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Sea lamprey *Petromyzon marinus*: an exception to the rule of homing in anadromous fishes

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Anadromous fishes are believed to make regular circuits of migration in the sea before homing to their natal rivers. Sea lamprey *Petromyzon marinus* is an anadromous fish that is an exception to this life-history pattern. It also differs from other anadromous fishes in that its adult phase is parasitic, a feeding strategy that should make homing problematic for lamprey cohorts that become widely dispersed through transport by the diverse hosts they parasitize. We sequenced a portion of the mitochondrial DNA control region from sea lampreys collected from 11 North American east coast rivers to test for genetic evidence of homing. There were no significant differences ($\chi^2=235.1$, $p=0.401$) in haplotype frequencies among them, with almost 99 per cent of haplotypic diversity occurring within populations. These findings, together with concordant genetic results from other geographical regions and ancillary information on pheromonal communication, suggest that sea lamprey does not home but rather exhibits regional panmixia while using a novel 'suitable river' strategy to complete its life cycle.

Keywords: anadromous; homing; mitochondrial DNA; parasitism; pheromone

1. INTRODUCTION

Anadromous fishes undertake regular seasonal and life-stage-consistent migrations between freshwaters, where they begin life, and the sea. Anadromy occurs in less than 1 per cent of the world's fishes but it has evolved multiple times across a broad phylogenetic distribution (McDowall 2001). Some taxa in which anadromy are represented include petromyzontids, acipenserids, osmerids, salmonids, alosines and moronids. Anadromous fishes may have substantial osmotic, bioenergetic and predation-exposure costs in moving between the two environments, but they benefit from the generally reduced predation on early life stages in rivers and access to the greater trophic resources of marine waters (Gross 1987).

As a group, anadromous fishes are believed to show homing to their natal rivers (McDowall 2001). One benefit of homing is that it allows individuals to return to habitats of established spawning success (McDowall 2001). Homing mechanisms have not been studied in all anadromous taxa, but in salmonids (Dittman & Quinn 1996), alosines (Dodson & Leggett 1974) and acipenserids (Boiko *et al.* 1993) it is completed with olfactory recognition of the natal river following imprinting prior to outmigration. Homing in anadromous fishes allows genetic differentiation among populations, even between neighbouring populations, through genetic drift and selection (DeWoody & Avise 2000). Thus, within-population variation is accompanied by significant among-population variation in anadromous fishes that home.

Evidence that sea lamprey *Petromyzon marinus* might not show homing fidelity emerged from Lake Huron of the Great Lakes watershed, where a tagging study of 555 outmigrating individuals from Devil River to Lake Huron recaptured 42 in-migrating spawning adults in four other rivers but none in Devil River (Bergstedt & Seelye 1995). To test whether this apparent absence of homing in its non-native landlocked range (Waldman *et al.* 2004) is a species-wide characteristic, we examined the population structure of anadromous sea lampreys in their native range collected from rivers within the Acadian and Virginian zoogeographic provinces, between Quebec and New York.

2. MATERIAL AND METHODS

Adult lampreys ($n=314$) were collected in rivers extending from St Lawrence River, Quebec, to Delaware River, New York (figure 1). Total DNA was isolated from fin clips stored in 95 per cent EtOH using proteinase K digestions in CTAB buffer (Waldman *et al.* 2006). A 511 bp portion of the mtDNA control was PCR amplified and 333 bp were sequenced in both directions using sea lamprey-specific primers (Waldman *et al.* 2004). Composite haplotypes were generated and their frequencies among collection sites were compared for statistical significance using a Monte Carlo-based χ^2 approach (Roff & Bentzen 1989). Haplotypic variation within versus among rivers was conducted using analysis of molecular variance (AMOVA; Excoffier *et al.* 1992). Sequence differences among haplotypes and GenBank accession numbers are available in the electronic supplementary materials.

3. RESULTS

There were no significant differences ($\chi^2=235.1$, $p=0.401$) in haplotype frequencies among these collections of sea lampreys as seen in other anadromous fishes across all or part of this range that home, including Atlantic salmon *Salmo salar* (King *et al.* 2001), striped bass *Morone saxatilis* (Wirgin *et al.* 1997), Atlantic sturgeon *Acipenser oxyrinchus* (Grunwald *et al.* 2007) and American shad *Alosa sapidissima* (Bentzen *et al.* 1989). AMOVA showed extremely low haplotypic variation among sea lamprey collection sites (1.3%); virtually all haplotypic diversity, almost 99 per cent, occurred within populations.

4. DISCUSSION

Our results indicate that sea lampreys from western Atlantic rivers, even across two zoogeographic provinces, exhibit regional panmixia. This corresponds with our findings of no significant differences ($p>0.05$) in haplotypic frequencies among collections in other discrete regions, including native landlocked populations in Lake Ontario (three rivers; Waldman *et al.* 2004), in Lake Champlain (four rivers;

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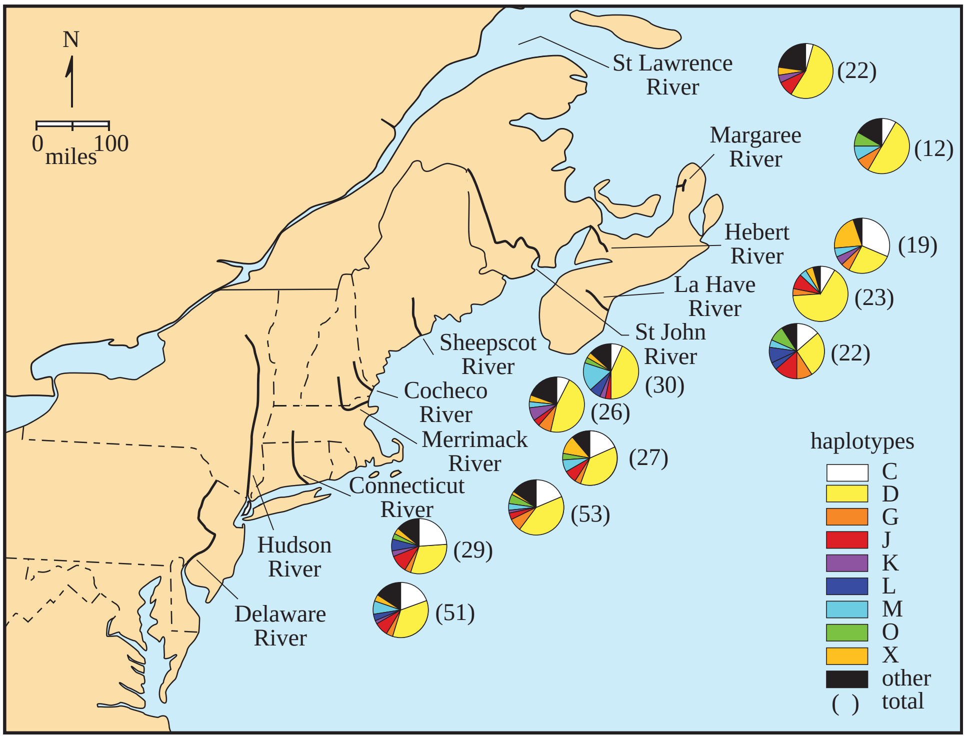

Figure 1. Mitochondrial DNA haplotype proportions in sea lamprey collections from 11 North American east coast rivers. Sample sizes in parentheses.

Waldman *et al.* 2006) and between two rivers in Portugal ($p=0.8643$; Rodríguez-Muñoz *et al.* 2004). Moreover, it is congruent with findings from nuclear DNA microsatellite analyses for Atlantic coast anadromous sea lamprey populations and among populations in Lakes Ontario and Champlain (Bryan *et al.* 2005). We hypothesize that this panmixia is one outcome of an alternative life-history strategy from that employed by other anadromous fishes, and that this strategy is directly allied with its parasitism.

Other anadromous fishes such as salmon (Groot & Margolis 1991), striped bass (Boreman & Lewis 1987) and shads (Dadswell *et al.* 1987) maintain regular circuits of migration in the sea, which facilitate feeding in productive marine waters together with coordinated returns to their natal rivers for reproduction. Sea lampreys, however, leave their natal rivers and feed sanguivorously for as much as 3 or 4 years, for several days to over two weeks per host, during which time they are transported by their hosts' movements (Beamish 1980). The spectrum of potential hosts in marine waters is extensive; documented prey off North America include but are not limited to pelagic fishes such as Atlantic salmon, bluefish *Pomatomus saltatrix*, Atlantic mackerel *Scomber scombrus*, menhaden *Brevoortia tyrannus*, bluefin tuna *Thunnus thynnus*, swordfish *Xiphias gladius* and basking shark *Cetorhinus maximus*; benthic fishes such as Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, hakes *Urophycis* spp., Atlantic sturgeon; and cetaceans (Collette & Klein-MacPhee 2002). There is little commonality among these and other possible hosts in seasonal and annual movement patterns, many of which are considerable, and include much of the western Atlantic Ocean when summed across species.

Probably owing to this non-specificity in host selection and its consequent implications for transport, sea lamprey has been found in the ocean from the surface to over 4000 m in depth (Beamish 1980). The horizontal spatial consequences of such diverse feeding opportunities are even more profound. Unlike for an outmigrating cohort of a non-parasitic anadromous fish, which may maintain cohesion by following a migratory circuit, a cohort of sea lamprey that emigrates from a river, after completing its marine feeding phase on a diverse suite of hosts, should be widely dispersed in ocean waters.

Such a broad geographical distribution, in the absence of homing, raises the question of how sea lampreys locate suitable spawning rivers inasmuch as many drainages do not provide both appropriate spawning and rearing habitats (Beamish 1980). Sea lampreys build nests only in shallow riffle areas with rubble of a particular size range, but their larvae inhabit sandy and silty backwaters where they develop in burrows for 2–8 years (Quintella *et al.* 2003) before transforming to the adult phase and outmigrating. The subsequent choice of river for spawning is critical in that sea lampreys expend considerable energy reserves before and during spawning (Beamish 1979) and then die shortly thereafter. However, many rivers are unsuitable for sea lamprey reproduction. In the Great Lakes, where sea lampreys became very abundant, only 8 per cent of tributaries have supported populations of sea lamprey larvae (Morman *et al.* 1980).

Strong evidence exists that chemical means afford an alternative 'suitable river' strategy to homing based on recognition of the presence of conspecifics ('kin recognition'; McDowall 2001). Larvae have been shown to release a bile acid-based pheromone detectable to adults in marine waters (Bjerselius *et al.* 2000), with individual larvae activating approximately 400 l water h^{-1} (Sorensen *et al.* 2003). Adult males that ascend to the gravel-bed spawning grounds then use powerful pheromones to communicate their presence to females downstream (Li *et al.* 2002).

Our genetic results, considered with ancillary information, suggest that we have identified a new relationship among two fundamental life-history characteristics, i.e. the presence of parasitism has coevolved with an alternative reproductive strategy for an anadromous fish species, and the use of a suitable river strategy, instead of homing. Both strategies involve olfactory certification of the reliability of the spawning habitat prior to bioenergetically costly upriver migration, but the one used by salmonids and alosines is based on within-individual 'memory', whereas the other is based on contemporaneous chemical signalling.

Our data combined with the information on chemical communication also suggest a strategy for sea lamprey control. Destructive parasitism by sea lampreys within their non-native range in the Great Lakes and also in Lakes Ontario and Champlain has caused substantial economic damage to fisheries (Holeck *et al.* 2004). In the absence of homing, the application of sea lamprey pheromones to rivers believed to be unsuitable for their spawning and nursery purposes might divert reproductive effort unproductively with little risk of establishing a new population.

Approximately half a dozen marine lamprey species exist elsewhere in the world (Nelson 1976). We predict that this same relationship holds for them too, as indicated for Pacific lamprey *Entosphenus tridentatus* where no significant haplotypic differences were seen among collections from 81 rivers across six zoogeographic regions between British Columbia and California, and where within-river differences also accounted for 99 per cent of the variation (Goodman *et al.* 2008). The life-history pattern identified for marine lampreys appears unique for diadromous fishes, but we note that it is the converse of catadromous anguillid eels that too are panmictic, but where for eels disaggregation occurs as individuals enter freshwaters, not as they exit them.

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