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Walleye egg deposition and survival on reefs in Western Lake Erie (USA)

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Variation in egg survival has been suspected to be a major source of walleye (*Stizostedion vitreum*) recruitment variability in Lake Erie. We sampled walleye eggs and larvae in western Lake Erie in 1994–95. Densities of eggs and larvae were higher in 1994 than 1995. Egg survival for depths and reefs pooled averaged 37% in 1994 and 13% in 1995. We found white perch (*Morone americana*) to consume large numbers of walleye eggs on reefs in 1995. Mean density of larvae from the date of first hatch through the end of May was 14 times higher in 1994 than 1995. Relatively slow water warming rates and frequent intense winds contributed to the low density and survival of eggs on reefs in 1995 by prolonging incubation periods and increasing the vulnerability of eggs to predation and severe wind events.

1. Introduction

Lake Erie walleye (*Stizostedion vitreum*) populations exhibit wide fluctuations in recruitment (Hatch *et al.* 1987). Interannual variation in the abundance and first year survival of walleye cohorts is considered a major source of recruitment variability for many walleye populations (Carlander & Payne 1977, Koonce *et al.* 1977, Ney 1978, Forney 1980). Many naturally spawning walleye populations experience high levels of mortality during the egg stage (Priegel 1970, Forney 1976, 1980). Observed egg survival rates range from 0.00003 in Spirit Lake, Iowa (Jennings 1969) to 0.357 in Lake Winnibigoshish, Minnesota (Johnson 1961). Substantial egg mortality is thought to be caused by dislodging from severe wind and wave action and temperature reversals during spawning and incubation periods (Johnson 1961, Busch *et al.* 1975, Koonce *et al.* 1977, Forney 1980, Serns 1982). Walleye egg survival has been directly

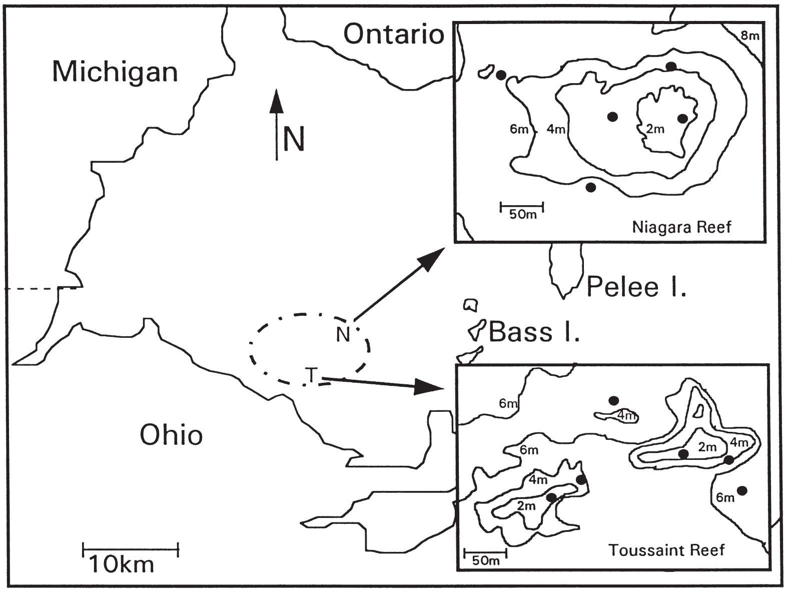

Fig. 1. Western basin of Lake Erie and reefs examined in this study. Dotted ellipse circumcises reef complex. Letter codes show locations of reefs. Filled circles identify egg sampling sites.

related to fluctuations in water temperature during incubation periods (Johnson 1961, Allbaugh & Manz 1964, Hurley 1972, Serns 1982), with optimal egg survival occurring when water temperatures increase from 5°C at a rate of 1°C/day (Smith & Koenst 1975). Incubation periods are lengthened when water warms more slowly thereby increasing vulnerability to severe wind events and predation (Carlander *et al.* 1960, Hartman 1969, Wolfert *et al.* 1975).

Research investigating walleye egg deposition on western Lake Erie reefs conducted from 1960–70 revealed that walleye spawning usually peaks during the third week of April when water temperatures range from 5.4 to 8.3°C (Baker & Manz 1971). Walleye spawning and egg density were higher at depths < 5 m where hard substrates persist which walleyes actively spawned over. No relationship was observed between egg deposition, viability, and year class strength, but a direct relationship between walleye year-class strength and water temperatures was observed (Busch *et al.* 1975) with the strength of the incoming year-class being inversely proportional to incubation time (Baker & Manz 1971, Busch *et al.* 1975).

In this study we investigated walleye egg deposition and survival across a range of depths on Toussaint and Niagara reefs in western Lake Erie in 1994 and 1995. While we do not believe that Lake Erie walleye year-class strength is determined exclusively in the egg stage, this life stage does present tremendous potential to introduce interannual variability in survival which can influence the abundance of larvae entering the system (Dahlberg 1979, Houde 1987). The purpose of this study was to identify factors limiting walleye egg survival on reefs in western Lake Erie and see how egg density and survival translate into larval abundance.

2. Methods

2.1. Study area description

Toussaint and Niagara reefs are the largest reefs among a large bedrock reef complex located in the western basin of Lake Erie (Fig. 1). This complex of reefs encompasses over 70 km^2 of surface area and extends to within 1.5 m of the surface. The surfaces of the reefs have numerous crevices and cavities as well as a varied substrate composition ranging from silt to boulders and exposed bedrock. The relative shallowness of the reefs allows their surface to be scoured by ice movements as well as wind-generated wave and current action. The lake bottom surrounding the reefs has low relief at depths from 7 to 10 m and is covered with silt and mud (Hartley 1961, Herdendorf & Braidech 1970, Bolsenga & Herdendorf 1993).

2.2. Egg collection

We sampled walleye eggs during 1994 and 1995 on Toussaint and Niagara reefs beginning in late March continuing through to mid-May when spawning ceased and catches of walleye eggs were negligible. We used a 39-kg iron sled (Stauffer

1981) attached to a diaphragm pump at the surface by a flexible hose 5 cm in diameter for egg collections. At each site, the sled was towed for 2 min at 0.5 m/s. Egg sampling was stratified by depth to examine egg deposition density; depths of < 3 m, 3–5 m, and 5–7 m were sampled (Fig. 1). These depth strata encompass the range of depths where walleye eggs were collected in previous studies (Baker & Manz 1971). Three samples were taken at each depth on each sampling day. We located sample sites by global positioning system coordinates and marked them with an anchored buoy.

Eggs and benthic debris (Dreissenid mussels and shells, sand, benthic organisms) were deposited from the pump apparatus into a 0.5 m^3 basket lined with 0.5 mm square mesh netting. The net liner containing the sample was then removed and placed in a labeled plastic bag. Samples were refrigerated at 5°C until they could be sorted at the laboratory which typically took from 2.5 to 24 hours. We found no indication that delays in processing of up to 24 hours influenced viability or survival estimates.

At the laboratory, samples were rinsed through a galvanized steel wire screen (6 mm bar mesh) to separate large debris from finer particles and eggs. The small particulate matter was then examined for walleye eggs which were counted entirely or subsampled. A single subsample was taken when there appeared to be more than 1 000 eggs in the total sample. Subsamples were typically 10% of the mass of the drained fine particulate matter. Identification of eggs was based on egg diameter (mm), egg color, and subsequent hatching of eggs. We found 3 sizes of eggs on the reefs during this study; 3 mm, 2 mm and 1.5 mm. Several eggs of each size category were placed in aquaria with aerated lake water and incubated at 15°C. Hatched larvae were identified according to Auer (1982). Collected eggs were examined with 10× magnification for viability and measured (nearest 0.1 mm) before being preserved in Stockards solution (Galat 1972). All eggs that were ruptured or showed signs of opaqueness or fungal growth were classified as dead eggs. All clear or eyed eggs were classified as viable eggs.

Walleye eggs were classified by developmental stage (Nelson 1968, McElman & Balon 1979) using a compound microscope with variable magnification. Stage 1 eggs are pre-organogenesis stage (28 thermal units (TU); a thermal unit is each degree C above a daily base temperature of 0°C; Allbaugh & Manz 1964) and stage 3 eggs are late embryonic stage with developed eyes, pectoral fin buds, and caudal mesenchyme rays as well as chromatophores along the ventral line and yolk sac (> 97 TU). Stage 2 eggs show intermediate development. Hatching normally occurs when at least 115 TU's have accumulated (Nelson 1968, Hurley 1972, McElman & Balon 1979). Egg survival (s) was estimated as:

$$s = (\text{No. stage 3 on day } x)/(\text{No. stage 1 on day 0})$$

Day x was a function of the temperature dependent development rate. We pooled egg survival data from all depths on each reef because wind and wave action displaced eggs from shallow sites to deep sites over the study period.

2.3. Physical, limnological, and climatological parameters

Water temperatures (°C) on the reef complex were recorded with continuous monitoring thermographs (Ryan Instruments, Inc.). Bottom dissolved oxygen was measured on the bottom at each sampling site using a calibrated YSI Model 50B dissolved oxygen meter. Secchi disk readings (nearest 0.1 m) were taken at each egg sampling site as an index of water clarity. Wind direction, intensity, and duration at South Bass Island, Ohio were recorded daily from the National Oceanographic and Atmospheric Administration weather observation broadcasts. Additional wind speed and direction data recorded at South Bass Island were obtained from the National Climatological Data Center in Asheville, North Carolina. We used criteria described by Busch *et al.* (1975) to determine the significance of wind events. Busch *et al.* examined a time series of water temperature and wind direction and intensity data from western Lake Erie and concluded that winds from N to NE exceeding 14.5 km/h, from the S to SW exceeding 17.5 km/h, and from the W to NW exceeding 20.5 km/h mixed western basin waters enough to reduce water temperatures by 0.5°C/day and be detrimental to incubating walleye eggs.

Substrate composition was examined by SCUBA diving at each egg sampling site. Divers measured substrate composition at three to five points at each egg sampling site in 1994 and 1995. Substrate particle sizes are based on the modified Wentworth scale (Cummins 1962).

2.4. Egg predator diet examination

Variable mesh gillnets were fished overnight during the peak spawning period in 1994 and 1995 to collect potential walleye egg predators. Two 40 m gillnets were fished simultaneously in 1994 and 3 were fished in 1995. The nets consisted of a single 8 × 2 m panel of each of the following stretch mesh sizes: 2.2 cm, 4.4 cm, 5.5 cm, 6.6 cm, and 8.8 cm. Gillnets were fished on the bottom in 2.3 m to 4.2 m of water on Toussaint reef. Upon capture, potential egg predators were measured to the nearest 1 mm and stomachs were removed and preserved in 10% formalin. We counted all eggs in stomachs anterior to pyloric caecum and in the anterior portion of the gut prior to the first flexure for greater redhorse sucker (*Moxostoma valenciennesi*). Identification of eggs in fish stomachs was based on egg size and color. We matched eggs observed in stomachs with concurrent catches from egg pump samples. We also examined the gut contents of fishes captured incidentally in egg pump samples in 1995. These fish were preserved whole in 10% formalin and dissected later.

2.5. Larval and juvenile abundance

We used a 2.0 m^2 framed ichthyoplankton net fitted with 583 mm mesh netting to sample pelagic larval fishes. A flow meter was positioned in the centre of the mouth of the net to

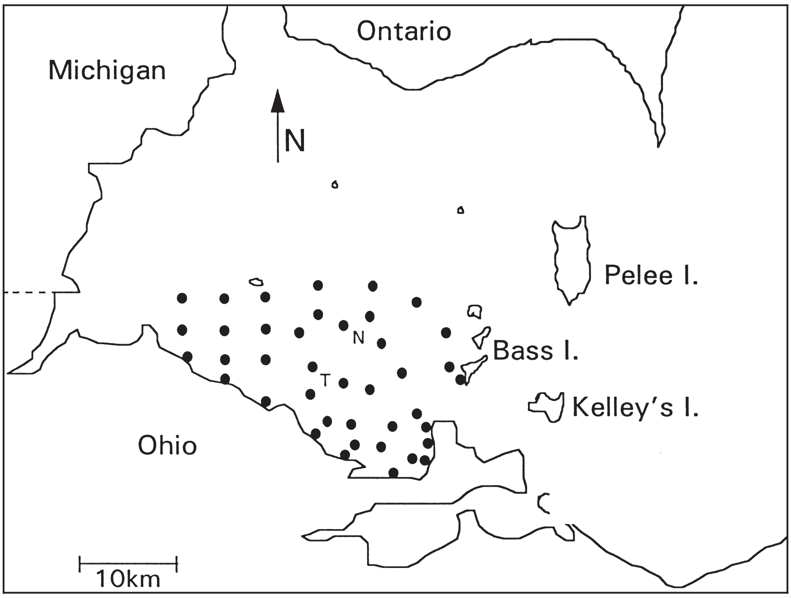

Fig. 2. Larval sampling sites in western Lake Erie. N = Niagara reef, T = Toussaint reef.

record the volume of water sampled. The net was towed in the upper 2.0 m of the water column at approximately 1.0 m/sec. for 5 min. We sampled from 15 to 40 sites (Fig. 2) per sample day and typically filtered 600 m^3 of water during each tow. Larval fishes were preserved in 95% ethanol and identified following Auer (1982). Catches of larval fish were $\mathrm{Log_e}(x+1)$ transformed to produce normalized data with homogeneous variance (O'Gorman 1984). We used mean larval density for the period from the first hatch through 31 May as an index of larval abundance to compare between years. We used the catch of age-0 walleye in assessment bottom trawl surveys in August (Ohio Division of Wildlife 1995, Sandusky Fisheries Research Unit, unpubl. data) as an index of relative year-class strength.

2.6. Statistical analysis

We calculated weighted averages of the numbers of walleye eggs collected per 2 min tow on each reef. We used the proportion of the reef surface area shallower than 7.0 m that each depth strata contributes to the total area as weighting factors. Surface area proportions were estimated from bathymetric maps of the reefs (Herdendorf & Braidech 1970). We used general linear models for an unbalanced design (SAS 1985) to detect differences in the numbers of stage-1 eggs collected per 2 min tow between depth strata and reefs as well as to investigate differences in viability between depth strata and reefs. Because total egg density is not independent between sample dates, we used estimates of newly deposited stage-1 eggs to compare densities between reefs and depths. Our design variables were reef, depth, and year and our parameters were numbers of stage-1 eggs and egg viability. In all analyses we used an α-level of 0.05.

3. Results

3.1. Reef substrates

Substrate composition varied at each depth stratum on both reefs. In general, the upper portions of the reefs (< 3 m) were composed of primarily large and small cobble (> 10 cm) and coarse gravel with little or no sand and silt. Sites with depths 3–5 m had highly variable substrates ranging from 40% exposed bedrock to 50% silt. Silt depths at the 3–5 m sites ranged from 2 to 20 cm. Gravels, cobbles, and boulders composed from 5 to 50% of the substrate at these sites. Sites 5–7 m deep were observed to have from 50–75% silt ranging from 2 to 40 cm deep with a conglomeration of gravels and small cobbles underneath.

3.2. Walleye egg deposition

Reefs were first sampled on 31 March 1994 but no walleye eggs were collected. Walleye eggs first appeared in samples from all depths at both reefs on 8 April 1994 when the water temperature was 4.2°C. In 1994 only walleye eggs were collected until 18 May when yellow perch (*Perca flavescens*) and *Morone* spp. eggs also appeared in the samples. Equipment failure prevented any egg sampling between 28 April and 17 May 1994. Walleye eggs

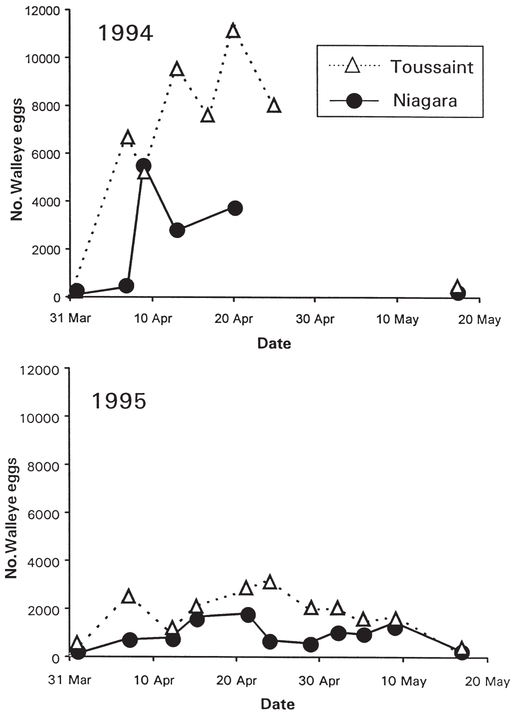

Fig. 3. Weighted mean numbers of walleye eggs collected per 2-min tow on Toussaint and Niagara reefs, 1994 and 1995. No eggs were collected in samples taken on 31 March 1994; no egg samples were taken between 28 April and 17 May 1994.

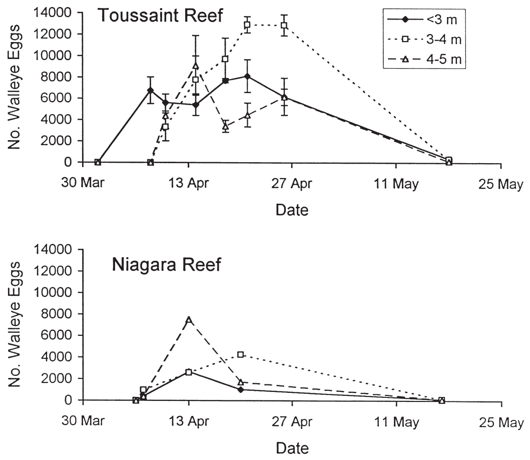

Fig. 4. Mean numbers of walleye eggs (± *S.E.*) collected per 2-min tow from different depth strata on Toussaint and Niagara reefs, 1994. No eggs were collected in samples taken on 31 March 1994; no egg samples were taken between 28 April and 17 May 1994.

appeared in samples on 31 March 1995 when the water was 4.8°C. No samples were taken prior to this date in 1995. In 1995, lake whitefish (*Coregonus clupeaformis*) eggs were collected in the earliest samples and yellow perch, *Morone* spp. and sucker (*Catostomidae*) eggs were collected in late April and May. Lake whitefish eggs were the only large eggs (> 3.0 mm) identified. Walleye and sucker eggs accounted for all the intermediate sized eggs (approximately 2.0 mm); sucker eggs were rare and had a much darker pigmentation than walleye eggs which were clear to yellow. The smallest eggs (< 1.5 mm) were those of yellow perch and *Morone* spp.

Walleye egg density peaked on 20 April 1994 on Toussaint reef, and on 10 April 1994 on Niagara reef when an average of over 11 300 and 5 500 eggs were collected per 2 min tow respectively (Fig. 3). Viable eggs persisted in samples at all sites through 18 May 1994 when less than 100 walleye eggs were collected per 2 min tow.

Egg densities were roughly 50% lower on Toussaint and Niagara reefs in 1995. Densities peaked on Toussaint reef on 24 April 1995 and on 21 April 1995 on Niagara reef when only 3 300 and 1 900 eggs were collected per 2 min tow respectively (Fig. 3). Viable walleye eggs were collected through 17 May 1995 when less than 50 walleye eggs were collected per 2 min tow.

In 1994, total egg density was generally higher at sites < 5 m deep than at sites 5–7 m on both reefs (Fig. 4), but in 1995, more eggs were consistently collected from sites < 5 m deep only on Toussaint reef. Egg density at sites > 5 m deep on Niagara reef actually appeared to increase in May (Fig. 5). Significantly more stage-1 eggs were collected from sites < 5 m deep on both reefs in 1994 ($p < 0.02$). In 1995, significantly more stage-1 eggs were collected from sites < 5 m deep on only Toussaint reef ($p < 0.3$). No significant difference in egg densities between depths was observed on Niagara reef in 1995 ($p = 0.17$). Significantly more stage-1 eggs were collected per unit effort from Toussaint reef than Niagara reef in both 1994 and 1995 (mean = 1 723 and 867 per tow respectively for 1994 and 571 and 280 per tow respectively for 1995; $p < 0.05$).

3.3. Walleye egg viability and survival in 1994

Egg viability estimates at Toussaint reef were generally higher in 1994 than 1995 (Fig. 6) with the

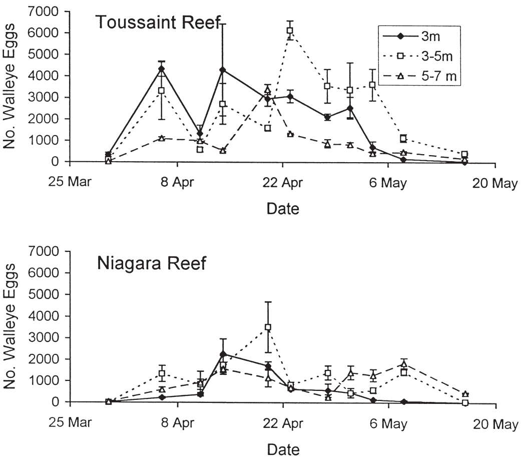

Fig. 5. Mean numbers of walleye eggs (± *S.E.*) collected per 2-min tow from different depth strata on Toussaint and Niagara reefs, 1995.

exception of three sample dates in mid-April 1995. Egg viability ranged from 41 to 74% between depths and reefs over the 1994 sampling period (mean = 56%) and did not differ significantly between depths or reefs ($p = 0.46$). In 1995, walleye egg viability ranged from 6 to 76% across the sampling period and did not differ significantly between depths or reefs ($p = 0.22$). Viability estimates generally increased in early April 1995 reaching 70% by mid-April and declined to less than 40% in late April and May.

Estimates of walleye egg survival were higher in 1994 than 1995. Our samples allowed for a single estimate of egg survival from 10 April to 21 April 1994 (102 TU's). Egg survival for pooled depths was calculated at 43% for Toussaint reef and 30% for Niagara reef and did not differ significantly between reefs ($p = 0.48$). We calculated 2 separate survival estimates for each reef in 1995. Walleye egg survival to stage 3 for the period 7 April through 29 April 1995 (99 TU's) was estimated at 14% for Toussaint reef and 7% for Niagara reef. Survival for the period 15 April through 9 May (113 TU's) was estimated at 16% and 15% for Toussaint and Niagara reefs respectively.

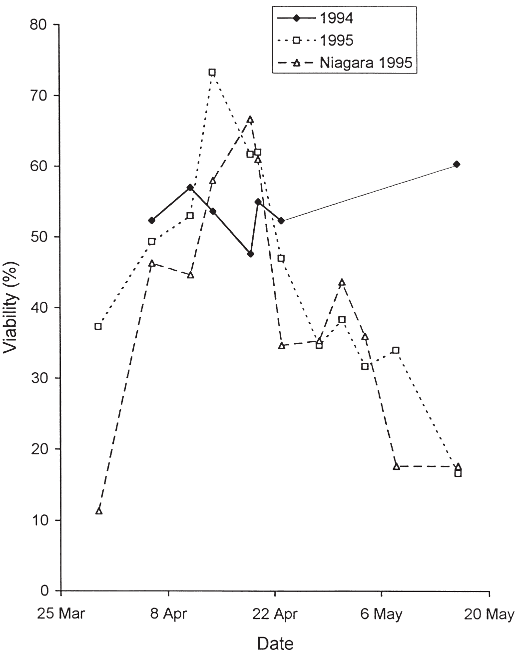

Fig. 6. Walleye egg viability estimates for pooled samples from Toussaint and Niagara reefs, 1994 and 1995. No viability estimates were made for samples from Niagara reef in 1994.

3.4. Egg predator diet examination

No fish other than spawning walleye were collected in gillnets fished overnight on 20 and 26 April 1994. In 1995, a total of 49 fish were captured in 3 nights of gillnetting from 12 April through 3 May and an additional 6 fish were collected with the egg pump. Few fish were captured in gill nets set on 12 April ($n = 4$) but the catch increased on subsequent nights, especially of white perch (*Morone americana*), the most common species collected. Only clear and yellow colored eggs were identified from fish stomach contents. All eggs in stomachs were of the mid-sized range (2 mm diameter). Walleye eggs were most abundant of any eggs on the reefs during this phase of our study. Sucker eggs occurred at a rate of about 1 in 1 000 eggs during late April and May 1995. We therefore feel confident that the majority of eggs observed in stomachs were walleye eggs and the contribution of eggs of other species is insignificant.

The stomachs of trout perch (*Percopsis omiscomaycus*), one yellow perch, log perch (*Percina caprodes*), one johnny darter (*Etheostoma nigrum*), white perch, and an unidentified sculpin (*Cottidae*) contained walleye eggs. The stomachs of one rock bass (*Ambloplites rupestris*) and one greater redhorse sucker did not contain walleye eggs. Walleye eggs appeared in 86% of white perch stomachs and each white perch stomach contained an average of 349 walleye eggs (Table 1).

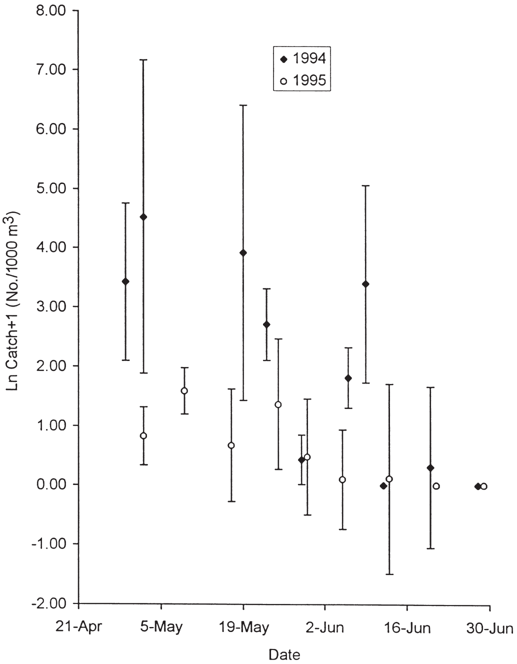

Fig. 7. Densities of larval walleyes collected at sites on and adjacent to reef complex in western Lake Erie, 1994–95.

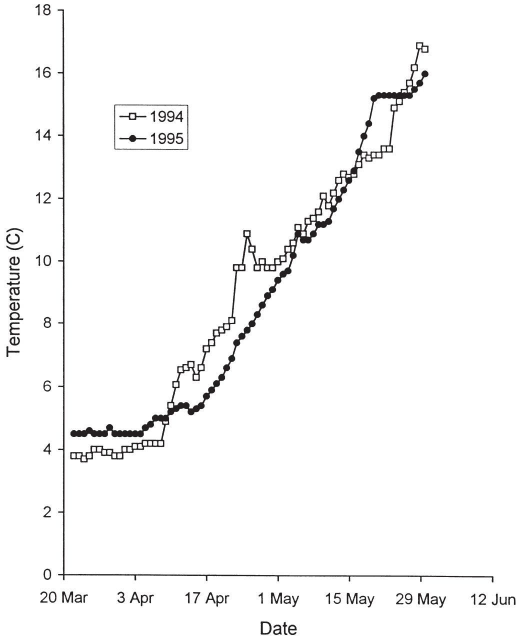

Fig. 8. Mean daily water temperatures observed on Niagara reef in western Lake Erie, 1994 and 1995.

3.5. Larval and juvenile abundance

We collected the first walleye fry on 29 April 1994 and 3 May 1995. In 1994, our catch peaked on 2 May when we captured 1 328 fry in 33 tows for an average density of 95.2 fry/1 000 m^3 (Fig. 7). Equipment failure prevented any larval sampling between 2 May and 18 May 1994. In 1995, the peak catch occurred on 11 May when a total of 85 walleye fry were captured in 40 samples for an average density of 3.5 fish/1 000 m^3. Mean density of walleye fry for the sample period was 14 times higher in 1994 than 1995 (28.4 and 2.0 fry/1 000 m^3 respectively).

The abundance of age-0 walleye in August bottom trawls was also greater in 1994 than 1995. Ohio Division of Wildlife (1995, Sandusky Fisheries Research Station unpubl. data) reported a geometric mean catch of 9.6 fish/hour in 1994 and only 1.2 fish/hour in 1995.

3.6. Physical, limnologic, and climatological parameters

Water temperatures warmed steadily in April and May 1994. Water temperatures were slightly warmer in late March and early April 1995 but warming was slower than in 1994 (Fig. 8). We calculated the average rate of warming per day from 1 April through 15 May which historically encompassed the walleye spawning and incubation periods in western Lake Erie. The average rate of warming per day for this 45-day period was 0.19°C/day in 1994 and 0.18°C/day in 1995. In contrast, the average rate of warming per day from the date eggs were first observed on the

Table 1. Average numbers of walleye eggs observed in fish stomachs collected from Toussaint and Niagara reefs, 1995. No. = number of fish examined, *TL* = fish mean total length (mm), *MT* = number of empty stomachs, Eggs = mean number of eggs observed in stomachs, Freq. = frequency of occurrence (%) of eggs in fish stomachs.

	No.	*TL*	*MT*	Eggs	Freq.
Grtr. redhorse	1	225	1	0	0
Johnny darter	1	44	0	2	100
Logperch	3	68	1	10	66
Rock bass	1	195	1	0	0
Sculpin	1	76	0	21	100
Trout perch	13	107	6	4	38
White perch	35	225	6	349	86
Yellow perch	1	81	0	5	100

reefs to the date fry were first observed in samples was more rapid at 0.22°C/day in 1994 and lower in 1995 at 0.16°C/day.

Major wind events were more frequent in 1995 than 1994 (Table 2). We found 21 days to have winds qualifying as detrimental to incubating walleye eggs in 1995 whereas only 14 days were identified in 1994. Winds were primarily from the W-NW in 1994 where E-NE winds predominated in 1995.

Secchi disk readings were generally greater on Toussaint Reef in 1994 than 1995 ranging from 0.3 m to 2.3 m in 1994 and 0.2 to 1.3 m in 1995. On Niagara reef, secchi disk readings ranged from 0.5 m to 1.2 m in 1994 and 0.3 to 1.9 m in 1995. Low secchi readings in 1995 were a result of the continued mixing of the water due to the persistent winds.

Bottom dissolved oxygen levels ranged from 3.8 mg/l to 6.2 mg/l on Toussaint Reef and remained above 5.0 mg/l at all sites on Niagara Reef over the 1994 walleye egg incubation period. In 1995, bottom dissolved oxygen levels were greater than 6.0 mg/l at all sites on both reefs through 15 April. We observed a decline in bottom dissolved oxygen levels at sites > 3 m after 15 April when dissolved oxygen levels declined to a low of 1.3 mg/l at one site 5–7 m deep on Niagara reef on 17 May.

4. Discussion

A combination of frequent intense winds, lower water warming rate, and egg predation appear largely responsible for the reduced egg densities and lower survival rates observed in 1995. Intense wind events cause mixing of lake waters which retards water warming and creates currents that dislodge walleye eggs from shallow reef substrates and deposit them in areas unsuitable for incubation (Eschmeyer 1950, Johnson 1961, Busch *et al.* 1975). We observed more intense wind events in 1995, especially winds from the E-NE which have long fetches, contributing to the slow water warming rate and displacing walleye eggs from reef habitats.

Table 2. Number of wind events that caused significant mixing of western Lake Erie waters in 1994 and 1995. Wind direction and intensity criteria based on Busch *et al.* (1975).

Wind direction and intensity	1994	1995
N-NE ≥ 14.5 km/h	4	12
S-SW ≥ 17.5 km/h	0	6
W-NW ≥ 20.5 km/h	10	3
Total	14	21

Many displaced eggs are likely deposited in deeper waters where silt substrates and reduced bottom dissolved oxygen levels can suffocate the embryos. We observed lower secchi readings in 1995 due to the continued mixing of lake waters caused by the relatively frequent intense winds. Precipitation of suspended particles from the water column contributes to low bottom dissolved oxygen readings (Zapotsky & Herdendorf 1980) and can cover deposited walleye eggs. We observed bottom dissolved oxygen levels as low as 1.3 mg/l at a site 5–7 m deep on Niagara reef in 1995 and presume that oxygen levels were also low at deeper sites surrounding the reefs. McMahon *et al.* (1984) maintain that dissolved oxygen levels above 6.0 mg/l are necessary for optimal walleye embryo development and survival. Therefore, it is likely that the majority of walleye eggs displaced to deep, silt habitats experience high mortality.

The warming rate of western Lake Erie waters was greater in 1994 than 1995, especially during the period from the first observation of eggs on the reefs to the time fry were first observed. Other studies have concluded that spawning and incubation temperatures are strongly related to hatching success (Busch *et al.* 1975). Rapid warming reduces incubation time and consequently reduces vulnerability to low oxygen, siltation, disease, predation, and storm generated turbulence and currents that can occur on the reefs.

Prolonged walleye egg incubation periods increase the potential for predation on walleye eggs. Wolfert *et al.* (1975) observed that yellow perch were the most consistent predators of walleye eggs on Kelley's Island Shoal in a study conducted in 1969–71. These authors conclude that the loss of walleye eggs to fish predation appeared to be important only when the rate of water warming slowed or stopped and the walleye and yellow perch reproductive periods overlapped. Our study shows the same temperature effect on incubation periods, but with white perch as the most abundant fish on the reef and the most important walleye egg predator.

Because we caught no potential egg predators in our gillnets in 1994, we feel that the reproductive periods of walleye and potential egg predators probably did not overlap to any point that could have significantly impacted the incubating walleye eggs. We did observe clearer water on Toussaint reef in 1994 than in 1995 which may have contributed to low gillnet catches in 1994. Hanson and Rudstam (1995) conclude that increased water clarity can lead to reduced catches and consequently diminish the effectiveness of sampling programs. Additionally, the faster water warming rate in 1994 may have allowed many of the walleye eggs to hatch before substantial numbers of white perch occupied the reef.

Our gillnet catches in 1995 show a gradual increase in the number of white perch inhabiting Toussaint reef and that there was a significant temporal overlap with the incubating walleye eggs in late April and May. Examination of gut contents indicate that white perch were the most important consumers of walleye eggs, though it is difficult to assess the impact that their predation may have on the reproductive success of walleye. We can only concur with Wolfert *et al.* (1975) that an overlap in reproductive periods when waters warm slowly gives potential predators more opportunity to consume the incubating walleye eggs as seen in 1995. The longer the walleye eggs incubate, the more opportunity there is for predation and the greater the potential for deleterious effects on walleye reproductive success.

Changes in the abundance of adult fish in Lake Erie do not appear to explain the differences in egg densities between 1994 and 1995 on Toussaint and Niagara reefs. The Lake Erie walleye population (age 2 and older) was estimated at 40.2 million fish in 1994 and was projected to increase by 6% to 42.8 million fish in 1995 (Lake Erie Walleye Task Group 1995). Shuter and Koonce (1977) deduced that stock size explains only a small part of the variation in recruitment of the western Lake Erie walleye population.

Energy surplus and allocation in female walleyes may partially explain the lack of consecutive strong year classes. Walleye growth rate was higher in 1993 than in 1994, likely due to a preponderance of gizzard shad (*Dorosoma cepedianum*) in 1993 (Ohio Division of Wildlife 1995), the preferred prey of walleye in western Lake Erie (Knight *et al.* 1984). The abundant gizzard shad may have provided the energy surplus needed to produce gametes and allowed the majority of females to spawn in 1994 possibly accounting for the higher egg densities observed in 1994. Henderson and Nepszy (1994) propose that good year-classes of walleye are only possible if most spawning females accumulate a surplus of energy the previous growing season and can direct this energy towards gamete production. Replenishment of energy depleted by reproduction may not be accomplished by all females thus limiting the number of fish capable of spawning the next year. Additionally, some females may resorb their eggs in order to satisfy their own metabolic needs if conditions are bad (i.e. harsh winter, cold spring, lack of prey), (Henderson & Nepszy 1994). Presently, we do not know how many females actually spawn on reefs in any given year nor do we fully understand the mechanisms that determine which females will spawn.

Additionally, females can allocate more or less energy to gametes depending on conditions encountered during the growing season (Roff 1983). Gamete size and energy content can vary from year to year influencing the survival probability of different sized eggs (Moodie *et al.* 1989, Brown & Taylor 1992). Larger eggs generally contain more energy and produce larger larvae upon hatching providing a stronger survival probability than small eggs (Miller *et al.* 1988, Moodie *et al.* 1989). Brown and Taylor (1992) discovered that lake whitefish eggs with higher caloric content produced larger larvae and that the endogenous growth of larvae was highly dependent on egg lipid content. Moodie *et al.* (1989) found that large walleye eggs contained more energy than small eggs and the subsequent larvae from the large eggs hatched at a larger size, began exogenous feeding sooner, and had greater survival than fry from small eggs.

Great disparity in apparent year-class strength of reef spawned walleye in Lake Erie is immediately evident in the egg stage. Egg density in 1994 was approximately twice that observed in 1995 and egg survival was 2.8 times better in 1994. The product of these factors provides an initial year-class disparity factor of nearly 6. We observed pelagic walleye larvae to be 14 times more abundant in 1994 than 1995. Because white perch were present on the reefs during late April and May 1995, the walleye hatch period, significant numbers of emerging walleye larvae may have been removed by predation. We performed no further examination of potential predator stomach contents during the larval emergence period thus missing the opportunity to identify predation on newly emerged larvae. The year-class disparity was reduced to a factor of 9.6 by August as estimated by relative abundance in bottom trawls (Ohio Division of Wildlife, Sandusky, Ohio, unpubl. data) indicating that either mortality was greater during the summer months in 1994 or walleye larvae immigrated from other areas in 1995 (i.e. river spawned fish, Regier *et al.* 1969) reducing the relative difference in year-class strength between years.

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