002), quantitative estimates of homing and straying are also largely unknown. Some inferences can be made from tagging studies (Jessop 1994), and genetic techniques offer hope of refining these estimates (Palkovacs et al. 2013). Although information is currently limited, there is substantial life history variation (e.g., Limburg 1998) including population-specific iteroparity rates and ages at maturation (Leggett and Carscadden 1978) in American shad. Leggett and Carscadden (1978) concluded that the higher rate of iteroparity in the northern portion of the American shad's range was a bet-hedging strategy because of the more unpredictable spring and early summer climatic conditions. For river herring, Gahagan et al. (2012) recently described high movement rates across salinity boundaries for age-0 alewives and blueback herring, particularly in systems where movement between riverine and estuarine habitats was unrestricted. Roughly 16 % of all fish examined moved between freshwater and marine habitats multiple times in their early life history (Gahagan et al. 2012). This finding contrasts sharply with the widely held view that juvenile river herring emigration is unidirectional and deterministic (i.e., always proceeds directly downstream). Limburg (1998) hypothesized that recurring migrations of juvenile alosines between lower river and near shore marine habitats were the

result of schooling, whereby juvenile alosines are entrained in schools of adult spawners. Limburg (1998) further hypothesized that this may be an important exploratory mechanism for potential colonizers. Unfortunately, there is great uncertainty regarding the heritability of these patterns of life history, habitat use, and migration timing. There is, however, more historic (Nolan et al. 1991) and recent work describing patterns of genetic structure in American shad (Hasselman et al. 2010, 2013) and river herring (Palkovacs et al. 2013).

Third, at high latitudes American shad may exhibit serial spawning and batch fecundity, whereby spawning events occur in several pulses and progress in a downstream direction as the season advances (Maltais et al. 2010). This has been observed in both semelparous and iteroparous populations of American shad (Olney et al. 2001). The phenomenon of serial spawning, coupled with higher degrees of iteroparity at higher latitudes (Leggett and Carscadden 1978), suggests that poor downstream survival of adults (Leggett et al. 2004) as well as juveniles (Harris and Hightower 2012) may negate otherwise effective restoration actions. Serial spawning is poorly understood in river herring as well as American shad. Frank et al. (2009) recently hypothesized that the phenomenon commonly referred to as “fallback” may actually be part of the normal spawning migration behavior of anadromous alewives. This would have substantial ramifications for how we view alosine migrations. In an undammed system, serial spawning would ensure substantial variation in life history even within a family group. Prior to the observations by Maltais et al. (2010), Olney et al. (2001) hypothesized that serial spawning may increase the probability of finding favorable environmental conditions for the survival of the larval American shad by dispersing them over time and space. Thus, life history variation may be environmentally mediated by processes such as serial spawning, but the extent to which these characteristics (i.e., tendency to spawn serially) may be heritable is largely unknown. Further refinement and testing of hypotheses regarding the genetic and environmental influences of serial spawning and other life history variants in alosines is needed.

Among the least studied of the east coast diadromous fishes is the sea lamprey (*Petromyzon marinus*; Clemens et al. 2010), for which even basic assessments such as regional abundance trends of adult

returns are unavailable (Nislow and Kynard 2009). Sea lamprey are best known for the extensive control programs in the Great Lakes where they are a non-native invasive species but they are native to the east coast and there is building evidence that they provide important ecological services to the watersheds, and that efforts to restore sea lampreys may assist the restoration attempts for other species (Hogg 2012). Recent evidence indicated that they quickly re-colonized upstream habitat after removal of small dams (Hogg et al. 2013).

On the east coast, true re-colonization studies are quite rare even though there have been many dam removals during the past 15 years, and we focus here on responses of alosines. Removals of Edwards Dam (Kennebec River, Maine) and Quaker Neck Dam (Neuse River, North Carolina) (Fig. 2) resulted in upstream migration of alosines and other anadromous fishes (O'Donnell et al. 2001; Burdick and Hightower 2006), yet the observations of these species upstream of the recently removed Embry Dam (Rappahannock River, Virginia) have been limited in distance and numbers (Allan Weaver, Virginia Dept. Game Inland Fisheries, pers.com.). When dams are removed or planned to be removed, various types of stocking are often implemented. For example, prior to the removal of the Edwards Dam in 1999, the Maine Department of Marine Resources had already transferred roughly 600,000 adult alewife and 8.4 million American shad fry to upstream reaches. Millions of adult alewives now return to the Kennebec River annually but the question remains whether the dam removal or the stocking led to the “success”.

Numerous rivers flowing into Long Island Sound did not have dams removed but have had fish passage facilities constructed and now have fish runs which are monitored at those facilities. Shad runs occur in the Housatonic, Naugatuck, Shetucket, and Pawcatuck rivers (S. Gephard, unpublished data) (Fig. 2). The Connecticut River hosts the largest run of American shad in Long Island Sound; in 2012, nearly 490,000 American shad were passed at the first dam (<http://www.fws.gov/r5crc/Stuff/stuff.html>). To the west, the Quinnipiac River had a shad count of seven for the first time at the first dam in 2012 (Connecticut Department of Energy and Environmental Protection (CTDEEP), Old Lyme, CT, unpublished data). Shad have been reported in only 2 of the last 15 years at the first dam on Whitford Brook (20 km east of the Connecticut

River) but other rivers have had far more consistent counts. The Pawcatuck River, 8 km west of Whitford Brook, has averaged 888 at the first dam over the past 34 years (RI DEM Arcadia, RI, unpublished data). No shad are observed in other numerous streams along the shoreline of Long Island Sound, suggesting that straying may be relatively rare.

Shad re-colonization of reconnected habitat within a natal river in the northeastern United States can proceed quickly, regardless of the low population levels. Immediate use of upstream habitats was seen in the Westfield River, a tributary to the Connecticut River at river kilometer (RKM) 95 and Farmington River at RKM 80 once fishways were installed at their respective dam sites (Fig. 3). Both rivers had shad runs to the base of the dams prior to fishway construction but the increase in shad abundance over time was greater in the Westfield River than the Farmington River. The Farmington River fishway at Rainbow Dam is considerably larger than the one at the Westfield River dam site (approximately 15 m high and 241 m long), making ascent difficult for shad. In the Shetucket River, draining directly into Long Island Sound, shad immediately moved upstream once fish passage facilities were installed (Fig. 2).

Self-sustaining populations above these dam sites are likely constrained by anthropogenic factors unrelated to the species' tendency for colonization. For example, the Rainbow Dam fishway is an unsuitable design for shad and many die attempting to ascend (S. Gephard, personal observation). Thus, the lack of population rebuilding observed over the last two decades is not surprising. The Greeneville Dam fish lift on the Shetucket River provides access to only a small area of upstream habitat that may be near its carrying capacity, resulting in a relatively stable but small population. The West Springfield Dam fishway on the Westfield River is the most effective fishway of the three and provides access to 21 km of suitable habitat, resulting in an expanding shad population in the Westfield River. While long-term success of restoration efforts has varied between the three locations, the data demonstrate the species' strong urge to continue upstream into habitat not previously occupied.

Until recently, empirical evidence of straying by river herring (alewife and blueback herring) has been completely lacking. Hogg (2012) and Gardner et al. (2011) captured adult alewife in previously

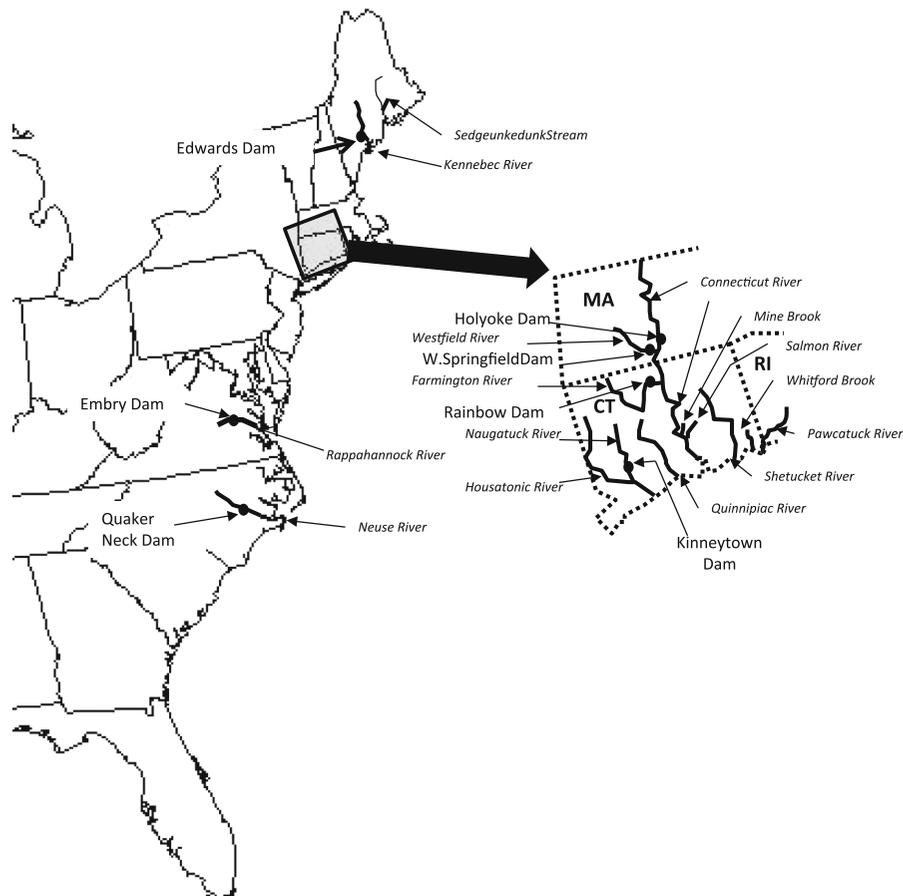


Fig. 2 Select rivers and dams along the Eastern seaboard of the United States. Inset map includes detailed area of rivers draining into Long Island Sound and their associated dams

inaccessible reaches of Sedgeunkedunk Stream, Maine shortly after dam removals in 2008 and 2009. Further, Hogg (2012) observed downstream emigration of juvenile alewife at the outlet of Fields Pond on this stream, confirming successful reproduction and recolonization of alewives in a pond that had been inaccessible prior to dam removal. Alewives have also been observed spawning in Connecticut River tributaries where there is no nursery habitat. For example, Mine Brook in East Hampton, CT has very limited (<300 m) fast flowing rocky habitat before alewives encounter a 6 m barrier waterfall yet alewives have been observed spawning there in some of the last 10 years (S. Gephard, pers. obs.). Residence time of drifting larvae would be extremely limited in this small brook so imprinting seems unlikely, leading to the conclusion that this spawning run and others like it

may represent straying. Moreover, recent studies have inferred straying rates from genetic analyses. Palkovacs et al. (2013) examined genetic patterns of isolation by distance (IBD) to conclude that straying rates are generally higher in alosines than salmon, and that blueback herring stray more than alewife. Notwithstanding the limitations of the IBD analysis (Bradbury and Bentzen 2007), this conclusion is consistent with observations from these New England streams (S. Gephard, pers. obs.).

Sea lamprey runs in Long Island Sound tributaries have been limited to a very few streams after industrialization (Whitworth 1996). The Connecticut River hosts the largest run in Long Island Sound, averaging 38,000 lamprey lifted annually during the last 20 years (<http://www.fws.gov/r5src/Stuff/stuff.html>). Only eight tributaries in Long Island Sound in

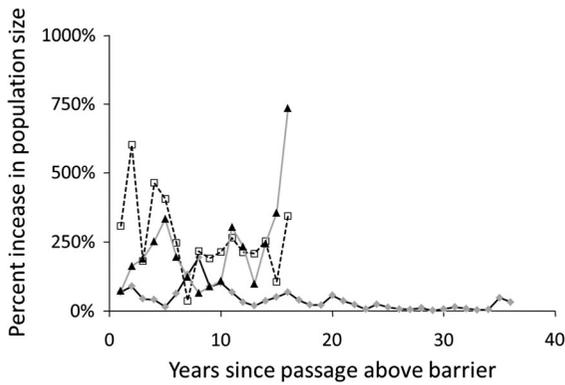


Fig. 3 Shad counts at three Long Island Sound fishways beginning the first year of operation of each fishway (CTDEEP and USFWS unpublished data). *Open squares with dashed black lines* is the Shetucket River (Greenville dam fishlift) (ave. shad population 2.317 ± 1.287), *grey diamond with solid black line* is the Farmington River (Rainbow dam fishway) (ave. shad population 504 ± 491), and the *black triangle with grey solid line* is the Westfield River (West Springfield dam fishway)) (ave. shad population 3.038 ± 2.300)

Connecticut host sea lamprey runs, and most of them are believed to number <1,000 and in most cases <100 individuals per year (CTDEEP, Old Lyme, CT, unpublished data). The tendency to be attracted to the pheromones produced by resident ammocoetes (noted previously), coupled with the paucity of established runs in Connecticut streams, suggest low re-colonization potential for the species.

Results from different restoration strategies in two Long Island Sound tributaries support the view that sea lamprey have limited re-colonization ability. The Shetucket River Greenville Dam Fishlift and the Naugatuck River Kinneytown Dam Fishway were operated for the first time in 1996 and 2000, respectively, with no prior stocking of sea lamprey and the assumption that no lampreys were present downstream of the dams (Whitworth 1996). No lampreys were passed in the 6–8 years of operation (Fig. 4), though a few lamprey were counted at the Greenville Fishlift on the Shetucket River during the past 17 years, demonstrating that some straying occurred (Fig. 4). Un-spawned adult lamprey were transplanted into habitat upstream of the Kinneytown Dam in 2004 (N = 63) and 2005 (N = 110) to support a re-colonization study that successfully produced ammocoetes (Starr 2007). During the next several years, the number of adult sea lampreys counted at the Kinneytown Fishway increased dramatically, presumably in

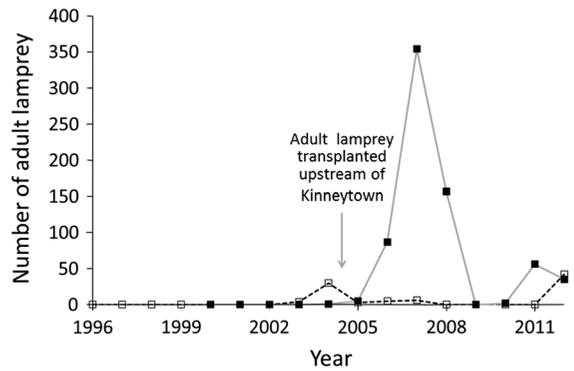


Fig. 4 Adult sea lamprey counts on the Shetucket River (Greenville dam fishlift), Shetucket River and Naugatuck River (Kinneytown dam fishway, Naugatuck River. *Open rectangles with a hashed black line* denote the Shetucket River, while the *solid grey line and solid black rectangles* denote the Naugatuck River (CTDEEP, unpublished data)

response to the presence of ammocoete pheromones (Fig. 4). Similar returns were not seen at the Greenville Fishlift where no transplanted occurred, suggesting that sea lamprey colonization of unoccupied streams is slower compared to streams with ammocoetes.

The Westfield River’s West Springfield fishway and the Farmington River’s Rainbow fishway both had sea lampreys nesting below the dams but no transplanted of sea lampreys above the dams prior to fishway operation. In both cases, sea lamprey immediately used the fishways in large numbers, resulting in consistent counts of lamprey in the thousands (Fig. 5). Sea lamprey nest surveys on the Salmon River, a Connecticut River tributary, documented many nests in headwater habitat approximately 5 rkm upstream of typical ammocoete habitat (CTDEEP, Old Lyme, unpublished data) demonstrating that upstream penetration is common and likely evolved to ensure that eggs and larvae drift downstream into suitable habitat. Similar patterns with sea lamprey in the Sedgeunkedunk Stream, Maine have recently been observed. A spawning population of sea lamprey existed below two impassable dams prior to their removal beginning in 2008. Within 1 year of dam removal, sea lamprey re-colonization proceeded as far upstream as the first natural barrier (roughly 5 km; Hogg et al. 2013). These data and observations demonstrate that lateral colonization of unoccupied streams by sea lamprey may be slow but upstream colonization of unoccupied habitat within occupied streams can be rapid.

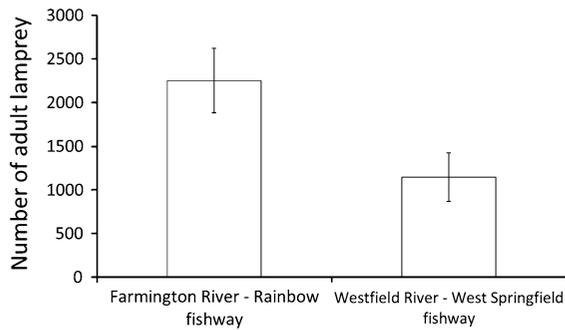


Fig. 5 Average number of sea lamprey passed in the Farmington River (Rainbow fishway) (1976–2012) and the Westfield River (West Springfield fishway) (1996–2012). Lines with perpendicular hash marks are standard error estimates, respectively. Lampreys were not counted at the Rainbow fishway in 1976–1977 (CTDEEP and MDFW unpublished data)

A colonization model

The preceding observations lead us to offer a conceptual model to compare the relative tendency for prominent North American east and west coast diadromous species to colonize new habitat (Fig. 6). This conceptual model between species provides a starting point for those involved in management actions associated with the elimination of migratory barriers and expansion of diadromous fish populations. For example, given the apparent tendency of sea lamprey to not stray (laterally across watershed boundaries) and apparent genetic panmixis in the Atlantic population (Bryan et al. 2005) there may be no reason not to transplant adults to accelerate colonization of vacant streams.

Alosines, on the other hand, have an intermediate tendency to stray and the decision to re-introduce fish may be influenced by local conditions. If a vacant stream is located between two streams with strong runs of the targeted alosine species, re-colonization may occur without reintroduction. Rivers that are distant or unique from extant runs may slow to re-colonize, so reintroduction may accelerate the pace of recolonization. If stocking is used, other issues of population structure and the swamping of native genotypes require careful consideration. Lastly, some rivers targeted for Atlantic salmon restoration in New England (e.g., the Connecticut) are over 500 km away from the nearest extant population. Given the species' limited tendency to stray, natural re-colonization

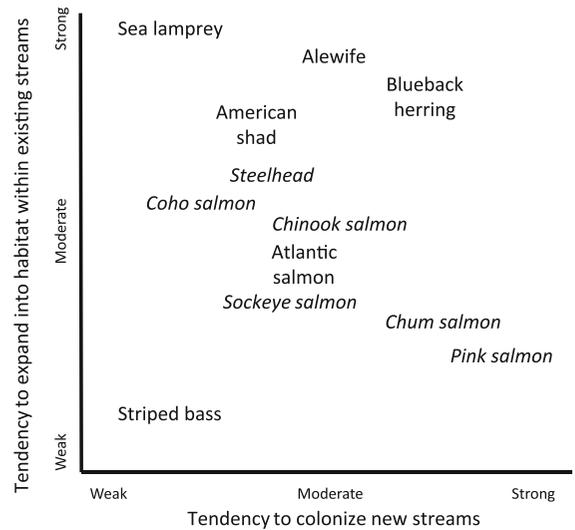


Fig. 6 A conceptual model of the potential for recolonization by East and West Coast of North America diadromous fish species. Italicized species are West Coast salmonids

would likely take an extremely long time or might not occur in the foreseeable future without assistance.

The tendency for west coast salmonids to colonize new streams or expand into habitats within existing streams is ultimately related to the compatibility between specific life history adaptations of each species and the physical and ecological characteristics of the new habitats (Quinn 1984; Allendorf and Waples 1996; Burger et al. 2000). Several specific factors will also directly affect colonization by salmon. These include natural barriers (assuming artificial barriers are removed), distance from the source population, initial population size, straying rate, interactions with existing fish populations, and intraspecific competition for food and space (Pess 2009; Pess et al. 2012). Identifying and understanding how each of the variables affects species-specific salmonid recolonization provides a template for salmonid response in any watershed. For example, pink salmon which typically have larger but highly variable population sizes, higher straying rates, minimal variation in life history characteristics, and a short freshwater residence are prime candidates for the colonization of newly opened habitats (Quinn 2005). Other species such as steelhead have lower population sizes, lower straying rates, greater variation in their life history, and greater freshwater residence time are thus less likely to establish spawning populations first.

Conversely, pink salmon colonization may be limited in their more modest jumping ability and ability to maneuver past barriers compared to steelhead.

One important factor to consider is metapopulation dynamics. A metapopulation can be broadly defined a suite of local populations inhabiting distinct patches of suitable habitat, which interact through dispersal, and persist through time between stochastic extinctions and re-colonizations (Schtickzelle and Quinn 2007). Both theoretical and empirically derived metapopulation models have been used and developed to explain the interaction of local populations and the potential for colonization of diadromous fishes (Cooper and Mangel 1999; Young 1999; Thorrold et al. 2001; Pess et al. 2012) but in general this body of theory has not been as strongly linked to conservation efforts for migratory fishes as it might be.

Conclusions and recommendations

Diadromous fishes can re-colonize newly available habitats, though life history patterns, proximity to source populations, physical capacity to surmount barriers or use artificial ladders, and diversity of habitats available may control the patterns and rates of recolonization. Straying and life history variation are integral parts of the biology of each species, allowing it to persist in the face of varying environmental conditions. These features, inferred from the west coast salmonid examples, and east coast alosine restoration efforts, function at the population level. However, the genetic architecture behind these life history traits at the individual level, where selection occurs, is even less well understood than it is at the population level. To advance the understanding of re-colonization we have offered several examples to illustrate the likely factors influencing the pace of natural re-colonization in previous sections. Re-colonization rate is most likely affected by four factors: accessibility, proximity to a donor stock, productivity and condition of the donor stock, and habitat suitability for the species and life history variant. These factors are the basis of our conceptual model to assist those weighing various re-colonization options. This conceptual model requires refinement and scrutiny through the development of quantitative models and empirical evidence.

Regardless of the factors that influence recolonization, barrier removal and assisted migration are the two main restoration actions that can be utilized as a restoration strategy. Identifying the targeted species, understanding the life history patterns between and within species, having information on the four preceding factors affecting colonization rate, and knowing if the focal populations are natural, transplanted, or of hatchery origin will help identify which restoration strategy is utilized (Anderson et al. 2013). Species with higher stray rates across watersheds, a relatively simple set of life history patterns, and are naturally occurring may not need any prompting, thus barrier removal could suffice to bring colonizers. Conversely, a species that seldom strays, does not move much within a stream, and has a relatively complex life history and specific habitat needs may need assisted migration or reintroduction.

Lastly, few examples of true re-colonization experiments exist, partly because they are often confounded by the artificial re-introduction of fish. There is typically more effort to stock streams to accelerate the pace of restoration but less effort to evaluate the costs and benefits of natural re-colonization versus stocking. Regardless of whether or not fish are stocked into a stream as part of a restoration plan, our review suggests that the elimination of migratory barriers will often result in upstream colonization of vacant habitat, even if different species do so at different rates.

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