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## Notes

## Predation by alewife on lake trout fry emerging from laboratory reefs: Estimation of fry survival and assessment of predation potential

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## ABSTRACT

Alewife (*Alosa pseudoharengus*) predation may be an important mortality source on lake trout fry (*Salvelinus namaycush*), and could affect the success of lake trout restoration in the Great Lakes. This study tested the prediction that fry showing typical swimming and avoidance behavior over artificial reefs will differ in survival when alewives are present versus when alewives are absent. Six tanks with cobble substrate were each stocked with 153 lake trout fry (density = 131 m<sup>-2</sup>), a density comparable to that recorded at Stony Island reef, Lake Ontario during the early 1990s. Four treatment tanks each contained ten alewives (density = 8 m<sup>-2</sup>) and two control tanks contained no alewives. After 12 days, mean recovery of fry was less in treatment tanks (31.5 fry per tank) than in control tanks (150 fry per tank;  $P < 0.009$ ). Fry mortality in control tanks was about 2% in contrast to 46 to 91% mortality in tanks containing alewives. Alewife predation effects were evident early in the experiment as the mean daily capture of fry by traps set in each tank was always lower after day two in treatment tanks than in control tanks. The rate of consumption of lake trout fry by alewives ranged from 0.57 to 1.16 fry alewife<sup>-1</sup> day<sup>-1</sup> (mean = 0.99 ± 0.141; median = 1.12). The results of this study support the hypothesis that predation by alewives could cause a high level of lake trout fry mortality, and thus affect natural recruitment of lake trout and the success of population rehabilitation.

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## Introduction

Non-native alewives *Alosa pseudoharengus* have been implicated as contributors to the inability to reestablish lake trout *Salvelinus namaycush* in the Laurentian Great Lakes (Jones et al., 1995; Krueger and Ebener, 2004; Madenjian et al., 2008; Muir et al., 2012). In lakes Huron, Michigan, and Ontario, where alewives have been abundant, lake trout rehabilitation efforts have met with little success (Elrod et al., 1995; Eshenroder et al., 1995; Holey et al., 1995; Muir et al., 2012). Alewives cause indirect mortality of lake trout fry by inducing early mortality syndrome, also known as thiamine deficiency complex (TDC; Fitzsimons et al., 1999; Honeyfield et al., 2005). Alewives have high thiaminase levels — TDC has been linked to thiamine deficiency in adult female lake trout that have fed on alewives. Embryos spawned by these adults died after hatching (Fitzsimons et al., 2010).

Alewives also cause direct mortality through predation on lake trout fry. Predation of lake trout fry was observed in the gut contents of

alewives caught at Stony Island reef, Lake Ontario in 1993 by Krueger et al. (1995) and continued to be observed over the next two years (C.C. Krueger, unpublished data). Alewife catches in gillnets on Stony Island reef peaked during mid May and coincided with peak emergence of lake trout fry at that site. Fry after absorption of the yolk sac swim at night from the lake bottom to the surface to gulp air, fill their swim bladders, and become free swimming (Balon, 1980). Likely, emergent fry making this transition between sac fry to the free swimming stage are highly vulnerable to predation. In a review of long-term (50 years) data series, Madenjian et al. (2008) concluded that circumstantial evidence supported that alewife predation on larval fishes, including lake trout, was the most likely primary cause of fish community disruption in the Laurentian Great Lakes. Recent resurgences of lake trout and native coregonines (e.g., bloater), in Lake Huron have coincided with dramatic declines (>99%) in alewife abundance (Madenjian et al., 2008; Riley et al., 2007; Schaeffer et al., 2005; Warner et al., 2005).

Alewife predation on lake trout fry is difficult to detect, much less investigate when alewives are abundant and fry are rare. Under these circumstances, alewives would have their greatest effect on limiting lake trout recruitment and potentially prevent species reestablishment. When predator (alewife) abundance is high relative to prey abundance (lake trout fry), as it has been in lakes Michigan, Huron, and Ontario since the 1950s, prey encounter probability and consumption rates per alewife will be low, hence difficult to detect. However, in this case

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the overall total mortality of fry will be high. Conversely, when predator abundance is low relative to prey abundance, we expect prey encounter probability to be high and easy to detect. In this case, the overall prey mortality will be low and unlikely to affect recruitment because prey abundance will overwhelm the effects of predation. Consequently, due to the combined effects of predation and TDC, lake trout recruitment could be substantially affected when lake trout abundance is low and alewife abundance is high. Effects of TDC on lake trout recruitment in the Great Lakes have been well studied; however, the predation potential of alewives on lake trout fry remains unknown due to the logistical difficulties associated with studying these interactions in the field, such as the rapid digestion of fry in alewife stomachs (Krueger et al., 1995) and the difficulty of accurately estimating alewife and fry abundance per unit area (e.g., on a spawning reef).

Under conditions of high alewife abundance, three conditions are necessary for alewife predation to induce enough fry mortality to affect lake trout recruitment. First, predator and prey must overlap in space and time. Spatio-temporal overlap of alewives and pre-emergent and emergent lake trout fry was observed in lakes Michigan, Huron, and Ontario with alewives moving inshore during spring for spawning (Wells, 1968) corresponding to the time when lake trout fry are emerging from the substrate (Krueger et al., 1995). During May–June, alewives inhabit waters over nearshore and offshore lake trout spawning reefs as well as soft sediments adjacent to the base of these reefs (Krueger et al., 1995; Madenjian and DeSorcie, 1999; Madenjian et al., 2006, 2008). Thus, alewives have access to lake trout fry during the period of emergence when fry are vulnerable to predation.

Second, the predator must possess the physical and physiological means to acquire and metabolize the prey. Previous laboratory predation studies demonstrated that alewives are capable of preying on different sizes of lake trout fry (Krueger et al., 1995; Strakosh and Krueger, 2005). Fry, sometimes partially immobilized, were introduced under daylight conditions at the water surface of treatment tanks, and alewives readily and aggressively fed on them (Krueger et al., 1995). In addition, lake trout fry in alewife guts were rapidly digested (e.g., 1 h after ingestion a 15-mm larvae was almost completely digested; Krueger et al., 1995). These laboratory observations were validated by finding wild lake trout fry in the stomachs of alewives caught from Lake Ontario at night just after sunset (Krueger et al., 1995; C.C. Krueger, unpublished data).

Third, the behavior of both predator and prey under natural conditions must render the prey susceptible to the predator. Lake trout embryos typically hatch during April and May in the Great Lakes where they inhabit the interstices of rocky shoals until emergence (Bronte et al., 1995). Lake trout fry are probably most vulnerable to predation during the period from just after hatching (sac fry stage, F<sup>2</sup>10 stage from Balon, 1980) through the transition to the emergent life stage (free-swimming stage, A<sup>2</sup>12 stage; Strakosh and Krueger, 2005) because it is at this stage that they begin moving outside of the substrate and ascend to the surface to fill the swim bladder. Sac fry prior to emergence begin to show short distance movements out of the substrate at night (Krueger et al., 1995) providing some limited exposure of fry to predators in the water column. Laboratory experiments demonstrated that pre-emergent lake trout sac fry recognized alewives as predators and responded by fleeing into the rock substrate or upward in the water column to the surface (Strakosh and Krueger, 2005). Emergence and free-swimming behavior require inflation of the gas bladder. First filling of the lake trout bladder occurs by swimming at night from the bottom to the surface to gulp air (Gustafson-Marjanen and Dowse, 1983; Tait, 1960). Fry showing this behavior are exposed to high predation risk for a considerable period of time because they are poor swimmers and unable to regulate their buoyancy until their bladder is inflated. After the swim bladder is filled, fry are better swimmers and should be better able to avoid alewife predation. Therefore, on the basis of field and laboratory observations, lake trout fry behavior renders them vulnerable to pelagic predators, such as alewives during

night-time emergence when fry are swimming up through the water column to fill their swim bladder.

Alewives forage in large schools and use vision and the acoustico-lateralis system to feed on pelagic prey. Alewives as planktivores filter feed on zooplankton but can switch at night to feeding on large individual prey items such as *Mysis diluviana* (Janssen and Brandt, 1980) using vision (Boscarino et al., 2010). Alewives are known to prey in the Great Lakes on the larvae of lake whitefish *Coregonus clupeaformis* (Hoagman, 1974), bloater *Coregonus hoyi* (Luecke et al., 1990; Rice et al., 1987), walleye *Sander vitreus* (Brooking et al., 1998), and yellow perch *Perca flavescens* (Brandt et al., 1987). Based on integrated laboratory and field studies, the light sensitivity of alewives was reported to be sufficient for night-time visual feeding, especially during moonlit periods, on large (5 to 15 mm) prey items such as *Mysis* at depths of <20 m in Lake Ontario (Boscarino et al., 2010), and by inference likely capable of feeding on even larger, more visible emerging lake trout fry  $\geq 23$  mm swimming to the surface.

Optimal foraging theory predicts that when a school of alewives encounters a patch of food, the environment provides a choice, and selecting the highest energy, largest food morsel available within gape size limitations can be advantageous (Brooks and Dodson, 1965; MacArthur and Pianka, 1966). Therefore, switching from predation on zooplankton to ichthyoplankton could be energetically advantageous for alewives. Size-selective predation of large over small zooplankton has been shown in alewives in Lake Ontario (e.g., O'Gorman et al., 1991). Luecke et al. (1990) reported that the presence of alternative food sources (i.e., zooplankton) did not reduce predation by alewives on larval bloater. For this reason, we expect that if patches of emergent lake trout fry are available for short periods of time, alewives that encounter these prey patches could induce high mortality.

Given the spatio-temporal overlap of alewives and lake trout fry, the ability of alewives to use this prey resource, and the occurrence of behaviors that render early life stages of lake trout susceptible to alewife predation, we sought to determine the potential of alewife predation to affect the abundance of lake trout fry as they transitioned from pre-emergent (F<sup>2</sup>10 stage; Balon, 1980) to the free-swimming emergent stage (A<sup>2</sup>12; Balon, 1980) while inhabiting artificial reefs. The fry during this transition would show typical diel movement in and out of stony substrate as sac fry, a brief night-time period of swimming to the surface to fill their swim bladders, and then become free swimming as emergent fry. We hypothesized that alewives would affect fry abundance over a 12 day time period that approximated the length of the developmental interval required to transition from the sac fry to the emergent life stages observed during the 1990s at Stony Island reef, Lake Ontario. Our objective was to determine whether lake trout fry showing typical swimming and avoidance behavior over artificial reefs differ in survival when alewives are present versus when alewives are absent. Our experimental design provided typical reef habitat (i.e., stony reef structure with interstices), springtime photoperiod, water temperatures similar to those in Lake Ontario during lake trout emergence, and densities of predators and prey that approximate those reported from Lake Ontario (Krueger et al., 1995). Motivation to conduct this study was further provided by spirited discussions at the 1994 RESTORE Conference (Selgeby et al., 1995) and subsequent discussions over the decade that followed at Lake Committee meetings (Great Lakes Fishery Commission, 2007) as to whether alewives, under any circumstances, could actually exert enough predation to measurably reduce lake trout fry numbers.

## Methods

### Laboratory reefs

Six identical, 1.22-m-diameter, circular fiberglass tanks served as laboratory reefs (1.17 m<sup>2</sup> surface area); four tanks were used as experimental treatments and two as controls. The bottom of each tank was lined with a 3-dimensional grid of plastic 1.0-cm high with 1.3

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