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

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ABSTRACT

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 loss 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 Olver, 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. Janssen, UW, Milwaukee, 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-

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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 m^2) submerged plateau extending approximately 23 m to the west of the breakwall. The plateau is composed of the same 10–50 cm angular cobble 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 homogenous 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

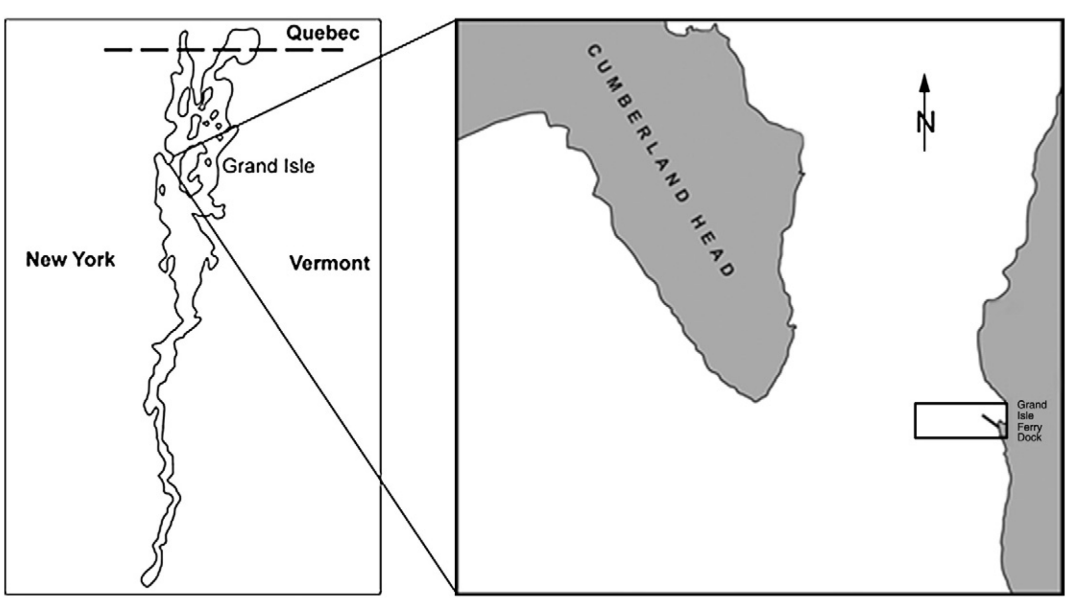

Fig. 1. Map of Lake Champlain showing the location of the study site at the Grand Isle Ferry Dock.