Predation on emergent lake trout fry in Lake Champlain

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A R T I C L E   I N F O

Article history:
Received 4 February 2008
Accepted 29 January 2009
Communicated by John Janssen

Index words:
Lake trout
Fry
Predation
Recruitment

A B S T R A C T

The rehabilitation of extirpated lake trout (Salvelinus namaycush) in the Great Lakes and Lake Champlain has been hindered by various biological and physiological impediments. Efforts to restore a lake trout fishery to Lake Champlain include hatchery stocking and sea lamprey control. Despite these management actions, there is little evidence of recruitment of naturally-produced fish in annual fall assessments. Spawning occurs at multiple sites lake-wide in Lake Champlain, with extremely high egg and fry densities, yet sampling for juvenile lake trout has only yielded fin-clipped fish. To investigate this recruitment bottleneck, we assessed predation pressure by epi-benthic fish on emergent fry on two spawning reefs and the subsequent survival and dispersal of fry in potential nursery areas. Epi-benthic predators were sampled with 2-h gillnet sets at two small, shallow sites in Lake Champlain throughout the 24-h cycle, with an emphasis on dusk and dawn hours. In total, we documented seven different species that had consumed fry, with consumption rates from 1 to 17 fry per stomach. Rock bass and yellow perch dominated the near-shore fish community and were the most common fry predators. Predator presence and consumption of fry was highest between 19:00 and 07:00. Predators only consumed fry when fry relative abundance was above a threshold of 1 fry trap−1 day−1. We used an otter trawl to sample for post-emergent fry adjacent to the reef, but did not capture any age-0 lake trout. Due to the observed predation pressure by multiple littoral, species on shallow spawning reefs, lake trout restoration may be more successful at deep, offshore sites.

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Introduction

Lake trout (Salvelinus namaycush) is the focus of intensive restoration efforts in the Great Lakes and Lake Champlain, due to the ecological, economic, and recreational importance of this top predator. Although the events leading to the extirpation of lake trout from the lower four Great Lakes in the 1960s are understood, causes of the decline and disappearance of this species in Lake Champlain by 1900 are unclear (Ellrott and Marsden, 2004). Thus far, efforts to re-establish self-sustaining populations in the lower four Great Lakes and Lake Champlain have resulted in limited success (Cornelius et al., 1995; Eilrod et al., 1995; Eshenroder et al., 1995; Holey et al., 1995; Reid et al., 2001; Ellrott and Marsden, 2004). In Lake Champlain, high fry densities have been measured at several reefs, but naturally-recruited juveniles and adults (identified by having a fin clipped) are rare to absent. Therefore, a recruitment bottleneck most likely occurs between fry emergence and the yearling life stage (Ellrott and Marsden, 2004, Marsden et al., 2005).

The decline of lake trout in Lake Champlain in the late 19th century has been attributed to overharvest (Plosila and Anderson, 1985), predation by rainbow smelt (Osmerus mordax; Halnon, 1963), and predation by sea lamprey (Petromyzon marinus; Fisheries Technical Committee, 1977). However, the shoreline seine fishery in Lake Champlain is unlikely to have driven the population to extinction (Ellrott and Marsden, 2004). Rainbow smelt are native to Lake Champlain, and recent genetic studies suggest that sea lamprey may also be native to the lake, indicating that native lake trout coexisted with these species (Bryan et al., 2005, Waldman et al., 2006).

Another possible reason for the decline is land use changes; over 40% of Vermont was deforested by 1900 (Foster and Aber, 2004). This may have resulted in silation that could have simultaneously improved sea lamprey spawning habitat in streams and degraded lake trout spawning habitat in the lake. Increased sea lamprey abundance coinciding with augmented sea lamprey spawning habitat from anthropogenic land use was also noted in Lake Ontario (Christie 1972, Jude and Leach, 1999).

Efforts to restore a self-sustaining lake trout population in Lake Champlain have included stockling lake trout yearlings and sea lamprey control. Since 1973, annual stocking rates have fluctuated between 39,000 and 271,863 lake trout yearlings, but for the past 12 years have stabilized between 68,000 and 90,000 yearlings (Ellrott and Marsden, 2004). Stocking since 1988 has focused on the Seneca Lake strain and its progeny; this strain has exhibited the most evidence of successful reproduction and higher survival rates in the presence of sea lamprey (Marsden et al., 1993, Schneider et al., 1996, Bronte et al., 2007). Sea lamprey control was initiated in 1990 with an experimental program; although control has resulted in decreased...
lake trout wounding rates, recent wounding rates have been alarmingly high, approaching 100 wounds per100 fish (Marsden et al., 2003, Vermont Department of Fish and Wildlife, unpublished data).

Despite these high wounding rates, the high adult stock size of lake trout in Lake Champlain should be more than adequate for successful reproduction. Bronte et al. (2007) set a target of 164 fish km\(^{-1}\) of net as minimum spawning stock size for restoration in Lake Michigan, assessed using index gillnets comprised of two panels each of 114, 127, 140, and 152 mm stretch mesh multifilament nylon, 1.8 m high. The same index gillnets employed in the Great Lakes yielded relative abundances at two sites in Lake Champlain that exceeded these criteria for stock size necessary for recruitment. In the fall of 2006, two sets at Arnold Bay (Fig. 1) resulted in an average relative abundance of 258 fish km\(^{-1}\) and four sets at Grand Isle had an average stock size of 377 fish km\(^{-1}\) (Riley, 2007). By-catch from lake whitefish (Coregonus clupeaformis) gillnet surveys recorded even higher lake trout spawner abundances at two additional sites in Lake Champlain (Riley, 2007).

Stocked lake trout in Lake Champlain are reproducing at multiple sites lake-wide, with high egg densities in the fall and high fry densities in the spring (Ellrott and Marsden, 2004). Between 2001 and 2003, the egg and fry relative abundances at several sites in Lake Champlain were much higher than densities in Parry Sound, Lake Huron, where there is substantial recruitment and a local lake trout population has been restored (Reid et al., 2001, Marsden et al., 2005). Egg densities recorded in Lake Champlain are well above the suggested threshold egg density of 500 eggs m\(^{-2}\) presumed to be necessary to withstand predation rates observed in the Great Lakes (Jones et al., 1995). Furthermore, the density of interstitial egg predators in Lake Champlain is less than in Lake Huron and the ratio of eggs to predators was six times that of Parry Sound (Jonas et al., 2005).

Despite high egg and fry abundances in Lake Champlain, there has been almost no recruitment of wild lake trout. In fall population assessments since 1982, the percentage of wild lake trout (assessed as fish lacking hatchery fin clips) has never exceeded 10.6% and has predominantly been between 2% and 6%. The background level of missed fin clips is presumed to be around 4% (Ellrott and Marsden, 2004). Targeted trawling and incidental catches of juvenile lake trout in 2001 and 2005–2007 yielded 50 age-1 to age-3 lake trout, of which all were fin-clipped (Ellrott and Marsden, 2004, unpublished data).

Given the high densities of lake trout adults, eggs, and fry, and the lack of recruitment, it is apparent that high mortality is occurring after fry emergence (Marsden et al., 2005). This mortality could be driven by a number of factors, including disease, starvation, and predation. In the Great Lakes, lake trout recruitment has been impacted by Early Mortality Syndrome (EMS) in emerging fry, related to a thiamine deficiency resulting from a diet of alewife (Alosa pseudoharengus; Fitzsimons and Brown, 1998, Brown et al., 2005). However, alewife were not present in Lake Champlain until 2003, and did not reach substantial population numbers until 2007. In the spring of 2001, 150 eggs that were monitored until the absorption of their yolk sac showed no signs of EMS and had a 90% survival rate (Ellrott and Marsden, 2004). Eggs taken from 19 lake trout had an average total thiamine level of 11 nmol g\(^{-1}\); no total thiamine levels were below the EMS threshold of 4 nmol g\(^{-1}\) (Dale Honeyfield, USGS, unpublished data).

Predation may be a more influential process than starvation in driving variable recruitment levels of different fish species (Houde, 1987). Laboratory studies on the behavior of lake trout fry have shown that they have a propensity to vertically migrate into the water column at night, thereby increasing their vulnerability to predation by epi-benthic predators (Krueger et al., 1995, Baird and Krueger, 2000). Very little is known about the fate of lake trout fry in the wild after they emerge from spawning substrate. Stauffer and Wagner (1979) sampled native predators of lake trout fry by trawling adjacent to a lake trout spawning reef in Lake Superior. Although overall consumption of fry was considered to be minimal, fry predation was documented by yellow perch (Perca flavescens), sculpins (Cottus spp.), and burbot (Lota lota), and burbot were identified as the major predator of lake trout fry (0.2 fry per stomach). Population models for lake trout in the Great Lakes on near-shore reefs suggest that fry predation between 4 and 8 fry per m\(^2\) day\(^{-1}\) could significantly affect lake trout recruitment (Savino et al., 1999). In addition to predation by indigenous species, predation pressure from exotic alewives (Krueger et al., 1995) and smelt (Schneberger, 1936, Hassinger and Close, 1984) may contribute to the poor natural recruitment of wild lake trout. The effect of the overall fish community on the survival of lake trout fry has been identified by the Great Lakes Fishery Commission as a first order research priority for investigating restoration failures (Eshenroder et al., 1999). More specifically, Savino et al. (1999) suggested that “future studies should provide simultaneous measures of interstitial and fry predator densities, predation rates, predator duration, and prey densities.”

The goal of this study was to determine whether predation is a potential cause of the lack of wild recruitment of lake trout in Lake Champlain. The specific objectives of this study were to (1) identify the community assemblage of fry predators on shallow spawning reefs, (2) document how fry predation and predator relative abundances varied diurnally and throughout the period of fry hatch, (3) examine relationships between biotic variables that may affect levels fry predation, and (4) document the survival and dispersal rates of post-emergent lake trout fry off the spawning reef.

![Fig. 1. Study sites in Lake Champlain.](image-url)
Methods

Study sites

Data on relative abundance of lake trout fry and potential fry predators were collected at Grand Isle and Arnold Bay, Lake Champlain, in 2006, and solely at Grand Isle in 2007 (Fig. 1). Both of these sites were artificially constructed to protect a water intake pipe (Arnold Bay) and support a breakwall (Grand Isle). Arnold Bay is a small (189 m²), shallow (1–7 m) reef, with a slope of 60°, located in southern Lake Champlain (Ellrott and Marsden, 2004). The substrate is comprised of angular rubble and cobble ranging from 10 to 60 cm with an interstitial depth of 20 cm. The Grand Isle breakwall site, located in northern Lake Champlain, has 570 m² of spawning substrate at depths between 0.3 and 4 m, with a slope between 35 and 60° (Ellrott and Marsden, 2004). The angular rubble and cobble substrate ranges in size between 13 and 99 cm, with an interstitial depth of 15–86 cm.

Fry collection

Emergent fry traps were used to document the relative abundance of fry during the spring hatching period (Marsden et al., 1988, Chotkowski et al., 2002). In 2006, 10 traps were deployed at both Arnold Bay and Grand Isle on 13 April. Traps were checked at least once a week, and were retrieved from Arnold Bay on 31 May 06 and Grand Isle on 5 June 06. In 2007, 15 traps were deployed only at Grand Isle and monitored between 25 March and 5 June 07. For this study, “fry” refer to the development stage immediately after hatching through yolk-sac absorption and “post-emergent fry” refer to fry that have dispersed from their natal reef and are feeding exogenously.

Predator sampling

Potential fry predators were sampled using two different gillnets. A standard gillnet with a float line and lead line was fished on the bottom in the conventional orientation (i.e., with the long axis parallel to the substrate); the net had 4 panels, 7.3 m long by 1.90 m high, with 24 cm, 35 cm, 50 cm, and 164 cm stretch monofilament mesh. The second, “blanket” gillnet had two lead lines and no float line and was laid over the substrate to capture demersal predators actively feeding between the interstitial spaces within the reef. The blanket gillnet had five panels, 7.3 by 1.9 m, of 38 cm, 50 cm, 76 cm, 113 cm, 150 cm stretch monofilament mesh. Each set used one of each net type.

In 2006, gillnets were set for approximately two hours (to minimize digestion of fry) once per week, on the day fry traps were checked. The gillnets were mostly set 1 h before sunset and lifted 1 h after sunset; additional sets were made to identify additional periods of predator abundance. Of the eight sets at Arnold Bay between 20 April and 31 May 06, two sets were fished overnight and one set was fished from 1 h before sunrise to 1 h after sunrise. Of the eight sets at Grand Isle between 24 April and 5 June 06, the first set was overnight and one set was fished from 1 h before sunrise to 1 h after sunrise. Fish were immediately preserved on dry ice to reduce further digestion of stomach contents.

In 2007, predators were only sampled at Grand Isle. In order to sample all 24 h with at least two or more replicates each hour, a systematic schedule was implemented that focused sampling during the crepuscular hours, with at least one set during dusk and dawn in each week. Using the same gillnets described above, 46 2-h gillnet sets were conducted between 2 April and 8 June. Over the 10 week period, there was an average of four 2-h gillnet sets per week. Each captured fish was identified, weighed and measured (nearest mm TL) in the laboratory. All stomach contents were individually weighed and identified to order.

For this study, “potential predators” refers to any fish caught in gillnets, “confirmed predators” refers to fish that consumed fry, and the frequency of fry predation occurrence is the percentage of confirmed predators that consumed one or more fry.

Post-emergent fry sampling

Following the methods of Bronte et al. (1995) for capturing post-emergent fry on their nursery ground, we used a 5 m otter trawl with a 6 mm cod end lining. In 2006, we trawled along and across contour adjacent to the Arnold Bay and Grand Isle spawning sites to 60 m depth, with an average speed of 2.5 knots. We sampled for 443 min of bottom time (29.8 km) on 5 days between 30 May and 6 July 06 at Grand Isle, and 393 min of bottom time (35.4 km) on four days between 13 June and 19 July 06 at Arnold Bay. In 2007, we sampled for 433 min of bottom time (34.7 km) in three days between 11 June and 29 June 07, to 20 m depth, adjacent to the Grand Isle breakwall. On 24 July, we trawled for 162 min of bottom time (14.5 km) to a depth of 80 m in a deep trench south of the Grand Isle breakwall. All fish caught were counted, with a subset measured for total length. Captured lake trout were examined for fin clips.

Statistical analysis

All statistical analyses were conducted in SPSS (version 15.0) software with significance levels set at $\alpha = 0.05$ (SPSS Inc. 2006). A Pearson’s correlation was used to determine whether there was a relationship between fry abundance, consumption rates, and the frequency of fry predation occurrence. However, limitations of the data suggest that statistically significant relationships should be interpreted with caution. Fry abundance data were limited to one estimate per week. In an effort to sample all 24 h over the season, we were not able to sample the same hours each week. The sampling design did not allow for sufficient replicates between 21:00 and 07:00 to determine whether there was a period when predator presence or fry consumption were concentrated within the nocturnal period. In addition, only a small proportion of the total catch consumed fry.

Results

Fry collection

Lake trout fry were collected between late April and late May at Arnold Bay and Grand Isle in 2006, and until early June at Grand Isle in 2007. Average CPUE of fry was similar at Arnold Bay in 2006 (11 fry trap$^{-1}$ day$^{-1}$) and Grand Isle in 2007 (1.2 fry trap$^{-1}$ day$^{-1}$), but higher at Grand Isle in 2006 (4.7 fry trap$^{-1}$ day$^{-1}$).

Predator sampling

A total of 1179 potential predators were caught and dissected. In 2006, 311 fish of eight different species were caught at Arnold Bay, and 323 fish of 11 species were caught at Grand Isle (Fig. 2). Increased gillnetting efforts at Grand Island in 2007 captured 545 fish of 17 species (Fig. 2). The total catch was dominated by yellow perch and rock bass (Amblopites rupestris) which comprised 85% of the total catch in 2006 and 87% of the total catch in 2007 at Grand Isle. The two different gill net types did not affect the total catch or number of fish containing lake trout fry.

Seven species were documented to be lake trout fry predators in Lake Champlain (Fig. 2). At Arnold Bay in 2006, three species (yellow perch, rock bass, and white perch Morone americana) consumed a total of five fry (2, 1, and 2, respectively). A smallmouth bass (Micropterus dolomieu) was incidentally caught while electrofishing on the reef and two fry were found in its stomach. At Grand Isle, 35 predators (6.5% of total catch) contained a total of 96 fry in 2007 and...
17 predators (5.3% of total catch) contained a total of 63 fry in 2006. The common predators in both years were yellow perch, rock bass and burbot; in addition, two rainbow trout (Oncorhynchus mykiss) contained a total of eight fry in 2006 and one whitefish consumed 10 fry in 2007. The three most common predator species exhibited diverse consumption patterns (Fig. 3). A single rock bass consumed 8 fry but 68% of the 31 rock bass that consumed fry had only one fry in their stomach. In contrast, all five burbot that ate fry had more than one fry in their stomach (average 7 fry per stomach; Fig. 3). There was no clear consumption trend by yellow perch; a single yellow perch contained 17 fry, but 54% of the 13 yellow perch that ate fry only consumed 1 fry (Fig. 3).

A large proportion of fish that consumed lake trout fry did not have other items in their stomachs: 8 of 17 fish (47%) of fish at Grand Isle in 2006, 9 of 37 fish (24%) of fish at Grand Isle in 2007, and 3 of 5 (60%) fish at Arnold Bay in 2006. Additional prey items included gastropods, bivalves, crayfish, and insect larvae. When predators consumed fry and other prey items, fry comprised a small percentage of total stomach weight: on average, lake trout fry represented 33% of the stomach contents by weight at Grand Isle in 2006, 20% at Grand Isle in 2007, and 15% at Arnold Bay in 2006.

Temporal trends

In 2007 at Grand Isle, predator presence and fry consumption were heavily concentrated between dusk and dawn (Fig. 4). The average potential predator CPUE at Grand Isle was 9.6 fish h$^{-1}$ for gillnet sets between 19:00 and 07:00 ($N=29$ sets) versus 0.47 fish h$^{-1}$ during daytime hours ($N=17$ sets). Fry consumption only occurred between 19:00 and 07:00 (Fig. 4). We caught confirmed predators in 2-h gillnets centered on every hour from 19:00 to 07:00 except 02:00 and 03:00. This gap is likely due to the fact that those hours were sampled early in the season when fry abundance was very low, and we assume that fry are being consumed throughout the night. However, it is interesting that ten of the 35 confirmed predators in 2007 were caught during two gillnet sets from 04:00 to 06:00. In 2006 at Grand Isle, six of 17 confirmed predators were caught in the one dawn gillnet set from 05:00 to 07:00.

All three data sets of fry relative abundance (Grand Isle 2006 and 2007 and Arnold Bay 2006) indicated that fry hatched over approximately a 30–60 day period (Fig. 5). As the spring season progressed, predator abundance increased with fry abundance. In 2006 at Grand Isle, our second week sampling for predators coincided with the peak in fry relative abundance; thus, there were only two data sets sufficient for determining the relationship between fry and predator CPUE. The seasonal variation in fry relative abundance was not correlated with the frequency of fry predation occurrence and consumption rates, but did determine when predators began and discontinued consuming fry. The proportion of the total catch represented by rock bass and yellow perch did not change over the season. There was no significant relationship between the percentage of predators who consumed fry and the
relative abundance of fry during the 13 weeks when fry were consumed ($r(11) = -0.197, p < 0.519$). There was also no significant relationship between fry relative abundance and the number of fry consumed per predator ($r(54) = 0.008, p < 0.951$). No fry were consumed when fry abundance was below 1 fry trap$^{-1}$ day$^{-1}$ (Fig. 5). However, fry were consumed in 13 out of the 14 weeks when fry relative abundance was above 1 fry trap$^{-1}$ day$^{-1}$ (Fig. 5). Of the 57 confirmed predators, the highest consumption in three of the top four cases (17, 14 and 11 fry/stomach) occurred when the fry relative abundance was just above 1 fry trap$^{-1}$ day$^{-1}$.

**Post-emergent fry sampling**

No lake trout fry were caught while trawling in presumed nursery grounds adjacent to Arnold Bay and Grand Isle in 2006 and 2007. Eight juvenile (2 and 3 year old) lake trout were caught at Grand Isle, but they were all stocked (as denoted by a fin clip). Fourteen additional species ranging in size from 17 mm to 343 mm were caught while trawling. The frequently captured species (>4 individuals) were 1758 sculpins (*Cottus* spp.), 6 tessellated darters (*Etheostoma ohlmstedi*), 27 unidentified darters, 556 smelt, 52 spottail shiners (*Cyprinella spiloptera*), 97 trout-perch (*Percopsis omiscomaycus*), 97 trout-perch (*Percopsis omiscomaycus*), 87 trout-perch (*Percopsis omiscomaycus*), 6 white perch, and 1030 yellow perch. The sizes of the fish we caught overlapped with the size of 0+ lake trout and the species composition indicated that we were sampling on bottom, where we would expect lake trout young-of-year to be during the day (Bronte et al., 1995).

**Discussion**

Our data show that emergent lake trout fry are vulnerable to nocturnal predation by multiple epi-benthic littoral predators at two near-shore, shallow artificial spawning reefs in Lake Champlain. While the proportion of fish we collected that ate fry was low, the abundance and diversity of predator species may present a significant impediment to lake trout recruitment.

The results from this study confirm the observation of Krueger et al. (1995) and Baird and Krueger (2000) that the nocturnal movements of lake trout fry make them more vulnerable to epi-benthic predation at night, as we only noted nocturnal consumption. In contrast to Jansen and Mackay (1992), who found Eurasian perch (*Perca fluviatilis*) foraging only during the day, all of the fry predation by yellow perch occurred at night or very early in the morning. This is likely due to the local high abundance of a prey item, lake trout fry, which may be sufficient to overcome the relatively low efficiency of yellow perch prey detection in low light conditions (Janssen, 1997). The low catches of potential predators during the day may have been due to net avoidance; if this is the case, then diurnal predation could be a more significant factor than we observed.

We collected five species (rock bass, smallmouth bass, lake whitefish, white perch and rainbow trout) that have not previously been documented as predators of lake trout fry (reviewed by Jones et al., 1995). White perch is exotic to Lake Champlain, as is the stocked rainbow trout. Rock bass and yellow perch were the most common

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**Fig. 4.** Catch per unit effort (fish h$^{-1}$) for predators containing or not containing lake trout fry; predators were caught in two gillnets at Grand Isle, 2007. The value for each hour represents the middle of a 2-h set and the average CPUE from April 2 to June 8, 2007.

**Fig. 5.** Weekly predator CPUE (fish h$^{-1}$) and fry relative abundance (fry trap$^{-1}$ day$^{-1}$) for (a) Arnold Bay 2006, (b) Grand Isle 2006, and (c) Grand Isle 2007. The predator CPUE (bars) was the average of each gillnet set between 7 pm and 7 am during that week. Asterisks above the bars indicate that fry were consumed by predators during that week. The fry relative abundance (line) was recorded once a week. The horizontal dashed line denotes the threshold of fry relative abundance at 1 fry trap$^{-1}$ day$^{-1}$. 
predators and were the dominant species in the littoral community assemblage. Given both their high population abundance and ability to consume large numbers of fry, rock bass and yellow perch are likely the two species having the most impact on fry survival in Lake Champlain. Only 12 out of 745 rock bass and yellow perch caught in both years were smaller than the lower limit for piscivory by rock bass and yellow perch (100 mm), as reviewed by Mittelbach and Persson (1998).

The survival and recruitment of stocked lake trout has been negatively correlated with the presence of complex fish communities (Gunn et al., 1987, Evans and Oliver, 1995). Self-sustaining lake trout populations do coexist with littoral species; however, generally lake trout first colonize habitats and establish populations in the absence of late successional species (Evans and Oliver, 1995). The results from this study suggest that predation could be a mechanism impeding restoration in lakes where there has been a net gain in species or simply an anthropogenic reversal in the order of colonization by different fish species. As early colonizers on the top of the food chain, lake trout were presumably able to maintain an ecological balance through predation over nascent populations of emigrating or introduced warm-water species. Lake Superior has fewer invasive species and a lower species richness than the lower four Great Lakes and, perhaps coincidently, it is the only Great Lake with successful lake-wide lake trout restoration (Hansen et al., 1995, Eshenroder et al., 1999). It is of interest that lake trout, as an invasive species, are easily able to successfully colonize oligotrophic lakes (e.g., Yellowstone Lake; Ruzicky et al., 2003) with depauperate species abundance. Similarly, in the southern edge of their range lake trout tend to inhabit only large lakes, such as the Great Lakes and Lake Champlain, that have large, deep- and cold-water refuges from littoral communities. Recent anthropogenic influences, such as shoreline stocking and construction of attractive spawning habitats in shallow water, may be responsible for the presence of fry in littoral areas where fry survival is severely threatened by littoral predators.

Although we had a low total catch of other confirmed predators, rainbow trout, burbot, and whitefish all exhibited a higher number of fry per stomach than previously recorded for other species, including rainbow smelt (Schnepberger, 1936, Hassinger and Close, 1984), alewife (Krueger et al., 1995), sculpins, yellow perch, and burbot (Stauffer and Wagner, 1979). The observed 5% frequency of overall fry predation occurrence is similar to results in other studies; 3–6% by sculpin and 9.6% by alewives (Savin et al., 1999, Krueger et al., 1995). The sampling gear used in this study did not target interstitial fry predators and it is likely that there is additional predation pressure by sculpins and also crayfish in Lake Champlain (Stauffer and Wagner, 1979, Savino and Henry, 1991, Savino and Miller, 1991).

The large variety and relative weight of other prey items in predator stomachs suggests that the fish we sampled were not necessarily attracted to the reefs due to the presence of lake trout fry; these fish would normally be moving inshore in spring to begin post-winter feeding. It is of interest that a relatively large proportion of predators in each year consumed only lake trout fry; we also noted a similar pattern for other prey items, e.g., stomachs that contained large numbers of one species of snail, or Hexagenia. This focus on a single prey item within a foraging period may indicate that prey switching occurs when an optimal food item is found early in the night. Thus, lake trout fry may be incidental items in the diet of many predators, but may also be a focus of foraging by individuals on some nights.

There was evidence of a minimum threshold of fry abundance at which predators consumed fry. Fry were only preyed upon when their relative abundance was above one fry trap⁻¹ day⁻¹. In Parry Sound, fry relative abundance has never exceeded this threshold and there is recruitment of fry. Thus, there may be a density-dependence effect on fry, perhaps based on competitive exclusion from protective interstitial spaces that occurs at approximately one fry trap⁻¹ day⁻¹ and triggers predation. The abundance of potential predators rose with increasing fry abundance, but predators continued to be abundant after fry emergence declined. Increasing temperatures increase fish inshore movements in spring; however, while predators are directly affected by spring temperatures, the timing of lake trout fry emergence is influenced by temperatures in the fall and winter, which affect the timing of egg deposition and rate of embryonic development. A late fall, coupled with a cold winter and rapid warming from an early spring, could coincide the peak of fry emergence with increased predator presence and exacerbate the impact of predation on fry survival.

Given the relatively high fry abundances in Lake Champlain and the low frequency of fry predation occurrence, it is surprising that not a single 0+ lake trout was found while trawling adjacent to the spawning reefs. We used the same methods that successfully captured 0+ lake trout in Lake Superior and the trawling by-catch indicated that we were correctly targeting potential nursery grounds (Bronte et al., 1995). It is unlikely that competition for food is a factor in the absence of juveniles; laboratory experiments indicate that lake trout fry are intrinsically resistant to starvation, making them more likely vulnerable to predation (Edsall et al., 2003). Furthermore, Mysis relicta, an important food source for lake trout young, is abundant in the nursery area adjacent to Grand Isle. Regardless of whether predation is the “smoking gun” behind the lack of lake trout recruitment in Lake Champlain, results from this study have narrowed the scope of the recruitment bottleneck to the post-emergent fry stage.

Although predation is likely not the sole cause of the recruitment bottleneck in Lake Champlain, its effect is augmented by the location of spawning reefs in shallow habitats that have a high abundance and diversity of littoral predators. In addition, fry predation in Lake Champlain is likely to soon be affected by the recent introduction of alewives in 2003 (Bernie Pientka, Vermont Department of Fish and Wildlife, personal communication). In other bodies of water that have lower densities of eggs and fry, the levels of fry predation observed in Lake Champlain would have a more severe impact. A reduction in the quantity and diversity of alternative food sources and an increase in the temporal and spatial overlap of fry and their predators could also exacerbate the effect of predation on fry survival.

Stocked lake trout are attracted to spawning on shallow reefs, perhaps due to the unintended imprinting of hatchery rearing conditions (Marsden et al., 1995, Gunn, 1995). Predation by littoral epi-benthic species in Lake Champlain illustrates why onshore, shallow sites may be detrimental for fry survival. In addition to increased density and species richness of predators, these sites are exposed to zebra mussels, high wave currents, and anthropogenic influences on water quality that negatively affect egg and fry survival (Marsden et al., 1995, Marsden and Chotkowski, 2001, Janssen et al., 2007). Consequently, lake trout recruitment may be more successful if focused on deep/offshore spawning reefs, as suggested by Eshenroder et al. (1999) and Eshenroder and Krueger (2002).

Acknowledgements

This study was funded by the Great Lakes Fishery Trust. We would like to thank Jeff Jones and the crew of the Monitor and Dick Furush and the crew of the Melosira for their trawling support. We thank Alan Howard for providing statistical assistance. We also thank the individuals who assisted us in the lab and field during some bizarre hours: Josh Ashline, Chelsea Martin, Erika Partee, Mike Harrington and Steve Smith.

References
