J. Great Lakes Res. 28(3):421–436 Internat. Assoc. Great Lakes Res., 2002

# Sculpins and Crayfish in Lake Trout Spawning Areas in Lake Ontario: Estimates of Abundance and Egg Predation on Lake Trout Eggs

John D. Fitzsimons<sup>1,\*</sup>, David L. Perkins<sup>2</sup>, and Charles C. Krueger<sup>3</sup>

<sup>1</sup>Great Lakes Laboratory of Fisheries and Aquatic Sciences, Bayfield Institute P.O. Box 5050 867 Lakeshore Road Burlington, Ontario, Canada L7R 4A6

> <sup>2</sup>U.S. Fish and Wildlife Service 300 Westgate Center Drive Hadley, Massachusetts, USA 01035

<sup>3</sup>Great Lakes Fishery Commission 2100 Commonwealth Blvd. Ann Arbor, Michigan, USA 48105

ABSTRACT: Crayfish (Orconectes spp.) and sculpins (Cottus spp.) were collected at eight lake trout spawning reefs in Lake Ontario to assess abundance and potential to consume lake trout eggs. Abundance of crayfish ranged from a high of 9.5/m<sup>2</sup> in eastern Lake Ontario to 0/m<sup>2</sup> in western Lake Ontario where the absence or near absence at four reefs sampled was attributed to cold water upwelling. Sculpin abundance ranged from 4.2 to 50.1/m<sup>2</sup>. Mean daily egg consumption (eggs/stomach) for sculpins 50 to 75 mm in length, ranged from 0 to 0.9 but differences among reefs were not significant. At one reef, significantly more eggs (2.5 eggs/stomach) were consumed by large sculpins (> 75 mm) than by small (44-49 mm) sculpins (0.2 eggs/stomach). Estimated egg consumption (eggs/stomach/ $m^2$ ) for sculpins > 43 mm for the eight reefs for the period between estimated date of peak lake trout spawning and a standardized 30-d period post spawning, ranged from 0 to 496  $eggs/m^2$  consumed or from 0 to 54% of estimated egg abundance. No lake trout eggs were found in crayfish stomachs, because of their mode of feeding. Estimated egg consumption by crayfish was indirectly estimated from a relationship developed between carapace length and egg consumption using published literature and experimental work. Using this procedure, estimated egg consumption by crayfish for a standardized 30-d period after the date of peak spawning ranged from 0 to 65 eggs/m<sup>2</sup> consumed, or from 0 to 82% of potential egg abundance for the eight reefs. At low egg abundance (<  $100/m^2$ ), the density of crayfish and sculpin observed in Lake Ontario could result in sufficient egg consumption to cause almost 100% mortality of lake trout eggs. At higher egg abundance, however, mortality due to crayfish and sculpins appears to be relatively low. Deposition was sufficiently low at 5 of 8 sites to suggest the possible importance of sculpin and crayfish predation on lake trout recruitment failure in Lake Ontario.

**INDEX WORDS:** Lake trout, sculpins, crayfish, predation, Lake Ontario.

### **INTRODUCTION**

Restoration of lake trout (*Salvelinus namaycush*) in Lake Ontario has been underway since 1973 when stocking first began. Native stocks historically supported important sport and commercial fisheries although by 1960 these stocks were virtually extinct due in part to overfishing and sea lam-

\*Corresponding author. E-mail: fitzsimonsj@dfo-mpo.gc.ca

prey (*Petromyzon marinus*) predation (Christie 1973). Since 1973, over 30 million fingerling and yearling lake trout have been stocked in Lake Ontario. Between 1986 and 1999 an average of 1 to 2 million fish were stocked annually. Despite the relatively good survival of hatchery-reared yearlings when stocked in the lake (Elrod and Schneider 1992), and resulting high abundance of adults (Jones *et al.* 1993), the occurrence of naturally pro-

duced yearling and older fish remains extremely low (O'Gorman et al. 1998; R. O'Gorman, USGS, Oswego, NY, pers. comm.). Up until 1992, spatially and temporally extensive sampling had resulted in the capture of only seven lake trout that, based on morphological characteristics, appeared to have a high probability of being produced naturally (Casselman 1991). An additional forty-four 1-year-old naturally produced lake trout were collected between 1994 and 1998, but the proportion of naturally produced yearlings in 1995 remained below 10%. In addition, the actual proportion is misleading because fewer hatchery yearlings survive in the lake than in the past (J. Elrod, U.S. Geological Survey, Oswego, N.Y. pers. comm.). Collectively this information suggests that high mortality occurs during the interval between the time of egg deposition and the first year of life.

Several factors may contribute to the lack of natural recruitment of lake trout in Lake Ontario. They include low egg deposition rates (Fitzsimons 1995a, Perkins and Krueger 1995), low reproductive success of some strains (Marsden et al. 1988, Grewe et al. 1993, Perkins et al. 1995), high swimup stage mortality related to a thiamine deficiency (Fitzsimons 1995b, Fitzsimons et al. 1995, Fitzsimons and Brown 1998), and predation by alewife (Alosa pseudoharengus) on lake trout fry (Krueger et al. 1995). Egg predation by sculpins and crayfish may also limit natural recruitment of lake trout in Lake Ontario, although few data are available to judge their importance. A general model developed by Savino et al. (1999) to examine the effects of multiple predators on lake trout egg survival predicted that interstitial predators, like sculpins and crayfish, could account for much higher predation than either epibenthic predators or fry predators. Egg predation per sculpin has only been documented at two lake trout spawning reefs, both in Lake Superior (1.2 eggs/day, Stauffer and Wagner 1979; 1 to 2 eggs/day, Peck 1986; 0.5 eggs/day, Hudson et al. 1995). Laboratory studies have estimated in the absence of other food that sculpins can consume 1 to 2.5 egg/day (Savino and Henry 1991, Miller et al. 1992, Chotkowski and Marsden 1999) and that crayfish can consume 2 to 4 eggs/day (Horns and Magnuson 1981, Miller et al. 1992, Savino and Miller 1991). Whether these rates are representative of predation in the wild and can cause high mortality of lake trout eggs at Great Lakes spawning reefs is not clear. Assessing the effect of egg consumption by sculpins and crayfish relative to other sources of mortality requires the integration of egg consumption and abundance of predators with egg abundance (prey density).

Recent studies that estimated the abundance of lake trout eggs on eight reefs in Lake Ontario also provided an opportunity to assess predation effects by sculpins and crayfish that were collected at the same time (Fitzsimons 1995a, Perkins and Krueger 1995). This study presents data on abundance and egg consumption by sculpins and crayfish in relation to egg abundance as determined in the previous studies. The hypothesis tested is that egg consumption by these two predators has a significant effect on lake trout recruitment in Lake Ontario.

# **METHODS**

#### **Field Collections of Sculpins and Crayfish**

Mesh bags, buried in the substrate prior to lake trout spawning, were used to capture sculpins and crayfish at eight lake trout spawning reefs in Lake Ontario in 1991 to 1993 (Fig. 1). Water temperatures during the time that bags were in the substrate are shown in Figure 2. Bags were deployed generally over a month before spawning. This was intended to allow the abundance of predators in the bags to equilibrate with that of the surrounding habitat that was essentially identical to what was placed back in the bags at the time bags were buried by divers. Bags were retrieved in November and December, 1992, approximately 1 to 2 months after spawning (Table 1, Fitzsimons 1995a). Details on the date that nets were deployed and retrieved, the time period that nets were in place, before and after the date of peak spawning, and temperatures on the date peak lake trout spawning occurred and the nets were retrieved are given in Table 1. At Stony Island, bags were also retrieved in November and December 1990 and 1991 as well as April and mid-May after the 1991 and 1992 spawning season (Perkins and Krueger 1995). Sampling design, mesh bag construction, burial, and retrieval and details of estimates of lake trout egg abundance are described in Fitzsimons (1995a) and Perkins and Krueger (1994, 1995). At the time of bag retrieval, sculpins and crayfish were removed and preserved in 10% formalin, within 24 hours after bags were retrieved from the substrate. Total length (mm), weight (gm wet weight), sex, mouth gape (mm), and species were determined for sculpins at all locations except for Stony Island where only total length was recorded. Mouth gape and total length was measured for an additional 40



FIG. 1. Map of Lake Ontario showing locations of eight lake trout spawning reefs sampled in 1990 to 1992.

sculpins captured in trawls at two other Lake Ontario locations (Port Dalhousie and Cobourg) to more accurately determine the relationship between size and mouth gape. Mouth gape was used as an indication of the potential to consume lake trout eggs. Stomach contents were removed and examined for evidence of lake trout eggs, fish, or invertebrates. Invertebrates were identified to family but only assessed for occurrence. Crayfish were identified to species and sex. They were measured for total and carapace length (mm), and weight (gm), except those at Stony Island where only total length was recorded. Stomachs were examined for evidence of lake trout eggs and other food items. Abundance of crayfish and sculpins at each site was calculated as the mean number of individuals/m<sup>2</sup> based on the sum of the number caught in the bags divided by the surface area of the bag opening divided by the total number of bags retrieved.

# **Sculpin Egg Consumption**

The number of whole lake trout eggs, including chorions, in individual sculpin stomachs was assumed to represent those eaten within the last 24 hours and thus represented daily consumption. For large (100 to 125 mm) slimy sculpins (Cottus cognatus) fed rainbow trout (Oncorhynchus mykiss) eggs, 67% of the eggs were recognisable after 24 hours at an average temperature of 8°C (J. Savino, U.S. Geological Survey, Ann Arbor, MI, personal communication). The nets were held at approximately 5°C prior to sorting so most eggs, including chorions, would still be recognizable. Mean daily consumption (eggs/fish/day) was calculated at each site for three size categories of sculpins (44 to 49, 50 to 75, and > 75 mm) as egg consumption is size dependent (Miller et al. 1992). Consumption was then multiplied by sculpin abundance (no./m<sup>2</sup>) in each size category to determine daily size-specific



FIG. 2. Mean daily temperature recorded by temperature loggers buried at seven Lake Ontario lake trout spawning sites during the fall of 1992 (PW-Port Weller, FP-Fifty Point, SC-Stoney Creek, BP-Burlington Pier, SI-Simcoe Island, GI-Galloo Island, SB-Snowshoe Bay).

consumption. By summing across the three size categories, total daily egg consumption for all sculpins present (eggs consumed/m<sup>2</sup>/day) was determined. To estimate egg consumption (no./m<sup>2</sup>) that occurred between spawning and the time of bag retrieval, the total daily egg consumption was multiplied by the number of days elapsed between the estimated date of peak spawning (Fitzsimons 1995a) (Table 1) and when bags were removed from the substrate. It was assumed that both the predator density and their egg consumption of eggs were constant over this period. Peak spawning was estimated by back calculating from the temperature record, the date on which each egg of a 50 egg sample would have had to have been fertilized and hence spawned, to reach its embryonic stage (Balon 1980) at retrieval and then using the spawning date of the dominant embryonic stage as the peak spawning date. Because the interval between estimated peak spawning date and the date when nets were retrieved varied from site to site from 15 to 44 days, a standardized 30-d period was also used to facilitate comparison among sites.

### **Crayfish Egg Consumption**

Direct estimation of lake trout egg consumption from crayfish stomach contents was not possible because crayfish, especially small ones, macerate their food and no eggs were found in stomachs. Instead, egg consumption was indirectly estimated using data from Miller et al. (1992) and laboratory studies conducted in this study that sought to determine the minimum size of crayfish capable of consuming lake trout eggs. Nine crayfish (Orconectes propinguus) captured in Lake Ontario (carapace length 4 to 33 mm) were held individually for 5 days in a partitioned raceway (3 m  $\times$  0.3 m) at 7°C without any cover, and with a 12 h light:12 h dark photoperiod. The only food given to the crayfish was five lake trout eggs provided at the beginning of each trial. Two trials were conducted in succession over a 10-d period. Consumption rates were

substrate	Date Set	Date Retrieved	Total days in sibstrate (Days after spawning)	Temperature at peak spawning (°C)	Temperature at bag retrieval (°C)
Port Weller	2-Oct-92	27-Nov-92	56 (42)	10.8	5.3
Fifty Point	6-Oct-92	16-Nov-92	41 (22)	6.6	6.2
Stoney Creek	7-Oct-92	17-Nov-92	41 (22)	6.6	6.4
Burlington	6-Oct-92	4-Dec-92	59 (48)	10.8	4.9
Simcoe Island	29-Sep-92	9-Dec-92	71 (29)	8.3	6.7
Galloo Island	30-Sep-92	2-Dec-92	63 (29)	8.4	7.3
Snowshoe Bay	1-Oct-92	1-Dec-92	61 (28)	8.0	6.3
Stony Island	15-Sep-90	30-Nov-90	75 (15)	8.0	6.0
Stony Island	15-Sep-91	10-Dec-91	86 (25)	8.0	6.0
Stony Island	15-Sep-91	10-Apr-92	177	_	_
Stony Island	15-Sep-91	15-May-92	212	_	_
Stony Island	15-Sep-92	4-Dec-92	80 (19)	8.0	6.0
Stony Island	15-Sep-92	23-Apr-93	190	_	
Stony Island	15-Sep-92	14-May-93	211		

TABLE 1. Details of mesh bag deployment and retrieval and temperatures for eight Lake Ontario lake trout spawning reefs sampled 1990-1993. Temperature data for Stony Island are approximate.

based on the average of the two trials and expressed as the number of eggs consumed/day. Data from these studies were combined with those of Miller et al. (1992), and using linear regression we determined the relationship between crayfish size (carapace length) and daily egg consumption rate. Only data for crayfish that were feeding in Miller et al. (1992) were used. The regression equation was used to estimate daily egg consumption for each crayfish caught and these estimates were summed to determine estimated daily egg consumption for each site (no. consumed/m<sup>2</sup>/day). Total egg consumption was estimated by multiplying the egg consumption per day times the number of days between the calculated date of peak lake trout spawning and when bags were removed from the substrate. As this period varied from site to site a standardised 30-d period was also used to facilitate comparison among sites. Because only measurements of total length (mm) (TL) were available for crayfish from Stony Island, these were converted to carapace length (mm) (CL) by the relationship:

$$CL = 0.50 \text{ TL} - 0.06, F_{[1,62 \text{ df}]} = 1220.3,$$
$$p < 0.0001, r^2 = 0.95 \tag{1}$$

prior to calculating daily egg consumption rate.

# **Total Egg Abundance**

Potential total egg abundance (no./m<sup>2</sup>) was calculated by adding the estimated egg consumption by sculpins and crayfish to the egg abundance measured by Fitzsimons (1995a) or Perkins and Krueger (1995). This procedure assumes that the total number of eggs present in bags at the time of egg deposition was the sum of eggs found at the time of bag retrieval plus eggs consumed by sculpins and crayfish over the period from the date of peak spawning to the date when bags were removed from the substrate. It also assumes that sculpin and crayfish densities in the bags were the same as outside the bags. As above, data were also calculated for a 30-d period to facilitate comparisons among sites.

### **Statistical Analysis**

Site-to-site variation was assessed with one-way ANOVA and means were compared by Newman-Keuls multiple range test. Linear regression models were used to assess linear relationships between variables. All statistical tests were made at the  $p \le 0.05$  level. All statistical tests were done using RS/1 (Bolt Baraneck and Newman Inc.) software.

# Fitzsimons et al.

TABLE 2.	Sculpin and crayfish abundance (no./m <sup>2</sup> ), sex ratio, length, and weight (mean (standard	error
of the mean	n)/N) at eight Lake Ontario lake trout spawning reefs sampled 1990–1993. Sample size (1	N) for
sculpin and	l crayfish abundance refers to the number of mesh bags used. Sample sizes followed l	by the
same letter	and case are not significantly different from means in the same column with the same	letter
and case.		

Location	Date Mesh Bags Retrieved (Depth (m))	Abundance (no./m <sup>2</sup> ) [Sex ratio (M:F)]	Sculpin Length (mm)	Sculpin Weight (gm)	Crayfish Abundance (no./m <sup>2</sup> ) [Sex ratio (M:F)]	Crayfish Total Length (mm)	Crayfish Carapace Length (mm)	Crayfish Weight (gm)
Port Weller	26 Nov. 1992 (4.6)	9.1(1.7) 52b [0.4:0.6]	50.4(2.3) 32cb	2.4(0.5)1 32bc	0.3(0.3) 52b	41.0 1	21.0 1	2.8 1
Fifty Point	16 Nov. 1992 (8.7)	5.3(1.1) 59b [0.4:0.6]	52.1(4.8) 21cb	3.5(0.9) 21ac	0			
Stoney Creek	17 Nov. 1992 (10.8)	6.2(1.1) 46b [0.1:0.9]	58.9(4.3) 16b	3.9(0.8) 16ac	0			
Burlington Pier	4 Dec. 1992 (6.3)	50.1(7.2) 3a [0.8:0.2]	71.3(7.2) 4a	6.4(1.8) 4a	0			
Simcoe Island	9 Dec. 1992 (5.0)	7.2(1.0) 60b [0.3:0.7]	50.9(1.2) 30cb	2.0(0.2) 30bc	4.1(0.9) 60b [0.2:0.8]	39.1(0.9) 16b	19.3(0.5) 16	2.2(0.2) 16b
Galloo Island	2 Dec. 1992 (7.2)	6.7(1.0) 60b [0.2:0.8]	48.0(0.7) 27c	1.8(0.1) 27bc	9.5(1.3) 60a [0.6:0.4]	36.3(1.3) 38b	18.1(0.7) 38	2.2(0.2) 38b
Snowshoe Bay	1 Dec. 1992 (2.2)	11.9(3.4) 48b [0.1:0.9]	53.8(1.1) 33cb	3.0(0.2) 33bc	2.7(0.8) 48b [0:1.0]	48.8(0.7) 9b	23.7(0.3) 9	4.0(0.2) 9a
Stony Island	30 Nov. 1990 (4.0)	17.6(2.7) 27B	49.5(1.0) 38A		3.3(1.3) 27A	44.7(2.1) 7		
Stony Island	10 Dec. 1991 (4.0)	6.3(1.6) 30A	54.1(2.1) 15B		6.6(1.6) 30A	47.4(1.7) 16		
Stony Island	10 Apr. 1992 (4.0)	4.2(1.4) 30A	50.9(1.7) 11		4.6(1.3) 30A	43.3(3.8) 10		
Stony Island	15 May 1992 (4.0)	4.2(1.3) 30B	52.2(1.7) 10		5.4(1.4) 30A	34.3(3.3) 14		
Stony Island	4 Dec. 1992 (4.0)	39.0 (4.8) 17aB	52.1(0.8) 52cb,B		5.1(1.9) 17bA	50.7(7.8) 7a		
Stony Island	23 Apr. 1993 (4.0)	9.7 (2.8) 18A	56.0(3.8) 14		4.2(1.4) 18A	36.8(7.1) 6		
Stony Island	14 May 1993 (4.0)	8.8 (2.1) 17A	60.3(5.3) 12		5.1 (1.9) 17A	41.7(7.0) 7		

426

			Mean a	bundance (no	o./m <sup>2</sup> )	
Location	Year	< 44 mm	>43  mm	44–49 mm	50–75 mm	>75 mm
Port Weller	1992	3.4	7.8	4.1	2.7	1.0
Fifty Point	1992	1.5	4.5	1.5	1.0	1.0
Stoney Creek	1992	0.6	4.1	0.3	2.8	1.0
Burlington	1992	0	49.8	0	35.8	14.0
Simcoe Island	1992	0.2	6.9	3.3	3.6	0
Galloo Island	1992	0.7	5.8	2.9	2.9	0
Snowshoe Bay	1992	0.3	9.6	2.4	7.2	0
Stony Island	1990	1.9	15.7	7.4	8.3	0
Stony Island	1991	0	6.3	2.1	4.2	0
Stony Island	1992	0.7	37.5	8.8	28.7	0
-						

TABLE 3. Mean abundance  $(no/m^2)$  of sculpins by size class at eight lake trout spawning reefs in Lake Ontario sampled during the fall of 1990 to 1992.

#### RESULTS

#### **Sculpins - Abundance and Size**

Abundance of sculpins (*Cottus* spp.) in the bags during the fall of 1992 ranged from 4.2 to 50.1 individuals/m<sup>2</sup> for the eight reefs (Table 2) and these tended to be of intermediate size (Table 3). Amongreef variation in sculpin abundance (SA) in 1992 was not correlated with the number of days or degree-days that bags were in the substrate, wind fetch, reef size, or water depth but was related to mean lake trout egg abundance (EA) by the relationship:

$$SA = 6.7 + 0.01 \text{ EA}, F_{[1,6 \text{ df}]} = 66.24,$$
  
p = 0.0002, r<sup>2</sup> = 0.92 (2)

At Stony Island, however, neither the number of sculpins/bag ( $\geq$  50 mm) (F<sub>[1,49 df]</sub> = 0.06, p = 0.815, r<sup>2</sup> = 0.001) or the number of eggs/stomach (F<sub>[1,34 df]</sub> = 1.03, p = 0.317, r<sup>2</sup> = 0.03) were related to the number of eggs/bag during the fall of 1990 to 1992.

There was significant year-to-year variation in sculpin abundance during the fall (1990 to 1992) but not during the spring (1992 and 1993) at Stony Island. Sculpin abundance in December 1992 at this site was significantly higher than in either April or May of 1993 (p < 0.05).

Mean length (48.0 to 71.3 mm) and weight (1.8 to 6.4 gm) of sculpins, showed site-to-site variation during 1992 (Table 2). At Stony Island, sculpins collected during the fall of 1990 were significantly shorter (p < 0.05) than those collected during the fall of 1991 or 1992 although no differences in

lengths during the spring were evident for sculpins collected in 1992 and 1993 for either April or May.

#### **Sculpins - Diet**

Sculpins consumed lake trout eggs at all sites sampled in 1992, except Burlington Pier and Snowshoe Bay. Eggs per stomach ranged from 0 to 0.9 for sculpins > 43 mm in length, the shortest sculpin sampled that had consumed an egg (Table 4). The relationship between mouth gape (mm) ( $5.8 \pm 0.2$ ; range 2.2 to 11.3 mm) (GAPE) and total length (mm) ( $63.6 \pm 1.6$ ; range 36.3 to 116.6 mm) (TL) was:

$$GAPE = 0.10TL - 0.71, F_{[1,141 df]} = 624.7,$$
  
p = 0.0001, r<sup>2</sup> = 0.82 (3)

Egg consumption by sculpins appeared to be size dependent but the limited size range at individual sites prevented a thorough assessment of the effect of sculpin size. At Port Weller, the only site that had a large range in sculpin size, egg consumption increased with sculpin size (p < 0.05) (Table 4). Overall egg consumption for sculpins collected during the fall of 1992 was weakly related to length for all sculpins ( $F_{[1,161 df]} = 22.4$ , p < 0.001, r<sup>2</sup> = 0.12) and for those that had eaten eggs ( $F_{[1,20 df]} = 5.31$ , p = 0.032,  $r^2 = 0.21$ ), but overall length explained a relatively small proportion of the variation in egg consumption. Egg consumption rates were similar among the eight sites, based on sculpins 50 to 75 mm in length, a size range that bracketed the mean size of sculpins at most sites.

Sculpin gut contents contained amphipods and

			Mean no.	/stomach	
Location	Year	44–49 mm	50–75 mm	> 75 mm	> 43 mm
Port Weller	1992	0.2(0.2) 12	0.9(0.5) 8	2.5(1.5) 2	0.6(0.3) 22
Fifty Point	1992	0.3(0.2) 6	0.5(0.3) 4	0.8(0.8) 5	0.5(0.3) 15
Stoney Creek	1992	1.0(0) 1	0.9(0.4) 9	1.0(1.0) 4	0.9(0.3) 14
Burlington	1992		0 2	0 2	0 4
Simcoe Island	1992	0 14	0.1(0.1) 15		0.03(0.03) 29
Galloo Island	1992	0 12	0.3(0.3) 12		0.2(0.1) 24
Snowshoe Bay	1992	0 8	0 24		0 32
Stony Island	1990	0 16	0.5(0.2) 18		0.3(0.1) 34
Stony Island	1991	0 5	0.9(0.4) 10		0.6(0.3) 15
Stony Island	1992	0 12	0.6(0.1) 40		0.4(0.1) 52

TABLE 4. Mean number of lake trout eggs/stomach (mean (standard error of the mean)/N) by size category for sculpins collected at eight lake trout spawning reefs in Lake Ontario, 1990 to 1992.

isopods in addition to lake trout eggs (Table 5). Amphipods occurred more frequently in eastern, than western Lake Ontario. Isopods were more common in sculpins from western than eastern Lake Ontario (Table 5). Other items such as sphaerid clams, snails, and chironomids were also eaten by sculpins at western Lake Ontario sites. Few stomachs were empty and those that were empty were from western Lake Ontario. At Stony Island, the only site where spring collections were made, no lake trout fry were found in sculpins collected during the spring of 1992 or 1993.

# Crayfish - Abundance, Size, and Diet

Crayfish abundance ranged from 2.7 to 9.5 individuals/m<sup>2</sup> in eastern Lake Ontario, but crayfish were nearly absent from the four western Lake On-

tario sites (Table 2). Variation in abundance among sites was unrelated to substrate size, water depth, wind fetch, lake trout egg abundance or the number of days that bags were in the substrate. At Stony Island, crayfish abundance did not differ either among the falls of 1990 to 1992 or between the spring of 1992 and1993, or between spring and fall in 1992.

Crayfish collected during the fall of 1992 were similar in length regardless of location with the exception of Stony Island where crayfish were significantly larger (Table 2). Crayfish were significantly heavier at Snowshoe Bay than at Simcoe or Galloo Islands during this same time period. No recognizable lake trout eggs or other food items were found in the gut of any crayfish collected.

Based on laboratory observations of egg con-

TABLE 5.	Occurrence	of amphip	ods, iso	pods,
other items	(sphaerid class	ms, snails,	chirono	mids)
and empty s	tomachs for s	culpins fro	m seven	Lake
Ontario lake	e trout spawni	ng reefs in	1992.	

	Per	cent of all	l sculpins	
Site	Amphipods	Isopods	Other	Empty
Port Weller (N = 32)	9.4	34.4	9.4	9.0
Fifty Point (N = 21)	14.3	19.0	14.3	9.0
Stoney Creek (N = 16)	0	37.5	12.5	4.0
Burlington (N = 4)	66.7	0	25.0	1.0
Simcoe Island (N = 30)	28.0	3.3	0	0
Galloo Island (N = 30)	92.6	3.7	0	0
Snowshoe Bay (N = 33)	90.9	9.0	0	0

sumption by nine crayfish and the data of Miller *et al.* (1992), the  $\log_{10}$  of the number of eggs consumed per day (CC) was related to carapace length (mm) (CL) as follows:

$$CC = 0.009CL - 0.09, F_{[1,21 df]} = 82.0,$$
  
p < 0.0001, r<sup>2</sup> = 0.80. (4)

# Estimated Egg Consumption by Sculpins and Crayfish

Estimated daily egg consumption at the eight sites by all sculpins > 43 mm averaged 3.6 and ranged from 0 to 17 eggs/m<sup>2</sup>/day (Table 6). Based on these values, egg consumption for the period that nets were in the substrate after the estimated date of peak spawning was from 0 to 314 eggs/m<sup>2</sup> and averaged 89.1. For a standardized 30-d postspawning period, egg consumption was from 0 to 496 eggs/m<sup>2</sup> and averaged 109.4. Based on estimated egg abundance (the sum of the measured egg abundance and potential egg consumption by sculpins), in 1992 the proportion potentially lost to sculpin predation during a standardized 30-d period would represent from 0 to 54% (Table 6) with a mean of 23%. For crayfish, calculated total daily egg consumption ranged from 0 to 2 eggs/m<sup>2</sup>/day, for the eight sites (Table 7). Potential egg consumption for the period that nets were in the substrate after the estimated date of peak spawning ranged from 0 to 54 eggs/m<sup>2</sup> and averaged 20.6. For a standardized 30-day period egg consumption was from 0 to 65 eggs/m<sup>2</sup> and averaged 25.7. Based on potential egg abundance (the sum of the measured egg abundance and potential egg consumption by crayfish) the proportion potentially lost to crayfish predation would represent from 0 to 82% with a mean of 22% for a standardized 30-d period (Table 7).

When predation by sculpins and crayfish on lake trout eggs was combined, consumption represented from 0 to 82% of potential egg abundance or on average 40%, for a 30-d period in 1992 (Table 8). In 1992, potential consumption by both predators combined as a proportion of eggs collected in bags was negatively related ( $F_{[1,6 df]} = 8.6$ , p = 0.03,  $r^2 = 0.59$ ) with measured egg deposition; at sites with high deposition predators potentially consumed a lower proportion of this deposition. Nevertheless daily consumption that same year was positively related ( $F_{[1,5 df]} = 53.2$ , p = .0008,  $r^2 = 0.91$ ) to egg abundance if the data for Burlington, where no crayfish were collected and no sculpin contained eggs, were not included.

#### DISCUSSION

Sculpin abundance  $(5.3 \text{ to } 50.1/\text{m}^2)$  at the Lake Ontario sites was not unusually high, being similar to abundances reported for other large lakes where passive sampling gear was used. For example, at a small man-made reef in Lake Superior, the estimated sculpin abundance using pails buried in the substrate was 13 individuals/m<sup>2</sup> (Peck 1986). The estimates obtained in this study were also similar to those calculated from egg baskets buried in the substrate of Lake Simcoe (3 to 14/m<sup>2</sup>, Hindley 1984). Conversely, the estimates of sculpin abundance were much higher than estimates from visual counts made by divers in southwestern  $(0.1/m^2, Janssen$ and Quinn 1985) and southeastern (2/m<sup>2</sup>, Rutecki et al. 1985) Lake Michigan and Lake Huron (5/m<sup>2</sup>, Emery 1970). Given the cryptozoic nature of sculpins, these lower densities suggest that sculpins hide from divers such that abundance estimates made by divers are not comparable to estimates made from buried sampling gears.

Crayfish abundance in eastern Lake Ontario ranged from 2.7 to 9.5 individuals/m<sup>2</sup> and was

ght lake trout spawning reefs in Lake Ontario sampled 1990 to 1992 ( <sup>a</sup> SEC-	<sup>2</sup> abundance (no./m <sup>2</sup> ) and egg consumption rate (eggs/stomach) for each size	calculated date of peak spawning to date mesh bags removed from the sub-	and the potential egg consumption).
lake trout spawning reefs in La	undance (no./m <sup>2</sup> ) and egg consu	culated date of peak spawning t	<i>d the potential egg consumption)</i>
nsumption by sculpins at eight	calculated as the product of ab	ggg consumption days from cal	he measured egg abundance an
ABLE 6. Estimated egg co.	ze specific egg consumption	ttegory from Table 4; <sup>b</sup> CD-e	rate; <sup>c</sup> based on the sum of th

Location	Year	Daily SEC <sup>a</sup> (44–49 mm) (no./m <sup>2</sup> )	Daily SEC (50-75 mm) (no./m <sup>2</sup> )	Daily SEC (> 75 mm) (no./m <sup>2</sup> )	Daily SEC (> 43 mm) (no./m <sup>2</sup> )	Egg CD <sup>b</sup>	Estimated total egg consumption for CD (no./m <sup>2</sup> ) [for 30-d]	Measured egg (no./m <sup>2</sup> )	Estimated total egg abundance (no./m <sup>2</sup> ) [for 30-d]	Potential consumed as a % of estimated total egg abundance for CD [for 30-d]
Port Weller	1992	0.8	2.4	1.7	4.9	44	216 [147]	1,422	1,638 [1,569]	13.2 [9.4]
Fifty Point	1992	0.4	0.5	1.0	1.9	22	42 [57]	52	94 [109]	44.7 [52.3]
Stoney Creek	1992	0.3	2.5	1.2	4.0	32	128 [120]	103	231 [223]	55.4 [53.8]
Burlington	1992	0	0	0	0	41	0	6,178	6,178 [6,178]	0
Simcoe Island	1992	0	0.2	0	0.2	29	6 [6]	64	70 [70]	8.6 [8.6]
Galloo Island	1992	0	1.0	0	1.0	29	29 [30]	30	59 [60]	49.2 [50.0]
Snowshoe Bay	1992	0	0	0	0	28	0	Q	6 [6]	0
Stony Island	1990	0	4.2	0	4.2	15	63 [126]	069	753 [816]	16.7 [15.4]
Stony Island	1991	0	3.7	0	3.7	25	93 [112]	3,197	3,290 [3,309]	2.8 [3.4]
Stony Island	1992	0	16.5	0	16.5	19	314 [496]	3,205	3,519 $[3,701]$	8.9 [13.4]

# 430

# Fitzsimons et al.

Location	Year	Estimated daily egg consumption (no./m <sup>2</sup> )	Egg CD <sup>b</sup>	Estimated total egg consumption for CD (no./m <sup>2</sup> ) [for 30-d]	Measured egg abundance (no./m <sup>2</sup> )	Estimated total egg abundance (no./m <sup>2</sup> ) [for 30-d]	Potential consumed as a % of estimated total egg abundance for CD [for 30-d]
Port Weller	1992	0.07	44	3 [2]	1,422	1,425 [1,424]	< 1 [< 1]
Fifty Point	1992	0	22	0 [0]	52	52 [52]	0 [0]
Stoney Creek	1992	0	32	0 [0]	103	103 [103]	0 [0]
Burlington	1992	0	41	0 [0]	6,178	6,178 [6,178]	0 [0]
Simcoe Island	1992	0.81	29	23 [24]	64	87 [88]	26 [27]
Galloo Island	1992	1.69	29	49 [51]	30	79 [81]	62 [63]
Snowshoe Bay	1992	0.88	28	25 [27]	6	31 [31]	81 [82]
Stony Island	1990	0.93	15	14 [28]	690	704 [718]	2 [4]
Stony Island	1991	2.16	25	54 [65]	3,197	3,251 [3,262]	2 [2]
Stony Island	1992	2.02	19	38 [60]	3,205	3,243 [3,265]	1 [2]

TABLE 7. Estimated egg consumption by crayfish at eight lake trout spawning reefs in Lake Ontario sampled in 1990 to 1992.

abased on the sum of potential consumption by all crayfish using the relationship log (no. of eggs consumed/day + 1) = .009 carapace length(mm) - .091.

<sup>b</sup>CD—consumption days, based on the no. of days between peak spawning and the when nets were removed from the substrate.

<sup>c</sup>based on the sum of the measured egg abundance and the potential egg consumption.

somewhat lower than that previously reported for Lake Ontario and other large lakes. Gannon *et al.* (1985) reported maximum abundance at two reefs in eastern Lake Ontario that ranged from 6 to 30/m<sup>-2</sup> based on samples collected with a dome suction sampler. Similarly average crayfish abundance in Lake Simcoe, estimated with egg baskets, ranged from 8 to 22/m<sup>2</sup> (Hindley 1984). The estimates of crayfish abundance tended, like those of sculpins, to be somewhat higher than those (2.2 to 4.0/m<sup>2</sup>) calculated from estimates made by divers in Lake Michigan (Janssen and Quinn 1985, Rutecki *et al.* 1985).

The marked difference in crayfish abundance observed between western and eastern Lake Ontario has been reported by others and may relate to thermal stress from upwelling of cold water in the west basin. Gannon *et al.* (1985) caught no crayfish at three reefs in western Lake Ontario but found them to be abundant at two reefs in eastern Lake Ontario. Cold-water upwelling is common along the north shore of western and central Lake Ontario (Arajs and Farooqui 1974), and the south shore of western Lake Ontario (Mortimer 1980, Gannon *et al.* 1985). In Lake Ontario, upwelling has been associated with temperature drops of up to 14°C over a 48hour period (Haffner *et al.* 1984). Rapid changes in temperature associated with upwelling can be lethal to crayfish. Crayfish mortality was observed after a sudden decrease in temperature from 18.7 to 7°C

#### Fitzsimons et al.

<u> </u>	3	00				
Site	Measured egg abundance (no./m <sup>2</sup> )	Estimated egg consumption for 30-d by sculpins (no./m <sup>2</sup> )	Estimated egg consumption for 30-d by crayfish (no./m <sup>2</sup> )	Overall potential egg abundance (no./m <sup>2</sup> )	Potential consumed as % of overall estimated egg abundance for 30-d	Daily consumption rate by all predators (no./m <sup>2</sup> d <sup>1</sup> )
Port Weller	1,422	147	2	1,571	10	5.0
Fifty Point	52	57	0	109	52	1.9
Stony Creek	103	120	0	223	54	4.0
Burlington	6,178	0	0	6,178	0	0
Simcoe Island	64	6	24	94	32	1.0
Galloo Island	30	30	51	111	73	2.7
Snowshoe	6	0	27	33	82	0.9
Stony Island	3,205	496	60	3,761	15	18.5

TABLE 8. Individual and combined estimated egg consumption for a 30-d period by sculpins and crayfish as a proportion of overall estimated egg abundance.

associated with an internal seiche in Georgian Bay (Emery 1970). The absence of crayfish on nearshore boulder substrates between the Niagara River and Brighton on the northcentral shore of Lake Ontario (Barton 1986), where upwelling occurs frequently, is consistent with the explanation that upwelling of cold water limited crayfish abundance in the collections. In eastern Lake Ontario where upwelling is infrequent, crayfish are abundant.

Lake trout egg consumption by sculpins, even at sites with high egg abundance, such as at Stony Island and Port Weller (0.3 to 0.6 and 0.6 eggs/stomach/day), was lower than the mean (1.0 to 2.5) estimated from laboratory studies (Savino and Henry 1991, Miller et al. 1992, Chotkowski and Marsden 1999). The absence of eggs in any of the sculpins collected at Burlington and Snowshoe Bay may be anomalous because of the small area and associated smaller sampling size. The difference between the observations and laboratory studies is unlikely attributable to temperature. Chotkowski and Marsden (1999) could not find a temperature effect on lake trout egg consumption by mottled sculpins (Cottus bairdi) over a range in water temperature from 4.5 to 14°C. The difference, however, may be the result of the rate of food passage in the

gut (Hershey and MacDonald 1985) and an ability to recognize eggs, although samples were preserved within a 24-h period and well within the reported gut passage time with at most an underestimate of 33% because of egg digestion. In addition, the effect of substrate (Biga *et al.* 1998, Chotkowski and Marsden 1999) and alternate sources of food (Savino and Henry 1991) may have also affected egg consumption in the sculpins that were collected. This disparity emphasizes the need to establish predation rates under natural conditions. Higher consumption rates were observed for larger (> 75 mm) than smaller sculpins in this study but the abundance of large sculpins based on the collections was generally low.

Egg consumption by sculpins tended to occur at a smaller size than would have been predicted by mouth gape with sculpins as small as 43 mm containing eggs. Using the relationship developed between sculpin mouth gape and length, and the smallest mean egg diameter of 5.5 mm that was observed at Stony Creek (Fitzsimons 1995a), it was predicted that only sculpins  $\geq 62$  mm in length would have been able to consume eggs. This ability of sculpins to eat eggs at smaller sizes than predicted was consistent with observations by Chotkowski and Marsden (1999) who found an egg in a 42 mm sculpin. The presence of yolk debris when small sculpins ate eggs in their study suggests that small sculpins may break eggs during ingestion such that mouth gape is not a good predictor of the potential to consume eggs.

Sculpin abundance at the eight reefs was correlated with egg abundance, although at Stony Island neither the number of sculpins per bag or the number of eggs per sculpin were related to the number of eggs in a bag. Hence, the relationship between sculpin and egg abundance observed may represent a similarity in the habitat used for spawning and that used by sculpins. However, it is possible that high egg abundance may attract an increased number of sculpins, although Dittman *et al.* (1998) noted that the use of chemoreception by slimy sculpins to detect salmon eggs was limited to a short period immediately after eggs were spawned.

Sculpins could cause a serious increase in total mortality at spawning reefs where lake trout egg abundance is low. At an egg abundance of 100 eggs/m<sup>2</sup> or less, such as was found at many natural spawning areas in the Great Lakes (Fitzsimons 1996), sculpin densities and size distributions similar to those observed in this study could result in 100% egg mortality. This is consistent with the modeling results of Savino et al. (1999). Conversely, at higher egg abundance such as occurs at artificial spawning areas in the Great Lakes (Fitzsimons 1996), a much smaller proportion of the mortality due to predators would be expected which is again consistent with what was predicted by Savino et al. (1999). Although it is not clear whether there is a critical egg to predator ratio, at one artificial reef in Lake Superior, where significant natural recruitment of lake trout occurs, average egg abundance was 290/m<sup>2</sup> and average sculpin abundance was 13/m<sup>2</sup> (Peck 1986).

The potential for crayfish to seriously contribute to lake trout egg mortality at the reefs in eastern Lake Ontario remains unclear. Because crayfish masticate eggs, calculation of *in situ* consumption was not possible. In the absence of direct evidence of egg consumption by crayfish, laboratory studies alone were used but these estimates probably represent the maximum potential for egg predation. Estimated egg consumption in the laboratory for sculpins was several-fold higher than that estimated from stomach contents from the wild and similar overestimation of egg consumption by crayfish would be expected. Laboratory studies have indicated that egg consumption rates by crayfish can be affected by substrate size (Horns and Magnuson 1981, Savino and Miller 1991), water temperature (Horns and Magnuson 1981), and the presence of sculpins (Miller *et al.* 1992) which all could be important. With these caveats, the data indicated, as with sculpins, that at low egg abundance ( $< 100/m^2$ ) mortality due to egg consumption by crayfish could potentially result in almost complete egg mortality. Similarly, at higher egg deposition rates, mortality caused by crayfish may be relatively low.

Although uncertainty exists as to the importance of egg mortality by crayfish predation in eastern Lake Ontario, this was not the case for western Lake Ontario. As virtually no crayfish occurred at the four western Lake Ontario sites, mortality due to crayfish at these locations had to be near zero. Moreover, based on the reported absence of crayfish on boulder substrates from the Niagara River to Brighton (Barton 1986), egg mortality due to crayfish appears low for a large part of Lake Ontario.

The fall period that was sampled probably represents the period of maximum predation on lake trout eggs because of the temporal nature of egg deposition, access to eggs by predators, and activity of predators. Immediately after spawning there is a high initial availability of eggs before they settle deep into the interstitial spaces where predators may have trouble accessing them (see Biga *et al.* 1998). Eggs can be dislodged from the substrate in large numbers at this time (Marsden and Krueger 1991) which could lead to high egg consumption, although these eggs may be lost to other sources of mortality anyway such as physical shock (Fitzsimons 1994). The higher proportion of empty stomachs in sculpins from western Lake Ontario where temperatures were generally colder, compared to eastern Lake Ontario sites, suggests either reduced food intake at these colder temperatures or difficulty in finding eggs in the interstitial spaces. Fitzsimons (1995) noted that spawning occurred earlier and, on average, collection nets remained in the substrate longer in western Lake Ontario. Consumption of lake trout eggs by crayfish at temperatures below 2.5°C was found to drop to zero (Horns and Magnuson 1981) while Van Vliet (1964) reported that predation by sculpins decreased greatly below 3°C, although the effects of declining temperature on egg consumption by sculpins are not known. Temperature at the time of net retrieval ranged from approximately 5 to 7°C.

Work by Stauffer and Wagner (1979) suggested that while predation pressure on lake trout eggs by most fish in the Great Lakes is generally low, consumption by sculpins tends to be the highest of the species examined. For several lake trout spawning reefs in Lakes Superior and Michigan, Stauffer and Wagner (1979) reported less than 0.1 egg/stomach in lake trout, longnose suckers (Catostomus catostomus), lake chubs (Couesius plumbeus), white suckers (Catostomus commersoni), and lake whitefish (Coregonus clupeaformis). Consumption by sculpins that averaged 1.2 eggs/stomach was slightly higher than round whitefish (Prosopium cylindracem) that contained 1 egg/stomach but considerably less than for burbot (Lota lota) (29 eggs/stomach). Egg consumption by burbot, however, was only observed in 2 out of the 5 years sampled. Moreover, the high consumption rates for these 2 years may have been atypical. Because of their size, burbot probably cannot readily feed on eggs within the interstitial spaces of cobble substrates, where eggs would normally incubate. They could, however, easily consume drifting eggs or eggs sitting on bare rock or sand. Indeed, immediately after Stauffer and Wagner (1979) seeded reefs with lake trout eggs, average egg consumption rates for lake trout, round whitefish, and longnose sucker of 515, 44, and 16 eggs/stomach were well above rates observed for naturally deposited eggs. Similarly Fitzsimons (1990) reported exceptionally high lake trout egg consumption by yellow perch (Perca flavescens) in Keuka Lake that he thought was related to spawning over non-protective substrate, an observation similar to that made by Hacker (1956), Prevost (1956), and DeRoche (1969) for other predators.

In summary, egg consumption by sculpins could be a significant source of mortality at some Lake Ontario reefs where egg abundance is low (<  $100/m^2$ ). In contrast, the apparent absence of crayfish from much of western Lake Ontario likely means that egg predation by cravfish is relatively unimportant at many spawning areas. In eastern Lake Ontario, however, crayfish could be a major mortality factor when lake trout egg abundance is low (<  $100/m^2$ ). Where egg abundance was high, such as occurred at Burlington and Port Weller in western Lake Ontario and Stony Island in eastern Lake Ontario, mortality due to egg predation by sculpins and crayfish would be relatively unimportant. However, only three of the eight sites examined had high egg abundance. In conclusion, at some sites predation could be significant suggesting a possible lake-wide impact on recovery of lake trout in Lake Ontario, but more definitive statements are not possible until a greater proportion of the active spawning reefs in Lake Ontario have been assessed.

# ACKNOWLEDGMENTS

The authors would like to thank Bill Williston for his efforts in the field and laboratory, and Cliff Schneider and the crew of the *Seth Green* for their assistance with the field work. We would also like to thank the Department of the Environment dive team in Burlington (H. Don, B. Gray, K. Hill, and M. Dahl) for their assistance with field work. We are indebted to Murray Johnson, John Leslie, Jacqueline Savino, and one anonymous reviwer for their constructive reviews of earlier drafts.

#### REFERENCES

- Arajs, A.A., and Farooqui, R. 1974. Nearshore currents and water temperatures along the north shore of Lake Ontario between Pickering and Cobourg. In *Proc. 17th Conf. Great Lakes Res.*, pp. 348–357. Internat. Assoc. Great Lakes Res.
- 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
- Barton, D.R. 1986. Nearshore benthic invertebrates of the Ontario waters of Lake Ontario. *J. Great Lakes Res.* 12:270–280.
- 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.
- Casselman, J.M. 1991. Research Project: Lake trout rehabilitation studies. In *Lake Ontario Fisheries Unit*, 1990 Annual Report, LOA 91.1 (Chapter 24), pp. 1–12. Ontario Ministry of Natural Resources.
- 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.
- Christie, W.J. 1973. A review of the changes in the fish species composition of Lake Ontario. Great Lakes Fishery Commission Tech. Report No. 23:1–65.
- DeRoche, S.E. 1969. Observations on the spawning habits and early life of lake trout. *Prog. Fish-Cult.* 31:109–113.
- 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.
- Elrod, J.H., and Schneider, C.P. 1992. Effect of stocking season and technique on survival of lake trout in Lake Ontario. *North Am. J. Fish. Manage*. 12:131–138.
- Emery, A.R. 1970. Fish and crayfish mortalities due to

an internal seiche in Georgian Bay, Lake Huron. J. Fish. Res. Board Can. 27:1165–1168.

- Fitzsimons, J.D. 1990. Yellow perch predation on lake trout eggs in Keuka Lake, New York. J. Great Lakes Res. 16:130–132.
- . 1994. Survival of lake trout (*Salvelinus namay-cush*) embryos after receiving physical shock. *Prog. Fish-Cult.* 56:149–151.
- \_\_\_\_\_. 1995b. The effect of B-vitamins on swim-up syndrome in Lake Ontario lake trout. *J. Great Lakes Res.* 21 (Supplement 1):286–289.
- \_\_\_\_\_. 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 (Supplement 1):142–151.
- \_\_\_\_\_, and Brown, S.B. 1998. Reduced egg thiamine levels in inland and Great Lakes lake trout and their relationship with diet. In *Early life stage mortality syndrome in fishes of the Great Lakes and Baltic Sea*, ed. G. McDonald, J.D. Fitzsimons, and D.C. Honeyfield, pp. 160–171. American Fisheries Society, Symposium 21, Bethesda, Maryland.
- ———, Huestis, S., and Williston, B. 1995. Occurrence of a swim-up syndrome in Lake Ontario lake trout and the effects of cultural practices and contaminants. *J. Great Lakes Res.* 21(Supplement 21):277–285.
- Gannon, G.E., Danhey, R.J., Anderson, J.W., Merritt, G., and Bader, A.P. 1985. The ecology of natural shores in Lake Ontario and their importance to artificial reef development. In *Artificial Reefs: Marine and Fresh Water Applications*, ed. F.M. D'Itri. pp. 113–139. Chelsea: Lewis Publishers Inc.
- Grewe, P.M., Krueger, C.C., Marsden, J.E., Aquadro, C.F., and May, B. 1993. Hatchery origins of naturally produced lake trout fry captured in Lake Ontario: temporal and spatial variability based on allozyme and mitochondrial DNA data. *Trans. Am. Fish. Soc.* 123: 309–320.
- Hacker, V.A. 1956. Biology and management of lake trout in Green Lake, Wisconsin. *Trans. Am. Fish. Soc.* 86:71–83.
- Haffner, G.D., Yallop, M.L., Hebert, P.D.N, and Griffiths, M. 1984. Ecological significance of upwelling events in Lake Ontario. J. Great Lakes Res. 10:28–37.
- 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.
- Hindley, B.A. 1984. Lake trout and lake whitefish egg survival in Lake Simcoe. MSc. thesis. York University, Downsview, Ontario.
- 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.

- 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.
- Janssen, J., and Quinn, J. 1985. Biota of the naturally rocky area of south-western Lake Michigan with emphasis on potential fish prey. In *Artificial Reefs: Marine and Fresh Water Applications*, ed. F.M. D'Itri, pp. 432–432. Chelsea: Lewis Publishers Inc.
- Jones, M.L., Koonce, J.F., and O'Gorman, R. 1993. Sustainability of hatchery-dependent salmonine fisheries in Lake Ontario: the conflict between predator demand and prey supply. *Trans. Am. Fish. Soc.* 122: 1002–1018.
- Krueger, C.C., Perkins, D.L, 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.
- Marsden, J.E., and Krueger, C.C. 1991. Spawning by hatchery-origin lake trout (*Salvelinus namaycush*) in Lake Ontario: data from egg collections, substrate analysis, and diver observations. *Can. J. Fish. Aquat. Sci.* 48:2377–2384.
- \_\_\_\_\_, Krueger, C.C., and Schneider, C.P. 1988. Evidence of natural reproduction by stocked lake trout in Lake Ontario. *J. Great Lakes Res.* 14:3–8.
- 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.
- Mortimer, C.H. 1980. Inertial motion and related internal waves in Lake Michigan and Lake Ontario as responses to impulsive wind stresses. I. Introduction, descriptive narrative, and graphical archive of IFYGL data. Univ. Wisconsin-Milwaukee, Center for Great Lakes Studies, Spec. Rept. No. 37.
- O'Gorman, R., Elrod, J.H., and Schneider, C.P. 1998. Reproductive potential and fecundity of lake trout strains in southern and eastern waters of Lake Ontario, 1977–1994. J. Great Lakes Res. 24:131–144.
- 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.. 1994. Design and use of mesh bags to estimate egg deposition and embryo survival in cobble substrate. N. Am. J. Fish. Manage. 14:866–869.
- \_\_\_\_\_, 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.
- \_\_\_\_\_, Fitzsimons, J.D., Marsden, J.E., Krueger, C.C., and May, B. 1995. Differences in reproduction among hatchery strains of lake trout at eight spawning areas in Lake Ontario:Genetic evidence from mixed-stock

analysis. J. Great Lakes Res. 21(Supplement 1):364-374.

- Prevost, G. 1956. Use of artificial and natural spawning beds by lake trout. *Trans. Am. Fish. Soc.* 86:258–260.
- Rutecki, T.L., Dorr III, J.A., and Jude, D.J. 1985. Preliminary analysis of colonization and succession of selected algae, invertebrates, and fish on two artificial reefs in inshore southeastern Lake Michigan. In Artificial Reefs: Marine and Freshwater Applications. ed. F.M. D'Itri, pp. 459–489. Chelsea: Lewis Publishers Inc.
- 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.
- , and Miller, J.E. 1991. Crayfish (Orconectes virilis) feeding on young lake trout (Salvelinus

namaycush): effect of rock size. J. Fresh. Ecol. 6: 161–170.

- \_\_\_\_\_, 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.
- Stauffer, T.M., and Wagner, W.C. 1979. Fish predation on lake trout eggs and fry in the Great Lakes, 1973–1978. Michigan Dept. of Natural Resources-Fisheries Division. Fisheries Research Report No. 1864.
- Van Vliet, W.H. 1964. An ecological study of *Cottus cognatus* Richardson in northern Saskatchewan. M.S. thesis. University of Saskatchewan, Canada.

Submitted: 10 June 2000 Accepted: 9 May 2002 Editorial handling: Donald A. Jackson