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Notes

Potential for carbon dioxide to act as a non-physical barrier for invasive sea lamprey movement

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ABSTRACT

Invasive sea lampreys have had substantial negative ecological and economic impacts on the Laurentian Great Lakes region. Control efforts, such as lampricide application and barriers, have resulted in a reduction in number of sea lampreys in the Great Lakes. Due to environmental and non-target impacts of existing control mechanisms, coupled with the fact that no non-physical barrier is completely effective at stopping fish movement, there is a critical need to develop novel control technologies to assist with the control and suppression of sea lamprey populations. Recent work has indicated that carbon dioxide gas (CO_2) applied to water will influence the movement and behavior of fishes, providing the potential for CO_2 to act as a non-physical barrier that can exclude fish from a target area. To date, the effectiveness of CO_2 at influencing the movement and behavior of sea lampreys has not been explored. The current study showed that CO_2 applied to water will result in behavioral agitation for both adult and transformer sea lampreys, and will eventually result in equilibrium loss. More importantly, both adult and transformer sea lampreys will 'choose' to avoid water with CO_2 concentrations of 85 and 160 mg/L (respectively). Together, results from this study suggest that CO_2 applied to water has the potential to act as a non-physical barrier to deter the movement of free-swimming lamprey in the wild. Carbon dioxide gas can be integrated with existing control technologies to act as a novel barrier technology and augment existing control strategies for sea lampreys.

Introduction

Invasive species can cause tremendous ecological, economical, and social damages (e.g., recreational, ecosystem services) on the receiving environment (Pimentel et al., 2005; Ricciardi and MacIsaac, 2011). In the Laurentian Great Lakes, biologists and managers have struggled to contain the spread and minimize the impacts of biological invaders (e.g., sea lamprey (*Petromyzon marinus*), alewife (*Alosa pseudoharengus*), zebra mussels (*Dreissena polymorpha*)) over the past 50 years (Rasmussen et al., 2011). Invasive species have been shown to have direct (e.g., competition, predation) and indirect (e.g., habitat modification, disease transfer, hybridization) impacts on native species that can result in population declines and the eventual reduction of species biodiversity within the invaded landscape (Clavero and García-Berthou, 2005; Ricciardi and MacIsaac, 2011). The establishment of invasive species can also result in negative economic consequences due to declines in the abundance of native species (Pimentel et al., 2005). As management strategies to extirpate already established invasive species have tremendous monetary costs and are often ineffective, one cost-effective and efficient management strategy for invasive species control is preventing the initial colonization event through the use of prevention technologies (Finnoff et al., 2007; Lodge et al., 2006).

Since the 1930s, sea lampreys have been an invasive species of particular concern in the Great Lakes region (Smith and Tibbles, 1980). The introduction and establishment of sea lampreys within the Great Lakes remain one of the most potent examples of how invasive species can impart negative biological and economic impacts on an ecosystem level. The biological impacts of sea lamprey invasion were evident relatively soon after introduction (~5 years) with declines in native fish populations, especially lake trout (*Salvelinus namaycush*) and burbot (*Lota lota*), which resulted in the restructuring of aquatic communities in these lakes (Smith and Tibbles, 1980). Sea lampreys are obligate migrants, with adults migrating into streams to spawn, and transformers (juveniles) outmigrating after a variable period of stream residency. This life history makes sea lampreys vulnerable to a variety of control measures. With the discovery and application of lampricides, along with other control measures such as traps and barriers, sea lamprey populations have been suppressed relative to historical levels (Christie and Goddard, 2003; McLaughlin et al., 2007; Smith and Tibbles, 1980). However, lampricide treatments must be applied annually to control sea lampreys within the Great Lakes (Irwin et al., 2012). A recent study by Irwin et al. (2012) suggests that current lampricide

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treatments would need to be increased 25–50% to maximize the economic benefit of fisheries within the Great Lakes (i.e., lower sea lamprey abundances yield greater fish harvest), resulting in substantial additional cost to apply lampricide. Other control mechanisms exist to prevent fish movement; however, physical, in-stream barriers vary in effectiveness across sites and can have negative impacts on native communities by impairing movements (McLaughlin et al., 2007). Thus, there is a critical need to develop additional techniques to facilitate the control and removal of sea lampreys that would supplement or enhance existing control efforts, particularly during juvenile migration events from spawning grounds and adult migration events to spawning grounds.

Carbon dioxide gas applied to water has recently shown promise as a physiological and behavioral deterrent to fish movement (Clingerman et al., 2007; Kates et al., 2012; Ross et al., 2001). An elevated carbon dioxide barrier initially acts as a behavioral modifier, with fishes actively avoiding hypercarbic water (Clingerman et al., 2007; Kates et al., 2012). If fish are resistant to the deterrence aspect of the carbon dioxide barrier, individuals will eventually succumb to the anesthetic effects of hypercarbia resulting in loss of consciousness and equilibrium (Iwama et al., 1989). Previous research on two species of invasive cyprinids (silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Hypophthalmichthys nobilis*)), along with two centrarchids native to North America (largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*)) has shown that CO_2 concentration of 70 mg/L will result in behavioral modifications (changes in ventilation frequency, loss of equilibrium, and irregular behaviors), while CO_2 concentrations of 120 mg/L will induce active avoidance of hypercarbic waters (Kates et al., 2012). These results suggest that zones of carbon dioxide gas applied to water have the potential to act as a non-physical barrier and deter movements for these species. Unfortunately, only a few studies have investigated behavioral responses of fishes to hypercarbia, and none have examined the behavioral impact of elevated carbon dioxide on sea lampreys. As such, it is presently not known if zones of elevated carbon dioxide gas have potential to act as a non-physical barrier for lamprey movement; and, if feasible, what concentrations of carbon dioxide should be targeted.

Based on this background, the overall goal of this study was to quantify the influence of elevated CO_2 on the behavior of sea lamprey transformers (juveniles) and adults. This goal was achieved by completing two complementary series of experiments. The first experiment quantified the behavioral consequences of elevated CO_2 exposure to sea lampreys by determining the concentration of hypercarbia needed for these fishes to elicit agitation responses (i.e., elevated activity levels, twitching, erratic swimming) and eventual equilibrium loss, while the second experiment used a behavioral choice arena to define the concentration of carbon dioxide necessary to induce behavioral avoidance. The comparison of two distinct life stages was important to ensure that any target concentration of CO_2 identified as a barrier be effective against both adults and transformers to ensure maximum effectiveness. When combined, results from these two experiments will define the target concentrations that would be required if carbon dioxide gas were to be considered as a non-physical barrier to influence the movement of naturally migrating sea lampreys, potentially providing managers and invasive species biologists with a novel 'tool' to help control the abundance, distribution and spread of invasive sea lampreys (McLaughlin et al., 2007).

Materials and methods

Experimental animals

Sea lamprey transformers and adults were collected by U.S. Geological Survey (USGS) biologists and transported to the Hammond Bay Biological Station (HBBS, Millersburg, MI). Lamprey transformers were housed indoors in 200 L plastic holding tanks continuously supplied with fresh water from Lake Huron, while adult sea lampreys were housed outdoors in 1000 L plastic holding tanks, also continuously supplied with fresh water from Lake Huron. Lampreys did not receive supplemental food while being held at HBBS prior to experiments.

Agitation response and equilibrium loss

To quantify the concentration of carbon dioxide that induced agitation and equilibrium loss, sea lampreys were subjected to incremental increases in CO_2 concentrations. Studies with incremental increases in CO_2 were conducted with transformers at HBBS on March 25–27, 2014, while experiments with adult sea lampreys occurred at HBBS on July 10–13, 2014. Trials were performed in complete darkness, and behavioral responses were recorded by a single observer using a headlamp producing a low-intensity red light, as previous research has shown this light source has a minimal impact on lamprey behavior (Hárosi and Kleinschmidt, 1993). Experiments began by placing an individual lamprey into a 15 L cooler that contained an air stone and water from Lake Huron. Lampreys were allowed 30 min to acclimate to the cooler, and the following water quality parameters were measured: water temperature and dissolved oxygen using a portable dissolved oxygen meter (YSI, 550A Yellow Springs Instruments, Irvine, California); pH using a WTW pH 3310 meter with a SenTix 41 probe (Germany); dissolved carbon dioxide and total alkalinity using a digital titration kit (Hach Company, titrator model 16900, kit 2272700 for CO_2 and kit 2271900 for total alkalinity). The sensitivity of the pH meter was ±0.01 pH units, and the sensitivity of the digital titration kits was ±1%. Temperature, pH, and total alkalinity were subsequently combined to generate values for pCO_2 (μatm) using CO_2Calc (version 1.2.0, U.S. Geological Survey, Reston, VA, USA) (Robbins et al., 2010). Initial water quality measurements for all experiments are provided in Table 1. Following this acclimation period, carbon dioxide levels were increased using the common technique of bubbling CO_2 gas into the water until a target pH was reached (Munday et al., 2009; Dixson et al., 2010), which, in the current study, was a pH decrease of 0.25 units (corresponding to an increase in carbon dioxide of approximately 25 mg/L, or 30,000 μatm). Once this target pH was achieved, lampreys were observed over a 5 min period for indications of 'agitation' that included erratic swimming, elevated activity levels or twitching (Gattuso et al., 2010; Kates et al., 2012). Following this 5 min observation period, CO_2 gas was added to the cooler to generate a second reduction in pH of 0.25 units, and animals were again observed over a 5 min period for behavioral responses. This process of CO_2 addition coupled with behavioral observations continued until lampreys lost equilibrium, at which point lampreys were removed from the cooler, weighed to the nearest tenth of a gram (g), measured to the nearest millimeter (mm) and placed in a separate holding tank. Lamprey sizes were 152 ± 5 mm standard error (SE) and 4.5 g ± 0.5 g for transformers, and 489 mm ± 16 mm and 215 g ± 18 g for adults (N = 8 animals of each life stage for all experiments).

Hypercarbia avoidance

Hypercarbia avoidance was quantified using a "shuttle box" choice arena (Loligo Inc., Hobro, Denmark), which consists of two circular chambers (1.5 m diameter, 0.5 m depth) connected by a narrow tunnel (0.2 m wide × 0.5 m deep) (described in detail in Kates et al., 2012). Briefly, external pumps moved water from one circular chamber into an external buffer column where it could be treated and returned to the choice arena via gravitational force. One buffer column was dedicated to one of the circular chambers of the arena, and the system allowed water chemistry in one circular chamber to be independently manipulated without affecting water chemistry in the other chamber. Water quality in each circular chamber was manipulated using a computer and software package (Shuttlesoft 2.6.0, Loligo Inc., Hobro, Denmark), and two pH probes, connected to two portable pH meters, were placed