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Effects of Egg and Fry Predators on Lake Trout Recruitment in Lake Michigan

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ABSTRACT

Lake trout (*Salvelinus namaycush*) restoration in the lower four Great Lakes has apparently been hampered by excessive mortality occurring between spawning and the first year of life. Review of the factors that affect lake trout egg and fry mortality suggests that predation on early life stages may be an important factor in lack of recruitment. We collected data on egg deposition densities, predator densities, and overwinter survival of eggs to hatching in Parry Sound, Lake Huron, where there is a self-sustaining population of lake trout, and Lake Champlain, where the status of restoration is unknown.. These data were compared with similar information from a parallel study in northern Lake Michigan. Egg deposition was lowest in Lake Michigan (0.4 – 154.5 eggs/m^2), intermediate in Parry Sound (39 – 1,027 eggs/m^2), and highest overall in Lake Champlain but with higher variation among sites (0.001 – 9,623 eggs/m^2). Fry collections in fry traps followed the same trend: no fry in Lake Michigan, 0.005 – 0.06 fry per trap day in Parry Sound, and 0.08 – 3.6 in Lake Champlain. Egg survival to hatch in overwinter egg bags was similar in Lake Michigan (7.6%) and Parry Sound (2.3 – 8.9%) in 2001-02, and varied in Lake Champlain (0.4-1.1% in 2001-02, and 1.8 – 18.2 in 2002-03). Predator densities were lowest at most sites in Lake Champlain, intermediate in Parry Sound, and highest in Lake Michigan. Egg seeding experiments showed that egg losses from the substrate were high, but were likely due to density-independent factors such as water movement. Laboratory experiments were conducted to compare egg consumption of native deep-and shallow-water predators (slimy and mottled sculpin, *Cottus cognatus* and *C. bairdi*) and a native vs. exotic crayfish (*Orconectes propinquus* and *O. rusticus*), using predator density, temperature, and predator species as co-factors. Temperature, intraspecific density, and interspecific effects did not significantly alter crayfish feeding rates. Comparison of data among the lakes indicates that lake trout restoration should be possible at current spawning levels in Lake Champlain, but is unlikely to occur at current adult stock sizes in northern Lake Michigan.

INTRODUCTION

Historically Lake Michigan had the highest production of lake trout of all of the Great Lakes. Yields were relatively constant from 1910 to 1945, but from 1946 to 1950, annual yield declined precipitously from approximately 3 million kilograms to 25 thousand kilograms. The presumed causes for this decline were lamprey predation, exploitation and habitat degradation (Eschmeyer 1957). Based on commercial catch reports, in the period leading up to the decline, nearly half of the entire catch came from the northeast section of Lake Michigan, suggesting that a high proportion of spawning reefs were also located there. Consequently, conditions at these spawning reefs must figure prominently in evaluations of the current lack of significant natural reproduction in Lake Michigan, a situation that exists despite the stocking of over 83 million lake trout in the last 35 years.

Nearly two thirds of the historic lake trout production in northern Lake Michigan came from offshore reefs, but the reasons why offshore reefs were more productive have not been identified (Dawson et al. 1997). In northern Lake Michigan, a large refuge area has been established that is now an important area protecting all age groups of lake trout. The U.S. Fish and Wildlife Service created a lake trout stocking plan in 1985 that incorporated a greater emphasis on stocking lake trout into refuge and primary rehabilitation zones in Lake Michigan. Revised stocking strategies and the existence of the refuge have not produced the anticipated increase in natural reproduction (Madenjian and DeSorcie 1999). Increasing adult lake trout populations in Lake Superior were associated with natural reproduction; in Lake Michigan, despite increasing adult lake trout populations, lake trout have yet to produce significant natural reproduction, suggesting that a bottleneck or bottlenecks exist elsewhere.

Current research suggests that the reason for the lack of lake trout recruitment is excessive mortality occurring between the time of spawning in the fall and the first year of life. At a GLFC sponsored conference in 1995, fisheries professionals reviewed several factors to determine their potential to affect lake trout reproduction (RESTORE; Krueger et al 1995). All of the factors discussed were relevant to Lake Michigan, including the level of stocking, size of the resulting population, egg deposition rates, contaminants in the eggs, thiamine deficiency, and egg and fry predators.

For significant natural reproduction to occur at a spawning reef and be measurable, sufficient numbers of males and females must congregate in the fall and deposit a sufficient number of fertilized eggs. Hatched fish must then develop over winter into successfully emergent fry. A range of adult abundance was measured at historic sites in northeastern Lake Michigan in the early 1990s (Dawson et al. 1997). Some sites were considered to have adequate numbers of adult spawners, based on a comparison with self-sustaining stocks in Lake Superior (Selgeby et al. 1995). However, it has not been determined whether significant spawning is occurring at these same sites. Sites located in northern Lake Michigan can provide an opportunity to identify potential bottlenecks and establish their relative importance.

Contaminant levels in Lake Michigan lake trout have been in decline for a number of years and Fitzsimons (1995) concluded that contaminant levels in eggs of lake trout had declined to the extent that acute toxicity would no longer be expected. The potential still exists, however, for sublethal effects. Similarly, a thiamine deficiency has been associated with early mortality syndrome (EMS; Fitzsimons et al. 1998, 1999, Brown et al. 1998), that averages 30% in southern Lake Michigan lake trout and close to 100% in northern Lake Michigan so is not sufficient to completely block reproduction.

Egg and fry predation has been a persistent but relatively unstudied concern that may be related to the lack of natural reproduction by lake trout in the Great Lakes including Lake Michigan. At the RESTORE conference it was concluded that biotic effects, like predation, should be considered a potential constraint to lake trout rehabilitation (Jones et al. 1995). The problem may be of increasing importance due to the recent addition of gobies and rusty crayfish to spawning reef fauna that already included native egg predators such as sculpins and crayfish. Recent modeling work suggests that there are three potential groups of egg and fry predators (Savino et al. 1999); epibenthic egg predators that consume eggs on the substrate surface during spawning, interstitial egg predators that can move in rock substrate and consume incubating eggs, and fry predators that consume pre-emergent and emergent fry in the spring. While modeling efforts have predicted that interstitial predators are most important, model predictions have never been verified in the wild. Moreover, the effect of interstitial predators is strongly dependent on the species of predator, predator numbers, the density of eggs, and the duration of predation, all of which are currently unknown for most lake trout spawning reefs in Lake Michigan. The model produced by Savino et al. (1999) concluded that there was a relatively small effect from fry predation on lake trout recruitment, although these authors were limited by a paucity of information available on lake trout fry predation. The importance of fry predation depends very much on the spatial-temporal overlap of lake trout fry and their predators, most notably alewives (Krueger et al. 1995). If alewives move onshore during lake trout emergence, losses to predation could be very high, but if alewives move onshore after emergence has occurred, losses may be quite low. The extent to which alewife feed on post-emergent fry is unknown. Additional challenges to the assessment of the relative importance of alewives as lake trout fry predators include knowledge of individual alewife consumption rates and alewife abundance levels. The product of consumption and abundance will equal the net consumption of fry in an area. The potential of alewives to consume lake trout fry is high. As many as 18 individual fry were found in the stomach of an alewife captured at a spawning reef in Lake Ontario during emergence, although most alewives appeared not to have eaten fry (J. Fitzsimons, unpublished data).

To address the impacts of egg and fry predators on lake trout recruitment, we compared egg, fry, and predator abundance among Lake Champlain, where most Great Lakes exotic predators (alewife, rusty crayfish, round goby) are absent, Lake Huron (Parry Sound), where lake trout are self-sustaining, and Lake Michigan. We used standard methods including gill-netting surveys, SCUBA surveys, egg collectors, and fry traps. Additional experimentation was conducted with seeded egg bags, exclosures, and laboratory tank studies. We assessed the adequacy of egg deposition and fry emergence at selected sites, relative to spawner abundance and relative to existing predator abundance and levels of physical disturbance. We also assessed the effect of temperature, predator abundance, and predator species composition on egg and fry consumption rates in the laboratory. We are currently synthesizing and integrating our findings into a predictive model that can be used to assess the importance of predators under various scenarios. This model will be supported by several summary reports from different aspects of the project.

OBJECTIVES

This work is linked with a project funded by the Great Lakes Fishery Trust that focuses on Lake Michigan. This project, funded by the Great Lakes Fishery Commission, was focused on collecting data on egg deposition densities, predator densities, and overwinter survival of eggs from two ‘control’ sites, Lake Champlain and Parry Sound, Lake Huron; these data will be compared with similar information from Lake Michigan. Specifically, the objectives of this proposal were:

1. Survey Lake Champlain for lake trout spawning sites.
2. Assess egg deposition and interstitial predator abundance at two sites in Lake Champlain and three in Parry Sound.
3. Conduct field sampling and field egg seeding experiments to measure egg losses in Lake Champlain and Parry Sound for comparison with Lake Michigan.
4. Measure fry emergence and relate to levels of egg deposition and survival.

5. Conduct laboratory experiments to compare egg consumption of native deep-and shallow-water predators (slimy and mottled sculpin, *Cottus cognatus* and *C. bairdi*) and a native vs. exotic crayfish (*Orconectes propinquus* and *O. rusticus*), using predator density, temperature, and predator species as co-factors.

RESULTS

1. Reconnaissance surveys of spawning reefs

Fifteen reefs in Lake Champlain, five in Parry Sound, and ten in Lake Michigan were surveyed by scuba divers. At each reefs we measured or recorded depth at top and base of the reef, reef area (defined by the area encompassed by cobbles), slope angle of the reef contour, substrate type, particulate substrate size, interstitial depth, presence of silt or organic debris, and presence of zebra mussels. Substrate at the majority of sites in all three lakes was adequate for attracting spawners and supporting egg incubation, based on comparison with previous studies. Data from these surveys are given in Appendices 1 and 2.

2. Assess egg deposition and interstitial predator abundance at two sites in Lake Champlain and three in Parry Sound.

We used egg bags buried into the substrate to acquire quantitative data on egg deposition and predator abundance in Lake Champlain and Parry Sound, and compared these samples with collections made in Lake Michigan. Overall we found the highest egg densities and lowest predator densities in Lake Champlain; densities of eggs and predators were intermediate in Parry

Sound, and in Lake Michigan egg densities were very low and predator densities were high (Appendices 2 and 3). Sculpins were more abundant in Lake Champlain than Parry Sound, whereas crayfish were less abundant in Lake Champlain than Parry Sound (Table 1). Lake Michigan had more predator species that the other lakes, and a higher proportion of exotic predators.

3. Conduct field sampling and field egg seeding experiments to measure egg losses in Lake Champlain and Parry Sound for comparison with Lake Michigan.

Egg seeding experiments were conducted in 2002 to estimate the depletion rates of trout eggs of varying densities when exposed to natural predator abundance, temperature and current regimes. To determine the level at which predators become satiated we planted eggs into 30 individually numbered egg bags at two sites in Lake Champlain, four sites in Parry Sound, and six sites in Lake Michigan. Bags at each site were randomly seeded with one of five densities (100, 250, 500, 1000, and 10,000 eggs/m^2) of trout eggs during the peak spawning period; five bags received each seeding density. The bags were retrieved approximately three weeks after seeding and processed within 24 hours. The proportion of eggs remaining to eggs seeded was determined. To distinguish a seeded egg from a naturally deposited lake trout egg, we seeded the bags with artificially pigmented lake trout eggs; lake trout broodstock was fed a high carotenoid diet, which produced an orange/red coloration in the eggs that was highly distinct from the yellow coloration in natural eggs.

Despite higher predator abundance at the Lake Michigan reefs, a greater predation effect was evident for the Parry Sound reefs with intermediate effects on the Lake Champlain reefs

(Appendix 4). We attribute this deviation from the expected direct relationship between predator density and predator effect to the generally lower levels of physical disturbance at the Parry Sound reefs that we suspect allowed more efficient egg foraging by predators. In contrast, egg recovery at the highest seeding density (5000 eggs$\cdot$m^{-2}), where egg recovery was relatively predator independent because of satiation, was directly related to wind fetch for Lake Michigan. We conclude that the high levels of physical disturbance in Lake Michigan cause high levels of egg loss, and potentially ameliorate overall losses by affecting egg predator foraging efficiency.

4. Measure fry emergence and relate to levels of egg deposition and survival.

Emergent fry traps were deployed at six sites in Lake Champlain, four sites in Parry Sound, and three sites in Lake Michigan over the three years of the project. We used two designs of surface-deployed traps, a traditional rigid fry traps and a modified design constructed of nylon fabric (Chotkowski et al. 2003). We also used a steel fry trap similar in design to the surface-deployed rigid trap, but deployed and checked by divers. Traps were checked approximately every 1-2 weeks throughout the fry emergence period.

Fry were collected at all sites in Parry Sound, five of six sites in Lake Champlain, and at none of the sites sampled in Lake Michigan. Catches per unit effort ranged from 0.08 to 3.6 fry/trap/day in Lake Champlain, and 0.005 to 0.06 fry/trap/day in Parry Sound (Appendix 2). The number of fry produced per 100 eggs was calculated using the quantitative estimates of egg deposition from egg bags, and ranged from 11.7-14.5% in Lake Champlain and 0.12 – 6.8 in Parry Sound (Appendix 2). These estimates presume that the collections of fry in fry traps represent a production of fry per unit area of the reef; since only the diver-checked fry traps remained in one place throughout the emergence period, we only used data from these traps to calculate fry-per-egg estimates.

Fry were also collected in egg bags left in the substrate over the winter in Lake Champlain. These bags were covered with fine-mesh lids in late fall, after the majority of spawning had been completed. Use of the bags allowed us to make a second estimate of percentage egg hatch, by comparing the mean number of fry in bags retrieved in spring to the mean number of eggs collected in bags in fall. Hatch estimates per 100 eggs were similar in Lake Michigan (7.6%) and Parry Sound (2.3 – 8.9%) in 2001-02, and lowest in Lake Champlain (0.4 – 1.1%; Appendix 2). Hatching was likely severely underestimated in Grand Isle, Lake Champlain, in 2001-02 due to the large number of eggs deposited in the bags; several bags were retrieved with masses of fungus resulting from infection of the closely-packed eggs. In a second year of sampling in Lake Champlain (2002-03), egg deposition was lower on Grand Isle, and an estimated 18.2% of the eggs hatched

5. Conduct laboratory experiments to compare egg consumption of native deep-and shallow-water predators (slimy and mottled sculpin) and a native vs. exotic crayfish (Orconectes propinquus), using predator density, temperature, and predator species as co-factors.

Laboratory experiments were used to test the effect of several variables on egg predation. We tested native predators (slimy sculpin *Cottus cognatus,* mottled sculpin *Cottus bairdi*), and a native crayfish (*Orconectes propinquus*) and two exotic species counterparts, round gobies (*Neogobius melanostomus*) and rusty crayfish (*O. rusticus*). Consumption by individual predators was tested at three temperature levels (4-5, 7-8, and 10-12^{0}C) for each of these species.

Predation by slimy sculpin, mottled sculpin, and round gobies was also tested at 1-2^0C. Three levels of predator density were tested in single-species tanks to establish the relationship between density and egg consumption. The levels of crayfish density were 3, 15, and 29/m^2, while the fish species were tested at 0.8, 4, and 8/m^2. Experiments were conducted at the Canada Centre for Inland Waters (CCIW) and the University of Vermont Rubenstein Ecosystem Science Laboratory.

Lake trout eggs and rainbow trout eggs (used as a surrogate when lake trout eggs were not available) were obtained from local state or federal fish hatcheries, and held in incubators until needed. Sculpins, gobies, and crayfish were obtained from the wild. All predators were held in tanks with shelters in the laboratory for 3-5 days prior to experimentation, to acclimatize them to captive conditions. Each predator was used only once. Prior to each experiment, predators were deprived of food for 24 hrs. Eggs were introduced to an aquarium at the start of an experiment at a density of 500 eggs/m^2, providing unlimited opportunities for predator consumption. The predators and substrate (if present) were removed after 7 days, and the remaining eggs were counted. Experiments were replicated six times.

Egg consumption by fishes was unaffected by temperature except for slimy sculpins, which ate more eggs at 10-11ºC than at 1-2ºC or 4-5ºC (Appendix 5). Both round gobies and slimy sculpins ate fewer eggs per individual at a density of 5 or 10 per tank than 1 individual per tank that was not compensated for by the higher predator density. There was no evidence of intraspecific competition between slimy sculpins and round gobies at various species combinations (10:0, 9:1, 5:5, 1:9, 0:10) at a density of 10 individuals per tank. Satiation appeared to regulate egg consumption under conditions of increasing egg density with little evidence of increased consumption at higher egg density.

Temperature had a significant effect only on the feeding rate of *O. rusticus* on rainbow trout eggs (Appendix 6). Egg consumption rate was significantly higher at low crayfish abundance (1 crayfish/tank) than at medium (5 crayfish/tank) or high (10 crayfish/tank) crayfish abundance for *O. rusticus*. Intraspecific predator density had no effect on the feeding rate of *O. propinquus*. The effect of interspecific predator density on rainbow trout egg consumption was explored by comparing feeding rates at high levels of crayfish abundance in single and mixed species treatments. Interspecific effects did not significantly alter crayfish feeding rates.

DISCUSSION

Previous work on lake trout restoration has focused on bottlenecks to survival during the stages between egg deposition and emergence. Our results provide comparative estimates of egg abundance, egg hatching success, fry abundance, and *in situ* egg mortality two Great Lakes and Lake Champlain, and represent a considerable improvement in our ability to assess the importance of egg predators. Our results suggest that, if we use Parry Sound as a benchmark for successful restoration of trout, then there is insufficient use of spawning reefs, insufficient spawner density, and egg densities are too low to support recruitment of lake trout in northern Lake Michigan. Lake trout assessment data indicate that adult stocks are too low in northern Lake Michigan for restoration to occur. Stocking rates may be too low in the northern lake to build sufficiently large adult populations, or mortality may be too high. In contrast to Lake Michigan, in Lake Champlain the spawning reef use, adult densities, egg densities, and fry hatch are high enough, or considerably higher, than is needed to support recruitment. The absence of large numbers of unclipped fish in the adult population suggests that there are sources of high mortality beyond fry emergence; these sources of mortality may also be present in other lakes. Predator densities were highest in Lake Michigan, and predator communities in this lake were dominated by recently introduced exotic species, the rusty crayfish and the round goby. Exotic species provide a unique challenge to rehabilitation efforts, as their interactions within the community are poorly understood. Our laboratory egg consumption data, combined with field data on egg density and predator abundance, provide important inputs to modeling efforts that may ultimately enable managers to predict whether spawning activity is sufficient in a given system to support natural recruitment of lake trout.

LITERATURE CITED

Brown, S.B., Fitzsimons, J.D., Palace, V.P., Vandenbyllaardt, L., and Klaverkamp, J.F. 1998. Thiamine and early mortality syndrome in lake trout (*Salvelinus namaycush*). In: McDonald, G., Fitzsimons, J.D., Honeyfield, D.C. (Eds.). Early life stage mortality syndromes in fishes of the Great Lakes and Baltic Sea. Trans. American Fisheries Society, Bethesda, MD 20814, pp. 18-25.

Chotkowski, M. A., J. E. Marsden, and B. J. Ellrott. 2003. An inexpensive modified emergent fry trap. N. Am. J. Fish. Manage. 22:261-164.

Dawson, K. A., R. L. Eshenroder, M. E. Holey and C. Ward. 1997. Quantification of historic lake trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. Can. J. Fish. Aquat. Sci. 54: 2290-2302.

Eschmeyer, P. H. 1957. The near extinction of lake trout in Lake Michigan. Trans. Am. Fish. Soc. 85:102-119.

Fitzsimons, J. D. 1995. A critical review of the effects of contaminants on early life stage (ELS) mortality of lake trout in the Great Lakes . J. Great Lakes Res. 21 Suppl. 1:267-276.

Fitzsimons, J.D., and Brown, S. B. 1998. Reduced egg thiamine levels in inland and Great Lakes lake trout and their relationship with diet. In: McDonald, G., Fitzsimons, J.D., D.C. Honeyfield, D.C. (Eds.). Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea. American Fisheries Society Symposium 21, Bethesda, MD, pp. 160-171.

Fitzsimons, J.D., Brown, S.B, Honeyfield, D.C., and Hnath, J.G. 1999. A review of early mortality syndrome (EMS) in Great Lakes salmonids: Relationship with thiamine deficiency. Ambio 28, 9-15.

Jones, M. L., Eck, G.W., Evans, D.O., Fabrizio, M.C., Hoff, M.H., Hudson, P.L., Janssen, J., Jude, D., O'Gorman, R., and J. F.Savino.1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages J. Great Lakes Res. 21 Suppl. 1:505-517.

Krueger, C.C., Jones, M.L., and W. W. Taylor. 1995. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management . J. Great Lakes Res. 21 Suppl. 1:547-558.

Madenjian, C. P., DeSorcie, T. J. 1999. Status of lake trout rehabilitation in the northern refuge of Lake Michigan. N. Am. J. Fish. Manage. 19:658-669.

Savino, J. F., P. L. Hudson, M. C. Fabrizio and C. A. Bowen. 1999. Predation on lake trout eggs and fry: a modeling approach. Great Lakes Res. 25: 36-44.

Selgeby, J.H., Bronte, C.R., Brown, E.H., Hansen, M.J., Holey, M.E., Vanamberg, J.P., Muth, K.M., Makauskas, D.B., Mckee, P., Anderson, D.M., Ferreri, C.P., and S.T. Schram. 1995. Lake trout restoration in the Great Lakes: Stock-size criteria for natural reproduction . J. Great Lakes Res. 21 Suppl. 1:498-504.

List of Appendices

Appendix 1. Ellrott, B. J. and J. E. Marsden. Lake trout reproduction in Lake Champlain. (manuscript in press., Trans. Am. Fish. Soc.)

Appendix 2. Marsden, J. E., B. J. Ellrott, J. Jonas, R. Claramunt, and J. Fitzsimons. A comparison of lake trout spawning, emergence, and habitat use in lakes Michigan, Huron, and Champlain.

Appendix 3. Jonas, J. L., R. M. Claramunt, J. F. Fitzsimons, J. E. Marsden and B. J. Ellrott. Estimates of abundance and the effect of lake trout egg predators on egg survival for Lakes Michigan, Huron (Parry Sound), and Champlain.

Appendix 4. Fitzsimons, J., B. Williston, G. Fodor, J. L. Jonas, R. M. Claramunt, J. E. Marsden, B. J. Ellrott, and D. C Honeyfield. Assessing the effects of physical disturbance and egg predation on lake trout egg mortality and its application to Lake Michigan.

Appendix 5. Fitzsimons, J., B. Williston, G. Fodor, G. Bravener, J. L. Jonas, R. M. Claramunt, J. E. Marsden, and B. J. Ellrott. Salmonine egg predation by round gobies, mottled and slimy sculpins, and crayfish (*Orconectes propinquus*): factors affecting laboratory derived predation rates.

Appendix 6. Ellrott, B. J., J. Fitzsimons, and J. E. Marsden. Effects of temperature and density on consumption of trout eggs by *Orconectes propinquus* and *O. rusticus*.

Lake trout reproduction in Lake Champlain

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Abstract

Native lake trout (*Salvelinus namaycush*) were driven to extirpation in Lake Champlain in the early 1900s. Possible causes of extirpation include overharvest, predation on adults by sea lamprey (*Petromyzon marinus*) , and predation on fry by rainbow smelt (*Osmerus mordax*). Efforts to restore a lake trout fishery began in 1972 when a coordinated lake trout stocking program was initiated. Attempts to control sea lamprey populations began in 1990. Despite these management actions, reproduction by stocked fish has not produced large naturally-produced year classes. This is the first formal study to quantitatively assess the level of natural reproduction by lake trout in Lake Champlain. In 2000 through 2002, we located 14 potential lake trout spawning sites and evaluated habitat characteristics and level of spawning activity at each site. Passive egg collectors revealed that eggs were deposited at 8 of 14 sites, with egg abundance ranging from 1.9 to 9,623 eggs/m^2. In 2001 and 2002, lake trout fry were collected in emergent fry traps at three of five sites; catch per unit effort ranged from 0.08 to 2.38 $\text{fry} \cdot \text{trap}^{-1} \cdot \text{day}^{-1}$. We were unable to collect naturally-produced juvenile lake trout through bottom trawling. We also examined adult lake trout size structure and abundance data collected annually by state agencies to determine if a trend existed in the percentage of unmarked lake trout in the population. The percentage of unclipped lake trout in Lake Champlain decreased steadily from 1982 (7.4%) to 1988 (1.7%), was variable from 1989 to 1991, then increased from 1992 (2.6%) to a maximum in 2000 (10.4%). The percentage decreased to 5.7% in 2001. The high levels of egg and fry abundance, the failure to collect lake-produced juveniles, and the low percentage of unclipped adult fish all suggest a recruitment bottleneck is present during the post-emergent fry life stage.

Introduction

Lake Champlain supported self-sustaining populations of lake trout (*Salvelinus namaycush*) prior to and during the 19th century when the Lake Champlain valley was settled and developed (Plosila and Anderson 1985). A commercial fishery was not present, though lake trout populations were large enough to allow seine harvests of spawning stocks during the fall. In the mid- to late 1800s, lake trout populations began to decline in Lake Champlain and became extinct by 1900 (Plosila and Anderson 1985). No data were collected on population characteristics or abundance prior to and during the period of decline.

Lake trout populations also underwent catastrophic collapses throughout most of the Great Lakes during the 19th and 20th centuries (Hansen 1999), but in contrast to these declines, the reasons for the population crash in Lake Champlain are poorly understood. It is generally accepted that a combination of overharvest, sea lamprey predation (*Petromyzon marinus*), and cultural eutrophication caused lake trout populations to crash throughout the Great Lakes basin (Eschmeyer 1957; Eshenroder 1992; Cornelius et al. 1995; Elrod et al. 1995; Hansen et al. 1995). Possible explanations for the decline of lake trout in Lake Champlain include overharvest (Plosila and Anderson 1985), predation by rainbow smelt (*Osmerus mordax*) (Halnon 1963), and predation by sea lamprey, but historical data do not exist to support or refute these explanations for Lake Champlain. A commercial lake trout fishery did not exist in Lake Champlain and subsistence fishing in the 1800s probably had no significant impact on lake trout populations considering there were sparse human populations and the fishing methods (seine) employed were inefficient at the depths at which lake trout are generally found. Rainbow smelt are native to Lake Champlain and co-evolved with lake trout, suggesting that rainbow smelt predation on lake trout was not likely to have caused the lake trout population to decline. Sea lamprey populations were described as common and abundant in Lake Champlain in the early to mid-1800s (Halnon 1963). It is unclear whether sea lampreys are native or exotic to Lake Champlain and this is currently a topic of substantial debate. If sea lampreys are native, they would have entered Lake Champlain approximately 10,000 years ago and have co-existed with lake trout. If they are exotic to Lake Champlain, they would have entered in the mid- to late 1800s, after construction of the Champlain and Chambly canals, and may have been a significant factor in lake trout population declines. However, anecdotal evidence suggests that sea lamprey populations were at low levels in the late 1800s when lake trout populations were declining, because forestry practices made tributaries unsuitable for sea lamprey reproduction (B. Chipman, Vermont Department of Fish and Wildlife, personal communication).

The first attempts to restore lake trout in Lake Champlain took place in the late 19th century. Sporadic stockings were unsuccessful in re-establishing naturally reproducing populations (Plosila and Anderson 1985). In the late 1950s and the 1960s, the New York State Department of Environmental Conservation (NYSDEC) and the Vermont Department of Fish and Wildlife (VTDFW) stocked limited numbers of lake trout. This stocking attempt was successful in developing a small lake trout fishery, but also failed to produce a self-sustaining lake trout population. Stocking levels increased in 1973 when the NYDEC, the VTDFW, and the United States Fish and Wildlife Service (USFWS) signed an agreement to form the Lake Champlain Fish and Wildlife Management Cooperative (LCFWMC). A primary goal of the cooperative was to re-establish a lake trout fishery in the lake. In the absence of information about historic stock characteristics, the goals of the restocking program focused on re-establishing a fishery rather than restoring a lake trout population. The specific objective developed by the cooperative in 1977 was to "Re-establish a lake trout fishery by 1985 that will annually provide at least 45,000 additional man-days of fishing with an approximate yield of 18,000 lake trout averaging 5 pounds each." (Fisheries Technical Committee 1977) Since 1973, nearly 5 million lake trout have been stocked; annual stocking rates have been variable and range from 39,000 to 271,863 yearling equivalents (5 fall fingerlings = 1 spring yearling) (Fisheries Technical Committee 1999; Figure 1). Stocking rates were decreased by approximately half in 1995 after bioenergetics modeling suggested that the higher stocking levels coupled with increased survival from the experimental sea lamprey control program could potentially cause the rainbow smelt forage base to crash (LaBar 1993). Since this reduction, annual stocking rates have stabilized between 68,000 and 90,000 yearlings. Several different lake trout strains have been stocked including the Adirondack (Raquette Lake, Lake George), Finger Lakes (Seneca Lake), Lake Michigan (Green Lake), Manitoba (Clearwater), Lake Superior (Marquette), Maine (Allagash Lake), and Jenny Lake (Wyoming) (Fisheries Technical Committee 1999). More recently, a "Lake Champlain" strain, progeny of feral lake trout from Lake Champlain, has been produced and stocked (Figure 1). Since 1990, only the Seneca Lake and Lake Champlain strains have been stocked in the system; these strains were selected because the Seneca Lake strain may be more resistant to sea lamprey attacks than other strains (Swink and Hanson 1996), and the Lake Champlain strain was primarily produced from Seneca Lake strain parents.

A second strategy to increase lake trout populations involved controlling populations of sea lamprey. An eight-year experimental sea lamprey control program was initiated in 1990, and used larval lampricides applied to 13 tributary systems and 5 deltas (Marsden et al., in press). The program reduced wounding rates (Type AI-AIII) of stocked lake trout and consequently increased survival. Prior to sea lamprey control, wounding rates were greater than 50%; during the period of experimental sea lamprey control, wounding rates fluctuated between 30 and 50%

(Marsden et al., in press). Sea lamprey control increased mean survival rate of age-3 to 4 lake trout from 0.35 to 0.43 and age-5 to 9 from 0.51 to 0.59; this mortality rate includes the fisheries exploitation rate, which varied from 0.11 to 0.14 between 1991 and 1997 (Fisheries Technical Committee 1999, Marsden et al., in press). Stocked lake trout have established a recreational fishery that has exceeded the management goal set by LCFWMC in 1977. In summer gillnetting conducted by LCFWMC from 1982 to 1997 (see methods), CPUE (fish/net) ranged from 3 to 11 and multiple year classes of sexually mature (>age-5) fish were collected each year (Fisheries Technical Committee 1999). Since 1991, repeat spawners (⩾ age-7) have represented between 19 and 47% of all lake trout sampled. However, reproduction by these fish has not contributed significantly to the adult population.

It is unlikely that the same impediments to lake trout rehabilitation in the Great Lakes are occurring in Lake Champlain. Adult stock size appears to be adequate; Selgeby et al. (1995) developed stock-size criteria for the Great Lakes and determined that areas with recruitment of age-1 and older lake trout had a CPUE in fall gillnets of 17-135 fish/305 m. In Lake Champlain, sampling with gillnets was conducted in summer, when lake trout are more highly dispersed; nevertheless, the equivalent catch was 7.5 to 27.5 fish/305 m of gillnet, partially within the range of naturally reproducing populations analyzed by Selgeby et al. The failure of lake trout to reproduce in the Great Lakes has been attributed to the accumulation of contaminants by lake trout (Mac and Edsall 1991). Madenjian et al. (2001) reviewed research on the role that contaminants may have played on lake trout reproductive success and concluded that contaminants have had very little effect on lake trout recruitment in Lake Michigan. Contaminant concentrations in Lake Champlain lake trout (R. Langdon, Vermont Department of Environmental Conservation, unpublished data) are lower than recent concentrations found in

Lake Michigan lake trout (Madenjian et al. 2001) and therefore are unlikely to inhibit natural recruitment of lake trout in Lake Champlain. The lack of genetic diversity in stocked lake trout populations is also considered an important constraint to lake trout rehabilitation in the Great Lakes (Burnham-Curtis et al. 1995). Natural reproduction may be enhanced when genetic diversity is maximized by stocking multiple strains and appropriate strains are matched with stocking locations (Burnham-Curtis et al. 1995; Perkins et al. 1995). In the 1970s and 1980s seven different lake trout strains were stocked into Lake Champlain, including strains from the Great Lakes and Finger Lakes of New York. The Seneca Lake strain, which was stocked in the highest frequency, has shown consistent reproductive success lakewide in Lake Ontario (Grewe et al. 1994). Early mortality syndrome (EMS) is another important source of lake trout mortality in the Great Lakes that is absent in Lake Champlain. EMS is linked to a diet high in exotic alewife (*Alosa pseudoharengus*) that contain high levels of thiaminase (Fitzsimons 1995a). Alewives are not present in Lake Champlain and the main forage fish, rainbow smelt, contain approximately one-half the level of thiaminase found in alewives (J. Fitzsimons, Canadian Center for Inland Waters, personal communication). Native lake trout in Lake Champlain were self-sustaining with a diet of native smelt, as there are few other forage species in the lake; the decline of Great Lakes lake trout did not occur for almost six decades after the introduction of smelt into the lakes in the 1920s and 1930s (Christie 1974). In the spring of 2001, approximately 150 lake trout sac-fry were collected from the Grand Isle breakwall and held at the Grand Isle Fish Hatchery until the yolk sac was fully absorbed; fry survival was greater than 90% and no signs of EMS were detected (D. Marchant, VTDFW, personal communication). Jones et al. (1995) developed a quantitative model of lake trout egg and fry predation and concluded that predation mortality could block natural recruitment, especially in systems where exotic predators have become established. To date, Lake Champlain has had no additions of known lake trout egg or fry predators.

Despite the efforts of managers to increase lake trout populations in Lake Champlain, lake trout have not re-established self-sustaining populations. Since the mid-1980s, adult lake trout in Lake Champlain have exhibited typical spawning behavior by aggregating during autumn at sites with appropriate spawning substrate (B. Chipman, VTDFW, personal communication), i.e., clean rock substrate with deep interstitial spaces. However, prior to this study there was no attempt to confirm lake trout natural reproduction at these sites. The goal of this study was to determine the level of lake trout natural reproduction in Lake Champlain. The objectives were to: 1) identify potential lake trout spawning sites, 2) intensively assess lake trout reproductive success (egg deposition, fry hatch, and fry survival) at identified sites, and 3) evaluate the contribution of unclipped lake trout to the juvenile and adult population.

Methods

Lake description

Lake Champlain forms the boundary between Vermont and New York and extends north into the Canadian province of Quebec (Figure 2). The lake is 193 km long, has a maximum width of 19 km, and a surface area of 1,127 km^2 (Lake Champlain Basin Program 1999). The mean depth is 19.5 m and the maximum depth is approximately 120 m; the main basin of the lake is primarily meso- to oligotrophic (Lake Champlain Basin Program 1999).

Assessment of unclipped lake trout

Annual assessment surveys for adult lake trout have been conducted since 1982 by VTDFW and NYDEC. From 1982 to 1997, the surveys were conducted during June, July, and August using nylon multifilament gill nets 122 m long and 1.8 m deep. Gill nets were composed of eight 15-m panels of different stretch mesh sizes (64, 76, 89, 102, 114, 127, 140, and 152 mm) and were fished for 24 hours. Age-4 and older (>400 mm) lake trout are fully selected to the gear while age-3 fish (<400 mm) are only partially selected (Fisheries Technical Committee 1999). Beginning in 1989, state agencies started fall electrofishing surveys to provide a second index of population abundance, size and age structure. In 1997, agencies converted from summer gillnetting to electrofishing only. Because all lake trout stocked into Lake Champlain are marked with a fin clip, an individual fish is assumed to be naturally produced if it has no fin clips. However, unclipped fish may also include those that were mistakenly not clipped prior to stocking or regenerated the clipped fin and were not recognized as clipped. The surveys provided an extensive data set to evaluate the proportion of unclipped age-3 and older lake trout and changes in abundance, age, and size structure through time.

Spawning site surveys

In the summers of 2000 and 2001, we located potential spawning sites using bathymetric charts, observations of shoreline geology, scuba observations, remotely operated video, and discussions with Lake Champlain fisheries biologists. We were seeking sites with habitat characteristics believed to be important for lake trout spawning including: cobble or boulder substrate, deep (>10 cm) interstitial spaces, low amounts of silt present, and adjacency to a steep slope (Marsden et al. 1995; Fitzsimons 1995b). Cobble is defined as particles with diameters of

25.7 to 99.9 cm; particles larger than cobbles are defined as boulders, as used in previous examinations of lake trout spawning habitat (Marsden et al. 1995). Spawning habitat quality and lake trout spawning levels were evaluated at selected sites. Variables measured to evaluate spawning habitat quality included reef depth, reef slope, substrate size, and interstitial depth. The approximate area of spawning sites was estimated using a combination of measurements of reef dimensions conducted by divers with a 100 m measuring tape, and visual estimates of small areas by divers. Divers made visual observations of the relative abundance of macrophytes and zebra mussels (*Dreissena polymorpha*), and estimated abundance of egg and fry predators such as sculpins (Cottidae) and crayfish as frequency of sightings of each species observed while burying egg bags, or surveying a reef. These observations provided a crude estimate of relative abundance.

Lake trout spawning activity assessment

Once potential spawning sites were identified we assessed egg deposition in fall of 2000 and 2001 using quantitative and qualitative passive egg collectors. The qualitative egg collection gear consisted of 15 egg nets (Horns et al. 1989) and 15 egg traps (Marsden et al. 1991) attached alternately 1 m apart to a 30-m line with anchors and buoys at each end. The gangs of traps and nets were deployed in early fall just prior to spawning and checked for the presence of eggs weekly until spawning was finished. The quantitative egg collectors (bags) consisted of a 45.7-cm deep cloth bag (3-mm mesh) attached to a 29.8 cm diameter PVC ring (Perkins and Krueger 1994). Scuba divers buried the bags by excavating a 40-50 cm deep pit, placing an individual bag into a pit, and backfilling the bag with the removed substrate. Egg bags were buried prior to spawning (August-October) and were retrieved when spawning was believed to have finished (late November-early December). During the 2000 spawning season, five sites were sampled using one gang of the qualitative egg collectors (15 traps and 15 nets) per site. Additionally, a remotely operated vehicle (ROV) equipped with a suction sampler was used in a related study to explore for lake trout spawning in deep water. In 2001, 10 sites were sampled using quantitative egg collectors and two sites were sampled using qualitative egg collectors. Eggs collected from each site were counted and preserved in Stockard's solution. Empty egg shells (chorions) also supplied evidence of the presence of eggs, and were counted and included with egg totals.

A subset of sites where lake trout deposited eggs were sampled for fry in the spring of 2001 and 2002 using two types of surface deployed qualitative emergent fry traps. A rigid steel trap (Marsden et al. 1988) and a similarly designed nylon mesh trap (Chotkowski et al. 2002) were deployed from ice-out (April) through mid-June. In 2001, fry sampling was conducted at the Grand Isle breakwall, Whallon Bay, Ore Den Bay, and Arnold Bay. In 2002, fry sampling was conducted at the Grand Isle breakwall, Saxton Cove, Whallon Bay, and Arnold Bay. Each site was sampled with 7 to 20 traps that were checked weekly for the presence of fry.

Juvenile lake trout sampling

In summer of 2001, we used a bottom trawl (7.62 m headrope, 6.35 mm stretched-mesh cod end) to sample for yearling and older lake trout at Shelburne Bay, Whallon Bay, and Willsboro Bay. Sampling occurred on May 18 and July 18, 2001 at Shelburne Bay, on July 18, 2001 at Whallon Bay, and on August 16, 2001 at Willsboro Bay. Depths sampled ranged from 15 to 40 m. The duration of bottom trawling at 2.2 knots was 79 minutes at Shelburne Bay, 26 minutes at Whallon Bay, and 70 minutes at Willsboro Bay. All lake trout captured were examined for fin clips, measured for total length, and then released.

Results

Assessment of unclipped lake trout

The percentage of unclipped lake trout in Lake Champlain decreased steadily from 1982 (7.4) to 1988 (1.7), fluctuated from 1989 to 1991, and increased from 1992 (2.6) to 2000 (10.6) (Figure 3). In 2001, the percentage decreased to 5.7.

Spawning site surveys

Since the mid-1980s, New York and Vermont state biologists have observed large aggregations of adult lake trout at two sites (Grand Isle breakwall and Whallon Bay) during the fall, providing indirect evidence of spawning. In 1998 and 1999, preliminary studies (JEM, unpublished data) sampled eggs and fry at the Grand Isle breakwall and Whallon Bay, confirming spawning activity at these sites. The Grand Isle breakwall consists of angular cobbles and boulders 13 to 105 cm in diameter, piled 15 to 86 cm deep on a 35 to 60^0 slope (Table 1). In fall, the water depth above the cobble substrate ranges from 0.3 to 5 m. The area of cobble is approximately 570 m^2. Whallon Bay has round substrate composed of natural, rounded cobble and boulder ranging from 17 to 106 cm in diameter with interstitial spaces 4 to 29 cm deep (Table 1). Whallon Bay is a moderately sloping, north facing shoreline, approximately 64,372 m^2 in area, and ranges from 0.3 to 14 m in depth.

Four sites in 2000 and 8 sites in 2001 were chosen as potential lake trout spawning areas (Figure 2, Table 1). Burlington breakwall (north and south), Willsboro Bay, Saxton Cove, Iron Bay, Ore Den Bay, and Arnold Bay are artificial sites either intentionally created to protect water intake pipes or to construct piers, or unintentionally created through mining or railroad construction. Shelburne Point, Allen Hill, Cannon Point, Thompson’s Point, and Button Bay are sites composed of natural rock materials. In total, 14 sites were evaluated for biotic and abiotic habitat characteristics and for assessment of lake trout spawning (Table 1). Macrophytes were sparse or absent at all sites except Iron Bay, Ore Den Bay, and Button Bay. Egg and fry predator abundance was observed to be low at most sites (< 5 predators/m^2). Zebra mussel abundance was moderate to dense at all sites except the two Burlington breakwall sites and Cannon Point. At moderate densities zebra mussels covered over 90% of hard surfaces in at least a single layer, and at higher densities they formed colonies several individuals thick over all hard surfaces.

Lake trout spawning activity assessment

Egg deposition occurred at 8 of 14 sites sampled in 2000 and 2001. In 2000, eggs were collected at 4 of 5 sites from November 13 to December 11 (Table 2). Catch per unit effort ranged from 0.002 to 4.08 $\text{eggs} \cdot \text{trap}^{-1} \cdot \text{day}^{-1}$. Eggs were collected at a rate of 14.5 per minute from one additional site (Ore Den Bay) using a suction sampler mounted on a remotely operated vehicle. In 2001, eggs were collected from 6 of 12 sites sampled. Mean egg density at sites where eggs were collected was lowest at Iron Bay (1.9 ±1.3 SE eggs/m^2) and highest at Grand Isle (9,623 ±1,658 SE eggs/m^2). Chorions comprised less than 12.1% of the collections at any site and was less than 4% at most sites.

In 2001, fry were caught at three of four sites (Grand Isle breakwall, Whallon Bay, and Arnold Bay) from the beginning of the sampling period to the second week in June (Table 3). Total CPUE ($\text{fry} \cdot \text{trap}^{-1} \cdot \text{day}^{-1}$) among these three sites was highest at Arnold Bay (2.38), intermediate at the Grand Isle breakwall (0.33), and lowest at Whallon Bay (0.14). Ten fry traps were set at Ore Den Bay and yielded no fry.

In spring 2002, fry were collected from three of four sites sampled. Fry CPUE remained high at Arnold Bay (1.73), intermediate at the Grand Isle breakwall (0.32), and lowest at Whallon Bay (0.08).

Juvenile lake trout sampling

In 175 minutes of bottom trawling at 2.2 knots, we collected 11 clipped and zero unclipped lake trout. All 11 fish were collected from Shelburne Bay at a rate of 0.14 fish/min bottom time and ranged from 217 to 396 mm total length. No lake trout were collected from either Whallon Bay or Willsboro Bay.

Discussion

This is the first formal study of lake trout spawning activity in Lake Champlain. Our survey of lake trout spawning habitat revealed the presence of multiple artificial and natural reefs with substrate suitable for egg incubation. With the exception of Willsboro Bay, Iron Bay, and Ore Den Bay, where human-deposited cobble extended down steep slopes to depths up to 20 m, all of the spawning substrate was in shallow water (< 8 m). Lake charts and anecdotal information from lake biologists suggest that there are additional sites not examined in the present study that have appropriate lake trout spawning habitat; with the exception of the Grand Isle site, we focused our work only on the middle third of the lake. Based on this information, the availability of spawning habitat does not appear to limit lake trout production.

Lake trout spawned at several sites throughout the main lake, with relatively high rates of egg deposition at three locations compared to the Great Lakes. Lake trout egg deposition in Lake Champlain is an order of magnitude greater than in Parry Sound, Lake Huron where the lake trout population is considered to be restored based on several criteria (Reid et al. 2001). Maximum CPUE (eggs · $trap^{-1}$ · day^{-1}) using egg nets and traps was 4.08 in Lake Champlain, whereas the maximum CPUE from lakes Superior (0.06), Michigan (0.07), Huron (0.46), and Ontario (0.45) were much lower (Schreiner et al. 1995). Extremely high lake trout egg deposition occurred at the Grand Isle breakwall in 2001; mean egg density was 9,623 eggs/m^2 compared to mean densities of 6,178 at Burlington Pier, Lake Ontario (Fitzsimons 1995b) and 4,250 at Stony Island, Lake Ontario (Perkins and Krueger 1995). Mean egg density (eggs/m^2) among all sites using egg bags was 2,273 (mean = 436 excluding the Grand Isle breakwall) in Lake Champlain, 30.1 in Lake Superior (Kelso et al. 1995), 1,150 in Lake Ontario (Fitzsimons 1995b), 221.7 in Parry Sound, Lake Huron (J. Fitzsimons, Canadian Center for Inland Waters, unpublished data), and 17.8 in Lake Michigan (J. Jonas and R. Claramunt, Michigan Department of Natural Resources, unpublished data).

Artificial reefs comprised over half of the spawning sites we located; eggs were collected at five of eight artificial sites and three of six natural sites. Ore Den Bay and Iron Bay are adjacent to abandoned iron mining sites where large quantities of mine tailings have trickled down steep shorelines into the bays. Both sites have steep slopes and deep interstitial spaces. Hatching may be compromised at these sites as dense macrophyte beds develop during the summer and decompose over the winter, contributing organic matter to the substrate. Low egg densities at both sites and the failure to collect fry at Ore Den Bay suggest that these sites are relatively unproductive compared to other spawning sites within the lake. The Arnold Bay site is a small cobble crib covering a water intake line used as a lake trout stocking site from 1989 to 1994. It is unknown whether lake trout show spawning site fidelity, however, considerable evidence suggests that fish in general recognize and return to specific sites when displaced

(Dodson 1988; Gunn 1995). Adequate egg incubating substrate and possible imprinting to the stocking site may explain the high egg and fry densities at Arnold Bay. The Saxton Cove site is located over a small, ruined breakwall with deep and extremely clean interstitial spaces. Although the rate of egg deposition was moderate compared to other sites within the lake, no fry were collected in spring; however, fry were subsequently collected at this site in 2003. The highest egg deposition rates of all sites occurred at the Grand Isle breakwall. The breakwall protects a ferry dock and is situated parallel to the ferry path and perpendicular to the prevailing winds. Both the ferry and the winds generate water currents around the breakwall, keeping the substrate clean of sand, silt, and fine organic matter. Water flowing through the Grand Isle state fish hatchery empties into Lake Champlain approximately 200 m from the breakwall. Chemical cues from several salmonid species, including lake trout, reared at the hatchery may aid in attracting spawning lake trout to the area. Egg deposition levels at this site may have had a negative effect on overall survival as fungus can rapidly spread if egg densities are too high. Several egg bags collected in the spring from the Grand Isle breakwall site had large fungus patches attached to the mesh resulting from decomposing eggs. While this is an artifact of the artificially high egg clustering within egg bags, it is still indicative of potential problems in the natural substrate.

Artificial sites without lake trout egg deposition include the two Burlington breakwall sites and Willsboro Bay. During the summer of 2001, the northern and southern ends of the Burlington breakwall were repaired by the U. S. Army Corps of Engineers. Angular cobble was piled at the base of the breakwall, creating deep, clean interstitial spaces. Prior to the repairs, no lake trout egg incubating substrate was present, so lake trout likely did not use those areas for spawning. Recent renovations to the two Burlington breakwall sites may explain why eggs were not collected from either site. The site in Willsboro Bay is a steep, straight shoreline where angular rock from railroad tracks has trickled into the water. Although this substrate is clean of organic matter and has deep interstices, spawning lake trout may have been attracted to other sites within the bay that we did not sample. Spawning behavior has been observed by lake biologists at Willsboro Point, which is in close proximity to the site we sampled.

Whallon Bay, Shelburne Point, and Button Bay are natural sites where eggs were collected. Although Arnold Bay and the Grand Isle breakwall had the highest densities of eggs and fry, Whallon Bay may be the most productive site based on reef area. Arnold Bay and the Grand Isle breakwall are small sites, approximately 189 and 570 m^2 in area, respectively. The area of appropriate spawning substrate at Whallon Bay is over a hundred times larger at approximately 64,372 m^2. Egg bags were buried in a line at depths of 3 to 4 m. We did not observe any differences in habitat characteristics, such as substrate size or reef slope along the line of bags. However, egg distribution among egg bags was not uniform; possibly lake trout identified substrate characteristics that we could not. There was an obvious peak of egg deposition in the bags buried in the center of the line. We also observed eggs at depths of < 2 m down to 9 m, suggesting that deposition is extensive at the Whallon Bay site. Low numbers of eggs were collected from Button Bay and Shelburne Point. Extensive habitat surveys have not been conducted at either site. Surface observations at these sites suggest that appropriate lake trout spawning substrate appears to be limited, as bedrock is the dominant substrate type.

Several seemingly adequate natural sites where eggs were sampled for, but not collected, included Allen Hill, Cannon Point, and Thompson's Point. Allen Hill and Cannon Point both have relatively shallow interstitial spaces that were "cleaner" during the summer, when habitat evaluations were conducted, than in the fall spawning season. Thompson's Point was chosen for egg sampling because in fall of 2001, scuba diver observations revealed over twenty adult lake trout at the site. These fish may have been staging to spawn somewhere else since the substrate here (bedrock covered with zebra mussels) is of low egg incubating quality and no eggs were collected.

Fry trapping efforts in 2001 and 2002 provided evidence that eggs were successfully incubating and hatching. Lake Champlain mean fry CPUE ranged from 0.08 to 2.38 compared to mean estimates of 0.35 in Lake Michigan, 0.04 in Lake Ontario, 0.02 in Lake Huron, and 0.57 in Lake Superior (Marsden et al. 1988). Considering the high levels of egg deposition at Grand Isle, fry CPUE was lower than expected; however, our traps may not have always been effectively fishing. The cobble substrate used to construct the breakwall does not extend very far from the base of the wall and is adjacent to sand. Some traps may not have been set on the cobble or may have slid off on to the sand; this would artificially lower CPUE. Also, predation by slimy sculpins (*Cottus cognatus*) may have lowered fry catch rates. For the first two weeks of fry trapping in spring 2002 up to 12 slimy sculpins were captured per trap and were likely feeding on lake trout fry in the traps. No fry were found in stomach contents, but this is not unexpected as digestion would have occurred before the traps were checked. We modified the fry traps to exclude predators and saw a decrease from 46 to 5 total sculpins collected from all traps and an increase in fry • trap^{-1} • day^{-1} from 0.47 to 0.71.

Our data indicate that lake trout spawn at multiple sites throughout Lake Champlain and mean egg density was higher than mean density at an already restored population in the Great Lakes (Parry Sound, Lake Huron). In 2001 and 2002, mean fry CPUE in Lake Champlain exceeded maximum estimates from Lake Superior where lake trout are self-sustaining. It is important to note that although egg density and fry CPUE in Lake Champlain are high compared to the Great Lakes, total egg and fry production among these systems cannot be compared because the geographic extent of spawning is unknown . Spawning sites and egg deposition were easy to locate in Lake Champlain, and have been difficult to find in portions of the Great Lakes (e.g., Horns et al. 1989, Edsall et al. 1995). This difference is likely a consequence of scale; there are few if any extensive (> 1 km) areas of cobble in Lake Champlain and few are far (> 1 km) from shore, so spawning appears to be concentrated in small, readily accessible areas. Given the high numbers of eggs and fry we detected, we would expect to collect unclipped juveniles and adults in assessment surveys. There has been a very limited amount of sampling for unclipped juvenile lake trout in Lake Champlain; state assessments for lake trout focus on adult sampling. In limited sampling efforts, we did not collect any unclipped juvenile lake trout. The decrease in the percentage of unclipped adult lake trout during the early years (1980s) of adult sampling may be explained by an improvement in fin clipping and clip identification practices. If the entire fin is not clipped, regeneration occurs and can be difficult to identify. Data beginning in the early 1990s are likely a more accurate representation of unclipped and presumably lake-produced fish as hatchery and sampling crews gained experience. Since 1990, a sub-sample of 100 lake trout have been checked for clips each year prior to stocking; 97 to 99% of these fish are clipped (B. Chipman, VTDFW, personal communication). Schneider et al. (1990) and Holey et al. (1995) suggested that successful natural recruitment beyond the fry stage can be construed when the number of unclipped adult lake trout in the population exceeds 2%, although examination of an extensive tagging and clipping dataset in Lake Michigan suggests that 5% should be used as a baseline (J. Jonas, Michigan Department of Natural Resources, personal communication). The recent increase in percentage of unclipped lake trout from just above 2% in 1993 to over 10% in 2000 suggests that lake trout spawned in the lake are recruiting to age-3 and older. However, from 1994 to the present, the length frequency of unclipped adult lake trout has also increased. In 1994, the most numerous size class of unclipped lake trout was 350-450 mm and each year since then th*e majority has come from a slightly larger length class. In 2001, the 650-750mm length class contained the majority (75%) of unclipped lake trout. This suggests that in the late 1980s or early 1990s one naturally-produced year class may have had particularly high survival or fish were mistakenly stocked without being clipped. The decrease in unclipped lake trout from 2000 (10.4%) to 2001 (5.7%) could potentially be a result of mortality of this larger and older year class; very few lake trout caught in the assessment surveys are larger than 750 mm. Even if the unclipped lake trout were mostly natural recruits, the percentage of unclipped lake trout is lower than expected considering the high levels of egg and fry production.

A decrease in stocking rate could potentially over-inflate the percentage of unclipped lake trout in the population. Because the annual stocking rate in Lake Champlain was variable and decreased by half since 1995, we examined whether this variation affected the ratio of unclipped to clipped fish. The percentage of unclipped lake trout was adjusted by the number of yearling equivalents stocked, i.e., each age class of clipped lake trout recovered in a given year was adjusted by the total number of yearlings stocked that made up that year class. This adjustment produced a trend identical to the non-adjusted percentage of unclipped lake trout, indicating that variation in stocking rate did not affect the percentage of unclipped fish.

Many of the factors impeding lake trout recruitment in the Great Lakes are lacking in Lake Champlain, e.g., insufficient spawning stock, contaminants, lack of genetic diversity, EMS, and predation on age-0 lake trout by exotic species. The high levels of egg and fry abundance in Lake Champlain, the failure to collect lake-produced juveniles, and the pattern of increasing length in the percentage of unclipped fish all suggest a bottleneck during the post-emergent fry life stage. Little is known about habitat for, or predators of, this life stage. Potential lake trout fry predators in the lake include slimy sculpins, yellow perch (*Perca flavescens*), and rainbow smelt (Jones et al. 1995). Yellow perch are very abundant and have been observed at several spawning sites during fall and spring. Further studies that examine egg and fry production and survival are necessary to better understand impediments to lake trout restoration in Lake Champlain. In particular, studies of the abundance and diets of potential predators of eggs, sac-fry, and post-emergent fry may explain why the high levels of egg abundance we document have not resulted in recruitment of naturally-produced lake trout.

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Literature Cited

Burnham-Curtis, M. K., C. C. Krueger, D. R. Schreiner, J. E. Johnson, T. J. Stewart, R. M. Horrall, W. R. MacCallum, R. Kenyon, and R. E. Lange. 1995. Genetic strategies for lake trout rehabilitation: a synthesis. Journal of Great Lakes Research 21 (Supplement 1): 477-486.

Chotkowski, M. A., J. E. Marsden, and B. J. Ellrott. 2002. An inexpensive modified emergent-fry trap for lake-spawning salmonids. North American Journal of Fisheries Management 22:621-624.

Christie, W. J. 1974. Changes in the fish species composition of the Great Lakes. J. Fish. Res. Board Can. 31:827-854

Cornelius, F. C., K. M Muth, and R. Kenyon. 1995. Lake trout rehabilitation in Lake Erie: a case history. Journal of Great Lakes Research 21 (Supplement 1): 65-82.

Dodson, J. 1988. The nature and role of learning in the orientation and migratory behavior of fishes. Environmental Biology of Fishes 23: 161-183.

Edsall, T. A., M. E. Holey, B. A. Manny, and G. W. Kennedy. 1995. An evaluation of lake trout reproductive habitat on Clay Banks reef, northwestern Lake Michigan. Journal of Great Lakes Research 21 (Supplement 1): 418-432

Eshenroder, R. L. 1992. Decline of lake trout in Lake Huron. Transactions of the American Fisheries Society 121:548-554.

Eschmeyer, P. H. 1957. The near extinction of lake trout in Lake Michigan. Transactions of the American Fisheries Society 85(1955):102-119.

Elrod, J.H., R. O'Gorman, C. P. Schneider, T. H. Eckert, R. Schaner, J. N. Bowlby, and L. P. Schleen. 1995. Lake trout rehabilitation in Lake Ontario**.** Journal of Great Lakes Research 21 (Supplement 1):83-107.

Fisheries Technical Committee. 1977. A strategic plan for development of salmonid fisheries in Lake Champlain. Lake Champlain Fish and Wildlife Management Cooperative. U. S. Fish and Wildlife Service, Essex Junction, VT. 20 pp

Fisheries Technical Committee. 1999. A comprehensive evaluation of an eight year program of sea lamprey control in Lake Champlain. Lake Champlain Fish and Wildlife Management Cooperative, Essex Junction, VT. 209pp.

Fitzsimons, J. D. 1995a. The effect of B-vitamins on a swim-up syndrome in Lake Ontario lake trout. Journal of Great Lakes Research 21 (Supplement 1):286-289.

Fitzsimons, J. D. 1995b. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. Journal of Great Lakes Research 21 (Supplement 1):337-347.

Grewe, P. G., C. C. Krueger, J. E. Marsden, C. F. Aquadro, and B. May. 1994. Hatchery origins of naturally produced lake trout fry captured in Lake Ontario: temporal and spatial variability based on allozyme and mitochondrial DNA data. Transactions of the American Fisheries Society 123:309-320.

Gunn, J. M. 1995. Spawning behavior of lake trout: effects on colonization ability. Journal of Great Lakes Research 21 (Supplement 1):323-329.

Halnon, L. C. 1963. Historical survey of Lake Champlain's fishery. Vermont Fish and Game Job Completion Report F-1-R-10 Job 6. Essex Junction, VT. 96pp.

Hansen, M. J. 1999. Lake trout in the Great Lakes: basinwide stock collapse and binational restoration. Pages 417-453 in W. W. Taylor and C. P. Ferreri, editors. Great Lakes

Fisheries Policy and Mangagement: A Binational Perspective. Michigan State University Press, East Lansing, Michingan.

Hansen, M. J., J. W. Peck, R. G. Schorfhaar, J. H. Selgeby, D. R. Schreiner, S. T. Schram, B. L. Swanson, W. R. MacCallum, M. K. Burnham-Curtis, G. L. Curtis, J. W. Heinrich, and R. J. Young. 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959-1993. Journal of Great Lakes Research. 21(Supplement 1):152-175.

Holey, M. E., R. W. Rybicki, G. W. Eck, E. H. Brown Jr., J. E. Marsden, D. S. Lavis, M. L. Toneys, T. N. Trudeau, and R. M. Horrall. 1995. Progress toward lake trout rehabilitation in Lake Michigan. Journal of Great Lakes Research 21 (Supplement 1):128-151.

Horns, W. H., J. E. Marsden, and C. C. Krueger. 1989. An inexpensive method for quantitative assessment of demersal egg deposition. North American Journal of Fisheries Management 9:280-286.

Jones, M. L., G. W. Eck, D. O. Evans, M. C. Fabrizio, M. H. Hoff, P. L. Hudson, J. Janssen, D. Jude, R. O'Gorman, and J. F. Savino. 1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages. Journal of Great Lakes Research 21 (Supplement 1):505-517.

Kelso, J. R. M., W. R. MacCallum, and M. L. Thibodeau. 1995. Lake trout spawning at five sites in Ontario waters of Lake Superior. Journal of Great Lakes Research 21 (Supplement 1):201-211.

LaBar, G. W. 1993. Use of bioenergetics models to predict the effect of increased lake trout predation on rainbow smelt following sea lamprey control. Transactions of the American Fisheries Society 122:942-950.

Lake Champlain Basin Program. 1999. The basin, fact sheet number 3. Available: www. anr.state.vt.us/champ/Basinfs.pdf. (August 2002).

Mac, M. J. and C. C. Edsall. 1991. Environmental contaminants and the reproductive success of lake trout in the Great Lakes: an epidemiological approach.. Journal of Toxicology and Environmental Health 33:375-394.

Madenjian, C. P., G. L. Fahnenstiel, T. F. Nalepa, E. S. Rutherford, G. W. Fleischer, H. A. Vanderploeg, T. H. Johengen, P. J. Schneeberger, D. S. Lavis, J. R. Bence, D. J. Jude, and M. P. Ebener. 2001. Dynamics of the Lake Michigan Food Web, 1970-1999. Available: www.glfc.org/bote/upload/chapter1.rtf. (September 2002).

Marsden, J. E., C. C. Krueger, and C. P. Schneider. 1988. Evidence of natural reproduction by stocked lake trout in Lake Ontario. Journal of Great Lakes Research 14:3-8.

Marsden, J. E., C. C. Krueger, and H. Hawkins. 1991. An improved trap for passive capture of demersal eggs during spawning: an efficiency comparison with egg nets. North American Journal of Fisheries Management 11:364-368.

Marsden, J. E., J. M. Casselman, T. A. Edsall, R. F. Elliot, J. D. Fitzsimons, W. H. Horns, B. A. Manny, S. C. McAughey, P. G. Sly, and B. L. Swanson. 1995. Lake trout spawning habitat in the Great Lakes---a review of current knowledge. Journal of Great Lakes Research 21(Supplement 1):487-497.

Marsden, J. E., B. D. Chipman, L. J. Nashett, J. K. Anderson, W. Bouffard, L. E. Durfey, J. E. Gersmehl, W. M. Schoch, N. R. Staats, A. Zerrenner. In press. Evaluation of the eight-year sea lamprey control program on Lake Champlain. Journal of Great Lakes Research

Perkins, D. L., and C. C. Krueger. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush)* at Stony Island Reef, Lake Ontario. Journal of Great Lakes Research 21 (Supplement 1):400-417.

Perkins, D. L., and C. C. Krueger. 1994. Design and use of mesh bags to estimate egg deposition and embryo survival in cobble substrate. North American Journal of Fisheries Management 14:866-869.

Perkins, D. L., J. D. Fitzsimons, J. E. Marsden, C. C. Krueger, and B. May. 1995. Differences in reproduction among hatchery strains of lake trout in eight spawning areas in Lake Ontario: genetic evidence from mixed-stock analysis. Journal of Great Lakes Research 21 (Supplement 1):364-374.

Plosila, D. S. and J. Anderson. 1985. Lake Champlain salmonid assessment report. Vermont Department of Fish and Wildlife. Essex Junction, Vermont. 125pp.

Reid, D. M., D. M. Anderson, and B. A. Henderson. 2001. Restoration of lake trout in Parry Sound, Lake Huron. North American Journal of Fisheries Management 21(1):156-169.

Schneider, C.P., T. H. Eckert, R. O'Gorman, J. H. Elrod, R. W. Owens, T. Schaner, P. Grewe, J. E. Marsden, and C. C. Krueger. 1990. Lake trout rehabilitation in Lake Ontario, 1989. 1990 Lake Ontario Committee report. Great Lakes Fishery Commission, Ann Arbor, Michigan 359pp.

Schreiner, D. R., C. R. Bronte, N. R. Payne, J. D. Fitzsimons, and J. M. Casselman. 1995. Use of egg traps to investigate lake trout spawning in the Great Lakes. Journal of Great Lakes Research 21 (Supplement 1): 433-444.

Selgeby, J. H., C. R. Bronte, E. H Brown Jr., M. J. Hansen, M. E. Holey, J. P. VanAmberg, K. M. Muth, D. B Makauskas, P. McKee, D. M. Anderson, C. P. Ferreri, and S. T. Schram. 1995. Lake trout restoration in the Great Lakes: stock-size criteria for natural reproduction. Journal of Great Lakes Research 21 (Supplement 1):498-504.

Swink, W. D., and L. H. Hanson. 1986. Survival from sea lamprey (*Petromyzon marinus*) predation by two strains of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 43:2528-2531.

Table 1. Spawning habitat of 14 potential lake trout spawning reefs in Lake Champlain. Sites are listed from north to south (Figure 2).

Site	Depth range (m)	Approx. area of substrate (m^2)[a]	Slope[b]	Substrate type	Substrate size range (cm)	Interstitial depth (cm)[c]
Grand Isle breakwall	0.3-4	570	35-60°	angular rubble/ cobble	13-99	15-86
Burlington breakwall (North)	0.3-8.0	500	30-50°	angular rubble/ cobble	15-80	>20
Burlington breakwall (south)	0.3-8.0	450	30-50°	angular rubble/ cobble	15-80	>20
Shelburne Point	0.3-4	----------	---------	bedrock	----------	<10
Allen Hill	0.3-8	4,000	45-65°	angular rubble/ cobble	15-35	10
Willsboro Bay	0.3-18	----------	0-45°	angular cobble/ boulder	40-300	>20

Table 1, continued.

Saxton Cove	2.6-5.0	320	10-60°	angular rubble/ cobble	10-60	10-30
Cannon Point	0.3-4.0	----------	70°	cobble	30-80	5-15
Whallon Bay	0.3-14	64,372	20-85°	rounded rubble/ cobble/ boulder	17-106	4-29
Thompson's Point	1-10	----------	65°	bedrock	----------	<10
Iron Bay	0.3-20	800	0-30°	mine tailings	10-152	20-100
Ore Den Bay	0.3-20	1000	0-10°	mine tailings	30-90	10-30
Button Bay	1-4	200	--------	angular cobble	----------	----------
Arnold Bay	1-7	189	60°	angular rubble/ cobble	10-60	20

[a] Area extrapolated from a combination of actual measurements of reef dimensions and visual estimations.

[b] A slope of 0° is vertical; 90° is horizontal.

[c] Measured vertically using a rigid ruler; interstices may extend below these depths.

Table 2. Summary of data from lake trout egg collections conducted in Lake Champlain during 2000 and 2001. Mean egg abundance in egg bags are presented as eggs/m^2. Eggs collected with egg traps and nets presented as eggs · trap^{-1} · day. Total number of eggs includes egg chorions (outer embryonic membrane). Sampling dates include the entire sampling period; dates of collections include only dates when eggs were collected.

Location and year	Collection gear	# collectors	Sampling dates (dates of collections)	# eggs	Mean egg abundance ± SE
2000					
Grand Isle breakwall	traps and nets	30	7 Nov- 8 Dec (13 Nov- 8 Dec)	3,799	4.08[a]
Cannon Point	traps and nets	30	14 Nov- 29 Nov	0	0
Whallon Bay	traps and nets	30	2 Nov- 4 Dec (14 Nov- 28 Nov)	1	0.002 ± 0.03
Button Bay	traps and nets	30	4 Nov- 11 Dec (19 Nov- 11 Dec)	10	0.02 ± 0.21
Arnold Bay	traps and nets	30	3 Nov- 11 Dec (3 Nov- 11 Dec)	85	0.12 ± 0.33
2001					
Grand Isle breakwall	Bags	59	10 Oct- 27 Nov	39,593	9,623 ± 1,658
Burlington breakwall (north)	Bags	15	23 Oct- 3 Dec	0	0

Table 2, continued

Burlington breakwall (south)	Bags	15	15 Oct- 29 Nov	0	0
Shelburne Point	traps and nets	30	23 Oct- 29 Nov (30 Oct- 29 Nov)	1	0.001 ± 0.03
Willsboro Bay	Bags	19	16 Oct- 5 Dec	0	0
Allen Hill	Bags	15	5 Sept- 29 Nov	0	0
Saxton Cove	Bags	15	11 Oct- 30 Nov	116	118 ± 59
Cannon Point	Bags	15	21 Aug- 4 Dec	0	0
Whallon Bay	Bags	60	21 Aug- 4 Dec	2,728	652 ± 158
Thompson's Point	traps and nets	30	8 Nov-13 Nov	0	0
Iron Bay	Bags	15	6 Sep- 4 Dec	2	1.9 ± 1.3
Arnold Bay	Bags	15	30 Aug- 30 Nov	949	972 ± 289

[a] Eggs from nets and traps were not tallied separately on this date, so the SE could not be calculated.

Table 3. Lake trout fry collections in Lake Champlain, 2001 and 2002, using emergent fry traps. CPUE is fry • trap^{-1} • day^{-1}. Totals and CPUE at a site only include data from first fry collection to the last.

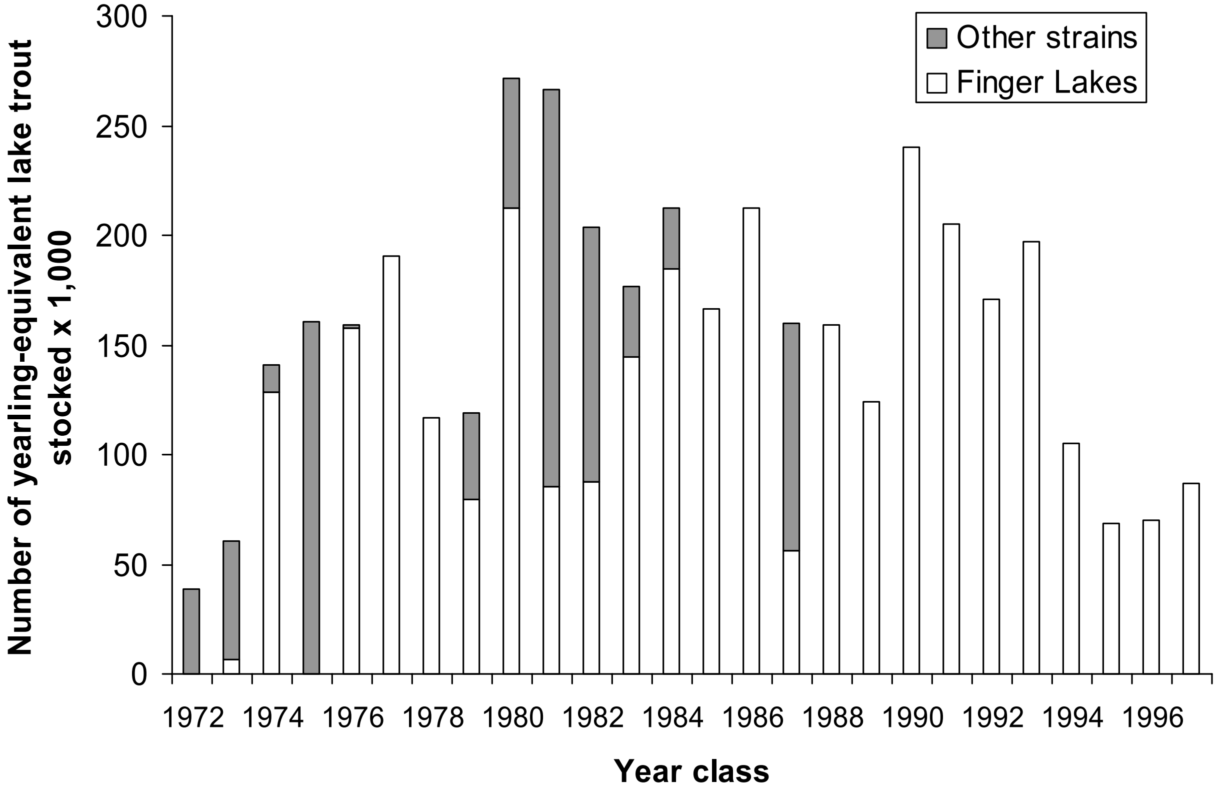
Location and year	Set	Lifted	Days	# Traps	# Fry	CPUE
2001						
Grand Isle breakwall	16-Apr	6-Jun	52	10	173	0.33
Whallon Bay	20-Apr	13-Jun	55	19	146	0.14
Ore Den Bay	3-May	19-Jun	48	10	0	0
Arnold Bay	2-May	4-Jun	25	10	594	2.38
2002						
Grand Isle breakwall	5-Apr	6-Jun	62	12	237	0.32
Saxton Cove	26-Apr	3-Jun	41	7	0	0
Whallon Bay	10-Apr	4-Jun	55	20	89	0.08
Arnold Bay	26-Apr	20-May	24	6	249	1.73

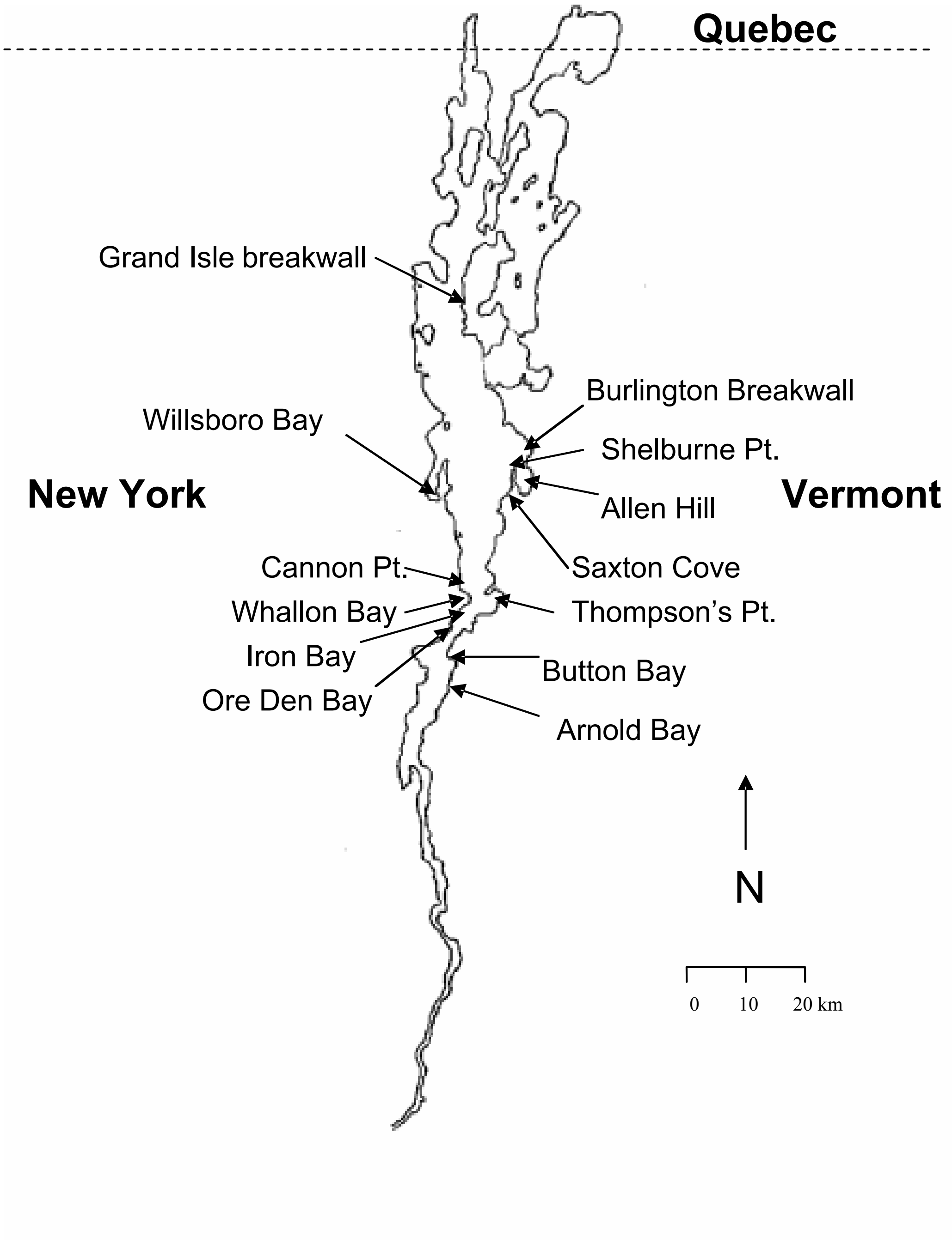
Figure Captions

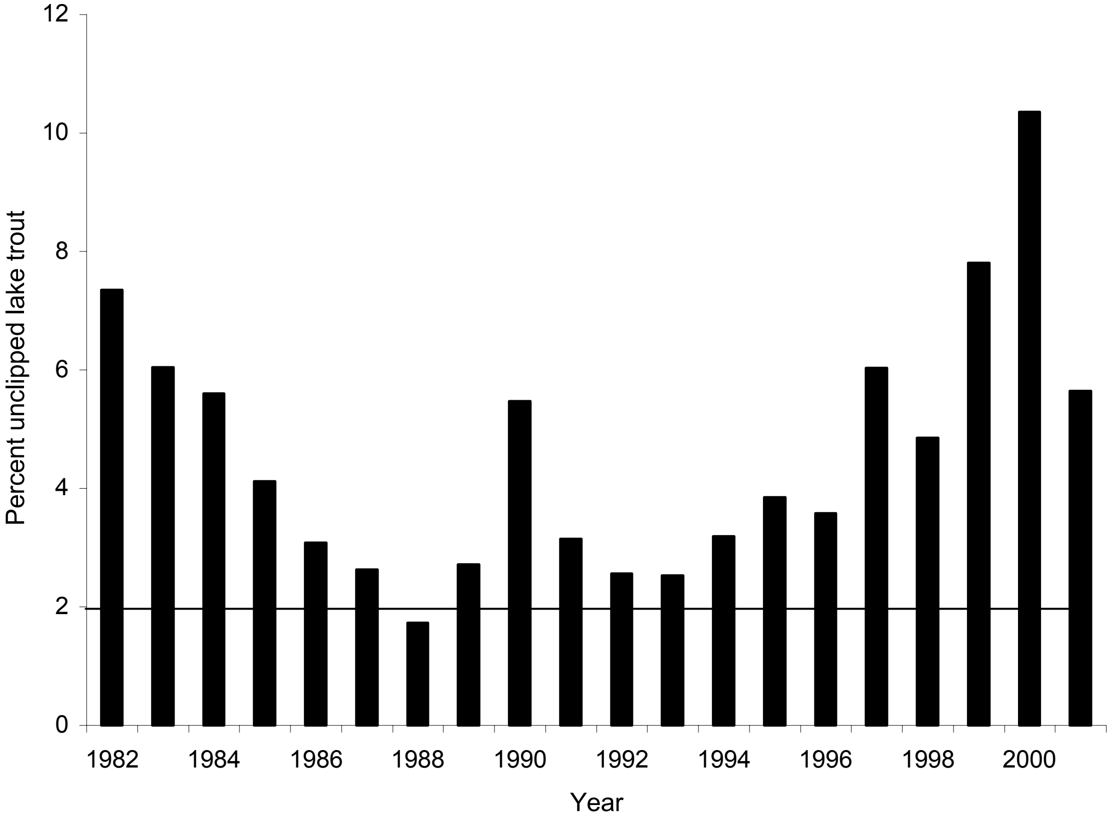
Figure 1. Numbers of yearling-equivalent lake trout stocked into Lake Champlain by year class and strain, 1972-1997. “Finger Lakes” represents Seneca Lake strain, and also includes composite strains of progeny from feral lake trout in lakes Ontario and Champlain, which were assumed to be largely of Seneca Lake origin. “Other strains” include Jenny Lake, Lake Michigan, Lake Superior (Marquette), Manitou (Clearwater), Adirondack (Raquette Lake, Lake George), and Maine (Allagash Lake).

Figure 2. Locations of areas examined for lake trout spawning in Lake Champlain.

Figure 3. Percentage of unclipped lake trout collected in adult population assessments in Lake Champlain. The line at 2% represents the estimated level of missed fin clips or unidentified hatchery fish, above which recruitment is presumed to be occurring (Schneider et al. 1990, Holey et al. 1995).


Other strains
Finger Lakes
Number of yearling-equivalent lake trout stocked x 1,000
0
50
100
150
200
250
300
1972
1974
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
Year class


Quebec
Grand Isle breakwall
Burlington Breakwall
Willsboro Bay
Shelburne Pt.
New York
Vermont
Allen Hill
Cannon Pt.
Saxton Cove
Whallon Bay
Thompson's Pt.
Iron Bay
Button Bay
Ore Den Bay
Arnold Bay
N
0
10
20 km



12
10
8
6
4
2
0
Percent unclipped lake trout
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
Year

A comparison of lake trout spawning, fry emergence, and habitat use in lakes Michigan, Huron, and Champlain

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Keywords: lake trout, restoration, habitat, spawning, fry emergence

Abstract

Restoration of self-sustaining populations of lake trout are underway in all of the Great Lakes and Lake Champlain; to date, restoration has only been achieved in Lake Superior and in Parry Sound, Lake Huron. We evaluated the potential for current stocks of lake trout to achieve restoration by comparing spawning habitat availability, relative abundance of spawners at spawning reefs, egg and fry density and egg survival in Parry Sound with similar data from Lake Michigan and Lake Champlain. Five to 15 sites in each lake were surveyed by divers, who also made visual assessments of the presence of adult lake trout in fall. Spawning adults were sampled at two to four reefs in each lake using standardized gillnets in 2002. Eggs were sampled using egg bags at two to 12 reefs per lake in fall, 2000-2002; eggs were also sampled using egg traps and nets in Lake Champlain in 2000 and 2001. Fry were sampled using emergent fry traps at two to four sites in each lake in spring, 20001-2003. Fry were also collected in egg bags left on the reefs overwinter in Parry Sound in each lake in 2001-2002, and in Lake Champlain in 2002-2003. Most of the sites surveyed had excellent spawning habitat. Adult lake trout were seen in low numbers at 1-2 sites in lakes Michigan and Champlain, in very high numbers at one site in Lake Champlain, and were not seen in Parry Sound. No lake trout were collected in gillnets in Lake Michigan, 0.16/hr were caught in Parry Sound, and 7.5 hr were caught in Lake Champlain. Eggs were collected at all five sites surveyed in Parry Sound, nine of 15 sites sampled in Lake Champlain, and six of ten sites in Lake Michigan. Egg deposition was lowest in Lake Michigan ((0.4 – 154.5 eggs/m^2), intermediate in Parry Sound (39 – 1,027 eggs/m^2), and highest overall in Lake Champlain but with higher variation among sites (0.001 – 9,623 eggs/m^2). Fry collections in fry traps followed the same trend: no fry in Lake Michigan, 0.005 – 0.06 fry per trap day in Parry Sound, and 0.08 – 3.6 in Lake Champlain. Egg survival to hatch in

overwinter egg bags was similar in Lake Michigan (7.6%) and Parry Sound (2.3 – 8.9%) in 2001-02, and varied in Lake Champlain (0.4-1.1% in 2001-02, and 1.8 – 18.2 in 2002-03. Using Parry Sound as a benchmark for successful restoration, recruitment of age 1+ lake trout is highly unlikely in northern Lake Michigan. The low levels of recruitment in Lake Champlain suggest that there are sources of high mortality that occur after fry emergence.

Introduction

Populations of lake trout (*Salvelinus namaycush*) were extirpated from the Great Lakes by the 1960s, and from Lake Champlain (Vermont and New York) by 1900 (Eschmeyer 1957, Plosila and Anderson 1985, Eshenroder 1992, Cornelius et al. 1995, Elrod et al. 1995, Hansen et al. 1995). The causes for the decline in the Great Lakes are generally understood to be commercial fishing and mortality from sea lamprey (*Petromyzon marinus*) attacks; however, the cause of the extirpation of lake trout from Lake Champlain is unknown (Ellrott and Marsden in press). In each of the lakes, restoration of lake trout populations has involved sea lamprey control, annual stocking of one or more strains of lake trout, and regulation of harvest. Lake trout populations became self-sustaining in Lake Superior in the 1990s, but are sustained by stocking in each of the other lakes. Evidence of spawning by stocked fish is extensive in most of the lakes, but there has been little to no evidence of sustained recruitment to age-1 and older except in Lake Superior and at two sites in Lake Huron (Cornelius et al. 1995, Elrod et al. 1995, Eshenroder et al. 1995, Hansen et al. 1995, Holey et al. 1995, Ellrott and Marsden in press). Since lake trout stocked as fingerlings or yearlings survive and grow well to maturity, it is generally hypothesized that the impediments to successful lake trout reproduction likely occur between spawning in fall and emergence of fry from spawning reefs in spring.

The purpose of this study was to compare lake trout spawning populations, habitat use, and fry emergence among three lakes at different stages of lake trout population restoration. In Lake Michigan, the restoration program has been underway since 1965; evidence of reproduction (egg deposition and/or fry hatch) was documented in Grand Traverse Bay area in the early 1970s, and along the southern shoreline in the early 1980s and 1990s, but wild year classes of age-1+ fish have not been detected (Holey et al. 1995). In Lake Huron, restoration stocking began in the early 1970s, and reproduction has been detected since the mid-1980s in South Bay and near Thunder Bay (Anderson and Collins 1995, Johnson and VanAmberg 1995). In Parry Sound, on the north-east shoreline of Georgian Bay, recruitment of naturally-produced fry has been sufficient to produce substantial year classes of wild lake trout since 1988 and restoration was considered to be achieved by 1997 (Reid et al. 2001). Lake trout stocking began in Lake Champlain in 1973, with the goal of restoring a fishery. Starting in 1999, a search for evidence of reproduction by stocked fish revealed numerous sites where spawning and fry hatch occurred, but recruitment of wild fish has been limited (Ellrott and Marsden in press). A comparison among these three lakes may indicate the spawning population size, levels of spawning habitat availability, use by stocked fish, and successful emergence of fry that are necessary for restoration to succeed. Our study focused on northern Lake Michigan, Parry Sound in Lake Huron, the southern half of the main basin of Lake Champlain.

Methods

Spawning site surveys

In all three lakes, potential spawning sites were located using data on fall aggregations of lake trout, and lake bottom topography and substrate composition. Information on lake trout aggregations was available in historic records from fall commercial fishing (lakes Michigan and Huron), and modern lake trout assessment work (Goodyear et al. 1982, Ellrott and Marsden in press). Spawning reefs generally have deep cobbles that protect eggs over the winter, and a steep contour that may aid in increasing water currents that keep the substrate scoured of silt (Fitzsimons 1994, Marsden et al. 1995). We examined bathymetric charts for areas of steep contour, then examined promising sites using scuba. If rubble/cobble substrates were present, we measured the following characteristics at each site: depth at top and base of the reef, reef area (defined by the area encompassed by cobbles), slope angle of the reef contour, substrate type, particulate substrate size, interstitial depth, presence of silt or organic debris, and presence of zebra mussels. Reef area was measured by divers using a 100 m tape. Slope angle was measured using a protractor and plumb line. We measured 20 to 60 substrate particles along their longest axis to estimate mean size. In Lake Michigan and Parry Sound each reef was videotaped and substrates were measured from the videotape images. We used the Wentworth scale as described in Marsden et al. (1995) to classify substrate: gravel is < 65mm, rubble is 65-256 mm, and cobble is 257-999 mm in the longest dimension. Interstitial depth was measured by inserting a rigid ruler vertically into the substrate several times until a maximum depth was found; interstices likely extend substantially below these depths on most reefs. Substrate shape (angular versus rounded) and presence of silt and zebra mussels were evaluated visually. We also determined from charts the longest fetch and direction of fetch; this information defines how much water movement can be expected on the reefs due to wind-generated water movements.

Subsequent work in each lake focused on sites that had the highest predicted potential to attract spawning lake trout, or yielded the largest egg collections in the first year of work. Additional sites were sampled as time allowed. In Lake Champlain the focal sites were Grand Isle and Whallon Bay; in Parry Sound they were Davy Is., Bar Is., Horse Is., and Mowat Is.; in Lake

Michigan they were the LTB crib, Bay Harbor, and Fishermens Is. An additional 13 sites in Lake Champlain, one site in Parry Sound, and seven sites in Lake Michigan were studied.

Adult lake trout assessment

The density of spawning lake trout aggregated at spawning sites was assessed in fall, 2002, using multipanel multifilament gillnets set for 1.5 hr between dawn and noon. Each net consisted of four 30.5 m panels of mulitfilament mesh, 1.6 m high, set on the bottom; panels were 11.4, 12.7, 14, and 15.2 cm stretch mesh. Gill nets were fished on one to three days at two sites in Lake Champlain, three sites in Lake Michigan, and four sites in Lake Huron (Table 2). All lake trout captured were measured for total length, and sex and reproductive status were assessed by expressing gametes. All fish in good condition were released.

Divers made observations during the spawning season at all sites where egg bags were buried and at sites where fall diver reconnaissance was done. These observations provided a qualitative evaluation of the presence and relative density of lake trout. Divers made estimates of the number of lake trout seen within an approximate time interval during these dives; while these estimates are not highly quantitative or replicable, they do provide an estimate of the differences in density among sites.

Spawning assessment

To determine whether reefs were used by spawning lake trout, we used two types of egg sampling equipment in the fall of 2000, 2002, and 2003. Egg traps and nets were 20 cm diameter passive egg collectors deployed from the surface in gangs of 30 collectors 1 m apart on a buoyed, anchored line (Horns et al. 1989, Marsden et al. 1991). These collectors were deployed in late October or early November and checked approximately every 5-10 days. The trap/net gangs provided data on presence or absence of eggs and relative egg deposition per collector per day (e.g., Schreiner et al. 1995). Egg bags were 45.7-cm deep cloth bags constructed of 3-mm Ace mesh attached to a 29.8 cm diameter PVC ring (Perkins and Krueger 1994). The bags were set into a hole dug by a diver into cobble substrate, and were filled with the excavated material. Thirty to 60 egg bags were deployed in early fall before the initiation of spawning activity, and retrieved after spawning had mostly or completely ended; the bags therefore provided cumulative, quantitative data on the density of eggs deposited per unit of substrate. The bags were set approximately 1 m apart in lines along the contour on each reef, in areas with the deepest interstitial spaces. Bags were retrieved by carefully removing substrate to ensure that eggs remained in the bags; the bag was then tied closed with a cable tie before transport to the surface. In 2000 we sampled eggs using trap/net gangs in Lake Champlain, and egg bags in Lake Michigan; we used egg bags in all three lakes in 2001 and 2002.

Bags were generally set along the edge of each reef, at the top of a slope. To test the assumption that this is the area where lake trout focus spawning effort, we set 15 egg bags across the contour at Whallon Bay, Lake Champlain, from 2.3 to 10 m depth, in 2002. This line of bags crossed the center of the line of bags set along the contour.

Egg survival and fry hatch

Survival of eggs over the winter was assessed using fine-mesh (1.5 mm) egg bags that would retain hatched fry. Egg bags were deployed in early fall as described above. The bags were closed with a 1.5 mm mesh, close-fitting cover at the end of the spawning season, and retrieved in spring as soon as ice thaw allowed access to the reefs (mid to late April). The bags were retrieved by leaving the cover on and substrate inside to ensure that hatched fry did not escape. Presence of any holes in the bags or covers that may have allowed escape of fry was noted as they were processed; if large holes were present, the bag contents were not included in the data analysis. Overwinter egg bags were used at two to found sites in each lake in 2001-2002; they were also used at two sites in Lake Champlain in 2002-03.

Fry densities on the reefs were also assessed in spring using two designs of emergent fry traps. Both designs consisted of a pyramid of metal mesh, open at the bottom, with a capture bottle at the top. The capture bottle had an inverted funnel set into the opening, so that fry which emerged from substrate beneath the trap and entered the bottle would be unlikely to escape. Emergent fry traps described by Collins (1975), and modified by Marsden et al. (1988), were deployed with buoyed lines from the surface, and were checked by lifting them to the surface. A second design had a 6 cm ledge with a 6 cm rim around the outside edge, into which rocks could be placed to anchor the trap to the substrate. These traps were checked by divers, who would remove and replace the capture bottles and check each bottle for fry at the surface. Both types of traps were deployed as early in the season as ice thaw allowed, and were checked for fry every 7-16 days until no more fry were captured. Diver traps were set approximately 1 m apart in lines along the reef contour, in a similar position to the egg bags; we attempted to place the surface fry traps in the same location, but there was variation in their location from set to set. Fry traps were used at two to four sites in each lake, and were deployed in lakes Champlain and Michigan in 2001, and in all three lakes in 2002 and 2003.

Results

Spawning site surveys

In Parry Sound and Lake Michigan, all sites surveyed had rounded cobble/rubble substrates, primarily limestone. Silt and organic material were absent or present in small quantities (Table 1). Natural sites surveyed in Lake Champlain were characterized by rounded or angular cobble/rubble substrate, or bedrock (Table 1). Fine silts were not present above a depth of 22 m except at Allen Hill, which was thickly coated with fines; at sites where surveys extended below 22 m we found thick (> 2 cm) deposits of silt that filled interstitial spaces. Ten of the fifteen sites in Lake Champlain and one site surveyed in Lake Michigan were man-made (breakwalls, mine tailings, water intake lines covered with rip-rap, and a ruined pier), with angular rubble-cobble substrates. These areas were generally in shallow water (< 7 m). The three deeper sites in Lake Champlain (Willsboro Bay, Ore Den Bay, Iron Bay) were located below steep shorelines and were comprised of rubble that had slipped into the water from mine tailings and railroad bed construction. At each of these sites, thick silt was found below 22 m.

Eggs were collected at all five sites surveyed in Parry Sound, nine of 15 sites sampled in Lake Champlain, and six of ten sites in Lake Michigan. Reefs where we found evidence of spawning generally had cobble/rubble substrate with interstitial spaces at least 20 cm deep, with a steep slope and absence of fines (Table 1). Only two sites were classified as poor spawning sites, both in Lake Champlain. These sites were primarily bedrock with no interstices; a single egg was collected on one of these sites (Shelburne Bay).

Adult lake trout assessment

Gillnet surveys on two to four reefs per lake collected 1.3 lake trout/hr in Lake Champlain and 0.16 lake trout/hr in Parry Sound (Table 2). No lake trout were caught during 11.6 hr of gillnetting in Lake Michigan, an effort intermediate between the other two lakes. Other species caught in the gillnets were lake whitefish and smallmouth bass, species which have preferences for rocky substrates similar to lake trout.

An alternate method for assessing relative lake trout abundance at spawning reefs is via observations of adult lake trout. We observed lake trout occasionally at Whallon Bay while diving (less than two sightings per hour); in addition, lake trout were seen and heard leaping at the surface during most visits to the sight, though this behavior was most frequently noted at night. Lake trout were observed from the surface near the spawning substrate at Arnold Bay in low numbers (less than 5 sightings per hour). Lake trout were always seen in extremely high numbers at Grand Isle during dives in the spawning season. The lake trout were aggregated toward the end of the breakwall, and were usually seen in dense, horizontal columns of fish approximately 5-7 fish wide and extending over 30 m; divers estimated that several hundred fish were present at the site. Spawning was observed and videotaped at the site; as many as 10% of the lake trout were carrying sea lamprey. Leaping at the surface was occasionally seen at Grand Isle. Lake trout were not observed at any other site in Lake Champlain. In Lake Michigan, lake trout were only seen in low numbers at the LTB crib. Lake trout were never observed at the Parry Sound sites; this is particularly puzzling, as the sites were very limited in area, and the divers traversed the entire area of available spawning substrate during their work each day.

Spawning assessment

CPUE and numbers of eggs collected per square meter varied substantially among reefs within each lake, among years at each reef, and also among lakes (Table 3). Across all sampling years, egg densities were the lowest in Lake Michigan (0.4 – 154.5 eggs/m^2), intermediate in Parry Sound (39 – 1,027 eggs/m^2), and highest overall in Lake Champlain but with higher variation among sites (0.001 – 9,623 eggs/m^2; Table 3). Some of the variation among sites may be explained by the location of the sampling equipment; small variations in trap or bag location may have substantial effects on catch. However, this does not entirely explain variance among years; for example, bags were buried in almost identical locations at the sites in Parry Sound in 2001 and 2002, because the small size of the reefs limited the possible positions of the bags. Egg collections increased over 5-fold at Davy Is. (from 186 to 1,027 eggs/m^2), but decreased at Horse Is. and Mowat Is.. Similarly, bag locations at Grand Isle in Lake Champlain were similar between sampling years, but egg collections decreased from 9,623 eggs/m^2 in 2001 to 3,183 eggs/m^2 in 2002. In 2001, a windrow of eggs estimated to contain millions of eggs was observed at the base of the breakwall, but no eggs were seen at the base of the reef in 2002 (Ellrott and Marsden in press).

The line of bags set across the contour at Whallon Bay, Lake Champlain, collected 709 eggs; the bags at either end of the line had few (< 15 per bag) or no eggs, whereas the bags in the center of the line, at the edge of the reef slope, contained the most eggs (45 to 243 eggs per bag. Collections of eggs in egg traps and nets provided data on when eggs were being deposited in Lake Champlain (Table 3). The last date on which egg traps and nets were retrieved with eggs in then was between late November and mid-December. Egg bags were retrieved each year between mid-November and early December; thus, we may not have collected eggs deposited late in the spawning season. This would reduce the total count of eggs, but likely does not affect the relative estimates of egg deposition among reefs.

Egg survival and fry hatch

Lake trout fry hatch measured as number of fry collected per fry trap per day was highest in Lake Champlain (0.08 – 3.6), and lower in Parry Sound (0.005 – 0.06); no fry were collected in fry traps in Lake Michigan (Table 4). Because the diver-deployed traps remained in place throughout the emergence period, catches may represent the number of fry emerging from a given area, in which case the number of fry per trap can be compared to the egg density in fall to calculate the proportion of eggs that hatched. The number of fry emerging per 100 eggs was 0.12 to 6.8 in Parry Sound in 2002 and 2003, and 11.7 to 14.5 in Lake Champlain in 2003. However, fry move laterally within the substrate prior to emergence (Marsden, unpublished data), so that a given trap likely collects fry from an area greater than that covered by the trap. In egg bags that were covered and left in the substrate overwinter, the number of hatched fry compared with egg density estimated in bags removed in fall was lowest in Lake Champlain (0.4 – 1.1%), and similar in Lake Michigan (7.6%) and Parry Sound (2.3 – 8.9%) in 2001-02 (Table 5). Hatching was likely severely underestimated in Grand Isle, Lake Champlain, in 2001-02 due to the large number of eggs deposited in the bags; several bags were retrieved with masses of fungus resulting from infection of the closely-packed eggs. In 2002-03, when egg deposition was lower on Grand Isle, an estimated 18.2% of the eggs hatched.

Discussion

Progress towards lake trout restoration, evaluated by the appearance of wild year classes in assessment samples, is most highly advanced in Lake Huron, virtually absent in Lake Michigan, and unknown in Lake Champlain. Adult spawning stock size in northern Lake Michigan and in Lake Champlain is marginal for restoration, using stock-size criteria developed by Selgeby et al. (1995; Jonas unpublished data, Ellrott and Marsden in press). Additional potential impediments to restoration in Lake Michigan include predation of early life stages (eggs and fry) by exotic species such as alewife (*Alosa pseudoharengus*), round goby (*Neogobius melanostomus*) and rusty crayfish (*Orconectes rusticus*). In Lake Champlain, these exotic predators are absent, but sea lamprey wounding rates are extremely high, such that the amount of energy allocated to spawning may be compromised. Using Parry Sound as a model of conditions that were adequate for restoration, we examined progress toward lake trout restoration in lakes Michigan and Champlain by comparing spawning habitat availability, use by spawners, egg densities, and fry hatch.

In all three lakes, spawning reef availability and spawning habitat quality were high. The number of reefs visited by lake trout, numbers of adult lake trout colleted and observed, and the number of eggs and fry collected at each site were all greatest in Lake Champlain, intermediate in Parry Sound, and lowest in Lake Michigan.

Among all three lakes there was no obvious difference in substrate size, substrate cleanliness, reef contour, or reef size between sites where we found evidence of spawning, and sites where no eggs or fry were collected. Sites were readily found in all three lakes that appeared to meet criteria for good lake trout spawning sites, as evaluated by the accumulated experience of the investigators (e.g., Fitzsimons 1994, 1995, 1996, Marsden 1994, Marsden et al. 1991, 1995a and b). In general, however, sites in Lake Michigan had higher levels of periphyton, lower water clarity, and more interstitial egg predators than in Lake Champlain; predator levels in Parry Sound were intermediate between the other two lakes, water clarity was greater, and the substrate was cleaner. More artificial sites than natural sites (3 versus 6) were used by spawning lake trout in Lake Champlain, whereas only one of the six sites where eggs were found in Lake Michigan was man-made. No artificial sites were sampled in Parry Sound. The high proportion of man-made spawning sites used in Lake Champlain may in part be an artifact of the small size of the lake, and our focus on areas where cobble was readily observed; many areas of the shoreline have been altered by human activity, resulting in highly visible areas of cobble.

Observations of adult lake trout at sites in fall have been suggested as a criterion to evaluate use of spawning sites, given that lake trout aggregate in order to spawn (e.g., Marsden and Janssen 1997). Lake trout have been observed by divers and remotely operated videos at reefs in lakes Michigan, Huron, and Ontario and the observations have been quantified at rates from 0.2 to 2 lake trout seen per minute during the day (Marsden and Janssen 1997). Adult lake trout were not observed in Parry Sound, and were seen in low numbers at one site in Lake Michigan and two sites in Lake Champlain. We observed extraordinary numbers of adult lake trout on several occasions at one site (Grand Is.) in Lake Champlain. These fish were not sampled in our daytime gillnet sets, likely because the nets were highly visible in daylight. Gillnet collections also reflect the difference in density of adults in each lake; the most adults were collected in Lake Champlain, and none were found with comparable effort in Lake Michigan (Table 2).

The highest spawning activity, evaluated by densities of eggs and fry, occurred at the smallest sites in lakes Champlain and Michigan (Tables 1, 3). It is possible that the smaller sites concentrated spawning activity, making detection of eggs more likely. The extreme spawning density noted at the Grand Isle site in Lake Champlain may be due to adult lake trout attraction the proximity of hatchery effluent where lake trout are reared, approximately 200 m from the breakwall (Ellrott and Marsden in press). In each lake the largest sites surveyed also yielded catches of eggs and fry. Spawning may have occurred at additional sites, and our sampling effort was too either small to detect eggs or was in the wrong place on a particular reef. However, given that we focused our efforts on the best substrate we could find at each site, spawning activity was probably very minor if we collected no eggs or fry. The distribution of egg collections in the cross-contour line of egg bags at Whallon Bay, Lake Champlain confirmed that we were generally setting egg bags in the optimum location, i.e., at the edge of the downward slope on each reef.

Egg density data and egg survival in Lake Champlain and Parry Sound are comparable to or greater than those measured in the other Great Lakes, whereas egg and fry densities in Lake Michigan are lower. Mean egg density has been measured at 122-518 eggs/m^2 in Lake Superior (Peck 1986), and 700 – 4,290 eggs/m^2 in Lake Ontario (Perkins and Krueger 1995); the range we measured was 118 – 9,623 eggs/m^2 in Lake Champlain, 39 – 1,027 eggs/m^2 in Parry Sound, and 0.4 – 154.5 in Lake Michigan.

Fry collections in egg bags were highest in Lake Champlain, and similar in Lake Michigan and Parry Sound; fry were collected on both reefs sampled in Lake Champlain, two of three sampled in Parry Sound, and one of four sampled in Lake Michigan. Fry traps yielded similar results – high fry density and CPUE in Lake Champlain, lower catches in Parry Sound, and no fry from Lake Michigan. Mean hatch data from egg bags were compromised in Lake Champlain due to the density of eggs in the bags. In 2003, when egg densities were lower, there was a striking difference in fry hatch (fry per 100 eggs) at the two sites in Lake Champlain (18.2 at Grand Isle versus 1.8 at Whallon Bay). Estimates of fry hatch were similar between fry traps and egg bags: 6.8 and 8.9, respectively, at Davy Is., and 0.8 and 2.3 at Bar Is. in 2002, 14.5 and 18.2, respectively, at Grand Is. in Lake Champlain. However, fry traps at Whallon Bay in Lake Champlain collected a considerably higher number of fry, relative to eggs caught at the site (11.7 fry per 100 eggs) than egg bags (1.8 fry per 100 eggs). These estimates of egg survival were similar to mean egg survival to mid-April measured in egg bags in Lake Ontario ranged from 12.4 – 16.5% (Perkins and Krueger 1995).

Our results suggest that, if we use Parry Sound as a benchmark for successful restoration of trout, then there is insufficient use of spawning reefs, insufficient spawner density, and egg densities are too low to support recruitment of lake trout in northern Lake Michigan. Lake trout assessment data indicate that adult stocks are too low in northern Lake Michigan for restoration to occur. Stocking rates may be too low in the northern lake to build sufficiently large adult populations, or mortality may be too high. Exploitation by sport and tribal fisheries is still high, and in recent years mortality due to sea lamprey has increased substantially, presumably due to sea lamprey reproduction in the St. Mary's River. In contrast to Lake Michigan, spawning reef use, adult densities, egg densities, and fry hatch are high enough, or considerably higher, in Lake Champlain than is needed to support recruitment. The proportion of unclipped lake trout in the adult population in Lake Champlain is low, with the apparent exception of one year class (Ellrott and Marsden in press). Previous work on lake trout restoration has focused on bottlenecks to survival during the stages between egg deposition and emergence. Data from Lake Champlain suggest that there are sources of high mortality beyond fry emergence; these sources of mortality may also be present in other lakes. Further research in Lake Champlain and other lakes that also lack exotic species as a source of post-emergent mortality may further our understanding of lake trout recruitment failure in the Great Lakes.

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Literature Cited

Anderson, D.M.and J.J. Collins. 1995. Natural reproduction by stocked lake trout (*Salvelinus namaycush*) and hybrid (backcross) lake trout in South Bay, Lake Huron . J. Great Lakes Res. 21 Suppl. 1:260-266

Collins, J. J. 1975. An emergent fry trap for lake spawning salmonines and coregonines. Prog. Fish-Cult. 37:140-142

Cornelius, F.C., K.M. Muth, and R. Kenyon. 1995. Lake trout rehabilitation in Lake Erie: a case history. J. Great Lakes Res. 21(sup1):65-82.

Ellrott, B. E. and J. E. Marsden. In press. Lake trout reproduction in Lake Champlain. Trans. Am. Fish. Soc.

Elrod, J.H., R. O'Gorman, C.P. Schneider, T.H. Eckert, T. Schaner, J.N. Bowlby, and L.P. Schleen. 1995. Lake trout rehabilitation in Lake Ontario. J. Great Lakes Res. 21(sup1):83-107.

Eschmeyer, P. H. 1957. The near extinction of lake trout in Lake Michigan. Transactions of the American Fisheries Society 85(1955):102-119.

Eshenroder, R. L. 1992. Decline of lake trout in Lake Huron. Transactions of the American Fisheries Society 121:548-554.

Eshenroder, R.L., N.R. Payne, J.E. Johnson, C. Bowen II, and M.P. Ebener. 1995. Lake trout rehabilitation in Lake Huron. J. Great Lakes Res. 21(sup1):108-127.

Fitzsimons, J. D. 1994. An evaluation of lake trout spawning habitat characteristics and methods for their detection. Can. Tech. Rep. of Fish. Aquat. Sci. No. 1962, 26 pp.

Fitzsimons, J. D. 1995. Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario . J. Great Lakes Res. 21 Suppl. 1:337-347

Fitzsimons, J. D. 1996. The significance of man-made structures for lake trout spawning in the Great Lakes: are they a viable alternative to natural reefs? Can. J. Fish. Aquat. Sci. 53:142-151

Goodyear, C. D., T. A. Edsall, D. M. Ormsby Dempsy, G. D. Moss, and P. E. Polanski. 1982. Atlas of the spawning and nursery areas of the Great Lakes fishes. Vol. XI: Lake Ontario. U. S. Fish & Wildlife Service, Washington, DC FWS/OBS-82/52

Hansen, M. J. 1999. Lake trout in the Great Lakes: basinwide stock collapse and binational restoration. Pages 417-453 in W. W. Taylor and C. P. Ferreri, editors. Great Lakes Fisheries Policy and Management: A Binational Perspective. Michigan State University Press, East Lansing, Michigan.

Holey, M.E., R.W. Rybicki, G.W. Eck, E.H. Brown, J.E. Marsden, D.S. Lavis, M.L Toneys, T.N. Trudeau, and R.M. Horrall. 1995. Progress toward lake trout restoration in Lake Michigan. J. Great Lakes Res. 21(sup1):128-151.

Horns, W. H., J. E. Marsden and C. C. Krueger. 1989. An inexpensive method for quantitative assessment of demersal egg deposition. N. Am. J. Fish. Manag. 9:280-286.

Johnson, J. E. and J.P. VanAmberg. 1995. Evidence of natural reproduction of lake trout in western Lake Huron. J. Great Lakes Res. 21 Suppl. 1:253-259

Marsden, J. E. 1994. Spawning by stocked lake trout on shallow, inshore reefs in south-western Lake Michigan. *J. Great Lakes Res.* 20:377-384

Marsden, J. E., and C. C. Krueger. 1991. Spawning by hatchery-origin lake trout in Lake Ontario: data from egg collections, substrate analysis, and diver observations. *Can. J. Fish. Aquat. Sci.* 48:2377-2384.

Marsden, J. E., and J. Janssen. 1997. Evidence of lake trout spawning on a deep reef in Lake Michigan using an ROV-based egg collector. *J. Great Lakes Res.* 23:450-457.

Marsden, J. E., C. C. Krueger and C. P. Schneider. 1988. Evidence of natural reproduction by stocked lake trout in Lake Ontario. J. Great Lakes Res. 14:3-8

Marsden, J. E., C. C. Krueger, and H. Hawkins. 1991. An improved trap for passive capture of demersal eggs during spawning: an efficiency comparison with egg nets. N. Am. J. Fish. Manage. 11:364-368.

Marsden, J. E., D. L. Perkins, and C. C. Krueger. 1995a. Recognition of spawning areas by lake trout: deposition and survival of eggs on small, man-made rock piles. *J. Great Lakes Res.* 21 (suppl. 1):330-336.

Marsden, J. E., J. M. Casselman, T. A. Edsall, J. D. Fitzsimons, W. H. Horns, B. A. Manny, S. C. McAughey, P. G. Sly, and B. L. Swanson. 1995b. Lake trout spawning habitat - a synthesis of current knowledge. *J. Great Lakes Res.* 21(suppl. 1):487-497.

Perkins, D.L., and C.C. Krueger. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at Stony Island reef, Lake Ontario . J. Great Lakes Res. 21 Suppl. 1:400-417

Plosila, D. S. and J. Anderson. 1985. Lake Champlain salmonid assessment report. Vermont Department of Fish and Wildlife. Essex Junction, Vermont. 125pp.

Reid, D. M., D. M. Anderson, and B. A. Henderson. 2001. Restoration of lake trout in Parry Sound, Lake Huron. N. Am. J. Fish. Manage. 21:156-169.

Schreiner, D.R., Bronte, C.R., Payne, N.R., Fitzsimons, J.D., and J.M. Casselman. 1995. Use of egg traps to investigate lake trout spawning in the Great Lakes . J. Great Lakes Res. 21 Suppl. 1:433-444

Selgeby, J. H., C. R. Bronte, E. H Brown Jr., M. J. Hansen, M. E. Holey, J. P. VanAmberg, K. M. Muth, D. B Makauskas, P. McKee, D. M. Anderson, C. P. Ferreri, and S. T. Schram. 1995. Lake trout restoration in the Great Lakes: stock-size criteria for natural reproduction. Journal of Great Lakes Research 21 (Supplement 1):498-504.

Table 1. Spawning habitat on potential lake trout spawning reefs in lakes Champlain, Michigan, and Huron (Parry Sound). Site ratings are based on cleanliness of substrate, depth of interstitial spaces, and presence of a contour.

Site	Depth range (m)	Approx. area (m^2)[a]	Slope[b]	Substrate type	Mean substrate size (range) in cm	Interstitial depth (cm)[c]	Presence of silt[d]	Longest fetch (km)	Zebra mussel density[e]	Rating
Lake Champlain										
Grand Isle breakwall	0.3-4	570	35-60°	angular rubble/ cobble	13-99	15-86	low		high	excellent
North of Burlington	0-3.5	250	30-50°	cobble	15-80	>20	low		low	very good
Burlington breakwall (north)	0.3-8.0	500	30-50°	angular rubble/ cobble	15-80	>20	low		low	very good
Burlington breakwall (south)	0.3-8.0	450	30-50°	angular rubble/ cobble	15-80	>20	low		low	very good
Shelburne Point	0.3-4	----------	---------	bedrock	----------	<10	low		low	poor
Allen Hill	0.3-8	4,000	45-65°	angular rubble/ cobble	15-35	10	high		moderate	moderate
Willsboro Bay	0.3-18	----------	0-45°	angular cobble/ boulder	40-300	>20	low		high	
Saxton Cove	2.6-5.0	320	10-60°	angular rubble/ cobble	10-60	10-30	moderate		high	excellent
Cannon Point	0.3-4.0	----------	70°	cobble	30-80	5-15	moderate		moderate	very good
Whallon Bay	0.3-14	64,372	20-85°	rounded rubble/ cobble/ boulder	17-106	4-29	low		moderate	excellent
Thompson's Point	1-10	----------	65°	bedrock	----------	<10	low		moderate	poor
Iron Bay	0.3-20	800	0-30°	angular cobble	10-152	20-100	low		high	excellent
Ore Den Bay	0.3-20	1000	0-10°	angular cobble	30-90	10-30	low		high	excellent
Button Bay	1-4	200	--------	angular cobble	----------	----------	low		high	very good
Arnold Bay	1-7	189	60°	angular rubble/ cobble	10-60	20	moderate		high	excellent

Site	Depth range (m)	Approx. area (m²)[a]	Slope[b]	Substrate type	Mean substrate size (range) in cm	Interstitial depth (cm)[c]	Presence of silt[d]	Longest fetch (km)	Zebra mussel density	Rating
Lake Michigan										
Bay Harbor	1-9	11,235	25-50°	rounded rubble/cobble	1.7-3,900	30-45	low	104 (NW 306°)	high	very good
Dahlia Shoal	3.5-7	142,010	40-50	rounded rubble/cobble	203.1 (2.9-1,057)	>100	low	82 (SW 235°)	high	excellent
Fishermans Island	1.5-4	195,390	30-45	rounded rubble/cobble	242.3 (2.8-1,305)	>100	low	119 (W 278°)	high	excellent
Gull Island Shoal	1-7	7,600,000	15-30	rounded rubble/cobble	59.0 (1.6-581)	>100	low	185 (SW 232°)	high	excellent
Hog Island Reef	2-5	60,493	30-45	rounded rubble/cobble	64.9 (6.5-457)	>100	low	104 (SSW 199°)	high	excellent
Ingals Point	1-1.5	650	50-60	rounded rubble/cobble	479.9 (82-2,929)	20-30	moderate	26 (NE 42°)	high	moderate
Leland	1-2	825	50-60	rounded rubble/cobble	280.3 (18-955)	20	moderate	96 (W 276°)	high	moderate
LTB Crib	1.5-3.5	100	35-45	rounded rubble/cobble	364.3 (25-1,913)	>100	low	22 (SW 259°)	high	excellent
Middle Ground	7-10	245,900	40-50	rounded rubble/cobble	451.7 (54-3,640)	45	low	69 (NW 322°)	high	good
Richards Reef	8-12	1,242,313	20-30	rounded rubble/cobble	494.9 (130-1,118)	>100	low	70 (W 282°)	high	excellent
Parry Sound										
Davy	1.5	30	30-40	rounded cobble	13.9±0.9	> 30	low	1.1	moderate	excellent
Bar Is.	1.5	30	30-40	rounded cobble	15.1±0.8	> 30	low	2.4	moderate	excellent
Horse Is.	1.6	30	30-40	rounded cobble	12.3±0.6	> 30	low	0.7	moderate	excellent
Mowat Is.	1.8	30	25-30	rounded cobble	13.0±0.7	> 30	low	3.5	moderate	moderate
Mary Is.	0.9	30	20-30	rounded cobble	13.8±0.7	> 30	low	6.5	moderate	moderate

[a] Area extrapolated from a combination of actual measurements of reef dimensions and visual estimations.

[b] A slope of 0° is vertical; 90° is horizontal.

[c] Measured vertically using a rigid ruler; interstices may extend below these depths.

[d] Silt was classified as low if it was barely visible, moderate if there was a thin coating of silt on hard substrates, and high if there was a > 1cm coating of silt on hard substrates

[e] zebra mussel density was classified as low if mussels were scattered on the substrate, moderate if there was a monolayer of mussels, and high if there were dense, multi-layer colonies that occluded interstitial spaces.

Table 2. Gillnet sampling for adult lake trout in lakes Champlain, Huron, and Michigan, 2002. All nets were set between 0730 and 1200 EST. M = male, F = female, U = unknown sex; ND = no data, fish fell out of net before capture. LAW = lake whitefish, SMB = smallmouth bass, SL = sea lamprey.

Lake/Site	Date	Depth (m)	Lake trout (TL in mm, sex)	Other fish
Lake Champlain				
Grand Isle	12 Nov	3–11.6	1 (668M)	5 LAW
		3-7	4 (720F, 580M, 697M, 605U)	2 LAW, 2 SL
Grand Isle	13 Nov	3 – 5.2	3 (752U, 673M, 592M)	1 LAW
Whallon Bay	14 Nov	1.5–36.9	0	2 SMB
Whallon Bay	14 Nov	2-18	2 (655F, ND)	4 SMB
Total effort = 7.5 hr				
Total CPUE = 1.3 lake trout/hour				
Lake Michigan				
Fishermans Island	17 Oct	6-8	0	0
Fishermans Island	21 Oct	10-16	0	0
Gull Island Reef	24 Oct	15-18	0	0
Gull Island Reef	25 Oct	21-23	0	0
Gull Island Reef	05 Nov	20-22	0	0
Richards Reef	24 Oct	30-38	0	0
Richards Reef	25 Oct	26-30	0	0
Richards Reef	05 Nov	24-32	0	0
Total effort = 11.6 hr				
Total CPUE = 0 lake trout				
Parry Sound				
Davy Is.	22 Nov	2-18	0	0
	23 Nov	2-18	0	0
	24 Nov	2-18	0	0
Mowat Is.	22 Nov	4-13	0	334
	23 Nov	2-25	0	0
	24 Nov	2-23	1 (681 M)	0
Bar Is.	22 Nov	2-10	0	0
	23 Nov	2-10	1 (661 F)	0
	24 Nov	2-11	0	0
Horse Is.	22 Nov	2-21	1 (572 U)	316 (3)
	23 Nov	2-22	0	91, 334
	24 Nov	2-22	0	0
Total effort = 18 hr				
Total CPUE = 0.16 lake trout/hr				

Table 3, Lake trout egg collections in Lake Champlain, Parry Sound, and Lake Michigan, 2000-2002. Eggs were collected in arrays of 15 egg nets and 15 fry traps ("traps") or in egg bags buried in the substrate. At Ore Den Bay eggs were collected with a suction sampler mounted on a remotely operated vehicle. Collections in egg traps and nets are reported as mean number of eggs per net or trap per day; collections from egg bags are reported as mean number of eggs per m^2 ± SD.

Location and year	Collection gear	# collectors	Sampling dates (dates of collections)[a]	# eggs	CPUE or # eggs/m2
2000					
Lake Champlain					
Grand Isle breakwall	traps	30	7 Nov- 8 Dec (13 Nov- 8 Dec)	3,799	4.08[b]
Cannon Point	traps	30	14 Nov- 29 Nov	0	0
Whallon Bay	traps	30	2 Nov- 4 Dec (14 Nov- 28 Nov)	1	0.002 ± 0.03
Button Bay	traps	30	4 Nov- 11 Dec (19 Nov- 11 Dec)	10	0.02 ± 0.21
Arnold Bay	traps	30	3 Nov- 11 Dec	85	0.12 ± 0.33
Lake Michigan					
Bay Harbor	bags	59	29 Nov	4	0.95 ± 3.6
Dahlia	bags	59	29 Nov	0	0
Fishermens Is.	bags	46	29 Nov	0	0
GTB New Mission	bags	30	27 Nov	0	0
Hog Is.	bags	60	2 Dec	0	0
Ingals Point	bags	30	Nov 27	2	0.94 ± 3.6
LC Hemingway	bags	30	28 Nov	0	0
LC Stoney Pt	bags	29	28 Nov	0	0
LTB crib	bags	33	13 Nov	362	154.5 ± 255.9
Middle Ground	bags	60	14 Dec	0	0
2001					
Lake Champlain					
Grand Isle breakwall	bags	59	27 Nov	39,593	9,623±1,658
Burlington breakwall (north)	bags	15	3 Dec	0	0
Burlington breakwall (south)	bags	15	29 Nov	0	0
Shelburne Point	traps	30	23 Oct- 29 Nov (30 Oct- 29 Nov)	1	0.001±0.03
Willsboro Bay	bags	19	5 Dec	0	0
Allen Hill	bags	15	29 Nov	0	0
Saxton Cove	bags	15	30 Nov	116	118 ± 59
Cannon Point	bags	15	4 Dec	0	0
Whallon Bay	bags	60	4 Dec	2,728	652 ± 158

Thompson’s Point	traps	30	8 Nov-13 Nov	0	0
Iron Bay	bags	15	4 Dec	2	1.9 ± 1.3
Arnold Bay	bags	15	30 Nov	949	972 ± 289
Parry Sound					
Davy Is	bags	29	14 Nov	377	186±224
Bar Is.	bags	29	14 Nov	775	519±411
Horse Is.	bags	29	14 Nov	563	278±258
Mowat Is.	bags	29	14 Nov	577	284±362
Mary Is.	bags	24	14 Nov	67	39±46
Lake Michigan					
Bay Harbor deep	bags	60	09 Nov	0	0
Bay Harbor shallow	bags	42	13 Nov	2	0.67±4.3
Bay Harbor	bags	37	21 Nov	16	6.1±14.3
Dahlia Reef	bags	47		0	0
Fishermen's Island	bags	84	26 Nov	35	5.9±15.9
Gull Island Shoal	bags	49	11 Dec	6	1.7±5.5
Hog Is.	bags	50		0	0
Ingals Point	bags	70		2	0.4±3.4
LTB crib	bags	30	19 Nov	107	50.2±53.8
2002					
Lake Champlain					
Grand Isle	bags	60	26 Nov	16,037	3,832±3,571.1
Whallon Bay	bags	45	25 Nov	1,033	342.8±872.5
Parry Sound					
Davy Is.	bags	60		4,297	1,027±1,052
Horse Is.	bags	59		776	189±228.6
Mowat. Is	bags	60		783	187±271.5
Bar Is.	bags	60		3,975	950±990.8
Lake Michigan					
Bay Harbor	bags	137		30	±
Dahlia	bags	58		0	0
Fishermen's Island	bags	58		2	0.54±3.9
Gull Is. shoal-east	bags	57	26 Nov	0	0
Gull Is. shoal-west	bags	54	26 Nov	0	0
Hog Is.	bags	59		0	0
Ingals Point	bags	60		0	0
Leeland	bags	48	1/19	0	0
LTB crib	bags	60		194	45.5±73.5
Middle Ground	bags	57		0	0
Richards Reef	bags	59	26 Nov	0	0

[a] Egg bags were all deployed in late summer prior to the onset of spawning; only retrieval dates are given.

[b] Eggs from nets and traps were not tallied separately on this date, so the SE could not be calculated.

Table 4. Lake trout fry collections in fry traps in Lake Champlain and Parry Sound, 2001-2003. Fry were collected in three designs of emergent fry traps: steel traps checked by divers (diver), and steel traps or soft traps checked by lifting to the surface (surface). Fry/m^2 was calculated as total number of fry divided by the total area under all the traps at a given site. CPUE = number of fry collected per trap-day. Number of fry per 100 eggs was calculated from quantitative estimates of eggs (from fall egg bags – Table 1) divided into quantitative estimates of fry (from diver traps) x 100. Surface fry traps did not yield quantitative estimates of fry per unit area.

Site	Trap type	Deployed	# Traps	# Fry	Fry/m^2	CPUE	Eggs/ m^2	Fry/ 100 eggs
2001								
Lake Champlain								
Grand Isle	surface	4/16-6/16	10	173	225.4	0.33	---	---
Whallon Bay	surface	4/20-6/13	19	148	63.0	0.14	---	---
Ore den Bay	surface	5/3-6/19	10	0	0.0	0.00	---	---
Arnold Bay	surface	5/2-5/4	10	594	228.5	2.38	---	---
Lake Michigan								
LTB crib	diver	4/5-6/5	16	0	0	0	0	0
Bay Harbor	diver	4/5-6/5	24	0	0	0	0	0
2002								
Lake Champlain								
Grand Isle	surface	4/5-6/6	12	237	105.0	0.32	---	---
Saxton Cove	surface	4/26-6/3	7	0	0	0	---	---
Whallon Bay	surface	4/10-6/4	20	89	31.0	0.08	---	---
Arnold Bay	surface	4/26-5/28	6	249	170.2	1.73	---	---
Parry Sound								
Davy Is.	diver	4/16-6/18	8	25	9.3	0.05	136	6.8
Bar Is.	diver	4/16-6/18	8	11	4.1	0.02	519	0.8
Horse Is.	diver	4/16-6/18	8	3	1.1	0.006	277	0.4
Mowat Is.	diver	4/16-6/18	8	0	0	0	219	0.0
Lake Michigan								
LTB crib	diver	4/10-6/10	16	0	0	0	0	0
Bay Harbor	diver	4/10-6/10	24	0	0	0	0	0
Fishermans Is.	diver	4/10-6/10	24	0	0	0	0	0
2003								
Lake Champlain								
Whallon Bay	diver	4/22-6/19	13	152	297.9	0.29	1,299	11.7
Grand Is.	diver	4/22-6/12	12	463	907.5	1.10	3,183	14.5
Grand Is.	surface	4/23-6/12	7	176	704.0	0.74	---	---

Arnold Bay	surface	4/30-6/4	10	4	16.4	0.02	---	---
Saxton Cove	surface	4/29-6/10	10	1,008	4,032.0	3.60	---	---
Parry Sound								
Davy Is.	diver	4/25-6/11	14	37	8.0	0.06	1,017	0.79
Bar Is.	diver	4/25-6/11	14	5	1.2	0.008	941	0.12
Horse Is.	diver	4/25-6/11	14	3	0.6	0.005	187	0.32
Mowat Is.	diver	4/25-6/11	14	5	1.1	0.005	171	0.63
Lake Michigan								
Fishermans Is.	diver	4/17-5/15	12	0	0	0	0	0

Table 5. Lake trout fry collections in egg bags retrieved in spring from Lake Champlain and Parry Sound, 2001-02 and 2002-03. No egg bags were left overwinter in Lake Michigan. Number of fry per 100 eggs was calculated from quantitative estimates of eggs (from fall egg bags – Table 1) divided into the mean fry/m^2 x 100.

Site	# bags	Dates deployed	# Fry	Mean fry/m^2	Mean % hatch
2001-02					
Lake Champlain					
Grand Isle	29	10/10 - 4/1	3,006	107 ± 98	1.1
Whallon Bay	26	8/21, 9/6 - 4/11	72	2.8 ± 8.0	0.4
Parry Sound					
Davy Is	25	9/4-5 - 4/16	23	12±26.9	8.9
Bar Is.	27	9/4-5 - 4/16	22	12±32.0	2.3
Mary Is.	14	9/4-5 - 4/16	0	0	0
Lake Michigan					
LC - Hemingway	25	9/13 – 4/19	0	0	0
LC - Stoney Point	27	9/13 – 4/19	0	0	0
LTB Crib	30	9/20 – 4/16	22	12±25.6	7.6
Bay Harbor	24	9/20 – 4/11	0	0	0
2002-03					
Lake Champlain					
Grand Isle	29	8/27 - 4/25	1,013	581 ± 85	18.2
Whallon Bay	27	9/9 - 4/22	44	23 ± 12.6	1.8

Estimates of abundance and the effect of lake trout egg predators on egg survival for Lakes Michigan, Huron (Parry Sound), and Champlain

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Introduction —

Results from evaluations of current research suggest that excessive mortality occurring between the time of spawning in the fall and the first year of life is likely the reason for the recognized lack of recruitment in lake trout populations in most of the Great Lakes. For significant natural reproduction to occur at a spawning reef and be measurable, sufficient numbers of males and females must congregate in the fall and deposit a sufficient number of fertilized eggs. Hatched fish must then develop over winter into successfully emergent fry. A range of adult abundance was measured at historic sites in northeastern Lake Michigan in the early 1990s (Dawson et al. 1997). Some sites were considered to have adequate numbers of adult spawners, based on a comparison with self-sustaining stocks in Lake Superior (Selgeby et al. 1995). However, it has not been determined whether significant spawning is occurring at these same sites. Lake trout populations in Parry Sound are relatively abundant and adult fish are known to deposit significant numbers of eggs on spawning reefs. The Parry Sound region has been declared a successful lake trout rehabilitation effort and as a result, supplemental stocking in the region has been discontinued (Reid et al. 2001). Lake Champlain also has abundant populations of spawning lake trout, though recruitment is considered to be low. Evaluation of spawning success at sites located in northern Lake Michigan, Parry Sound and Lake Champlain provide an opportunity to identify potential bottlenecks and establish their relative importance.

In addition to evaluations of adult abundance and egg deposition rates it is important to understand the dynamics of egg and fry predators. Predation on early life-stages has been a persistent but relatively unstudied concern that may be related to the lack of natural reproduction by lake trout in the Great Lakes. At the RESTORE conference it was concluded that biotic effects, like predation, should be considered a potential constraint to lake trout rehabilitation (Jones et al. 1995). The problem may be of increasing importance due to the recent addition of gobies and rusty crayfish to spawning reef fauna in Lake Michigan that already included native egg predators such as sculpins and crayfish.

The potential effect of interstitial predators is strongly dependent on the density of naturally deposited eggs and the density of predators. The goals of our study were to (1) determine the density of naturally deposited eggs on several spawning reefs in Lakes Michigan, Parry Sound, and Champlain, (2) determine the density and species composition of interstitial predators on several spawning reefs in Lakes Michigan, Parry Sound, and Champlain, and (3) compare egg and predator densities to determine minimum egg deposition rates that will lead to successful emergence of fry in the spring given variable predator densities.

Methods —

Three regions of the Great Lakes were evaluated to determine lake trout egg deposition rates and the abundance of interstitial predators. Regions were selected based on their unique qualities in regard to progress toward lake trout restoration. Lake Michigan represented the worst case scenario; with low egg deposition rates, high predator abundances (both native and non-native), and no remnant stocks of lake trout. Parry

Sound in Lake Huron represented the best case, high egg deposition rates, intermediate levels of native predators, remnant stocks of naturally reproducing lake trout, and abundant spawning lake trout in the population (Reid 2001). The intermediate location was Lake Champlain, where egg deposition rates were high, predators were mainly native species and of intermediate abundance. There were no remnant stocks of lake trout, and only 5 to 10 percent of the adult lake trout sampled in Lake Champlain are naturally produced and not stocked (Ellrott and Marsden in press).

Within a given region, spawning sites were identified based on reconnaissance diving surveys to evaluate habitat, past experience with evaluations of lake trout egg deposition, and current knowledge of sites known to attract spawning lake trout in the fall. In Parry Sound, a total of five sites were identified based on the above criteria. These included Davy, Bar, Mowat, Horse, and Mary Islands. Perry Sound is the region that we had the greatest knowledge of lake trout spawning sites, based on previous investigations (Fitzsimons; Reid et al. 2001). In Lake Champlain, six sites were identified, these included Grand Isle, Arnold Bay, Saxon Cove, Iron Bay, Whallon Bay, and the Coast Guard. Less information was available regarding spawning behaviors in Lake Champlain when compared with Lake Huron or Lake Michigan. Sites in Lake Huron and Lake Champlain were all near shore locations. In Lake Michigan, nine sites were identified. Because a significant portion of lake trout spawning habitat in northern Lake Michigan is offshore, we chose to evaluate five off shore sites and three near shore sites. The offshore sites include Dahlia Shoal, Middle Ground, Hog Island Reef, Gull Island Shoal and Richards Reef. The near shore locations included Little Traverse Bay-North, Little

Traverse Bay-South (Bay Harbor), Fisherman's Island, and Ingalls Point (Grand Traverse Bay).

Diving surveys were used to further identify habitat within sites. Divers would survey an entire reef looking for areas with substrate, slope, and depth characteristics appropriate for attracting spawning lake trout (Fitzsimons 1994; Marsden et al. 1995). When specific locations were identified within a reef structure, a 100-m transect was established to record interstitial depth, slope, percent periphyton, zebra mussel coverage, and observations of interstitial predators.

To evaluate the amount of egg deposition at a given location, we buried nets using standard methods (Perkins and Krueger 1994, 1995; Fitzsimons 1995). Prior to the spawning season, sixty individually numbered egg collection nets were buried at each location. The nets were placed in pairs along either side of a 30-m-long marked line at 1-m intervals. The nets were positioned at the top of the drop-off at each location. Each net was constructed of a 0.5-m-deep cloth bag (3-mm mesh) attached to a PVC ring (0.35-m diameter or 0.96-m^2 in area). Divers deployed nets by excavating a hole 40-50 cm deep, placing the net in the hole, and back filling with the removed substrate.

Nets were retrieved after the spawning season (typically late November early December). To retrieve nets, divers would carefully remove the substrate from the inside of the net while preventing interstitial predators from escaping. After the substrate was removed the net would be twisted at the top and sealed with a cable tie. Any eggs or predators would remain in the net bag.

The recovered nets were then brought to the lab in water. The contents of each net bag would be evaluated in a clear glass pan placed on a light table. All eggs were counted and preserved in Stockard's solution to determine stage of development. Interstitial predators were identified, counted, weighed (g) and measured (mm). Total lengths were recorded for all fish species and carapace lengths were recorded for all crayfish species. All predators were preserved in ethanol, and later dissected to determine whether the diet included lake trout or other fish eggs.

For each site we estimated the average number of eggs per net and the variance. To estimate the number of eggs per square meter, we multiplied the average number of eggs per net by an adjustment factor of 14.085 that is based on the surface area of the egg nets.

For each site we estimated the total number of predators that were large enough to prey on lake trout eggs. For crayfish the length was greater than 19 mm carapace length and only sculpin and gobies greater than 42 mm were used (citations?). We estimated the number of crayfish and sculpin at each location. In each case we multiplied the number of predators per net by an adjustment factor of 14.085 to obtain the number per square meter. For a given region we report the density and percent species (native crayfish, exotic crayfish, sculpin, and other) of interstitial predators.

The mean and standard error of the number of eggs and predators were estimated for each site and region. Data did not meet assumptions of normality or homogeneity of variance. Analysis of variance (ANOVA) was used to test for differences in egg density and predator densities among sites and between regions. ANOVA is justified based on the underlying distribution of the data is likely normal. The ratio of eggs per predator was calculated and compared for sites that were found to have emerging fry in the spring (indication of success), and those that had none.

Results —

The density of eggs after lake trout have completed the spawning run in Lake Champlain was different between sites (ANOVA, df=9, P=0.000) and highest among the regions evaluated averaging 2,354±319 eggs per M^2 (ANOVA, df=6, P=0.000). Eggs were collected at six of the ten sites evaluated in Lake Champlain (Table 1). The Grand Isle location had the greatest number of eggs deposited of all sites at 6,584±676 eggs per M^2. Other locations were variable but lower in egg density ranging from 2 to 891 eggs per M^2. Site differences in the egg density were also apparent among the five sites evaluated in Parry Sound (ANOVA, df=4, P=0.000). Sites in Parry Sound were less variable and in general lower in egg density (455±36 eggs per M^2) than those observed in Lake Champlain (Table 1). The highest egg densities occurred at Bar and Davy Islands averaging 700 to 800 eggs per M^2, the other three Parry Sound locations had egg densities of less than 200 eggs per M^2. Sites in Lake Michigan had significantly fewer egg deposited than in either Lake Champlain or Parry Sound. A man-made crib located in northern Little Traverse Bay provided the highest egg density estimates at 76 eggs per M^2. Densities at all other locations were estimated at less than 3 eggs per M^2 (Table 1).

The density of interstitial predators varied between sites within regions and among regions. Lake Champlain and Parry Sound contained the lowest predator densities averaging 6±1 predators per M^2 (Table 1). Within Lake Champlain we observed 7 native interstitial predator species; 6 fish and 1 crayfish. The Grand Isle and Arnold Bay locations had the greatest number of predators averaging 11 predators per M^2. It is interesting to note that the two sites with the highest egg densities (Grand Isle and Arnold Bay) were also sites with the highest predator densities (Table 1). In Parry Sound we observed 9 native predator species; 5 fish and 4 crayfish. Mowatt Island had the highest predator densities at 8±1 predators per M^2. An inverse relationship was observed between egg and predator density in this system, the greater the density of predators the lower the density of eggs (Table 1). Lake Michigan contained the highest predator densities observed averaging 15 predators per M^2 ranging from a low of 7 to a high of 31. We observed 9 native and 2 exotic predator species (1 fish and 1 crayfish) in Lake Michigan. Of the native predators, seven were species of fish, three were crayfish, and an occasional mudpuppy was observed.

The predator species observed in each region can be summarized in the following categories, native crayfish, O. rusticus (exotic), sculpin, round goby (exotic), and other. When viewed in this way, it is apparent that sculpin are the major players in Lake Champlain, while native crayfish dominate in Parry Sound, Grand Traverse Bay and

Offshore in Lake Michigan. The Leeland location in Lake Michigan is dominated by native crayfish and the “other” category. A large number of longnose dace were observed at this location and account for the majority of the “other” category. The nearshore zone in northeastern Lake Michigan is now dominated by exotic predators such as the round goby and rusty crayfish. As a consequence, numbers of native crayfish and sculpin are declining in this region.

When compared among regions, reefs with the highest egg deposition and lowest predator abundance are best for overwintering lake trout eggs to emergence. In order to better understand the interactions between egg and predator abundance levels, we calculated a ratio of the number of eggs per predator and compared these values for sites that had successful emergence of lake trout fry in the spring and those that did not. The lowest level at which fry emergence was observed was at 24 lake trout eggs per predator, and the highest ratio recorded at sites without emergence was around 10 eggs per predator. Therefore we conclude that successful egg densities relate to the abundance of predators at a given location. Further, the number of eggs deposited per predator should be greater than 24 to ensure success to emergence, though the actual threshold lies somewhere between 10 and 24 eggs per predator (Table 1).

Discussion —

Egg deposition rates are relatively high in Parry Sound and Lake Champlain, yet barely detectable in Lake Michigan. The densities of predators were relatively low in these systems when compared to Lake Michigan. The composition of interstitial predator species varied among the regions evaluated. In Lake Champlain predators were mainly sculpin, while in Parry Sound the primary predators were native crayfish species. In Lake Michigan on the other hand, offshore and Grand Traverse Bay predator communities were similar to Parry Sound and dominated by native crayfish. The nearshore zone presented a much different picture than all other locations, as it was dominated by two recently introduced exotic species, the rusty crayfish and the round goby. Exotic species provide a unique challenge to rehabilitation efforts in that their interactions within the community are poorly understood.

The influence of predation on lake trout eggs and its affect on recruitment to the fry stage is not clear. An understanding of the interstitial predator densities in conjunction with lake trout egg deposition rates is essential to evaluating this influence. We have observed that lake trout must deposit eggs at a rate between 10 and 34 eggs per predator in a square meter area. The target density of eggs per predator is based on initial egg deposition minus the affect of predation in the first three weeks after deposition. The results of this investigation could be used to determine target densities of eggs deposited in a given location, through establishing target adult spawning biomass.

References:

Ellrott, B. E. and J. E. Marsden. In press. Lake trout reproduction in Lake Champlain. Trans. Am. Fish. Soc.

Fitzsimons, J. D. 1994. An evaluation of lake trout spawning habitat characteristics and methods for their detection. Can. Tech. Rep. Fish. Aquat. Sci. No. 1962.

Fitzsimons, J. D. 1995. Asessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. J. Great Lakes Res. 21(Supplement 1):337-347.

Jones, M. L., G. W. Eck, D. O. Evans, M. C. Fabrizio, M. H. Hoff, P. L. Hudson, J. Janssen, D. Jude, R. O'Gorman, and J. F. Savino. 1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages. Journal of Great Lakes Research 21 (Supplement 1):505-517.

Marsden, J. E., Casselman, J. M., Edsall, T. A., Elliott, R. F., Fitzsimons, J. D., Horns, W. H., Manny, B. A., McAughey, S. C., Sly, P. G., and Swanson, B. L. 1995. Lake trout spawning habitat in the Great Lakes a review of current knowledge. J. Great Lakes Res. 21(Supplement 1):487-497.

Perkins, D. L., and Krueger, C. C. 1994. Design and use of mesh bags to estimate deposition and survival of fish eggs in cobble substrate. N. Am. J. Fish. Manage. 14:866-869.

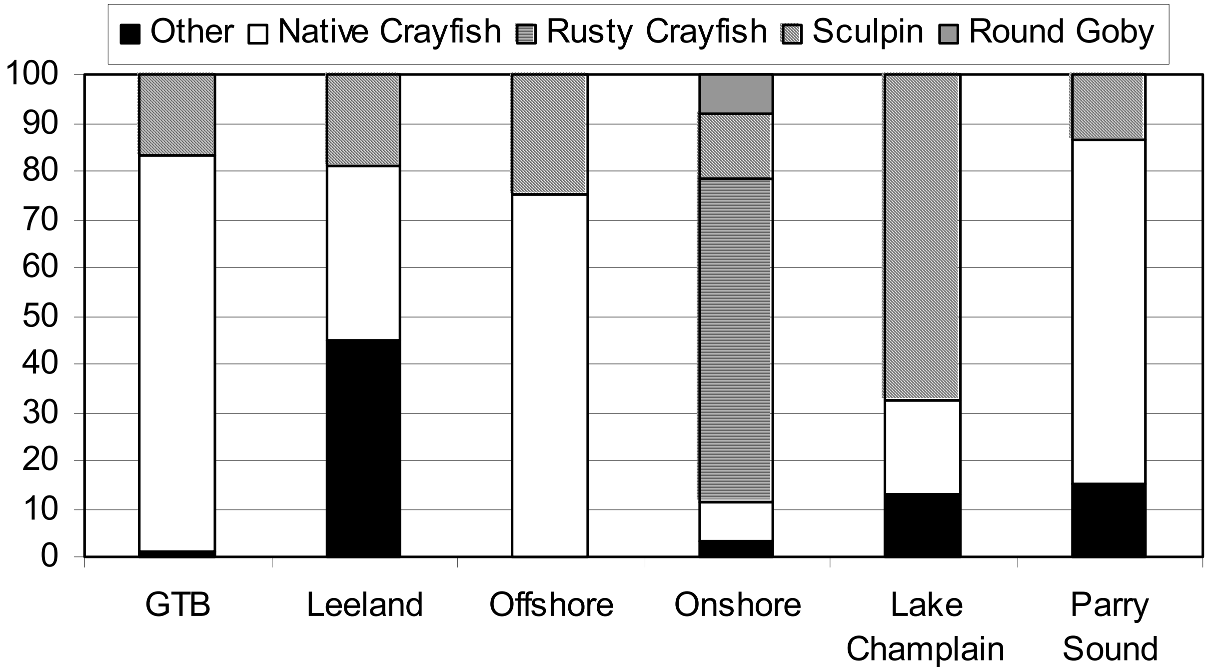
Perkins, D. L., and Krueger, C. C. 1995. Dynamics of reproduction by hatchery-origin lake trout (Salvelinus namaycush) at Stony Island Reef, Lake Ontario. J. Great Lakes Res. 21(Supplement 1):400-417.

Reid, D. M., Anderson, D. M., and Henderson, B. A. 2001. Restoration of lake trout in Parry Sound, Lake Huron. N. Am. J. Fish. Manage. 21:156-169.

Table 1. Comparison of lake trout egg deposition rates, abundance of predators of viable length, and ratios of eggs to predators among sites and among regions. A Y in the fry column indicates that fry emergence was measured from the site in the spring.

Site		Eggs per M^2±SE	Total predators per M^2±SE	Egg to predator ratio	Fry?
Parry Sound		455±36	6±1	82	Y
	Bar Island	808±91	4±1	222	Y
	Davy Island	724±100	5±1	147	Y
	Horse Island	214±25	6±1	38	Y
	Mary Island	30±9	7±2	4	
	Mowatt Island	185±29	8±1	24	Y
Lake Champlain		2,354±319	6±1	384	Y
	Allen Hill	0±0	5±2	-	
	Arnold Bay	891±284	11±2	79	Y
	Burlington Breakwall	0±0	2±1	-	
	Cannon Point	0±0	8±2	-	
	Coast Guard	4±4	6±2	1	
	Grand Isle	6,584±676	11±1	591	Y
	Iron Bay	2±1	3±2	1	
	Saxon Cove	109±58	2±2	58	Y
	Whallon Bay	680±143	2±1	276	Y
	Willsboro Bay	0±0	7±2	-	
Lake Michigan					
Onshore		20±4	14±1	1	
	Bay Harbor-Deep (9 m)	0±0	23±2	-	
	Bay Harbor-Shallow (3 m)	1±1	7±2	<1	
	Bay Harbor (1-2 m)	3±1	10±1	<1	
	Fishermans Island	3±1	8±1	<1	
	LTB-Crib	76±14	22±1	4	
GTB					
	GTB-Ingalls Point	0.4±0.2	26±2	<1	
Leeland					
	Leeland	0±0	16±2	-	
Offshore		0.2±0.1	14±1	<1	
	Hog Island	0±0	11±1	-	
	Gull Island Shoal	1±1	27±1	<1	
	Dahlia Shoal	0±0	9±1	-	
	Middle Ground	0±0	13±1	-	
	Richards Reef	0±0	10±1	-	

Figure 1. Proportion of predator species within each of the six regions identified. Native Crayfish include observations of O. propinqus, O. virilis, O. limosus, and Cambarus. The other category includes smallmouth bass, largemouth bass, longnose dace, common white suckers, longnose suckers, banded killifish, Johnny darters, log perch, rock bass, bluntnose minnows and mudpuppies.



Assessing the Effects of Physical Disturbance and Egg Predation on Lake Trout Egg Mortality and Its Application to Lake Michigan

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Abstract: Directly assessing the effects of egg predators on lake trout survival in the Great Lakes is difficult but a necessary part in quantifying their role in the continued lack of lake trout restoration, particularly in Lake Michigan. We developed an egg seeding method to separate the effects of physical disturbance and egg predation. We used distinctively coloured high-carotenoid lake trout eggs seeded into egg nets and quantified their loss at five different densities (100, 250, 500, 1000, and 5000 eggs·m^{-2}) over a three to four week period. We applied the method at six reefs in Lake Michigan with relatively high abundance of egg predators, four reefs in Parry Sound where egg predator abundance was lower and lake trout are self-sustaining, and two reefs in Lake Champlain where egg predator abundance was also low. Using the method we noted that despite higher predator abundance at the Lake Michigan reefs, a greater predation effect was evident for the Parry Sound reefs with intermediate effects indicated for the Lake Champlain reefs. We attribute this deviation from the expected direct relationship between predator density and predator effect to the generally lower levels of physical disturbance at the Parry Sound reefs that we suspect allowed more efficient egg foraging by predators. In contrast, egg recovery at the highest seeding density (5000 eggs·m^{-2}), where egg recovery was relatively predator independent because of satiation, was directly related to wind fetch for Lake Michigan. We conclude that the high levels of physical disturbance in Lake Michigan, that cause high levels of egg loss, potentially ameliorate overall losses by affecting egg predator foraging efficiency. Nevertheless given the extremely low rates of natural egg deposition that we noted over a three-year period (2000-2002) in northeastern Lake Michigan, we suggest that current egg predator densities there are likely limiting lake trout restoration.

Introduction

The lake trout of Lake Michigan, like those of almost all of the Great Lakes with the exception of Lake Superior fail to show the anticipated natural reproduction expected from several decades of stocking and chemical control of sea lamprey to control predation on lake trout (Holey et al. 1995, Madenjian and DeSorcie 1999, LMLTTG 2003). After lake trout were driven to extinction by 1956 from the combined effects of overfishing and sea lamprey predation (Wells and MacLain 1973), lakewide stocking of lake trout began in 1966, approximately 5 years after sea lamprey control by lampricide application in streams was initiated (Smith and Tibbles 1980). By 1991 over 60 million fish had been stocked with stocking from 1966 to 1991 usually in excess of 2 million fingerlings and yearlings per year (Holey et al. 1995).

Several potential impediments to natural reproduction by lake trout in Lake Michigan exist including low spawner abundance, high rates of exploitation, inappropriate spawning site selection that may be affected by stocking sites, low genetic diversity, habitat degradation, contaminants, a thiamine deficiency that results in a type of larval mortality known as EMS, and predation of eggs and fry (LMLTTG 2003). Of this list probably the least is known about the effects of egg and fry predators in part because of a lack of information on the location of current spawning sites relative to historic (Dawson et al. 1997), and the abundance of naturally deposited eggs and egg and fry predators at these sites, and information on what proportion of eggs and fry are being consumed by predators. Based on Lake Ontario where more is known about egg and predator densities, five out of eight spawning reefs were considered to have sufficiently low egg densities that egg predators could seriously affect reproductive success (Fitzsimons et al. 2002)

Models have been used previously to assess the effect of multiple predators on survival of eggs and fry of lake trout (Jones et al. 1995, Savino et al. 1999). While these models were useful in assigning relative predation risks from epibenthic predators, interstitial egg predators and fry predators at present they seem under parameterized given all the possible factors impinging on predation risk from a particular predator. Factors like temperature, predator species and size, inter-and intra-specific competition, and substrate size all have the potential to affect predation but have not explicitly been accounted for in models used to date (Chotkowski and Marsden 1999, Fitzsimons et al. 2003, Ellrott et al 2003) . Moreover even when data is available, much of it is obtained under controlled laboratory conditions and conditions in the wild may have either positive or negative effects on such data.

A comprehensive study to assess the effects of egg and fry predators in northeastern Lake Michigan on lake trout reproduction that was begun in 2000 (Jonas et al. 2003), provided an opportunity to determine where contemporary stocks are spawning, what range of egg abundance is occurring and what the potential for egg and fry predation is. Although simultaneous collection of eggs and egg predators were part of the project objectives and will provide valuable insights as to the potential of predation to limit reproduction, they have their limitations (Fitzsimons et al 2002). Egg predation can only be confirmed in such studies by examining stomach contents but stomach contents represent only a relatively short period of time and predation rates can be affected by a number of factors including egg density, species of egg predator and temperature that can change during the egg incubation period (Savino et al. 1999, Savino and Henry 1991, Miller et al. 1992, Horns and Magnuson 1981, Biga et al 1998, Chotkowski and Marsden 1999). For predators that macerate their food like crayfish, stomach contents provide almost no information as to what was consumed. Similarly in the case where egg density is so low as to make it almost impossible to find eggs in stomach contents, the predators may still have the potential to eat eggs if eggse present and so represent a latent mortality factor, but there is no way of determining what that potential is. Moreover there is no way in such studies to know how many eggs were present initially which is important to calculate what proportion of eggs arensumed by predators relative to other sources of egg loss.

Given the problems inherent and assumptions involved in assessing the significance of egg predators taking either a modeling approach or an approach involving the simultaneous collection of eggs and predators and examination of stomach contents suggests that the only way of reliably assessing the effect of a given predator community in limiting lake trout reproduction is the use of mesocosms containing known number of eggs and predators. Mesocosms have been used to assess the effects of predators in freshwater and marine systems (Gleason and Bengtson 1996, Rooker et al. 1998, Turner et al 199, Moksnes, 2002). The results of such studies can be difficult to interpret because mesocosms can introduce artifacts that cannot be separated from predatory effects requiring that 'open' mesocosms be used (Steel 1996).

In open lake environments used by lake trout for spawning, factors other than predation are active and have the potential to influence the outcome of mesocosm type studies. Likely the most significant cause of egg loss relative to egg predation is that caused by physical disturbance. Egg loss resulting from physical disturbance can be significant and can occur either by direct loss of eggs (Clady 1976, Ventling-Schwank and Livingstone, 1994, Roseman et al 2001) or indirect loss through death and subsequent disintegration of eggs that are extremely sensitive to physical disturbance during the early stages of embryogenesis (Fitzsimons 1994, Fitzsimons et al 1995, Eschenroder et al. 1995, Perkins and Krueger 1995). Nevertheless for a given location,losses from physical disturbance are likely density-independent.

Separating the effects of physical disturbance from egg predation using mesocosms seems at first an intractable problem until one considers the type of processes at work for each factor. Losses due to physical disturbance are likely density-independent suggesting that regardless of the number of eggs initially added to a mesocosm, a relatively constant proportion would be recovered but that this proportion would be inversely proportional to the amount of physical disturbance. Wave energy models developed by physical limnologists indicate that shear stress (ie. the amount of energy necessary to move bottom particles or in this case eggs) decreases with depth (Miller et al. 1977). Similarly the square of bottom velocities encountered during storms for a given depth, particularly at shallow depths, increases rapidly up to some wind fetch distance which is dependant on the duration of the event asuch as a storm that produced them (M. Skafel, NWRI, pers. comm.). It follows that on average the amount of physical disturbance and in turn the potential for egg loss increases from inland lakes to the Great Lakes, where it would be greater in open lake areas relative to embayments.

In contrast to the density independence associated with egg loss resulting from physical disturbance, that associated with predation may be density dependent because the ability of a given predator or group of predators has a physical limit. This limit is set ultimately by the size of a predator (Biga et al. 1998) but is more likely under the more immediate control of other factors controlling metabolism like temperature and activity (Diana 1995). Prey appear to profit from this limit under what has become known as the predator satiation or predator swamping hypothesis, and is found in such diverse phyla as corals (Hughes et al 2000), crabs (Van Montfrans et al. 1995), terns (Becker 1995), sea turtles (Eckrich and Owens 1995), and mayflies (Sweeney and Vannote 1982) and seems to be strongly associated with reproductive synchrony. Salmonines including lake trout show a high level of reproductive synchrony (MacLean et al, 1981, Tallman 1990, Fitzsimons 1995) that along with predator satiation may provide other benefits like mate finding, genetic divergence through temporal isolation, and synchrony with limited food resources. Predator satiation appears to operate with known and potential egg predators of lake trout as well. Fitzsimons et al (2004) noted that lake trout egg predation in controlled laboratory studies using a range of egg densities from 5 to 500 eggs per aquaria, by the crayfish *Orconectes propinquus*, the slimy sculpin (*Cottus cognatus*), and the round goby (*Neogobius melanostomus*), showed evidence of reaching an asymptotic egg consumption as a proportion of eggs available or satiation. Beyond this point the proportion of eggs consumed was independent of egg density. The relationship between egg density and egg consumption for each predator varied, however. Most notably the crayfish was relatively inept compared to the two fish species, while within the two fish species, the goby was better able to detect and consume eggs at lower concentrations in the substrate and consumed more eggs at higher densities than the sculpin. At extremely low egg densities the crayfish and sculpins were less able to find and consume eggs than gobies

Taken together it is evident that for eggs released into a mesocosm, the proportion of eggs recovered will be under the control of density independent (ie. physical disturbance) and density dependent (ie. egg predation) factors. One can envisage a number of scenarios for a range of egg densities (Fig. 1). In situations with either low or high physical disturbance but relatively low predation there is a change in the proportion of eggs recovered but no relationship with egg density such that egg recovery is density independent. When the effect of a predator is added, he proportion of eggs recovered increases up to some inflection point above which satiation occurs and egg recovery becomes limited by the amount of physical disturbance. The resulting curve is asymptotic in nature. As the amount of physical disturbance and predation is increased the relationship still follows an asymptotic curve however the inflection point is shifted to the right to a higher egg density while the horizontal asymptote declines such that a smaller proportion of eggs are recovered. Fig. 1 shows four scenarios but seemingly an almost endless number are possible depending on the particular predator community and physical process active at a location. To compare sites having different levels of physical disturbance it is possible to calculate the point at which egg recovery switches from being density dependant to density independent or the Km which is analogous to the Km from enzyme kinetics. Since Km has the same units (e.g. eggs·m^{-2}) as natural egg deposition it is possible to compare the two and determine if the natural deposition rate is above the satiation point. For those locations where natural deposition is below the satiation point it would seem that the effect of predation could be significant but as natural egg deposition reaches and exceeds the satiation point, egg predation will become relatively insignificant.

Given the above conceptual understanding of how physical disturbance and egg predation might interact and affect egg mortality we developed a multidensity (100 to 5000 eggs·m^{-2}) egg seeding method to estimate the separate effects of physical disturbance and egg predation at spawning reefs in Lake Michigan. We compared these reefs with reefs in Parry Sound where lake trout are self-sustaining (Reid et al 2001), so co-existing with the current predator community, and reefs in Lake Champlain where there are few egg predators, none of which are exotic (E. Marsden, UVN, Burlington, Vermont, pers. comm.). The nucleus of our approach was an open egg net that we have used previously to estimate lake trout egg deposition rates and predator abundance in the Great Lakes (Fitzsimons 1995, Fitzsimons et al. 2002) and that functioned here as a microcosm. Its small size (28 cm dia. 0.02 cu. m.) permitted abundant replication and was readily deployed by SCUBA divers. The eggs used were obtained from captive brood stock fed a high carotenoid diet so as to distinctively colour eggs and help in distinguishing natural from seeded eggs. Eggs at one of the 5 different densities were added to the nets at random by SCUBA divers at the time of estimated peak spawning and the nets retrieved approximately three weeks later when we evaluated the number of seeded eggs remaining and determined the average abundance of crayfish and sculpins and assessed the relationship between egg recovery and predator abundance and physical disturbance. As a surrogate for physical disturbance we used wind fetch. Herein we describe the results of our collections and an analysis of the relative effects of egg predation and physical disturbance at the three locations.

Methods

Sites used

Lake Michigan

Five natural reefs and one man-made crib located in northeastern Lake Michigan were used, 3 of which were offshore submerged reefs (e.g. Middle Ground, Hog Island Reef, and Dahlia Reef) while the other 3 reefs were all located at the shoreline (Fig. 2). Habitat characteristics for each of the reefs are given in Table 1.

Lake Huron

Four natural reefs in the Parry Sound area of Georgian Bay, a large bay to the east of Lake Huron, were used. All four (Davy Island, Mowat Island, Bar Island, Horse Island) were located at the shoreline of islands (Fig. 3). Habitat characteristics are given in Table 1.

Lake Champlain

One natural reef (Whallon Bay) and one man-made reef (Grand Isle) located in central Lake Champlain were used. Both sites are located on the shoreline (Fig. 4). Habitat characteristics for the two reefs are given in Table 1.

Construction, deployment, and retrieval of egg nets

A net previously described by Fitzsimons (1995) having a diameter of x mm and a depth of x mm was used with the following modifications. The ring had the following dimensions: I.D. 28 mm, O.D. 30 mm, thickness 5 mm. Nets were constructed of synthetic fabric with a pore size of 3 mm, small enough to retain eggs and predators but large enough to allow the passage of silts and sands. At each site, a total of 60 nets were used only 25-30 of which were seeded depending on location although all were used to calculate the amount of natural deposition. Numbers of seeded eggs found in non-seeded nets provided an opportunity to look at near-field resuspension-deposition relative to far-field resuspension-deposition.

Nets were buried in pairs approximately 1 m apart along a 30 m line set parallel and at the top of the dropoff at each location. Divers would excavate sufficient substrate to accommodate the net, position the net in the excavation created, then backfill the net up to the rim of the net with the material excavated. When completed the rims of the egg nets were generally level with the surrounding substrate. Nets were placed in the substrate approximately 30 days prior to seeding (Table 2) to allow the substrate within each net to re-equilibrate with the predator community in the surrounding substrate. A tidbit temperature logger used to determine temperature over the period of seeded egg incubation. It was attached to one of the nets at the time of deployment where it remained until the time that nets were removed from the substrate.

Approximately 19-29 days after egg nets had been seeded (Table 2) SCUBA divers removed all nets from the substrate at each of the reefs. Divers would carefully remove all substrate so as not to disturb the predators or the eggs in the nets, and then sealed the net with a plastic closure. This was generally successful for sculpins and crayfish that were photophobic and generally quite lethargic at the time of retrieval. Smallmouth bass that were only found at the Parry Sound sites and two of the Lake Michigan sites, tended to be more active such that some escaped. Because of good visibility where this occurred, it was readily noted by divers and later added to the contents of the net although no information for these fish was available for length or weight. Because the size of smallmouth bass was so uniform, sizes of those fish that remained in nets ware considered representative of those that escaped. Gobies were considerably more active at the time nets were removed from the substrate with many escapees, not all of which were noted by divers because of poor visibility. As such the densities for the sites where gobies occurred in Lake Michigan are considered highly conservative.

Assessment of spawning period

Spawning date in Lake Michigan was determined directly by successively collecting and removing eggs with an airlift from 30 cm dia. plastic funnels buried in the substrate at the Menonoqua site. The funnel to which was attached a 5 cm plastic hose that exited from the side of the reef, allowed SCUBA divers to regularly remove eggs with a diver operated airlift and track the level of egg deposition over time. As Menonoqua was the only site where significant lake trout spawning occurred and was close enough to shore it was the only location sampled and we assume that it is representative for the other reefs used in Lake Michigan.

For Parry Sound, spawning date was estimated from intensive trap netting undertaken by the Ontario Ministry of Natural Resources at Davy and Horse Islands during the fall of 2001. As with Lake Michigan we assumed there was no reef-to-reef variation in spawning date such that all of the four reefs within the Parry Sound area were treated the same.

Spawning at the two locations in Lake Champlain was ascertained by SCUBA divers who regularly visited the sites during the fall of 2002 and looked amongst cobbles for evidence of eggs.

Assessment of spawning

Typically at each site, the 60 egg nets were examined for evidence of naturally deposited eggs. This included live and dead eggs as well as assigned chorions but did not include any classes of seeded eggs. Assigning chorions to a particular group (ie seeded or naturally deposited) was based on the proportion of live eggs in those two groups. Egg deposition was determined as the average total number of eggs divided by the cross-sectional area of the net ($0.0710\ m^2$) and expressed as $eggs \cdot m^{-2}$.

Eggs used for seeding

To provide eggs for the seeding experiments that we could distinguish from naturally deposited eggs that tend to be varying shades of yellow we fed brood fish in a hatchery a high carotenoid diet. For the studies in Lake Michigan and Parry Sound brood fish were a combination of Seneca and Green Lake strain lake trout held at the USGS laboratory in Wellsboro, Pennsylvania fed a commercial diet (Mellick Aquafeed Inc., Catawissa, PA 17820) containing 4.4 mg/kg of the carotenoid canthaxanthin. Eggs were stripped , fertilized, and held at 9-10ºC until just past epiboly at this same facility when they were transported to CCIW. Fitzsimons (1994) noted that once this stage had been reached, eggs were relatively insensitive to physical shock. At CCIW, all deformed or unfertilized eggs were removed and the eggs held for 7 days at 9-10ºC until just before seeding.

For the Lake Champlain studies, brood fish held at the Salisbury Fish Hatchery in Salisbury, Vermont, were fed a commercial diet containing 100 mg/kg of canthaxanthum Eggs were stripped, fertilized and held at 9-10ºC until just past epiboly at this same facility when they were transported to the Rubenstein Laboratory at University of Vermont in Burlington. Here all deformed or unfertilized eggs were removed and the eggs held for 7 days at 9-10ºC until just before seeding.

Seeding protocols

One to two days prior to when eggs were to be seeded, eggs were hand counted out in water filled glass trays for the following egg densities in units of eggs·m^{-2} (numbers of eggs added per net): 100 (7), 250 (17), 500 (34), 1000 (68), and 5000 (340). Five replicates were used at each density. Eggs were placed in water filled plastic bottles, completely filled with water and left in a large tank at 5-6ºC until they could be transported on ice by road to the field site. At the field site all the eggs to be seeded at a particular reef were added to large net bags and transported by a SCUBA diver to the bottom. Here divers randomly drew a bottle from a bag and in turn randomly selected one of the nets from the 30 pairs and gently added the eggs to the net. Prior to releasing the eggs the diver would remove one to two cobbles to permit the eggs to settle deep into the interstial spaces of the cobbles within a bag using gentle hand motion. This ensured that no seeded eggs were visible once any cobbles removed had been replaced.

To assess egg survival five replicate samples of 100 eggs for each of the batches of eggs (Lake Michigan, Parry Sound, Lake Champlain) were held in the lab until hatch at 9-10ºC. Dead eggs were removed on a daily basis and survival calculated on the basis of percent eye-up and percent hatch. As an additional control, 8 plastic incubators (Marsden et al. 1994) were loaded with the same eggs as used for Parry Sound. These were buried by divers at Mowat Island on the same date as eggs were seeded and removed on the same date as egg nets were removed from the substrate.

Net sorting and predator densities

Once nets were returned to the laboratory their contents were sorted within 28-hr. Predators that included crayfish, sculpins, gobies and smallmouth bass were removed first and placed in screened containers until they were identified to species and their length and weight determined. Eggs were then placed in water filled glass dishes, removed with a siphon tube and placed in one of four categories depending on whether they were live or dead and whether they were orange (seeded) or yellow (naturally deposited). Chorions were assigned to the seeded or naturally deposited groups by the proportion of total live eggs in each of the groups.

Predator densities were calculated as the average number·m^{-2} for each of the types of predators wherin we pooled all crayfish into one group and all sculpins into one group. Only sculpins with a total length of >43 mm and crayfish with a carapace length >19 mm were included as it was only these sizes that were capable of eating eggs.

Calculation of Km

The proportion of the total seeded eggs recovered, both live and dead at each density were averaged and semi-log plots made of the average proportion of eggs recovered for each density at each site and the initial density. This plot was visually inspected to determine the nature of the relationship, specifically to see if there was a part where the proportion of eggs recovered was density dependant and decide at what densities eggs were vulnerable to egg predators. Fitzsimons et al. (2003) had found that at very low egg densities, crayfish and sculpins were unable to locate and consume eggs in small aquaria such that the functional relationship was truncated. Accordingly where we saw evidence of a truncated relationship we removed those densities from the plots. Of the remaining data points we fitted an asymptotic relationship of the form $y=a-b(e^{-cx})$ by fitting a straight line ($y=ax+b$) to the relationship between the reciprocal of the proportion of eggs recovered and the reciprocal of the starting egg density (eggs·m^{-2}) for the edited data. Km was then calculated as the reciprocal of the quotient of the intercept of the above straight line relationship divided by its slope. Where visual inspection did not indicate any density dependence in egg recovery we arbitrarily assumed that it was less than the lowest egg density and in this instance one-half of the lowest egg density used or 50 eggs·m^{-2}.

We assessed relationships between egg predator density and Km and between Km and natural egg abundance using linear regression. We compared the mean Km for Lake Michigan and Parry Sound using a t-test. Test were considered significant at $p<0.05$.

Assessing the amount of physical disturbance

To provide a measure of the effect of physical disturbance we used the proportion of eggs recovered at 5000 eggs·m^{-2} as visual inspection of the plots of proportion of eggs recovered and seeding density indicated that recovery of eggs was always density independent at this point. Because we did not directly measure physical disturbance at each of the sites as a surrogate we used wind fetch for the prevailing wind during the period that seeded eggs were in nets for each of the sites. Wind fetch was defined as the linear distance (km) between the reef and the closest point of land 180º to the direction of the prevailing wind. In the absence of wind observations for Lake Michigan we drew upon local knowledge that placed the prevailing wind directly from the west. For Parry Sound we used wind data collected at the Parry Sound Coast Guard Base only used daily average wind data for winds equal to or in excess of 10 km·hr^{-1}. Data for Lake Champlain was obtained from the Burlington National Airport Weather Offfice. We used linear regression to look at the relationship between our measure of effect and wind fetch. Tests were considered significant at $p<0.05$.

Results

Natural egg deposition

Despite considerable variability within areas, egg deposition was generally highest at Lake Champlain, followed by Parry Sound, and lowest at Lake Michigan (Table 3). The range of egg deposition among the three areas was over 80-fold. Lake Michigan was notable as at only one site was their evidence of significant spawning (e.g. Ingles Point 46 eggs$\cdot m^{-2}$) and this was considerably less than that for any of the reefs at the other two areas.

Predator abundance

Unlike egg deposition, there was considerably less variability in abundance of sculpins and crayfish that varied by over six-fold (Table 4). Crayfish were the dominant predator in Lake Michigan, Parry Sound and Lake Champlain. Smallmouth bass were also found at sites in Lake Michigan and Parry Sound (Table 5) while round gobies were restricted to the nearshore reefs Menooqua and Fisherman's Island where mean density was 2.1 and $0.5 \cdot m^{-2}$, respectively.

Predator abundance relative to seeding level

There were no significant relationships for any of the sites between either the initial or final number of eggs per net and predator abundance per net, determined as all sculpins (>43 mm), all crayfish (>19 mm), or the sum of all sculpins (>43 mm) and all crayfish (>19).

Temperature

Temperatures for the date of egg seeding and reteival of seeded eggs varied from site-to-site although the average egg incubation temperature was within 2.3ºC for all sites (Fig. 5, Table 6).

Egg recovery from seeded nets

Egg recovery varied within sites and among sites with evidence of variation in both the amount of physical disturbance and egg predation based on the shape of the curves (Figs. 6-9). Km was similar across the range of natural egg deposition declining at the higher densities of eggs for Parry Sound and Lake Champlain (Fig. 10). There was no significant variation in Km among the three areas (Fig. 11)

At Parry Sound where the amount of physical disturbance based on the number of eggs recovered at 5000 eggs·m^{-2} was relatively low, averaging 63%, Davy Island showed no evidence of predation because of the lack of a density dependence on egg recovery (Fig. 6). In contrast at Bar, Horse and Mowat Islands, there were indications of a progressive increase in the amount of egg predation and a similar but with a progressive reduction in the ability of predators to find and consume eggs at low seeding densities.

For Lake Champlain, both sites showed the effects of increased physical disturbance expected in a larger body of water with egg recovery averaging 44 % at 5000 eggs·m^{-2} (Fig. 7). Predation was only noted for the reef at Grand Isle.

With the greatest amounts physical disturbance expected so too was there the greatest amount of physical disturbance indicated for Lake Michigan with egg recovery averaging 10% at 5000 eggs ·m^{-2} (Figs. 8,9). Predation was only indicated at Ingles Point and Hog Island with the predation effect being evident at intermediate egg densities at both reefs. Overall, Km did not seem to vary with distance offshore.

Km and its relationship with predator abundance

Across all sites no significant statistical relationships were evident between the densities of sculpin, crayfish, or sculpin and crayfish combined, and Km. There was considerable scatter in this relationship, however (Fig. 12). When just the Parry Sound data was considered there was a significant relationship between Km and the combined density of sculpins and crayfish (F=20.51, p=0.05, r^2=0.91) while the relationship between crayfish alone and Km was not quite as strong (F=14.69, p=0.06, r^2=0.88) (Fig. 13). When the plots for Lake Michigan and Parry Sound are compared (Figs. 13, 14) it was evident that increasing Km occurred at approximately one-fifth the total predator density in Parry Sound that it did in Lake Michigan.

Relationship between wind fetch and egg recovery and survival..

Using wind fetch as a surrogate for physical disturbance, egg recovery for the six reefs in Lake Michigan at 5000 eggs·m^{-2}, was strongly related to a west wind fetch (F= 38.3, r^2= 0.91, p=0.0035 (Fig. 15). No such relationship was noted between percent of eggs live at retrieval and wind fetch (Fig. 15). For Parry Sound, where wind fetch was on average one-twentieth that of Lake Michigan, egg recovery at 5000 eggs·m^{-2} for the four reefs was unrelated to southwest wind fetch but was consistent with the relationship between wind fetch and egg recovery for Lake Michigan. In Lake Champlain, the shorter north wind fetch for Grand Isle of almost 0 and higher egg recovery at 5000 eggs·m^{-2} of 61% contrasted with the longer north wind fetch for Whallon Bay of almost 50 km and lower egg recovery at 5000 eggs·m^{-2} of 27%.

Discussion

The method we used here provided the first estimates of *in situ* egg mortality in the Great Lakes basin and as such represents a considerable improvement in our ability to assess the importance of eggs predators. Previous work has been limited to capture of predators in the wild that upon dissection showed evidence of eggs in the gut from which the level of predation was inferred (Fitzsimons et al. 2002, Stauffer and Wagner 1979, Peck 1986, Hudson et al 1995). However, assessments based on the number of eggs in the stomachs of predators may be misleading. Even self-sustaining populations appear to be able to sustain fairly significant amounts of predation as evidenced by the number of eggs found in stomachs. Fitzsimons (1990) found that the stomachs of yellow perch (*Perca flavescens*) at several spawning locations in Keuka Lake (New York), where lake trout are self-sustaining, contained large numbers of lake trout eggs, during and just after spawning had occurred. It could be argued that these eggs would have died anyway due to physical disturbance and that it is the eggs that settle into the interstitial spaces that are more important because of the higher survival afforded by protection from egg predators and physical disturbance (see Jones et al. 1995). However, based on more detailed examination of the spawning habitat used in Keuka Lake it is evident that lake trout here are spawning on shale substrate with almost no interstitial space in depths of 25-28 m (unpublished data). Hence, while eggs are to a certain extent outside of the influence of physical disturbance, which would be minimal on a small inland lake like Keuka Lake, yellow perch in this case would have ready and prolonged access to most of the eggs spawned. The real strength of our approach over that of previous investigators, has been in knowing the initial number of eggs present and of being able to differentiate the effect of predation from physical disturbance. As expected from laboratory studies where satiation of predators fed eggs was observed (Fitzsimons et al. 2003), the higher rates of egg deposition in Parry Sound and Lake Champlain (Marsden et al. 2003) were associated with reduced loss of seeded eggs based on Km. This suggests that the predation effect can be overcome once egg deposition is high enough.

The method we used here showed considerable site-to-site variability in both a predation effect and a physical disturbance effect based on the relationship between egg seeding density and egg recovery. The amount of physical disturbance assessed as the recovery of eggs at 5000 eggs·m^{-2}, where predators would be unable to influence egg density, was consistent with wind fetch similar to the relationship that Fitzsimons (1995) developed between wind fetch and egg survival, post spawning for Lake Ontario. Obviously physical disturbance can account for a significant loss of eggs particularly in large bodies of water like Lake Michigan but this does not include the losses of eggs that died in place such as the losses that Fitzsimons (1995) measured for eggs in egg nets from Lake Ontario. Those types of losses were not measured here since eggs were added to nets post epiboly, a stage by which eggs are relatively unaffected by physical disturbance (Balon 1980, Fitzsimons 1994). If those loses are added by adjusting the number of eggs recovered at 5000 eggs·m^{-2} by the equation Fitzsimons (1995) developed between fetch and egg survival, the overall losses of eggs are even greater (Fig. 16), approaching 100% at a fetch of approximately 70 km. Prior to this study it has been rare in the Great Lakes where it has been possible to assess the effect of physical disturbance as in very few cases is there information on the initial egg abundance (Roseman et al. 2001). Given the high level of physical disturbance indicated for Lake Michigan in our study. it would seem if predators were active and eating eggs, they could impose a very high mortality rate on the remaining eggs.

In Lake Michigan where total predator levels were higher than for Parry Sound, where lake trout are self-sustaining, predators did not seem to be imposing an inordinate effect on egg survival based on our results. Indeed contrary to the effect of physical disturbance, the effect of predators based on Km, seemed more evident in Parry Sound than Lake Michigan. In addition this was despite the fact that at the offshore reefs in Lake Michigan because of logistics, eggs incubated a further 9-10 days over the Parry Sound sites and at the inshore reefs in Lake Michigan, eggs incubated a further 1-3 days over the Parry Sound sites. Not only was Km generally higher for the Parry Sound reefs but also higher relative to the abundance of predators compared to Lake Michigan by a factor of almost four-fold. Based on the two reefs examined in Lake Champlain it appears to be intermediate between the two. What this suggests is a higher activity level by the predators at the Parry Sound reefs compared to the other two areas. This is unlikely related to temperature, since temperatures among sites were similar during the time of egg incubation suggesting instead that differences are related to an effect of the level of physical disturbance on predator foraging activity. Similarly it seems unlikely to be related to either the size of substrate or the size of the predators present at the Parry Sound reefs, both of which can affect egg consumption (Biga et al. 1998, Chotkowski and Marsden 1999). Ellrott et al (2003) was unable to find any evidence of an effect of interspecific competition on egg consumption by crayfish. However, Fitzsimons et al. (2003) noted it for both slimy sculpins and round gobies, both of which were generally more abundant at the reefs in Lake Michigan than Parry Sound. Nevertheless depite their higher abundance, most egg nets on retrieval for the Lake Michigan reefs contained usually one or less than one individual sculpin or goby.

Obviously by residing in the cobble substrate predators are being afforded some measure of protection from physical forces that can be particularly strong during the fall especially in a larger body of water like Lake Michigan. Just how important this protection might be was the observation that young-of-the-year (YOY) smallmouth bass were using cobble substrate as over-wintering habitat. The highest abundance of YOY smallmouth bass occurred at Bar Island, a relatively protected site, while at Davy Island, a relatively exposed location, they were absent.

The highest abundance of predators for the Lake Michigan sites occurred at Ingles Point, the site having the lowest fetch for a west wind, as well as northwest and southwest winds, and so this location is likely to experience the lowest levels of physical disturbance of the six Lake Michigan reefs we used. During the fall of 2002, Claramunt et al (2003) found that at a site in Little Traverse Bay which is exposed to west winds, the highest abundance of predators occurred at 9 m with fewer at 3 and 1 m. The shallower sites were obviously zones of greater physical activity as the cobbles there were almost devoid of mussels or periphyton. This state could not be explained on the basis of the abundance of round gobies. This species, whose preferred prey in the Great Lakes appears to be zebra mussels, were nearly absent at 1 and 3 m but were very abundant at 9 m where zebra mussels were also very abundant (Claramunt et al. 2003, Djuricich and Janssen 2001).

Apparently because of the higher levels of physical disturbance at lake trout spawning reefs in large lakes like Lake Michigan such as we used here, they may be able to sustain higher abundances of egg predators relative to more protected embayments like Parry Sound, or inland lakes. This has to be balanced off, however, with the greater levels of physical disturbance occurring in large lakes. Part of the greater amount of physical disturbance indicated for the Lake Michigan reefs may be the result of depth although we were able to account for over 90% of the variation in recovery at 5000 eggs·m^{-2} by fetch alone. Depths of the reefs used in this study were, however, relatively shallow, the greatest being 8 m at Middle Ground with the average being 5 m. In this zone, current velocities are still expected to be high and under the influence of wind-driven currents. It is not until a depth of approximately 12 m. is reached that these become relatively insignificant (Skafel, pers. comm). There are other deeper reefs in Lake Michigan, like the mid-lake reef complex and Julian's Reef located in southwestern Lake Michigan (Marsden and Janssen 1997) with average depths of 30-40 m that are probably outside of the influence of most wind-driven currents. However, egg predators like sculpins appear to be relatively abundant and have been found to contain lake trout eggs at these locations. Moreover it is not known how important sculpins are here in affecting egg survival and how it might be affected by the level of physical disturbance.

Despite the apparent greater capacity of these Lake Michigan spawning sites to sustain egg predators, current levels of egg deposition in northeastern Lake Michigan are extremely low (Marsden et al. 2003). The highest was 46 eggs·m^{-2} but most were near zero. Egg density at the sites we used here were not exceptionally low either, since similar results were seen at a number of other locations evaluated in northeastern Lake Michigan (Marsden et al. 2003). Even for Gull Island reef, where Madenjian and DeSorcie (1999) determined based on the number of spawners, that there should have been evidence of significant natural reproduction by 1997, egg deposition in 2002 was extremely low (<1 egg·m^{-2}, Marsden et al. 2003) Since Km in eggs·m^{-2} is a measure of the point at which egg density goes from being predator-dependant to physical disturbance-dependant, and hence a threshold to at least reach and likely exceed for natural reproduction to occur, deposition falls far short at the reefs we assessed. At Menonoqua, where we had the highest egg deposition (46 eggs·m^{-2}), it was still somewhat less than the Km suggesting that egg survival while still possible could be seriously affected by the current predator community. At Ingles Point, the site having the highest Km, egg deposition was so low as to be undetectable during 2002 and barely detectable in 2000 and 2001 (Marsden et al. 2003). For Hog Island the site having the second highest Km, egg deposition was never detected over the period 2000-2002 (Marsden et al. 2003). Obviously there is no potential at either of these reefs for egg survival unless egg deposition is increased dramatically to compensate for the number of eggs likely to be eaten by predators. At the three other locations where predation was not indicated by the relationship between egg seeding and egg recovery (e.g. Fishermans Island, Dahlia Reef and Middle Ground), we arbitrarily assumed that Km was one half the lowest egg density used (e.g. 100 eggs·m^{-2}) or 50 egs·m^{-2}. However, even compared with this modest level of egg deposition, current rates of egg deposition are well short. Of these three sites, it is only at Fishermans Island (<1 egg·m^{-2}) where over the three year period 2000-2002 there werdetectable levels of spawning albeit extremely low (Marsden et al. 2003).

Because the current egg predator community at the Lake Michigan sites is dominated by crayfish and is likely to change to gobies, even greater egg deposition may be required to compensate for the number of eggs eaten by predators (Diana et al. 2003). In laboratory tests, consumption by a single goby (7 eggs·day^{-1}) was 7 times that of a single crayfish (1 egg·day^{-1}) while that of a single slimy sculpin was 2.5 (2.5 eggs·day^{-1}) that of a single crayfish (Ellrott et al. 2003, Fitzsimons et al. 2003). At Bay Harbour, the site having the highest abundance of gobies in 2002, Claramunt et al. (2003) found that only 5 % of eggs seeded at 9 m at 1000 eggs·m^{-2} were recovered over a three week period compared to 20 % and 16 % at Fishermans Island and Menonoqua respectively for this study when seeded at the same rate. Given the depth range over which gobies are found and their capacity to move offshore it would seem that even the offshore reefs may eventually be vulnerable but this may be tempered somewhat by the abundance of dreissenids, their preferred food (Diana et al. 2003, Djuricich and Janssen 2001).

The prospects for increased spawning in northeastern Lake Michigan in future, such that egg deposition can overcome the current egg predation effect, are not encouraging. If the numbers of spawners are any indication of the potential for spawning to occur, current estimates of spawners suggest this is unlikely to occur in the foreseeable future (Jonas et al. 2003). Although there are plans for further restricting the stocking to even fewer sites so as to potentially increase egg deposition at these sites, it will take years for this action to have an effect if in fact it is successful. Actions in past to stock fish at particular reefs with the intent of increasing the number of spawners there, have not been all that successful with most fish concentrating near shore particularly in northeastern Lake Michigan (R. Claramunt , MDNR, Charlevoix, pers. comm.). Greater knowledge of the factors that attract fish to particular spawning sites will help in this endeavour and this is seen as an important research activity missing from the current restoration effort being undertaken by state and federal fisheries management agencies.

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References

Balon, E.K. 1980. Early ontogeny of the lake charr, *Salvelinus (Cristivomer) namaycush,* In *Charrs: salmonids fishes of the genus Salvelinus*, E.K. Balon (ed.), pp 462-485. The Hague, The Netherlands: Dr. W. Junk Publishers

Becker, P.H. 1995. Effect of coloniality on gull predation on common tern (*Sterna hirundo*) chicks. Colonial Waterbirds 18:11-22.

Biga, H., Janssen, J., and Marsden, J.E. 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. J. Great Lakes Res. 24:464-473

Chotkowski, M.A., and Marsden, J.E. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. *J.* Great Lakes Res. 25:26-35

Claramunt, R., Jonas, J.L., Fitzsimons, J.D., and Marsden, J.E. 2003. Effect of time and depth on the rate of egg loss at a lake trout spawning reef in northeastern Lake Michigan. Draft.

Clary, J.R. 1972. Predation on brown trout by the slimy sculpin. Prog. Fish-Cult. 34:91-95.

Dawson, K.A., Eshenroder, R.L., Holey, M.E., and Ward, C. 1997. Quantification of historic lake trout (*Salvelinus namaycush*) spawning aggregations in Lake Michigan. Can. J. Fish. Aquat. Sci. 54:2290-2302.

Diana, J.S. 1995. Biology and Ecology of Fishes. Cooper Publishing Group LLC. Carmel. IN 441p.

Diana, C., Jonas, J.L., Claramunt, R.M., Fitzsimons, J.D., and Marsden, J.E. 2003. Abundance of round gobies (*Neogobius melanostmus*) in littoral habitats of northeastern Lake Michigan. Draft.

Djuricich, P., and Janssen, J. 2001. Impact of round goby predation on zebra mussel size distribution at Calumet Harbour, Lake Michigan. J. Great Lakes Res. 27:312-318.

Ellrott, B.J., Marsden, J.E., Claramunt, R.M., Fitzsimons, J.D., and Jonas, J.L.2003. Effects of temperature and density on consumption of trout eggs by *Orconectes propinquus* and *O. rusticus*. Draft.

Eckrich, C.E., and Owens, D.W. 1995. Solitary versus arribada nesting in the olive ridely sea turtles (*Lepidochelys olivacea*): A test of the predator satiation hypothesis. Hepetologia 51:349-354.

Eshenroder, R.L., Bronte, C.R., and Peck, J.W. 1995. Comparison of lake trout-egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. J. Great Lakes Res. 21(Supplement 1):313-322.

Fitzsimons, J.D. 1990. Yellow perch predation on lake trout eggs in Keuka Lake, New York. J. Great Lakes Res. 16:130-132.

Fitzsimons, J.D. 1994. Survival of lake trout (*Salvelinus namaycush*) embryos after receiving physical shock. Prog. Fish-Cult. 56:149-151.

Fitzsimons, J.D. 1995. Assessment of lake trout spawning habitat and egg deposition in Lake Ontario. J. Great Lakes Res. 21(Supplement 1):337-347.

Fitzsimons, J.D., B. Lantry, and R. O'Gorman. 2003. The status of a lake trout resurgence in Lake Ontario from an early life stage perspective. Accepted. Chapter XX in State of Lake Ontario (SOLO). Ed. M. Munawar.

Fitzsimons, J.D., D.L. Perkins, and C.C. Krueger. 2002. Sculpins and crayfish on lake trout spawning areas in Lake Ontario: Estimates of abundance and egg predation. J. Great Lakes Res, 28:421-436.

Fitzsimons, J.D. Claramunt, R.M., Ellrott, B.J., Jonas, J.L., and Marsden, J.E. 2003. A comparison of trout egg predation by sculpins and gobies: Effect of temperature, inter- and intra-specific competition, egg density, tank size and alternate food source. Draft

Gleason, T.R., and Bengtsson, D.A. 1996. Growth, survival, and size-selective predation mortality of larval and juvenile inland silversides, *Menidia beryllina* (Pisces;Atherinidae). J. Exp. Mar. Biol. Ecol. 199:165-177.

Holey, M. E., Rybicki, R.W., Eck, G.W., Brown, E.H., Marsden, J.E., Lavis, D.L., Toneys, M.L., Trudeau, T. N., and Horall, R.M. 1995. Progress towards lake trout retoration in Lake Michigan. J. Great Lakes Res. 21(Supplement 1):128-151.

Horns, W.H., and Magnuson, J.J. 1981. Crayfish predation on lake trout eggs in trout lake, Wisconsin. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 178. 299-303.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Motschaniwskyj, N.A., Pratchett, M.S., Tannner, J.E., and Willis, B.L. 2000. Supply-side ecology works both ways: The link between benthic adults, fecundity, and larval recruits. Ecology 81:2241-2249.

Hudson, P.L., Savino, J.F., and Bronte, C.R. 1995. Predator-prey relations and competition for food between age-0 lake trout and slimy sculpins in the Apostle Island region of Lake Superior. J. Great Lakes Res. 21(Supplement 1):445-457

Jones, M.L., Eck, G.W., Evans, D.O., Fabrizio, M.C., Hoff, M.H., Hudson, P.L., Janssen, J, Jude, D., O'Gorman, R., and Savino, J.F. 1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages. J. Great Lakes Res. 21(Supplement 1):505-517.

Jonas, J.L., Claramunt, R.M., Ellrott, B.J., Fitzsimons, J.D., and Marsden, J.E. 2003. Estimates of abundance and the effect of lake trout egg predators on egg survival for Lakes Michigan, Huron, and Champlain. Draft.

Krueger, C.C., Jones, M.L., and Taylor, W.W. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management. J. Great Lakes Res. 21(Supplement 1):547-558.

Krueger, C.C., Perkins, D.L, and Mills, E.L., and Marsden, J.E. 1995. Predation by alewives on lake trout fry in Lake Ontario: Role of an exotic species in preventing restoration of a native species. J. Great Lakes Res. 21(Supplement 1):458-469.

Lake Michigan Lake Trout Task Group (LMLTTG). 2003. Possible impediments to lake trout restoration in Lake Michigan. Prepared by LMLTTG for the Lake Michigan Committee. Contributors C.R. Bronte, J. Jonas, M.E. Holey, M.L. Toneys, P. McKee, B. Breidert, R.M. Claramunt, M.P. Ebener, R.L. Eshenroder, C.C. Krueger, G. Wright and R. Hess.

Madenjian, C.P. and DeSorcie, T.J. 1999. Status of lake trout rehabilitation in the Northern Refuge of Lake Michigan. N.A. J. Fish. Manage. 19:658-669.

Marsden, J.E., and Janssen, J. 1997. Evidence of lake trout spawning on a deep reef in Lake Michigan using an ROV-based egg collector. J. Great Lakes Res. *23*:450-457.

Marsden, J.E., Ellrott, B.J., Claramunt, R.M., Fitzsimons, J.D. and Jonas, J.L. 2003. A comparison of lake trout spawning, emergence, and habitat use for Lakes Michigan, Huron (Parry Sound) and Champlain. Draft.

MacLean, J.A., Evans, D.O., Martin, N.V., and DesJardine, R.L. 1981. Survival, growth, spawning distribution, and movements of introduced and native lake trout (*Salvelinus namaycush*) in two inland Ontario lakes. Can. J. Fish. Aquat. Sci. 38:1685-1700.

Miller, M.C., McCave, I.N., and Komar, P.D. 1977. Threshold of sediment motion under unidirectional currents: Sedimentology 24:507-527.

Miller, J.E., Savino, J.F., and Neely, R.K. 1992. Competition for food between crayfish (*Orconectes virilis*) and the slimy sculpin (*Cottus cognatus*). J. Fresh. Ecol. 7:127-137.

Moksnes, P_O. 2002. The relative importance of habitat-specific settlement, predation and juvenile dispersal for the distribution and abundance of young juvenile shore crabs *Carcinus maenas* L. J. Exp. Mar. Biol. Ecol. 271:41-73.

Peck. J.W. 1986. Dynamics of reproduction by hatchery lake trout on a man-made spawning reef. J. Great Lakes Res. 12:293-303.

Perkins, D.L., and Krueger, C.C. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at Stony Island reef, Lake Ontario. J. Great Lakes Res. 21(Supplement 1):400-417.

Reid, D., Anderson, D.M, and Henderson, B.A. 2001. Restoration of lake trout in Parry Sound, Lake Huron. N.A. J. Fish. Manage. 21:156-169.

Rooker, J.R., Holt, G.J., and Holt, S.A. 1998. Vulnerability of newly settled red drum (*Sciaenops ocellatus*) to predatory fish: Is early-life survival enhanced by seagrass meadows? Mar. Biol. 131:145-151.

Roseman, E.J., Taylor, W.W., Hayes, D.B., Knight, R.L., and Hass, R.C. 2001.Removal of walleye eggs from reefs in western Lake Erie by a catastrophic storm. Trans. Am. Fish. Soc. 130:341-346.

Savino, J.F., and Henry, M.G. 1991. Feeding rate of slimy sculpin and burbot on young lake charr in laboratory reefs. Envir. Biol. Fish. 31:275-282

Savino, J.F, Hansen, P.L., Fabrizio, M.C., and Bowen, C.A. II. 1999. Predation on lake trout eggs and fry: a modelling approach. J. Great Lakes Res. 25: 36-44.

Smith, B.R., and Tibbles, J.J. 1980. Sea lamprey (*Petomyzon marinus*) in Lakes Huron, Michigan, and Superior: history of invasion and control, 1936-78. Can. J. Fish. Aquat. Sci. 37:1780-1801.

Stauffer, T.M., and Wagner, W.C. 1979. Fish predation on lake trout eggs and fry in the Great Lakes. 1973-1978. Mich. Dep. Nat. Res. Fish. Res. Rep. No. 1864.

Steel, M.A. 1996. Effects of predators on reef fishes: Separating cage artefacts from effects of predation. J. Exp. Mar. Biol. Ecol. 198:249-267.

Sweeney, B.W., and Vannote, R.L. 1982. Population synchrony in mayflies: A predator satiation hypothesis. Evolution 36:810-821

Tallman, R.F. 1990. Seasonal isolation and adaption among chum salmon, *Oncorhynchus keta* (Walbaum), populations. Diss. Abst. Int. Pt. B.- Sci. & Eng. Vol. 50, No. 12.

Turner, A.M, Fetterolf, S.A., and Bernot, R.J. 1999. Preator identity and consumer behaviour:differential effects of fish and crayfish on the habitat use of a freshwater snail. Oecologia 2:242-247.

van Montfrans, J., Epifanio, C.E., Knott, D.M, Lipcius, R.N., Mense, D.J., Metcalf, K.S., Olmi, E.J., Orth, R.J., Posey, M.H., and Wenner, E.L. 1995. Settlement of blue crab postlarvae in western North Atlantic estuaries. Bull. Mar. Sci., vol. 57, no. 3, pp. 834-854.

Ventling-Swank, A.R., and Livingstone, D.M. 1994. Transport and burial as a cause of whitefish (*Coregonus* sp.) egg mortality in a European lake. Can. J. Fish. Aquat. Sci. 51:1908-1919.

Wells, L., and McClain, A.L.1973. *Lake Michigan, man's effects on native fish stocks and other biota*. Great Lakes Fishery Commission, Tech. Rep. No. 20

Table 1: Summary of habitat information for the 12 reefs used.

Site	Depth range (m)	Slope (º)	Substrate type	Substrate size range (cm)	Interstitial depth range (cm)
Lake Champlain					
Grand Isle breakwall	0.3-4	35-60	cobble	13-99	15-86
Whallon Bay	0.3-14	20-85	cobble	17-106	4-29
Lake Huron (Parry Sound)					
Davy Island	1.5	30-40	cobble	13.9	>30
Mowat Island	1.8	25-30	cobble	13.0	>30
Bar Island	1.5	30-40	cobble	15.1	>30
Horse Island	1.6	30-40	cobble	12.3	>30
Lake Michigan					
Ingles Point	1-1.5	50-60	cobble	82-2929	20-30

Fisherman's Island	1.5-4	30-45	cobble	3-1305	>100
Menonoqua	1.5-3.5	35-45	cobble	25-1913	>100
Middle Ground	8-9	30-40	cobble	15-25	>30
Dahlia Shoal	3.5-7	40-50	cobble	3-1057	>100
Hog Island Reef	2-5	30-45	cobble	7-457	>100

Table 3: Summary of natural egg deposition and Km calculated for the 12 reefs.

Lake	**Location**	**Natural egg deposition (no./m2) (X±SEM)**	**Km**
Parry Sound	**Davy Island**	**1009 (126)**	**50**
	Mowat Island	**170 (31)**	**1412**
	Bar Island	**933 (134)**	**298**
	Horse Island	**185 (29)**	**589**
Champlain	**Grand Isle**	**3748 (454)**	**262**
	Whallon Bay	**717 (240)**	**50**
Michigan	**Ingles Point**	**0**	**1561**
	Fishermans Island	**<1**	**50**
	Menonoqua	**46 (10)**	**61**

	Middle Ground	**0**	**50**
	Hog Island	**0**	**358**
	Dahlia Reef	**0**	**50**

Table 2: Summary of net seeding and retrieval dates and period in substrate for each of the 12 seeded reefs

Site	**Date Nets Buried**	**Date Nets Seeded**	**Date Nets Retrieved**	**Days Eggs Incubated**
Lake Huron				
Davy Island	**Sept 4**	**Oct 24**	**Nov 12**	**19**
Mowat Island	**Sept 4**	**Oct 24**	**Nov 12**	**19**
Bar Island	**Sept 3**	**Oct 24**	**Nov 13**	**20**
Horse Island	**Sept 3**	**Oct 24**	**Nov 13**	**20**
Lake Champlain				
Grand Isle	**Aug 27**	**Nov 6**	**Nov 26**	**20**

Whallon Bay	**Sept 9**	**Nov 5**	**Nov 25**	**20**
Lake Michigan				
Ingles Point	**Aug 21**	**Oct 28**	**Nov 19**	**22**
Fishermans	**Aug 20**	**Oct 28**	**Nov 20**	**23**
Menonoqua	**Aug 20**	**Oct 28**	**Nov 18**	**21**
Middle Ground	**July 30[1]**	**Oct 28**	**Nov 26**	**29**
Hog Island	**Aug 23**	**Oct 28**	**Nov 26**	**29**
Dahlia Reef	**Aug 23**	**Oct 28**	**Nov 26**	**29**

[1] 2001

Table 4: Summary of density and length and weight of crayfish and sculpins in egg nets at each of the 12 reefs seeded in 2002.

Site	**Crayfish**				**Sculpins**			
	Abundance (no./m^2)	**Length (mm)**	**Weight (gm)**	**N**	**Abundance (no./m^2)**	**Length (mm)**	**Weight (gm)**	**N**
Lake Huron								
Davy Island	**3.8 (0.9)**	**27.9(2.0)**	**6.0(1.5)**	**15**	**0.2 (0.2)**	**45.5(1.5)**	**0.7(0.1)**	**3**
Mowat Island	**6.4 (1.0)**	**26.0(2.1)**	**4.3(0.3)**	**27**	**0.7 (0.4)**	**75.3(7.7)**	**5.5(0.8)**	**4**
Bar Island	**3.6 (0.9)**	**24.7(0.8)**	**4.5(0.6)**	**17**	**0**			
Horse Island	**5.3 (1.1)**	**25.6(1.0)**	**5.3(0.7)**	**22**	**0**			
Lake Champlain								

Grand Isle	**9.7 (1.3)**	**33.5(2.5)**	**10.6(2.3)**	**4**	**1.5 (0.2)**	**51.2(1.6)**	**1.6(0.2)**	**38**
Whallon Bay	**4.1 (1.0)**				**0.2 (0.1)**	**55.1(5.1)**	**2.0(0.7)**	**7**
Lake Michigan								
Ingles Point	**15.7 (1.9)**	**27.7(0.6)**	**7.5 (0.4)**	**70**	**6.5 (1.2)**	**63.9 (2.4)**	**4.0 (0.5)**	**28**
Fisherman's Island	**5.4 (1.2)**	**25.3 (1.0)**	**5.4 (0.7)**	**19**	**1.9 (0.7)**	**68.4 (3.5)**	**4.0 (0.6)**	**8**
Menonoqua	**14.3 (1.6)**	**30.4 (0.8)**	**9.9 (0.7)**	**61**	**2.9 (0.8)**	**79.8 (2.1)**	**7.6 (0.6)**	**22**
Middle Ground	**10.4 (1.5)**	**22.2 (0.4)**	**3.2 (0.3)**	**45**	**5.3 (1.1)**	**73.1 (2.3)**	**5.1 (0.6)**	**24**
Hog Island	**6.9 (1.2)**	**28.3 (1.0)**	**7.4 (0.7)**	**31**	**6.7 (0.9)**	**70.1 (1.7)**	**4.9 (0.3)**	**31**
Dahlia Reef	**3.6 (1.0)**	**24.7 (1.3)**	**4.7 (0.8)**	**16**	**5.8 (1.3)**	**63.8 (3.1)**	**4.0 (0.6)**	**25**

Table 5: Summary of abundance and lengths and weights of smallmouth bass at reefs in Parry Sound and Menonoqua and Ingles Point in Lake Michigan.

Location	**Abundance ($no./m^2$)**	**Length (gm)**	**Weight (mm) N**	**N**
Mowat Island	**2.4 (0.7)**	**83.4 (1.1)**	**8.0 (0.8)**	**8**
Bar Island	**5.5 (1.0)**	**83.4 (1.8)**	**9.1 (0.6)**	**16**
Horse Island	**1.5 (0.6)**	**82.3 (4.3)**	**8.1 (0.7)**	**3**
Menoqua	**1.6**			
Ingles Point	**0.5**			

Table 6: Summary of egg incubation temperature data for the 12 reefs seeded in 2002.

Site	**Date Seeded**	**Temperature At Seeding (ºC)**	**Temperature At Retrieval (ºC)**	**Average Incubation Temperature (ºC)**
Lake Huron				
Davy Island	**Oct 24**	**10.6**	**8.0**	**9.0**
Mowat Island	**Oct 24**	**10.9**	**8.1**	**9.2**
Bar Island	**Oct 24**	**10.5**	**8.2**	**9.4**
Horse Island	**Oct 24**	**10.8**	**7.9**	**9.1**
Lake Champlain				

Grand Isle	**Nov 6**	**9.7**	**7.6**	**8.4**
Whallon Bay	**Nov 5**	**10.4**	**9.0**	**9.5**
Lake Michigan				
Ingles Point	**Oct 28**	**11.1**	**7.4**	**9.1**
Fishermans	**Oct 28**	**11.7**	**6.0**	**9.3**
Menonoqua	**Oct 28**	**12.2**	**8.4**	**10.0**
Middle Ground	**Oct 28**	**12.5**	**7.8**	**9.6**
Hog Island	**Oct 28**	**10.1**	**5.5**	**7.7**
Dahlia Reef	**Oct 28**	**12.0**	**5.1**	**8.8**

Fig. 1: Hypothetical patterns of egg recovery for a range of starting egg abundances for scenarios involving low predation and physical disturbance, moderate predation and low physical disturbance, high predation and high physical disturbance, and low predation and high physical disturbance**.**

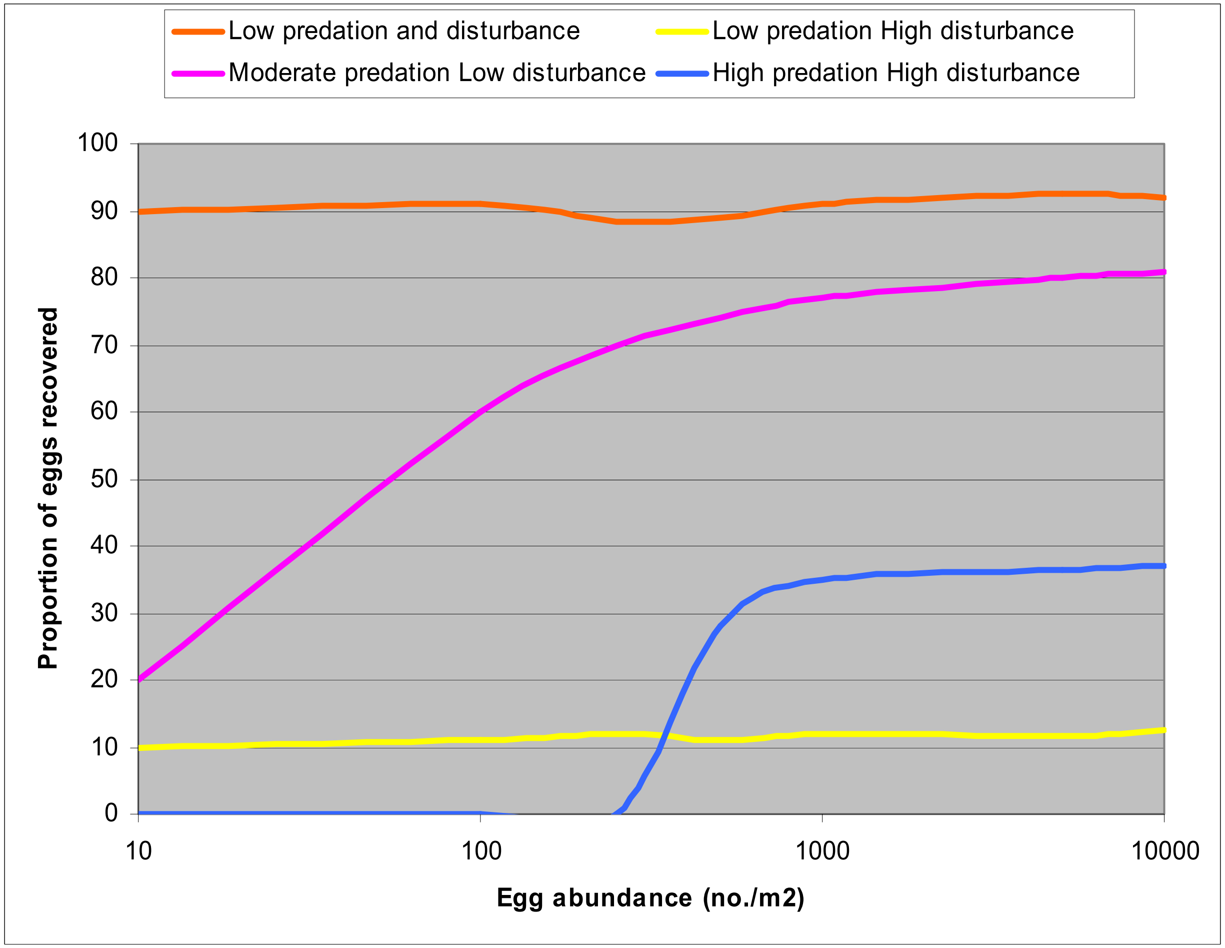
Low predation and disturbance
Low predation High disturbance
Moderate predation Low disturbance
High predation High disturbance
Proportion of eggs recovered
100
90
80
70
60
50
40
30
20
10
0
10
100
1000
10000
Egg abundance (no./m2)

Fig. 2: Map of northeastern Lake Michigan showing location of six reefs used for seeding

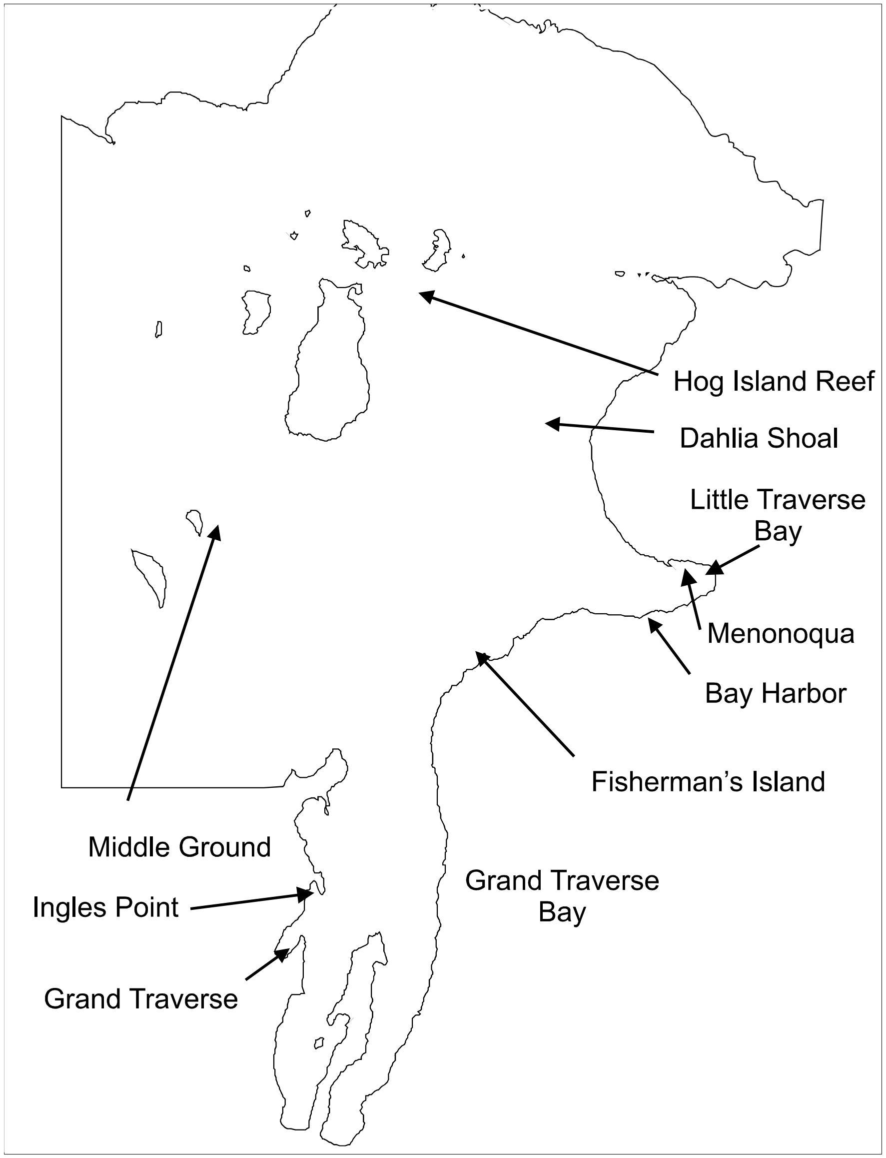
Hog Island Reef
Dahlia Shoal
Little Traverse Bay
Menonoqua
Bay Harbor
Fisherman's Island
Grand Traverse Bay
Middle Ground
Ingles Point
Grand Traverse

Fig. 3: Map of Parry Sound showing location of four reefs used for seeding

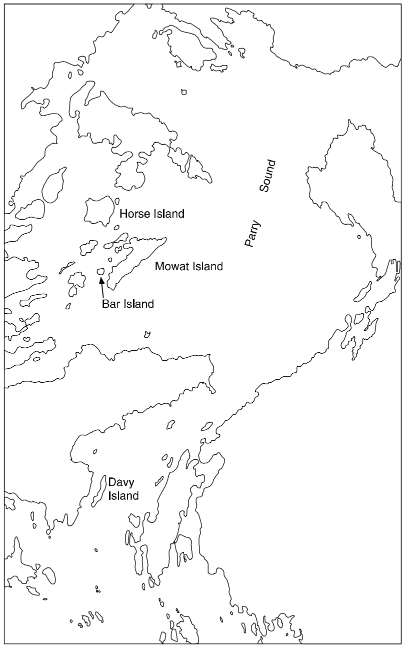

Fig. 4: Map of Lake Champlain showing location of six reefs used for seeding

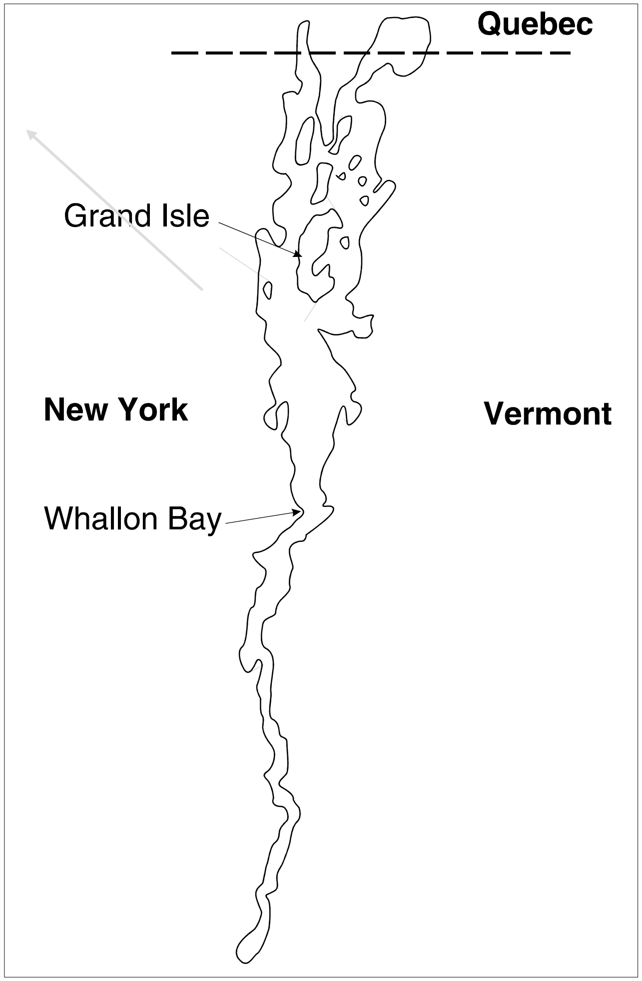

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Fig. 5: Temperature during egg incubation for reefs at Parry Sound, Lake Champlain, and Lake Michigan, 2002.

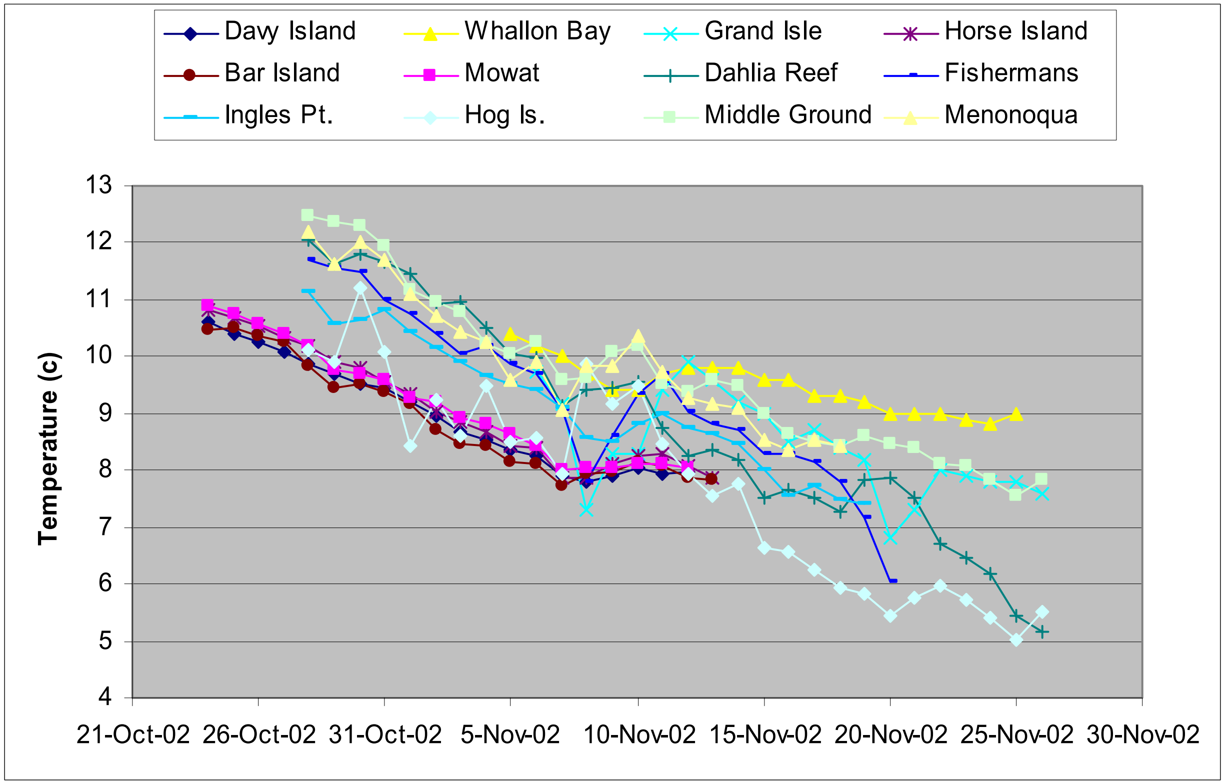


Fig. 6: Proportion of eggs recovered at five egg densities at four reefs in Parry Sound, 2002

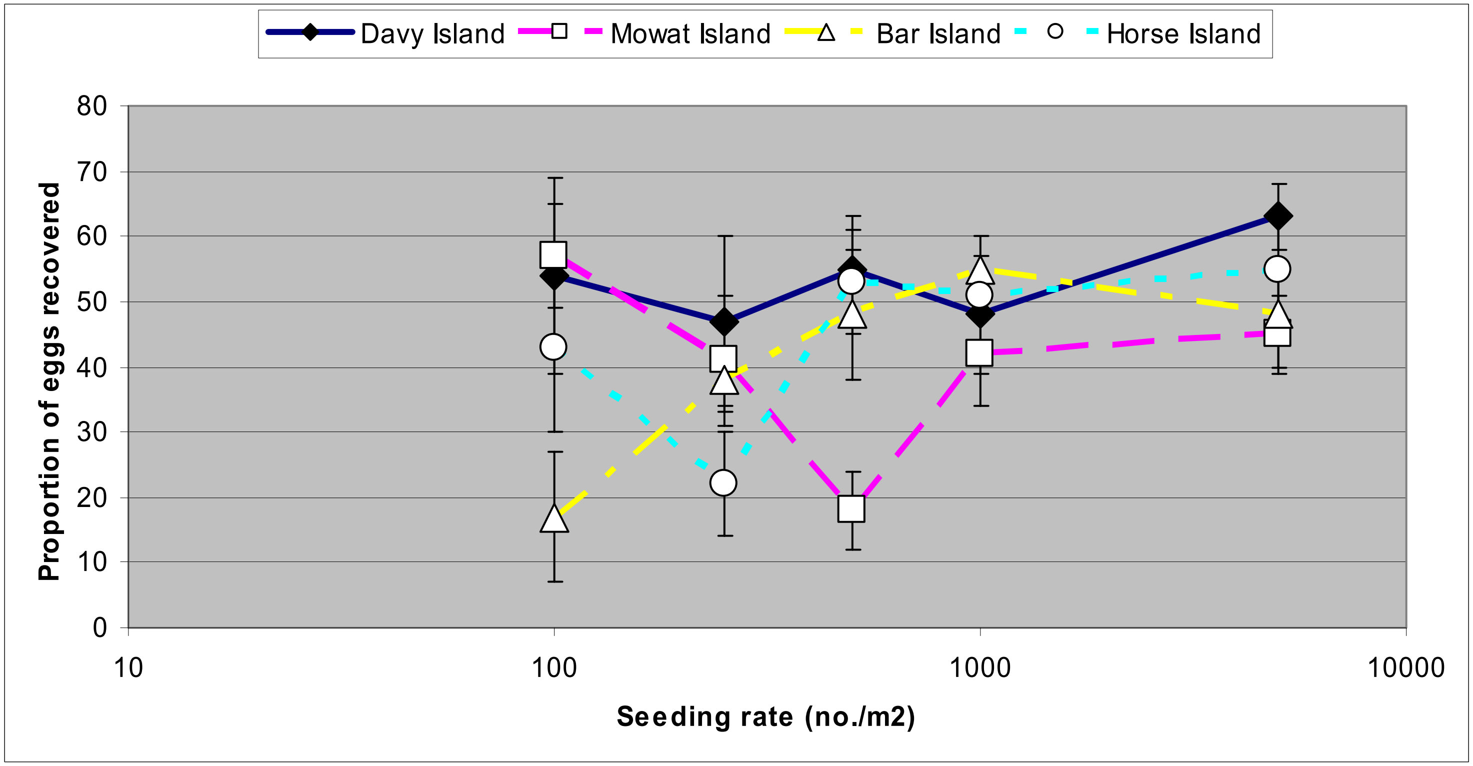


Fig. 7: Proportion of eggs recovered at five egg densities at two reefs in Lake Champlain, 2002

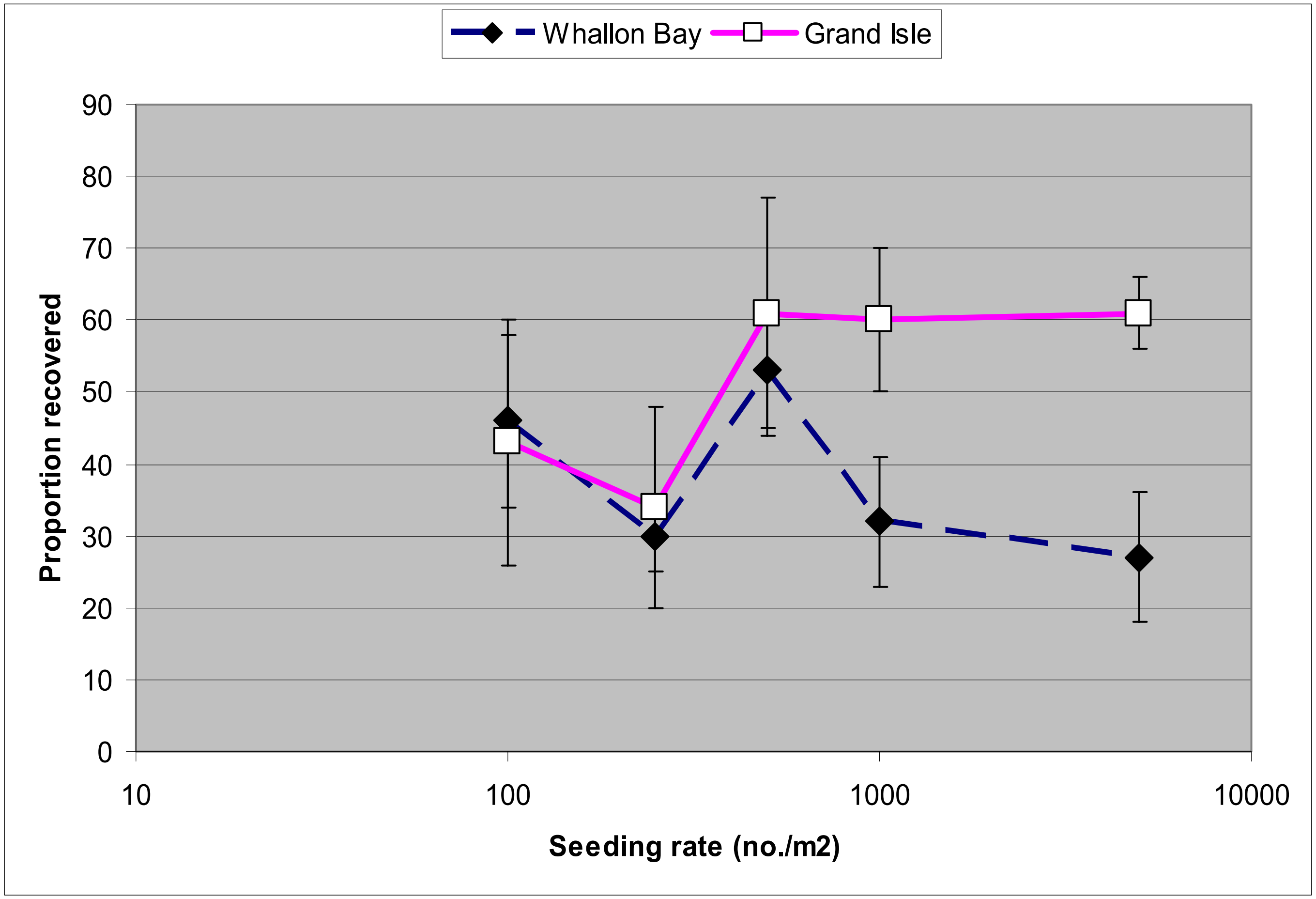


Fig. 8: Proportion of eggs recovered at five egg densities at three nearshore reefs in Lake Michigan, 2002

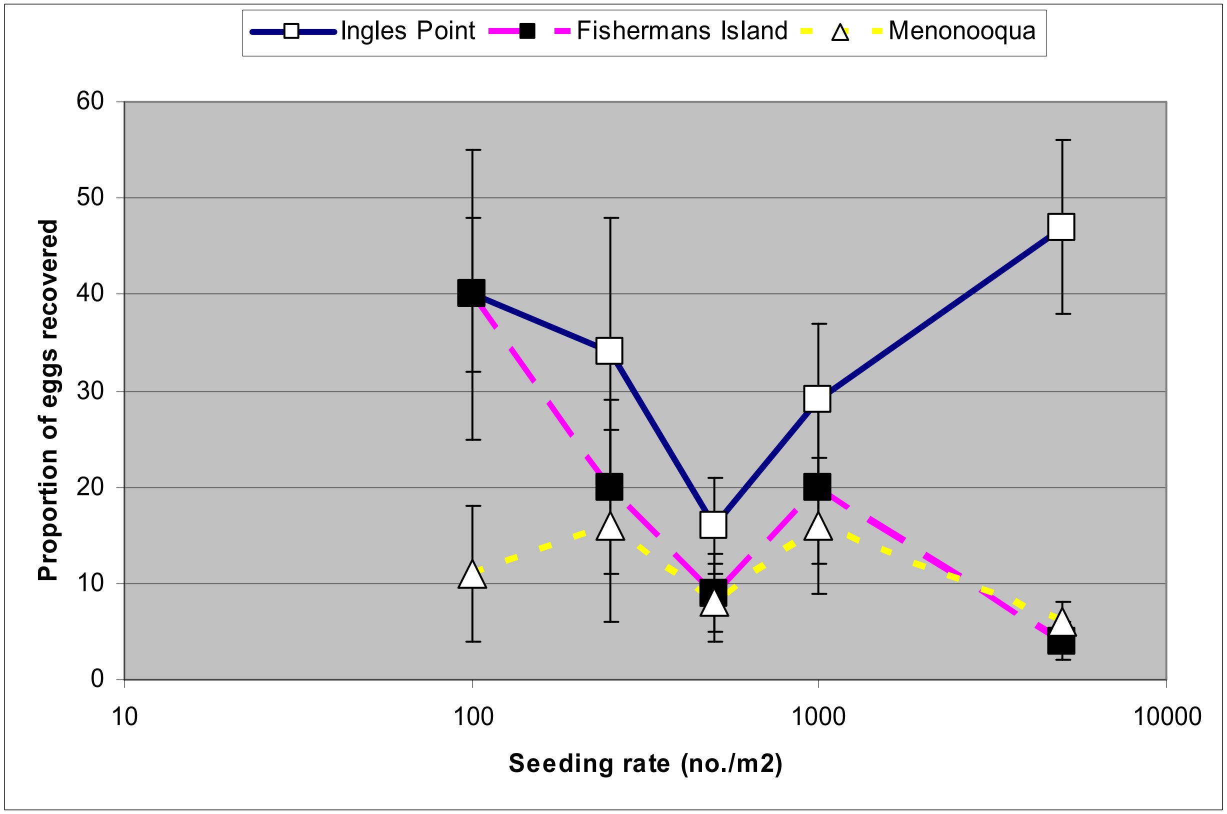


Fig. 9: Proportion of eggs recovered at five egg densities at three offshore reefs in Lake Michigan, 2002

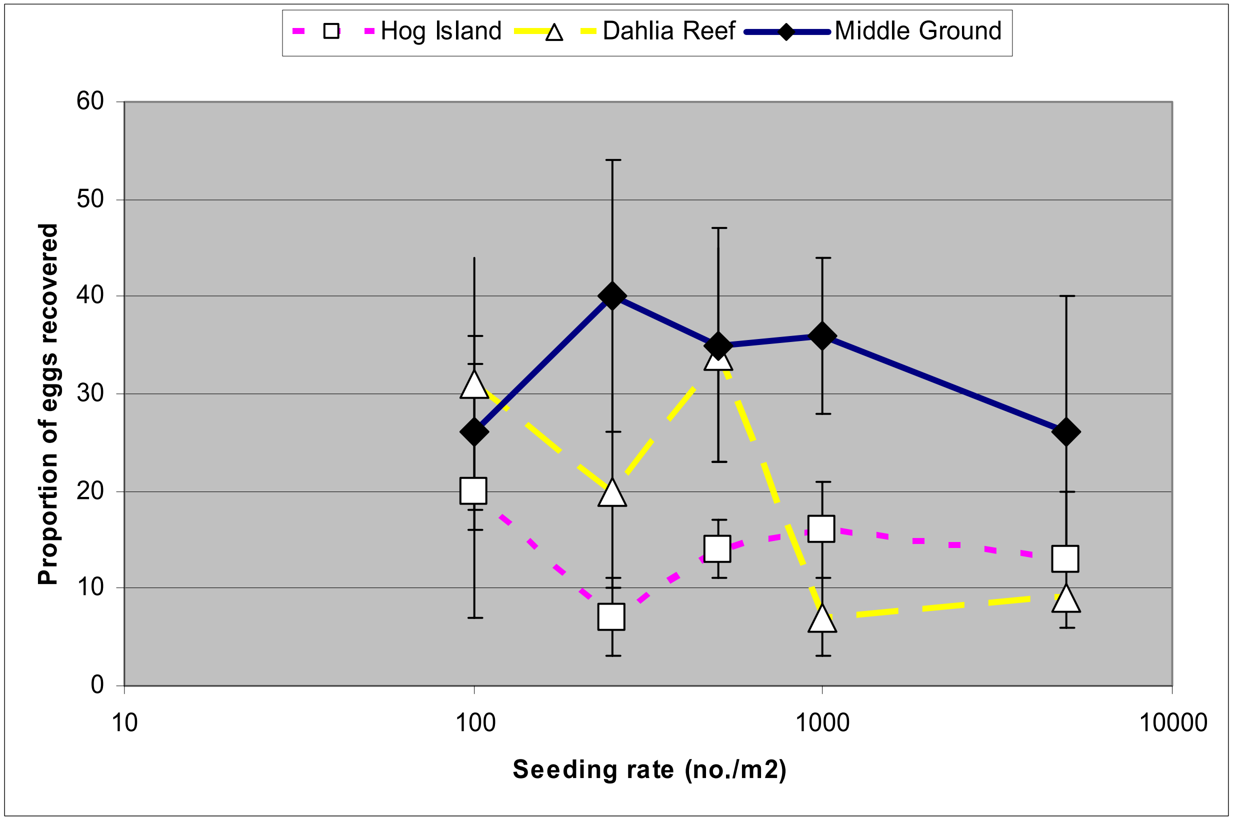


Fig. 10: Relationship between natural egg density and Km for the 12 reeefs. Line indicates 1:1 line where Km equals natural egg deposition.

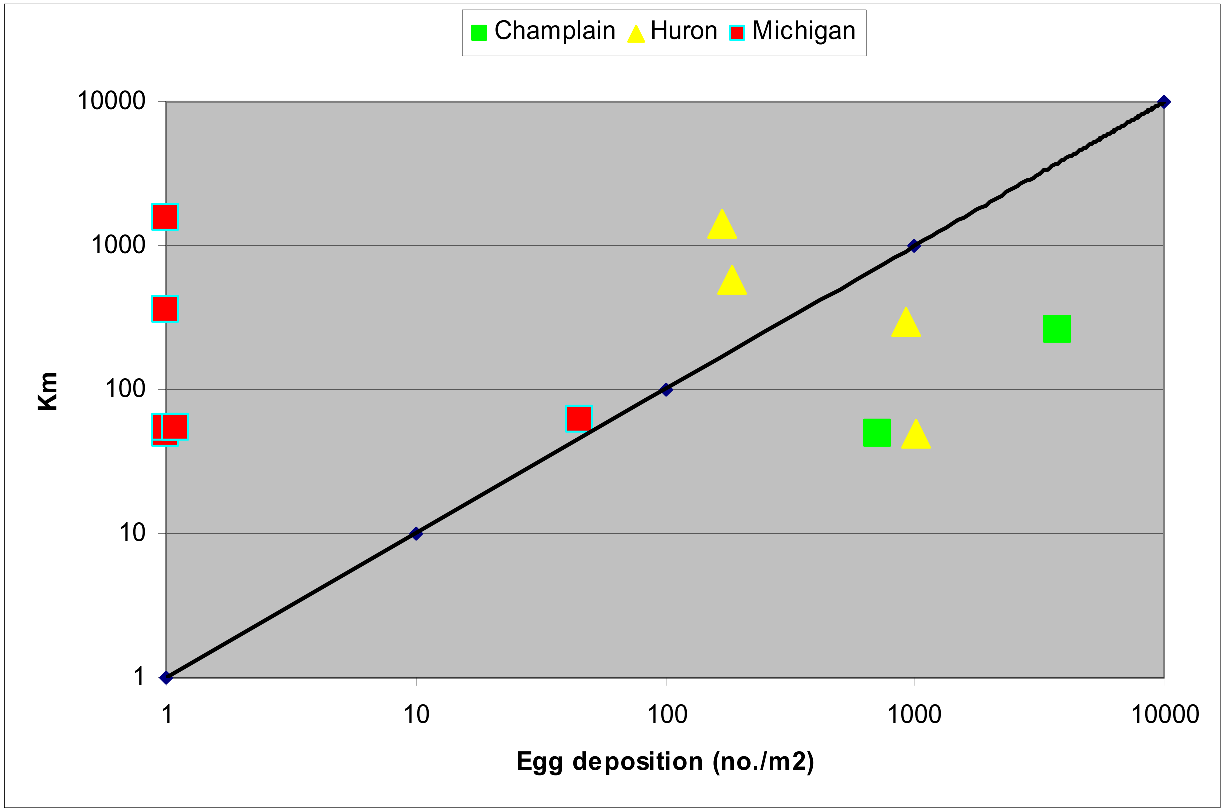


Fig. 11: Average Km (±SEM) for the three areas.

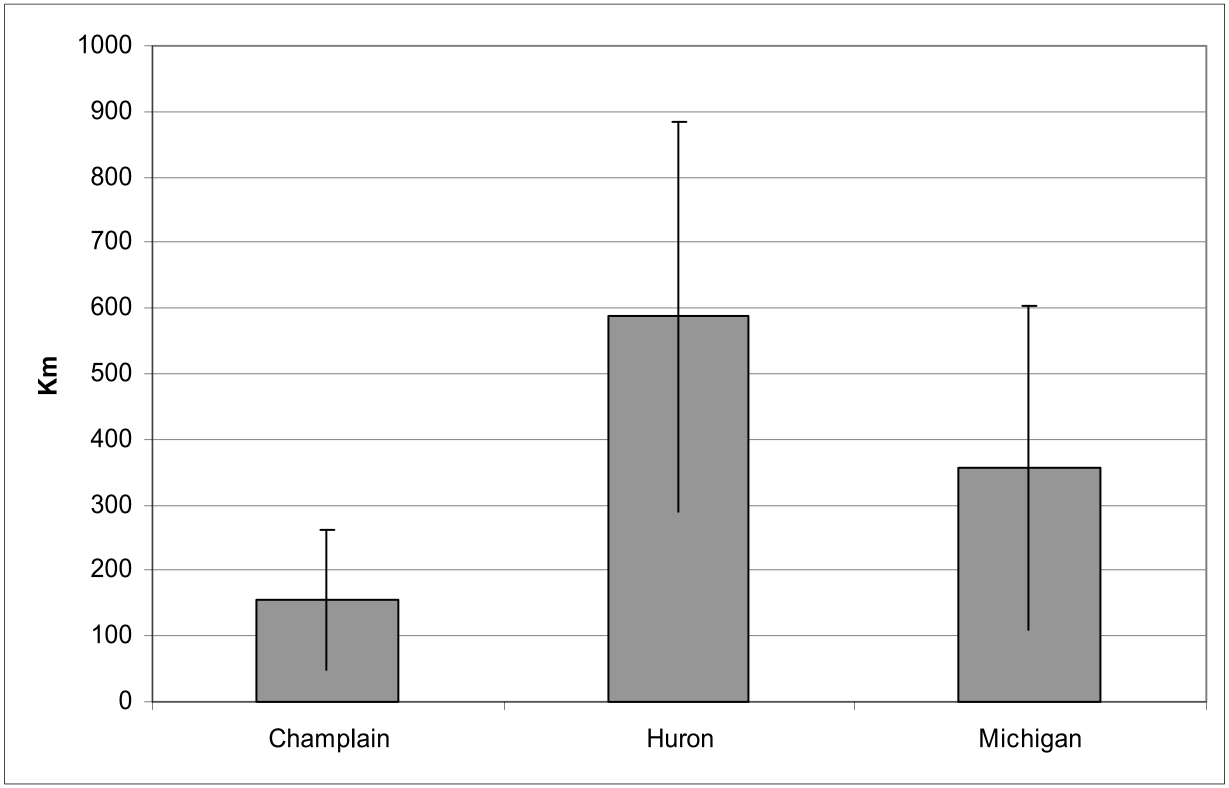


Fig. 12: Relationship between density of crayfish, sculpins and crayfish and sculpins combined and Km for each of the 12 reefs.

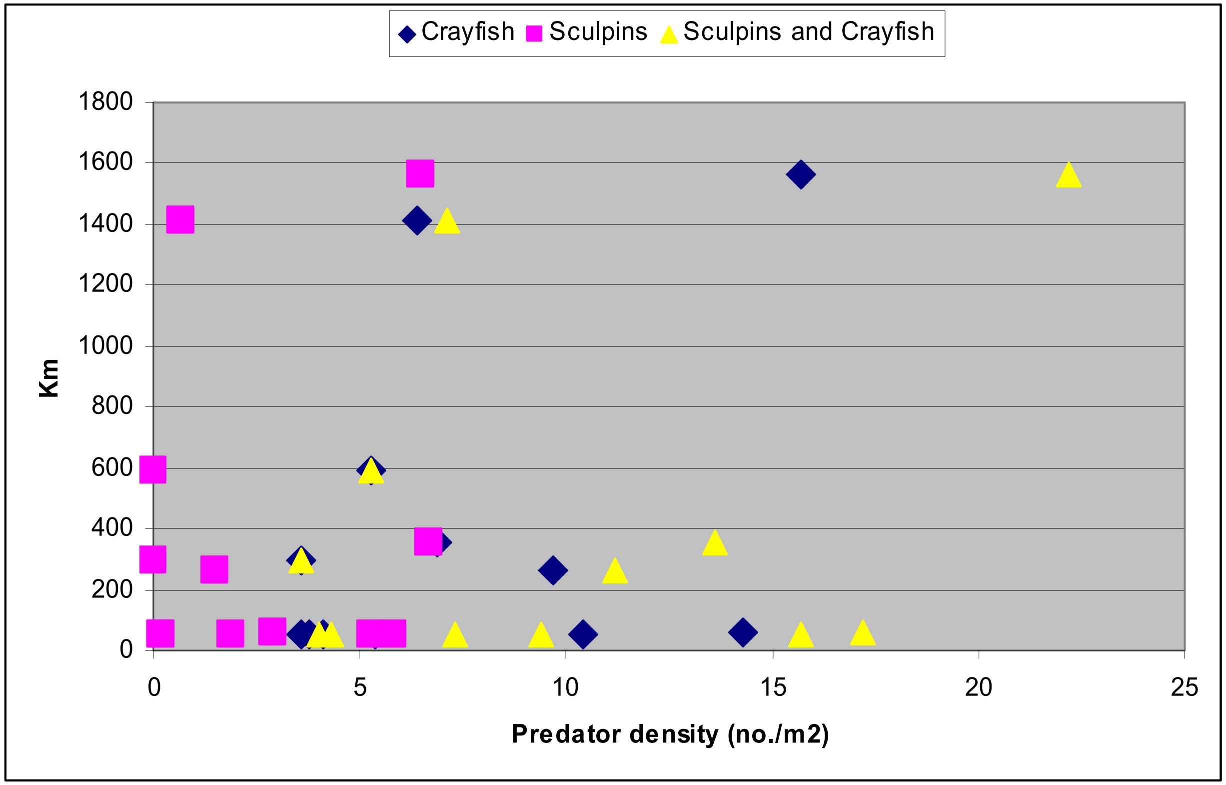


Fig. 13: Relationship between density of crayfish, sculpins and crayfish and sculpins combined and Km for Parry Sound (PS) and Lake Champlain (LC) reefs.

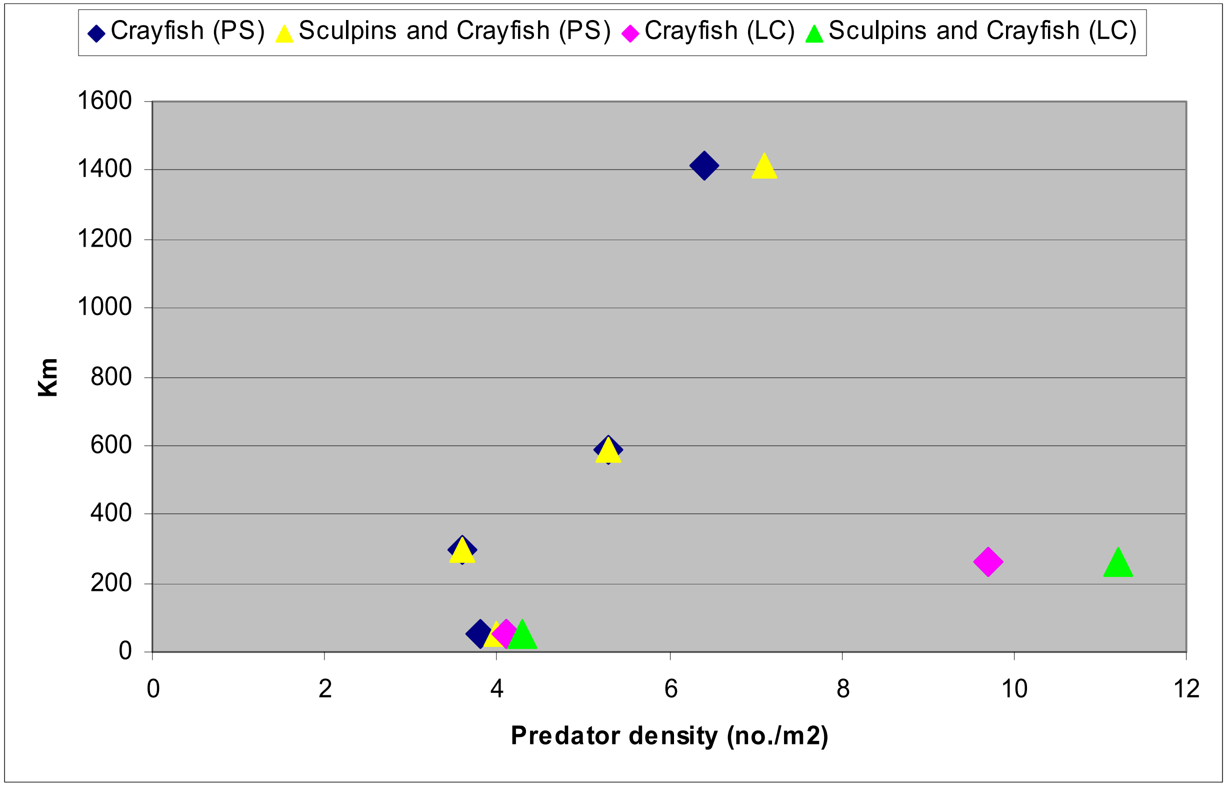


Fig. 14: Relationship between density of crayfish, sculpins and crayfish and sculpins combined and Km for each of the 6 Lake Michigan reefs.

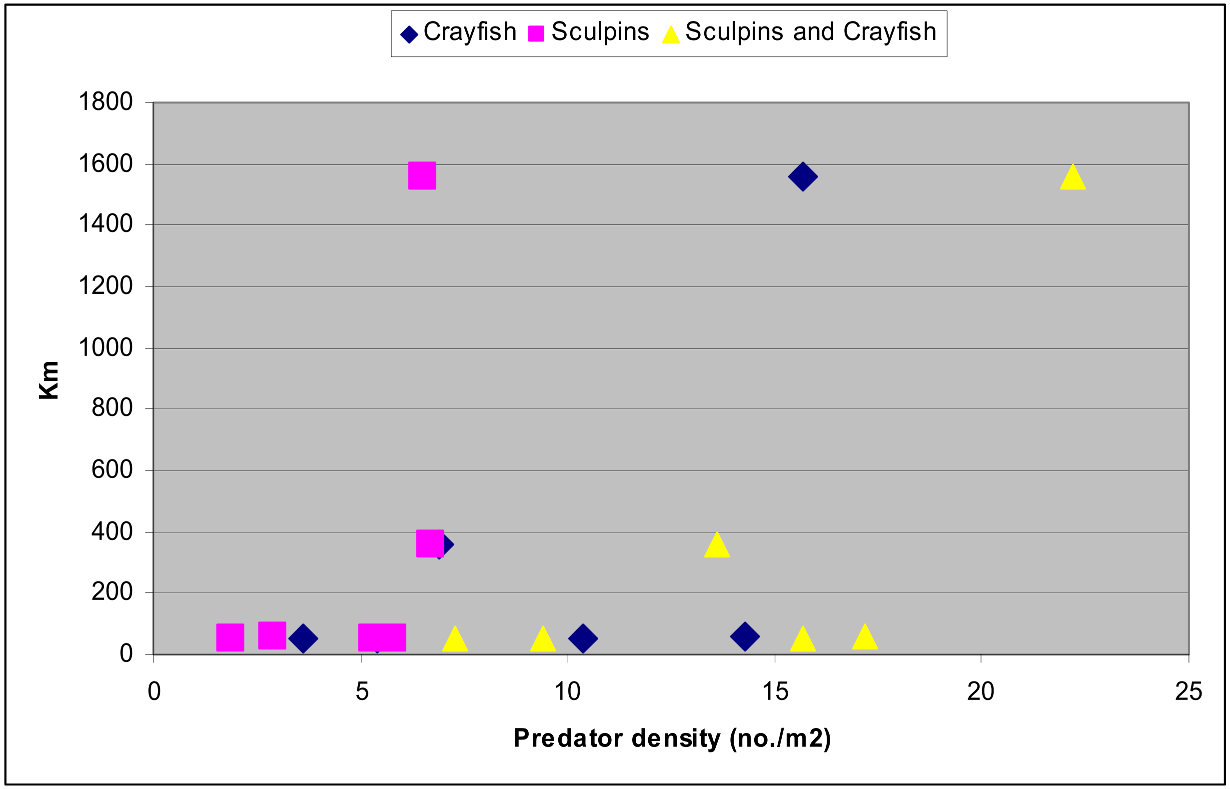


Fig. 15: Relationship between west wind fetch and egg recovery and survival at 5000 eggs·m^{-2} for 6 lake trout spawning reefs in Lake Michigan and Huron 2002. Curve is for Lake Michigan data.

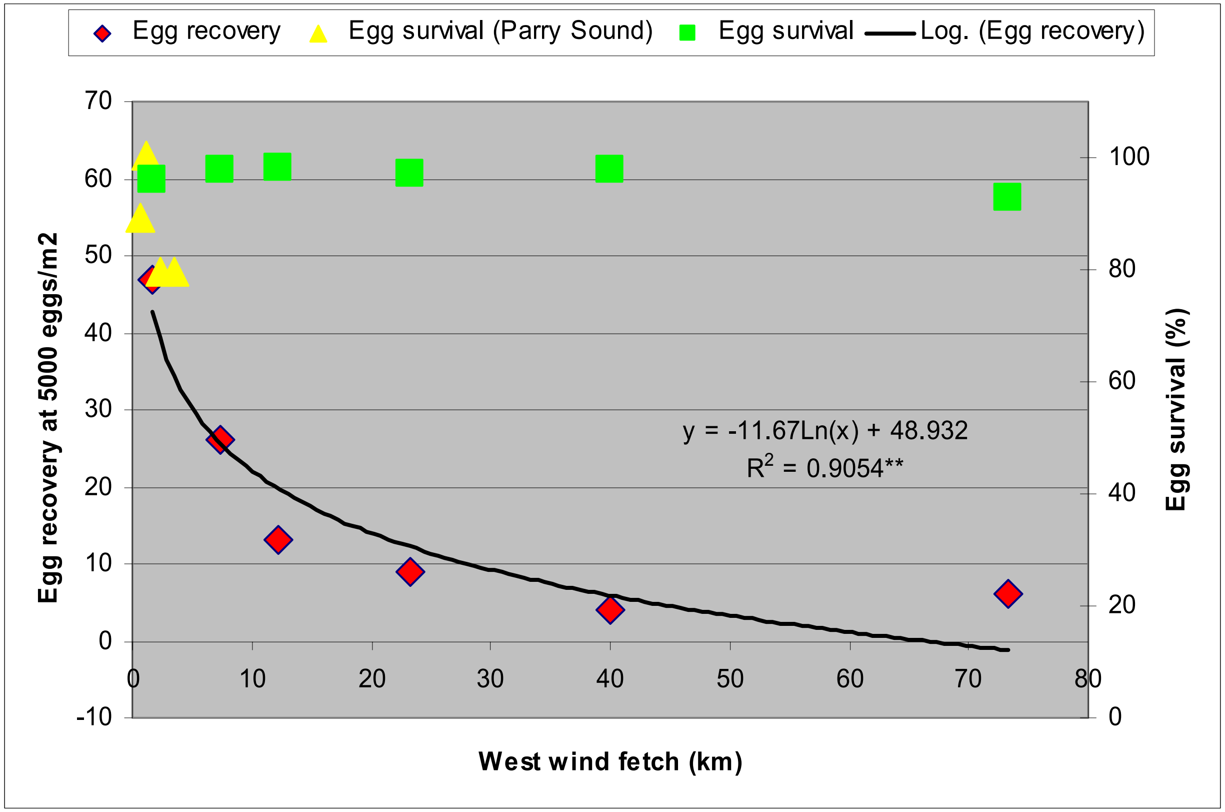
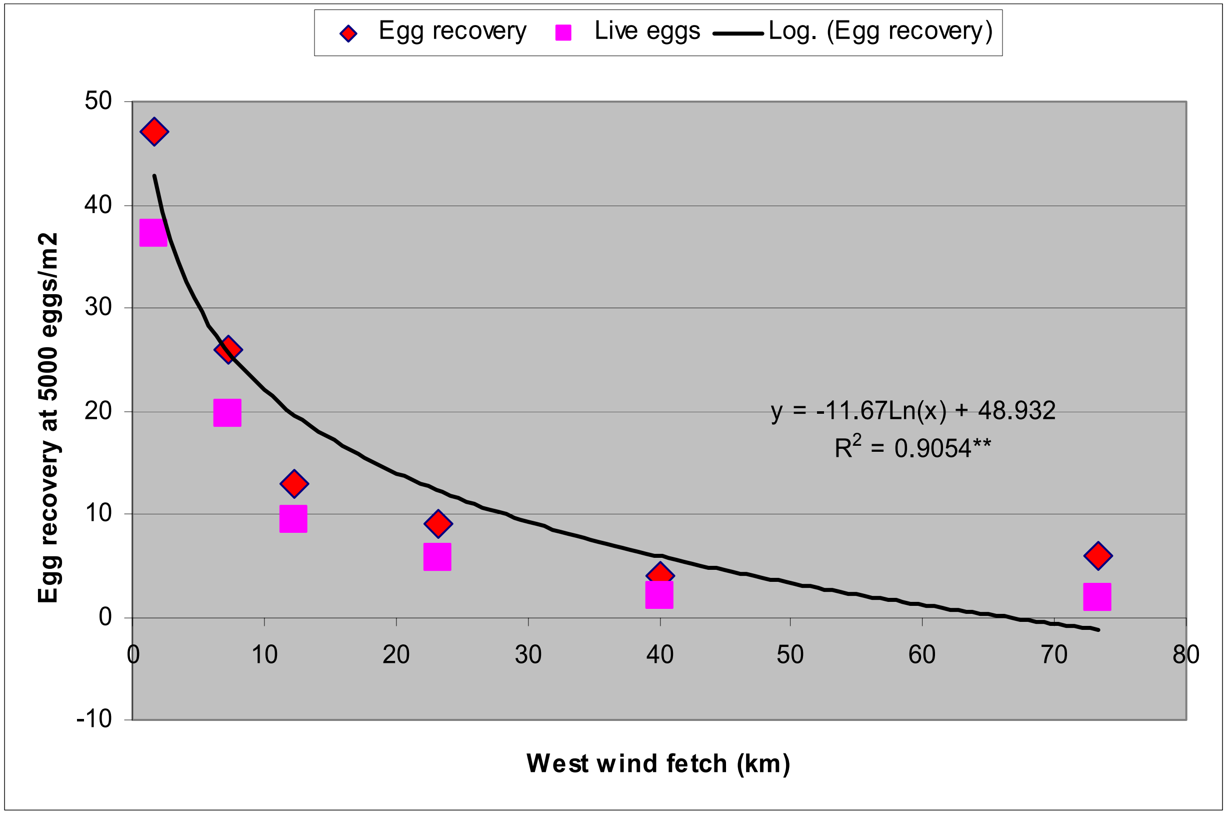


Fig. 16: Relationship between west wind fetch and estimated egg recovery and live egg recovery using the relationship from Fitzsimons (1995) for the 6 Lake Michigan sites.



Salmonine egg predation by round gobies, mottled and slimy sculpins, and crayfish (*Orconectes propinquis*): Factors affecting laboratory derived predation rates.

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Abstract: Recent modeling efforts, prompted in part by the ongoing lack of natural reproduction by lake trout (*Salvelinus namaycush*) in the Great Lakes, have focused attention on the potential negative effects of interstitial predators like sculpins, crayfish and gobies. For these models to become more useful, however, there is a need to better understand a number of factors that potentially affect egg consumption by interstitial predators and incorporate these in models. In this study we investigated in the laboratory the effect of temperature (1-2ºC, 4-5ºC, 7-8ºC, and 10-11ºC), egg density, interspecific and intraspecific competition and an alternate food source on egg consumption by slimy (*Cottus cognatus*) and mottled sculpins (*Cottus bairdi*), round gobies (*Neogobius melanostomus*), and the native crayfish (*Orconectes propinquis*). Egg consumption was unaffected by temperature except for slimy sculpins where more eggs were eaten at 10-11ºC than at 1-2ºC or 4-5ºC. Both round gobies and slimy sculpins ate fewer eggs per individual at a density of 5 or 10 per tank than 1 individual per tank that was not compensated for by the higher predator density. There was no evidence of intraspecific competition between slimy sculpins and round gobies at various species combinations (10:0, 9:1, 5:5, 1:9, 0:10) at a density of 10 individuals per tank. Satiation appeared to regulate egg consumption under conditions of increasing egg density with little evidence of increased consumption at higher egg density. The presence of zebra mussels (*Dreissena polymorpha*) did not affect the number of eggs eaten by round gobies which ate approximately 75% of their body weight in mussels per day when rainbow trout eggs were present. Based on comparative studies round gobies overall appeared to be the most adept egg predator, followed by sculpins with crayfish the least efficient.

Introduction

Stocking of lake trout to rebuild populations decimated by the combined effects of overfishing and sea lamprey predation has produced little tangible evidence that all of the barriers to restoration have been removed (Krueger et al . 1995). It is only in Lake Superior where with the aid of 45 years of stocking, populations are considered fully restored to the extent that further stocking is unnecessary (Hansen et al. 1995). For Lake Ontario while there is evidence of natural reproduction as evidenced by survival past the young-of-the-year stage (YOY), it is geographically and temporally sporadic and overall remains at a low level despite improvements in water quality, reductions in contaminant burdens, and high spawner abundance (Fitzsimons et al. 2003, Fitzsimons 1995, Fitzsimons et al. 1995, Selgeby et al 1995). Lake Ontario's small size and relatively high stocking rate per unit area, may have resulted in higher adult abundance and as a consequence have enhanced opportunities for natural reproduction there. For Lakes Erie, Huron, and Michigan, lakes that are 1.3 to 3 times the area of Lake Ontario but with much lower area based stocking rates there is almost no evidence of survival past the YOY stage. Nevertheless Lake Superior is the largest of the Great Lakes, and while it had significant remnant stocks, it has been determined that stocking made a significant contribution to restoration of lake trout in this lake even though the area-based stocking rate was extremely low (Hansen et al. 1997). This suggests looking elsewhere, and likely at density independent factors, to develop a better understanding of the bottelenecks to restoration of lake trout stocks in the Great Lakes.

Jones et al (1995) provided convincing arguments of the potential of predators to affect lake trout restoration. Their ideas were further developed by Savino et al (1999) who of the three types of predators (eg. epibenthic predators, interstitial predators, fry predators) implicated interstitial predators as causing the highest mortality. However the ability of both authors to predict actual predation was hampered by limited or non-existent model parameterization. Notably these authors referred to the need for assessing the effect of the prey and predator density, the presence of other competing predators, availability of alternate prey, and predation duration. Even for Lake Ontario where there is limited natural reproduction, there appears to be evidence of the potential effects of predators. Fitzsimons et al. (2002) using the abundance of simultaneously collected lake trout eggs and their major interstitial predators, sculpins and crayfish, predicted that at 5 out of 8 reefs examined, predation could be a significant mortality factor. Even though these authors evaluated one of the conditions necessary for assessing effect, namely having prey and predator density, they used relatively simple models of effect however, over a 30 day period and assumed an additive interspecific competition-free model. While their assumptions that the initial 30 days post spawning where temperatures were relatively warm was likely the most significant and was supported by models of predator effect (Jones et al. 1995, Savino et al. 1999), predation over the winter months could still be important. With an estimated egg incubation period of 180 days (Savino et al. 1999), over 150 of which occurs at temperatures less than 4ºC, even low rates of egg consumption could be important. Fitzsimons et al's. (2002) assumption of an additive interspecific competition-free model, or that the predation effect is directly proportional to predator density and unaffected by competing predators, is also evident in models of predator effect (Savino et al. 1999, Jones et al. 1995). However, there was little real support for this assumption in the literature. Most predation studies have used either a single sculpin (Savino et al 1991, Biga et al 1998, Chotkoski and Marsden 1999) or a single crayfish (Savino and Miller 1991, Horns and Magnuson 1981), to infer predator effects when in the wild, density can range over at least an order of magnitude (Fitzsimons et al 2002). Moreover sculpins and crayfish can co-occur on the same reef but to the authors knowledge there is only one instance where investigators simultaneously assessed the effect of competition for lake trout eggs between a crayfish and a sculpin (Miller et al. 1992).

In a similar vein the effect of varying egg density on the effect of predators has received little attention although a predator swamping effect (Sweeney and Vannote 1982, van Montfrans 1995) is liable to modulate the effect of predators particularly at high egg densities. In the Great Lakes, lake trout egg density can vary by over four orders of magnitude and it is not clear if the density of egg predator populations either expands or contracts to meet the size of this potential but seasonably restricted food source (Fitzsimons 1995, 1999). Of the 8 spawning reefs evaluated by Fitzsimons et al. (2002), deposition at two reefs was so high that the authors concluded based on the predator density at the time, that egg predation at these sites would be relatively unimportant.

Deposition of lake trout eggs is a seasonally limited occurrence and it seems unlikely that a predator could exist on the nutrition obtained from eggs alone. Accordingly other food items must also be important to the diet of species like sculpins and crayfish to sustain populations found on spawning reefs. Fitzsimons et al (2002) noted a variety of items in sculpin stomachs other than lake trout eggs including isopods and amphipods but relative volumes were not determined. There is only one study so far that has looked at the importance of an alternate food source on egg predation. Savino and Henry (1990) noted that the presence of the amphipod *Diaporeia* did not affect the egg consumption by slimy sculpins. For other egg predators like round gobies the presence of an alternate food source especially if that alternate food source is zebra mussels has a strong potential to influence egg predation. Round gobies prefer zebra mussels, particularly small ones (Ghedotti et al. 1995), and given the nature of lake trout spawning habitat it is likely that lake trout eggs would co-occur with zebra mussels (Marsden et al. 2001).

Addition of new exotic egg predators further complicates estimates of the effects of egg predators on lake trout restoration. The rusty crayfish (*Orconectes rusticus*) while present in Wisconsin inland lakes for several years has recently spread to Lake Michigan where it co-occurs with native crayfish that over time appears to displace them completely (Capelli 1982,Lodge et al. 2000, Olsen et al 1991, Jonas et al 2003). Of even greater significance has been the more recent but much more rapid spread of round gobies after being accidentally introduced through ship's ballast into the St. Clair River in 1990 (Jude et al. 1992). This species has now been sited at lake trout spawning areas in lakes Erie, Michigan, Huron, and Ontario with densities as high as $116 \cdot m^{-2}$ being observed (unpublished data).

To help resolve a number of the uncertainties regarding the effects of egg predators on lake trout egg mortality and aid in the development of more realistic models of effect we undertook a number of studies over a three year period to examine the following:

1. The effect of temperature on egg consumption by round gobies and slimy and mottled sculpins.

2. The effect of interspecific competition on egg consumption by round gobies and slimy sculpins.
3. The effect of intraspecific competition between round gobies and slimy sculpins on egg consumption
4. The effect of egg density on egg consumption by round gobies, slimy sculpins and crayfish.
5. The effect of an alternate food source (e.g. zebra mussels) on egg consumption by round gobies.

Herein we report the results of our investigations.

Methods

Fish and egg collections and holding

Collections of slimy sculpins were made with bottom trawls towed in depths of 50-70 in western Lake Ontario over a three year period (2000-2002). They were transported back to CCIW where they were held in dechlorinated Lake Ontario water at ambient temperature (8-10ºC), in 1-m square tanks with various ABS pipe fittings and cobbles provided as cover. Sculpins were fed lake and rainbow trout eggs along with frozen blood worms and brine shrimp. Mottled sculpins were collected by back pack electrofisher in the upper Credit River and transported back to CCIW where they were held in similar conditions to slimy sculpins.

Round gobies were collected initially by bottom trawl in western Lake Erie and transported back to CCIW where they were held under similar conditions to sculpins above. Because of a massive die off during the spring of 2001, additional collections were made by beach seine along the north shore of Lake Erie in the summer of 2001. These collections were supplemented in the summers of 2002 and 2003 by trawl collections made off the mouth of the Niagara River in western Lake Ontario.

Lake trout eggs were obtained from various sources including Keuka Lake and Lake Ontario. These were fertilized at CCIW where they were held at 8-10ºC until the time of testing usually between epiboly and eye-up as earlier developmental stages, particularly for eggs from Lake Ontario suffered high mortality if handled before epiboly. While the source of eggs may have varied across experiment type, within a particular set of experiments (ie. temperature) the same source of eggs was used.

Rainbow trout eggs were used to supplement tests with lake trout eggs as well as provide comparative data. Eggs were obtained from Rainbow Springs Hatchery in Thamesford, Ontario; eggs were generally available all year long from this facility except for a period in July and August.

Effect of experimental conditions

To assess the effect of the presence of substrate and egg condition (ie live or dead) in the system being used to evaluate temperature effects, egg predation by slimy sculpins on lake trout eggs was tested with and without substrate. The substrate used was round river stones obtained from a local garden supply. Substrate averaged 8 cm in diameter and was

10-15 cm deep. In addition we tested whether predation on lake trout eggs differed depending on whether they were live or dead but in the absence of substrate. Use of dead eggs potentially allowed testing of eggs over a much broader seasonal range than live eggs that are only available in the fall through to the late spring.

Effect of temperature

The temperature of CCIW water feeding individual glass aquaria (40 cm long x 20 cm wide 25 cm high) containing approximately 2 layers of round river stones (8 cm dia.), was adjusted to a flow of approximately 100 ml/minute using a combination of cold- and hot-water, to one of four target temperature ranges: 1-2ºC, 4-5ºC, 7-8 ºC, and 10-12ºC prior to experimentation. Each temperature and predator combination was replicated 6 times. Water depth was held at 20 cm with a standpipe. Light was maintained at __ lux with a 12 hr. light: 12 hr. dark photoperiod. Predators were acclimated to test temperatures for one week prior to testing. For 24 hr. prior to the initiation of a particular study all predators (mottled sculpin, slimy sculpin, round goby) were starved. On the date a particular experiment was to start, 50 live eggs, either rainbow trout or lake trout, were gently spread over the entire surface of the rocks and allowed to settle into the interstices for an hour before a single predator was added and allowed to forage for 7 days. Temperature of each aquaria was monitored daily. At the end of the 7-day exposure period, numbers of live eggs, dead eggs and chorions were removed and counted while the length (mm) and weight (gm) of each predator was determined.

Effect of tank size

To assess the effect of tank size on egg predation buy round gobies, the glass aquaria and 1–m fiberglass tanks used above along with a 4-m dia. plastic pool were used to create five different areas (0.08, 0.25, 0.50, 1.0 and 10 m^2). The fiberglass tanks were either divided in half or quarters using bricks to obtain areas of 0.25 or 0.50 m^2. To obtain an egg density of approximately 500 eggs·m^{-2}, 50, 125, 250, 500 or 5070 lake trout eggs were added to the areas of 0.08, 0.25, 0.50, 1.0 and 10 m^2 respectively. Six replicates were used for all of the above areas with the exception of the 10 m^2 where only three replicates were used. As above, a single predator was starved for 24 hr. prior to being added to the tank, one hour after eggs were added. Light was maintained at ____ lux with a 12 hr. light: 12 hr. dark photoperiod. A single temperature range was used (7-8ºC) that was maintained with a combination of cold- and hot-water with a flow rate of 100-5000 ml/minute. Temperature of each aquaria, tank, or pool was monitored daily. At the end of the 7-day exposure period numbers of live eggs, dead eggs and chorions were removed and counted while the length (mm) and weight (gm) of each predator in each tank was determined

Effect of interspecific competition

Tests to assess the effect of interspecific competition on egg consumption by slimy sculpins and round gobies (1, 5 or 10 per tank) were conducted in 1 m square fiberglass tanks containing two layers of rounded river stones (8 cm dia.). A total of 500 eggs were used for each of the six replicates (five for gobies), and these were poured evenly over the entire surface of the tank and allowed to settle for an hour before a single predator was added. As above predators were starved for 24 hr. prior to testing while light was maintained at XX lux with a 12 hr. light: 12 hr. dark photoperiod. A single temperature range was used (7-8ºC) that was maintained with a combination of cold- and hot-water with a flow rate of 1000 ml/minute. Each density and predator combination was replicated 6 times. Temperature of each tank was monitored daily. At the end of the 7-day exposure period numbers of live eggs, dead eggs and chorions were removed and counted while the length (mm) and weight (gm) of each predator in each tank was determined.

Effect of intraspecific competition

The effects of intraspecific competition between slimy sculpins and round gobies was evaluated at the following treatments of numbers of slimy sculpin to numbers of round goby: 10:0, 9:1, 5:5, 1:9, and 0:10. Six replicates were used for all of the treatments with the exception of 9:1 sculpins :gobies and 1:9 gobies:sculpins where only three replicates were used. The same environmental conditions were used as for the interspecific experiments. Light was maintained at ___ lux with a 12 hr. light: 12 hr. dark photoperiod. A single temperature range was used (7-8ºC) that was maintained with a combination of cold- and hot-water with a flow rate of xx ml/minute. Temperature of each tank was monitored daily. At the end of the 7-day exposure period, numbers of live eggs, dead eggs and chorions were removed and counted while the length (mm) and weight (gm) of each predator in each tank was determined.

Effect of egg density

Tests to determine the effect of egg density on lake trout egg consumption by slimy sculpins, round gobies and native crayfish (*Orconectes propinquis*) were run in small glass aquaria used above for temperature studies. The same substrate was also used. One of seven different densities of eggs (5, 10, 25, 50, 100, 250 or 500) were added to each aquaria to produce egg densities of 63, 125, 313, 625, 1250, 3125 or 6250 eggs·m^{-2} respectively. A total of three replicates per egg density were used. As above, a single predator was starved for 24 hr. prior to being added, one hour after eggs were added. Light was maintained at ___ lux with a 12 hr. light: 12 hr. dark photoperiod. A single temperature range was used (10-12ºC) that was maintained with a combination of cold- and hot-water with a flow rate of 100 ml/minute. Temperature of each aquaria was monitored daily. At the end of the 7-day exposure period numbers of live eggs, dead eggs and chorions were removed and counted while the length (mm) and weight (gm) of each predator in each tank was determined.

Effect of zebra mussels on egg consumption by round gobies

Small zebra mussels (5-10 mm) were scraped from docks at a marina in the Severn River in the summer of 2003. They were transferred to water filled coolers, and returned to CCIW where they were reared for 30 days until 750 grams was added to each of six 40 x 20 cm aquaria containing approximately two layers of 8 cm dia. cobbles. Once added, the mussels covered approximately 50-75% of the rock surface. A separate sample of mussels was measured to determine the length frequency and average mussel weight before the predation tests were begun. Mussels were allowed a period of one month to adjust to the aquaria and reattach to rocks with their byssal threads. Tests made over the course of this period indicated that this was indeed the case although no objective tests of the degree of adherence were made. Over the one month period mussels were held at 12-13ºC and fed various forms of *Spirulina* and were observed to be actively filtering water during the adjustment period.

A second set of six aquaria of the same dimensions and with the same size and density of cobbles as the mussel aquaria, were set up prior to the experiment. Water temperature in both sets of aquaria was adjusted to 10-12ºC two days before tests were begun. Gobies were starved for 24 hr prior to being added to the aquaria to which had been added 50 eyed rainbow trout eggs obtained from a local hatchery. Eggs were added in such a way that most settled down into the spaces around and beneath the cobbles although some were evident on the surface.

A subsample of approximately 200 mussels was measured for length prior to the experiments. In addition approximately 200 mussels from each of the six tanks was measured at the end of the experiment and these were used to assess whether there had been any qualitative changes in the lengths of the mussels due to predation by gobies.

The weight of all mussels remaining in each aquaria at the end of the experiment was determined and used to calculate the weight of mussels eaten by each goby.

Statistics

The General Linear Model procedure of Systat was used to assess treatment differences. Pairwise comparisons were made using the Bonferroni procedure. All count data was log transformed while all percentage data was arc sine transformed prior to analysis to stabilize variance. The Kolmogorov-Smirnoff procedure was used to compare the size distribution of zebra mussels before and after goby predation. All tests were considered significant at $p \leq 0.05$

Results

Effect of substrate

In the small aquaria used for the temperature tests, the presence of substrate had a significant ($p=0.043$) effect on the number of lake trout eggs eaten per day by slimy sculpins that was temperature dependant ($p<0.001$) (Table 1). Accordingly all other tests were performed with substrate present

Effect of egg condition

The condition of the egg, whether it was alive or dead, had no significant ($p>0.05$) effect on how many rainbow trout eggs were consumed by round gobies (Table 2). In contrast the condition of the egg had a significant effect on whether lake trout eggs were eaten by slimy sculpins. Significantly ($p=0.001$) more live eggs were eaten than dead, although the number depended on temperature ($p<0.01$) (Table 3). Accordingly all other experiments were performed with live eggs only.

Temperature

Temperature had a significant ($p=0.001$) effect on how many lake trout eggs were consumed but it depended on the species of predator ($p=0.028$) but with no interaction ($p>0.05$) between species and temperature (Table 4). Overall slimy sculpins consumed significantly ($p=0.026$) more eggs than round gobies but similar amounts to mottled sculpins. In addition mottled sculpins and round gobies consumed similar numbers of eggs. Significantly more eggs were consumed in the 10-11ºC range than at 2-4ºC ($p=0.006$) or 4-6ºC ($p=0.001$) but not 7-8ºC ($p>0.05$). Consumption at 2-4ºC, 4-6ºC, and 7-8ºC was similar.

When species were tested individually, slimy sculpins ($p=0.002$), but not mottled sculpins ($p>0.05$) or round gobies ($p>0.05$), showed evidence of a temperature effect (Table 4). In no case was there a significant effect of predator size on consumption. With slimy sculpins, the number of eggs consumed in the temperature ranges 2-4ºC ($p=0.005$) and 4-6 ºC ($p=0.006$) were significantly less than for the temperature range 10-11ºC (Table 4).

Tank size

Size of tank that experiments were conducted in, had a significant (p=0.023) effect on the number of rainbow trout eggs consumed by round gobies (Table 5). In no case was there a significant effect of predator size on consumption. The number of eggs consumed in a 1 m^2 tank was significantly greater (p=0.043) than a 0.08 m^2 tank but not a 0.25, 0.5 or 10 m^2 tank. As a result all experiments involving interspecific or intraspecific competition were conducted in 1 m^2 tanks.

Interspecific competition

For slimy sculpins and round gobies fed lake trout eggs, there was evidence of interspecific competition. For slimy sculpins, the number of eggs eaten per individual when only one sculpin was present, was significantly greater than if five (p=0.049) or ten (p=0.007) sculpins were present although there was no difference between five and ten sculpins (Table 6). In no case was there a significant effect of predator size on consumption. Despite these differences, ten sculpins ate significantly (p=0.007) more lake trout eggs than one sculpin but not five sculpins, although the number eaten was not proportional to the number of predators present.

With round gobies, a similar pattern was evident in that the number of lake trout eggs eaten per individual when only one goby was present, was significantly greater than if five (p=0.015) or ten (p=0.006) gobies were present although there was no difference between five and ten gobies (Table 6). In no case was there a significant effect of predator size on consumption. As a result, the total number of lake trout eggs eaten by one, five or ten gobies was similar (Table 6).

When gobies were fed rainbow trout eggs neither the number of eggs consumed per individual nor the number of eggs consumed when one, five or ten gobies were present showed a significant density effect (Table 6).

Intraspecific competition

Using various combinations of slimy sculpins and round gobies (10:0, 9:1, 5:5, 1:9, 0:10) we were unable to detect any evidence of intraspecific competition with regards to how many lake trout eggs were consumed. (Table 7).

Egg density

All predators including crayfish ($p=0.039$), slimy sculpin ($p<0.001$) and round goby (<0.001) showed evidence of an egg density effect on the proportion of lake trout eggs consumed over a one week period (Figs. 1-3)

For crayfish, the proportion of eggs consumed at 10 eggs per tank was significantly ($p=?$) less than at 500 eggs per tank but was similar to the other egg densities (Fig. 1). The absolute number of eggs consumed per day by crayfish was not affected by egg density.

The proportion of lake trout eggs consumed by slimy sculpins for a one week period at 10 eggs per tank was significantly less than the number of eggs consumed at 25 ($p=0.003$), 50 (0.001), 100 (<0.001), 250 (<0.001) and 500 (<0.001) eggs per tank (Fig. 2). In addition a significantly (<0.001) smaller proportion of eggs were consumed at 5 eggs per tank than at 10 eggs per tank. The absolute number of eggs consumed per day by slimy sculpins was unaffected by egg density except at 5 eggs per tank where significantly fewer eggs were consumed than at 10 ($p=0.002$), 25 ($p=0.006$), 50 ($p=0.001$), 100 ($p=0.003$), 250 ($p=0.001$) and 500 ($p=0.001$) eggs per tank. Absolute consumption at all other densities was similar.

With round gobies, the proportion of eggs consumed over a one week period at 5 eggs per tank was significantly less than at 25 ($p=0.001$), 50 ($p<0.001$), 100 ($p<0.001$), 250 ($p=0.002$) and 500 ($p<0.001$) eggs per tank (Fig. 3). Similarly the number of eggs consumed at 10 eggs per tank was significantly less than at 25 ($p=0.046$), 50 ($p=0.011$), 100 ($p=0.005$), and 500 ($p<0.001$) but not 250 ($p>0.05$) eggs per tank. The absolute number of eggs eaten per day showed a significant ($p=0.001$) effect of egg density. Specifically the number of eggs eaten at 25 ($p=0.006$), 50 ($p=0.012$), 100 ($p=0.003$) were significantly less than at 250 eggs per tank but not at 5, 10 or 500 eggs per tank.

Alternate food source

The consumption of rainbow trout eggs by round gobies was unaffected by the presence of zebra mussel encrusted cobbles. The number of eggs eaten per day with mussels present (0.78±0.28 (X±SEM)) was not significantly ($p>0.05$) different from where mussels were absent (0.33±0.13). In addition, in the presence of mussels, 5.9 (±0.13) grams of mussels were eaten per day, representing 75.6 (±8.0) percent of body weight per day. Based on the length frequency of mussels used at the start of the experiment and those remaining at the end, gobies appeared to prefer mussels in the size range 6-11 mm (Fig. 4).

Discussion

The temperature range that we used that spanned the temperatures occurring just before (10-11ºC) and at lake trout spawning (7-8ºC), for the first month after spawning (4-5ºC), and well into the winter (1-2ºC), did not have a large effect on egg consumption except for slimy sculpins. This was surprising given that fish are poikilotherms for which we would have expected that egg consumption may have been more dependant on temperature. Sculpin gut passage time was found to be inversely related to temperature (Hershey and McDonald 1985). Some of the lack of a temperature effect was due to variability within treatments that limited our ability to detect among temperature range effects. In support of this is that for slimy sculpins, that showed the greatest range in consumption between low and high temperatures, we saw the greatest number of significant differences.

The fact that egg consumption occurs at temperatures as low as 1-2ºC and perhaps lower still, has implications for modeling of the effect of egg predators like sculpins and gobies. Savino et al. (1999) maintained that predation by interstitial predators like sculpins would slowly decline post spawning to near zero over temperature ranges that are similar to what we used here. Our results do not support that for mottled sculpins and round gobies. Even for slimy sculpins where there was more evidence of a temperature effect, daily consumption at 1-2ºC (0.43 eggs·day^{-1}) was approximately 25% of the starting egg predation rate used by Savino et al. (1999) of 2 eggs·day^{-1}·predator^{-1} that was similar to the average consumption rate of slimy sculpins at 10-11ºC we observed (1.67 eggs·day^{-1}·sculpin^{-1}). With regards to egg consumption at low temperatures during winter, the modeling efforts of Jones et al. (1995) regarding interstitial predators seem more realistic. They assumed predation would occur over a longer period (200 instead of 160 days) and at a higher rate at the end of the period (close to 0.5 compared to near 0 eggs·day^{-1}·predator^{-1}) than Savino et al. (1999).

The continuing consumption of eggs even at low temperatures is perhaps of greater concern for round gobies than sculpins because of differences in abundance. In Lake Ontario Fitzsimons et al. (2002) reported that densities of sculpins on spawning reefs based on egg nets ranged from 4 to 50·m^{-2} with most less than 10. In contrast estimates using the same nets at one site in western Lake Ontario have indicated densities as high as 116 gobies·m^{-2} (unpub. data), some 25-times the abundance of sculpins reported for this same location.

The predation rates that we observed for sculpins and gobies from the temperature studies were generally lower than those that have been reported previously from the literature. Savino and Henry (1991) reported that slimy sculpins at 6-7ºC ate 2 lake trout eggs·day^{-1} whereas we found slimy sculpins to consume approximately half this amount (1.06 eggs·day^{-1}) at a temperature range of 7-8ºC. Similarly Miller et al (1992) noted that at 7ºC, slimy sculpins ate 2.5 eggs·day^{-1}. Based on data provided by Chotkowski and

Marsden (1999) for a 75 mm mottled sculpin with a temperature range of 4.5-14ºC, the daily consumption was 2 lake trout eggs was estimated. Based on this same study, a 75 mm round goby was estimated to eat about 1.5 eggs·day^{-1}.

Part of the difference for egg consumption rates between our study and those in the literature may be the tank size used for the temperature studies of 0.08 m^2. Daily consumption rates for individual slimy sculpins and round gobies in 1 m^2 tanks at a water temperature of 7-8ºC were 2.5 and 7.0 eggs·day^{-1} respectively and are similar to higher than those reviewed above. These consumption rates represent increases for the sculpin and goby of 2.5- and 14-fold respectively over that at the same temperature but for tanks that were one-twelfth the volume. Further increases in tank size of up to 10-times did not increase the daily consumption of rainbow trout eggs by round gobies suggesting that the 1 m^2 tank we used for a number of our studies did not constrain egg consumption and probably provides a reasonable estimate of egg consumption rates in the wild. The reason why egg consumption should increase with tank size is not clear. If a predator like a round goby was foraging on the eggs closest to the surface it could at an egg density of 500 eggs·m^{-2}, such as we used, quickly deplete eggs in this zone in a 0.08 m^2 tank but have more difficulty doing this in a 1 m^2 tank. Obviously in our case the 10 m^2 tank, also with 500 eggs·m^{-2}, did not significantly increase the availability of eggs to round gobies.

Substrate and the size of predators used may also play a role since Biga et al. (1998) noted that mottled sculpins had more difficulty feeding on lake trout eggs in 10-22 cm glacial till than 5 to 10 cm stream. The substrate we used that averaged 8 cm in diameter was near the middle of the range represented by this study and certainly reduced lake trout egg consumption by slimy sculpins when substrate was present relative to a bare tank. Biga et al. (1998) also noted that small sculpins were able to penetrate interstitial spaces to a greater degree than large sculpins.

Perhaps the most striking result of our studies was the strong effect of interspecific competition. Both five and ten slimy sculpins when held in the same tank ate significantly fewer eggs per individual than a single individual. Moreover although the greater density resulted in greater overall consumption it was far from additive. The total number of eggs consumed by five and ten sculpins per day of 5.9 and 8.6 respectively were still well short of the 12.5 and 25.0 eggs per day expected if consumption was directly proportional to density and they ate the same number of eggs as an individual slimy sculpin (2.5 eggs·day^{-1}). Similar results were seen for goby although the deviation from expected was even greater. Based on a per individual consumption of 7 eggs·day^{-1}, we would have expected 35 and 70 eggs per day to be eaten by 5 and 10 gobies respectively. Instead the 5 and 10 gobies ate only 8.9 and 14 eggs·day^{-1} respectively which were not significantly different from consumption by a single individual. The results for rainbow trout eggs and round gobies were no different from those with lake trout eggs. In our interspecific competition experiments we were unable to examine feeding by individual fish so we don’t know how distributed the effect was and whether one fish did all the egg consuming as conspecifics were added or whether egg consumption was shared among conspecifics albeit at a low level.

The lack of any intraspecific competition when ten predators were present may be a reflection of the process operating when 10 conspecifics as present noted above. Furthermore once density is at this level whether they are conspecifics or not does not seem to matter even for unrelated species like mottled sculpins and round gobies that in single individual pairings showed considerable aggression on the part of the round goby (Dubs and Corkum 1996). Nevertheless there is evidence of intraspecific competition leading to the recruitment failure of mottled sculpins in habitats invaded by round gobies but this appears to be the result of spawning interference by round gobies (Janssen and Jude 2001.

The presence of a strong interspecific effect has significant implications to assessing the effects in the wild and in modeling efforts. Fitzsimons et al. (2002) assumed an additive model in his calculations such that egg consumption by both sculpins and crayfish was directly proportional to numbers. Our results here do not support an additive model. Similarly in the modeling efforts of Savino et al. (1999) and Jones et al. (1995) an additive model was assumed but again does not appear justified.

The reason for the strong interspecific competition effect may relate to behavioural interactions especially between gobies. Dubs and Corkum (196) reported that at night when mottled sculpins and round gobies were most active outside or refuges, and when they would probably be eating more eggs, more time was spent in a refuge by a resident fish if a single conspecific intruder was present. There was no clear difference in the time spent in the refuge by the two species. If another species, instead of a conspecific was added instead, the time in the refuge was even greater. Associated with these behavioural changes were increased amount of aggression shown by a resident goby relative to an intruding goby, behaviours that appeared to be absent with mottled sculpins. This greater aggression shown by gobies to other gobies compared to mottled sculpins may explain the relatively greater effect of interspecific competition in depressing overall consumption that we observed with round gobies compared to slimy sculpins.

The mechanism by which egg predators like sculpins and gobies find eggs is not known but appears to involve chemosensory cues that may involve taste or olfaction or some combination for which the stage of the egg appears to be very important (Dittman et al. 1998). These authors noted that there was a limited window, post spawning when salmon eggs were actually detectable by sculpins using chemical cues. When Clary (1972) and Biga et al. (1998) seeded artificial salmon redds with fertilized water-hardened eggs, there was no attraction to redds by slimy sculpins. How the death of an egg interacts with this process not known although we found that slimy sculpins preferred live eggs over dead eggs and that this preference increased with temperature. Round gobies in contrast showed no preference for live over dead rainbow trout eggs. Many of the eggs deposited on a spawning reef die immediately after spawning either as a result of lack of fertilization, physical disturbance, or wave action (Fitzsimons 1995, Perkins and Krueger 1995, Jones et al 1995). Therefore goby predation on dead eggs, that will not contribute to reproduction anyways, may buffer effects on live eggs whereas with slimy sculpins this is not the case.

At very low egg densities there appears to be some variation in the ability of different egg predators to find and consume eggs. The crayfish that we used appeared to be relatively inept based on the small proportion of eggs consumed at low densities. In contrast the slimy sculpin was able to find and consume most eggs down to125 eggs$\cdot$m^{-2} while the round goby could find and consume most eggs down to 63 eggs$\cdot$m^{-2} or half this density. This suggests that the round goby could be a superior predator a standing enhanced by its high population abundance and greater individual egg consumption rate.

Satiation appears to be strong regulator of egg predation over a number of phyla based on our studies. Crayfish but more so with round gobies and slimy sculpins, the proportion eggs eaten decreased with egg density. The point at which this started to occur was at a relatively low egg density of 125-300 eggs·m^{-2} suggesting that without a lot of use a spawning stock of lake trout could potentially overwhelm a group of interstitial predators. Although egg predators can sometimes increase egg consumption in the face of greater egg availability, this was limited and appeared to occur only after quite high egg. abundances were achieved (ie 3000-6000 eggs·m^{-2}), and it is not known if these rates of consumption are sustainable and are likely ultimately controlled by fish size (Biga et al. 1998).

The presence of zebra mussels did not diminish consumption of rainbow trout eggs by round gobies even when over 50% of the substrate was covered and with mussels of the appropriate size. Whether eggs were taken incidental to feeding on the mussels, their typical diet in the Great Lakes (Jude et al. 1995, Ray and Corkum 1997), or selected for, is not known. Selection for smaller mussels is similar to what has been observed in the wild (Djuricich and Janssen 2001). The very high consumption rate of mussels by gobies on a percent body weight basis and the number of mussels that would have to be ingested for this to occur, would suggest a high potential for the incidental ingestion of fish eggs during the feeding process. Conversely because of their preference for zebra mussels, when mussels are absent or present at low abundances they may be inadequate to support large populations of gobies on an ongoing basis. As a result, areas like Georgian Bay that have very low densities of mussels currently, may encounter smaller densities and attendant effects of gobies compared to other areas like northeastern Lake Michigan where goby abundance has increased dramatically over the past three years (Marsden et al. 2003, Diana et al. 2003).

Based on the factors we have investigated here there are some very clear messages as to what factors will enhance reproduction by a species like lake trout that is impacted by interstitial predators like gobies and sculpins in an environment now heavily colonized by dreissenids. Although the diversity of egg predators has lately increased with the addition of round gobies that appear to eat twice the eggs of native egg predators, it is likely the pre-invasion by dreissenids facilitated this growth in goby populations. This is evident in the marked contrast in density of sculpins, that that are unable to eat all but the smallest mussels, and gobies that are. While the increased density of species like gobies is of concern we have seen that in higher densities, interspecific competition can be a strong regulator of egg consumption. Further there seems to be limits to consumption such that with progressive increases in egg density, a smaller and smaller percentage of eggs will be lost to egg predators. All of this seems to point to the need to concentrate restoration efforts on a small number offshore reefs where zebra mussels and goby abundance is currently low such that the mortality can be overcome and so minimized.

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References

Biga, H., Janssen, J., and Marsden, J.E. 1998. Effect of substrate size on lake trout egg predation by mottled sculpin. J. Great Lakes Res. 24:464-473

Balon, E.K. 1980. Early ontogeny of the lake charr, *Salvelinus (Cristivomer) namaycush,* In *Charrs: salmonids fishes of the genus Salvelinus*, E.K. Balon (ed.), pp 462-485. The Hague, The Netherlands: Dr. W. Junk Publishers

Capelli, G.M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnol. Oceanogr. 27:741-745.

Chotkowski, M.A., and Marsden, J.E. 1999. Round goby and mottled sculpin predation on lake trout eggs and fry: Field predictions from laboratory experiments. J. Great Lakes Res. 25:26-35

Clary, J.R. 1972. Predation on brown trout by the slimy sculpin. Prog. Fish-Cult. 34:91-95

Diana, C., Jonas, J.L., Claramunt, R.M., Fitzsimons, J.D., and Marsden, J.E. 2003. Abundance of round gobies (*Neogobius melanostmus*) in littoral habitats of northeastern Lake Michigan. Draft

Dittman, A.H., Brown, G.S., and Foote, C.J. 1998. The role of chemoreception in salmon egg predation by coastrange (*Cottus aleuticus*) and slimy (*C. cognatus*) sculpins in Iliamna Lake, Alaska. Can. J. Zool. 76:406-413.

Djuricich, P., and Janssen, J. 2001. Impact of round goby predation on zebra mussel size distribution at Calumet Harbour, Lake Michigan. J. Great lakes Res. 27:312-318.

Dubs, D.O.L., and Corkum, L.D. 1996. Behavioural interactions between round gobies (*Neogobius melanostomus*) and mottled sculpins (*Cottus bairdi*). J. Great Lakes Res. 22:838-844.

Fitzsimons, J.D. 1995a. Assessment of lake trout spawning habitat and egg deposition in Lake Ontario. *J. Great Lakes Res. 21(Supplement 1*):337-347.

Fitzsimons, J.D. 1995. A critical review of the effects of contaminants on early life stage (ELS) mortality of lake trout in the Great Lakes. *J. Great Lakes Res. 21(Supplement 1*):267-276

Fitzsimons, J.D. 1996. The significance of man-made structures for lake trout spawning in the Great Lakes: Are they a viable alternative to natural reefs? Can. J. Fish. Aquat. Sci. 53:142-15.

Fitzsimons, J.D., B. Lantry, and R. O'Gorman. 2003. The status of a lake trout resurgence in Lake Ontario from an early life stage perspective. Accepted. Chapter XX in State of Lake Ontario (SOLO). Ed. M. Munawar.

Fitzsimons, J.D., D.L. Perkins, and C.C. Krueger. 2002. Sculpins and crayfish on lake trout spawning areas in Lake Ontario: Estimates of abundance and egg predation. J. Great Lakes Res, 28:421-436.

Ghedotti, M.J., Smihula, J.C., and Smith, G.R. 1995. Zebra mussel predation by round gobies in the laboratory. J. Great lakes Res. 21:665-669.

Hansen, M.J., Peck, J.W., Schorfaar, R.G., Selgeby.J.H., Schreiner, D.R., Schram, S.T., Swanson, B.L., MacCallum, W.R., Burnham-Curtis, M.K., Curtis, G., Heinrich, J.W., and Young, R.J. 1995. Lake trout (Salvelinus namaycush) population sin Lake Superior and their restoration in 1959-1993. J. Great Lakes Res. 21(Supplement 1):152-175.

Hansen, M.J., Bencew, J.R., Peck, J.W., and Taylor, W.W. 1997. Evaluation of the relative importance of hatchery-reared and wild fish in the restoration of Lake Superior lake trout. In *Developing and Sustaining World Fisheries Resources. The State of Science and Management*. pp. 492-497 Eds D.A. Hancock, D.C. Smith, A. Grant, and J.P. Beumer. CSIRO, Collingwood, Australia.

Hershey, A.E., and McDonald, M.E. 1985. Diet and ingestion rate of slimy sculpin*, Cottus cognatus*, in an Alaskan arctic lake. J. Fish. Aquat. Sci. 42:483-487.

Horns, W.H., and Magnuson, J.J. 1981. Crayfish predation on lake trout eggs in trout lake, Wisconsin. Rapp. P.-v. Reun. Cons. Int. Explor. Mer. 178. 299-303.

Janssen, J., and Jude, D.J. 2001. Recruitment failure of the mottled sculpin *Cottus bairdi* in Calumet Harbour, southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. J. Great Lakes Res. 27:319-328.

Jones, M.L., Eck, G.W., Evans, D.O., Fabrizio, M.C., Hoff, M.H., Hudson, P.L., Janssen, J, Jude, D., O'Gorman, R., and Savino, J.F. 1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages. J. Great Lakes Res. 21(Supplement 1):505-517.

Jonas, J.L., Claramunt, R.M., Ellrott, B.J., Fitzsimons, J.D., and Marsden, J.E. 2003. Estimates of abundance and the effect of lake trout egg predators on egg survival for Lakes Michigan, Huron, and Champlain. Draft

Jude, D.J., Reider, R.H., and Smith, G.R. 1992. Establishment of Gobiidae in the Great Lakes basin. Can. J. Fish. Aquat. Sci. 49:416-421.

Jude, D.J., Janssen, J., and Crawford, G. 1995. Ecology, distribution and impact of the newly introduced round and tubnose gobies on the biota of the St. Clair and Detroit Rivers. In *Lake Huron Ecosystem: Ecology, Fisheries and Management*, ed. M.Munawar, T. Edsall and J. Leach, pp. 447-460. SPB Academics Publishing, Amsterdam, The Netherlands.

Krueger, C.C., Jones, M.L., and Taylor, W.W. Restoration of lake trout in the Great Lakes: Challenges and strategies for future management. J. Great Lakes Res. 21(Supplement 1):547-558.

Lodge, D.M., Taylor, C.A., Holdrich, D.M., and Skurdal, J. 2000. Nonindigeous crayfishes threaten North American freshwater biodiversity: Lessons from Europe. Fisheries 25:7-20

Marsden, J.E., and Chotkowski, M.A. 2001. Lake trout spawning on artificial reefs and the effects of zebra mussels: Fatal attraction?. J. Great Lakes Res. 27:33-43.

Marsden, J.E., Ellrott, B.J., Claramunt, R.M., Fitzsimons, J.D. and Jonas, J.L. 2003. A comparison of lake trout spawning, emergence, and habitat use for Lakes Michigan, Huron (Parry Sound) and Champlain. Draft

Miller, J.E., Savino, J.F., and Neely, R.K. 1992. Competition for food between crayfish (*Orconectes virilis*) and the slimy sculpin (*Cottus cognatus*). J. Fresh. Ecol. 7:127-137.

Olsen, T.M., Lodge, D.M, Capelli, G.M, and Houlihan, R.J. 1991. Mechanisms of impact of an introduced crayfish (*Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Can. J. Fish. Aquat. Sci. 48:1853-1861.

Perkins, D.L., and Krueger, C.C. 1995. Dynamics of reproduction by hatchery-origin lake trout (*Salvelinus namaycush*) at Stony Island reef, Lake Ontario. J. Great Lakes Res. 21(Supplement 1):400-417.

Ray, W.J., and Corkum, L.D. 1997. Predation of zebra mussels by round gobies, *Neogobius Melanostomus.* Envir. Biol. Fish. 5:267-273.

Savino, J.F., and Henry, M.G. 1991. Feeding rate of slimy sculpin and burbot on young lake charr in laboratory reefs. *Envir. Biol. Fish.* 31:275-282

Savino, J.F, Hansen, P.L., Fabrizio, M.C., and Bowen, C.A. II. 1999. Predation on lake trout eggs and fry: a modelling approach. J. Great Lakes Res. 25: 36-44.

Selgeby, J.H., Bronte, C.R., Brown, E.H., Hansen, M.J., Holey, M.E., VanAmberg, J.P., Muth, K.M. Makaukas, D.B., McKee, P, Anderson, D.M., Ferreri, C.P., and Schram, S.T. 1995. Lake trout restoration in the Great Lakes: Stock-size criteria for natural reproduction. J. Great Lakes Res. 21(Supplement 1):498-504.

Sweeney, B.W., and Vannote, R.L. 1982. Population synchrony in mayflies: A predator satiation hypothesis. Evolution 36:810-821

van Montfrans, J., Epifanio, C.E., Knott, D.M, Lipcius, R.N., Mense, D.J., Metcalf, K.S., Olmi, E.J., Orth, R.J., Posey, M.H., and Wenner, E.L. 1995. Settlement of blue crab postlarvae in western North Atlantic estuaries. Bull. Mar. Sci., vol. 57, no. 3, pp. 834-854

Table 1: Effect of substrate on feeding rate of slimy sculpins on lake trout eggs at 4 different temperature ranges. Means followed by the same letter are not significantly different from means with the same letter.

Substrate	Temperature range (ºC)	Temperature (ºC) (X±SEM)	Size (mm) (X±SEM)	N	Number of eggs eaten Per day (X±SEM)
Present	1-2	1.2(0.1)	87.3(3.3)	4	0.03(0.04)ac
	4-5	4.2(0.01)	81.0(3.0)	4	0.32(0.19)ac
	7-8	7.5(0.04)	80.5(2.9)	4	0.89(0.36)bc
	10-11	10.1(2.0)	91.5(2.9)	2	0.71(0.22)bc
Absent	1-2	1.1(0.05)	90.8(3.2)	5	0.03(0.03)ac
	4-5	3.9(0.02)	84.8(2.1)	4	0.36(.018)ac
	7-8	7.6(0.03)	84.8(3.8)	5	1.80(0.49)b
	10-11	10.0(0.03)	91.2(1.7)	4	2.36(0.68)b

Table 2: Effect of egg condition on feeding rate of round gobies on rainbow trout eggs. Means followed by the same letter are not significantly different from means with the same letter.

Egg condition	Length (mm)(X±SEM)	Number of eggs eaten per day (X±SEM)

live	75.8(1.4)	0.76(0.20)a
Dead	72.8(2.1)	0.43(0.23)a
live/dead (50/50)	72.2(2.5)	1.10(0.31)a

Table 3: Effect of egg condition on feeding rate of slimy sculpins on lake trout eggs. Means followed by the same letter are not significantly different from means with the same letter.

Egg condition	Temperature Range (ºC)	Actual Temperature (ºC) (X±SEM)	Length (mm) (X±SEM)	Eggs eaten per day (X±SEM)
Live	1-3	1.1(0.05)	90.8(3.2)	0.03(0.03)a
	4-5	3.9(0.02)	84.8(2.1)	0.36(0.18)abc
	7-8	7.6(0.03)	84.8(3.8)	1.80(0.49)bc
	10-11	10.0(0.03)	91.3(1.7)	2.36(0.68)ab
Dead	1-3	1.1(0.3)	93.8(2.8)	0.07(0.07)a
	4-5	3.9(0.02)	84.8(2.6)	0.23(0.19)a
	7-8	7.2(0.02)	85.0(2.7)	0.48(0.13)c
	10-11	9.4(0.03)	92.7(2.9)	0.10(0.10)a

Table 4: Effect of exposure temperature on daily feeding rates of round goby, slimy sculpin and mottled sculpin on lake trout eggs. Means followed by the same letter for the same species are not significantly different from means for the same species with the same letter.

Species	Temperature Range (ºC)	Actual Temperature (ºC) (X±SEM)	Length (mm) (X±SEM)	Eggs eaten per day(X±SEM)
Round goby	1-3	3.5(0.1)	79.8(1.7)	0.31(0.09)a
	4-5	4.6(0.1)	72.2(2.2)	0.12(0.04)a
	7-8	7.5	71.8(1.9)	0.48(0.14)a
	10-11	10.0(0.03)	76.2(3.1)	1.12(0.42)a
Slimy sculpin	1-3	2.4(0.03)	82.5(2.6)	0.43(0.12)a
	4-5	4.7(0.1)	89.7(1.6)	0.50(0.15)a
	7-8	7.5(0.1)	80.0(1.1)	1.06(0.27)ac
	10-11	10.3(0.03)	81.7(1.8)	1.67(0.22)bc
Mottled sculpin	1-3	2.7(0.2)	97.5(3.5)	0.60(0.22)a
	4-5	4.9(0.1)	95.2(3.9)	0.37(0.11)a
	7-8	7.5(0.1)	81.6(2.6)	0.34(0.18)a
	10-11	9.7(0.1)	91.7(4.0)	1.33(0.38)a

Table 5: Effect of tank size on feeding rate of round gobies on rainbow trout eggs. Means followed by

the same letter are not significantly different from means with the same letter.

Tank size (m^2)	Goby length (mm) (X±SEM)	Eggs per individual per day (X±SEM)
0.08	80.0(1.1)	1.06(0.27)a
0.25	81.7(1.7)	1.67(0.69)ab
0.50	85.3(0.3)	4.62(0.53)ab
1.00	81.0(1.5)	8.95(3.59)b
10.00	87.0(1.5)	12.76(0.21)ab

Table 6: Effect of interspecific competition on feeding rate of slimy sculpins and round gobies on lake and rainbow trout eggs. Means followed by the same letter for the same species are not significantly different from means for the same species of predator and eggs with the same letter.

Predator species	Egg species	Predators per tank	Length (mm) (X±SEM)	Eggs eaten per individual per day (X±SEM)	Eggs per treatment eaten per day (X±SEM)
Slimy sculpin	lake trout	1	85.5(1.0)	2.5(0.6)a	2.5(0.6)a
		5	86.0(0.7)	1.2(0.3)b	5.9(1.5)b
		10	87.1(0.3)	0.9(0.1)b	8.6(0.8)b
Round goby		1	76.0(1.4)	7.0(1.3)a	7.0(1.3)a
		5	77.2(1.6)	1.8(0.4)b	8.9(2.1)a
		10	76.8(0.7)	1.4(0.4)b	14.0(4.0)a
	rainbow trout	1	81.0(1.5)	7.8(2.6)a	7.8(2.6)a
		5	77.0(1.1)	2.1(0.3)a	10.6(1.6)a
		10	74.3(0.8)	0.6(0.2)a	8.1(1.6)a

Table 7: Effect of intraspecific competition on the feeding rate of combinations of slimy sculpins and round gobies on lake and rainbow trout eggs. Means followed by

the same letter are not significantly different from means with the same letter.

Number of gobies	Goby length (mm) (X±SEM)	Number of slimy sculpins	Sculpin length (mm) (X±SEM)	Eggs per individual per day (X±SEM)
0	-	10	87.1(0.3)	0.9(0.1)a
1	87.0(3.8)	9	88.1(0.3)	1.0(0.1)a
5	87.7(0.4)	5	88.7(0.6)	1.2(0.1)a
9	86.9(0.9)	1	89.7(2.3)	0.6(0.1)a
10	76.8(0.7)	0	-	1.4(0.4)a

Fig. 1


◆ Proportion of eggs not eaten
■ Number of eggs eaten per day
Proportion of eggs not eaten
120
100
80
60
40
20
0
Number of eggs eaten per day
1.4
1.2
1
0.8
0.6
0.4
0.2
0
1
10
100
1000
Number of eggs per aquaria

Fig. 2.


◆ Proportion of eggs not eaten
Number of eggs eaten per day
Proportion of eggs not eaten
0
20
40
60
80
100
120
Number of eggs eaten per day
0
0.5
1
1.5
2
2.5
3
1
10
100
1000
Num ber of eggs per aquaria

Fig. 3.

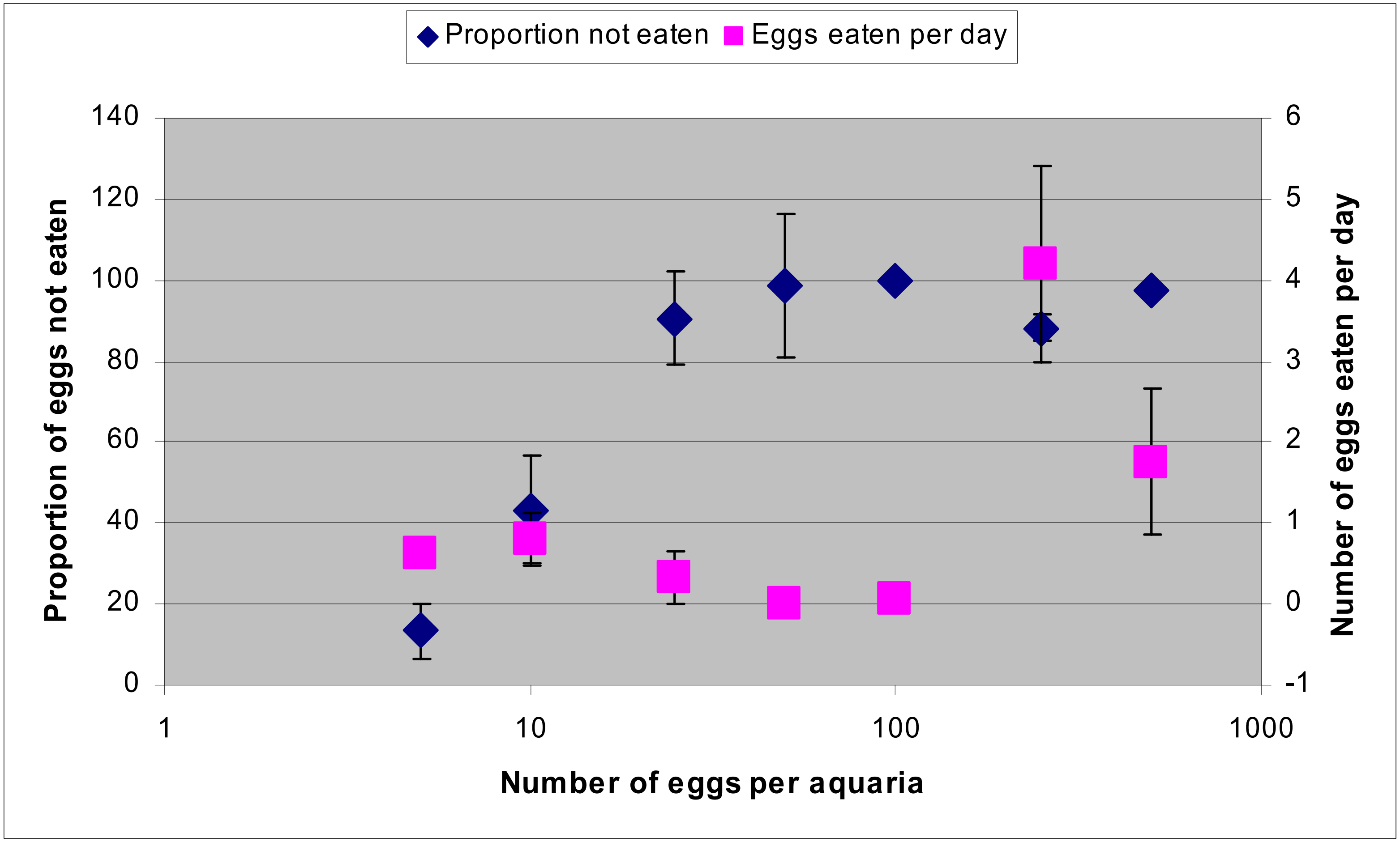
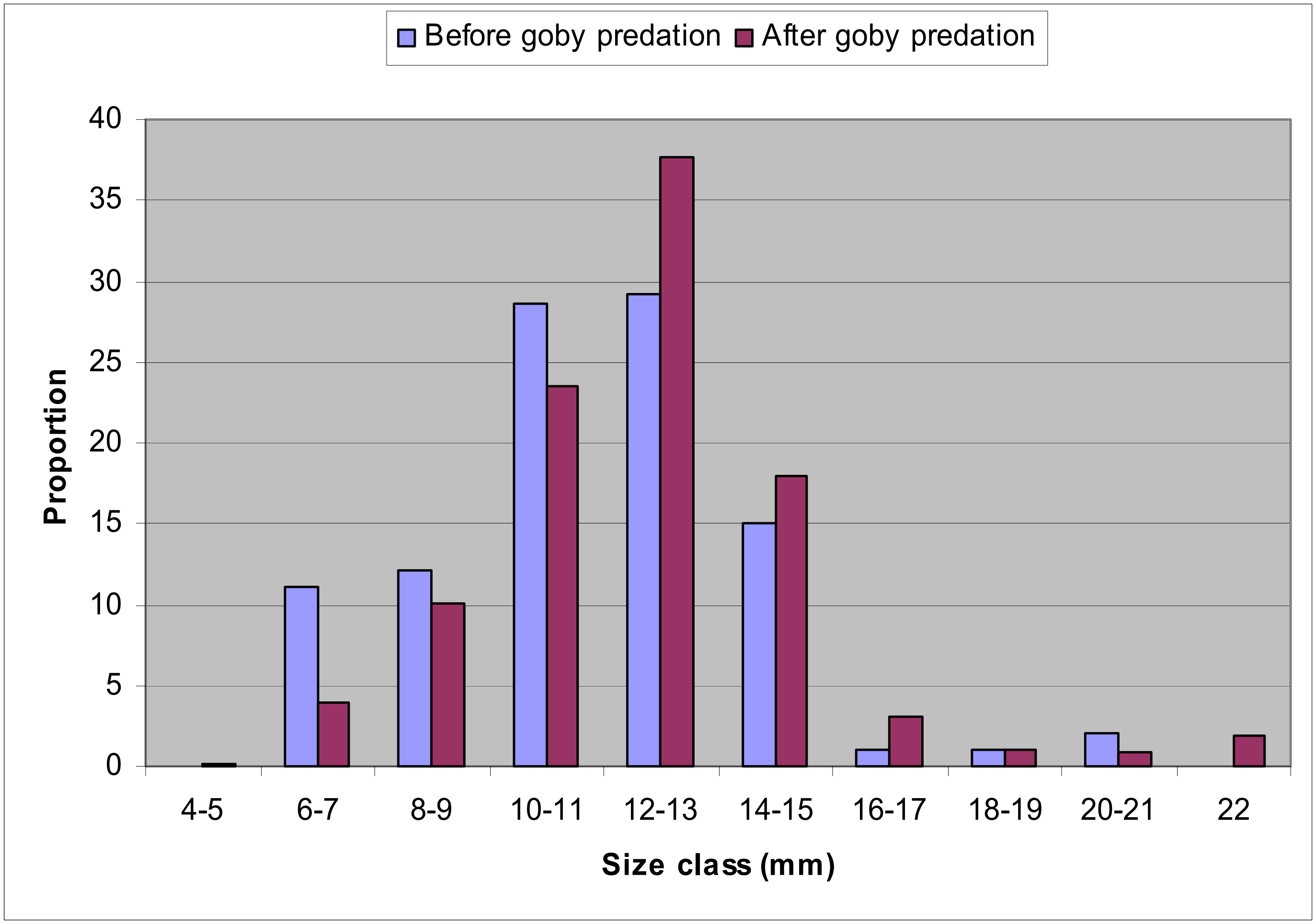

◆ Proportion not eaten
■ Eggs eaten per day
Proportion of eggs not eaten
140
120
100
80
60
40
20
0
Number of eggs eaten per day
6
5
4
3
2
1
0
-1
1
10
100
1000
Number of eggs per aquaria

Fig. 4


Before goby predation
After goby predation
Proportion
0
5
10
15
20
25
30
35
40
4-5
6-7
8-9
10-11
12-13
14-15
16-17
18-19
20-21
22
Size class (mm)

Effects of temperature and density on consumption of trout eggs by *Orconectes propinquus* and *O. rusticus*

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Abstract

Using laboratory experiments, we tested the effects of temperature and predator density on consumption of trout eggs. We quantified the effect of temperature on the predation rates of lake trout (*Salvelinus namaycush*) eggs and rainbow trout (*Oncorhynchus mykiss*) eggs by crayfish native (*Orconectes propinquus*) and exotic (*Orconectes rusticus*) to the Great Lakes. Feeding rates of individual crayfish on eggs were tested at four temperature ranges (2-3, 4-5, 7-8, and 10-12^0 C). Mean individual consumption ranged from 0.1 to 1.5 lake trout eggs per day and from 1.0 to 5.5 rainbow trout eggs per day. Temperature had a significant effect only on the feeding rate of *O. rusticus* on rainbow trout eggs. The effect of intraspecific predator density on rainbow trout egg consumption was determined by testing a single crayfish species at three levels of abundance. Egg consumption rate was significantly higher at low crayfish abundance (1 crayfish/tank) than at medium (5 crayfish/tank) or high (10 crayfish/tank) crayfish abundance for *O. rusticus*. Intraspecific predator density had no effect on the feeding rate of *O. propinquus*. The effect of interspecific predator density on rainbow trout egg consumption was explored by comparing feeding rates at high levels of crayfish abundance in single and mixed species treatments. Interspecific effects did not significantly alter crayfish feeding rates. Results from these experiments provide empirical data to aid in modeling how temperature and predator density affect lake trout egg predation rates in the field.

Introduction

Predation on early life stages of lake trout (*Salvelinus namaycush*) has been suggested as an important impediment to lake trout restoration in the Great Lakes (Jones et al. 1995; Savino et al. 1999). Models of lake trout egg and fry survival developed by Jones et al. (1995) and Savino et al. (1999) showed that predation by interstitial species such as sculpins and crayfish, could be a particularly significant source of lake trout mortality. Obtaining field estimates of interstitial predation on lake trout eggs in the Great Lakes can be difficult due to unfavorable weather conditions during fall and winter. Additionally, analysis of crayfish diets is problematic due to their “shredding” style of feeding. Estimated consumption rates of interstitial predators from laboratory studies have ranged up to 3 lake trout eggs per day for crayfish (Horns and Magnuson 1981; Savino and Miller 1991) and up to 2 lake trout eggs per day for sculpins (Savino and Henry 1990). Most of these estimates of egg consumption were obtained from single predator studies conducted using temperatures between 6 and 8°C. Savino and Miller (1991) stated that they chose 6 to 8°C for their feeding experiments because this temperature is within the thermal range in the Great Lakes from fall to spring. The models developed by Jones et al. (1995) and Savino et al. (1999) assumed that feeding by interstitial predators decreased with temperature, but this specific relationship has not yet been determined. Temperature is likely to significantly affect predation; predators that are more tolerant of low temperatures will forage more effectively later into the incubation period than less tolerant species and thus have a greater impact on egg mortality. Temperature has not previously been considered as a cofactor in lake trout egg predation experiments.

Predator density and predator interactions may also be important variables affecting egg predation on lake trout spawning reefs. Interspecific (Werner and Hall 1979) and intraspecific (Genner et al. 1999; Matsumoto 2001) competitive interactions have been shown to affect food resource availability within fish species and may affect feeding behavior of interstitial egg predators. Crayfish often display agonistic behavior during conspecific interactions (Goessmann et al. 2000; Stocker and Huber 2001), suggesting that feeding rates of individuals may be altered in the presence of conspecifics. Abundance of crayfish can vary dramatically on lake trout spawning reefs between and within systems; mean crayfish densities (#/m^2) assessed using the same methods in 2001 ranged from 3 to 10 in Parry Sound, Lake Huron (J. Fitzsimons, Canadian Center for Inland Waters, unpublished data), 4 to 54 in northern Lake Michigan (J. Jonas and R. Claramunt, Michigan Department of Natural Resources, unpublished data), and 0 to 2 in Lake Champlain (E. Marsden and B. Ellrott, University of Vermont, unpublished data). The relatively high crayfish abundance observed in some nearshore areas of northern Lake Michigan can be attributed to the recent introduction of *O. rusticus* to the system. Crayfish assemblages were once dominated by native crayfish (*O. propinquus* and *O. virilis*); these species are now competing with and being displaced by the more aggressive *O. rusticus* (Capelli 1982). The variation in crayfish species and abundance observed among lake trout spawning reefs may have important consequences for lake trout recruitment.

The goal of our study was to determine how temperature and predator density affect consumption rates of lake trout and rainbow trout (*Oncorhynchus mykiss*) eggs by crayfish species that are native (*Orconectes propinquus*) and exotic (*O. rusticus*) to the Great Lakes. For each species of crayfish, we wanted to establish the relationship between temperature and daily egg consumption. Next, we wanted to examine if the number of eggs eaten per crayfish per day changed as intraspecific crayfish density varied. Lastly, we tried to see if intraspecific crayfish interactions influenced daily egg consumption rates by crayfish differently than interspecific interactions.

Methods

General Experimental Methods

Experiments were conducted at the Rubenstein Ecosystem Research Laboratory, University of Vermont. *O. rusticus* were collected from the Connecticut River located near the eastern border of Vermont and *O. propinquus* were obtained from the Winooski River in Richmond, Vermont. Crayfish were held at ambient room temperature (15 to 20^0 C) in 114 L glass aquaria and were fed trout eggs, aquatic vegetation, and goldfish flake food. Prior to testing, crayfish were starved and allowed to acclimate to the experimental temperature for 24 h. Lake and rainbow trout eggs were obtained from the Salisbury Fish Hatchery in Salisbury, Vermont. Rainbow trout eggs were also obtained from White Sulfur Springs National Fish Hatchery in White Sulfur Springs, West Virginia. Lake trout eggs were not available year round, so rainbow trout eggs were used to test the effect of predator density and to examine temperature effects using a second prey type. The trout eggs were held at 2 to 5^0C. Experiments were conducted in black, rubber, circular aquaria (76 cm diameter) fed with dechlorinated water from a re-circulating system. Round cobbles with a mean diameter of 100 mm were piled 30 cm deep in each experimental aquarium. Prior to releasing the predator(s) in the aquarium, trout eggs were scattered over the substrate at a density of 500 eggs/m^2 in order to provide unlimited opportunities for egg consumption by predators and crayfish carapace length was recorded.

Predators were then allowed access to the eggs for 7 days and the remaining eggs were counted. Individual daily consumption was calculated by subtracting the number of live and dead eggs remaining from the initial number of eggs (176), dividing by the number of live crayfish, and then dividing by 7 days. Experiments were analyzed for each prey species separately. Analysis of variance (ANOVA) was used to detect differences among temperature and density treatments with crayfish size as a co-variate. A significance level of 0.05 was used to determine differences among treatments. The Student-Newman-Keuls multiple comparison procedure was used to distinguish among temperature treatments where appropriate.

Temperature Experiments

Feeding trials for an individual crayfish of each species were conducted at four different temperature ranges (1-2, 4-5, 7-8, 10-12 ºC). Trials were replicated six to seven times for each crayfish species using rainbow trout eggs and six times using lake trout eggs. A two-way analysis of variance model was used to detect differences among temperature treatments and between crayfish species. Since there was a positive relationship between the mean daily consumption of lake trout eggs and the variance, the data were square root transformed. When necessary a square root transformation is most appropriate for count data (Sokal and Rohlf 1969).

Intraspecific Predator Density Experiments

We tested crayfish in single-species aquaria at three densities to determine the relationship between density and rainbow trout egg consumption for *O. propinquus* and *O. rusticus*. Densities were low (one per tank, equivalent to $3/m^2$), medium (5 per tank, $14/m^2$), or high (10 per tank, $28/m^2$). Both crayfish species were tested at each density level six times. Two-way ANOVA was used to detect differences in consumption among the three treatments and between crayfish species. The data were square root transformed to achieve homogeneity of variance.

Intra- versus Interspecific Predator Experiments

To determine if there were differences in egg consumption related to intra- and interspecific effects, a mixed species treatment consisting of five *O. propinquus* and five *O. rusticus* was tested seven times and compared to high density single species treatments from the intraspecific tests. This design compared crayfish consumption of rainbow trout eggs among the following three treatments: 1) ten *O.propinquus*/tank, 2) ten *O. rusticus*/tank, and 3) five of each crayfish species. The data were square root transformed and analyzed with a one-way ANOVA model.

Results

The mean percentage of eggs remaining was over 56 % (100 eggs) for each experiment. No crayfish died in the temperature experiments and mortality was low in the low density (1 out of 12 crayfish), medium density (2 out of 60 crayfish), and high density experiments (3 out of 120 crayfish). No obvious wounds were identified in any of the mortalities.

Temperature Experiments - lake trout eggs

No consistent trend in consumption relative to temperature was observed for either *O. propinquus* or *O. rusticus* (Figure 1). Mean daily consumption ranged from 0.5 to 1.5 eggs for *O. propinquus* and from 0.7 to 1.2 for *O. rusticus*. The standard deviation of mean daily consumption ranged from 0.29 to 1.61 for a given species/temperature combination. Analysis of variance showed that crayfish size had no effect as a cofactor so size was dropped from the analysis. The two-way analysis of variance model showed that there was no significant difference in egg consumption between the crayfish species ($p < 0.25$) or among the temperature treatments ($p < 0.38$; Table 1). The interaction between crayfish species and temperature was also not significant ($p < 0.36$).

Temperature Experiments - r*ainbow trout eggs*

Mean consumption of rainbow trout eggs ranged from 1.0 to 5.5 eggs/crayfish/day and was positively related to temperature level for both *O. propinquus* and *O. rusticus* (Figure 2). The two-way analysis of variance model showed that there was a significant effect of temperature ($p < 0.002$) and that feeding rate of *O. propinquus* was not different from *O. rusticus* ($p < 0.81$; Table 2). Crayfish carapace length was not significant as a cofactor. One-way analysis of variance models showed that temperature significantly affected consumption by *O. rusticus* ($p < 0.03$; Table 3), but did not change the consumption rate of *O. propinquus* ($p < 0.12$). The Student-Newman-Keuls procedure detected that consumption by *O.rusticus* was higher at 10 - 12°C than at 2 - 3°C (Figure 2).

Intraspecific Predator Density Experiments

Mean daily consumption of rainbow trout eggs by both crayfish species at three densities ranged from 0.9 to 3.9 eggs/crayfish (Figure 3). The two-way analysis of variance showed that there was a significant interaction between predator density and predator species ($p<0.03$), but no effect of either crayfish species ($p<0.08$) or density ($p<0.06$) was detected (Table 4). When the crayfish species were analyzed separately using a one-way analysis of variance there was a significant effect of density for *O. rusticus* ($p<0.04$; Table 5), but not for *O. propinquus* ($p<0.77$). The Student-Newman-Keuls procedure failed to detect any differences in rainbow trout egg consumption by *O. rusticus* among the density treatments.

Intraspecific versus Interspecific Predator Experiments

Mean rainbow trout egg consumption rate by crayfish was similar among the three treatments (Figure 4). The mean rate of rainbow trout egg consumption was 0.9 eggs/crayfish/day in the high density *O. propinquus* treatment, 1.0 eggs/crayfish/day in the high density *O. rusticus* treatment, and 1.1 eggs/crayfish/day in the interspecific treatment. One-way ANOVA did not detect differences in crayfish feeding rate on eggs among the three treatments ($p<0.48$; Table 6).

Discussion

Since crayfish are ectothermic poikilotherms and metabolic rate increases linearly with temperature (Diana 1995), we expected food consumption to increase with each temperature level. The highest temperature level (10 to 12°C) chosen was not beyond the optimum temperature range for crayfish. Our results indicated that temperature did not significantly alter the feeding rate of lake trout eggs by *O. rusticus* or *O. propinquus*. This occurred because the variation around the mean consumption rate for *O. rusticus* and *O. propinquus* was high at each temperature treatment. Sample size calculations revealed that 13 more crayfish of both species needed to be tested at each temperature range to achieve an 80% chance of detecting differences among temperature treatments. We found contrasting results in the temperature experiments when rainbow trout eggs were used for prey, as temperature affected the feeding rate of *O. rusticus*, but not *O. propinquus*. It is unclear why there was an interaction between temperature and prey type. Possible reasons for this interaction include differences in prey size, color, and taste, all of which have been shown to affect animal feeding behavior (Diana 1995). Lake trout eggs are relatively large (4 - 5 mm diameter), have a yellow pigmentation, and likely have a specific taste; rainbow trout eggs are relatively small (2-3mm diameter), have a red/orange pigmentation, and also likely have a unique taste. The larger lake trout eggs likely incur longer handling times than rainbow trout eggs; both species crayfish consistently ate more rainbow trout eggs than lake trout eggs at each temperature.

We predicted that *O. rusticus* would consume trout eggs at a higher rate than *O. propinquus*. *O. rusticus* have a higher metabolic rate than their congeners and thus have larger appetites (Jones and Momot 1983). Overall, feeding rate did not differ between crayfish species for either prey type. However, due to the variability in the consumption rate of lake trout eggs by *O. rusticus* the power to detect differences between crayfish species was low. Sample size calculations showed that 34 additional crayfish needed to be tested of each species at each temperature range.

Compared to previous laboratory studies our estimates of daily lake trout egg consumption by *O. propinquus* were low although our estimates of the feeding rate on rainbow trout eggs were similar. Horns and Magnuson (1981) conducted feeding trials at 6 to 8°C and found daily consumption of lake trout eggs by *O. propinquus* and *O. virilis* to be between 1 and 2 eggs/crayfish when substrate size was similar to that used in our study. In our study at 7 to 8°C, *O. propinquus* consumed 0.7 eggs/crayfish/day and *O. rusticus* consumed 1.2 eggs/crayfish/day. Our results for crayfish consumption of rainbow trout eggs match those of Miller et al (1992) who found *O. virilis* to feed at a rate of 3 eggs/day; in our study *O. propinquus* consumed rainbow trout eggs at a rate of 3.2 eggs/day and *O. rusticus* fed at a rate of 3.4 eggs/day.

Our study indicates that crayfish consumption below 4°C is higher than has been previously assumed (Jones et al. 1995; Savino et al. 1999). Between 2° and 3°C individual *O. rusticus* consumed lake trout eggs at a rate of 0.7 eggs/day and *O. propinquus* consumed 0.5 eggs/day of rainbow trout eggs. Previous assumptions of interstitial egg predation rates (including sculpins and crayfish) calculated on a per area basis by Jones et al. (1995) and Savino et al. (1999) were less than 1 egg/m^2/day when temperatures were below 4^{0}C. Considering crayfish density on spawning reefs from 4 to 54/m^2 at several sites in northeastern Lake Michigan (J. Jonas and R. Claramunt, Michigan Department of Natural Resources, unpublished data)see previous comment and feeding rates of at least 0.5 eggs/crayfish/day, consumption by crayfish at temperatures below 4°C could account for much greater losses of lake trout eggs than 1/m^2/day. Temperatures on spawning reefs are in this range for much of the egg incubation period. At one spawning reef in Lake Champlain, temperatures during egg incubation were between 2 and 4°C for up to 60 days (B. Ellrott and E. Marsden, University of Vermont, unpublished data). At Mowat Island spawning reef in Lake Huron (Georgian Bay), temperatures during egg incubation were between 2 and 4°C for up to 23 days in the winter prior to hatch after which they fell below 2°C until the spring when temperatures between 2 and 4°C occurred for an additional 25 days with some level of hatch likely occurring (J. Fitzsimons, Canadian Center for Inland Waters, unpublished data). At a spawning site in Little Traverse Bay, Lake Michigan, temperatures during egg incubation were between 2 and 4°C for over 40 days (R. Claramunt, Michigan Department of Natural Resources, unpublished data). Our study provides new evidence supporting claims made by Savino et al. (1999) and Fitzsimons et al. (2000) that egg predation could be an important source of lake trout mortality on spawning reefs with low egg deposition and high crayfish abundance.

In the intraspecific predator density experiments we expected individual crayfish consumption to decrease as crayfish abundance was increased. Our understanding of crayfish behavior and competitive interactions support these expectations. From a behavioral standpoint, crayfish are territorial and often are agonistic when encountering conspecifics (Goessmann et al. 2000). Intraspecific territoriality has been shown to enhance competition between individuals with the same diet (Genner et al. 1999; Maher and Lott 2000; Matsumoto 2001). The need to search for accessible eggs combined with the aggressive nature of *O. rusticus* may be why consumption was higher when one versus multiple crayfish were tested. If substrate was not limiting access to eggs, an egg density of 500 eggs/m^2 would provide approximately five eggs for each crayfish at the medium crayfish abundance level and 2.5 eggs for each crayfish at the high crayfish abundance level. In the low density treatment, an individual *O. rusticus* was able to consume a mean of nearly four rainbow trout eggs per day while searching without the risk of encountering a competitor. Given that the presence of substrate would lower the number of accessible eggs below 5 eggs/crayfish for the medium density and below 2.5 eggs/crayfish for the high density, searching for eggs to consume may have been necessary. At the low predator density, crayfish likely were able to search and find more accessible eggs because there was no risk of encountering another crayfish. At the medium (5 crayfish/tank) and high (10 crayfish/tank) predator density levels the risk of encountering a conspecific and potentially engaging in combat may outweigh the risk of searching. Hazlett (1994) showed that an *Orconectes* congener, *O. virilis*, ceased movement when it chemically detected crushed conspecifics. This provides evidence that *O. rusticus* may decrease movement if a risk is perceived. Our results for *O. rusticus* support the notion that an increase in intraspecific interactions limits food resource availability and decreases overall predation rates. However, overall egg predation rate was not affected by density for *O. propinquus*. Chemical, behavioral, and morphological differences between *O. propinquus* and *O. rusticus* may explain why intraspecific competition affects their feeding behavior differently. First, Hazlett (1994) observed that *O. propinquus* showed no signs of alarm and did not alter behavior in the presence of chemicals released by crushed conspecifics. Next, *O. propinquus* are in general less aggressive than *O. rusticus*, and have smaller chela. Because *O. propinquus* are less aggressive, the risk of a conspecific interaction escalating to a fight may not be high enough to inhibit searching behavior. Furthermore, if a fight does ensue the risk of suffering a lethal wound may be lower than for *O. rusticus*. Lastly, unlike other *Orconectes* species, *O. propinquus* are active during the day and rely on visual cues more so than chemical cues to detect danger.

In the feeding trials involving ten crayfish per tank, the overall rate of egg consumption by crayfish was the same in single species and mixed species treatments, indicating that intra- and interspecific competitive interactions may not affect crayfish feeding differently. It is important to note that we were unable to determine how many eggs were consumed by an individual crayfish during an experiment and thus cannont determine if overall consumption was equally partitioned between *O. propinquus* and *O. rusticus*. Nevertheless, the overall affect of intra- and interspecific competition was similar.

Our results offer empirical data that can be used to improve estimation and modeling of lake trout egg predation. Previous models assumed that predation of lake trout eggs by crayfish decreased with temperature and did not account for competitive interactions between predators. We provide evidence that crayfish may feed on lake trout eggs throughout much of the incubation period at a higher rate than previously assumed and that intraspecific and interspecific competition may be an important factor affecting *O. rusticus*, but not *O. propinquus* foraging.

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Literature Cited

Capelli, G. M. 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnology and Oceanography 27:741-745.

Diana, J. S. 1995. Biology and Ecology of Fishes. Cooper Publishing Group LLC. Carmel, IN. 441pp.

Fitzsimons, J. D., Perkins, D.L., and Krueger, C.C. 2000. Sculpins and crayfish on lake trout spawning areas in Lake Ontario: estimates of abundance and egg predation. Journal of Great Lakes Research 28: 421-436.

Genner, M. J., G. F. Turner, and S. J. Hawkins. 1999. Resource control by territorial male cichlid fish in Lake Malawi. Journal of Animal Ecology 68:522-529.

Goessmann, C., C. Hemerlrijk, and R. Huber. 2000. The formation and maintenance of crayfish hierarchies: behavioral and self-structuring properties. Behavioral Ecology and Sociobiology 48:418-428.

Gunderson, J. 2000. Rusty crayfish factsheet. Minnesota Sea Grant. Available: www.seagrant.umn.edu/exotics/index.html. (March 2001).

Hazlett, B. A. 1994. Alarm responses in the crayfish *Orconectes virilis* and *Orconectes propinquus*. Journal of Chemical Ecology 20: 1525-1535.

Horns, W. H., and J. J. Magnuson. 1981. Crayfish predation on lake trout eggs in Trout Lake, Wisconsin. Rapp. P. –V. Reun. Conseil International pour l'Exploration de la Mer 178:299-303.

Jones, P. D., and W. T. Momot. 1983. The bioenergetics of crayfish in two pothole lakes. Freshwater Crayfish 5:193-209.

Jones, M. L., G. W. Eck, D.O. Evans, M. C. Fabrizio, M. H. Hoff, P. L. Hudson, J. Janssen, D. Jude, R. O'Gorman, and J. F.Savino.1995. Limitations to lake trout (*Salvelinus namaycush*) rehabilitation in the Great Lakes imposed by biotic interactions occurring at early life stages. Journal of Great Lakes Research 21 (Supplement 1):505-517.

Maher, C. R. and D. R. Lott. 2000. A review of ecological determinants of territoriality within vertebrate species. The American Midland Naturalist 143: 1-29.

Matsumoto, K. 2001. Overlapping territory of a benthophagus fish, *Goniistius zonatus* (Teleostei: Cheilodactylidae). Ecological Research 16:715-726.

Miller, J.E., J. F. Savino, and R. K. Neely. 1992. Competition for food between crayfish (*Orconectes virilis*) and the slimy sculpin (*Cottus cognatus*). Journal of Freshwater Ecology 7:127-136.

Savino, J. F. and M. G. Henry. 1991. Feeding rate of slimy sculpin and burbot on young lake charr in laboratory reefs. Environmental Biology of Fishes 31:275-282.

Savino, J. F., and J. E. Miller. 1991. Crayfish (*Orconectes virilis*) feeding on young lake trout (*Salvelinus namaycush*): effect of rock size. Journal of Freshwater Ecology 6:161-170.

Savino, J. F., P. L. Hudson, M. C. Fabrizio, and C. A. Bowen II. 1999. Predation on lake trout eggs and fry: a modeling approach. Journal of Great Lakes Research. 25(1):36-44.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company. San Fransico, California 776pp.

Stocker, A. M. and R. Huber. 2001. Fighting strategies in crayfish *Orconectes rusticus* (Decapoda, Cambaridae) differ with hunger state and the presence of food cues. Ethology 107: 727-736.

Werner, E.E. and D.J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology 60: 256-264.

Table 1. Two-way analysis of variance table from temperature experiments: effects of temperature and predator species on consumption of lake trout eggs by two crayfish species.

Source	DF	Sum of Squares	P-value
Predator species	1	0.420	0.25
Temperature level	3	0.960	0.38
Predator species * temperature level	3	1.377	0.36
Residual	40	13.159	

Table 2. Two-way analysis of variance table from temperature experiments: effects of temperature and predator species on consumption of rainbow trout eggs by two crayfish species.

Source	DF	Sum of Squares	P-value
Predator species	1	0.022	0.81
Temperature level	3	7.070	0.002
Predator species * temperature level	4	7.092	0.004
Residual	47	18.374	

Table 3. One-way analysis of variance table from temperature experiments: effect of temperature on consumption of lake trout eggs by *O. rusticus*.

Source	DF	Sum of Squares	P-value
Temperature	3	5.35	0.03
Residual	22	10.69	

Table 4. Two-way analysis of variance table from density experiments: effect of density and predator species on consumption of rainbow trout eggs by two crayfish species.

Source	DF	Sum of Squares	P-value
Predator species	1	0.714	0.08
Predator density	2	1.385	0.06
Predator density * predator species	3	2.186	0.03
Residual	31	0.797	

Table 5. One-way analysis of variance table from intraspecific density experiments: effect of density on consumption of rainbow trout eggs by *O.rusticus*.

Source	DF	Sum of Squares	P-value
Predator density	2	2.593	0.04
Residual	15	4.971	

Table 6. One-way analysis of variance table for intra- versus interspecific predator effects on crayfish consumption of rainbow trout eggs.

Source	DF	Sum of Squares	P-value
Treatment	2	0.072	0.48
Residual	16	0.047	

Figure captions

Figure 1. Effect of temperature on consumption of lake trout eggs by *O. propinquus* and *O. rusticus*. Solid bars represent treatment means (six replicates) and error bars represent one standard error.

Figure 2. Effect of temperature on consumption of rainbow trout eggs by *O. propinquus* and *O. rusticus*. Solid bars represent treatment means (six replicates) and error bars represent one standard error. Bars with different letters indicate significant differences for *O. rusticus*; no significant differences were observed for *O. propinquus*.

Figure 3. Effect of crayfish density on consumption of rainbow trout eggs by *O. propinquus* and *O. rusticus*. Solid bars represent treatment means (six replicates) and error bars represent one standard error.

Figure 4. Comparison of intra- and interspecific effects on rainbow trout egg consumption by *O. propinquus* and *O. rusticus*. Solid bars represent treatment means (six to seven replicates) and error bars represent one standard error.

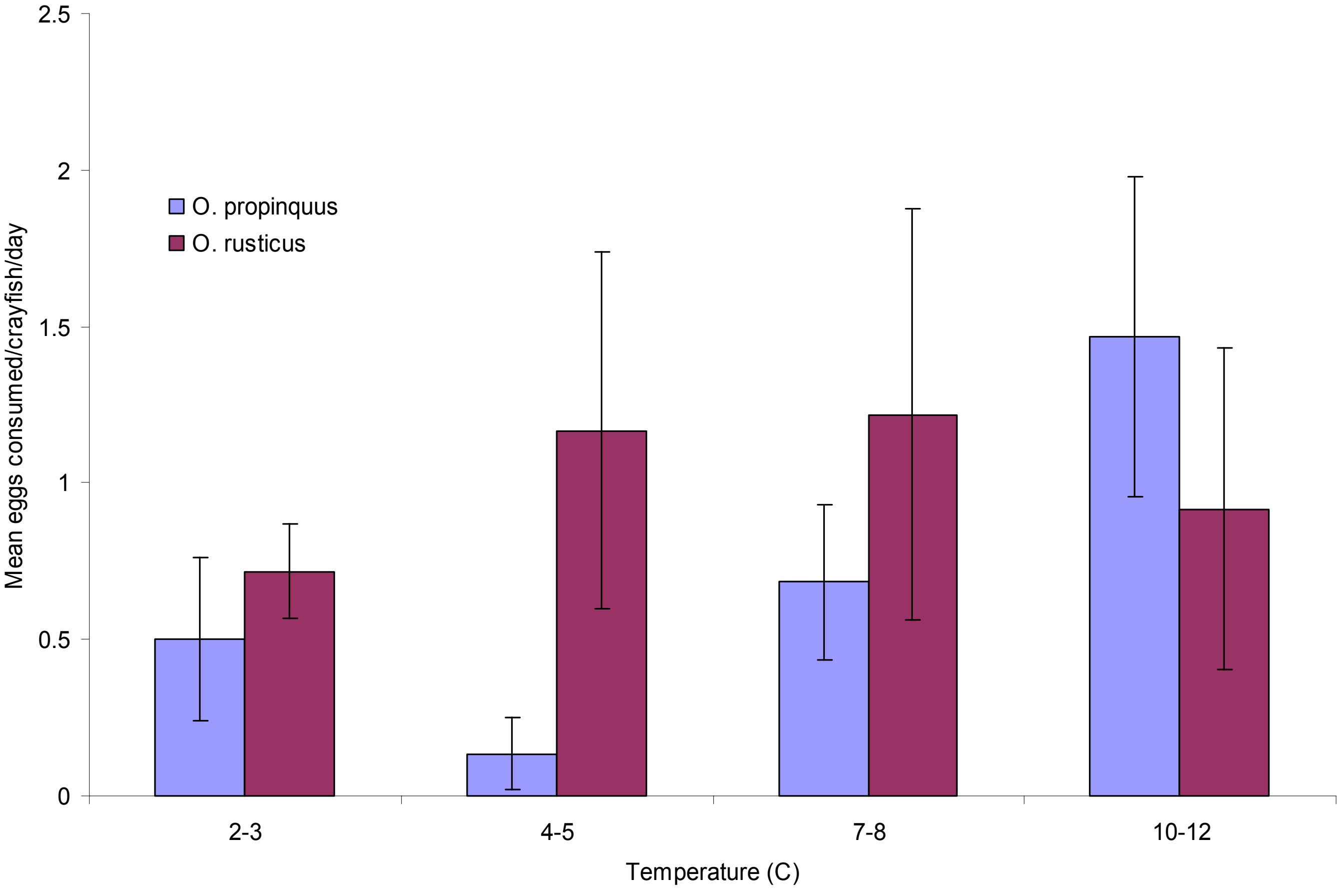
2.5
2
1.5
1
0.5
0
Mean eggs consumed/crayfish/day
O. propinquus
O. rusticus
2-3
4-5
7-8
10-12
Temperature (C)

Figure 1.

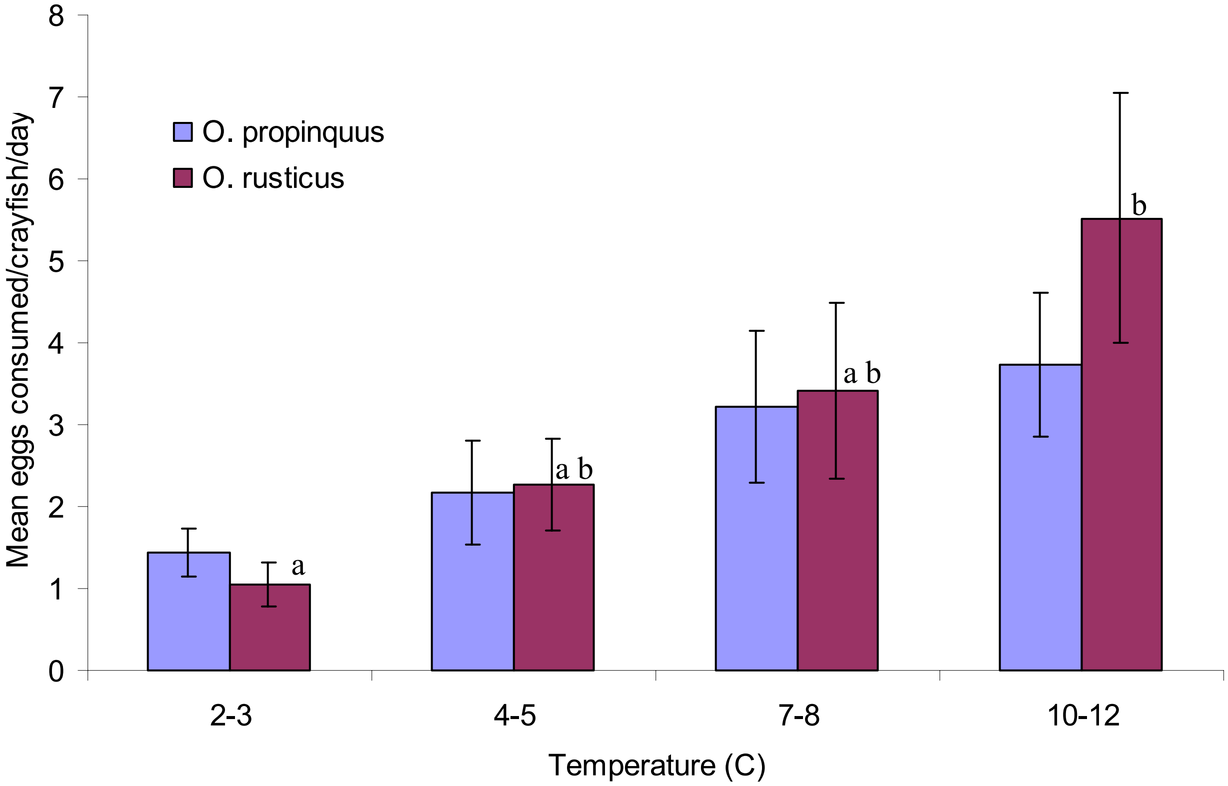
Mean eggs consumed/crayfish/day
0
1
2
3
4
5
6
7
8
O. propinquus
O. rusticus
a
a b
a b
b
2-3
4-5
7-8
10-12
Temperature (C)

Figure 2.

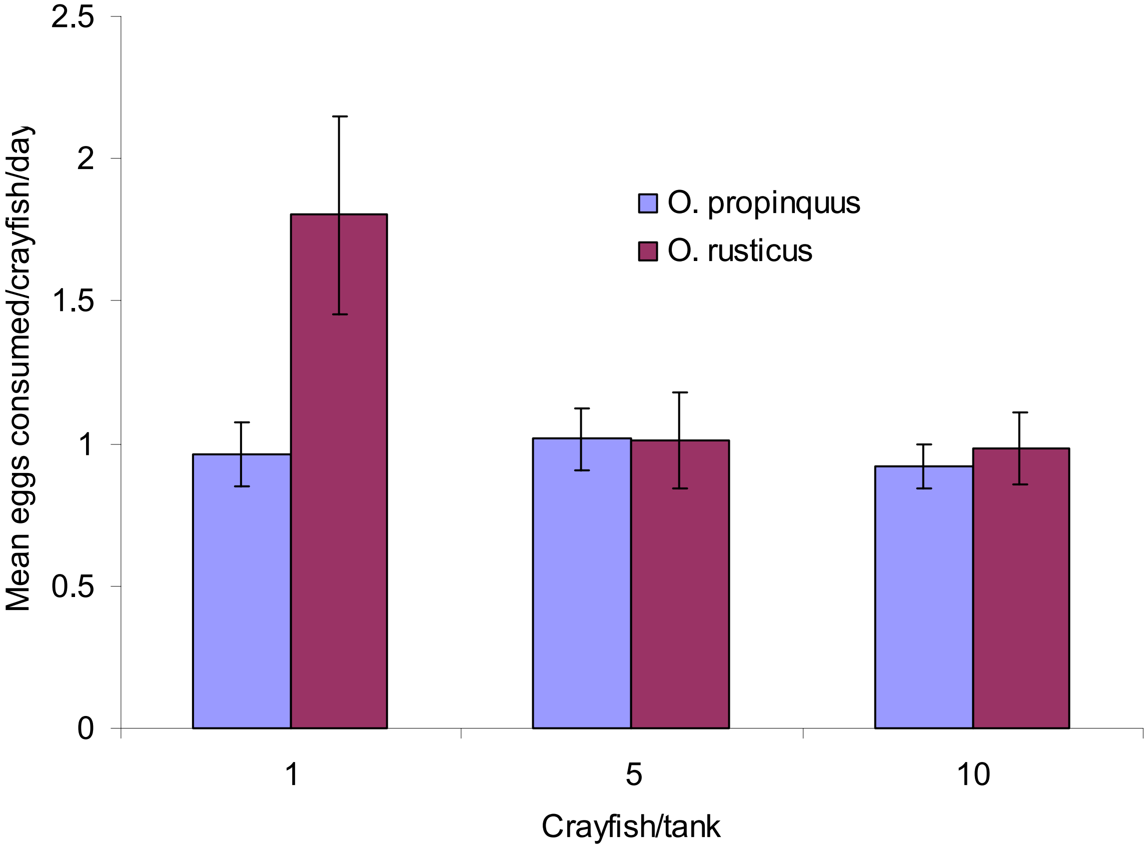
2.5
2
1.5
1
0.5
0
Mean eggs consumed/crayfish/day
O. propinquus
O. rusticus
1
5
10
Crayfish/tank

Figure 3.

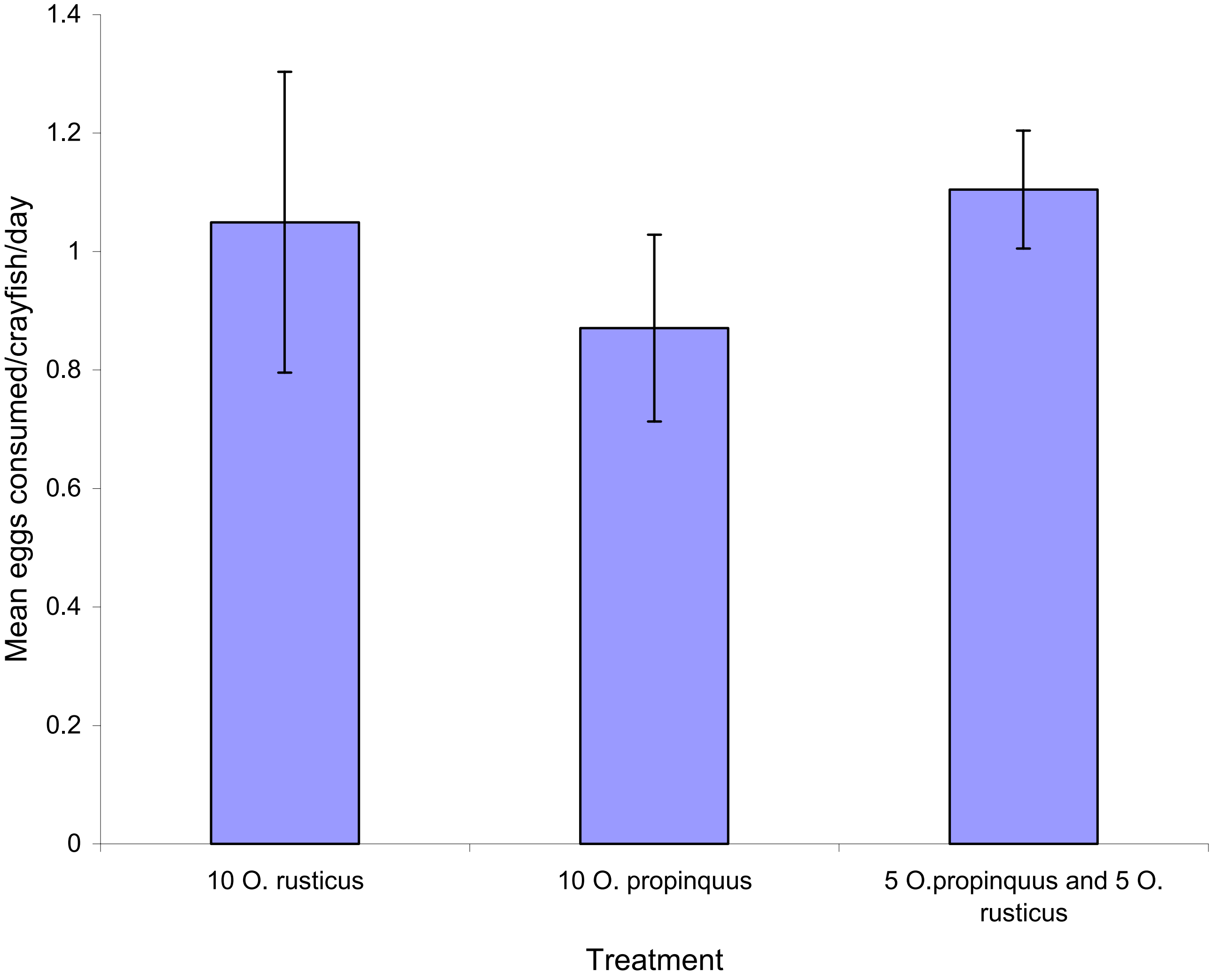
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Mean eggs consumed/crayfish/day
10 O. rusticus
10 O. propinquus
5 O.propinquus and 5 O. rusticus
Treatment

Figure 4.