

The Role of Anadromous Sea Lamprey in Nutrient and Material Transport between Marine and Freshwater Environments

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Abstract.—The sea lamprey *Petromyzon marinus* is a widely distributed anadromous species spawning in coastal rivers and streams throughout the north Atlantic basin. In this paper, we review aspects of sea lamprey migration and ecology that relate to the transport of nutrients and materials to and from freshwater ecosystems and provide an example of a long-term study of a native wild population. Several aspects of lamprey life history (rapid growth in marine phase, many adults spawn in upper reaches of small oligotrophic rivers, all adults die after spawning) suggest that anadromous sea lampreys contribute marine-derived nutrients and materials (MDNM) to freshwater ecosystems. We used long-term (20 years) data on spawner abundance, along with literature-derived concentration values, to estimate the import of nutrients and materials to a spawning reach of the Fort River, a tributary of the Connecticut River in western Massachusetts, USA. Sea lamprey imported as much as 0.26 g of P per square meter of stream, as much as of 20% of the total annual P loading to a similar system where a full P budget has been developed. While the MDNM contribution of sea lamprey may be substantial, other aspects of their life history and habitat use may limit the overall the magnitude and direction of lamprey influence on freshwater ecosystems. Spawning requirement for rocky substrate within a narrow size range may limit import at the watershed scale. In addition, marine survival rates of less than ~1% will result in a net export of nutrients and materials via out-migrating juveniles (transformers). While there is currently no information on survival rates in wild anadromous populations, the tight link between adult survival and prey/host fish populations observed in landlocked Great Lakes systems suggests that the ecological role of sea lamprey may be strongly related to the abundance of coastal marine fishes. Further research on adult survival, juvenile dispersal and distribution, and the paths of nutrient and material uptake in spawning streams are necessary to more fully evaluate the role of anadromous sea lamprey in the transport of MDNM.

Introduction

The sea lamprey *Petromyzon marinus* is a widely distributed anadromous species native to the North Atlantic and northern Mediterranean region (Maitland 2003). The species was highly valued as a food source during early European history (Dempson

and Porter 1993) and continues to be in some European rivers today (Almeida et al. 2002). In addition to its food value, sea lamprey are harvested by biological supply companies for use in laboratories (Kircheis 2004). However, in the past half century, sea lamprey research and management in North America has been dominated by efforts to monitor and eradicate invasive landlocked populations from the Great Lakes region of the United States, where

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they have had a devastating impact on valuable fisheries (Christie and Goddard 2003). In a Web-based literature search using the terms “sea lamprey ecology and management,” more than 90% of the first 100 papers dealt with Great Lakes issues. Even in wild anadromous populations, fears of negative effects on commercial and game fishes have led some managers to cull prespawning lampreys in rivers, despite no evidence that these negative impacts occur. For example, until recently in the Sheepscot River, Maine, USA, it was the policy to exclude prespawning lampreys from the fishway at the lowermost dam in the system (Kircheis 2004).

More recently, given declines and local extirpations of native populations (Renaud 1997), due in large extent to the barriers to migration (Beamish and Northcote 1989), there has been an acknowledgment of the conservation importance of sea lamprey in its native range. Conservation of native sea lamprey is currently part of river management plans in both Europe (Maitland 2003) and North America (Connecticut River Atlantic Salmon Commission 1998). Interest in the conservation of native anadromous lamprey stems in part from their potential role in freshwater ecosystems. Anadromous fish can impact freshwater ecosystems in a number of different ways, but the role of Pacific salmonids in the transport of nutrients to and from stream ecosystems has received particular attention from ecologists (reviewed by Gende et al. 2002; Naiman et al. 2009, this volume). However, there is relatively little research on the role of Atlantic-basin anadromous fish in nutrient and material transport (Nislow et al. 2004; Saunders et al. 2006; Jardine et al. 2009, this volume). Further, while the focus has been on nutrient transport, anadromous fish transport other important materials in the course of their migratory life cycle. For example, in the north Atlantic region, mercury contamination of freshwaters is a major problem for freshwater fisheries (Mergler et al. 2007), but we have little information of the role of anadromous fish in Hg transport. In this paper, we assess the potential role of sea lamprey in freshwater ecosystems. We review lamprey life history and habitat-use characteristics that influence the direction and magnitude of nutrient and material transport and estimate potential import using long-term data on spawner abundance in a tributary of the Connecticut River, USA. Our goal

is to establish a framework to evaluate the ecological role of sea lamprey, identifying important data gaps to help guide future research.

Factors Favoring Sea Lamprey as Important Nutrient and Material Importers

Life History Factors

Several life history attributes of anadromous sea lamprey point towards lamprey as significant importers of marine-derived nutrients and materials (MDNM). Adult growth rates in the marine environment are quite high, with adults increasing their body mass more than two orders of magnitude during an estimated 13–19 months at sea (Maitland 2003; Drevnick et al. 2006). This growth and sea age are similar to pink salmon *Oncorhynchus gorbuscha*, which are significant contributors of marine-derived nutrients to Pacific Northwest streams (Quinn 2005). Additionally, like all Pacific salmon (except for steelhead *O. mykiss* and cutthroat trout *O. clarkii*), sea lamprey are obligately semelparous, with all adults dying within a few days after spawning (Applegate 1950; Beamish 1980). This is in contrast to all other native Atlantic basin species in which some percentage of spawners survive to out-migrate, taking a considerable portion of their MNDM back out to the ocean (Lyle and Elliott 1998; Nislow et al. 2004).

In addition to the size, abundance, and fate of spawners, the timing of spawning and carcass availability may be key to the role of lamprey in nutrient and material transport. Studies in the Pacific Northwest (Gende et al. 2002) suggest that for some species in some systems, carcasses are present during a time when physical conditions (i.e., floods) prevent efficient uptake. Because lamprey generally spawn in late spring and die immediately after, carcasses are available at a time of the year characterized by relatively low flows, warm temperatures, and high fish growth rates. This makes the contribution of lamprey very well-timed to support instream production. Further, as a consequence of these conditions, carcasses decompose quickly. In the Fort River, western Massachusetts, USA, carcasses are essentially completely decomposed within 1–2 weeks after spawning (B. E. Kynard, personal ob-

servation). This is in strong contrast, for example, to decomposition rates observed for fall-spawning Atlantic salmon *Salmo salar* in Scottish Highland rivers (Nislow, unpublished data) where >50% of the carcass mass was still present months after placement in rearing streams in January. As a consequence, for the same nutrient and material total load (g) contained in spawners, loading rates (g/time) will be much greater for lamprey than for species with spawning timing and decomposition rates similar to Atlantic salmon (Figure 1).

Habitat Use Factors

In addition to life history characteristics, the types of spawning and juvenile rearing habitats used by anadromous species strongly influences their potential contribution to freshwater ecosystems. The ability of lamprey to access and use small, upland rivers makes it more likely that they will be important contributors of nutrients and materials. Total nutrient loading tends to be higher in larger, lowland rivers than in smaller upland rivers and streams (Lyle and Elliott 1998) due to greater residential, agricultural,

and industrial use (Stockner et al. 2000; Nislow 2005) along with longitudinal increases in the storage capacity of rivers and floodplains (Naiman et al. 1987; Montgomery and Buffington 1997), so that inputs from migratory fish are likely to be a smaller proportion of total budgets in these downstream reaches. Further, in the north Atlantic basin, small rivers and streams tend to be most vulnerable to nutrient depletion associated with timber harvest, acidification, dams, and other anthropogenic factors, a phenomenon known as cultural oligotrophication (Stockner et al. 2000). As an illustration of this difference, Lyle and Elliott (1998) found that anadromous salmonids accounted for a very small fraction (<0.1%) of the total annual flux of nutrients in large river systems in the UK, while in a small oligotrophic Norwegian river, Atlantic salmon could account for as much as 18% of the total annual P budget (Jonsson and Jonsson 2003).

Differential use of rearing habitats within rivers may also influence the magnitude and direction of nutrient transport. Sea lamprey larvae and ammocoetes generally show a directed downstream movement from spawning areas with increasing age in

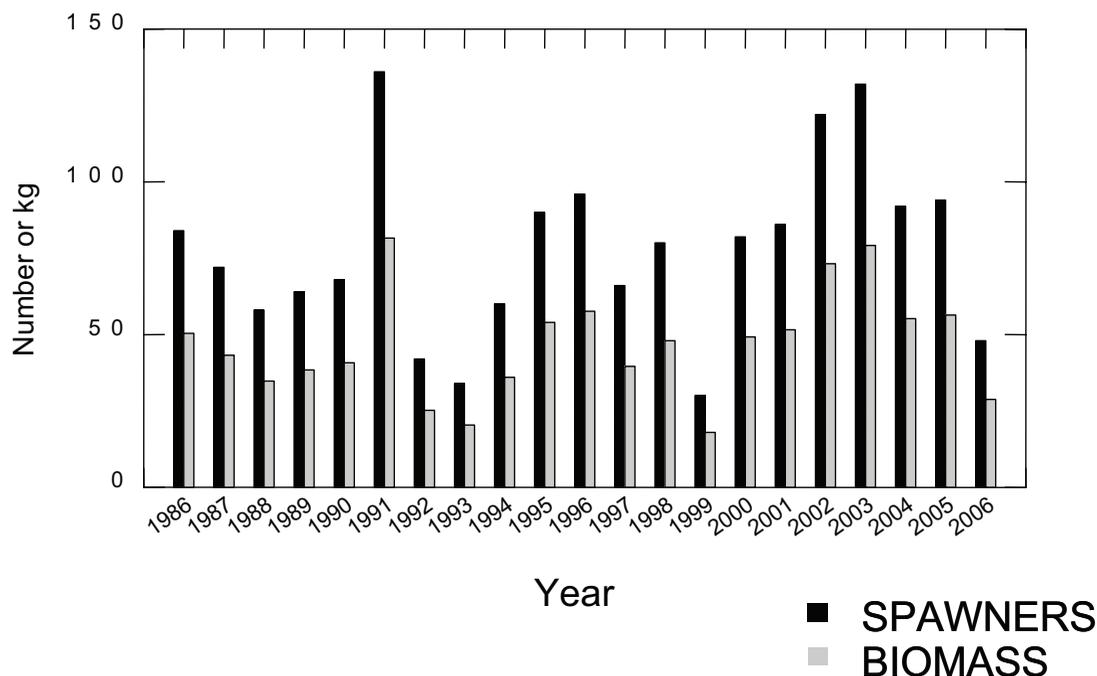


Figure 1.—Time series of estimated spawner abundance (numbers and biomass) for the upper spawning section of the Fort River, Massachusetts, USA from 1986 to 2006.

large river systems (Beamish and Potter 1975). In the Connecticut River, juvenile abundance tends to be very high in large tributary and main-stem habitats that are not appropriate for spawning (Kynard, unpublished data), an observation also made for Pacific lamprey *L. tridentata* (Torgerson and Close 2004). While some of this displacement is likely involuntary and associated with floods, an additional factor is the increase in productivity and growth potential of fish in downstream habitats, along with increased availability of fine-substrate (silt bed habitats) in lower-gradient reaches. As a consequence, a substantial percentage of the nutrients being exported by out-migrating juveniles are potentially not derived from the upstream spawning reach and does not subtract from net import by spawning adults.

Trophic Factors

One of the most striking aspects of sea lamprey life history is the major ontogenetic change in feeding strategy. As juveniles (ammocoetes), sea lamprey live in the stream bottom and filter-feed on diatoms and other algae, along with organic detritus (Maitland 2003). After developing into parasitic transformers, fish switch to feeding on coastal marine fishes and continue this foraging style as adults. This magnitude of change in trophic position (an increase of between two and three full trophic levels) is unique to north Atlantic anadromous fish and has important implications for mercury (Hg) accumulation and transport. Hg concentrations can increase by a factor of 10 with each increase in trophic level (Mergler et al. 2007). The combination of increased Hg concentration, along with increased biomass of spawning adults, suggests that lampreys may be net importers of Hg to stream ecosystems.

Case Study: Nutrient and Hg Import in a Wild Population in the Fort River, Western Massachusetts, USA

Study Site

The Fort River is a small (drainage area = 155 km²) tributary of the Connecticut River draining into

the main-stem Connecticut near the town of South Hadley, Massachusetts, USA. There are no barriers to fish migration in the Fort River, although access to the upper Connecticut and Fort rivers is regulated by Holyoke Dam ~20 river km downstream. Spawning occurs in several discrete sites where suitable gravel-cobble substrate is available (B. E. Kynard, unpublished data). The upper spawning site consists of a 300 m long (~5 m wide) section draining 39 km² of the upper Fort River watershed, which is largely an intact transitional hardwood forest (Fisher and Carpenter 1976). This river section that has been surveyed for the past 20 years by conducting a visual count of lamprey redds multiple times throughout the spawning period (late May through late June), depending on water temperature. To estimate spawner numbers, we multiplied the redd count by 2, as redds were generally used by single male–female pairs. This method yields a minimum estimate because it does not include a few males each year that build a late starter redd but do not spawn.

Calculating Nutrient and Hg Import

To calculate N and P import from spawning lampreys, we first multiplied spawner number by individual spawner mass to obtain total spawner biomass for a given year. This value is a slight underestimate of total adult lamprey biomass as those few adults that fail to find a mate and construct a redd also die on the spawning grounds. Individual spawner mass in the Connecticut River basin is 798 g (Stier and Kynard 1986) with very little variation (<2%) within and among years and sexes. We then multiplied total spawner biomass by standard N (0.03 g/g) and P concentrations (0.0047 g/g) for fish tissue (Lyle and Elliott 1998) and by Hg concentrations (400 ng/g) taken from Drevnick et al. (2006) to calculate total yearly import per square meter, based on a total spawning section area of 1,500 m². Finally, to give an estimate of the relative contribution of lamprey-derived nutrients, we compared lamprey-derived P to total annual P loading measured by Meyer and Likens (1979) in Bear Brook, New Hampshire, a stream with similar drainage area and land cover as the Fort River. As most MDNM from anadromous sea lamprey is imported, during 1 month, we also compared MDNM to monthly Bear Brook P loading.

Nutrient and Hg Import Results

Over the 20-year study period, an average of 40 redds (range, 15–68) were observed in the upper spawning site of the Fort River, translating into an average of 80 (range, 30–136) spawners and 46.7 kg total biomass (Figure 2). This biomass of spawners contributed an average of 0.15 g of P, 0.93 g of N, and 0.012 ng of Hg per square meter per year (Table 1). With respect to P, lamprey-derived contributions ranged from 5% to 20% of the total annual P loads in Bear Brook (Meyer and Likens 1979). However, given that almost all the lamprey-derived P loading occurs during 1 month (June), relative contribution for the month when carcasses are available is much higher, equal, or exceeding total Bear Brook P monthly loads in some years (Table 1.)

Factors Pointing Away from Sea Lamprey as Important Importers of MDNM

While consideration of several key life history, habitat, and trophic factors along with the results of a

case study suggest an important role for sea lamprey as MDNM, other factors point in a different direction.

Life History Factors

The duration of freshwater residence can be an important determinant of the magnitude and direction of nutrient flux via anadromous fishes. In species such as pink salmon and chum salmon *O. keta*, the juvenile freshwater stage is very short (several months) with juveniles emigrating at very small sizes (Quinn 2005). As a consequence, nutrient export via juveniles is negligible and generation time is short, both of which increase net import via returning adults. In contrast, sea lamprey have an extended freshwater juvenile residence. Connecticut River sea lamprey generally spend ~4–5 years in freshwater (M. Horgan, Miami University, Oxford, Ohio, personal communication), which is similar to the residence time observed in another southerly river in the eastern Atlantic, the River Mondego in Portugal (Quintella et al. 2003). However, in a more northerly river, the St. John in New Brunswick, where colder water temperatures likely limit

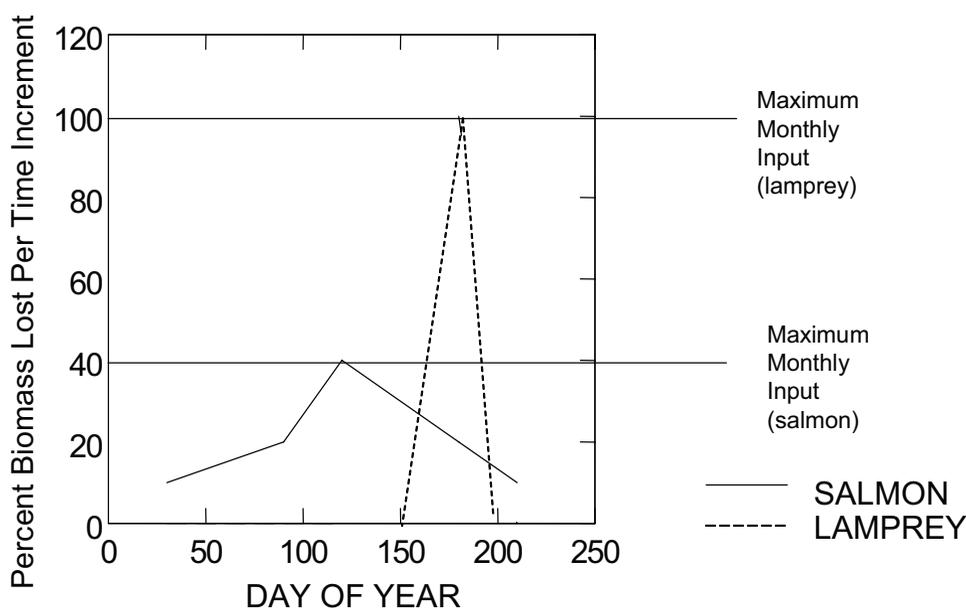


Figure 2.—Time course of carcass decomposition/disappearance of postspawned carcasses of sea lamprey (dashed line) compared to Atlantic salmon (solid line). Lines based on postspawning observations for lamprey in the Fort River, and on measured carcass mass loss rates for Atlantic salmon in a Scottish Highland stream.

Table 1.—Mean, minimum, and maximum annual transport of nitrogen, phosphorus, and mercury (Hg) from spawning sea lamprey to the upper spawning section of the Fort River, Massachusetts, USA based on a 20-year record of spawner abundance. Proportion of annual and monthly P load based on total annual loads measured at Bear Brook, New Hampshire (Meyer and Likens 1979).

	Mean	Minimum	Maximum
Hg (ng m ²)	0.012	0.005	0.022
Nitrogen (g m ²)	0.93	0.36	1.63
Phosphorus (g m ²)	0.15	0.06	0.26
Proportion of annual P load	0.12	0.05	0.20
Proportion of monthly P load	1.41	0.54	2.45

ammocoete growth, freshwater residence is 8–9 years (Beamish and Potter 1975).

Perhaps the key life history parameter determining whether lampreys represent a net gain or a net loss for freshwater ecosystems is the percentage of juveniles that survive to spawn (hereafter referred to as adult survival). The size ratio of adults to juveniles sets an approximate balance point for the direction of nutrient transfer with respect to adult survival. Lamprey increase their individual mass about two orders of magnitude while at sea. Assuming that proximate composition does not change markedly, adult survival of ~1% is the break-even point for nutrient and material transfer—below this value, lamprey represent a net loss to freshwater ecosystems. Unfortunately, we have essentially no information on adult survival rates in wild anadromous sea lamprey populations, and estimates from landlocked populations vary. In a widely used population model, transformer to spawner survival is assumed to be very high (50%) (Bence et al. 2003), which would make out-migrating juveniles largely inconsequential to the nutrient and material mass-balance. Other landlocked lamprey studies indicate significantly lower adult survival (minimum estimates of 4–8% based on tag recovery) (Stewart et al. 2003) which would, however, still result in substantial MDNM import if anadromous populations had similar adult survival rates. In general, however, survival rates for anadromous populations, which must contend with more extreme changes in habitats, as well as long and hazardous migrations, are considerably lower than landlocked populations (Jonsson and Jonsson 1993). In a 2-year study of a wild anadromous population of Pacific lamprey in Cedar Creek, Washington, USA (Stone et al. 2002), the population consisted of ~40 spawners and more than 3,000 juveniles (ammo-

coetes plus transformers). While the study did not measure survival per se, this ratio of adult to juvenile biomass is much closer to the break-even point for nutrient transport.

In the absence of data on adult survival in anadromous sea lamprey populations, it is worth considering several general aspects of sea lamprey life history and reproductive strategy that may influence whether they are a net nutrient/material gain or loss for freshwater. During transformation, sea lamprey shift to a parasitic existence and migrate to the sea. In many host–parasite systems, a very small percentage of individuals find suitable hosts (Anderson and May 1978). The reproductive strategies of spawning lamprey, which produce large numbers (hundreds of thousands) of small eggs, is consistent with overall high mortality rates characteristically experienced by parasites. These high fecundities may make it possible for populations to be sustained with low numbers of spawning adults, limiting potential nutrient and material import. Further, survival during parasitic life history stages is strongly dependent on host abundance and susceptibility (Anderson and May 1978). Evidence from landlocked populations indicates that spawner abundance is much more closely related to the abundance of important host fishes for newly transformed parasitic-phase lampreys than to the availability of spawning habitat (Young et al. 1996). Strong linkage between host abundance, adult survival, and nutrient and material import suggest that the role of sea lamprey may be dependent on the status of important marine and coastal host fishes. In the northwest Atlantic, anadromous and coastal clupeid fishes, which were likely important hosts for recently transformed parasitic-phase sea lampreys, have declined greatly as a consequence of river modification and overhar-

vest (Saunders et al. 2006), potentially impacting the adult survival and ecological importance of anadromous sea lamprey. However, in the Connecticut River, lamprey abundance has increased while clupeids have decreased (Stier and Kynard 1986), suggesting that anadromous clupeids may not be the key posttransformer host species in this system.

Habitat Factors

Sea lamprey have fairly stringent habitat requirements for nest building and spawning. Maitland (2003) reported that nests are generally constructed of gravels between 9 and 60 mm, a size range that is similar to but narrower than that required by anadromous Atlantic salmon and brown trout (also known as sea trout) *Salmo trutta* (Armstrong et al. 2003). It is thought that the upper size limit of spawning substrate is set by limits on the ability of spawners to move large rocks. However, sea lamprey in the Connecticut River appear to be able to use somewhat larger substrate sizes, with male and female spawners often working together to move larger rocks (Kynard, personal observation). As a result of these habitat constraints, a relatively small percentage of the total river area, even for small rivers and streams, may be suitable for spawning. For example, in the Fort River, more than 90% of the redds are found in less than 5% of the total river length. This limitation will ultimately constrain the size of the spawning run and the magnitude of nutrient and material transport.

Trophic Factors

The potential for sea lamprey to be net importers of Hg to freshwater ecosystems is co-determined by (1) increased biomass of adults and (2) higher Hg concentration per unit biomass. The ontogenetic change in trophic level associated with the parasitic phase in sea lamprey should, given all else equal, result in increased Hg concentration. However, Drevnick et al. (2006) found that Hg concentrations in adult sea lamprey from the Connecticut River basin were highly variable and overlapped broadly with concentrations in ammocoetes. If this is the case generally, then Hg net import would be the result only of increases in net biomass of spawners and subject to the same considerations and constraints discussed in the previous two sections.

Lack of increased Hg concentration in adults, in spite of higher trophic position, may be the result of several factors. Hg methylation rates, which control the conversion of inorganic Hg to toxic, bioavailable methyl Hg, tend to be lower in marine environments due to high chloride ion concentrations (Fitzgerald et al. 2007) so that fish growing in marine environments have lower Hg concentrations than fish growing in freshwaters. As an example, Riget et al. (2000) found that Hg concentrations were 10–15× higher in lake-resident Arctic char *Salvelinus alpinus* than in co-occurring anadromous individuals. In addition, given all else equal, animals that grow slowly and inefficiently have been shown to accumulate more Hg per unit biomass than animals that grow quickly and efficiently, a phenomenon known as growth dilution (Simoneau et al. 2005; Karimi et al. 2007). Given the differences in growth rates and feeding ecology of ammocoetes (slow, inefficient growth and poor quality food resources) versus parasitic-phase (rapid, efficient growth on a high quality food source) lamprey, growth dilution may play an important role in determining relative Hg concentrations and the magnitude and direction of Hg transport in lamprey and anadromous fish in general.

Conclusions, Management Implications, and Research Recommendations

The unique ecology and life history of anadromous sea lamprey has important implications for the role of this species in aquatic ecosystems. With respect to nutrient and material transport, lamprey generally appear to use the right habitats (small, oligotrophic rivers and streams), at the right time (late spring, a time of high nutrient demand in north temperate systems) and do the right thing (die after spawning) to make them potentially important contributors of marine-derived nutrients to freshwater ecosystems in the north Atlantic region. Further, the ontogenetic shift in feeding ecology and trophic level, which is not observed in any other anadromous species, has major implications for material transport, specifically for substances such as Hg, which biomagnify along aquatic food chains. A more thorough understanding of the fate and effect of these nutri-

ents and materials is necessary to evaluate ultimate impacts on freshwater ecosystems. For example, in the Pacific Northwest, salmon-derived MDNM is incorporated into fish and wildlife via direct consumption of carcasses, as well as indirectly via algal and invertebrate production (Kline et al. 1994). The relative importance of these two routes will strongly determine Hg transfer to higher trophic levels. Experimental additions of carcasses, coupled with isotope tracer experiments of the type used extensively in Pacific Northwest ecosystems (Bilby et al. 1998), would make a valuable contribution to this understanding.

While several attributes of sea lamprey point towards a significant ecological role other attributes suggest a lesser role under some circumstances. Perhaps most importantly, little information exists on adult survival rates in natural populations. However, the observed dependence of adult population size on the abundance of prey resources in landlocked populations has significant implications for management and conservation of anadromous populations. It suggests a strong connection between freshwater and coastal marine ecosystem health, as the ability of sea lamprey to import nutrients may depend strongly on the abundance of anadromous and coastal fishes. Many of these stocks have been declining for decades (Musick et al. 2000). Identifying key host species for anadromous sea lamprey, in the same way that bloater *Coregonus hoyi* was identified as a key species for Great Lakes populations, should help in this integrated conservation effort. In addition, it may be possible to use the frequency of lamprey marks on coastal fishes, which form at attachment and feeding sites on host fishes, to provide indices of lamprey abundance (Bence et al. 2003). Lamprey marks have been correlated to spawner abundance for landlocked Great Lakes populations (Smith et al. 1974).

One key question with respect to management and conservation is the extent to which population viability (an essential management target) coincides with ecological function. The high fecundity and parasitic life history of sea lamprey also suggest that population abundance sufficient to maintain population viability may be insufficient to fully achieve ecological contribution goals. Specifically, high adult fecundities may make it possible for relatively few adults to sustain local populations, but with either limited import or net export of nutri-

ents and materials. This issue has been considered for Pacific salmonids, leading to recommendations that escapement levels be set high enough to ensure both population viability and adequate provision of marine-derived nutrients (Bilby et al. 2001). Similar considerations should apply to sea lamprey populations, particularly those populations that are either currently exploited (Almeida et al. 2002) or being considered for exploitation.

Stringent habitat requirements may limit the import of marine-derived nutrients and materials via wild anadromous sea lamprey at the watershed scale. These habitat restrictions may make it more appropriate to evaluate lamprey contributions at a smaller scale within river systems (i.e., the spawning reach—100 m to km). Given these smaller-scale considerations, it is crucial to understand within-river dispersal and movements of juvenile-stage lampreys in order to develop accurate mass-balance models of nutrient and material transport. Long-term demographic studies that incorporate these movements, coupled with experimental manipulations of carcasses and isotope tracer experiments, are critically needed to better understand the present and potential future role of lamprey in the transport of marine-derived nutrients and materials.

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