Relationship between lake trout spawning, embryonic survival, and currents: A case of bet hedging in the face of environmental stochasticity?

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A B S T R A C T

Lake trout, Salvelinus namaycush, spawning in the Great Lakes occurs primarily on cobble substrate at relatively shallow water depths that can experience strong water currents. Strong currents may limit embryonic survival by damaging or displacing eggs, but may also reduce the accumulation of fine material and limit foraging by potential egg predators. To better understand the importance of currents, we evaluated the role of currents in spawning habitat selection, egg density and survival, and egg predator density at a spawning reef in Lake Champlain (USA). Most spawning occurred one week after the largest storm event associated with the strongest currents and greatest upwelling. Highest spawning activity was associated with a relatively shallow part of the reef that had the highest current velocity and greatest potential for egg displacement. Within the interstices, the survival of naturally deposited eggs was unrelated to the concurrent loss of artificial eggs. We propose that the reproductive strategy of spawning on shallow areas of a reef that have the highest current velocity and high potential for egg displacement represents a type of bet hedging to optimize survival of those embryos that remain within interstices. This strategy may have evolved in response to environmental stochasticity that resulted in higher egg survival.

Introduction

Currents have long been suspected of influencing lake trout, Salvelinus namaycush, spawning habitat selection and embryonic survival but have received scant quantitative analysis (Marsden et al., 1995; Martin and Oliver, 1980). Consequently, the role of water currents in the attraction of spawning lake trout and embryonic survival, and overall role in the reproductive strategy used by lake trout remains unclear (Marsden et al., 1995; Sly, 1988; Storr, 1962). The highest abundance of spawning lake trout and highest density of eggs in the Great Lakes are usually associated with relatively shallow submerged reefs or shorelines having sharp contour breaks (Bronte et al., 2007; Claramunt et al., 2005; Marsden, 1994; Marsden et al., 2005). Such habitat features could dramatically affect water current velocity and direction, leading to upwelling, locally increased or decreased current velocity, sediment resuspension/scouring and wake zones (Bronte et al., 2007; Fitzsimons, 1995; Marsden and Krueger, 1991; Marsden et al., 1995; Sheng, 2000; J. Jansen, UW, Milwauke, WI, pers. comm., unpub. data). If currents increase embryonic survival and therefore reproductive success, the detection of currents by spawners and use of currents to increase embryonic survival may play an important role in the reproductive strategy used by lake trout and may ultimately increase reproductive success. Whether spawning lake trout actually detect currents or habitat features that enhance local water velocity and use these factors to select desirable spawning habitat is not known.

Use of shallow reefs for spawning has been associated with egg displacement and mortality directly related to the physical disturbance accompanying wind-generated currents (Fitzsimons, 1995; Fitzsimons et al., 2007; Perkins and Krueger, 1995). As a result, the use of shallow spawning habitat in the Great Lakes has been posited by some as a major contributor to the low reproductive success of contemporary lake trout stocks relative to historic stocks (Bronte et al., 2003). However, historically large catches of lake trout in Lake Michigan were associated with the widespread use of relatively shallow spawning reefs throughout the lake (Dawson et al., 1997). Successful restoration of lake trout in Lake Superior was thought to be the result of spawning on relatively shallow reefs (Bronte et al., 1995; Hansen et al., 1995; Wilberg et al., 2003). Collectively, these observations suggest that the use of shallow spawning habitat, which has the potential to receive high current exposure, is not necessarily inconsistent with self-sustaining populations. A better understanding of the interaction between currents and lake trout reproductive success on shallow spawning habitat may help to resolve uncertainties regarding the suspected impediments to lake trout restoration in the Great Lakes (Bronte et al., 2003).

Historically spawning of lake trout on shallow reefs having strong currents may have resulted in some egg displacement and mortality but may have yielded net benefits for the remaining embryos (Fitzsimons, 1994; Perkins and Krueger, 1995). Such benefits may have been part of a ‘bet hedging’ spawning strategy by lake trout. Lake trout are long-
lived and have multiple spawning events during their lifetimes, so they may be able to integrate fluctuations in environmental factors such as currents by spawning eggs over habitat having a range of current velocity. This could result in a range of egg survival probabilities, dependent on environmental factors (Anderson et al., 2008; Berkely et al., 2004; Bobko and Berkley, 2004; Hutchings and Myers, 1993; Lambert, 1987; Marteindottir and Steinarsson, 1998). High egg survival may depend on the use of deep interstitial spaces often associated with high quality lake trout spawning habitat (Marsden et al., 1995). The reduction in current velocity and potential for egg displacement associated within deep interstitial spaces would need to be counterbalanced with the need for sufficient water currents for the effective delivery to and transfer of oxygen across egg membranes to optimize egg survival and yolk-sac utilization (Hamor and Garside, 1976, 1979; Silver et al., 1963). Spawning in areas of high currents may also be an effective means of reducing the density of epibenthic egg predators such as crayfish (Orconectes spp.) and sculpins (Cottus spp.) (Claramunt et al., 2005; Jones et al., 1995; Savino and Miller, 1991) that may have difficulty foraging in high currents (Flinders and Magoulick, 2007; Webb et al., 1996).

We hypothesize that lake trout balance current-related egg mortality with other factors that can act to improve egg survival; we further hypothesize that they select spawning habitat based on an optimal current velocity that maximizes egg distribution and ultimately egg survival over a gradient of conditions. To test these hypotheses we evaluated the predictions that 1) spawning habitat use, as measured by egg density, is directly related to current velocity, 2) displacement of eggs is directly related to current velocity, 3) egg mortality within interstitial spaces is unrelated to current velocity, and 4) the density of epibenthic predators is inversely related to current velocity.

To evaluate the effect of water currents on lake trout spawning, we assessed the relationship between spatial patterns of current velocity by measuring 1) natural egg deposition, 2) natural egg survival, 3) artificial egg displacement and 4) egg predator abundance during the fall of 2004 at a lake trout spawning reef in Lake Champlain (Marsden et al., 2005).

**Methods**

**Study site**

Our study was conducted on a spawning reef in Lake Champlain which is associated with the Grand Isle ferry dock breakwall located on the eastern shore of Lake Champlain (Fig. 1) (Marsden et al., 2005). The breakwall is 200 m long, oriented roughly northwest to southeast and consists of 1–2 m square emergent blocks sitting on a bed of 10–50 cm diameter angular cobble (see Marsden et al., 2005). The submerged part of this structure is steeply sloped and extends approximately 2 m out from the large blocks; water depth on top of the cobbles ranges from 1 to 2 m at the top to 2–3 m at the base. At the western end of the breakwall, there is a 12 × 20 m (240 m²) submerged plateau extending approximately 23 m to the west of the breakwall. The plateau is composed of the same 10–50 cm angular cobbles as the breakwall and has a steep drop-off around its perimeter. The water depth over the plateau ranges from 2 to 3 at the top and 3 to 8 m at the base.

Spawning by lake trout at the site is intense; egg densities for the entire reef average 3000 eggs m⁻², and windrows of eggs have been seen at the base of the reef (Marsden et al., 2005, J.E. Marsden, unpublished data). The high level of egg deposition is consistent with high spawner abundance, possibly influenced by pheromones released from a nearby hatchery (Ellrott and Marsden, 2004; Fitzsimons, 1995; Foster, 1985; Marsden, 1994; Marsden et al., 2005). Survival of eggs and resulting alevins at this site is high and similar to that for self-sustaining lake trout stocks (Marsden et al., 2005; Peck, 1986); therefore, understanding factors that affect egg survival is relevant to understanding the reproductive strategy used by lake trout in the Great Lakes. The areas of the breakwall used by spawning lake trout have homogeneous substrate and water depth (Marsden et al., 2005), so potentially confounding effects of large variation in substrate size or water depth are reduced. Egg predators (e.g., sculpins and crayfish Jonas et al., 2005) are present in low abundance and distributed homogeneously. Thus, the reef was ideally suited to assess the effects of currents on spawning.

**Lake trout spawning assessment**

Lake trout spawning was assessed using egg collection nets (Perkins and Krueger, 1995) (Fig. 1). Egg nets (35 cm dia., 50 cm deep, 3 mm mesh) were deployed by scuba divers on September 23, 2004, prior to lake trout spawning to allow time for interstitial predators to redistribute. Divers excavated enough substrate to accommodate an individual egg net, placed the net into the excavation, and then backfilled the net with the excavated material. A total of 90 nets were buried at the site. Nets were spaced approximately 1 m apart in a line along the southwestern one-third of the breakwall and in a grid of approximately 1–2 m spacing on the plateau at the western end of the breakwall. A

![Fig. 1](image_url)
temperature logger was attached to one of the nets to record temperature over the period that nets were deployed. Nets were removed on December 9, approximately 2 to 3 weeks after the peak of spawning activity based on observations of fish activity on the reef, and previous spawning investigations (Marsden et al., 2005).

**Use of artificial eggs to measure lake trout egg displacement**

Artificial eggs were used to examine post-spawning egg displacement, similar to their use with redbuilding salmonines (Crisp, 1989a, b). Artificial eggs were plastic beads with mean weight (mg), diameter (mm), and settling velocity (cm s⁻¹) comparable to lake trout eggs. To determine the settling velocity of artificial and lake trout eggs, a total of 10 individual artificial and 20 lake trout eggs were allowed to settle in a column of water at approximately 9 ºC. The distance and time of descent were used to calculate settling velocity (cm s⁻¹).

One hundred artificial eggs were added to each egg net by scuba divers on November 4, 2004, just prior to the expected spawning period. Scuba divers released the artificial eggs directly into the center of each egg net and then used gentle hand movement to ensure that all artificial eggs had settled below the surface of the substrate in the net and were no longer visible.

**Retrieval and sorting of egg net contents**

All egg nets were recovered by scuba divers on December 9, 2004 and transported to the laboratory in Burlington, Ontario. The contents of all nets were sorted over a one-week period during which time they were held at a temperature of 5 ºC to minimize consumption of lake trout eggs by crayfish and sculpins (Elliot et al., 2007; Fitzsimons et al., 2006). Eggs were classified as either alive (translucent) or dead (opaque). Dead eggs were placed in Stockard's solution (Fleming and Ng, 1987) for clearing to permit determination of egg fertilization. Percent fertilization of eggs in each net was based on the proportion of live and dead fertilized eggs present relative to the total number of eggs. Chorions where at least 50% of the chorion was present were included in total egg counts but were not used to determine fertilization rate. To determine egg density, we divided the total of dead and live eggs and chorions in each net by the net area (0.07 m²).

We used the reciprocal of the proportion of artificial eggs recovered multiplied by the number of natural eggs at the time of egg net recovery to estimate the number of natural eggs present immediately after spawning had ended. This assumed that natural eggs behaved the same way as artificial eggs and that the release of artificial eggs was coincident with spawning.

All egg predators were measured (fork length in mm for sculpin, carapace length in mm for crayfish) and weighed (g). Only sculpins >42 mm and crayfish >19 mm were included in predator densities as these are the only sizes capable of consuming lake trout eggs (Jonas et al., 2005).

To determine the stage of embryonic development reached at the time egg nets were retrieved, 100 translucent live eggs from each of nine randomly selected nets from the breakwall and eight randomly selected nets from the plateau were examined microscopically using published descriptions (Balon, 1980). The temperature record and predictive equations developed from Balon (1980) on the time to reach each of the embryonic stages observed were used to back-calculate putative spawning dates (Fitzsimons, 1995).

**Measurement of water currents**

To measure variation in water currents at the macro-habitat (e.g., the immediate area of Lake Champlain but away from the reef) and micro-habitat (e.g., the surface and just below the surface of the spawning reef) scale, we used a combination of a conventional current meter (Acoustic Doppler current profiler (ADCP)) and calibrated dissolvable plaster of Paris blocks (PPBs) (Leonetti, 1997). A priori we suspected that currents would behave differently in the area of the ADCP relative to the area associated with the reef. The reef itself was expected to create a vertically upwelled current (Otake et al., 1991) whereas in the open waters surrounding the ADCP vertical water motion was expected to be negligible compared to horizontal water movement (Sheng, 2000). We used the PPBs to examine current dynamics on the reef as it was the only practical means of evaluating currents over such a small scale and area involving both the surface of the reef and the area just below the surface of the reef. Due to logistical constraints, however, we were able to do this only prior to spawning and not during the actual spawning period. Although current measurements obtained with an ADCP or a PPB are not directly comparable, we used PPBs to infer the nature of the relationship between depth and current velocity. To examine a range of current velocities, we sampled the reef for evidence of spawning based on eggs at a range of depths assuming that current velocity decreases with depth.

**Construction of plaster of Paris blocks (PPB)**

We used plaster of Paris blocks (PPB) as described by Leonetti (1997) to measure water currents on a microhabitat scale (Fig. 2). The blocks were constructed from commercially available plaster of Paris and were formed by pouring a plaster slurry into each compartment of an ice cube tray; each compartment had a volume of approximately 16 ml. Enough plaster of Paris was prepared to fill all of the compartments (14) of a single ice cube tray. Once all compartments had been filled with a standardized volume of plaster of Paris, the tray was gently knocked to remove any trapped air. To serve as an attachment point, a single 8 cm long (5 mm dia.) size 10 stainless steel bolt was inserted vertically into the center of each filled compartment before the plaster set. The bolt head was placed flat and towards but not touching the bottom of the compartment. The tray was placed in a drying oven at 40 ºC for a period of 48 h. After drying, all PPBs were inspected for consistency, and any fine edges that could be easily abraded during handling were removed with a file. The finished PPBs were rhomboid in shape, approximately 28 mm high, with an upper face area of 28 x 42 mm and lower face area of 20 x 33 mm. A plastic numbered tag was inserted onto the protruding bolt end of each PPB and fastened in place with a rubber O-ring. The numbered PPB was weighed (±0.0001 g) and held at room temperature until used.

Two types of PPB deployment were used, one to measure currents at the substrate-water interface immediately over an egg net (surface PPB), and one to measure currents within the interstitial space of an egg net (interstitial PPB) (Fig. 2). Two surface PPBs were attached at opposite sides of the rim of an egg bag by inserting the bolt of each PPB into a hole on the rim, so that the bottom edge of the block was approximately 2 mm above the egg net. A single interstitial PPB was placed in a solid mesh (1 x 1 mm) polyethylene capsule, within the interstitial spaces of each egg net (Fig. 2). The block was fixed in the center of the rigid capsule by attaching the block bolt to the end cap of the capsule.

**Calibration of surface and interstitial PPBs**

The rate of dissolution or flux of the surface and interstitial PPBs and relationship with current velocity were determined using a large flume (0.75 m deep, 1 m wide, overall length 25.9 m long, working length 21.4 m) located at Canada Center for Inland Waters (CCIW, Burlington, Ontario). Loss of PPB weight (±0.0001 g) for duplicate pre-weighed surface and interstitial PPBs were determined at five different current velocities (0, 5.12, 10.56, 15.32, and 24.73 cm s⁻¹) and for five different time periods (0, 12, 24, 36, and 48 h) at an average water temperature of 18 ºC. Current velocity in the flume was measured with a SonTek Acoustic Doppler Velocimeter current meter, sampled at the rate of
was tested in succession for each of the water depths of 30 cm. Rods were located 2 m apart on the midline of the flume. PPBs were separated from the bottom end facing down, leaving the interstitial PPB approximately 5 cm below the surface of the substrate. For surface PPBs, divers inserted the bolt of an individual surface PPB into one of the holes located on the rim of each egg net, with each egg net receiving two PPBs. Once in place on a net, the rubber O-ring and numbered tag of a PPB separated the body of the PPB from the net ring by approximately 2 mm, allowing current to move freely around the block so the ring does not protect the base from dissolution (Fig. 2). In addition, care was taken to ensure that once deployed, no part of a PPB was in contact with the adjacent cobble that might abrade the PPB during the period of deployment and lead to erroneous current measurements.

Surface and interstitial PPBs were left in place for 5 days before retrieval by divers on November 9, 2004. Each surface PPB was carefully removed by a diver so as not to abrade the PPB, and placed into an individual section of an ice cube tray for transport to the surface. Interstitial PPBs were transported intact to the surface and disassembled at CCIW; all PPBs were dried overnight at 40 ºC, placed in a desiccator to cool, reweighed, and the weight loss over the period of deployment determined. The average current velocity (cm s⁻¹) was calculated for the period of deployment of each PPB by back-calculating the current velocity associated with the flux (e.g., gh⁻¹) using the appropriate calibration curve. Wind data (i.e., average wind speed and sustained wind speed) during the period of deployment of the PPBs and the ADCP (November 9 to December 9) were obtained from Plattsburgh (New York) Airport, located approximately 20 km from the field site.

Vertical current profiling

To determine temporal changes in the vertical current profile for the Grand Isle reef, an acoustic Doppler current profiler (ADCP) was placed on the bottom (7 m) approximately 50 m southwest of the spawning area. The ADCP recorded current velocity and direction at five discrete water depths (1, 2, 3, 4, and 5 m). The ADCP was deployed on November 9, 2004 after all PPBs had been recovered and retrieved one month later on December 9, 2004. To determine whether lake trout spawning was related to current velocity or direction, these metrics were compared among three periods corresponding to pre-spawning (November 9–15), spawning (November 18–24) and post spawning (November 25–December 9) (see below).
Statistics

Relationships between flux and current velocity were examined by linear regression; relationships between current velocity, artificial egg loss, egg density, and egg survival were examined by curvilinear regression using the procedures in SigmaPlot (Version 8.0). Data were transformed as necessary (arcsine transform for loss of artificial eggs and egg survival; log transform for current velocity and water depth) prior to analysis to meet the requirements of normality and homoscedasticity. All tests were considered statistically significant at $P < 0.05$.

Results

Water currents

There was a positive linear relationship between flux and current velocity determined using a flume for both the surface PPBs (Fig. 3a; $F_{1, 4} = 188.5$, $r^2 = 0.98$, $P < 0.0001$) and interstitial PPBs (Fig. 3b, $F_{1, 4} = 52.7$, $r^2 = 0.95$, $P = 0.005$). The flux for the interstitial PPB was related to that of the surface PPB (Fig. 3c, $F_{1, 4} = 248.4$, $r^2 = 0.99$, $P < 0.0001$).

In Lake Champlain, current velocity based on PPBs during the period November 4 to 9 was related to water depth by a curvilinear relationship for both surface ($F_{1, 73} = 8.76$, $r^2 = 0.18$, $P = 0.0004$), and interstitial ($F_{1, 64} = 19.87$, $r^2 = 0.37$, $P < 0.0001$) PPBs. Current velocity for the surface PPB ($C_S$) was linearly related to that of the interstitial PPB ($C_I$) (Fig. 5, $F_{1, 63} = 11.70$, $r^2 = 0.15$, $P = 0.0011$) by the equation $C_I = 0.2393 + 0.5841 \cdot C_S$. At low current velocity, current velocity measured by surface and interstitial PPBs was similar, but as current velocity increased, current velocity measured by the interstitial PPBs decreased relative to that of surface PPBs. During their deployment at an average depth of 3.0 ± 0.1 m, the estimated current velocity for interstitial PPBs ranged from 4.5 ± 0.2 cm s$^{-1}$ and for surface PPBs 5.2 ± 0.1 cm s$^{-1}$, a difference of 16%. Average current velocity for surface PPBs (5.2 cm s$^{-1}$) over the period November 4 to 9 at an average depth of 3 m was less than one-half that measured in the 3 m bin of the ADCP (9.6 cm s$^{-1}$) over the period November 9 to December 9, 2004 (Table 1).

Based on the current record for the ADCP (Table 1), current velocity did not differ ($P > 0.05$) over the period of investigation relative to spawning activity (i.e., pre-spawning, spawning, post-spawning) although there was a significant (Table 1) relationship between current velocity and water depth ($F_{1, 6} = 94.1$, $P < 0.0001$); current velocity at 1 m was higher than that at all other depths (i.e., 2, 3, 4, 5 m), but all other depths were not different from each other. There was no significant period × depth interaction ($P > 0.05$). For current direction, there was a significant period ($F_{2, 8} = 82.3$, $P < 0.0001$) and depth ($F_{2, 8} = 11.7$, $P < 0.0001$) effect but no significant period × depth interaction ($P > 0.05$). Mean current direction during the spawning period (289°) was significantly higher ($P < 0.05$) than that during the pre-spawning (234°) or post-spawning period (243°); pre- and post-spawning...
periods were not different from each other. Current direction was similar at depths of 5 (267°), 4 (264°), and 3 m (257°) but significantly higher than at 1 m (235°). Mean current direction at 2 m (243°) was similar to that at 1 and 3 m, but significantly ($P < 0.05$) less than at 4 or 5 m.

Lake trout spawning and relationships with artificial egg loss, water currents, and egg predators

The distribution of egg developmental stages in egg nets, evaluated with the temperature record (Fig. 6), indicated that there were two temporally separate spawning periods. The first occurred on or about November 18 at a water temperature of 9.0 °C and accounted for approximately 96% of egg deposition. A much smaller period of spawning occurred on or about November 24 at a water temperature of 8.2 °C, and resulted in deposition of the remaining 4% of the eggs. Currents during both spawning periods were predominately from the south-east and towards the windward side of the reef (Fig. 6). The approximately one-week period circumscribing the two spawning periods was not unique in terms of the rate of temperature change (Fig. 6), wind speed (Fig. 7), or current velocity or direction, based on measurements made with the ADCP (Fig. 6). Water temperature during this period was constant during the first spawning period and showed a slight decline during the second period, with wind speed relatively low. However, the two spawning periods were preceded by a large upwelling event indicated by a rapid temperature decline approximately one week prior to the first spawning period, when temperature declined by approximately $3 \, ^\circ C$ (Fig. 6). This upwelling event was associated with the strongest currents of the observation period, from the south-east. The south-east currents were followed by currents of much lower speed in the south-west and a temperature increase to approximately $3 \, ^\circ C$ ($T = 5.5, df = 28, P < 0.001$) but only slightly lower than that of lake trout eggs ($7.79 \pm 0.09 \, cm \, s^{-1}$). The difference between uncorrected and corrected lake trout egg density was approximately five-fold. Recovery of artificial eggs did not differ between the plateau and breakwall. The loss of artificial eggs was related to water depth by a curvilinear relationship (Fig. 8; $F_{2,75} = 10.57, r^2 = 0.20, P < 0.001$).

Lake trout egg density was related to water depth but only after egg density had been corrected for egg loss based on recovery of artificial eggs (Fig. 9; $F_{2, 3} = 5.88, r^2 = 0.12, P = 0.04$). Survival (%) of lake trout eggs averaged $77.4\%$ ($\pm 1.1$) and was related to water depth by a curvilinear relationship (Fig. 10, $F_{2, 72} = 4.59, r^2 = 0.09, P = 0.01$) but unrelated to the proportion of artificial eggs recovered ($P > 0.05$).

The combined density of the egg predator sculpins ($5.4 \pm 0.8 \, m^{-2}$) and crayfish ($0.9 \pm 0.4 \, m^{-2}$) averaged $6.3 \pm 0.8 \, m^{-2}$. Egg predator density was unrelated to depth, corrected or uncorrected lake trout egg density, or the proportion of artificial eggs recovered ($P > 0.05$).

Discussion

Relationship between spawning and current velocity

We found a direct relationship between current velocity, mediated by the effect of water depth, and egg deposition which we infer is a measure of spawning habitat selection. Lake trout spawning, inferred from corrected egg densities, was highest at approximately 2 m and lower in shallower and deeper water. By contrast, Claramunt et al. (2005) reported that for Bay Harbor Reef, a relatively large, shallow reef in northeastern Lake Michigan, the majority of naturally deposited eggs were found at the shallowest depth (1 m), compared with 3 and 9 m. The depth of highest egg density at Grand Isle was similar to the depth of highest current velocity measured by both surface and interstitial PPBs. Due to logistical issues, the PPBs measured currents for a period that preceded the estimated spawning period by 14 to 20 days, but we construe that the current patterns (though not current velocities) inferred from the PPBs are likely to apply during the spawning period. Based on the ADCP measurements which immediately followed the deployment of PPBs, current speed was relatively invariant for a given depth during the pre-spawning, spawning, and post-spawning periods; mean current speed during the spawning period based on the ADCP (9.6 cm s$^{-1}$) was higher than that measured with PPBs (5.2 cm s$^{-1}$) but of the same order of magnitude. Current speed in surface waters is generally under the control of wind speed (Beletsky and Schwab, 2001). Based on the wind record obtained from Plattsburgh airport, winds were higher during the period of PPB deployment than after their retrieval. If current measurements with PPBs and the ADCP were

![Figure 5](image-url) Relationship between log interstitial and surface current velocity (cm s$^{-1}$) ($r^2 = 0.15$) based on PPBs in Lake Champlain (solid line). Dotted line indicates 1:1 relationship.

![Figure 6](image-url) Water temperature during the spawning period was constant during the first spawning period and showed a slight decline during the second period, with wind speed relatively low. However, the two spawning periods were preceded by a large upwelling event indicated by a rapid temperature decline approximately one week prior to the first spawning period, when temperature declined by approximately $3 \, ^\circ C$ (Fig. 6). This upwelling event was associated with the strongest currents of the observation period, from the south-east. The south-east currents were followed by currents of much lower velocity from the south-west and a temperature increase to approximately $9 \, ^\circ C$. A second large upwelling event occurred around December 6, when water temperature averaged $6.7 \, ^\circ C$ and dropped by approximately $2 \, ^\circ C$. This second upwelling event was apparently not followed by a detectable increase in lake trout spawning based on the distribution of egg developmental stages at the time when nets were retrieved.

Lake trout egg density averaged $8759 \pm 779$ (mean $\pm$ SEM) eggs m$^{-2}$ overall for the entire reef. When lake trout egg density for each individual egg net was corrected for loss using the proportional recovery of artificial eggs (mean $\pm$ SEM; $37.1 \pm 3.0$%) from the same net, lake trout egg density averaged $41,550 \pm 5199 \, \text{eggs m}^{-2}$. The settling velocity of artificial eggs ($7.21 \pm 0.06 \, \text{cm s}^{-1}$) was significantly ($T = 5.5, df = 28, P < 0.001$) but only slightly lower than that of lake trout eggs ($7.79 \pm 0.09 \, \text{cm s}^{-1}$). The difference between uncorrected and corrected lake trout egg density was approximately five-fold. Recovery of artificial eggs did not differ between the plateau and breakwall. The loss of artificial eggs was related to water depth by a curvilinear relationship (Fig. 8; $F_{2,75} = 10.57, r^2 = 0.20, P < 0.001$).

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![Image](image-url)

**Table 1** Summary of mean ($\pm$SE) current velocity (cm s$^{-1}$) and direction (°) for an ADCP deployed at a depth of 7 m near Grand Isle Ferry Dock (Lake Champlain) (see Fig. 1) for the period November 9 to December 9, 2004. Note the direction is the direction the current is heading (PSP = prespawning period, SP = spawning period, PSTSP = post-spawning period).

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<th>Depth (m)</th>
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<td>299.0 (5.5)</td>
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<tr>
<td>5.0</td>
<td>251.1 (7.1)</td>
<td>290.7 (5.4)</td>
</tr>
</tbody>
</table>
directly comparable, estimated current speeds with PPBs should have been much higher. Thus, either current measurements are not comparable between the two methods, or the reef where the PPBs were deployed had a moderating effect on currents, or some combination of the two.

Although the pattern of variation in current velocity across depth with the ADCP was not comparable with that estimated with the PPBs, we suspect this may be related to the habitat in which each of the methods were deployed. The ADCP indicated highest current velocity at 1 m with a logarithmic decline at greater depths up to 5 m, whereas the PPBs, spanning a depth range of approximately 1.5 to 4 m, indicated highest current velocity at approximately 2 m. The ADCP was deployed in open water and vertical velocity was relatively low (results not shown), whereas the PPBs, being deployed on the reef itself, may have experienced considerable vertical and horizontal velocity in response to upwelling associated with the reef (Otake et al., 1991). Vertical upwelled currents can lead to transport of sediments from the bottom water column to surface water (Otake et al., 1991), and therefore are likely to also transport semi-buoyant lake trout eggs. In fact, the depth pattern of loss of artificial eggs reflected the current patterns inferred from surface and interstitial PPBs, with the greatest loss of artificial eggs occurring at the same depth (2 m) as the highest currents estimated with PPBs.

We measured currents associated with lake trout spawning for only one location and one year; inter-annual and spatial variation is likely to be high. We predict that lake trout spawning site selection may be related to a critical current velocity at a given depth, as observed for lingcod Ophiodon elongatus and Pacific cottids (DeMartini, 1978; DeMartini and Patten, 1979; Giorgi and Congleton, 1984). Critical current velocities...
may be important for establishing optimal conditions that optimize growth and survival of incubating embryos. Although we found highest egg deposition to occur at approximately 2 m, highest egg survival occurred at approximately 3.2 m. While the relationship between either corrected egg density or egg survival and water depth was dome shaped, in the case of egg survival, the relationship was shifted to a greater depth compared to that for corrected egg density.

The egg density we measured at Grand Isle in 2004, when not corrected for the effects of dislodgment, was very high, being 10- to over 1000-fold higher than that reported for other spawning reefs in the Great Lakes basin (Fitzsimons, 1995; Marsden et al., 2005). The average egg density measured in 2004 for Grand Isle was, however, within the range reported for this site by Marsden et al. (2005). It is difficult to compare the corrected egg densities for Grand Isle to other sites as there are few sites having egg densities similar to Grand Isle, the loss of artificial eggs or colored eggs has been evaluated at relatively few sites, and current velocities at none of these sites were similar to Grand Isle (Claramunt et al., 2005; Fitzsimons, 1995).

Knowledge of the importance of currents and their interaction with bottom topography will be important in identifying spawning habitat in deeper parts of the Great Lakes (Janssen et al., 2007). Deep-water spawning habitat may have advantages over shallower sites in terms of reduced physical forces or numbers of egg and fry predators, all of which have been associated with increased egg mortality (Fitzsimons et al., 2006, 2007; Jonas et al., 2005). However, in the absence of wave-generated turbulence in such habitats, presence of currents may be required to maintain interstices free of sediment and maintain adequate oxygen concentrations, habitat attributes to which lake trout are extremely sensitive (Sly, 1988).

Current velocities on Lake Champlain during the fall of 2004 averaged 10 cm s\(^{-1}\) between 2 and 5 m, approximately one-half the velocity reported for the much larger Lake Ontario, based on data for four satellite-tracked drogues approximately 4 m high suspended approximately 1.5 m below the surface (Simons et al., 1985). For the four drogues, mean current velocity ranged from 1.2 to 25.1 cm s\(^{-1}\) with highest currents associated with movement along the south shore. Although current velocities in Lake Champlain were considerably higher during storm events, at their peak slightly in excess of 50 cm s\(^{-1}\), current velocity at these times was still less than the maximum velocity based on the four drogues in Simons et al. (1985) that ranged from 61.2 to 77.6 cm s\(^{-1}\).

The spawning period for lake trout at Grand Isle in 2004 lasted approximately one week. This appears to have been an unusually concentrated spawning period, perhaps triggered by the high wind events that fall. In 2001, egg deposition was sampled throughout the spawning season at Grand Isle using egg funnels (McAughey and Gunn, 1995) buried on the same spawning substrate as in this study and sampled almost daily from Nov. 5 to Nov. 20, then on Nov 25 and Dec. 7 (J.E. Marsden, unpub. data). Forty percent of the total eggs collected were sampled on one date (Nov. 14), but eggs were collected over the entire period but were concentrated in a 12-day period. Spawning periods of from 2 to 39 days with an average of 17 days were reported by Fitzsimons (1995) for Lake Ontario based on the developmental stages of eggs collected at seven spawning reefs. The spawning period in an inland lake lasted an average 14 days over a three-year period, based on daily observations of egg deposition (McAughey and Gunn, 1995). Spawning over multiple dates, as with spawning over a range of depths and current velocities, is likely to be advantageous in a stochastic environment in which a diversity of strategies can be successful.

The shorter spawning period of lake trout in Lake Champlain in 2004 may reflect the effect of the large upwelling event that occurred prior to spawning in 2004. This event, because of its effect on water temperature, may have had the effect of synchronizing ovulation among the majority of females and hence the timing of their movement onto the spawning reef (Foster et al., 1993; Gillet, 1981). According to the temperature logger, a week of strong storms on Nov. 9 was associated with a strong upwelling event. The largest spawning period was estimated to have occurred on or about November 18, nine days later. Variation in water temperature, like variation in water currents, could also affect spawning period although little is known about the relative importance of water temperature and photoperiod in controlling spawning date (Martin and Oliver, 1980).

Nearsurface spawning has been assumed to be detrimental to lake trout egg survival, due to negative effects of high current velocity in shallow water (Bronte et al., 2003). Our data on egg retention and survival during relatively high current velocities in Lake Champlain indicate that nearsurface spawning may, in fact, be a robust strategy, and may not be a mal-adaptive behavior of stocked lake trout.

**Fig. 9.** Relationship between log corrected egg density (no. eggs m\(^{-2}\)) and log water depth (m) in Lake Champlain.

**Fig. 10.** Relationship between arc sine egg survival (%) and log water depth (m) in Lake Champlain.

Egg displacement and current velocity

The loss of artificial eggs in this study, while relatively high and possibly influenced by their lower settling velocity relative to natural eggs, was within the range observed in the Great Lakes. Lake trout egg loss at two spawning reefs ranging in depth from 5 to 11 m in southwestern Lake Ontario ranged from 35 to 50% (Fitzsimons et al., 2003). Wind fetch for these locations was however, relatively short (4–44 km) (Fitzsimons, 1995). By comparison, losses of lake trout eggs on six reefs in Lake Michigan were as high as 85% and related exponentially to wind fetch which ranged from 2 to 73 km. Detailed observations at one reef in Lake Michigan with a wind fetch of approximately 70 km
(Claramunt et al., 2005) indicated losses of trout eggs as high as 93%, three weeks after they were added to the reef. Spawning by lake trout in the area of highest current velocities and highest potential for egg displacement may represent a type of bet-hedging reproductive strategy by a broadcast spawner to optimize reproductive success (Easte et al., 2008; Gunn, 1995). Noakes (1989) argued that spawning habitat selection is particularly critical for a species, like lake trout, whose young spend considerable time in the spawning habitat. Lake trout fecundity is relatively high (1500 eggs kg⁻¹; Shuter et al., 1998), so by spawning thousands of eggs in areas with highest current velocity, females distribute their eggs across a broad area representing a gradient in both physical (e.g., currents) and chemical (e.g., dissolved oxygen) factors and their interaction.

Egg mortality and current velocity

Currents can result in the displacement of eggs, but elevated egg displacement in this study was not associated with poor survival of eggs that remained in the substrate. Egg survival was unrelated to the loss of artificial eggs, our surrogate for the effects of currents. We found that the water depth at which egg survival was highest was somewhat deeper than the depth with the highest corrected egg density. As a result of environmental stochasticity, the area on a reef that provides optimal conditions for embryo survival in one year may not be the same in a subsequent year. In a given year, however, the bet-hedging strategy of broadcasting eggs over a gradient of physical and chemical conditions may allow lake trout to exploit reef heterogeneity such that some portion of the reef will provide conditions for adequate embryo retention and survival.

Epibenthic egg predators and current velocity

We did not find any evidence that the distribution of egg predators (sculpins and crayfish) was related to depth, inferred current patterns, egg density, or amounts of physical disturbance. Perhaps eggs or other food sources were in sufficient supply to obviate the need for associating with certain areas on the reef. Jonas et al. (2005) indicated that for non-self-sustaining lake trout stocks, egg to predator ratios were much lower than for self-sustaining stocks. Egg predators can reach satiation on eggs (Fitzsimons et al., 2007), therefore once egg density reaches a certain point the effect of egg predation on probability of egg survival would decline. If a lake trout bet-hedging reproductive strategy exists, as proposed here, it likely evolved under the influence of variation in the physical and chemical attributes of spawning habitat but not variation in the biological attributes of spawning habitat. This would be consistent with the evolution of the species after glaciation (Martin and Olver, 1980). The use of reef spawning by lake trout in lakes likely evolved just after the last ice age (Eshenroder et al., 1995) when abundance of egg predators such as sculpins and crayfish in areas inhabited by lake trout were probably low to non-existent (Jackson and Harvey, 1989). As a result, such egg predators were unlikely to be present in sufficient numbers to influence the evolution of the reproductive strategy used by lake trout.

Conclusion

In conclusion, we found that spawning lake trout appear to make use of the habitat on a reef with the highest currents that provide high water quality but also have the greatest potential for egg dislodgement. This reproductive strategy may represent a type of bet-hedging to provide for optimal conditions for development of embryos in the face of environmental stochasticity. To better understand the direct and indirect effects of currents on lake trout spawning and egg survival, further work is needed to measure additional factors thought to affect egg survival but using equipment that is appropriate to the nature of gradients that may exist and to the high levels of physical disturbance that can occur.

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