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Use of chemosensory cues as repellents for sea lamprey: Potential directions for population management

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ABSTRACT

Sea lamprey invaded the Great Lakes in the early 20th century and caused an abrupt decline in the population densities of several native fish species. The integrated management of this invasive species is composed of chemical (lampricide) applications, low-head barrier dams, adult trapping and sterile male release. Recently, there has been an increased emphasis on the development of control methods alternative to lampricide applications. We propose as an alternative-control method the use of chemosensory cues as repellents for sea lamprey population management. Based on the available evidence at this time, we suggest that injury-released chemical alarm cues show promise as repellents for sea lamprey and further research should be directed at determining whether sea lamprey show an avoidance response to these types of chemosensory cues. From a management perspective, these chemosensory cues could be used to restrict sea lamprey access to spawning grounds. Repellents could also be used together with attractants like sex pheromones to manipulate sea lamprey behavior, similar to the "push-pull" strategies utilized with insect pests.

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Introduction

Sea lamprey (*Petromyzon marinus*), an exotic pest, invaded the Great Lakes in the early 20th century (Smith and Tibbles, 1980) causing declines in several economically and ecologically important fish species, especially lake trout, *Salvelinus namaycush* (Applegate, 1951; Smith and Tibbles, 1980; Eshenroder et al., 1992). Fisheries in the Great Lakes are enormous in value, with recreational fisheries alone estimated to exceed \$1.5 billion (Bence and Smith, 1999). Sea lamprey populations are subjected to a \$14 million/year extensive control program (Jones, 2007) in order to keep sea lamprey populations at low levels and protect fisheries. The integrated management of this invasive pest currently relies on the use of lampricides in tributary streams (Brege et al., 2003), low-head barrier dams to prevent adult lamprey from accessing spawning grounds (Lavis et al., 2003), trapping of adults and controlled sterile male release (Twohey et al., 2003). Due to rising lampricide costs and

mounting public disapproval of pesticides, the Great Lakes Fishery Commission has pledged to reduce its reliance on lampricides by 50% (Great Lakes Fishery Commission, 2001). This substantial decrease in chemical control will rely heavily on the successful development and integration of cost-effective alternatives for controlling sea lamprev populations. Efforts to reduce lampricide use are focused on: 1) intensification of existing alternative-control technologies, such as low-head barrier dams, trapping of adults and release of sterile male lamprey, and 2) implementation of at least one new alternativecontrol method by the end of 2010 (Great Lakes Fishery Commission, 2001). An alternative-control method that shows a great promise for rapid implementation is the use of sea lamprey pheromones to manipulate the behavior of spawning adults (e.g., Wagner et al., 2006; Li et al., 2007). Sea lamprey have a larval migratory pheromone (Bjerzelius et al., 2000; Vrieze and Sorensen, 2001; Li et al.;, 2007) that attracts spawning stage adults to streams where juveniles are present, and a sex pheromone released by spermiating males (e.g., Wagner et al., 2006; Li et al., 2007) that attracts females. Although there remain a number of critical research needs with respect to lamprey pheromones (Li et al., 2007), recent field tests supported the efficacy of sea lamprey pheromones as attractants in trap-based management strategies (Wagner et al., 2006).

We propose as a new alternative-control method the use of chemical repellents to manipulate sea lamprey behavior and ultimately contribute to sea lamprey management. There is extensive

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evidence indicating that the lamprey olfactory organ is welldeveloped and highly sensitive to a group of biologically relevant odorants. Not only is each developmental stage regulated to some extent by odorants, but also olfaction is thought to fundamentally influence and regulate important behaviors and physiological processes such as migration, mating behavior and sexual maturation (for a review see Li et al., 2007 and references therein). This evidence suggests that sea lamprey could respond to chemosensory cues that warn the presence of predators and facilitate predator avoidance behaviors.

While the conventional alternative methods are the focus of extensive research attention (e.g., Bergstedt and Twohey, 2007; Li et al., 2007; McLaughlin et al., 2007), the use of chemosensory cues as chemical repellents has remained completely unexplored. A Great Lakes Fishery Commission sponsored workshop (Sorensen and Hanson, 1993) raised the possibility that sea lamprey behavior could be controlled with chemosensory cues and recommended careful examination of the possibility of presence of lamprey alarm cues and sea lamprey responses to predator stimuli, human saliva and dead lamprey. We provide a short review of injury-released chemical cues in fishes and review the available evidence that supports the potential effectiveness of these substances as repellents for sea lamprey. Finally, we will discuss the potential application of these substances for sea lamprey management.

Predation is considered a major selective factor, with an immediate negative effect on the prey organisms' future fitness (Lima and Dill, 1990). Accordingly, natural selection favors the ability to recognize any source of information that allows receivers to sense the presence of predators early and reduce predation risk by behavioral or other means. Chemical cues can be more advantageous than visual cues because they can persist longer in the environment and can provide information about the presence of predators hidden behind structures or camouflaged by coloration, darkness or turbidity of the water (Wisenden, 2003). Examples of chemical cues used for predator avoidance abound both in marine and freshwater environments (see Table 12.1 in Wisenden, 2003). Based on the limited evidence available at the present time, injury-released chemical alarm cues hold promise as potential repellents for sea lamprey population control.

Injury-released chemical alarm cues

A wide range of aquatic vertebrate and invertebrate taxa exhibit antipredator behavior in response to injury-released chemical alarm cues, indicating the vital value of this type of chemical cue as antipredator information (Chivers and Smith, 1998). Perhaps most widely studied in fishes of the superorder Ostariophysi (Pfeiffer, 1977; Chivers and Smith, 1998; Brown et al., 2003;), injury-released alarm cues have been shown in a wide array of taxonomically diverse species, including salmonids, gobies, sticklebacks, poeciliids, sculpins, cichilds, cottids, percids, gobies and centrarchids (Chivers and Smith, 1998; Brown, 2003). The alarm cues are produced and/or stored in the epidermis (Chivers and Smith, 1998) and can only be released following mechanical damage to the skin as would occur during predation events. Once released into the water column, alarm cues can elicit a variety of species-specific antipredator behaviors, including increased shoal cohesion, increased swimming and area avoidance, freezing behavior and reduced feeding or mating (Pfeiffer, 1977; Chivers and Smith, 1998). It is worth noting that alarm cues have been shown to function as indicators of local predation threats for non-shoaling (i.e., territorial) juvenile salmonids (Leduc et al., 2006) under fully natural conditions. Moreover, recent evidence shows that the relative concentration of alarm cues detected provides valuable information regarding level of immediate (Brown et al., 2006a,b) and very low levels of risk (Brown et al., 2004). Chemical alarm cues can also induce long-term behavioral responses such as acquired recognition of new predators and morphological and life history changes (Brown, 2003; Chivers et al., 2008). Such dramatic increases in the predator avoidance behavior of individuals detecting alarm cues are known to increase survival during encounters with live predators (Mathis and Smith, 1993; Leduc et al., 2009). Given the demonstrated survival benefit associated with responding to alarm cues, there likely exists strong selection pressure on cue receivers for the 'innate' recognition of conspecific alarm cues and those of closely related species (Brown et al., 2003; Kelly et al., 2006; Chivers et al., 2007).

There are two lines of indirect evidence that suggest the existence of injury-released chemical alarm cues in sea lamprey. First, Namespetra (2008) has recently examined the behavioral response of sea lamprey to an extract of decaying lamprey, a biodegradable detergent solution, and undiluted human saliva. The study found that most of the experimental lamprey moved to the opposite end of the tank after the addition of decaying sea lamprey extract compared to no reaction to the control treatment using river water. The fact that lamprey avoided the scent of decaying sea lamprey suggests that sea lamprey possess chemicals that function as alarm substances similar to other species of fish. Second, Namespetra's (2008) finding is further supported by field observations by sea lamprey control officers who reported sea lamprey jumping out of the water to avoid the area where decaying sea lamprey were added to a stream (W. D. Swink, United States Geological Survey, personal communication). Decomposing shark flesh was also identified as a potential source for shark repellent chemical cues (Rasmussen and Schmidt, 1992). Anecdotal evidence from fishermen in support of decomposing shark flesh indicates that sharks avoid areas containing decomposing shark carcasses (Sisneros and Nelson, 2001).

In order to ascertain the existence and role of injury-released alarm cues in sea lamprey, further research should (1) investigate the presence of an avoidance response in sea lampreys in response to sea lamprey skin extract and/or sea lamprey internal tissue extract, (2) determine whether this is a general response to injured heterospecific fish/lamprey or a specific response to injured conspecific sea lamprey, (3) determine the length, latency and resistance to habituation of avoidance responses to these repellents and (4) determine whether the response is gender specific or time specific (i.e., does sea lamprey response differ early vs. late in the spawning season). A better understanding of these basic ecological questions will dictate the likelihood that alarm cues may play a role in future management considerations.

Population management considerations

From a management perspective, the best case scenario for the utilization of sea lamprey repellents would be to prevent migrating adult sea lamprey from accessing tributary streams where spawning would take place. This could be achieved by releasing repellents at very low concentrations during the sea lamprey spawning season at the mouth of the tributary to label the habitat as risky (a seasonal chemical barrier). If this method of complete exclusion would work, sea lamprey control agents could concentrate migrating sea lamprey populations to a small number of streams where extensive chemical or alternative biological control methods are already applied. If sea lamprey, in fact, show sensory adaptation to the repellent substance, a more realistic management scenario would include releasing repellents at regular intervals into a stream or part of a stream to concentrate migrating sea lamprey in the vicinity of biological control devices, such as traps. In addition, several different types of repellents could be released sequentially to induce an avoidance response in sea lamprey that might show habituation/olfactory adaptation to the previously released repellent. Daytime application of the repellents could induce hiding sea lamprey to become active and available to capture by nearby traps. Sea lamprey populations could be

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