Behavior of Post-emergent Lake Trout Fry in the Presence of the Alewife, a Non-native Predator

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ABSTRACT. Although predation by non-native alewife (Alosa pseudoharengus) on lake trout fry (Salvelinus namaycush) has been documented, whether or not emergent lake trout fry innately recognize alewives as predators is unknown. This study investigated the behavior of post-emergent, free-swimming lake trout fry in the presence of alewives. Study objectives were to determine (1) if fry respond to the presence of alewives and show an avoidance behavior, (2) if the fry behavior appeared to be innate or learned, and (3) whether alewives will catch and eat post-emergent fry. The influence of alewives on fry behavior and vertical distribution were determined by adding alewives to tanks containing lake trout fry. Fry immediately reacted to the introduction of alewives by fleeing even though alewives showed no predatory behavior. When lake trout fry were introduced into tanks with and without alewives, more fry were distributed near the top and fewer fry near the middle of the tanks with alewives. Predation of post-emergent fry occurred immediately in the second experiment. Survival of fry after 5 days in tanks with alewife averaged 57% in contrast to 94.5% in the control tanks. We conclude that post-emergent lake trout fry, while innately able to recognize alewives as a predator and show evasive behavior, are still vulnerable to predation.

INDEX WORDS: Larval fish, alevin, Lake Ontario, mortality, vertical distribution, innate, learned.

INTRODUCTION

The reintroduction and establishment of naturally reproducing populations of lake trout (Salvelinus namaycush) to Lake Ontario has been a fish management goal for several decades but little success has occurred (Krueger and Ebener 2004). One factor that may contribute to the lack of natural recruitment is predation on lake trout fry by the non-native alewife (Alosa pseudoharengus; Krueger et al. 1995, Johnson and V anAmberg 1995). Alewives have been documented to feed on fry of several species and could limit recruitment (Crowder 1980, Kohler and Ney 1980). Brandt et al. 1987 found that alewives in a Lake Ontario embayment heavily preyed upon larval yellow perch (Perca flavescens) and concluded that alewife predation may reduce recruitment of yellow perch lake wide. They reported that a large portion of alewife stomachs (30% in 1985 and 41% in 1986) contained larval yellow perch, with one stomach containing 361 larvae. Kohler and Ney (1980) identified six different fish species in alewife stomachs from Claytor Lake, Virginia. Species observed in the stomachs included alewives, white bass (Morone chrysops), largemouth bass (Micropterus salmoides), sunfish (Lepomis spp.), and golden shiner (Notemigonus crysoleucas). Alewives also have reported to eat larval lake whitefish (Cargonus clupeaformis; Hoagman 1974), rainbow smelt (Osmerus mordax; Smith 1970), and walleye (Sander vitreus; Brook- ing et al. 1998).

Lake trout fry are susceptible to alewife predation during the transition from sac fry to the free-swimming stage (between the eleutheroembryo F210 stage and the alevin A212 stage as described by Balon 1980), when they swim from rocky spawning substrate to the surface to fill their swim bladder. During this transition, lake trout fry leave the safety of the spawning reef, increasing their risk
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of a pelagic predator encounter, and swim poorly making them unlikely to successfully avoid a predatory attack (Baird and Krueger 2000). Krueger et al. (1995) reported that large schools of alewife aggregated over a lake trout spawning reef in Lake Ontario and that their presence coincided temporally with this transition period of the fry. Some alewife caught near the reef had fry in their stomachs. Laboratory experiments also showed that alewives readily fed on lake trout fry of this transition stage and that alewives could cause substantial fry mortality (Krueger et al. 1995). However, pre-emergent and emergent fry are closely associated with the rocky cover of the spawning reef that provides them refuge from pelagic predators. These fry are most exposed to alewife predation for the short period during the swim-up phase. In contrast, post-emergent fry leave the cover of the spawning reef and migrate to nursery areas that offer less protection from predation (Peck 1981, Bronte et al. 1995).

Ontogenetic habitat shifts tend to be size dependent and occur when fry become less susceptible to predation and strong intra-specific competition (Werner and Hall 1988, Werner and Anholt 1993). Werner and Hall (1988) reported that bluegill (Lepomis macrochirus) shifted habitats from vegetation to the pelagic zone, when they reached 50 to 83 mm in length. Although this habitat shift was energetically more profitable, the risk of predation increased 40 to 80 times for bluegill in open water compared to vegetative cover. Similarly, the predation risk experienced by lake trout fry may increase when fry move away from the cover of spawning reefs to nursery areas.

The risk of predation by alewife that post-emergent lake trout fry endure depends more on swimming ability and avoidance response than body size. Although Hoagman (1974) reported that alewives ignored larval lake whitefish > 19.5 mm, other studies found alewives readily preyed upon much larger fish. Alewives consumed lake trout fry up to 34 mm in laboratory experiments (Krueger et al. 1995) and post-emergent fry in nursery areas can be as small as 27 mm in length (Peck 1981, Bronte et al. 1995). Brooking et al. (1998) investigated the predation vulnerability of walleye at different sizes. They reported that alewives (122 ± 1.52 mm) aggressively fed upon walleye < 16 mm TL causing 100% mortality. As walleye grew their avoidance ability increased and when they reached 34 mm TL only 5% of the walleye were eaten by the alewives after a one-hour exposure. Because alewives readily fed upon walleye fry up to 34 mm, they concluded that the large fry, due to their swimming capabilities, were harder for alewives to capture than small fry and caused the low mortality rates. Lake trout fry past the A12 developmental stage are fully emergent, can regulate their buoyancy, and swim well. Thus, their ability to avoid predators should be improved over earlier life stages (Fuiman and Magurran 1994). However, if the lake trout fry do not recognize alewives as potential predators, fry may not show appropriate behaviors to reduce this predation risk even though they may swim well.

The behavioral responses of prey in the presence of a predator plays a major role in determining the success of an individual’s or species’ survival. Csanyi and Doka (1993) divided predator-prey interactions into four main categories; interactions at the individual level, interactions at the group level, interactions among prey, and learning by the predator. Individual-level actions by fish include recognition, inspection, defense responses, and decision-making (Fuiman and Magurran 1994). Group-level interactions can allow the fish to protect each other, and include shoaling, alarm responses, vigilance, and mobbing (Fuiman and Magurran 1994). Interactions among prey often involve the social facilitation of alarms to communicate predator presence. Learning by the predator allows the predator to adapt to the avoidance behavior of the prey. Of these four categories, individual-level interactions may be particularly important for lake trout fry responding to non-native alewife because, if a species is predator naïve, learning by the prey at the individual level plays an important role in developing avoidance behavior (Olla and Davis 1989, Csanyi and Doka 1993, Fuiman and Magurran 1994).

Prey naïveté of a predator can occur when the predator is a non-native species with no co-evolutionary history with the prey (Harvey and Greenwood 1978, Huntingford and Wright 1993). Because the alewife is a non-native species, lake trout fry may not immediately recognize the alewife as a predator, and thus fry may have no innate defensive response to the presence of alewives (Fuiman and Magurran 1994, Huntingford and Wright 1993, Magurran 1990). Defensive behavior may not occur until after the prey has had an aggressive experience with the predator. Patten (1977) found that naïve coho salmon (Oncorhynchus kisutch) fry suffered a 54.5% mortality rate when exposed to torrent sculpin (Cottus rhodius) predation, even though they have a long co-evolutionary
history, but did show rapid learning after exposure. Other studies have reported that naïve prey will show a strong avoidance response to predators only after having fed on prey conspecifics (Hirvonen et al. 2000, Vilhunen and Hirvonen 2003). Vilhunen and Hirvonen (2003) found that naïve age-0 Arctic char (S. alpinus) only showed a fright response to water from a tank containing pikeperch (Stizostedion lucioperca) had been fed age-0 Arctic char and not to tank water from pikeperch fed Arctic grayling (Thymallus thymallus). Unless alewives have been feeding on lake trout fry, chemical cues may not be given to alert fry that alewives are potential predators.

Even if lake trout fry immediately recognize alewives as predators, fry may not react appropriately and unsuccessfully avoid or prevent an attack. Vilhunen and Hirvonen (2003) reported that an anti-predator response of the closely related Arctic char was to freeze in the presence of a predator. If lake trout fry do not move in the presence of a school of alewives, fry may initiate an avoidance response too late to avoid an attack and be eaten. In an experiment conducted by Krueger et al. (1995), lake trout fry stocked into a tank containing alewives responded by initially swimming at the water's surface and then diving to the bottom after an alewife attack. However, stress of stocking may have caused the initial surface swimming behavior of the fry.

In this study, the potential vulnerability of free-swimming, post-emergent lake trout fry to predation by alewives was assessed by recording the behavioral responses of fry and alewives in laboratory tanks. The objectives were to determine (1) if lake trout fry respond to the presence of alewives and show an evasive or avoidance behavior, (2) if behavior of fry appeared to be innate or required learning, and (3) whether alewives will catch and eat post-emergent, free-swimming lake trout fry.

**METHODS**

**Laboratory Tanks**

Four rectangular flow-through tanks (1.8 m long × 0.6 m wide × 0.6 m high) with glass windows along the length of one side were used in the experiments. The bottom of the tanks was covered to a depth of 0.1 m with substrate composed of 60–80% cobble, 20–40% pebble, and < 5% boulder (Cummins 1962 classification) to simulate the substrate described for Stony Island reef in Lake Ontario (Marsden and Krueger 1991). Windows near the tanks provided natural day-night light cycle of March and April to all tanks with minimal shadows. Tanks were supplied with water from Cayuga Lake by the City of Ithaca water supply and dechlorinated at the laboratory. Tanks received an inflow of 37.5 L/h at one end and water drained out a screened 0.45 m tall standpipe at the opposite end. The slight current in the tanks had no notable effect on fish distribution. Water temperature in the tanks varied from 7.5 to 8.5°C.

**Study Fish**

Alewives were captured during the spring of 1995 by seining Cayuga Lake adjacent to Meyers Point near Lansing, N.Y. and were held over winter in 1.8 m diameter tanks. The alewives ranged in size from 120 mm to 177 mm total length and were not gape height or width limited in relation to the size of the lake trout fry used in these experiments. Alewives were fed a 4 g per alewife diet of bloodworms (Chironomidae) and brine shrimp (Artemia sp.) before and during all experiments to provide choice of prey and to avoid feeding behavior associated with starvation. Food was distributed evenly over the surface of all tanks. Before transfer to the rectangular study tanks, alewives were held in a salt solution of 3 g/L NaCl for 40 minutes to reduce the physiological effects associated with stress.

Newly hatched lake trout sac fry of the Seneca (Finger Lakes) strain were obtained from the Bath State Fish Hatchery, New York State Department of Environmental Conservation (strain described in Krueger et al. 1989). Fry originated from gametes collected from adults captured from Seneca Lake during the fall of 1995. Alewives invaded and colonized Seneca Lake during the mid to late 1800s (Smith 1985), and therefore, the strain has a limited co-evolutionary history with alewives. To slow development, pre-emergent fry were kept at 0.5 °C to ensure that the development stage was the same in all experiments. Lake trout used in all experiments were post-emergent, free swimming fry (alevin A212 stage as described by Balon 1980), were predator naïve, and ranged in size from 26 to 28 mm. This size and stage (A212) corresponds with those of lake trout fry found on the nursery areas of Lake Superior in June (Bronte et al. 1995). In all experiments, lake trout fry were fed a diet of bloodworms (Chironomidae) and brine shrimp (Artemia sp.). Food was added to the tanks until fry were observed to no longer actively feed. The number of fry stocked into each tank (144 fry) resulted in den-
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Two experiments were conducted. During both experiments, behavioral observations and counts of fry were recorded within three depth zones: the top zone—the surface to 0.1 m, the middle zone—0.1 m to 0.35 m, and the bottom zone including the substrate—0.35 m to 0.45 m of depth. The bottom zone included from just above the substrate and the substrate, which was approximately 0.1 m in depth. Lines drawn on the sides of each tank, the back wall, and window, delineated each zone.

In the first experiment, alewives were introduced to tanks with lake trout fry, and fry behavior was compared before and after the introduction. The purpose of this experiment was to determine if lake trout fry would innately respond to the presence of an alewife. Prior to the experiment, alewife diet only consisted of blood worms and brine shrimp, and no fry of any fish species. Four experimental tanks were stocked with 144 post-emergent, free-swimming lake trout fry and allowed to acclimate for three days before alewives were introduced. Three days was sufficient for lake trout fry to assume stable distributions prior to the experiment. Counts of lake trout fry in each zone were recorded every 5 min for 30 min before the introduction of alewives, and were averaged for data analysis. Five alewives were then introduced into one of the four tanks. The initial response of the lake trout fry to the alewife introduction was recorded to determine if predator naïve fry immediately (presumably innately) recognized alewives as predators. Beginning immediately after the alewives were added to the tanks, the number of fry in each zone (top, middle, bottom) was recorded every five min for 30 min. The experiment was sequentially repeated in each of the three remaining tanks. A day prior to alewife introduction water was poured into each tank to simulate the stocking disturbance to determine the fry’s reaction. No change in distribution or evasive behavior was observed.

In the second experiment, two treatment tanks were stocked with 10 alewives each and two tanks with no alewives served as controls. The purpose of this experiment was to determine if lake trout fry avoided the alewives (i.e., use the substrate for cover) while accounting for any temporal differences that may occur (i.e., alewives and/or fry may be more active at night), and if alewives would eat post emergent lake trout fry. Alewives were allowed to acclimate for 1 week. A plastic screen (3 mm mesh) barrier was placed in each tank to prevent alewives access to 1/4 of the tank and to create a small protected section where fry would be stocked. The barrier allowed fry and alewives to see each other and was used to initially protect fry from alewife attack. At night under a red light, lake trout fry were stocked in alewife (treatment) and non-alewife (control) tanks into the small sections behind the barriers and the fry’s initial reaction was recorded. Fry were allowed to acclimate in the small section of the tank for 10 min to provide some time for fry to become acclimated to the tank and recover from the stress of stocking. Observations of fry were recorded prior to removal of the barrier, and thus prior to their physical exposure to alewives. Predation of fry was recorded for the first 10 min after the barrier was removed and alewives had physical access to the fry. Vertical distribution of fry in both alewife (treatment) and non-alewife (control) tanks was recorded over a 2-day period. Counts within zones were made at the onset of each experiment and every 30 min thereafter within four three-hour periods of 05:00–08:00, 11:00–14:00, 17:00–20:00, and 23:00–0200. A total of 56 observations were made per tank. The nighttime observations were made using a red light (Sogard and Olla 1997, Miyasaka and Nakano 2001). Although fish do not show a fright response to red light (Yunker et al. 1999), it does enable the fish to see each other, therefore, the red light was only used during the observation period (Miyasaka and Nakano 2001). Five days after fry stocking, the tanks were drained, substrate removed, fry counted, and survival rates compared between treatments and controls.

Data Analysis

The observations from both experiments (i.e., number of lake trout fry in each zone) were changed into percentages and arc-sine transformed for analysis (Snedecor and Cochran 1989). A repeated measures analysis of variance (RANOVA), with repeated measures in time and in space (Maceina et al. 1994, Ott 1988, Milliken and Johnson 1998), was used to detect differences before and after alewife introduction in the first experiment. Multiple comparisons were made using Fisher’s LSD (least significant difference). This method only conducts multiple preplanned comparisons.
using LSD tests if the F-test in the RANOVA was significant \((P < 0.05)\), and controls the experiment-wise error rate making it approximately equal to \(\alpha\) (Milliken and Johnson 1998). For the first experiment, LSD comparisons were only made among the same zones between pre- versus post-alewife introduction.

Due to the availability of only four tanks and the limited number of appropriate age lake trout fry, we were unable to increase our sample size in the second experiment (2 controls and 2 treatments). Therefore, observations for each zone were averaged across time periods, and the analysis was limited to differences between treatment and control tanks. A RANOVA, with repeated measures in space (Maceina et al. 1994, Ott 1988, Milliken and Johnson 1998), was used to detect differences. The LSD comparisons were only made for the same zones between treatment vs. control. For example, the transformed percent of fry recorded in the bottom zone of tanks with alewives were only compared to the transformed percent of fry in the bottom zone of tanks without alewives using LSD tests.

All data analyses were performed using mixed model analysis (PROC MIXED) in the statistical software package SAS version 8.01 (SAS 2000) at an \(\alpha\) level of 0.05. Unlike the general linear models, PROC MIXED takes into account that observations may be correlated and show non-constant variability (Littell et al. 1996, SAS 2000). Tests of hypotheses were conducted with the Type III Tests of fixed effects, and compound symmetry was assumed for both analyses (Milliken and Johnson 1998). Correct degrees of freedom were calculated using the Satterthwaite method (Littell et al. 1996, Milliken and Johnson 1998).

**RESULTS**

In the first experiment, fry distribution was different before and after introduction of alewives to the tanks \((F\text{-value} = 6.95, \text{DF} = \{14, 63\}, P < 0.0001; \text{Fig. 1})\). Based on LSD comparisons, the number of fry in the bottom and middle zones prior to alewife introduction differed \((P < 0.001)\) from the number of fry in these zones after introduction. When alewives were introduced to tanks, fry occupying the middle zone immediately moved into the substrate, and fry at or near the surface, remained near the surface (Fig. 1). A few fry were observed to move from the middle zone to the top zone when alewives were introduced. The number of fry in the top zone did not change \((P \geq 0.18)\) over time. No predator inspection by the fry occurred during the 30-min period after alewife introduction and no aggressive response by alewives occurred towards the fry.

In the treatment tanks (with alewives) of the second experiment, fry placed in the side without alewives immediately darted into the bottom substrate (53% of fry) or remained near the surface (45%). Few fry used the middle zone (2%). No attempted inspection by alewife of lake trout fry was observed while the barrier was in place. In the tanks without alewives, fry occupied the bottom (42%), middle (35%), or top (23%) zones. Similar to the results of the first experiment (Fig. 1), over the 2-day period after the barrier was removed, lake trout fry in tanks with alewives held positions in the top or bottom zones, and avoided the middle zones used by the alewife (Fig. 2). Fry in the middle zone were positioned against the tank walls, in contrast to tanks without alewives where fry were distributed throughout the middle zone. In tanks without
alewives, more fry chose to occupy the bottom and middle zones than the top zone (Fig. 2). The RANOVA indicated a strong alewife by location interaction (F-value = 21.26, DF = {2, 6}, \( P = 0.002 \)). The LSD comparison found no difference \(( P = 0.27 \)) in the number of fry in the bottom zone between tanks with and without alewives. However, the number of fry in the top zone \(( P = 0.003 \)) and the middle zone \(( P = 0.005 \)) were different between treatment and controls.

In the second experiment, alewives were observed to locate, catch, and eat the free-swimming, post-emergent fry when the barriers were removed. Predation within the first 10 min after removal of the barrier was approximately 2%. Lake trout fry immediately showed evasive behavior when attacked. The survival of fry after five days in the two tanks with alewife was 53% and 61%, in contrast to 96% and 93% survival in the control tanks without alewife.

**DISCUSSION**

Predator naïve lake trout fry immediately showed avoidance behavior in response to the presence of alewives by fleeing to positions near the surface or into or just above the substrate. Neither predatory attacks nor inspections were required for fry to show this response. Although lake trout fry may have reacted to other conspecifics, they did not show any group-level behaviors (i.e., shoaling, group inspections) and appeared to respond on the individual level. Fry may have responded to chemical cues, but it was not from alewives previously feeding on conspecifics. The immediate anti-predator reaction observed is consistent with the interpretation that fry behavior is innate rather than learned and that the avoidance response does not require previous experience with the predator (Endler 1986, Fuiman and Magurran 1994, Csányi and Doka 1993).

Strong innate predator recognition has been reported for many fish species (e.g., Huntingford and Wright 1992, Fuiman and Magurran 1994, Brown 2003, Vilhunen and Hirvonen 2003), especially for populations from areas with high predator densities (Magurran 1990, Huntingford and Wright 1992). Magurran (1990) found that laboratory-reared young from a population of European minnow (Phoxinus phoxinus) that co-occurred with northern pike showed anti-predatory responses (i.e., reduced feeding rate, schooling, predator inspections) earlier than a population never exposed to northern pike. Similarly, Huntingford and Wright (1992) reported that laboratory-reared three-spined sticklebacks (Gasterosteus aculeatus) from a high predation risk site learned to avoid dangerous areas significantly faster than those from a low risk site. Hatchery-reared age-0 Arctic char were also reported to express innate responses to predator chemical cues (Hirvonen et al. 2000, Vilhunen and Hirvonen 2003).

Similar to the variation in innate predator recognition among populations, behavioral responses to predators vary widely. In response to alewives, post-emergent lake trout fry fled into or just above the substrate or near the surface. In contrast, the Arctic char froze when exposed to predatory threat (Hirvonen et al. 2000, Vilhunen and Hirvonen 2003). These differences between closely related taxa are not unexpected. Trinidadian guppy (Poecilia reticulata) populations have been well documented to show a wide variety of anti-predatory behaviors within the same stream (Magurran et al. 1993). For example, Templeton and Shriner (2004) reported guppies from upstream sites would freeze on the bottom of the tank while downstream fish would hide under shelter. Brown and Warburton (1997) also found behavioral differences between populations of rainbowfish (Melanotaenia eachamensis). Fish from an open lake population did not rely on cover provided within the tanks.
when exposed to a predator. Whereas rainbowfish from a stream with abundant complex habitat used cover when under the threat of predation.

Movement into substrate or to the surface by lake trout fry is an example of a fleeing response without predator inspection and could reduce predation risk depending on the species of predator and developmental stage of fry. Byran et al. (2002) reported similar results for the Little Colorado spinechase (Lepidomeda vittata). In the presence of Apache trout (Oncorhynchus apache), the spinechase increased the use of both the surface and bottom zones and decreased use of the middle zones. Seghers (1974) also found that a population of guppies would remain near the surface and move toward the edge of the river due to increased predation in deeper water. Similar to the open-lake population of rainbowfish (Brown and Warburton 1997), lake trout fry that fled to the surface may have reacted in a way representative of fry in cover-poor nursery areas and were no longer relying on the substrate for cover.

Most studies concur that variation in anti-predatory responses among populations is directly related to adaptation of the fish to local conditions, including both predator and habitat characteristics (Magurran 1990, Huntingford and Wright 1992, Magurran et al. 1993, Templeton and Shriner 2004, Brown and Warburton 1997). The fleeing response to the surface observed in our experiments may have been a tank effect. However, the behavior could be an adaptive evolutionary behavior that aided survival of lake trout fry exposed to benthic predation by native species. With the possible exception of lake herring (Coregonus artedi) as a pelagic species, most native species likely to be predators of lake trout fry are benthic. Burbot (Lota lota), slimy sculpins (Cottus cognatus), round whitefish (Prosopium cylindraceum) (Stauffer and Wagner 1979, Savino and Henry 1991), crayfish (Orconectes spp.), mudpuppies (Necturus maculosus), juvenile lake trout, and suckers (Catostomus spp.; Hacker 1956, Horns and Magnuson 1981, Savino and Miller 1991, Savino et al. 1993, Stauffer and Wagner 1979) have all been reported as predators of lake trout fry and are benthic in their life history.

Peck (1981) and Bronte et al. (1995) found that free-swimming fry dispersed away from the principal spawning area, and left the cover of the rocky substrate of spawning shoals in Lake Superior. Both reports describe nursery areas as sandy bottoms with little structural cover from predators. Hypothetically, if a benthic predator (e.g., burbot) approached, the response of a lake trout fry could be to move higher in the water column away from the path of the predator. The post-emergent lake trout fry in our study also started to develop counter-shading (i.e., light ventral to dark dorsal coloration). Thus, in the absence of cover, lake trout fry may swim upward and take advantage of their natural camouflage to avoid visual detection by a benthic predator.

In contrast to the potential advantages with benthic predators, fleeing to the surface by fry could increase their risk of predation when encountering a schooling pelagic fish, such as the alewife. Alewives often school in spring and early summer especially in near-shore areas of some of the Great Lakes (O’Gorman et al. 1991, Krueger et al. 1995), and have been found to concentrate in bottom areas during daytime hours (Janssen and Brandt 1980). Feeding strategies shown by alewives include darting, gulping, and filtering by approaching prey from behind or slightly underneath (Janssen 1978). Janssen et al. (1995) found that alewives were size selective and used their lateral line to focus on single prey items in the dark. Although alewives are not benthic feeders and usually approach prey from underneath, they will cruise within 8 cm of substrate and sometimes awkwardly attempt to ingest items off the bottom (Janssen 1978). Thus, if free-swimming lake trout fry in nursery areas encounter large schools of alewives near the bottom, fleeing to the surface could be a maladapted behavior that increases the risk of predation.

Some of the behavior of fry reported here could have been due to the experimental conditions of confinement to tanks. For example, some fry in the middle zone of tanks with alewives (experiment 2) were positioned next to the walls of the tanks. This position next to the wall protected fry on one side from attack. Possibly, with larger tanks or under field conditions, fewer fry would occupy this middle zone because the protection afforded by the tank sides would be reduced or absent. Additionally, due to the low number of replicates in experiment 2, diel differences in vertical distributions were not investigated and results should be viewed as preliminary.

Alewives readily caught and fed upon post-emergent, free-swimming lake trout fry in the second experiment. Predation occurred even though the alewives had alternative food resources available. The post-emergent fry eaten were a more advanced life stage (alevin) than the pre-emergent and emer-
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