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Year Class Recruitment Processes of Lake Trout: Role of Fry Predation by Alewives

Contract Period
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by
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GREAT LAKES FISHERY COMMISSION
Research Completion Report[1]

Year-class recruitment processes of lake trout: role of fry predation by alewives

by

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October 31, 1994

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[1] Project completion reports of Commission-sponsored general research are made available to the Commission's cooperators in the interest of rapid dissemination of information that may be useful in Great Lakes fishery management, research, or administration. The reader should be aware that project completion reports have <u>not</u> been through a peer review process and that sponsorship of the project by the Commission does not necessarily imply that the findings or conclusions are endorsed by the Commission.

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Executive Summary

Lake trout (*Salvelinus namaycush*) restoration efforts in Lake Ontario have resulted in an abundance of spawning fish of hatchery-origin but virtually no detectable natural recruitment. One explanation has been predation by non-native alewife (*Alosa pseudoharengus*) on lake trout fry. The purpose of the first part of this study was to determine if alewives could be important predators of lake trout fry. In the laboratory, behavior of fry was examined to ascertain when fry would be present in the water column during a 24-hour period and to determine the acceptability of fry as food for alewife. In aquaria exposed to ambient light regimes, sac fry activity in the water column was much greater at night than during daylight hours ($P < 0.001$). In laboratory tanks, lake trout fry (15-34 mm) were aggressively eaten by alewives (118-175 mm). Field studies were conducted at Stony Island reef, Lake Ontario from 1989-1993 to determine whether alewives and fry were present at the same time on the reef, if alewives fed when on the reef, and if alewives fed upon naturally-produced lake trout fry. Lake trout fry capture in traps indicated that sac and emergent fry were available as prey from the middle of April through the third week of May. The first capture of alewife in gill nets set adjacent to the fry traps was typically in early May and corresponded to the peak capture of sac fry in traps. Food was present in 86% of the 1239 alewife captured after sunset over the 5-year period. Ten lake trout fry were found in six of the 62 alewife captured after sunset on May 20, 1993 at Stony Island reef; no fry were observed in alewife stomachs caught on other dates.

The objectives of the second part of this study were to determine whether alewife could feed regularly upon fry that exhibited natural behavior, to compare the survival rates of fry in the presence and absence of alewife, and to estimate the mean daily consumption rate of fry by alewife over a twelve day period. Six tanks that contained cobble substrate were maintained under natural photoperiod and each stocked with 153 lake trout fry (densities similar to that observed at Stony Island reef, Lake Ontario). Four treatment tanks each contained ten alewives. The two tanks without alewives served as controls. After 12 days, mean recovery of fry was much less in the treatment tanks that contained alewife (31.5 fry per tank) than in the control tanks (150 fry per tank) ($P < 0.009$). Mortality in the control tanks was about 2% in contrast to the 46 to 91% mortality experienced in tanks with alewives. The effects of predation by the alewives were evident early in the experiment because the mean daily capture of fry in traps set in each tank was always lower after day two in treatment tanks than in control tanks. Alewife consumption rates of lake trout fry ranged from 0.57 to 1.16 fry $\text{alewife}^{-1}\ \text{day}^{-1}$ with a mean of 0.99 fry $\text{alewife}^{-1}\ \text{day}^{-1}$ (SE = 0.141) and a median of 1.12 fry $\text{alewife}^{-1}\ \text{day}^{-1}$.

Predation by alewives might have caused substantial mortality of lake trout fry from spawning areas in Lake Ontario where alewife were abundant and could also be an important source of mortality in similar areas of lakes Michigan and Huron. Increased stocking of predatory salmonids to suppress alewife could enhance survival of fry and speed restoration in Lake Ontario, but seems unlikely under current strategies to manage alewife as forage for non-native salmonids. In this context, lake wide goals should be re-focused on restoration in localized areas where alewife do not congregate during the spring and predation on lake trout fry would be minimal such as at offshore shoals.

Introduction

Lake trout (*Salvelinus namaycush*) were native to Lake Ontario until 1960. Prior to that time they provided a valuable sport and commercial fishing industry for both Canada and the U.S. The decline and eventual extinction of lake trout has been attributed to a combination of overfishing, predation by sea lamprey (*Petromyzon marinus*), and degradation of habitat. A program to restore a self-perpetuating population of lake trout to Lake Ontario has been underway since 1971. In the past decade, up to two million lake trout yearlings have been stocked in the lake each year. The survival of lake trout in Lake Ontario after stocking has been adequate to develop an important sport fishery in New York. In addition, assessment surveys conducted by the New York State Department of Environmental Conservation (DEC) have found large aggregations of mature lake trout at several sites in the eastern basin of the lake. The first evidence of successful reproduction by stocked lake trout was documented in 1982 by the capture of a single lake trout fry by DEC, and by our collection of 75 fry off the north end of Stony Island in 1986 (Marsden et al. 1988) Since this time, fry have been collected from the Stony Island reef every year through 1990. However, annual trawling assessments by DEC and the U.S. National Biological Survey (NBS) to capture naturally-produced fingerlings and yearlings have provided little evidence of survival of wild fry beyond the emergent life stage.

This research project investigated one possible explanation for the lack of recruitment to the yearling life stage -- the predation of lake trout fry by alewives. Alewives invaded Lake Ontario, possibly through the Erie Canal system, sometime prior to their first documentation in 1873 (Smith 1970). Alewives increased and became abundant just prior to 1900 at a time when predation pressure on alewives was diminished due to reduced lake trout abundance and the extinction of Atlantic salmon (*Salmo salar*). Concurrent with the increase of alewives in Lake Ontario was the decline of several important native species such as the lake herring (*Coregonus artedii*), a shallow-water planktivore. The role that alewives have played as a competitor, predator, and prey in Lake Ontario over the decades of the 1900s has not been clear and has served to stimulate considerable debate (e.g., Miller 1957; Smith 1970; Christie 1974). Alewives, however, have remained abundant in Lake Ontario through the 1980s (e.g., O'Gorman et al. 1987). Predation of larval fish by alewives has been proposed as possible factor that caused the decline of several native Great Lakes species such as emerald shiners (*Notropis atherinoides*), lake whitefish (*Coregonus clupeaformis*), and yellow perch (*Perca flavescens*) during the 1900s (e.g., Smith 1970; Crowder 1980; Jude and Tesar 1985).

This research project focused on determining the potential of alewife to be an important predator on lake trout fry. The objectives of this investigation were as follows:

1. To compare the temporal pattern of abundance of alewives and lake trout fry on a reef in the spring in order to identify whether the putative predator and prey exist at the same time and place.

2. To determine the proportion of alewives that are actively feeding on the reef in the spring.

3. To determine whether alewives will accept lake trout fry as a food item.

In addition, as a part of our laboratory studies we determined whether alewives would feed on lake trout fry emerging from simulated reefs over a twelve day period, and the predation effect of alewives on fry abundance when fry occurred at densities similar to those observed at Stony Island reef.

The results of this project were written into two manuscripts in styles suitable for submission for publication in scientific journals. The first manuscript entitled "Predation by Alewife on Lake Trout Fry in Lake Ontario: Role of an Exotic Species in Preventing Restoration of a Native Species" served as the content for an oral presentation at the GLFC sponsored RESTORE Conference (see Appendix 1). The paper has been submitted to the *Journal of Great Lakes Research* for publication as a contribution to the special RESTORE conference volume. This paper completes the first three objectives of this research project. The second paper entitled "Predation by Alewife on Lake Trout Fry Under Simulated Reef Conditions" will be submitted to the *Journal of Great Lakes Research* and completes the additional laboratory studies conducted under this research contract (see Appendix 2). As a complement to the data set presented in the first paper, additional field work was conducted at Stony Island reef during the spring of 1994. These data are presented in Appendix 3 and further contributes to the completion of objectives 1 and 2.

Appendix 1

Submitted to:

Rehabilitation of Lake Trout in the Great Lakes: A Critical Assessment

J. Great Lakes Res.
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Predation by Alewife on Lake Trout Fry in Lake Ontario: Role of an Exotic Species in Preventing Restoration of a Native Species

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ABSTRACT. *Lake trout (*Salvelinus namaycush*) restoration efforts in Lake Ontario have resulted in an abundance of spawning fish of hatchery-origin but virtually no detectable natural recruitment. One explanation has been predation by non-native alewife (*Alosa pseudoharengus*) on lake trout fry. The purpose of this study was to determine if alewives could be important predators of lake trout fry. In the laboratory, behavior of fry was examined to ascertain when fry would be present in the water column during a 24-hour period and to determine the acceptability of fry as food for alewife. In aquaria exposed to ambient light regimes, sac fry activity in the water column was much greater at night than during daylight hours ($P < 0.001$). In laboratory tanks, lake trout fry (15-34 mm) were aggressively eaten by alewives (118-175 mm). Field studies were conducted at Stony Island reef, Lake Ontario from 1989-1993 to determine whether alewives and fry were present at the same time on the reef, if alewives fed when on the reef, and if alewives fed upon naturally-produced lake trout fry. Lake trout fry capture in traps indicated that sac and emergent fry were available as prey from the middle of April through the third week of May. The first capture of alewife in gill nets set adjacent to the fry traps was typically in early May and corresponded to the peak capture of sac fry in traps. Food was present in 86% of the 1239 alewife captured after sunset over the 5-year period. Ten lake trout fry were found in six of the 62 alewife captured after sunset on May 20, 1993 at Stony Island reef; no fry were observed in alewife stomachs caught on other dates. Predation by alewives might have caused substantial mortality of lake trout fry from spawning areas in Lake Ontario where alewife were abundant and could also be an important source of mortality in similar areas of lakes Michigan and Huron. Increased stocking of predatory salmonids to suppress alewife could enhance survival of fry and speed restoration in Lake Ontario, but seems unlikely under current strategies to manage alewife as forage for non-native salmonids. In this context, lake wide goals should be re-focused on restoration in localized areas where alewife do not congregate during the spring and predation on lake trout fry would be minimal such as at offshore shoals.*

INDEX WORDS: *Great Lakes, food habits, diet, zooplankton, mortality, behavior, management*

INTRODUCTION

Lake trout (*Salvelinus namaycush*) have been the focus of a native species restoration program in Lake Ontario since the early 1970s. The decline and eventual extinction of lake trout around 1960 has been attributed to a combination of overfishing and predation by sea lamprey (*Petromyzon marinus*), and possibly degradation of habitat (Christie 1972, Elrod *et al.* this volume). A program to restore a self-perpetuating population of lake trout to Lake Ontario has been underway since 1971 when sea lamprey control efforts were initiated. In the past decade, up to two million lake trout yearlings have been stocked in the lake annually and their survival has resulted in large aggregations of mature lake trout at several potential spawning sites in the eastern basin of the lake during autumn. Evidence of successful reproduction by stocked lake trout was documented in 1982 with the capture of a single lake trout fry by the New York State Department of Environmental Conservation (NYDEC), and by a collection of 75 fry off the north end of Stony Island in 1986 (Marsden *et al.* 1988). Since 1986, fry have been collected from the Stony Island reef every year through 1993. However, annual bottom trawling assessments of fish stocks by NYDEC and the National Biological Survey (NBS, formerly part of the U.S. Fish and Wildlife Service) have indicated that the contribution of naturally-produced fingerlings and yearlings to the population has been virtually nil (Elrod *et al.* this volume). In Lake Ontario, though fry capture rates at Stony Island have steadily increased, only four yearlings suspected to be from natural spawning were captured in 1989, three were caught during 1990, and none were caught in 1991 by agencies conducting assessments (Casselman 1991, Schneider *et al.* 1992). Thus, few wild fry appear to survive beyond the emergent life stage.

Alewife (*Alosa pseudoharengus*) is a species exotic to Lake Ontario and may be responsible in part for the extinction or reduction of several native fish species through food competition and larval predation. Alewives probably invaded Lake Ontario during the 1860s through the Erie Canal system (Smith 1970) and were noted to be abundant by 1873 (Koelz 1926). Alewives remained abundant in Lake Ontario through the 1980s, although adult alewife biomass declined from 1986 to 1992 (*e.g.*, Jones *et al.* 1993). Alewives are highly dependent on zooplankton for food (Janssen and Brandt 1980, Keilty 1990, Mills *et al.* 1992) and have been shown to locally depress zooplankton body size and abundance through intense predation (e.g., Wells 1970, O'Gorman *et al.* 1991). Changes in zooplankton body size distribution have been used in Lake Ontario to track the movement and distribution of alewife in spring (O'Gorman *et al.* 1991). Alewife predation of larval fish has been proposed as a possible factor that caused the decline of several native Great Lakes species during the 1900s such as emerald shiners (*Notropis atherinoides*), lake whitefish (*Coregonus clupeaformis*), and yellow perch (*Perca flavescens*) (Smith 1970, Crowder 1980, Jude and Tesar 1985, Eck and Wells 1987). Competition for zooplankton food between alewives and native fish species has been frequently offered as an explanation for the decline of native populations; however, predation on early life stages of native species may be more important (Eck and Wells 1987).

Alewives have been observed to feed on larval fish in the laboratory and field. Hoagman (1974) observed that in laboratory tanks adult alewives from Lake Michigan readily ate larval lake whitefish about 16 mm long. In North Sandy Pond, a bay of eastern Lake Ontario, alewives fed intensively during late April and early May upon yellow perch larvae 7-8 mm long at levels that may have controlled year class strength (Brandt *et al.* 1987). In Cayuga and Seneca lakes, New York, alewives were reported to feed upon young-of-year alewife during summer months (Odell 1934, Rothschild 1966). Larval fish up to 26 mm long were a frequent component in stomachs of alewives collected from Claytor Lake, Virginia (Kohler and Ney 1980). Consumption of even larger sized fishes by alewives has been observed in Lake Ontario. Stomachs of four alewife (169 to 211 mm) captured in trawls contained from one to six young-of-year alewives 20-35 mm long (R. O'Gorman, NBS, personal communication 1993). One large alewife (211 mm) had eaten one young-of-year alewife and two rainbow smelt (*Osmerus mordax*) that were 55 mm and 65 mm long. Lake trout fry between the sac and emergent fry stages are 15 to 28 mm long, well within the size range acceptable by alewife. Thus, one possible explanation for the lack of lake trout recruitment to the yearling life stage in Lake Ontario is predation of fry by alewife.

Evidence necessary to demonstrate that a predator could control the abundance of a prey species is the observation that both species occur at the same time and place, and that the predator is actively feeding and will accept the prey as food. If these observations are true and predator consumption equals or exceeds prey production for a sufficient time, prey populations will be eliminated. In the case of alewives, the most likely intersection in time and space with lake trout fry would be in the spring as fry emerge from the stony substrates of spawning areas for feeding and for the filling of their swimbladder with air (Tait 1960). Timing of the emergence of lake trout fry in Lake Ontario (Marsden *et al.* 1988) roughly corresponds to the inshore movement of alewife in response to near-shore warming of water (Graham 1956, O'Gorman *et al.* 1991). However, not only is a seasonal correspondence required, but also diel behavior patterns of predator and prey must intersect. For example, emergence of salmonid fry to fill their swimbladder with air typically occurs at night (*e.g.*, Hoar 1956, Godin 1982, Gustafson-Marjanen and Dowse 1983). This behavior pattern may be true for lake trout fry and could indicate a higher activity level at night than during the day. Thus for alewife predation of lake trout fry to occur, alewives would need to feed at night in the spring on lake trout spawning reefs and accept fry as a food item.

This study used laboratory and field approaches to determine the potential of alewife to be an important predator on lake trout fry. Laboratory objectives were to describe diel behavior of lake trout fry (to ascertain when they are available as prey) and to determine whether alewife would accept fry as food. Field studies were conducted at

Stony Island reef in Lake Ontario from 1989-1993 to provide direct and indirect evidence of alewife predation on lake trout fry. These studies included: (1) use of gill nets and traps to determine if alewife and lake trout fry occupied the reef area at the same time, (2) indirect assessment of fish predation intensity through measurement of mean body size of crustacean zooplankton during spring and its association with the presence or absence of alewife, and (3) examination of the stomach contents of alewife captured on the reef to determine whether alewives were actively feeding, and whether alewives fed upon naturally-produced lake trout fry.

METHODS

Laboratory Studies

Diel availability of lake trout fry as a prey in the water column was investigated in glass aquaria (19.2 l) fitted with a trap to capture fry swimming upward out of stony substrate (Fig. 1). Stone from Lake Ontario was placed in the aquaria to a depth of 10 cm. Two square pieces of clear plexiglas were fitted and glued into each aquarium to funnel fry to two openings at the apex where the two pieces came together. Openings were located 5 cm away from the sides of the aquaria to inhibit fry from returning to the substrate after swimming upward through the opening. Preliminary tests indicated that after exiting upward through the opening, fry stayed near the sides and only returned to the substrate when the openings were located next to the side. Each piece of plexiglass had a mesh-covered hole to allow water circulation. Air was pumped into each aquarium through a small airstone to slowly circulate and oxygenate the water. Sides of the aquaria were covered with black plastic. During use, the aquaria were exposed to the ambient photoperiod of March and April. Fry used each year originated from gametes of

[Fig. 1 Near Here]

mature lake trout captured adjacent to Stony Island reef the previous autumn. In 1992, two aquaria were seeded with either 10, 20, 30, or 40 lake trout sac fry (total of eight aquaria). Water temperature in the aquaria over the 20 day study period gradually increased from 6 to 9°C. In 1993, each of six aquaria were seeded with 50 fry. Three aquaria were exposed to the natural photoperiod and three were exposed to constant light from fluorescent lamps. Water temperature over the 19 day study period gradually increased from 7.5 to 10.5°C. In both study years, fry were counted and removed (not replaced) from the aquaria traps twice daily, once immediately after sunrise to determine capture overnight and once during the day typically 1-2 hrs before nightfall to assess movement out of the substrate during night and day periods. Comparison of counts of fry captured during night versus counts of fry captured during day used the likelihood ratio test statistic *G* (Sokal and Rohlf 1981) to test the null hypothesis that fry had an equal probability of being captured during either period. A simultaneous test of the effect of density and night versus day was performed using 2-way ANOVA (Sokal and Rohlf 1981).

The suitability of lake trout fry as food for alewife was determined by visual observation of alewife behavior toward fry in two circular tanks (1.8 m diameter). Tanks at Cornell University's Resource Ecology and Management Laboratory (REM Lab) were filled to about 1 m depth with dechlorinated water(13°C, source Cayuga Lake, New York) and set up as flow-through systems. Alewives (115 to 175 mm) were seined from Cayuga Lake or gill netted from Lake Ontario and then transferred to the REM Lab. For about one week after arrival, salt was added to the tanks to maintain a 1% concentration to reduce the effects of stress from capture. Observations were begun after alewives had been actively feeding upon brine shrimp (*Artemia* sp.) for several days. Approximately 60 alewives were held in one tank and 15 alewives in the other. Live, partially immobilized, and dead fry (19-34 mm) were introduced to the tanks one at a time and the fate of fry was recorded. To determine the amount of time before a lake trout fry would become unrecognizable in an alewife stomach, a single, thawed fry (15-28 mm) was fed to an alewife held in the tanks described above. Immediately after the fry was eaten, the time was recorded and the alewife was transferred to a tank (also 13°C) that contained no fry or other alewives. This procedure was repeated with 10 alewives (each having eaten a single fry). Alewife were sacrificed at 1, 2, 2.5, or 3 hours after being fed, and were then dissected to determine the visual identifiability of the fry.

Field Studies

All studies were conducted on Stony Island reef, a shallow-water shoal in northeastern Lake Ontario (43° 55' 50" N, 76° 17' 50" W) that ranges in depth from 4 to 10 m (see Fig. 1 of Marsden *et al.* this volume). The reef is composed of limestone cobbles and boulders 25 mm to > 400 mm in size; detailed description of the site has been provided by Marsden *et al.* (1988) and Marsden and Krueger (1991).

To compare the temporal pattern of abundance of alewives and lake trout fry on the reef in the spring, traps were used to catch lake trout fry and gill nets were used to capture alewives. From 1989 through 1993, 60 to 62 steel-mesh, pyramidal fry traps (Marsden *et al.* 1988) were fished on the reef. Traps were placed on the bottom beginning in early April where they were deployed between the shallow and deep edges of the reef in the study area used by Perkins and Krueger (this volume). Traps were lifted, checked for fry, and reset at roughly weekly intervals until the end of May each year. Fry here refers to early developmental stages immediately after hatching (eleutheroembryo stage) through yolk-sac absorption (early alevin stage, see Balon 1980). Fry were classified at time of capture as to their developmental stage based on the degree of yolk sac absorption. Sac fry had rounded protruding yolk sacs and were typically < 19 mm long. Fry with partially absorbed yolk sacs were classified as between the sac and emergent stages (S/E). These fry had an oblong yolk sac that had lost its spherical globular shape and were typically 19 to 23 mm long. Fry classified as emergent had no yolk sacs and were typically > 23 mm long.

Alewives were captured by fishing two gill nets on the same dates that the fry traps were tended (with few exceptions). Each net consisted of two 30.5 by 1.83 m net panels. One panel was constructed of 2.5 cm stretch monofilament mesh and the other panel was 3.8 cm stretch monofilament mesh. One net was set on the deep side of the reef (bottom depth 10-13 m) and the other net was set on the shallow side (bottom depth 4-5 m). Nets were usually set parallel to the depth contours and within 20 m of the fry trapping area. Soak time for each set was one hour. Two sets were made on each sampling date. One set was made about one hour before nightfall. The second set fished during the first hour after nightfall. The short soak time was necessary to minimize the digestion of fry in alewife stomachs (to enhance the identifiability of fry in stomachs) and because longer soak times could have caused mesh saturation when alewife densities were high. All fish captured were immediately preserved in 10% formalin after their abdominal cavities were pierced and later each fish was identified and measured (nearest mm TL). Stomachs of preserved fish were dissected and examined under a microscope for the presence of fish larvae. Lake trout larvae in stomachs were identified with keys by Auer (1982), measured to the nearest mm TL, and counted. Presence or absence of food was noted for each fish.

Zooplankton were sampled each year on four to five dates in the spring with a conical plankton net 0.5 m in diameter, 2 m in length, and constructed of 153 μ mesh. The net was lowered to the bottom to a depth of about 10 m and retrieved vertically. Two to four tows were made on each collection date except in 1989 when only one tow was made on each date. Zooplankton were preserved in a sugar-formalin solution (Haney and Hall 1973) immediately after being rinsed from the net. Individual zooplankters were identified to species (Balcer *et al.* 1984), enumerated, and measured electronically in one to three 1 ml subsamples. Immature zooplankters (neonates and copepodites) were also counted and measured in all subsamples. Zooplankters were measured from the anterior margin of the head to the base of either the tail spine (in cladocerans) or the caudal rami (in copepods). Tests of contrast of mean sizes of zooplankton among dates were conducted according to Petersen (1985). Length-frequency distributions of zooplankters among dates were compared by use of the Kolmogorov-Smirnoff test (Conover 1980).

RESULTS

Laboratory Observations

Diel Behavior of Lake Trout Fry

Capture of lake trout sac fry rising above the substrate in aquaria was much greater at night than during daylight hours in 1992 and 1993 ($P < 0.001$, Table 1). In 1992, approximately 97% of the fry were captured at night. No density dependent effects were observed among aquaria with 10, 20, 30, and 40 fry ($P > 0.50$). On two occasions, the trap was checked about two hours after sunset. In both instances, several fry had been captured, indicating that fry activity began shortly after nightfall. In 1993, 82% of the fry were captured during night time periods in the aquaria with an ambient light regime. In aquaria exposed to constant light, fry capture at night was not different from that during day ($P > 0.50$). In both light regimes, more than 95% of the fry introduced to the aquaria were captured over the 19 day period (Table 1).

[Table 1 Near Here]

Feeding Response of Captive Alewives to Lake Trout Fry

In laboratory tanks, lake trout fry (15-34 mm) were actively fed upon by alewives (118-175 mm). Fry introduced to the surface of the tank would initially swim at the surface. An alewife (sometimes more than one) would orient to the fry, especially if the fry was actively swimming, and either engulf the fry completely and swallow, or hesitantly peck at the fry and get one-half to three-quarters of the fry in its mouth. If the fry was not engulfed, fry sometimes would then vigorously wriggle free and swim quickly to the bottom of the tank. Alewife rarely pursued fry that were within 2 to 4 cm of the tank bottom. Fry were eaten when other food items (brine shrimp) were abundant (>50 shrimp) and being fed upon by alewife. Small sac fry < 20 mm in length were more readily fed upon by alewife than 25 mm post-emergent fry. Partially immobilized and dead fry of all sizes were eaten readily by alewives.

Individual alewives varied considerably in their acceptance of lake trout fry as food. Some alewives never fed on fry whereas others fed on fry whenever fry were available. Some alewives approached a fry, examined it, and then swam away. Other alewives engulfed a fry, swam a meter or so, and then spit the fry out. Some alewife aggressively pursued, captured, and ate fry. One alewife ate five lake trout fry during one 0.5 hour feeding session.

Detectability of lake trout fry in alewife stomachs was dependent on the size of the fry and the length of time after ingestion. One hour after ingestion, two 15 mm TL sac fry were barely discernible in the gut and could have been missed easily whereas a 16 mm TL sac fry was more readily identifiable upon close examination (N=3 fry). Typically the head with paired black spots of the eyes was the easiest part of the fry to identify. Two hours after ingestion, 18 mm sac fry were not detectable in alewife stomachs (N=2 fry). After 2.5 hours, emergent fry >23 mm were still readily detectable in alewife stomachs (N=3 fry). After 3 hours of digestion, a 23 mm fry was barely discernible whereas a 28 mm fry was still easily identifiable.

Field Studies

Occurrence of Lake Trout Fry and Alewife on Stony Island Reef

Lake trout sac fry always were captured on the first date that traps were lifted in April, 1989-1993, and fry were typically vulnerable to the traps through the third week of May (Fig. 2). Variability in the first date when trapping occurred reflected differences among years when the ice cover disappeared, and hence our ability to reach the study site from the mainland. In every year, sac fry dominated the catch in April. Out of 1194 fry captured in April, 1144 (96%) were classified as sac fry. Catch of sac fry increased to a peak around the first week of May when water temperature was 6-8°C. Total number of fry captured was lowest in 1989 (135 fry) and increased to 1414 fry in 1993 (Fig. 2).

[Fig. 2 Near Here]

Over the five year study period, most S/E and emergent fry were captured in May (94%, Fig. 2). During the first four years (1989-1992), emergent fry were rarely captured; only 31 emergent fry were caught out of a total of 1345 fry; most fry (93%) were classified as sac fry. In 1993, S/E and emergent fry capture was proportionally much higher (55% of total) than in previous years (7%). Peak capture of this developmental stage occurred during the third week in May when water temperature was 9°C, approximately two weeks after the peak sac fry capture. Emergent fry comprised most of the fry catch on May 20 and 27, 1993; out of 640 total fry observed on these dates, 443 fry were classified as emergent.

Alewife were first captured in late April (rarely) or early May in the gill nets set adjacent to the fry traps (Fig. 2). Earliest capture of alewives roughly corresponded to peak capture of lake trout sac fry in traps. The catch of alewife usually increased during the middle of May when water temperatures were 9-11°C and emergent fry were available as prey. Thereafter, the alewife catch was variable. In 1993, the most alewife were caught on May 20 when peak numbers of emergent lake trout fry were captured.

Highest catches of alewives occurred after sundown; an average of 89% (range 64-100%) of alewives caught over the five years were captured in nets set after nightfall.

Eleven other species were caught in *gill net*s during April and May. These species were rainbow smelt, lake trout, American eel (*Anguilla rostrata*), lake chub (*Couesius plumbeus*), emerald shiner, spottail shiner (*Notropis hudsonius*), yellow perch, white perch (*Morone americana*), rock bass (*Ambloplites rupestris*), smallmouth bass (*Micropterus dolomieu*), and mudpuppy (*Necturus* sp.). With the exception of the non-native rainbow smelt, few species were captured in April. Of 174 smelt captured over five years, 157 smelt were caught in April.

Zooplankton Size Distribution

Fifteen different crustacean zooplankton species were identified over the five year study but only a few species were ever abundant. The three most abundant zooplankton were the copepods *Diacyclops thomasi*, *Skistodiaptomus oregonensis*, and *Leptodiaptomus minutus*.

For all years, mean lengths of zooplankters were greater in the absence of alewife when compared to sample periods when alewife were present ($P < 0.005$) (Fig. 3). Tests were made by comparison of the mean length of zooplankton on the two sample dates immediately preceding and two dates immediately following the first capture of alewives (in 1992 only one sample date occurred before alewives appeared). The presence of alewife on Stony Island reef coincided with a decline in mean length of crustacean zooplankton over a 4-5 week period (Fig. 3) and a virtual disappearance of large-bodied zooplankters ($\geq$ 0.9 mm) (Fig. 4). Although zooplankton size clearly declined when alewife moved nearshore, mean body lengths of zooplankton generally increased from 1989 (0.41mm) to 1993 (0.71 mm) in the presence of alewife suggesting that alewife abundance and predation intensity declined over the study period.

[Fig. 3 Near Here]

[Fig. 4 Near Here]

Stomach Contents of Alewife Captured At Stony Island Reef

Ten lake trout fry (20-25 mm) were found in the stomachs of six (149 - 165 mm) of the 62 alewife captured after nightfall from the shallow side of the reef on May 20, 1993 (Fig. 5). Stomachs of the six alewife contained one to three fry per alewife. Fry in stomachs were readily identifiable suggesting that the fry were eaten within 1-2 hours before the alewife were captured. The presence of lake trout fry in alewife stomachs coincided with the peak capture of emergent fry from the reef in 1993 (Fig. 2). No fry were observed in the stomachs of alewife captured on other sampling dates.

[Fig. 5 Near Here]

Over the five year period, food was present in 93% of 570 alewife captured before sunset and in 86% of the 1239 alewife captured after sunset. The most common food items observed were copepods, *Daphnia* sp., amphipods (*Gammarus* sp.), water mites (*Hydracarina* sp.), and Chironomidae larvae. No lake trout fry were eaten by the other fish species or mudpuppies captured from the reef.

DISCUSSION

Before one can reasonably conclude that a predator may be responsible for the absence of a prey species, four criteria should be satisfied (modified from Kitching and Ebling 1967 and Simberloff 1981):

1. one must know for certain, by prevention of predation, that other physical and ecological factors are not limiting,
2. geographic and temporal distribution patterns of predator and prey must overlap,
3. predation should occur not only in the laboratory but also in the field,

4. transplant experiments should be conducted in which the predator is observed to eat the putative prey and the prey population can not survive unless protected from predators.

The first three criteria listed above can be addressed with respect to alewife predation on lake trout fry.

The first criterion, that other variables provide a better explanation for the failure of lake trout recruitment than predation, seems unlikely based on several lines of evidence. Little evidence exists that suggests behavioral or physiological problems occur in recruitment between egg deposition and the fry stage. In Lake Ontario, adult lake trout of hatchery origin aggregate over spawning reefs, recognize appropriate incubation substrates for their eggs, successfully fertilize and deposit eggs, and, at least in the case of Stony Island reef, produce fry through the emergent stage (Marsden *et al.* 1988, Marsden and Krueger 1991, Perkins and Krueger this volume, Marsden *et al.* this volume, this study). The absence of sufficient spawning areas in the lake to produce a detectable natural year class (10,000 to 30,000 yearlings) also does not completely explain the lack of natural recruitment (Perkins and Krueger this volume). Though these aspects of reproductive ecology undoubtedly affect the amount of fry emergence, the primary blockage to natural recruitment seems most likely to be between the time of fry emergence and yearling life stages.

Mortality after fry emergence likely does occur due to a swim-up syndrome (*e.g.*, Mac *et al.* 1985, Mac and Edsall 1991), possibly caused by a thiamin deficiency in eggs (Fitzsimons *et al.* this volume). However, complete mortality after emergence due to the syndrome seems unlikely. During the last decade the NYDEC has collected gametes from adult lake trout captured adjacent to Stony Island for hatchery propagation (Marsden *et al.* 1993). Several year classes of the "Lake Ontario strain" were propagated and then stocked back into the lake as yearlings. In this case, no physiological barriers existed to prevent fry from growing to the yearling stage in the hatchery. Similarly, we have trapped fertilized eggs in the fall and fry in spring from the reef at Stony Island and transported them to the Cornell University hatchery (e.g., Perkins and Krueger this volume). Fry derived from both collection methods have been held for six months after emergence, well beyond the age where swim-up mortality has been reported. In 1993, the swim-up syndrome was observed in fry from Stony Island but this source of mortality did not provide a complete block to survival (roughly 50% survived). Other sources of fry mortality in Lake Ontario such as starvation also do not provide an adequate explanation for the absence of wild yearlings. For example, food such as Chironomidae, Amphipoda, and *Mysis relicta* typically consumed by young-of-year lake trout (e.g., Dryer *et al.* 1965, Swedberg and Peck 1984, Hudson *et al.* this volume) appears to be abundant and comparable to other Great Lakes (e.g., Johannsson 1992). Thus, the first criterion seems to be satisfied; variables other than predation do not completely explain the lack of natural recruitment to the yearling life stage.

The second criterion, that alewife and lake trout fry must occur at the same place and time, was satisfied by the present study (Fig. 2). The field and laboratory studies demonstrated that lake trout fry, of both sac and emergent life stages, occurred in the water column from early April through about the end of May and thus were vulnerable to predators over this time period. Alewife were first captured on the reef in gill nets at about the time of peak capture of lake trout sac fry in early May. Alewife capture in most years appeared to be greatest on the reef when emergent fry were most abundant and vulnerable. Studies of diel behavior of lake trout fry indicated that fry were primarily active at night. Similarly, most (68%) of the alewife were caught on the reef at night and of these, most (89%) were feeding. The gill net effort used in this study (four 1-hour sets per week) to assess alewives was probably inadequate to characterize relative abundance in general, especially when abundance was at low levels. Once alewife were present near Stony Island in early May, the number captured in subsequent sampling dates was highly variable with no trend (except in 1989, Fig. 2). The variability in the data was likely dependent on whether a school by chance moved onto the reef during the evening we sampled. The spring occurrence of alewife in the reef area was associated with an increase in water temperature and consistently coincided with a decline in the mean length of crustacean zooplankton (Fig. 3) and a virtual disappearance of large zooplankton (Fig. 4). One could argue that the warming of waters at Stony Island reef in the absence of alewife could have triggered zooplankton reproduction and reduced mean size while large zooplankters remained abundant. However, at Stony Island reef large zooplankters disappeared (Fig. 4), and thus the changes in mean zooplankton size and abundance likely reflected the presence and abundance of alewife. Alewife moving inshore to spawn in Lake Ontario waters have been shown to feed heavily on the largest zooplankters (O'Gorman *et al.* 1991). Our study supports the notion that the presence of alewife results in intense predation. In May, the loss of large crustacean zooplankton may have increased the predation pressure exerted by alewife on larger prey items such as lake trout fry. However, depletion of zooplankton food resources was clearly not a requirement for fry predation to occur. Alewives fed on fry in the laboratory when brine shrimp were present and fry predation occurred in the field even though zooplankton mean size in the presence of alewife steadily increased over the study period.

The third criterion, that alewife predation on lake trout fry occur in the laboratory and field, was satisfied by this study. Lake trout fry were readily eaten by alewives held in tanks. In addition, about 10% of the alewives captured from Stony Island reef in 1993 had eaten from one to three lake trout fry per alewife. Though the laboratory studies of alewife predation on fry were conducted during the day, the capture of alewife after nightfall with only sightly digested fry in their stomachs (Fig. 5) demonstrated that alewife were capable of feeding on fry at night. The lack of fry in alewife stomachs in other years may be explained, in part, by a change in the ratio of the abundance of fry to alewife. For example, in 1989 the abundance of alewife was high and abundance of fry was low (Fig. 2). Thus, the chance was remote of capturing an alewife that had recently eaten one of the few fry available. In addition, detection in an alewife stomach of the small, sac fry available as prey during these years was unlikely due to their rapid digestion by alewife. Larger, emergent fry (>23 mm) were rare during the first years of this study (Fig. 2). In 1993, the ratio between fry, especially large ones classified as emergent, and alewife abundance had likely increased. Total fry captured on the reef increased approximately 10-fold from 1989 to 1993 and the proportion of emergent fry increased from 13% to 35% of the total. Part of the increase in emergent fry capture was due to increased egg deposition and better survival of eggs and fry over winter (Perkins and Krueger this volume), but could also be due to reduced alewife predation of fry. At the same time the numbers of alewife declined in the eastern basin, possibly as much as 85% (discussed below). Locally, mean size of zooplankton in the presence of alewife increased and zooplanktivory declined during the five-year period. Thus in 1993, fewer alewives on the reef than in the past had much greater numbers of fry to feed upon and this situation probably explains why we captured alewife that had recently eaten lake trout fry.

To meet the fourth criterion, demonstrating control of prey populations through transplant experiments in the field, requires that predatory consumption exceeds prey production for a sufficient time to drive prey to low levels or extinction. Such experimentation is not logistically possible in the Great Lakes. Studies of this type could, however, be done in small inland lakes (*e.g.*, stocking alewife in lakes that contain naturally-reproducing lake trout). An alternative approach to address this criterion would be to model alewife consumption and fry production in Lake Ontario and examine whether alewife could control fry abundance. This approach has been developed by Jones *et al.* (this volume) based on plausible assumptions about prey densities, predator feeding rates, and duration of exposure of predator to prey. They concluded that alewives in Lake Ontario had the potential to consume a substantial fraction of the lake trout fry produced from 1987-1991 but not in 1992 and 1993. Evidence related to this criterion could also be provided by observing the failure and success of natural reproduction of lake trout before and after the extinction or large reduction of alewife in a lake. During 1992-1993, alewife numbers in Lake Ontario's eastern basin during late April - early May were 85% lower than during 1989-91 (C.P. Schneider, NYDEC, personal communication, 1993). Detection of natural recruitment of lake trout in Lake Ontario in the near future (1994-1995) would provide further evidence that alewife have impeded restoration through predation. The large numbers of emergent fry and large mean size of zooplankton observed in 1993 (Figs. 2 and 3) may already reflect reduced predation pressure by alewives.

We suspect that in Lake Ontario over the past decade predation by alewives on lake trout fry caused nearly 100% mortality of emergent fry in near-shore spawning areas where alewives were abundant. Alewife in the past have been the most abundant species of the open-water fish community in the lake (O'Gorman *et al.* 1987). The present study was originally stimulated by our night-time visual observations in 1988 of large numbers of alewives swimming near surface among floats that marked the locations of our fry traps on Stony Island reef. The abundance of alewives that we observed on the reef in 1988, that we documented in 1989 (Fig. 2) and that others documented lake wide during the past decade (O'Gorman *et al.* 1987, Johannsson *et al.* 1991), when combined with our laboratory observations of the aggressiveness of alewife while feeding on fry, makes fry survival seem a remote possibility. Fry would be especially vulnerable when they swam to the surface at night through a water column filled with alewives to inflate their swim bladders with air.

Alewife predation of fry also may explain the general failure of natural recruitment of lake trout from near-shore spawning areas of lakes Michigan and Huron where alewife have been abundant in the past (Holey *et al.* this volume, Eshenroder *et al.* this volume) and the reproductive success of lake trout in Lake Superior where alewife are rare (Hansen *et al.* this volume). Since 1975, natural fry production by hatchery lake trout has been documented in Lake Superior (Peck 1981), Lake Michigan (Wagner 1981, Jude *et al.* 1981), and Lake Huron (Nester and Poe 1984). Though fry were documented more than eight years ago in these Great Lakes, sizable numbers of yearling and older lake trout likely to be progeny of hatchery-origin fish have only been observed in Lake Superior and in limited areas of Lake Huron (Hansen *et al.* this volume, Johnson and VanAmberg this volume, Anderson this volume). Natural reproduction and recruitment to a spawning population has been observed on Parking Lot Reef located 4.6 km offshore in Thunder Bay, Lake Huron but not at near-shore spawning locations in the bay (Johnson and VanAmberg this volume). Alewife abundance in June from near-shore sites appeared much greater than at offshore Parking Lot Reef. Thus, high levels of alewife predation on fry would explain the lack of natural recruitment at in-shore reef sites in Thunder Bay and low levels of predation would explain successful natural recruitment at Parking Lot Reef. Similarly in Lake Superior, where alewives have been rare (Bronte *et al.* 1991), lake trout stocks, when protected from sea lamprey and fishing mortality, have increased through the natural reproduction of both hatchery and wild stocks (Hansen *et al.* this volume).

Lake-wide achievement of the lake trout restoration goal in Lake Ontario may not be possible unless alewife numbers decline and remain low. If the abundance of alewife increases, natural recruitment from adult lake trout of hatchery origin probably will not occur from near-shore spawning areas where alewife congregate and are abundant. Increased stocking of predatory salmonids to suppress alewife populations could enhance survival of lake trout fry and speed restoration. This management option, however, seems unlikely in the current cultural and institutional context. Concern by the public and fishery agencies over the decline of alewife as a source of prey for stocked non-native salmonids (*Oncorhynchus* sp. and *Salmo* sp.) has caused NYDEC and the Ontario Ministry of Natural Resources to reduce stocking of salmonids (including lake trout) in an effort to ensure that alewife remain abundant (Lange and Smith this volume). In light of the present study, lake-wide management seems headed away from restoration of native species toward managing for healthy populations of an exotic prey species through reductions in stocking of predatory salmonids. Besides lake trout, the abundance of native species, such as lake whitefish, yellow perch, emerald shiner, and other species with pelagic larvae vulnerable to alewife predation may be reduced by this management direction. Management for high abundance levels of alewife will foreclose the opportunity for successful reintroduction of extirpated species such as deepwater cisco (*Coregonus hoyi*) and deepwater sculpin (*Myoxocephalus thompsoni*) that also have pelagic larvae. If management for high alewife abundance continues, goals for lake trout restoration should be revised. In this context, current lake wide goals (Schneider *et al.* 1983) should be re-focused on restoration in localized areas where alewife do not congregate during the spring and predation on lake trout fry would be minimal such as at offshore shoals.

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Table 1. Day• night capture of lake trout fry with emergence traps in laboratory aquaria exposed to ambient daylight and constant light.

Experiment	Number of Fry Captured	
	Night	Day
1992		
Natural photoperiod -- 2 aquaria of each density		
10 fry per aquaria	17	2
20 fry per aquaria	33	3
30 fry per aquaria	57	0
40 fry per aquaria	76	1
Total	183	5
1993		
Natural photoperiod -- 3 aquaria of equal density		
50 fry per aquaria	117	26
Constant light -- 3 aquaria of equal density		
50 fry per aquaria	72	78

Figure Headings

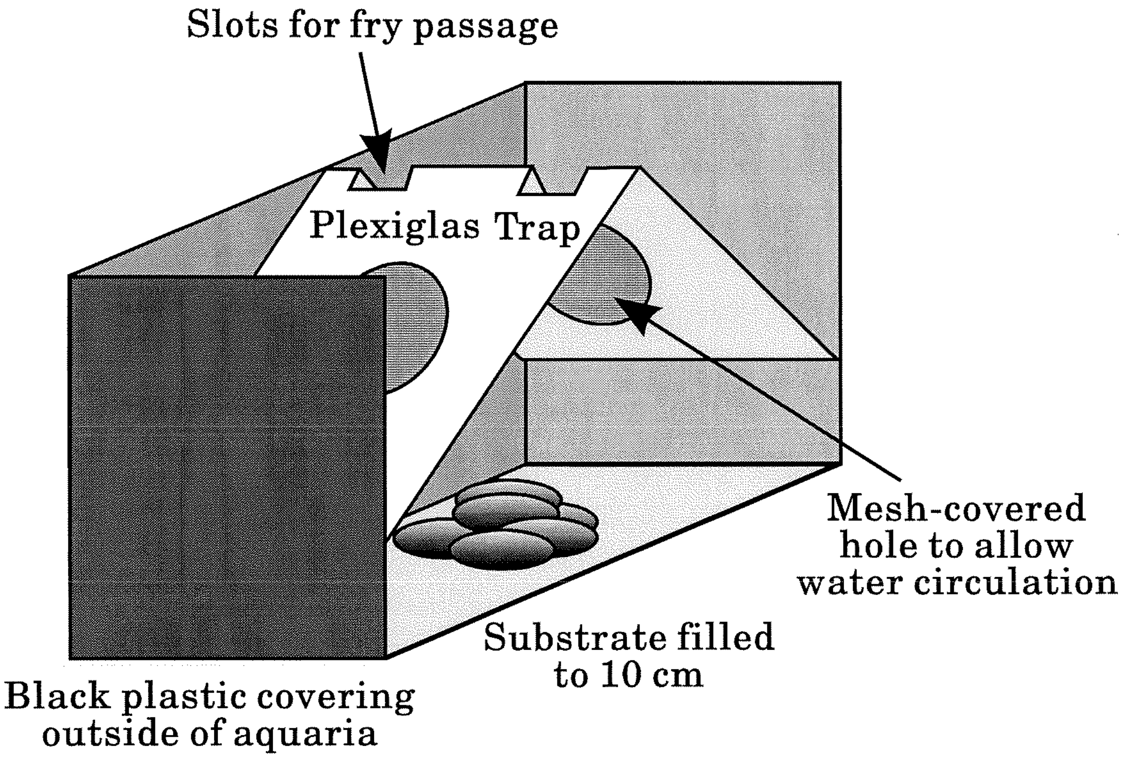
***Fig. 1.** Design of aquaria fitted with trap that was used to study day-night activity of lake trout fry in the laboratory.*

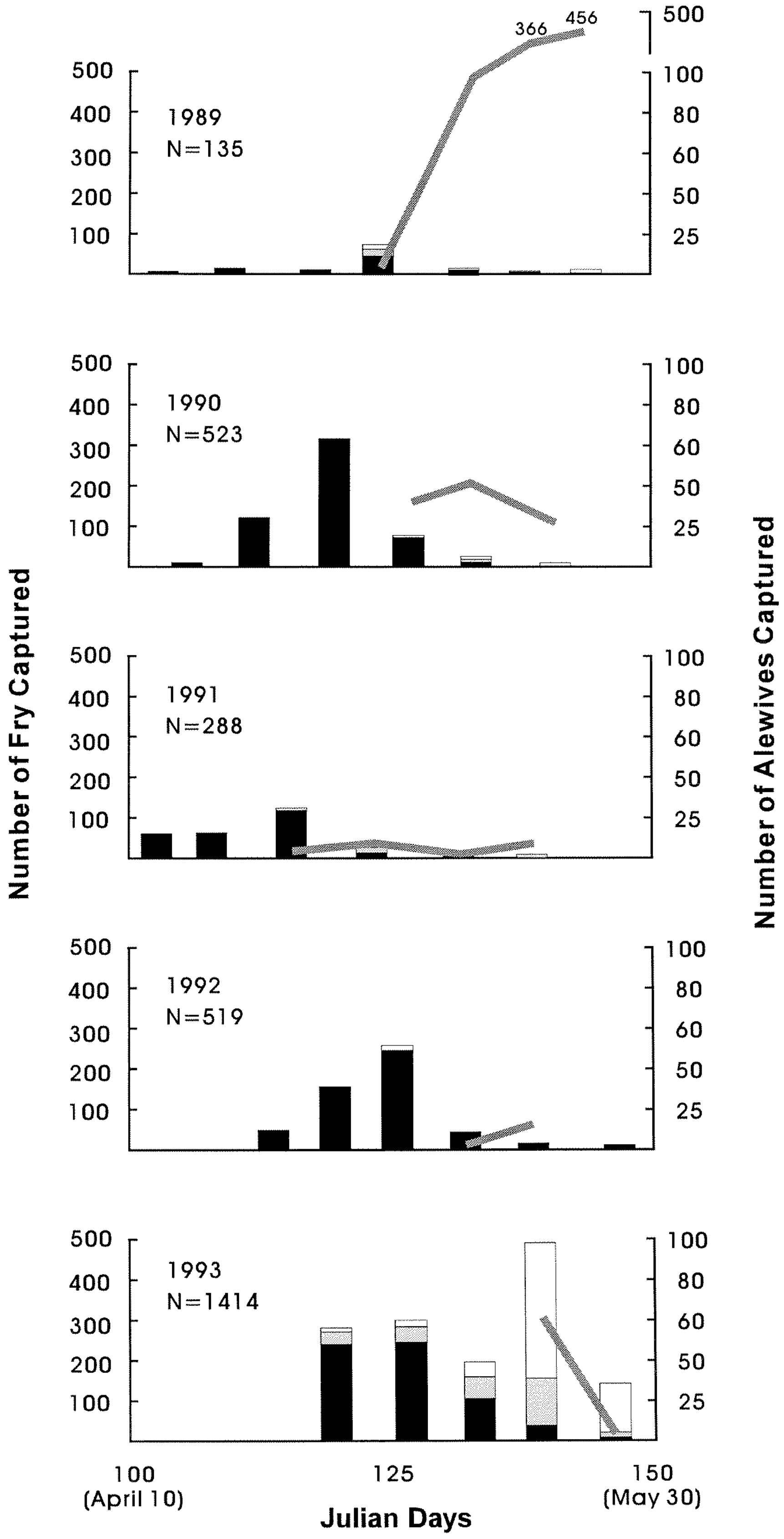
***Fig. 2.** Lake trout fry catch in traps (bar) and alewife catch in gill nets (line) from Stony Island reef, Lake Ontario, 1989-1993. Classification of fry as sac (black), sac/emergent (gray), and emergent (white) is described in the Methods. N = the total number of fry captured.*

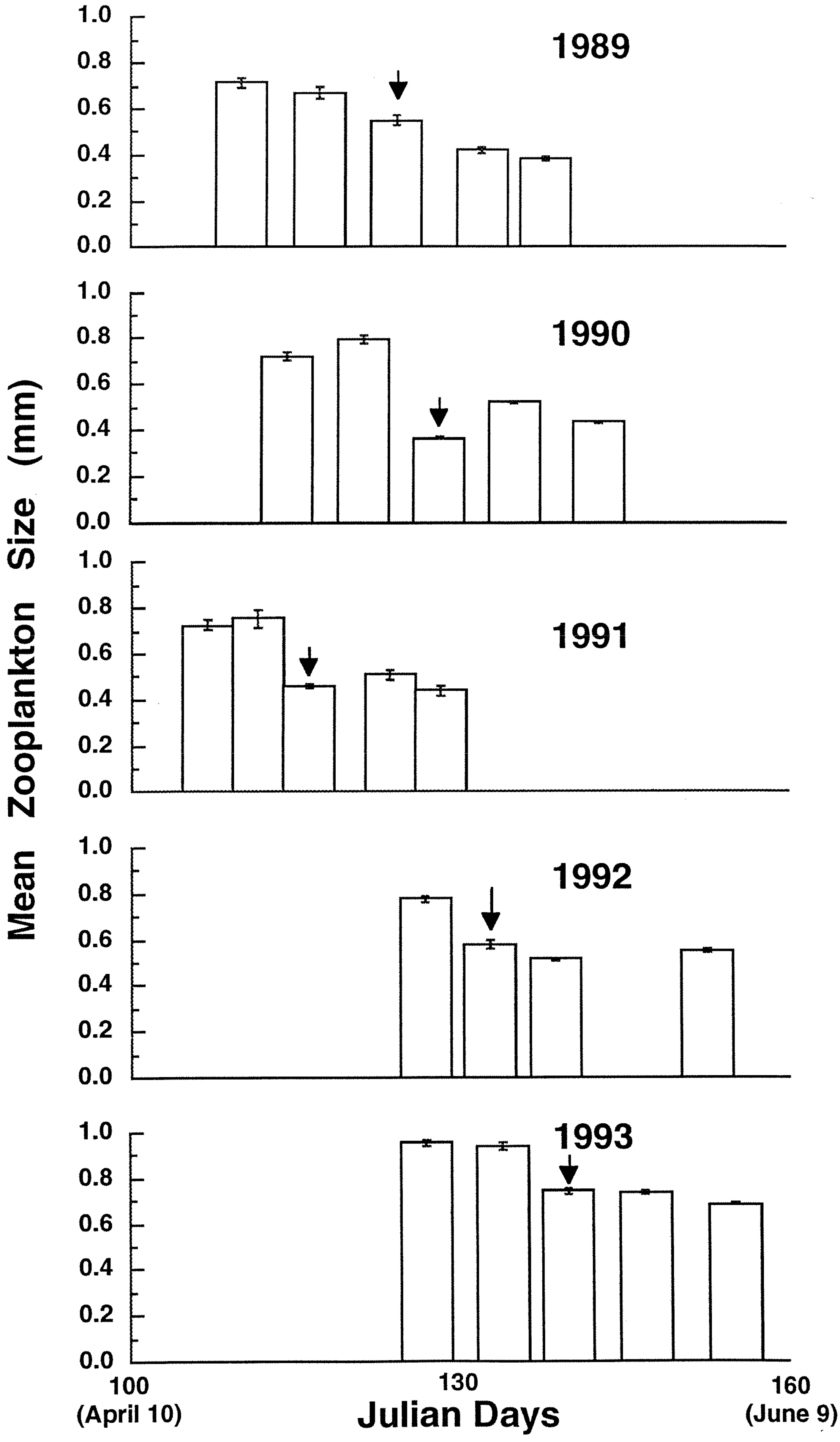
***Fig. 3.** Mean size of crustacean zooplankton sampled from Stony Island reef Lake Ontario at approximately weekly intervals April-May, 1989-1993. Arrows indicate the date of first captures of alewives in a field season. Error bars represent one standard error (only one sample was collected each date in 1989).*

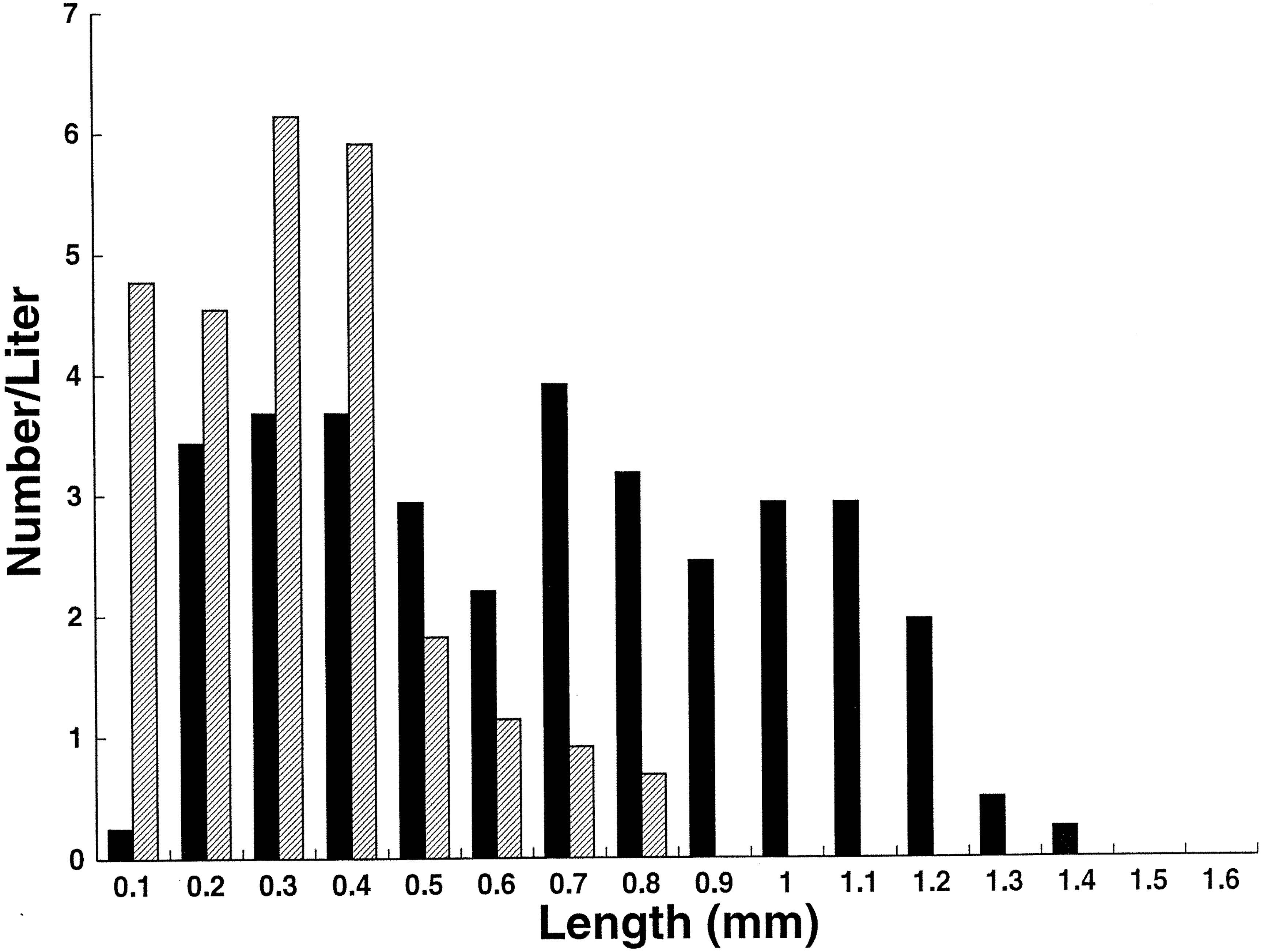
***Fig. 4.** Length-frequency distribution of crustacean zooplankton collected from Stony Island reef before (solid) and after (hatched) the presence of alewife on April 27 and May 12, 1989. Disappearance of large bodied zooplankton ≥ 0.9 mm in the presence of alewife was similar in other years sampled.*

***Fig. 5** An alewife (153 mm) captured from Stony Island reef on May 20, 1993 that contained two lake trout fry (both 25 mm) in its stomach.*


Slots for fry passage
Plexiglas Trap
Mesh-covered hole to allow water circulation
Substrate filled to 10 cm
Black plastic covering outside of aquaria


Number of Fry Captured
Number of Alewives Captured
1989
N=135
366
456
500
1990
N=523
1991
N=288
1992
N=519
1993
N=1414
500
400
300
200
100
100
80
60
50
25
100
(April 10)
125
150
(May 30)
Julian Days


1.0
0.8
0.6
0.4
0.2
0.0
1989
1990
1991
1992
1993
Mean Zooplankton Size (mm)
100
(April 10)
130
160
(June 9)
Julian Days


Number/Liter
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1
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1
1.1
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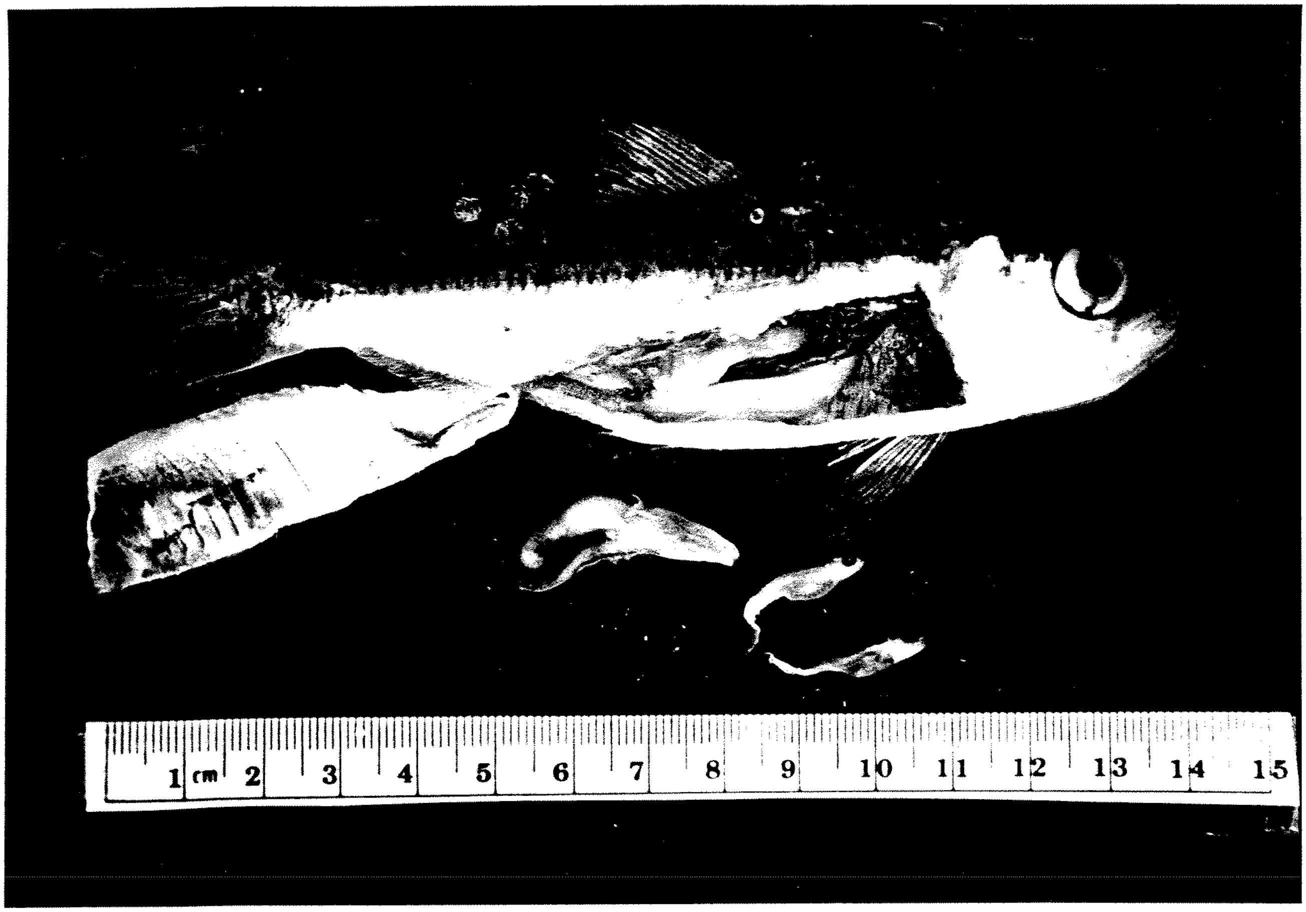
1.6
Length (mm)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Appendix 2

To be submitted to:

J. Great Lakes Res.
Internat. Assoc. Great Lakes Res.

Predation by Alewife on Lake Trout Fry Emerging from Laboratory Reefs

Version 10/27/94 15:00

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***ABSTRACT**. Predation by alewife (*Alosa pseudoharengus*) may be an important source of mortality to lake trout fry (*Salvelinus namaycush*), and could affect the success of lake trout restoration in the Great Lakes. The objectives of this study were to determine whether alewife could feed regularly upon fry that exhibited natural behavior, to compare the survival rates of fry in the presence and absence of alewife, and to estimate the mean daily consumption rate of fry by alewife over a twelve day period. Six tanks that contained natural cobble substrate were maintained under natural photoperiod and each stocked with 153 lake trout fry (densities similar to that observed at Stony Island reef, Lake Ontario). Four treatment tanks each contained ten alewives. The two tanks without alewives served as controls. After 12 days, mean recovery of fry was much less in the treatment tanks that contained alewife (31.5 fry per tank) than in the control tanks (150 fry per tank) ($P < 0.009$). Mortality in the control tanks was about 2% in contrast to the 46 to 91% mortality experienced in tanks with alewives. The effects of predation by the alewives were evident early in the experiment because the mean daily capture of fry in traps set in each tank was always lower after day two in treatment tanks than in control tanks. Alewife consumption rates of lake trout fry ranged from 0.57 to 1.16 fry alewife^{-1} day^{-1} with a mean of 0.99 fry alewife^{-1} day^{-1} (SE = 0.141) and a median of 1.12 fry alewife^{-1} day^{-1}. The results of this study support the contention that predation by alewife could provide a high level of lake trout fry mortality, and thus affect natural recruitment of lake trout and the success of population rehabilitation.*

***INDEX WORDS:** Restoration, exotic, non-native, consumption, diet, prey, abundance, recruitment, food habits*

INTRODUCTION

Predation by the non-native alewife (*Alosa pseudoharengus*) may be an important source of mortality to the fry of lake trout (*Salvelinus namaycush*) and could seriously affect the natural recruitment of lake trout in the Great Lakes. In lakes Huron, Michigan, and Ontario where alewife have been abundant, programs underway for many years to rehabilitate lake trout populations have met with little success (Eshenroder et al. in review, Holey et al. in review, Elrod et al. in review). Part of the explanation for the lack of successful natural reproduction in these lakes may be mortality of fry through predation by alewife (Jones et al. in review). For example, in Lake Ontario the deposition of lake trout eggs and emergence of fry in large numbers has been documented from one intensively-studied spawning area (Perkins and Krueger in review), yet capture of naturally-produced young of year and older fish occurs rarely (Elrod et al. in review). In contrast, hatchery-reared, yearling lake trout appear to survive well after stocking to maturity (Elrod et al. in review), and thus blockage to natural recruitment seems to occur between the fry and yearling life stages. In the recent past, alewives have been a dominant species in Lake Ontario's fish community (e.g., O'Gorman et al. 1987, Jones et al. 1993) and suspected to control the recruitment of other native species such as yellow perch (*Perca flavescens*) through intensive predation on young (Brandt et al. et al. 1987). Recently, confirmation of the acceptability of lake trout fry as a food item for alewife has occurred in laboratory studies and lake trout fry have been found in the stomachs of a few alewives captured from Lake Ontario (Krueger et al. in review).

Lake trout fry likely would be most vulnerable to predation between the sac fry stage just after hatching through the start of the emergent free-swimming stage. Sac fry exhibit regular movement out of the substrate during night periods and return to stony substrate during day light periods (Krueger et al. in review). This life stage would provide some limited exposure to predation. As the yolk sac becomes absorbed, fry become free swimming and no longer negative phototaxic. Emergence and free-swimming behavior requires the inflation of the gas bladder most likely by swimming from the bottom to the surface to gulp air most likely at night (e.g., Lagler et al. 1963; Gustafson-Marjanen and Dowse 1983). Fry exhibiting this behavior could be exposed to predation for a considerable period of time as they are likely poor swimmers until their bladder is inflated and they are able to regulate their buoyancy. At Stony Island reef in Lake Ontario, alewives have been documented to congregate in May during the time period that lake trout fry emerge from the reef (Krueger et al. in review). Once fry become emergent and better swimmers, they should be better able to avoid predation by alewife.

Neither laboratory or field studies have provided evidence that predation by alewife on fry exhibiting natural behavior could actually affect fry abundance. Previous experimentation in a laboratory setting of predation confirmed that alewife would feed upon lake trout fry. Fry, sometimes partially immobilized, were introduced at the water surface of tanks under daylight conditions and alewives were recorded to readily and aggressively fed on the fry (Krueger et al. in review). The conditions used in this study did not permit the fry to exhibit the natural behavioral movement out of the substrate during darkness. Recent field studies in Lake Ontario confirmed that lake trout can eat fry in a wild setting. In 1993, six alewives were captured from Stony Island reef, Lake Ontario that contained 10 lake trout fry (Krueger et al. in review). However, no evidence was provided that alewives will regularly feed on lake trout fry or that predation intensity would be sufficient to affect the abundance of fry.

This study used a laboratory approach to determine the potential of alewife to affect lake trout fry abundance in reef areas through predation. The approach used alewives held in tanks that contained natural cobble substrate stocked with lake trout fry at densities similar to that observed at Stony Island reef, Lake Ontario and maintained under natural photoperiod. The null hypothesis was that the presence of alewives in tanks containing fry in cobble substrates would not affect fry abundance over a twelve day period. The time period used embraced the natural transition period between the sac and emergent life stages. The objectives of the study were to determine whether alewife could feed regularly upon lake trout fry that exhibited natural behavior (avoidance, swimming, etc.), to compare the survival rates of fry in the presence and absence of alewife, and to estimate the mean daily consumption rate of fry by alewife under simulated reef conditions of no fry replacement.

METHODS

Laboratory Reefs

Six identical, 1.22 m diameter circular fiberglass tanks with stones placed in their bottoms served as the laboratory reefs (1.17 m^2 surface area). The tanks were filled to 0.55 m depth and set up as flow through systems with complete replacement of water occurring every four hours. Water used in the test was drawn from Cayuga Lake at approximately 19 m depth, chlorinated by the Town of Ithaca, NY, and then dechlorinated and delivered to the tanks at the Resource Ecology and Management (REM) Facility at Cornell University. Water temperature in the reef tanks followed the natural variation exhibited in Cayuga Lake and was measured with a mercury thermometer. Temperature differences between tanks was important to monitor because large differences could vary the rate of development of the lake trout fry, and hence affect their vulnerability to predation. The entire bottom of each tank was first lined with a plastic grid mesh that was 1.0 cm high and contained 1.3 cm by 1.3 cm squares to provide additional interstitial spaces. Over the top of the grid in each tank was placed two layers of stone (86-99% cobble, <15% pebble, and <2% boulder by count; classification of Cummins 1962). The photoperiod was maintained by natural light entering through two windows on one wall. Natural light was supplemented by one 15 watt incandescent light bulb placed over each tank, timed to turn on one hour after sunrise and one hour before sunset each day.

Fish

Alewives were obtained in 1993 from Cayuga Lake by seine and from Lake Ontario by gillnet, placed into holding tanks at the REM Facility, and held overwinter. These fish were fed predominately brine shrimp (*Artemia* sp.) and supplemented with blood worm (*Tubifex* sp.). Over the fourteen day period prior to the experiment, lake trout fry were introduced occasionally to the surface of each tank and fry were eaten occasionally by the alewives. However, during this period the diet of the alewives remained predominately brine shrimp and bloodworm.

Lake trout fry used in this experiment were propagated from eyed embryos obtained from the U.S. Fish and Wildlife Service National Fish Hatchery at Warren, PA. The embryos were derived from gametes stripped from adult lake trout captured from Lake Erie and artificially fertilized. Embryos were incubated in 2.0-3.0 ° C water at the REM facility until hatch. Sac fry ("eleutheroembryo" of Balon 1980 or free embryos) were kept from contact with the water surface to prevent swim bladder inflation. Fry were held under the surface of the water in sealed mesh and PVC pipe cages until stocking into the reef tanks. Water temperature of the tanks with fry cages was 1.0-3.0 ° C until five days prior to the experiment when the temperature was slowly raised to approximately 10.0 ° C.

Experimentation

The experiment was conducted over a twelve day period from 2 June 1994 through 14 June 1994 with each of the six tanks stocked with an equal number of lake trout fry. The length of the time period used was based on earlier observations from

Stony Island reef in Lake Ontario where fry emergence appears to occur over a ten to 14 day period in mid to late May (Krueger et al. in review). Water temperatures in the tanks were measured daily. Four treatment tanks each contained 10 alewives and two control tanks contained none. Six days prior to the onset of the test, 10 alewives randomly chosen were placed into each of four tanks. Alewives in each tank were fed 40 g of brine shrimp every day of the experiment during daylight hours. The same amount of brine shrimp also was placed in the control tanks daily.

At the start of day one, 153 lake trout fry were distributed into the bottom of each of the six tanks. The number of fry stocked into the tanks was chosen to provide a density of 131 fry m^2 identical to that measured in the spring of 1993 at Stony Island reef, Lake Ontario (Perkins and Krueger in review). A pipette was used to transfer fry from their cages to the tanks. Fry were released just above the substrate to prevent immediate predation of fry by the alewife. Fry were distributed over the bottom throughout each of the tanks. Developmentally the fry used in this experiment were at a stage just before onset of emergence (end of $F^2$10 stage and at the start of the to alevin stage of Balon 1980). Fry stocked were from 23 to 26 mm TL (0.07-0.12 g wet weight).

Small fry traps were placed on the bottom of each tank and used to monitor the daily movement of fry upward out of the substrate. Traps were made from minnow traps that contained a 16.0 cm diameter funnel opening (0.020 m^2) to lead fish to the inside of the trap. On the first day of the experiment, one trap was placed in each tank with the funnel opening down on the substrate. Traps were checked daily and the number of fry was recorded by tank. Fry were removed from the traps and returned to the reef substrate.

After twelve days, alewives and lake trout fry were removed from each of the tanks. Total lengths and wet weights were collected from every fish recovered and recorded by tank. Fry were captured by a small dip net after partially draining each tank and removing and washing each stone and the plastic grid.

Statistical Analyses

Two sample t-tests were used to compare treatment versus control tanks for water temperatures, alewife lengths and weights, lake trout fry lengths, number of fry recovered at end of test period, and fry capture in traps (Snedecor and Cochran 1989). Null hypothesis used was that no difference occurred between treatment and control tanks. One-way ANOVA was used to compare lengths and weights of alewives among treatment tanks (Snedecor and Cochran 1989). A significance level of $P \leq 0.05$ was used to reject null hypotheses. Alewife consumption rates of fry were calculated by assuming the number of fry eaten in each tank was the difference between the average number recovered in the control tanks and the number recovered in a treatment tank. The number eaten was then divided by the number of alewives (10) and by the number of days (12) to determine consumption rate (fry alewife^{-1} day^{-1}).

RESULTS

Water Temperature

No difference in mean water temperatures occurred between treatment and control tanks ($P > 0.50$). Mean water temperature in the treatment tanks of 11.6° C was nearly identical to the 11.3° C observed in the control tanks. On any day, between tank differences were never greater than 0.3° C.

Alewife Survival

No alewife mortality was observed in any of the four treatment tanks. Alewives removed from the tanks at the end of the experiment ranged from 123 to 174 mm TL (12.2 to 33.2 g wet weight). No significant differences among the tanks occurred in alewife mean TL or wet weight (one-way ANOVA, $P > 0.60$).

Fry Behavior and Survival

The transition from sac to emergent fry was completed at the end of 12th day. Fry after stocking on the first day appeared photophobic, immediately sought shelter in the substrate, and were not visible in the tanks. At the end of the experiment, fry were observed free swimming throughout the water column in the control tanks. The fry that remained in the treatment tanks at the end of the test period were observed hovering in spaces between rocks on the bottom apparently avoiding the alewives in the water column.

Mean recovery of the 153 lake trout fry stocked per tank was much less in treatment tanks that contained alewife (31.5 fry per tank) than in control tanks (150 fry per tank) ($P < 0.009$). In one treatment tank, 82 fry were removed whereas in the other three tanks only 11, 16, and 17 fry were recovered. Mortality in the control tanks over the 12 day period was about 2% in contrast to the 46 to 91% mortality experienced in tanks with alewives. Whereas most predation of fry likely occurred at night and was not directly observable, alewife were observed to eat fry (rarely) during daylight hours.

Fry captured by traps in treatment tanks changed little or slightly declined whereas fry capture in control tanks increased over the 12 days (Fig. 1). Mean daily number of fry captured in treatment tanks was significantly less than the number captured in control tanks on days 3 and 5-12 ($P \geq 0.05$). Mean fry capture in traps by tank was correlated with the number of fry recovered in each tank ($r = 0.98$).

Mean total length of fry recovered from the treatment tanks (26.8 mm) was not different from fry in the control tanks (26.6 mm; $P > 0.25$). Mean total length of fry was significantly greater in both treatment and control tanks than fry at the start of the experiment (24.7 mm). Fry were observed to feed upon brine shrimp in the tanks.

Estimates of alewife consumption rates of lake trout fry ranged from 0.57 to 1.16 fry alewife^{-1} day^{-1} with a mean of 0.99 (SE = 0.141) and a median of 1.12 fry alewife^{-1} day^{-1}.

DISCUSSION

High levels of predation by alewife of lake trout fry occurred as inferred by the apparent high mortality that occurred in treatment reef tanks when compared to control tanks. The hypothesis that the presence of alewife would not affect fry density was rejected. Alewife appeared quite capable of regularly feeding on lake trout fry that inhabited stony substrates and exhibited natural behavior. Three of the tanks were similar in the number of fry recovered (11, 16, 17 fry) and thus appeared to withstand a similar predation effect by alewives. However, the number of fry recovered was greater in the fourth treatment tank than in the other treatment tanks (82 fry). One explanation for the difference observed is that the ten alewives in this tank simply fed less readily upon fry than those alewives in the other tanks. Large individual variation in willingness to feed upon lake trout fry has been observed among alewives (Krueger et al. in review). Some alewife will feed upon fry at every opportunity whereas other alewife never feed upon fry. Use of larger numbers of alewives in experiments such as these likely would reduce the effect of this source of variation.

The effects of predation by the alewives were evident early in the experiment because the number of fry captured by traps was always lower after day two in treatment tanks than in control tanks (Fig. 1). Hence, high levels of predation must have occurred over the first three days that the fry were exposed to predation by alewife. Behavior of the fry would have affected the risk from predation. Fry at time of stocking for this experiment would have exhibited either the behavior of sac fry or that of fry that were entering the free swimming stage (emergent fry or alevin stage). Pre-emergent sac fry exhibit diel movements out of rock substrate at night and have been readily captured 40 cm off the bottom (Krueger et al. in review). Fry of this life stage would offer some opportunity for predation to occur. Salmonid fry that are ready to become emergent will swim to the surface to fill their gas bladders with air (Lagler et al. 1962). We suspect that most fry used in this experiment were at this stage. Once the gas bladder is filled, fry become free swimming and capable of altering their buoyancy. Fry in our tanks that swam to the surface through the alewives would likely have been highly vulnerable to predation. Thus, fry in this experiment regardless of life stage should have been immediately vulnerable to predation the first days of the experiment.

Improved swimming capability of emergent fry over sac fry should have reduced the predation risk of the fry during the later part of the experiment. Substantial numbers of emergent fry were observed swimming above the substrate in control tanks by the fifth day. We suspect that the process of emergence was nearly completed by this time. Thus, vulnerability of the fry to predation by alewives was probably much reduced from this time forward in the experiment.

Alewife consumption rates of lake trout fry must be interpreted as estimates that were less than maximum. Fry as a prey item were not replaced as they were eaten and densities declined sharply over time. Fry not only became scarce but also likely less vulnerable due to completion of emergence during the later days of the experiment. Thus, the opportunity for alewife to consume fry markedly declined over time. In addition, alewife were fed during the day an alternative food source in the form of brine shrimp and thus may have been less inclined to feed upon fry. Variables that would also affect consumption rates estimates include substrate size and quantity and water depth.

Quality of cover for fry in terms of the type and size of rock substrate used to simulate reefs could affect the ability of fry to escape and avoid predation. In addition, greater depth of water over the simulated reefs than that used here (0.55 m) would have required fry to swim a greater distance from the bottom to reach the surface and could have increased vulnerability to predation, and hence consumption estimates.

Estimates of alewife consumption rates of lake trout fry in this study were lower than previous estimates for other lake trout fry predators but were not directly comparable. Slimy sculpins (*Cottus cognatus*) were estimated to consume approximately two lake trout fry day^{-1} sculpin^{-1} in experimental test chambers (Savino and Henry 1991). Burbot (*Lota lota*) were estimated to consume as many as 200-300 fry day^{-1} burbot^{-1} in small test chambers with one burbot (Savino and Henry 1991). In both tests, fry were in numbers in excess of what could be consumed by one predator and the predators used were not fed for 24 hours prior to the experiments. The predation rate by crayfish (*Orconectes virilis*) of lake trout fry in laboratory tanks has been estimated to be about 2 fry day^{-1} crayfish^{-1} (Savino and Miller 1991). In the crayfish studies, substrate size, size of test chamber, and starvation for 48 hrs all affected consumption rate estimates.

The results of this study support the contention that predation by alewife could provide a high level of lake trout fry mortality (up to 91%), and thus affect natural recruitment of lake trout and the success of population rehabilitation. If our consumption estimates are approximately correct and their levels are low relative to other predators, predation by alewife would not be precluded from causing high levels of fry mortality to occur. In the Great Lakes, low consumption rates per individual would be compensated by the past high abundance of alewives in lakes Huron, Michigan, and Ontario (e.g., O'Gorman et al. 1987), and thus could have caused high mortality of lake trout fry in some spawning areas. Simple models of alewife predation of fry, built upon plausible assumptions about prey densities, predator feeding rates, and duration of exposure of predator to prey, have predicted high levels of fry predation, in some cases close to 100% mortality (Jones et al. in review). Expectations for the success of population rehabilitation of lake trout should be tempered by the potential negative effects on fry survival caused by alewife.

ACKNOWLEDGMENTS

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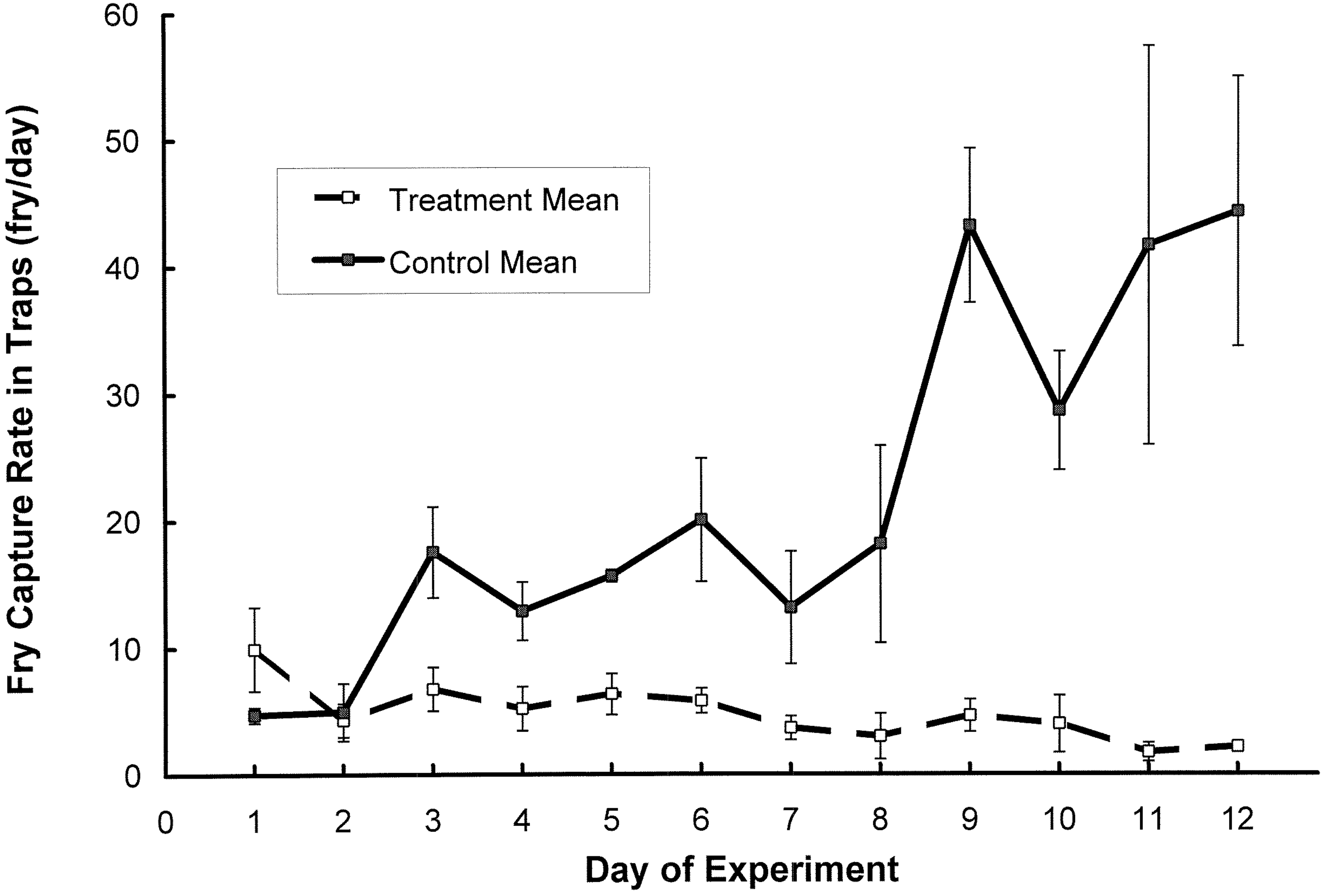
Figure Headings

Fig. 1. Mean number of lake trout fry captured per day in traps in treatment tanks (N = 4, dashed line) each with 10 alewives versus control tanks (N = 2, solid line) without alewives over a twelve day period. Vertical lines through data points represent one standard error of the mean.


Treatment Mean
Control Mean
Fry Capture Rate in Traps (fry/day)
60
50
40
30
20
10
0
0
1
2
3
4
5
6
7
8
9
10
11
12
Day of Experiment

Appendix 3

Field Data Taken At Stony Island Reef, Lake Ontario

During Spring 1994

Methods used to collect lake trout fry, alewives, and temperature/dissolved oxygen data follow those described on pages 10 - 14 in Appendix 1.

Appendix Table 1. Number of sac fry (S), sac fry/emergent (SE), and emergent (E) lake trout fry and adult alewives caught on and adjacent to, respectively, Stony Island Reef in the spring (22 April -9 June) of 1994. The total number of fish caught in gillnets is given with the alewife catch. Fry captured were electrophoretically analyzed and data were subjected to mixed stock analysis. Fry were estimated to be 80 % (SE=0.071) Seneca x Seneca strain parentage and 20% (SE=0.071) Killala/Superior x Seneca crosses. Strain contribution to the fry was estimated to be 89.8% from the Seneca strain and 10.2% from either the Killala or Superior strain.

	Fry Traps					**Gillnets**
Date	**#traps/days**	**S**	**SE**	**E**	**Total**	**#Alewives /Tot. # of fish**
29 April	61/7	93 (95%)	5 (5%)	0	98	0/6
4 May	61/5	179 (90%)	20 (10%)	0	199	2/5
13 May	61/9	258 (67%)	96 (25%)	31 (8%)	385	127/134
20 May	61/7	66 (12%)	197 (37%)	273 (51%)	536	1/4
24 May	60/4	6 (1%)	170 (37%)	280 (61%)	456	0/17
3 June	61/10	0	12 (5%)	221 (95%)	233	3/28
9 June	61/6	0	0	4 (100%)	4	22/38
Totals	60.9/48	602 (32%)	500 (26%)	808 (42%)	1911	155/232

Appendix Table 2. Stomach fullness and content description from fish caught in gillnets immediately adjacent to Stony Island reef in the spring (29 April - 9 June) of 1994. Stomaches were classified by volume as full (F), half-full (H), partially full (P), or empty (E). The food item classifications were: copepods and cladocerans (C & C); amphipods (*Gammarus* sp.; Amph.); chironomids (Chiro.); mollusc shell fragments (MSF); snail shell fragments (SSF); fish (non-lake trout; Fish); unidentified fish or amphibian eggs (Egg); isopods (Iso.); megaloptera (Meg.) and; unidentifiable contents (Unid.).

Species	**Total No. caught**	**Stomach Fullness (% of total volume)**				**Stomach Contents**		
		F	**H**	**P**	**E**	**Item - % Occurrence in Stomachs**		
Alewife	155	10.3	26.5	62.5	0.1	C & C - 98.1;	Chiro. - 8.4;	Amph. - 0.1;
						MSF - 0.1		
Trout-perch	56	3.6	3.6	12.5	80.4	Chiro. - 12.5;	Amph. - 7.1;	Fish - 1.8;
						MSF - 1.8;	Unid. - 1.8	
Spot-tail Shiner	10	10.0	50.0	30.0	10.0	MSF - 40.0;	Chiro. - 30.0;	SSF - 20.0;
						Iso. - 10.0;	Eggs - 10.0;	Meg. - 10.0
Rainbow Smelt	8	0.0	0.0	12.5	87.5	Unid. - 12.5		
Lake Chub	2	0.0	0.0	100.0	0.0	Chiro. - 50.0;	MSF - 50.0	
Yellow Perch	1	100.0	0.0	0.0	0.0	Amph. - 100.0;	Chiro. - 100.0	

Appendix Table 3. Water temperature, specific conductivity, and dissolved oxygen data from Stony Island Reef at 5 meters depth, from 10 November, 1993, to 17 June, 1994. Two DataSonde recorders (#1 & #2) were buried 20 cm in the substrate. The second recorder failed to record dissolved oxygen data.

Date	Time	Temperature		Specific Conductivity		Dissolved Oxygen	
		Temp #1	Temp #2	SpCond#1	SpCond#2	DO #1	DO #1
MMDDYY	HHMMSS	degC	degC	mS/cm	mS/cm	%Sat	mg/l
111093	115946	8.88	8.84	0.334	0.325	97.1	11.24
111193	115945	8.48	8.45	0.333	0.325	98.7	11.53
111293	115944	8.81	8.77	0.335	0.327	98	11.36
111393	115943	8.24	8.22	0.334	0.326	96.8	11.39
111493	115942	8.77	8.7	0.337	0.329	94.7	10.99
111593	115941	8.8	8.76	0.335	0.328	95.4	11.07
111693	115940	8.48	8.45	0.333	0.327	96.1	11.24
111793	115939	7.97	7.91	0.332	0.326	92.2	10.91
111893	115938	8.45	8.4	0.334	0.329	95.9	11.22
111993	115937	8.07	8.04	0.322	0.33	95.6	11.28
112093	115936	7.75	7.71	0.335	0.328	95.7	11.39
112193	115935	7.18	7.18	0.332	0.327	94.4	11.39
112293	115934	7.33	7.28	0.334	0.33	98.3	11.82
112393	115933	7.38	7.35	0.333	0.331	92.2	11.07
112493	115932	7.13	7.09	0.333	0.331	94.6	11.43
112593	115931	6.42	6.38	0.327	0.323	91	11.19
112693	115930	6.17	6.16	0.331	0.328	93.5	11.57
112793	115929	6.16	6.14	0.329	0.327	94.3	11.67
112893	115928	6.24	6.23	0.328	0.326	94.9	11.73
112993	115927	5.97	5.96	0.329	0.328	93.2	11.59
113093	115926	6.34	6.33	0.334	0.333	90.2	11.12
120193	115925	5.62	5.6	0.331	0.329	94.7	11.88
120293	115924	5.49	5.47	0.331	0.33	95.9	12.07
120393	115923	5.75	5.71	0.332	0.33	96.1	12.02
120493	115922	5.41	5.4	0.331	0.33	92.2	11.63
120593	115921	5.43	5.33	0.332	0.331	94	11.85
120693	115920	5.48	5.43	0.332	0.331	92.6	11.67
120793	115919	5.29	5.27	0.332	0.333	96.2	12.17
120893	115918	5.31	5.3	0.335	0.33	96.1	12.15
120993	115917	5.08	5.04	0.334	0.33	95.6	12.17
121093	115916	5.14	5.1	0.325	0.332	95.2	12.09
121193	115915	5.13	5.1	0.338	0.334	95.5	12.14
121293	115914	4.74	4.69	0.337	0.333	95.8	12.29
121393	115913	4.39	4.35	0.336	0.332	94	12.18
121493	115912	4.39	4.34	0.331	0.326	94	12.17
121593	115911	4.56	4.54	0.338	0.331	94.3	12.16
121693	115910	4.49	4.42	0.333	0.327	94.6	12.22
121793	115909	5.1	5.09	0.342	0.339	94.6	12.03
121893	115908	4.96	4.95	0.339	0.336	93.7	11.96
121993	115907	4.39	4.29	0.336	0.329	91.2	11.82
122093	115906	4.46	4.45	0.335	0.333	94.4	12.2
122193	115905	4.49	4.47	0.337	0.334	93.3	12.06

Appendix Table 3 continued.

Date	**Time**	**Temperature**		**Specific Conductivity**		**Dissolved Oxygen**	
		Temp #1	Temp #2	SpCond#1	SpCond#2	DO #1	DO #1
MMDDYY	HHMMSS	degC	degC	mS/cm	mS/cm	%Sat	mg/l
122293	115904	4	4	0.336	0.332	94.2	12.32
122393	115903	3.31	3.3	0.32	0.317	92.7	12.36
122493	115902	2.48	2.48	0.318	0.315	92.2	12.56
122593	115901	2.97	2.97	0.333	0.33	93.2	12.53
122693	115900	2.51	2.48	0.334	0.334	92.7	12.63
122793	115859	1.94	1.92	0.333	0.332	91.5	12.65
122893	115858	1.25	1.22	0.33	0.329	89.7	12.64
122993	115857	0.88	0.88	0.329	0.328	91	12.97
123093	115856	1.95	1.92	0.337	0.335	92.4	12.77
123193	115855	0.72	0.72	0.332	0.331	92.9	13.29
10194	115854	1.41	1.39	0.336	0.337	93.9	13.19
10294	115853	1.6	1.58	0.338	0.337	93.9	13.12
10394	115852	0.81	0.69	0.335	0.331	91.5	13.06
10494	115851	0.26	0.22	0.336	0.332	91.1	13.21
10594	115850	0.41	0.26	0.337	0.333	88.3	12.75
10694	115849	0.01	0.02	0.332	0.332	91.3	13.34
10794	115848	0.14	0.14	0.335	0.334	89.5	13.02
10894	115847	0.69	0.69	0.338	0.337	88.8	12.72
10994	115846	0.24	0.24	0.337	0.336	91.4	13.26
11094	115845	0.65	0.65	0.342	0.337	90.4	12.96
11194	115844	0.2	0.21	0.343	0.339	90.5	13.15
11294	115843	0.12	0.12	0.343	0.339	90.5	13.17
11394	115842	0.08	0.09	0.34	0.338	90.8	13.24
11494	115841	0.07	0.05	0.34	0.338	90.1	13.14
11594	115840	0.22	0.19	0.339	0.338	90.4	13.12
11694	115839	0.22	0.26	0.341	0.339	91.3	13.26
11794	115838	0.05	0.04	0.341	0.339	91.5	13.35
11894	115837	0.21	0.22	0.34	0.338	90.6	13.15
11994	115836	0.07	0.09	0.343	0.34	91.1	13.28
12094	115835	0.03	0.03	0.343	0.341	90.6	13.22
12194	115834	0.03	0.03	0.343	0.341	89.9	13.12
12294	115833	0.05	0.05	0.347	0.345	91.4	13.34
12394	115832	0.1	0.1	0.347	0.345	86.5	12.61
12494	115831	0.1	0.12	0.349	0.345	90.6	13.19
12594	115830	0.2	0.24	0.347	0.345	90.5	13.15
12694	115829	0.14	0.16	0.346	0.344	91.3	13.29
12794	115828	0.25	0.17	0.346	0.345	86.9	12.61
12894	115827	0.07	0.07	0.345	0.345	90.9	13.25
12994	115826	0.14	0.17	0.345	0.344	90.6	13.19
13094	115825	0.15	0.16	0.345	0.345	91.6	13.32
13194	115824	0.34	0.33	0.346	0.344	87.1	12.6
20194	115823	0.4	0.34	0.349	0.348	85	12.27
20294	115822	0.2	0.19	0.347	0.346	92	13.37
20394	115821	0.14	0.17	0.351	0.346	92.1	13.4
20494	115820	0.14	0.14	0.351	0.346	92.7	13.49

Appendix Table 3 continued.

Date	Time	Temperature		Specific Conductivity		Dissolved Oxygen	
		Temp #1	Temp #2	SpCond#1	SpCond#2	DO #1	DO #1
MMDDYY	HHMMSS	degC	degC	mS/cm	mS/cm	%Sat	mg/l
20594	115819	0.14	0.14	0.349	0.346	92	13.39
20694	115818	0.14	0.16	0.348	0.345	92.1	13.4
20794	115817	0.12	0.12	0.347	0.344	92.2	13.42
20894	115816	0.22	0.24	0.346	0.344	92.3	13.4
20994	115815	0.11	0.1	0.345	0.344	92.7	13.5
21094	115814	0.15	0.12	0.345	0.343	92	13.38
21194	115813	0.14	0.14	0.346	0.344	92.8	13.5
21294	115812	0.14	0.12	0.347	0.345	94.1	13.7
21394	115811	0.14	0.14	0.348	0.346	92.1	13.41
21494	115810	0.1	0.09	0.345	0.345	92.7	13.51
21594	115809	0.17	0.19	0.347	0.345	84.8	12.33
21694	115808	0.07	0.05	0.351	0.346	93.3	13.6
21794	115807	0.14	0.14	0.348	0.345	90.8	13.22
21894	115806	0.24	0.22	0.349	0.347	82.8	12.01
21994	115805	0.16	0.17	0.352	0.347	93	13.53
22094	115804	0.34	0.36	0.349	0.348	93.7	13.56
22194	115803	0.31	0.36	0.348	0.351	94.1	13.63
22294	115802	0.24	0.26	0.35	0.347	94.6	13.73
22394	115801	0.24	0.24	0.349	0.346	94.1	13.66
22494	115800	0.1	0.12	0.351	0.345	92.9	13.53
22594	115759	0.14	0.14	0.349	0.345	94.8	13.79
22694	115758	0.08	0.09	0.352	0.349	94.7	13.81
22794	115757	0.07	0.09	0.351	0.348	94.2	13.73
22894	115756	0.08	0.09	0.35	0.348	94.2	13.73
30194	115755	0.17	0.19	0.355	0.351	84.3	12.26
30294	115754	0.24	0.28	0.355	0.353	74	10.73
30394	115753	0.22	0.29	0.352	0.354	91.7	13.31
30494	115752	0.15	0.36	0.353	0.353	95.6	13.9
30594	115751	0.15	0.19	0.352	0.348	94.9	13.8
30694	115750	0.27	0.29	0.353	0.349	92.6	13.42
30794	115749	0.17	0.16	0.353	0.349	96.2	13.98
30894	115748	0.29	0.41	0.355	0.352	95.8	13.88
30994	115747	0.19	0.22	0.351	0.348	96.2	13.97
31094	115746	0.2	0.22	0.351	0.347	93.4	13.57
31194	115745	0.27	0.28	0.352	0.348	92.8	13.45
31294	115744	0.31	0.36	0.356	0.353	69	9.99
31394	115743	0.2	0.26	0.356	0.347	83.7	12.16
31494	115742	0.26	0.24	0.364	0.352	72.9	10.57
31594	115741	0.14	0.14	0.355	0.345	94.9	13.81
31694	115740	0.15	0.16	0.354	0.346	96.6	14.05
31794	115739	0.24	0.24	0.359	0.347	95.2	13.81
31894	115738	0.26	0.26	0.356	0.347	94.5	13.7
31994	115737	0.19	0.21	0.359	0.347	95.6	13.88
32094	115736	0.19	0.19	0.357	0.346	96.5	14.02
32194	115735	0.15	0.16	0.357	0.346	95.8	13.94

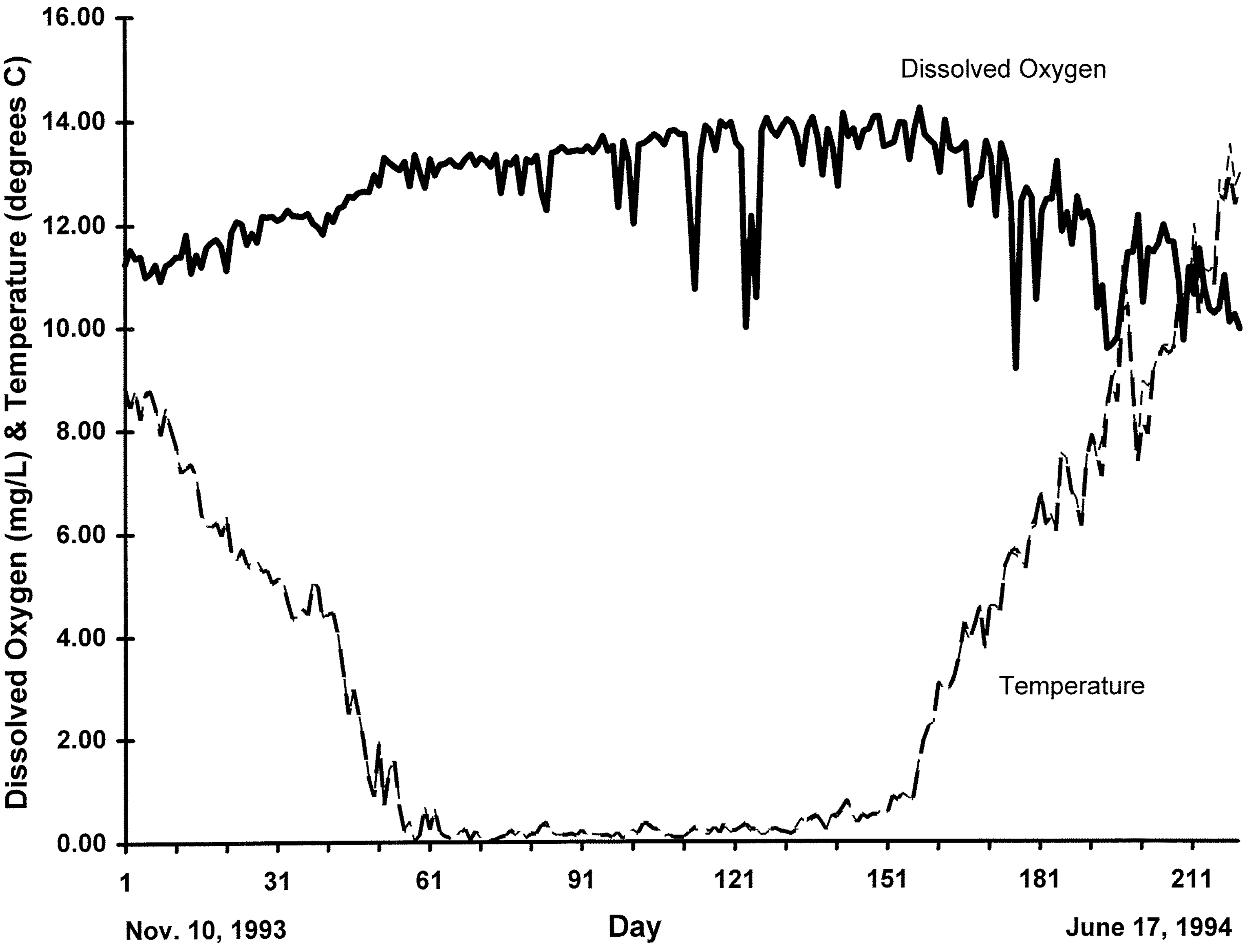
Appendix Table 3 continued.

Date	**Time**	**Temperature**		**Specific Conductivity**		**Dissolved Oxygen**	
		Temp #1	Temp #2	SpCond#1	SpCond#2	DO #1	DO #1
MMDDYY	HHMMSS	degC	degC	mS/cm	mS/cm	%Sat	mg/l
32294	115734	0.29	0.22	0.361	0.349	94.5	13.68
32394	115733	0.45	0.43	0.371	0.348	91.2	13.15
32494	115732	0.38	0.41	0.36	0.347	95.8	13.85
32594	115731	0.42	0.47	0.359	0.347	97.4	14.06
32694	115730	0.48	0.52	0.367	0.346	94.9	13.67
32794	115729	0.39	0.38	0.362	0.346	89.7	12.96
32894	115728	0.24	0.22	0.363	0.346	95.3	13.83
32994	115727	0.52	0.5	0.359	0.347	93.6	13.47
33094	115726	0.46	0.52	0.359	0.349	88.3	12.74
33194	115725	0.58	0.64	0.357	0.345	98.4	14.14
40194	115724	0.82	0.81	0.355	0.358	95.9	13.69
40294	115723	0.52	0.52	0.356	0.346	96.2	13.84
40394	115722	0.36	0.36	0.353	0.342	93.2	13.47
40494	115721	0.52	0.53	0.353	0.344	95.8	13.8
40594	115720	0.5	0.47	0.354	0.344	96.1	13.83
40694	115719	0.55	0.53	0.353	0.343	97.8	14.07
40794	115718	0.54	0.53	0.352	0.341	97.9	14.08
40894	115717	0.62	0.64	0.352	0.342	94	13.49
40994	115716	0.56	0.55	0.354	0.345	94.1	13.53
41094	115715	0.84	0.88	0.353	0.345	95.2	13.58
41194	115714	0.84	0.81	0.351	0.34	97.9	13.96
41294	115713	0.93	0.96	0.353	0.344	98	13.95
41394	115712	0.86	0.81	0.349	0.34	92.9	13.24
41494	115711	0.77	0.83	0.345	0.334	96.9	13.85
41594	115710	1.51	1.41	0.348	0.344	101.7	14.24
41694	115709	1.95	1.95	0.333	0.327	99.2	13.72
41794	115708	2.24	2.22	0.357	0.346	99.3	13.62
41894	115707	2.29	2.34	0.351	0.335	98.8	13.53
41994	115706	3.1	3.08	0.286	0.255	97.1	13.01
42094	115705	2.92	2.95	0.355	0.341	104.1	14.01
42194	115704	2.95	2.95	0.365	0.344	100.1	13.46
42294	115703	3.12	3.2	0.364	0.343	100	13.4
42394	115702	3.63	3.6	0.352	0.328	101.8	13.45
42494	115701	4.13	4.25	0.361	0.333	104.1	13.57
42594	115700	3.9	3.9	0.368	0.325	94.3	12.37
42694	115659	4.27	4.2	0.342	0.306	99.1	12.87
42794	115658	4.58	4.59	0.34	0.312	100.4	12.94
42894	115657	3.73	3.72	0.361	0.342	103.2	13.6
42994	115656	4.58	4.57	0.347	0.343	103.1	13.29
43094	115655	4.58	4.64	0.362	0.36	94.4	12.16
50194	115654	4.51	4.47	0.36	0.336	105	13.55
50294	115653	5.34	5.35	0.343	0.324	104.6	13.22
50394	115652	5.59	5.6	0.326	0.305	98.3	12.35
50494	115651	5.56	5.68	0.343	0.313	73.2	9.19
50594	115650	5.48	5.52	0.339	0.321	98.8	12.45

Appendix Table 3 continued.

Date	**Time**	**Temperature**		**Specific Conductivity**		**Dissolved Oxygen**	
		Temp #1	Temp #2	SpCond#1	SpCond#2	DO #1	DO #1
MMDDYY	HHMMSS	degC	degC	mS/cm	mS/cm	%Sat	mg/l
50694	115649	5.31	5.28	0.336	0.316	100.5	12.71
50794	115648	6.06	6.06	0.343	0.322	100.9	12.53
50894	115647	6.12	6.28	0.35	0.327	85	10.53
50994	115646	6.83	6.79	0.322	0.304	100.6	12.25
51094	115645	6.12	6.16	0.345	0.322	100.8	12.49
51194	115644	6.34	6.29	0.339	0.314	101.4	12.49
51294	115643	6.07	6.01	0.347	0.332	106.5	13.21
51394	115642	7.53	7.48	0.299	0.276	99.2	11.87
51494	115641	7.44	7.4	0.315	0.288	102	12.23
51594	115640	6.83	6.8	0.34	0.319	95.4	11.61
51694	115639	6.64	6.56	0.35	0.333	102.5	12.54
51794	115638	6.11	6.11	0.354	0.329	97.8	12.12
51894	115637	7.44	7.41	0.317	0.295	102.2	12.25
51994	115636	7.91	7.89	0.317	0.296	100.8	11.95
52094	115635	7.44	7.51	0.349	0.321	86.4	10.36
52194	115634	7.77	7.07	0.337	0.309	90.9	10.8
52294	115633	8.59	8.38	0.331	0.297	82.2	9.58
52394	115632	8.99	9.05	0.33	0.291	83.7	9.66
52494	115631	9.22	8.53	0.364	0.3	85.3	9.79
52594	115630	11.19	10.31	0.326	0.3	97	10.64
52694	115629	10.55	10.4	0.307	0.287	102.9	11.45
52794	115628	8.66	8.91	0.333	0.301	98.4	11.45
52894	115627	7.49	7.31	0.347	0.33	101.7	12.18
52994	115626	8.95	8.15	0.342	0.312	90.6	10.47
53094	115625	8.83	7.89	0.331	0.32	99.5	11.53
53194	115624	9.12	9.15	0.336	0.311	99.6	11.46
60194	115623	9.45	9.33	0.334	0.313	101.7	11.62
60294	115622	9.64	9.61	0.339	0.318	105.6	12
60394	115621	9.64	9.48	0.335	0.31	102.7	11.67
60494	115620	9.58	9.56	0.347	0.317	102.4	11.66
60594	115619	10.54	10.43	0.346	0.307	98.1	10.92
60694	115618	10.63	10.43	0.346	0.311	87.7	9.74
60794	115617	10.51	10.46	0.34	0.315	100.2	11.16
60894	115616	12.01	11.61	0.337	0.309	98.8	10.63
60994	115615	10.92	10.18	0.341	0.325	104.5	11.53
61094	115614	11.12	11	0.352	0.318	98	10.76
61194	115613	11.07	10.87	0.354	0.323	94.1	10.35
61294	115612	11.22	10.79	0.353	0.323	93.6	10.26
61394	115611	12.87	12.56	0.352	0.32	98.1	10.36
61494	115610	12.65	12.48	0.354	0.321	103.7	11
61594	115609	13.55	13.01	0.349	0.318	97	10.09
61694	115608	12.75	12.38	0.354	0.322	96.8	10.24
61794	115607	13.02	12.83	0.357	0.325	94.7	9.96

Appendix Figure 1. Dissolved oxygen (mg O^2/L) and temperature (^{o}C) in rock substrate at Stony Island reef, Lake Ontario November 10, 1993 through June 17, 1994.


Dissolved Oxygen
Temperature
Dissolved Oxygen (mg/L) & Temperature (degrees C)
16.00
14.00
12.00
10.00
8.00
6.00
4.00
2.00
0.00
1
31
61
91
121
151
181
211
Day
Nov. 10, 1993
June 17, 1994