



## A semelparous fish continues upstream migration when exposed to alarm cue, but adjusts movement speed and timing



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Animals make trade-offs between predation risk and pursuit of opportunities such as foraging and reproduction. Trade-offs between antipredator behaviours and foraging are well suited to manipulation in laboratory and field settings and have generated a vast compendium of knowledge. However, much less is known about how animals manage trade-offs between predation risk and pursuit of reproductive opportunities in the absence of the confounding effects of foraging. In the present study, we investigated how the nonfeeding migratory life stage of sea lamprey, *Petromyzon marinus*, responds to odour from dead conspecifics (a cue that induces avoidance behaviours in laboratory and field studies). We released groups of PIT-tagged sea lamprey 65 m from the shore of Lake Michigan or 287 m upstream in Carp Lake River and used antennas to detect their movements in the river. As the breeding season progressed, sea lamprey initiated upstream movement earlier and were more likely to enter the river. Sea lamprey that began the night in Lake Michigan entered Carp Lake River at higher rates and accelerated upstream when exposed to high concentrations of alarm cue, consistent with animals attempting to minimize time spent in risky areas. Sea lampreys that began the night in the river delayed upstream movement when exposed to alarm cue, consistent with animals sheltering and gathering information about a source of risk. We attribute this context-specific reaction to alarm cue to differences in perceived vulnerability to predation in sheltered positions in the river versus exposed positions in the lake. Once in the river, the vast majority of sea lamprey moved upstream independent of alarm cue or Julian date. Although life-history-induced time and energy budgets place rigid constraints on the direction of migration, sea lamprey attend to predation risk by modifying movement timing and speed.

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Antipredator behaviours are costly in that they require animals to reallocate time and or energy away from foraging or pursuing reproductive opportunities (reviewed in: Lima & Dill, 1990; Lind & Cresswell, 2005; Sih, 1994). Animals can manage this trade-off by responding to predator cues in a manner proportional to the immediacy and level of risk posed (e.g. Crawford, Hickman, & Luhring, 2010; Ferrari, Messier, & Chivers, 2008a, 2008b; Helfman, 1989) and the level of risk that forgoing an opportunity poses to future survival or reproductive success (e.g. Kohler & McPeck, 1989; Magnhagen, 1990; Morton & Chan, 1999; Tuttle & Ryan, 1982). To compensate for the costs of antipredator behaviours, animals can increase opportunity pursuits when predation

risk is lower (e.g. Daly, Behrends, Wilson, & Jacobs, 1992) or continue to pursue opportunities with less risky strategies when predation risk is high (e.g. Godin, 1995; Spencer, 2002). However, the utility of compensatory behaviours and the relative cost of antipredator behaviours are in part determined by the internal state of prey and the time remaining for important life history events such as migration and reproduction (Clark, 1994; Grand, 1999).

Iteroparous animals can trade off current reproductive opportunities for increased survivorship if doing so increases their lifetime fitness through subsequent breeding events (Bull & Shine, 1979; McNamara & Houston, 1996; Roff, 1992). Not surprisingly, iteroparous animals demonstrate a variety of reproductive trade-offs in response to predation risk that potentially decrease short-term reproductive output, but increase lifetime reproductive fitness through increased survivorship such as shortened brood

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times (Evans, Gasparini, & Pilastro, 2007) or brood size (Wisenden, 1993), decreased conspicuous courtship behaviours (Chivers, Wisenden, & Smith, 1995; Endler, 1987; Tuttle & Ryan, 1982), or selecting suboptimal nesting habitat (Spencer, 2002). Because semelparous animals and older iteroparous animals have little or no chance of future reproductive success if they forgo a current breeding opportunity, they should be increasingly willing to tolerate predation risk in pursuit of reproduction (gobiids: Magnhagen, 1990; eggplant lace bugs: Tallamy, 1982). For example, while young mature iteroparous gobies (sand goby, *Pomatoschistus minutus*) will forgo nest construction in the presence of predators, semelparous gobies (black goby, *Gobius niger*) and older *P. minutus* build nests regardless of predation risk (Magnhagen, 1990). Many semelparous fishes face similar trade-offs when migrating upstream through predator gauntlets on their way to spawning grounds.

Migrations are energetically demanding and hazardous endeavours requiring both careful timing and budgeting of stored energy reserves (Alerstam, Hedenström, & Åkesson, 2003; Dingle, 1996; Sillett & Holmes, 2002; Slotte, 1999). Anadromous fishes entering into nonfeeding life stages prior to terminal breeding migrations (e.g. salmonids: Hendry & Berg, 1999; Hinch, Cooke, Healey, & Farrell, 2005; sea lamprey: Larsen, 1980) use finite energy budgets to migrate, mature and breed during seasonally finite suitable environmental conditions (Brett, 1995; Burgner, 1991). A multitude of interacting factors can lead to failed breeding migrations (Cooke et al., 2004). Migration timing is constrained by the suitability of seasonal environmental conditions for migration to the spawning grounds and subsequent development of young (Hodgson & Quinn, 2002; Prop, Black, & Shimmings, 2003). Furthermore, migrating during suboptimal conditions is costly to endogenous energy reserves (e.g. temperature: Eliason, et al., 2011; high water flow: Standen, Hinch, Healey, & Farrell, 2002) and can lead to prespawning death (e.g. Macdonald, Williams, & Woodey, 2000).

Migrating anadromous fishes confront aggregations of unfamiliar terrestrial, aquatic and aerial predators in rivers during predictable seasonal migrations (e.g. bears preying on salmon: Gill & Helfield, 2012; Quinn, Wirsing, Smith, Cunningham, & Ching, 2014; pinnipeds preying on salmon and lamprey: Roffe & Mate, 1984; birds preying on lamprey: Sjöberg, 1989) that can exact high mortality rates (e.g. 40–63% of tagged chum salmon predated by bears or seals during 2 years of spawning runs; Peirce, Otis, Wipfli, & Follmann, 2013; 12–58% of sockeye salmon predated by bears across 13 streams during 1986–2002 in southwestern Alaska; Quinn, Gende, Ruggerone, & Rogers, 2003). Although predation risk may be high during breeding migrations, antipredator behaviours could compromise reproductive pursuits by altering the timing of migration or by increasing energetic expenditures prior to spawning. Because nonfeeding semelparous life stages are unable to compensate for expended energy and missed breeding opportunities, they should be especially sensitive to expenditure of time and energetic capital.

Sea lamprey, *Petromyzon marinus*, are a semelparous fish common to both eastern and western drainages of the Atlantic Ocean (Renaud, 2011). After at least 1 year in open water environments (marine or freshwater) where they are ectoparasites of a broad range of fishes (Silva, Araujo, Bao, Mucientes, & Cobo, 2014), sea lamprey cease feeding and return to river systems to reproduce (reviewed in Moser, Almeida, Kemp, & Sorensen, 2015). Physiological changes concurrent with this breeding migration cause an irreversible cessation of feeding in sea lamprey (Larsen, 1980), resulting in a finite store of energy available to complete their life cycle. In addition to energetic constraints, timing of upstream migration in sea lamprey is strongly tied to seasonal stream

temperatures (Binder & McDonald, 2008), which effect rates of sexual maturation (Sower, 2015) and set limits on embryonic development (Rodríguez-Muñoz, Nicieza, & Braña, 2001). In addition to temperature and rheotactic cues, migrating sea lamprey attend to a variety of odours expressed by conspecifics (Clemens, Binder, Docker, Moser, & Sower, 2010): larval odour, which may indicate suitable larval rearing habitat (Sorensen et al., 2005; Wagner, Twohey, & Fine, 2009), sex pheromones, which indicate mate availability (Li, Twohey, Jones, & Wagner, 2007), and a putative alarm cue, which would be present when predators are feeding on conspecifics (Bals & Wagner, 2012; Wagner, Stroud, & Meckley, 2011).

Lampreys are likely important prey to a variety of animals due to their relatively high lipid content (2.35–6.01 kJ/g), yet are under-recognized as such due to a cryptic life cycle (reviewed in Cochran, 2009). Much like salmonids, lampreys are particularly exposed to predation pressure while concentrated during upstream migration, such as in estuaries and in the mouths of rivers; where birds like gulls (*Larus* spp.) and mergansers (*Mergus* spp.) (Cochran, 2009), predatory fishes such as burbot, *Lota lota*, and walleye, *Sander vitreus* (Cochran, 1986), and pinnipeds congregate (Roffe & Mate, 1984). Few empirical studies of predation on sea lamprey are available, and we must therefore rely on scattered observations to infer the extent to which predation pressure may occur. Despite this limitation, at least two freshwater fishes (northern pike, *Esox lucius*, rainbow trout, *Oncorhynchus mykiss*), a snake (northern water snake, *Nerodia sipedon*), several bird species (great blue heron, *Ardea herodias*, *Larus* spp. gulls, double-crested cormorant, *Phalacrocorax auritus*) and a few mammals (North American river otter, *Lontra canadensis*, American mink, *Neovison vison*, raccoon, *Procyon lotor*) consume migratory sea lamprey (reviewed in Cochran, 2009).

Aquatic organisms, such as sea lamprey, are able to assess and mitigate predation risk in part by detecting and responding to chemical cues associated with predators or the act of predation (Mirza & Chivers, 2001). Sea lamprey avoid predator cues, particularly that of 2-phenylethylamine, a compound found in mammalian urine (Di Rocco, Belanger, Imre, Brown, & Johnson, 2014; Di Rocco, Imre, & Johnson, 2016; Imre, Di Rocco, Belanger, Brown, & Johnson, 2014). However, another class of chemical cues, 'alarm cues', indicates an immediate and high level of predation risk as these cues are released from specialized skin cells upon mechanical damage (i.e. following a predator attack) (reviewed in Chivers & Smith, 1998; Kats & Dill, 1998; Wisenden, 2003). Prey detecting an alarm cue often demonstrate antipredator behaviours such as flight, avoidance, reduced activity, or shelter seeking (Chivers & Smith, 1998; Wisenden & Chivers, 2006). Migrating sea lamprey demonstrate a strong and consistent avoidance response to a putative alarm cue extracted from conspecifics (Bals & Wagner, 2012; Imre et al., 2014; Wagner et al., 2011) and will avoid areas of a natural stream activated with this substance (i.e. seek a 'safe space') (Hume et al., 2015; Wagner et al., 2011). However, sea lamprey encountering sections of river where there is no 'safe space', face a potential dilemma: moving upstream in the presence of alarm cue brings them closer to the source of potential predation risk, whereas delaying upstream movement or choosing to avoid an otherwise suitable spawning river incurs costs in time and energy that may translate to reduced reproductive productivity. Furthermore, because alarm cues degrade over time (Ferrari et al., 2008a, 2008b), their utility for locating predators likewise diminishes with time from attack.

We tested the effects of a whole-river (i.e. bank-to-bank) application of the sea lamprey alarm cue at three concentrations (none, low, high; see Methods for details) on the willingness of migrating sea lamprey to confront the apparent risk of predation at

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