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Passage and freshwater habitat requirements of anadromous lampreys: Considerations for conservation and control

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ABSTRACT

Understanding the relationship between a species and its habitats is important for both conservation of imperiled species and control of invasive species. For migratory species, we hypothesize that maintaining connectivity between segregated habitats is more important than improving the quality of each habitat. In the case of anadromous lampreys of conservation concern, we posit that restoring passage routes between spawning, rearing and feeding habitats will result in higher larval abundance upstream from barriers than efforts to improve quality of these freshwater habitats. To explore this hypothesis, we reviewed conservation actions for native anadromous lampreys in freshwater and found that: i) improving passage between habitats results in immediate and quantifiable increases in larval abundance, ii) anadromous lampreys are capable of existing in suboptimal habitats, and iii) small reservoirs of production drive rapid expansion when anadromous lampreys are released from passage constraints. Hence, maintaining habitat connectivity is clearly crucial for conservation of anadromous lampreys. There are fewer examples of improvements to freshwater habitat that increased larval lamprey abundance, perhaps because lampreys are rarely the focus of these efforts. However, habitat limitations such as stream dewatering, chemical pollution, and scour occur and will likely be exacerbated by climate change. Documenting habitat actions that reverse these problems may provide evidence for the merits of lamprey-specific habitat improvement. Our observations are relevant to sea lamprey control in the Great Lakes because barriers and chemical treatment are key instruments of population regulation, and can be strategically deployed to limit production.

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Introduction

Species persistence requires maintenance of connectivity between habitats of sufficient quality for every stage of the life cycle. Erosion of habitat connectivity can lead to declines in species of conservation concern (Hodgson et al., 2011), but can also be exploited for pest control purposes (Rusch et al., 2010). Similarly, reducing habitat quality can limit recovery of imperiled species, while targeted reductions in habitat quality are often used in integrated pest management (Chaplin-Kramer et al., 2011).

The relative importance of these two elements, habitat connectivity and habitat quality, depends on the life history of the species in question (Fig. 1). Because migratory animals must pass between multiple segregated habitats (e.g., caribou *Rangifer tarandus* L. or Chinook salmon *Oncorhynchus tshawyscha* Walbaum 1792), they are likely to be most sensitive to loss of habitat connectivity (e.g., from pipelines or dams). In contrast, non-migratory animals spend their entire lives in a single habitat (e.g., desert pupfish, *Cyprinodon macularius* Baird and Girard 1853 or gopher tortoise *Gopherus polyphemus* Daudin 1802) and may be more sensitive to habitat degradation.

In pristine areas with complete connectivity between high-quality habitats, all species are likely to flourish, and where habitat quality is uniformly low and fragmented, all but the most resilient species are at risk (Fig. 1). However, when key habitats are disconnected, regardless of their quality, we propose that migratory species abundance will be most affected (Fig. 1). When habitat quality is low but continuous, we predict that non-migratory species would be most impacted (Fig. 1).

Anadromous lampreys appear to fall into the first category, as they must pass between different habitats at key transition points in their life history. Upon hatching in freshwater streams, prolarvae transition to silty areas for burrowing (Dawson et al., 2015). Upon metamorphosis, larvae transition from silty freshwater rearing areas and migrate downstream to lakes or the ocean where they begin the parasitic stage (Moser et al., 2015b; Silva et al., 2013). As they near sexual maturity, anadromous lampreys transition to a free-swimming migratory phase that takes them back to freshwater streams for spawning (Baker et al., 2017; Clemens et al., 2010; Johnson et al., 2015). These migrations often occur over great distances (>700 km, Moser et al., 2015a,b).

Anadromous lampreys also have stage-specific habitat requirements. Adults need clean gravel/cobble/boulder substrate for spawning (Baker et al., 2017; Johnson et al., 2015), while larvae develop in sand and silt (Dawson et al., 2015). Adults are parasitic and require relatively large-bodied marine or estuarine prey (Quintella et al., this issue), whereas larvae feed on low-quality micro-algae and detritus in freshwater (Dawson et al., 2015).

Both disruption of lamprey movement and degradation of habitat are well-recognized obstacles to recovery of imperiled lamprey species (Clemens et al., this issue), and important tools for control of invasive sea lamprey (*Petromyzon marinus* L.) in the Laurentian Great Lakes (Lavis et al., 2003). For example, the European river lamprey (*Lampetra fluviatilis* L.) in Finland was severely impacted by a combination of impassable dams and logging operations that reduced spawning and rearing substrate (Tuunainen et al., 1980; Ojutkangas et al., 1995). In the Iberian Peninsula, Mateus et al. (2012) estimated that 80% of sea lamprey habitat has been lost due to dam construction. Native sea lamprey historically ascended over 650 km from the sea to freshwater streams in Switzerland, but are now rare in the heavily impounded Rhine River (Baer et al., 2018). In the western U.S., Pacific lamprey (*Entosphenus tridentatus* Richardson 1836) has been extirpated from some California drainages due to a combination of water withdrawals and stream impoundment (Reid and Goodman, 2016) and pouched lamprey (*Geotria australis* Gray 1851) are threatened by habitat loss and/or barriers to passage (Clemens et al., this issue; Lucas et al., this issue). These four anadromous lampreys (sea, river, Pacific, and pouched) are relatively well-studied and are the main focus of our review.

If passage is crucial to the fitness of anadromous lampreys, how important is freshwater habitat quality? Lamprey are capable of adapting to habitat limitations and are able to take advantage of sub-optimal habitats for both rearing (e.g., large particle size, bank overhangs; Nazarov et al., 2016) and reproduction (e.g., under cover, in woody debris, deep water; Johnson et al., 2015). Channelization and dam construction in the 1980s restricted spawning of sea lamprey in the Mondego River, Portugal, to a 15-km artificial reach of sub-optimal habitat influenced by hydropeaking (Quintella et al., 2003). This was the only available freshwater reach for this species in the entire river basin. Yet this poor-quality area allowed for maintenance of sea lamprey production, which rapidly expanded upstream when a fishway was constructed in 2011 (Pereira et al., 2017). Spawning in suboptimal habitat immediately downstream from low-elevation dams that block passage has also been observed for sea lamprey in the north-eastern U.S. and other anadromous species (Gardner et al., 2012; Lucas et al., 2009; A. Jackson, Confederated Tribes of the Umatilla Indian Reservation, personal communication, 2019).

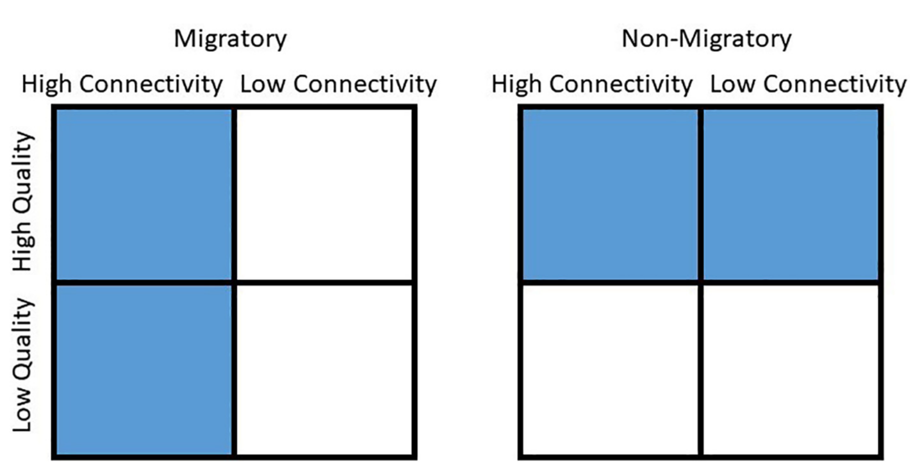

Fig. 1. Schematic of proposed vulnerability (low = shaded, high = white) to habitat quality (vertical axis) or connectivity (horizontal axis) for migratory animals (left panel) vs non-migratory animals (right panel).

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Table 1
Brief overview of evidence for responses of anadromous lampreys to landscape-scale restoration activities that improve habitat quality vs those that improve habitat connectivity.

	Summary of evidence	Source
Habitat quality	Increased Pacific lamprey (*Entosphenus tridentatus*) abundance following woody debris restoration	Roni, 2003; Nagayama et al., 2012; Gonzalez et al., 2017
	Increased river lamprey (*Lampetra fluviatilis*) abundance following riffle restoration and reduced hydropeaking	Aronsuu et al., 2019
	Immediate pouched lamprey (*Geotria australis*) spawning activity following large boulder placement in a wood-lined box drain	C. Baker, NIWA, pers. comm.
Habitat connectivity	Increased upstream abundance of sea lamprey (*Petromyzon marinus*) following dam removal or fishway improvements	Hogg et al., 2013; Lasne et al., 2015; Magilligan et al., 2016; Livermore et al., 2017; Pereira et al., 2017; Kynard and Horgan, 2019
	Increased river lamprey abundance following fishway improvements	Bracken et al., 2018
	Increased upstream abundance of Pacific lamprey following dam removal or fishway improvements	Hess et al., 2015; Moser and Paradis, 2017; Jolley et al., 2018; Reid and Goodman, 2020
	Increased upstream abundance of Pacific lamprey following translocation over dams	Close et al., 2009; Ward et al., 2012
	Increased upstream abundance of pouched lamprey adults following fishway improvements	Bice et al., 2019

A key prediction of our conceptual model in aquatic systems is that there will be more examples of increased abundance of migratory species upstream from a barrier when connectivity is restored than when habitat quality is improved. We used studies that measured larval abundance of native anadromous lampreys to explore this idea, conducting a systematic search and review of the lamprey literature (Grant and Booth, 2009). After summarizing the connectivity and habitat requirements of anadromous lampreys in freshwater, we tallied examples of passage improvement and freshwater habitat restoration actions that increased larval abundance in each study area (Habitat Connectivity vs Habitat Quality section, Table 1), while recognizing that it is often difficult to separate the effects of these actions).

Improvements in habitat connectivity and quality for lampreys can impact other aquatic species in myriad ways (Maine, 2020). Thus, in the course of our reivew, we also summarized examples of how conservation actions for lampreys have affected other freshwater species.

Habitat connectivity

For anadromous lampreys, high connectivity requires persistence of corridors between freshwater spawning and rearing habitats and estuarine/ocean feeding areas. For native sea lamprey, there are few examples of continuous freshwater habitats in either North American or European drainages to the Atlantic Ocean. In almost every watershed, lamprey habitats are fragmented by passage barriers. For example, the British river network is reportedly 97% fragmented (Jones et al., 2019). Consequently, robust populations of anadromous lampreys are rare in these areas. Both river and sea lampreys are listed in the European Union Habitats Directive as species whose conservation requires the designation of special areas of conservation (CEC, 1992). Similarly, the imperiled status of Pacific lamprey in the U.S. is recognized by tribal, federal, and state governments (Clemens et al., 2017; Clemens et al., this issue).

The literature abounds with examples of barriers to pre-spawning migrations of lampreys; from obstruction at tidal barrages in Britain (e.g., Silva et al., 2017) to barriers at culverts, dams, irrigation diversions, and weirs in North America and Europe (e.g., Almeida et al., 2002; Castro-Santos et al., 2017; Gargan et al., 2011; Jackson and Moser, 2012; Keefer et al., 2013; Moser et al., 2015a; Nunn et al., 2017; Silva et al., 2019). In some cases, dams have resulted in complete loss of habitat connectivity and extirpation of lamprey upstream (e.g., Beamish and Northcote, 1989; Larson et al., 2020; Wallace and Ball, 1978). However, there are also many examples of barriers that are semi-permeable to adult lamprey, allowing a percentage to pass based on lamprey size (Keefer et al., 2013), sexual maturation (Moser et al., 2019c), or migration timing (Keefer et al., 2009; Lucas et al., 2009).

Some low-head barriers block lamprey passage only during certain flow conditions. For example, the European river lamprey has an extended migration period, with adults moving into freshwater during late summer to overwinter and spawn the following spring. In Ireland, Kurz and Costello (1999) reported river lamprey spawning in the River Slaney upstream from a 2.5 m weir. High flow conditions in autumn presumably allow river lamprey to surmount such barriers; but migrations that occur immediately prior to spawning in spring can be blocked due to low flow. Successful passage at low-head barriers in the Yorkshire Ouse also requires high flows (Foulds and Lucas, 2013; Lucas et al., 2009).

There are also examples of barriers to pouched lamprey that become passable during high flow conditions. In New Zealand, adult pouched lamprey can climb past natural weirs and waterfalls, but poorly designed culverts are only passable during high flows (C. Baker, National Institute of Water and Atmospheric Research (NIWA), personal communication, 2019). Similarly, in the Donguil River, Chile, the 6 m high El Salto waterfall disrupts the upstream migration of adult pouched lamprey until rainfall raises the water level by about 15 cm, creating a fluvial terrace that enables passage around the waterfall (Reyes et al., 2014).

Even when there is a substantial area of suitable spawning habitat downstream from a barrier, pre-spawning anadromous lampreys continually endeavor to travel further upstream. These adults are likely attracted by larval pheromones (reviewed in Moser et al., 2015a). If no passage is available, this migratory imperative leads to spawning in graveled areas at the base of weirs (Gargan et al., 2011). Float-over surveys upstream from obstacles on the Munster Blackwater River in Ireland (3300 km^2, 189 km main stem) identified spawning gravels suitable for sea lamprey; but, an eDNA "snap shot" noted under-use of these habitats (Bracken et al., 2018). Bracken et al. (2018) also observed focused spawning activity in areas immediately downstream from the first two major weirs of 2.5 m head height. Barry et al. (2018) used the SNIFFER III (Scotland and Northern Ireland Forum for Environmental Research) coarse resolution barrier passability tool, which rated these weirs as either impassable or presenting high-impact risk to migration of adult sea lamprey. While barriers are required by Irish law to have a fish passage facility, Barry et al. (2018) opined that a majority of fishways at low-head weirs were failing to pass sea lamprey. For European river lamprey, strategies to mitigate the adverse impacts of such low-head barriers with technical solutions have also met with limited success (Tummers et al., 2018).

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Monitoring of larval abundance and distribution of anadromous lamprey upstream from barriers provides information on both adult passage success and larval production attributed to restored connectivity. Habitat available for spawning and rearing of sea lamprey doubled in the Connecticut River (northeastern U.S.) following fish passage improvements at Holyoke Dam (RKM 225) and three other main stem dams located upstream (Kynard and Horgan, 2019). While annual counts of adult sea lamprey passing Holyoke Dam after the improvements ranged from 15,000 to 95,000 during the period 1978–2014, there was no significant trend in adult counts with time (Kynard and Horgan, 2019). Unfortunately, the lack of larval sampling upstream from the dams made it difficult to determine whether increased adult abundance translated to improved recruitment. Ideally, larval sampling should assess age and stage structure to evaluate population growth, in addition to abundance and distribution.

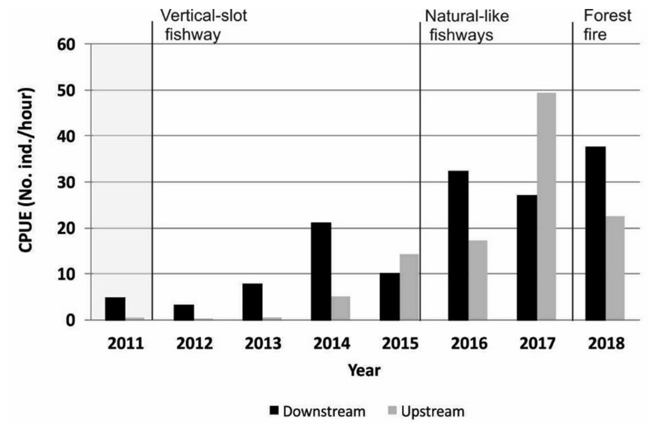

Fig. 2. Catch per unit effort (CPUE; larvae/h) of sea lamprey (*Petromyzon marinus*) electrofished between 2011 and 2018 in areas downstream (black bars) and upstream (gray bars) from the Coimbra Dam (RKM 45), Mondego River, Portugal. Occurrences of fishway openings and a severe forest fire are also noted.

Freshwater habitat quality

For lamprey, high-quality freshwater habitats are exemplified by uncontaminated streams, rivers, lakes, or tributary deltas where optimal adult spawning habitats are located upstream from optimal larval burrowing habitat. High-quality habitats are free of invasive predators and do not experience rapid de-watering or scour associated with hydropeaking or channelization. In the following paragraphs we summarize the substrate, depth, flow, and water quality conditions needed for spawning and rearing of anadromous lampreys.

Adult anadromous lampreys typically seek large substrate for spawning, such as gravel-cobble (Johnson et al., 2015; Silva et al., 2015) and boulder (Baker et al., 2015). Sea lamprey nests are clearly defined excavations of up to 1 m, with a depression on the upstream side of a gravel mound (Hogg et al., 2014; Pinder et al., 2016; Sousa et al., 2012; Inland Fisheries Ireland, unpublished data), while pouched lampreys spawn under boulders (Baker et al., 2015). Spawning is usually in areas where the bed slope changes and spawning is not typically observed in uniform hydraulic habitat (Pinder et al., 2016). In open water adjacent to spawning sea lamprey, depths range 0.3–1.0 m and velocity is typically 0.5–2.3 m/s (Johnson et al., 2015; Pinder et al., 2016; Sousa et al., 2012; Inland Fisheries Ireland, unpublished data).

In contrast, optimal larval rearing habitat is over fine substrate in low-velocity depositional areas that occur at pool tailouts, at the ends of bars, at overhangs, tributary deltas, in-line lakes, and/or in side channels (reviewed in Dawson et al., 2015). Granulometric composition must allow burrow construction and maintain a vital unidirectional water flux, essential to branchial aeration, food intake, and elimination of metabolic waste (Hardisty and Potter, 1971). The ideal particle size combination is dominated by fine/medium (0.05–0.6 mm diameter) and medium/coarse sand (0.2–2 mm diameter), with low quantities of gravel and silt (Taverny et al., 2012). Organic matter present in sediment provides food for the detritivorous larvae, but an excess of fines (e.g., clay, silt) can clog the gill lamellae (Dawson et al., 2015) and potentially increase predation risk (Smith et al., 2012). Such habitat must fulfill a number of conditions that maximize survival during the entire larval phase; however, larval lamprey are able to occupy marginal patches of habitat (Nazarov et al., 2016), and some are even found in the lower reaches of rivers exposed to tidal influence (e.g., Silver, 2015).

Lampreys have an anti-tropical distribution, generally found north and south of the 20 °C isotherm. Average lethal temperatures are around 28 °C (Potter, 1980), but temperature during the warmest month could be the true limiting factor (Ferreira et al., 2013). Larval lamprey generally require surface water year round; however, larvae of Pacific lamprey can survive for several weeks in the hyporheic zone of an intermittent stream in the absence of surface water (Rodríguez-Lozano et al., 2019). At the southern limits of the Petromyzontidae distribution, the increasing frequency of dry years with prolonged droughts followed by waterway siltation and fires, are expected to severely impact lamprey production. This is particularly of concern in the southern part of the Iberian Peninsula, where sea lamprey populations are already in decline due to river fragmentation (Mateus et al., 2012).

In addition to dewatering, unnaturally high scour can limit lamprey rearing habitat. Impervious surfaces surrounding urban streams can produce flashy hydrographs characterized by flows of greater magnitude and shorter duration than normal (Walsh et al., 2005). Such flows can scour fine-grain substrate used by larval lampreys for rearing. In New Zealand, pouched lamprey larval density dropped from 54 larvae per m^2 to 6 larvae per m^2 after sediment loss in a channelized box drain where sediment was not naturally replenished (unpublished data, C. Baker, NIWA).

Larval lamprey are also sensitive to chemical contaminants. Ash runoff from forest fires increases ammonium concentrations, trace metals, and ferrocyanides that lead to hypoxia (Bixby et al., 2015; Earl and Blinn, 2003; Gonino et al., 2019; Moyle et al., 2010). Severe droughts are increasingly frequent, as are the severity of forest fires. In the Mondego River, Portugal, larval abundance of sea lamprey decreased 46% in 2018 after a severe drought and forest fire upstream from the Coimbra Dam in summer 2017, followed by heavy rain (Fig. 2). Larval sensitivity to chemical contamination has also been reported for other native lamprey species and is a key component of the sea lamprey control program in the Great Lakes (Dawson et al., 2015; Moser et al., 2019b; Moyle et al., 2010).

Habitat connectivity vs freshwater habitat quality

For anadromous lampreys of conservation concern, does larval abundance recover faster with habitat connection or habitat improvement (Silva et al., 2015)? In the following sections, we review changes in larval abundance of native lampreys upstream from a barrier following actions that improved connectivity (e.g., dam removals) vs. those that improved freshwater habitat quality (as in Hodgson et al., 2011). Review keywords used were "lamprey" in combination with "passage", "barrier", "migration", "habitat improvement", "habitat quality", or "habitat restoration". The lamprey literature is relatively small and tractable; we were already familiar with almost all of the studies returned by our search. A secondary outcome of this review was a summary of how conservation actions for lampreys have impacted other aquatic species.

Improving connectivity

Actions to re-connect high-quality habitats by removing dams or otherwise providing passage for anadromous lampreys have resulted in immediate upstream colonization (likely facilitated by larval pheromone cues) and increased larval production. This is predicted in systems where anadromous lampreys already occur downstream from an obstacle or are established in neighboring basins (Pess et al., 2014); but, Pacific lamprey were also able to recolonize an isolated stream after barrier removal (Reid and Goodman, 2020). Hogg et al. (2013) demonstrated immediate use of upstream habitat by spawning sea lamprey in an eastern coastal U.S. river following barrier removal. Further upstream penetration was reported in subsequent years, likely due to successful spawning, more widespread larval colonization, and consequent pheromone attractant release (Neeson et al., 2011). Similar responses of sea lamprey to barrier removal were reported in another U.S. river draining to the Atlantic Ocean (Magilligan et al., 2016) and in France (Lasne et al., 2015).

Downstream pockets of production help to attract lamprey into impounded systems, allowing for rapid recolonization when some passage is restored. In Ireland, mitigation measures were undertaken at two weirs to facilitate upstream migration of sea lamprey into the Mulkear catchment (650 km^2, 65 km main stem). Telemetry studies indicated that these weirs were obstacles to pre-spawning sea lamprey, with many lamprey interrupting migration and returning downstream to the River Shannon where they were found spawning in suitable habitat (Rooney et al., 2015). During 2010–2014, the upper weir (Ballyclogh) was breached, and the lower weir (Annacotty) was modified with rigid plastic tiles that featured molded knob-like structures. Direct nocturnal observation indicated that migrating sea lamprey used the molded surfaces to pass upstream and did not use other areas of the weir face (Inland Fisheries Ireland, unpublished data). Environmental DNA studies further indicated that prior to mitigation this weir impeded sea lamprey (Gustavson et al., 2015); and that when the tiles were in proper repair, sea lamprey were able to pass upstream and spawn (Bracken et al., 2018).

Even fishways with low passage efficiency can allow enough lamprey passage for recolonization upstream. In central Portugal, upstream colonization by sea lamprey has been extensively catalogued in the Mondego River, a channelized and highly impounded river (Pereira et al., 2017) where several actions to restore river connectivity were implemented. Obstacles to migration identified through radiotelemetry (Almeida et al., 2000, 2002) were targeted for improvement. A vertical-slot fishway was built in 2011 at Coimbra Dam (the first impassable obstacle, RKM 45, Fig. 3) and adult passage was monitored using visual counts at the fishway and biotelemetry (i.e., passive integrated transponders, radio transmitters, transmitters equipped with physiological sensors that record muscle activity-EMG). Electrofishing surveys documented larval population responses and recolonization patterns. During peak migration, fishway passage efficiency was 31% and most upstream movements were observed when discharge from the dam was <100 m^3/s and temperature was 15–19 °C (Pereira et al., 2019). When dam discharge exceeded 100 m^3/s, tagged lamprey were attracted to the dam gates and away from the fishway entrance (flow controlled at 1.5 m^3/s). Pereira et al. (2017) found that sea lamprey could experience considerable passage delay (1.5–34 days), particularly if they remained immediately downstream from the dam gates. At this location, lamprey experienced high levels of muscle activity and energy costs associated with attempts to pass through the gates (Quintella et al., 2004). Once inside the Coimbra fishway, four of five EMG-tagged lamprey took 3–8 h to pass (Almeida et al., 2016; Pereira et al., 2017) and exhibited the characteristic burst and attach behavior described for this species during obstacle negotiation (Quintella et al., 2004). Within four spawning seasons, the vertical-slot fishway contributed to a 29-fold increase in larval abundance.

Lampreys can also respond positively to nature-like fishways. The Coimbra fishway construction was followed in 2016 by installation of five nature-like fishways at problematic low-head weirs (Fig. 3; Almeida et al., 2002). Passage at the first weir upstream from Coimbra Dam increased from 15% to 40% following the nature-like fishway installation (Almeida et al., 2016; Pereira et al., 2017). Most tagged sea lamprey (63%) passed this obstacle within 7 d and data from EMG tags suggested lower muscle activity than at Coimbra Dam (Oliveira, 2017). Two years after the construction of nature-like fishways, a 99-fold increase in larval abundance was observed compared to pre-fishway abundance in 2011 (Fig. 2). For European river lamprey, Aronsuu et al. (2015) opined that nature-like fishways are a preferred alternative, as all ten of ten observed lamprey were able to pass a nature-like fish ramp at a low-head barrier. At both nature-like and technical fishways, entrance designs with sufficient attraction flow that do not create a velocity barrier are critical (Castro-Santos et al., 2017; Moser et al., 2019a; Pereira et al., 2017).

When habitat connectivity is restored, anadromous lampreys are typically observed spawning upstream from former dam sites in the first spring after barrier removal (e.g., Hogg et al., 2013; Jolley et al., 2018; Moser and Paradis, 2017). Colonization by sea lamprey of the upstream reaches of the Mondego River occurred immediately after the Coimbra Dam fishway began to operate (Pereira et al., 2017). While the rate of colonization is usually rapid, it varies with stream size, downstream population abundance, and passage efficiency at barriers, both in the U.S. (Hogg et al., 2013; Jolley et al., 2018; Livermore et al., 2017; Moser and Paradis, 2017), and in Europe (Lasne et al., 2015; Pereira et al., 2017).

After lamprey passage is restored, proliferation of anadromous larvae occurs at upstream reaches, promoting a rapid colonization of tributaries and an expansion of main stem abundance. In the Mondego River, sea lamprey colonization followed this pattern of upstream adult dispersion, with initial expansion of larval abundance in the main stem upstream from the Coimbra Dam, followed by increased larval abundance in the lower Ceira River (the first tributary upstream from the dam, Fig. 2). Pacific lamprey in the Elwha River exhibited a similar pattern, with initial colonization of tributaries immediately upstream from former dam sites, followed by spawning in tributaries further upstream (R. Paradis, Lower Elwha/Klallam Tribe, personal communication).

These examples indicate that re-connecting habitats is particularly effective for anadromous lampreys for a number of reasons:

i) Pheromone cues produced by larvae can attract anadromous adults to areas downstream from an obstacle (reviewed in Moser et al., 2015a).
ii) Lamprey larvae can survive and adults can spawn in sub-optimal substrate (Almeida and Quintella, 2002; Dawson et al., 2015; Silva et al., 2015), thereby maintaining adult attraction and small pockets of production in dammed systems (Almeida et al., 2000; Lasne et al., 2015).
iii) Even a fishway with low passage efficiency (~30%) can allow for rapid lamprey colonization (Pereira et al., 2017).
iv) When an opportunity for escapement is provided, pioneering individuals rapidly disperse upstream (Almeida et al., 2002; Hogg et al., 2013; Moser and Paradis, 2017), establishing new core areas or larval production.

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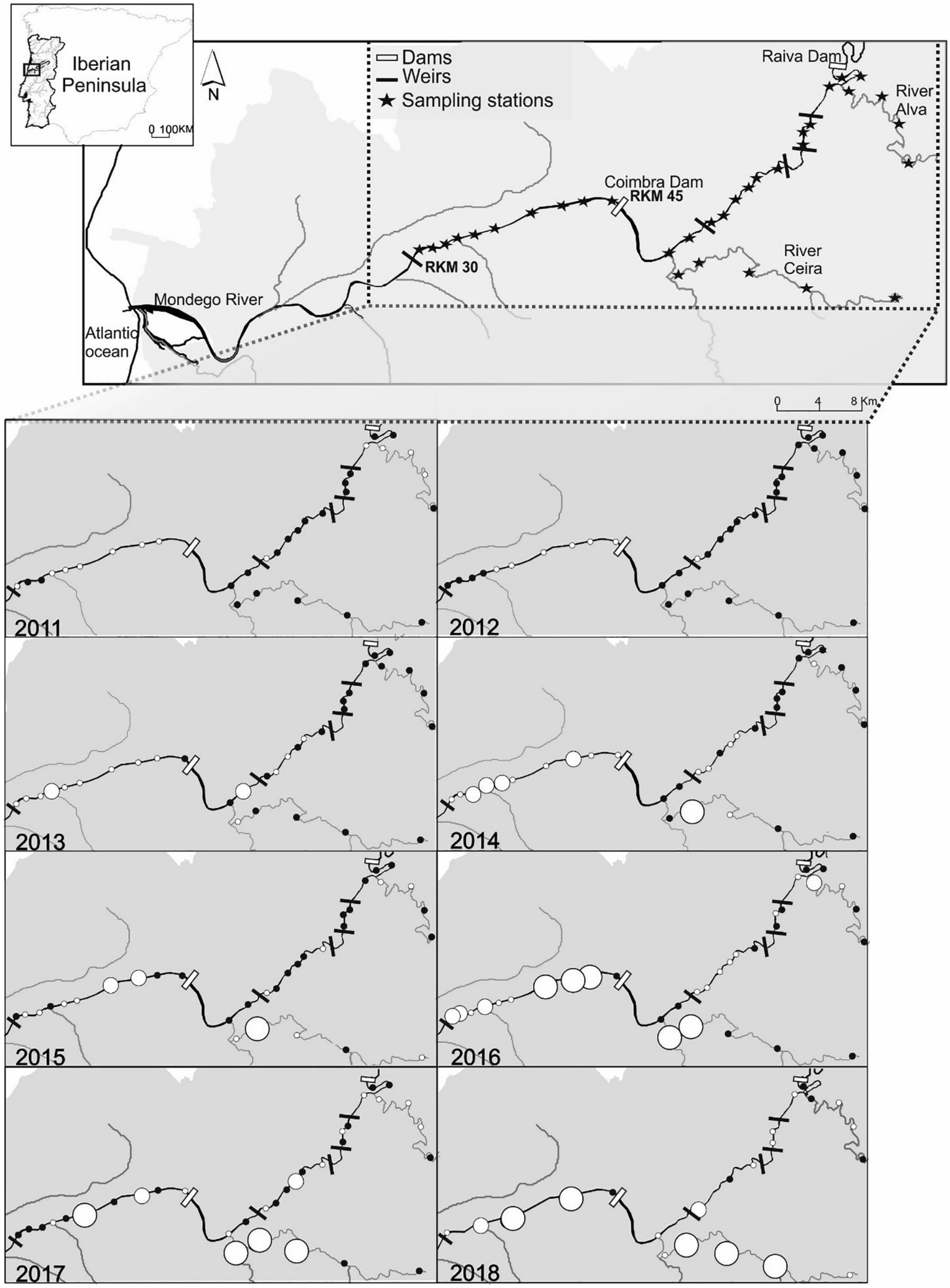

Fig. 3. Spatial distribution of sea lamprey (CPUE; larvae/h) in the Mondego River, Portugal between 2011 and 2018 for areas downstream and upstream of the Coimbra Dam (RKM 45). Larval abundance was classified as: absent (•); < 30/h (small ○); 30–60/h (medium ○); 60/h (large ○). Dams ([]) and low-head weirs (▬) are also represented.

v) Increased abundance of lamprey larvae at upstream reaches promotes rapid colonization of adjacent sites (Hogg et al., 2013; Pereira et al., 2017).

In some systems, translocation (transporting adults upstream from passage obstacles) can also improve recruitment of anadromous lampreys (Close et al., 2009; Salojkrvi et al., 1978; Ward et al., 2012). However, Aronsuu et al. (2015) observed that translocating adult river lamprey upstream from migration barriers requires attention to local environmental conditions. They cautioned that instream cover is critical for resting and that low levels of movement occur at water temperatures below 2 °C. Aronsuu

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et al. (2019) reported that 30 years (1981–2010) of intensive stocking (247 million sub-yearlings) and adult translocations (571 000) of river lamprey have not resulted in population recovery in River Perhonjoki (Finland). Moreover, Reid and Goodman (2020) advocate for low-cost removal of barriers to Pacific lamprey, rather than relatively costly and labor-intensive translocation schemes. In New Zealand, pouched lamprey have not become established above hydropower dams, despite intermittent trap and transfer operations for adults. Catches below the dams are highly variable, with fish absent in most years (Ryder, 2018). An assessment of lamprey bile acids from water samples at 15 sites above and 11 sites below Roxburgh Dam detected high concentrations of lamprey pheromone (petromyzonol sulfate) at all sites below the dam, but failed to detect the compound upstream from the dam (C. Baker, NIWA, unpublished data).

Improving habitat connectivity for anadromous lampreys is ongoing or planned in numerous river systems worldwide. Sea lamprey migration into the River Shannon, Ireland's largest catchment (16,800 km^2, 360 km), is impeded by two major hydroelectric dams immediately upstream from the tidal limit. Anadromous sea lamprey can utilise fish lifts at both barriers, enabling access to Lough Derg at the bottom of the Shannon catchment. A total of 49 upstream movements by anadromous sea lamprey were recorded in the fish lifts during May-July 2013. In addition, non-feeding sea lamprey outmigrants and lake-feeding juveniles in Lough Derg have been recorded (King and O'Gorman, 2018). These data suggest that sea lamprey persist, even though very low numbers of adults penetrate the catchment. Improved passage efficiency via the creation of a nature-like fishway is currently being investigated. That numerous lamprey would use such enhanced passage facilities is evidenced by studies of this species in the adjacent River Mulkear, the last major Shannon tributary un-impacted by hydroelectric weirs (Bracken et al., 2018; Gustavson et al., 2015; Rooney et al., 2015).

In the Rhine River basin, a substantial investment to improve ecological connectivity has been made during the past 20 years, with several fishways built in the Rhine main stem, delta, and tributaries (Griffioen and Winter, 2017; ICPR, 2009; Raat, 2001). However, sea lamprey colonization responses have been equivocal (Baer et al., 2018). At two vertical-slot fishways located in the southern, upper Rhine River (Iffezheim in 2000 and Gambsheim in 2006), approximately 1900 (Iffezheim) and 500 (Gambsheim) adult sea lamprey have used the fishways since their construction. Despite some annual variation, numbers at these fishways are consistently low. Reproduction occurs as far upstream as the Strasbourg Dam, and an increase in nests, lamprey larvae, and downstream movement has been observed (ICPR, 2013). Baer et al. (2018) also reported a high quantity of metamorphosing juveniles at this location (650 km from the river mouth), but only three adult sea lamprey and 40 river lamprey. The explanation for these results is unknown, but lamprey losses at downstream obstacles and/or during the early part of the spawning migration are suspected. For example, sea lamprey passage efficiency at the tidal barrier (Afsluitdijk) in the Netherlands is 16–33%. Improving this structure for lampreys could contribute to a faster recovery (Griffioen and Winter, 2017).

In the Garonne-Dordogne River in France, adult lamprey counts at fishways installed at hydropower dams have unfortunately shown a dramatic decrease, from tens of thousands during the 2000s to nearly zero recently (Lobry et al., 2016). Sea lamprey support an important commercial fishery in the Gironde estuary, and catch per unit effort did not decrease during this period (Beaulaton et al., 2008). This hampers identification of the reason for the decline in lamprey abundance recorded at the fishways and highlights the need to consider an integrated management approach for commercial species. For example, during lamprey restoration in the Mondego River, Portugal, the number of fishing licenses was adjusted and an intermediate fishing closure was established during the peak of spawning migration (Stratoudakis et al., 2020). These measures allowed an increase in lamprey numbers reaching the upstream river stretch (Almeida et al., this issue).

Within the Iberian Peninsula, several additional rivers are prime candidates for sea lamprey restoration work. In the Tagus and Douro Rivers of Portugal, two of the largest river basins, the existing Borland fish locks do not pass sea lampreys efficiently, most likely due to poor entrance attraction (Bochechas, 1998, 1995; Santo, 2005). Similarly, in the Ulla River of northwestern Spain, there is an urgent need to remove or improve low-head obstacles and curtail lamprey fisheries (Silva et al., 2019). Currently, several on-going projects to improve ecological connectivity and spawning habitat availability will hopefully benefit sea lamprey populations, along with other diadromous and potamodromous fishes.

Across the native distribution of European lampreys, there are few other rivers where rehabilitation projects include monitoring of lamprey fishway use, population demography, and/or patterns of recolonization. However, some studies have already provided insight into the main recovery obstacles, and this has led to prioritization of rehabilitation measures in European rivers (Van Puijenbroek et al., 2018). Such efforts will hopefully continue to develop, and in the near future, will provide more information on recovery of anadromous lampreys in their native range.

Improving habitat

There are few examples of habitat improvements in freshwater that have specifically targeted anadromous lamprey restoration. Even fewer invest in lamprey-specific monitoring. More common are habitat restoration actions directed at other species that either improve or, in some cases, diminish freshwater habitats for anadromous lampreys.

Habitat improvements designed specifically for anadromous lampreys are showcased by long-term research and monitoring in the Perhonjoki and Kalajoki rivers, Finland (Aronsuu et al., 2019). European river lamprey in these rivers are heavily impacted by dams in the lower reaches, channelization, acidification, upstream impoundment, and hydropeaking. Habitat improvements to restore river lamprey in the River Kalajoki contributed to increases in abundance of both subyearling and older larvae (Aronsuu et al., 2019). Most effective were restoration of substrate in riffles to provide winter holding areas for adults and reduction of hydropeaking to reduce larval mortality (Aronsuu et al., 2019).

Habitat improvements for salmonids and other species can result in collateral improvements for lamprey. For example, woody debris addition for salmonid restoration has resulted in increased depositional zones and concomitant increases in larval lamprey habitat and abundance (Gonzalez et al., 2017; Nagayama et al., 2012; Roni, 2003). However, addition of spawning substrates for salmonids in the River Perhonjoki, Finland, did not improve spawning habitat for river lamprey, as grain sizes added were too large (8–40 mm) for the lamprey to use (Aronsuu et al., 2019). Addition of these grain sizes would benefit sea lamprey, as spawning gravel used by Atlantic salmon in Irish rivers (Fluskey, 1989), closely matches that used by sea lamprey (Andrade et al., 2007; Sousa et al., 2012; Inland Fisheries Ireland unpublished data).

Increasing stream flows for salmon can also improve conditions for lamprey and other stream residents. In the Umatilla River (northwestern U.S.), increased minimum flow requirements have resulted in lower summer temperatures and expanded rearing and spawning habitat for Pacific lamprey (A. Jackson, Confederated Tribes of the Umatilla Indian Reservation, personal communication, 2019). As a result of population increases, 2019 was the first year that a tribal fishery for lamprey was permitted in the Umatilla

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River. Increased flow requirements in many small coastal Californian, Australian, and Portuguese streams would undoubtedly increase lamprey habitat, as these areas now are partially to completely de-watered in most summers (Oliveira et al., 2004; S. Reid, Western Fishes, personal communication, 2019; C. Baker, NIWA, personal communication, 2019).

In some cases, well-meaning efforts to improve salmon habitat have resulted in direct mortality and potential habitat degradation for anadromous lampreys (Maine, 2020). De-watering and substrate "improvement" can result in loss of lamprey larvae and their rearing habitats (Strief, 2009; R. Lampman, Confederated Tribes and Bands of the Yakama Nation, personal communication, 2019; S. Reid, Western Fishes, personal communication, 2019). Dredging and channel widening reduce larval habitat, but re-colonization of impacted habitat and colonisation of newly created habitat have been recorded within just three years (King et al., 2015). Lamprey exhibit wider thermal tolerance limits than salmonids and a flexible life history that allows for movement to new areas in the face of habitat degradation (e.g., Silva et al., 2015). Hence habitat quality may not be as key to their recovery as it is for other species.

If lamprey are not killed outright by dewatering or chemical pollution, they appear to tolerate small patches of suboptimal habitat—and persist. This characteristic, and their panmictic population structure, allows native anadromous lampreys to perpetuate in the face of habitat degradation; but it has also made invasive sea lamprey in the Laurentian Great Lakes very difficult to exterminate. It should be noted that native brook lampreys worldwide do not have the advantage of broad adult dispersal and are therefore far more vulnerable to local habitat degradation than anadromous or adfluvial forms (Maitland et al., 2015).

Effects of anadromous lamprey conservation on other species

In North America, most barrier removals are made to increase production of alosids and salmonids, with collateral benefits to lampreys (e.g., Hogg et al., 2013; Moser and Paradis, 2017). However, some efforts have been made to specifically provide lamprey passage. These have included installation of separate fishways designed to accommodate Pacific lamprey climbing abilities, and retrofits to traditional fishways (Goodman and Reid, 2017; Moser et al., 2019a,c, 2011). Studies were conducted to ensure no negative outcomes of these actions for salmonids; in most cases, improvements for lamprey were either neutral or improved salmonid passage (e.g., Johnson et al., 2012; Moser et al., 2019a).

In Europe, conservation measures targeting sea lamprey recovery, either by dam removal or implementation of fishways, have had mutual benefits for other diadromous fishes and the entire freshwater ecosystem. After providing a fishway targeting allis shad (*Alosa alosa* L.) and sea lamprey in central Portugal, increases in brown trout (*Salmo trutta* L.) abundance at upstream stretches was observed (Almeida et al., 2016). Anglers also started to report a reappearance of the anadromous form of this species (i.e., sea trout). The catadromous thin-lipped grey mullet (*Chelon ramada* Risso, 1827) is now able to use feeding habitats in upstream areas of the Mondego River (Almeida et al., 2016). As a result of the increased abundance of sea lamprey larvae, the number of mullet parasitized by juveniles has increased, being particularly conspicuous during the downstream mullet spawning migration (September–November).

In many European rivers, proliferation of non-native European catfish (*Silurus glanis* L.) has resulted in predation on sea lamprey larvae and adults, as well as other native fishes (M. Ferreira, personal communication, 2019; Boulêtreau et al., 2020). In the River Garonne in France, where European catfish have established self-sustaining populations, anadromous fish contributions to the catfish diet ranged between 53% and 65% (Poulet et al., 2011; Syväranta et al., 2009). Boulêtreau et al. (2020) reported that 50% of tagged lamprey were consumed within a week and at least 80% of them were preyed upon within one month. This emphasizes the potential importance of anadromous species in food webs where migration is currently prevented, but also the impact of non-indigenous species (i.e., European catfish) on native sea lamprey in European rivers.

At an ecosystem level, marine-derived nutrient subsidies from sea lamprey contribute to stream food webs either by direct consumption of lamprey eggs/carcasses or via indirect pathways (e.g., Dunkle, 2017; Nislow and Kynard, 2009; Samways et al., 2018; Weaver et al., 2015). This boosts the productivity of entire freshwater communities (Weaver et al., 2018a). Additionally, nest-building behaviors increase habitat heterogeneity and favor pollution-sensitive benthic invertebrates (Hogg et al., 2014; Sousa et al., 2012; Weaver et al., 2018b). Finally, by serving as a flagship species in their native range, lampreys provide indirect public support for restoration of other under-valued or cryptic species.

Conclusions

The importance of connectivity for conservation of anadromous lampreys is highlighted in our review of passage and freshwater habitat requirements. In recent years, numerous studies have documented the rapid recolonization of upstream areas following dam removal or modification (Table 1). These studies lend support to our hypothesis that improving habitat connectivity, as opposed to a focus on habitat quality, will increase larval abundance of anadromous lampreys. While re-establishing habitat connectivity may be scientifically defensible, we did not consider the attendant societal and economic costs, key elements in structured decision making (Gregory et al., 2012). Moreover, stream connectivity and habitat quality are not mutually exclusive, as restoring connectivity often results in improvements to riparian function (Pess et al., 2014). Indeed, the European Union's Water Framework Directive of 2000 identifies 'water quality' in terms of 'ecological quality', with benthic invertebrates and fish counted as indicators of 'quality'. The Directive also identifies the relevance of hydromorphology in waterbodies of 'high' quality, with longitudinal connectivity included as a criterion.

Our conclusion should not be extended to non-parasitic brook lampreys, which are not migratory and likely more susceptible to local habitat degradation (Maitland et al., 2015). It also may not apply to lampreys at the edge of their distribution, where effects of extreme climate change on habitat quality could accelerate extinctions (Maitland et al., 2015). Pouched lampreys in the Southern Hemisphere, lampreys of the Iberian Peninsula, southern California and Central America all face increased risks of de-watering, reduced attraction flows, scour, dredging, hypoxia, and chemical pollution (Wang et al., this issue). Freshwater habitat restoration efforts that target these effects and take into consideration the specific spawning and rearing requirements of lamprey are rare, but would likely contribute to recovery of both native brook and anadromous lampreys (Maitland et al., 2015; Clemens et al., this issue). Restoration that works to "restore natural river processes" (Addy et al., 2016) will, by definition, contribute to recovery of habitat types suitable for all life stages of anadromous lampreys.

The outcome of assessing our model prediction has clear management implications for recovery of native anadromous lampreys: every effort should be made to protect small reservoirs of production until habitat connectivity can be re-established (as in the Mondego River). Because fecundity of anadromous lampreys is about 10× higher than that of salmonids and because lampreys are able to survive suboptimal rearing and spawning substrates,

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even small levels of adult escapement at passage barriers can keep a population from going extinct. Indeed, these same characteristics thwart sea lamprey control efforts in the Great Lakes, where near-zero passage barriers can still result in some upstream production (Johnson et al., 2016).

Barriers to migration (decreased connectivity) and chemical application (decreased habitat quality) are already used to control sea lamprey in the Great Lakes (Vélez-Espino et al., 2008). Population matrix modeling predicted that use of lampricide to kill young-of-year, larvae and transforming juveniles would be more effective than methods targeting adult fecundity (via reductions in stream connectivity; Vélez-Espino et al., 2008). This goes against the predictions of our conceptual model. We suggest that this difference may arise because lampricides target lamprey directly, whereas typical habitat restoration actions (e.g., increasing stream sinuosity, reducing point and non-point source pollutants, restoring riparian function) do not.

Nevertheless, there is some evidence to suggest that populations of sea lamprey in the Great Lakes can rebound when highly contaminated sites are cleaned up (e.g., Mineral River, a tributary to Lake Superior; M. Steeves, Fisheries and Oceans, Canada, personal communication). While Pacific lamprey exist in highly contaminated sites (Nilsen et al., 2015), actions to alleviate chemical contamination could allow these populations to expand. For anadromous lampreys in Europe, efforts to improve water quality and reduce severe hypoxic zones have undoubtedly improved lamprey habitats, but these effects are often masked by the fact that these rivers are also heavily impounded (e.g., Baer et al., 2018).

The propensity for lamprey to exploit very small patches of low-quality habitat and still maintain residual populations is a recognized problem when targeting streams for sea lamprey control (Jubar et al., this issue). However, the attraction of adults to larval pheromones and larval sensitivity to chemical controls and/or de-watering events could be further exploited in control efforts. Morman et al. (1980) first noted that adult sea lamprey were attracted to and able to spawn in areas upstream from unacceptably polluted larval habitats, resulting in no larval production. For native lampreys, production can occur in unexpected areas (irrigation diversion canals, hatchery abatement reservoirs, dam forebays; see Lampman et al., this issue) with lethal consequences for larval production. Attracting and encouraging spawning of sea lamprey upstream from regularly de-watered, dredged, or degraded larval habitats in tributaries to the Great Lakes could have similar effects (e.g., Humber River, Pratt et al., this issue).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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