Challenges to Deep-water Reproduction by Lake Trout: Pertinence to Restoration in Lake Michigan

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ABSTRACT. *Restoration efforts for lake trout* Salvelinus namaycush *in Lake Michigan are increasingly being focused on re-establishment of the species in deep water. This focus is based in part on examination of historical records of indigenous lake trout, which suggest that offshore reefs, especially deep reefs, sustained the greatest numbers of lake trout. This focus is also based on the increasing impact of non-indigenous species, such as alewife and round goby, on lake trout survival on shallow reefs. Development of a successful strategy for re-establishing deep-water lake trout in Lake Michigan will require a better understanding of the challenges to a species that evolved in shallow water and whose nearest relatives are shallow-water fishes. The challenges include an annual temperature cycle with fall warming rather than cooling, which may impact reproductive timing and embryo incubation. Deep water presents challenges to fry in that there is no apparent physiological mechanism for producing swim bladder gas and initial filling of the swim bladder at the surface has little impact on buoyancy once a fry returns to depth and the swim bladder is compressed. First feeding is a challenge because there is no local primary production to support a rich prey supply and the phenology of zooplankton prey abundance differs from that in small lakes. We propose that plans for restoration of lake trout into deepwater habitats in Lake Michigan must proceed in concert with research leading to a better understanding of extant deepwater strains in Lake Superior.*

INDEX WORDS: *Genetic strains, constraints to reproduction, prey availability, predators, exotic species, early life history, swim-bladder inflation.*

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INTRODUCTION

Efforts to restore populations of lake trout *Salvelinus namaycush* to the Great Lakes, since their extirpation in most areas of the lower four lakes by the 1960s, have yielded limited success (Hansen 1999). Research and, to a large extent, management efforts, have focused on shallow (< 18 m), nearshore reefs, in part due to the logistical difficulties of working on offshore reefs in fall (Marsden *et al.* 1995). Substantial and sustained natural reproduction by lean lake trout has occurred only in Lake Superior (Hansen 1999, Sitar *et al.* 2007), where wild stocks are now at or close to pre-collapse levels (Wilberg *et al.* 2002), and in Parry Sound, Lake Huron (Reid *et al.* 2001). In northern Lake Michigan, adult populations (Bronte *et al.* 2007) and resulting densities of eggs and fry are low (Jonas *et al.* 2005, Marsden *et al.* 2005), suggesting that restoration in this area and elsewhere is unlikely at current stocking and mortality rates. Recommendations for future restoration strategies are now focused on concentrating most fish on offshore areas around Beaver Island in northern Lake Michigan and at deep offshore locations at the Mid-Lake Reef Complex (Bronte *et al.* 2007; Fig. 1). Both areas, especially the Mid-Lake Reef Complex (see Janssen *et al.* 2006), were important sources of recruitment prior to lake trout extirpation (Dawson *et al.* 1997). The Mid-Lake Reef Complex is comprised of three limestone cuestas, East Reef, Sheboygan Reef, and Northeast Reef, 40–60 m at their crests, with a total surface area of 2,859 km^2 (Holey *et al.* 1995). Redirecting the focus on deep reefs is also justified by analyses of commercial catch records that indicate the highest catch per effort per area by commercial fishers prior to lake trout extirpation was on the offshore deep reefs (Dawson *et al.* 1997).

Restoration and fishery management efforts and research have largely focused on lean lake trout, a shallow, nearshore morphotype that dominated the historical fisheries. Lean lake trout was one of many morphotypes found throughout the Great Lakes (Strang 1854, Smith and Snell 1891, Brown *et al.* 1981, Goodier 1981, Lawrie and Rahrer 1972) and some of this morphotypic diversity remains only in Lake Superior (Lawrie and Rahrer 1972, Krueger and Ihssen 1995, Moore and Bronte 2001). Lean lake trout occur in water less than 80 m deep and typically use nearshore shallow reefs for reproduction, although offshore reefs were also impor-

FIG. 1. *Map showing Beaver Island and the general area of Sheboygan Reef and East Reef. For more detail of the bathymetry of East Reef and Sheboygan Reef see Janssen* et al. *(2006). The areas designated as lake trout refuges are shown in Holey* et al. *(1995).*

tant sources of recruitment, especially in Lakes Huron and Michigan.

It is generally thought that lake trout populations were present in several riverine glacial refugia (Wilson and Hebert 1996) and, historically, there were river-spawning populations in Lake Superior and perhaps Traverse Bay in Lake Michigan (Loftus 1957). Eshenroder *et al.* (1995) and Sly and Evans (1996) suggested that contemporary deep reefs used by spawning lake trout were originally used as shallow reefs when waters levels were

much lower immediately after glaciation. Adaptations to deep water have had little time to evolve because there is no indication of a deep-water glacial refugium.

The information on reproduction and early life history of lake trout spawning on shallow reefs does not necessarily provide a good model for deep reefs, where thermal regimes, currents/water motion, substrates, contour, prey, and sedimentation dynamics may be substantially different. Herein we review current information on lake trout spawning on shallow reefs and compare/contrast this information with deep reefs to predict behavior and biological differences and highlight future research needs. Some new data are included where they are useful for justifying our arguments. We focus on potential bottlenecks in lake trout life history imposed by a deep-water habit.

Genetic Strains

The relative importance of genetic factors and hatchery origin in defining deepwater spawning behavior is unknown.

There are three extant lake trout phenotypes in Lake Superior: "siscowet" occurring from 50 m to perhaps the deepest water (406 m), "humper" occurring at isolated reefs surrounded by water more than 100 m deep and steep banks, and "lean" that inhabit waters shallower than 70 m (Lawrie and Rahrar 1972, Hansen *et al.* 1995, Moore and Bronte 2001, Bronte *et al.* 2003). Extirpated siscowet-like lake trout were reported for Lake Michigan (Brown *et al.* 1981), but it is not known whether these were genetically similar to Lake Superior siscowet. Spawning areas of humper and siscowet have only been inferred from collection of individuals in spawning condition at various times of the year. These data suggest that gene flow among the phenotypes may be limited due to selection of different spawning grounds (Hansen *et al.* 1995) and seasons (Bronte 1993). There are few if any accounts of siscowets spawning with leans at nearshore sites or at offshore sites in Lake Superior, although leans spawning at siscowet sites offshore has not been investigated. Depth distribution of potential spawners during the spawning season is similar to their distribution during the rest of the year, with leans found in 2–40-m depths, humpers in 50–70 m, and siscowets ranging from 91–182 m, although spawning siscowet were reported by Goodier (1981) as shallow as 45 m.

Stocking in the Great Lakes has incorporated genetic diversity (Krueger and Ihssen 1995), but has focused on lean lake trout. More recently, restoration strategies, particularly in Lake Michigan, have begun to examine stocking lake trout on deep reefs. This would involve continued use of the Seneca Lake strain, which has demonstrated good survival and resistance to sea lamprey (*Petromyzon marinus*) predation, and introduction of siscowet and humper morphotypes from Lake Superior. Predicting the spawning depth of the Seneca Lake strain is difficult, because spawning behavior may be flexible with respect to depth. Seneca Lake is 190 m deep, and lake trout eggs have been collected as deep as 35 m (Sly and Widmer 1984); however, eggs have also been collected at 3 m on a breakwater at the north end of the lake (J. E. Marsden, personal observations). The Seneca strain has been shown to produce high proportions of naturally spawned fry at multiple sites in Lake Ontario (Marsden *et al.* 1989, Perkins *et al.* 1995) and one site in Lake Michigan (Marsden, unpublished data), but in all cases, these reefs are less than 15 m deep (Marsden *et al.* 1989, Marsden 1994, Perkins *et al.* 1995, Fitzsimons 1995). The Seneca strain also produced the majority of embryos collected from East Reef on the Mid-Lake Reef Complex, Lake Michigan, at a depth of about 50 m (DeKoning *et al.* 2006). An important area for future research to advance the restoration program is to understand what constitutes a "deepwater spawner." If spawning location is primarily dictated by water temperature, day length, and presence of appropriate substrate (see below), then a stocked lake trout is likely to select areas at any depth that have the right combination of these factors. The prevalence of spawning on man-made substrates attests to this (Jude *et al.* 1981, Fitzsimons 1996, Marsden and Chotkowski 2001, Marsden *et al.* 2005). On the other hand, spawning in deep water may require a different set of behaviors and adaptations that would imply genetic differentiation from shallow water spawners. For example, first filling of the gas bladder by emergent fry is generally held to be vital for survival. Deep spawning strains may have evolved alternative strategies to avoid the challenge of swimming to the surface to acquire air (see below).

One of the substantial problems in predicting behaviors of lake trout on deep reefs is the paucity of information about behavior of native strains. Hatchery-reared fish may behave differently than wild fish, both because of genetic components to their

behavior and as a consequence of their early rearing under shallow, crowded hatchery conditions.

Timing of Reproduction

The cues that regulate timing of maturation and spawning on deep reefs, including interaction between temperature and day length, are unknown.

The seasonal nature of reproduction involves the timing of several physiological/ behavioral processes. While timing of these individual events may be coordinated, ultimate control of the processes can be independent and involve different cues. Salmonines reproduce once per year and, therefore, maturation of the ovaries (oogenesis) and testes (spermatogenesis) occurs at one particular time of the year and requires several months to complete. In most fish species, including salmonines, photoperiod is believed to be the primary environmental cue synchronizing gonadal maturation to a given time of the year (Bromage *et al.* 2001). While temperature affects gonadogenesis and spawning time (see below), it is usually considered to modulate rather than dictate the timing of reproduction (Davies and Bromage 2002). Even at great depths, it is possible that photoperiod is still an important cue that governs the overall seasonal synchronization of gonadal development.

There is a major difference between the fully mature ovaries and testes in fish; mature sperm are haploid, while mature oocytes have not yet completed meiosis. The completion of the reduction division in oocytes occurs in a terminal process called germinal vesicle breakdown (GVBD) or oocyte final maturation, and is followed shortly by ovulation; the release of the oocyte from the follicle wall. Ovulation and GVBD are controlled by different hormones than those controlling gonadogenesis (oogenesis and spermatogenesis), and GVBD/ovulation are most likely synchronized or controlled by different external cues. For these terminal processes, temperature probably plays a much greater role in many species. Spawning by lake trout is generally thought to be influenced by declining temperatures, and is triggered when water temperatures drop below 10–12°C (Martin and Olver 1980). On deep reefs, the primary cues for egg release are probably different, as water temperatures never rise above 10°C, and actually increase as the thermocline breaks down in autumn (Fig. 2).

Finally, release and fertilization of gametes, sometimes referred to as spawning, may involve
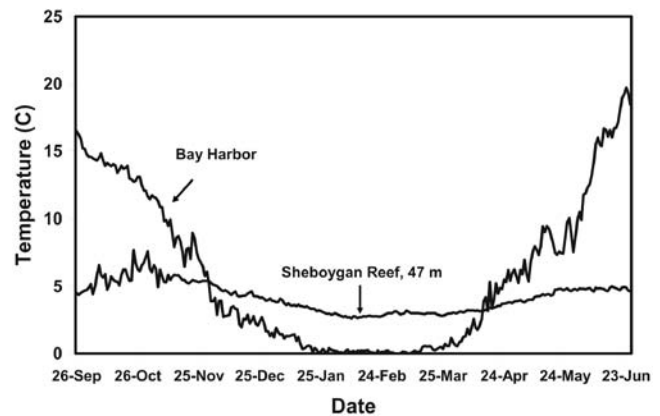
**FIG. 2.	Water temperatures during the spawning and likely egg incubation periods for a shallow reef in Little Traverse Bay (Marsden, unpublished temperature logger data) in Northern Lake Michigan (Bay Harbor) and Sheboygan Reef (47 m deep) in southern Lake Michigan (Gottlieb et al. 1989).**

complex behavioral and endocrine interactions that could be cued separately from gonadogenesis and GVBD/ovulation. In addition, since salmonines are capable of holding ovulated eggs in the body cavity for days to weeks, spawning would not necessarily have to occur immediately after ovulation. Thus, the precise timing of reproduction for any fish species would ultimately be a result of several timing mechanisms that could be cued by different environmental parameters.

In general, most lake trout strains appear to be fall spawners with spawning peaks from September (northerly, e.g., Alaska) to late October/early November in lakes in Ontario, Wisconsin, New Hampshire, and New York (Martin and Olver 1980). However, reports have suggested that different lake trout morphotypes may reproduce at different times of the year and, as a result, may constitute some degree of reproductive isolation. Eschmeyer (1955) reported that lake trout (presumably "lean" forms) in southern Lake Superior appeared to be fully mature with gonads comprising 12–18% of the total body weight in late October/early November. In contrast, lake trout classified as "siscowets" had ovaries consisting of 11.9–13.9% of the body weight by late September and in one case, 13% by late July. The differences in maturation time suggest that siscowet and lean lake trout forms in Lake Superior may reproduce at different times of the year. While Gonado-Somatic Indices were not recorded, Bronte (1993) observed one ripe male and
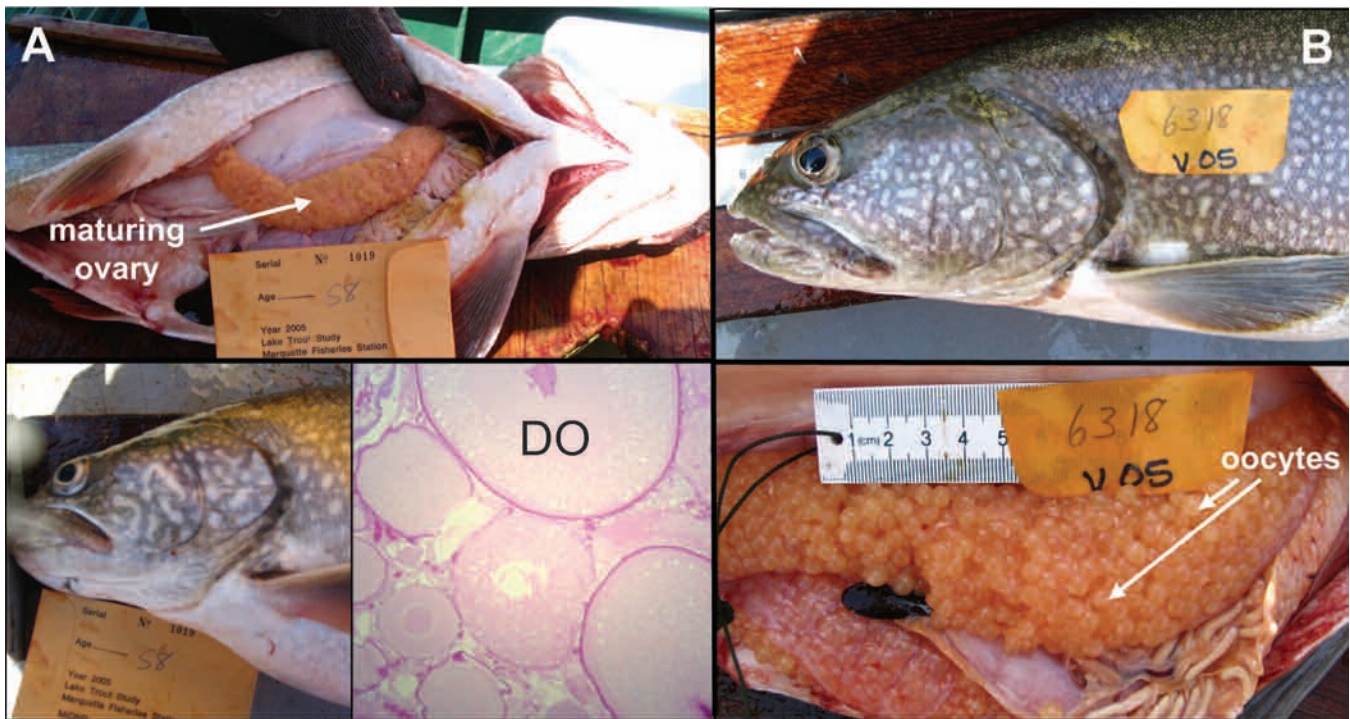
FIG. 3. A: Maturing ovary (top) of a 59-cm siscowet lake trout female (bottom left) collected 21 June 2005 in Lake Superior (Marquette, MI). Bottom right panel is histological section of ovary showing developing oocyte with central nucleus. B: Fully mature, postvitellogenic ovary (bottom) of a 69.3-cm siscowet lake trout female (top) collected 8 Sepember 2005 in Lake Superior (Marquette, MI).

one ripe female siscowet in late April in collections northeast of the Apostle Islands in Lake Superior. Humper lake trout evidently spawn in mid-September in Lake Superior off of Isle Royale (Rahrer 1965), and females with fully developed eggs have been observed in early August (C.R. Bronte, unpublished data). Finally, in preliminary sampling of siscowet populations in Lake Superior off Marquette, MI during 2004–2005, siscowet females were in the process of gonadal maturation by at least early June, and had fully mature ovaries (postvitellogenic oocytes) by early September (Fig. 3; Sitar and Goetz pers. obs.). One female collected in September had ovaries undergoing oocyte maturation and, thus, ovulation should have occurred within several days. This indicates that spawning could occur in early September for that particular siscowet population and would be consistent with that reported by Eschmeyer (1955). However, to accurately determine if leans and siscowets spawn at different times, reproductive sampling of both morphotypes in neighboring populations must be conducted within the same year and at the same time of year.

The circannual cycle of reproduction may be controlled by photoperiod to synchronize gonadal maturation to a given time of the year, which may differ among lake trout morphotypes. The consistency of reproductive timing may also be confounded by whether or not a fish reproduces every year. As summarized in Martin and Olver (1980), there have been many reports suggesting that lake trout do not reproduce every year and that the frequency may be related to latitude. Intermittent spawning, which occurs in long-lived species like lake trout, could explain asynchronous reproduction in certain lake trout populations. For example, in Lake Superior in late September, Eschmeyer (1955) observed a female siscowet with fully mature ovaries (13.9% gonadal weight) and a larger female with ovaries in a far less mature state (3.5% gonadal weight) in the same gill net catch. Tagged female lake trout with ripe, free-flowing eggs in fall have been recaptured in subsequent spawning seasons with undeveloped eggs in Lake Superior (C.R. Bronte, personal observation). Observations by Eschmeyer (1955) suggest that the more mature fish

would spawn the year observed, while the less mature fish might spawn the next year. It may be possible that in deepwater forms such as siscowet, intermittent spawning occurs, or that complete gonadal maturation might even require more than 1 year. Thus, populations may only appear to be unsynchronized in terms of reproductive timing. Depending on the latitude, lake trout may mature from 4–19 years, with longer ages at first maturity being observed at more northern locations (Martin and Olver 1980). Lake Superior siscowet and lean lake trout start to mature around age 7 and can live for 20 years or more, hence reproduction may not be required every year for sustainability.

While some information is available, there are still several fundamental questions concerning reproduction in lake trout morphotypes, such as siscowets, which live in deep water. These include: 1) Where and at what depths do siscowets spawn? 2) At what times of year do siscowet spawn, and is reproduction synchronized within and among populations of deepwater lake trout? 3) If siscowets mature and spawn at great depths, what are the cues that synchronize and determine reproductive timing?

Reef Location and Substrate

Lake trout spawning in deep water likely have different habitat constraints therefore characteristics that define spawning sites in shallow water may not apply.

Numerous studies have described shallow-water substrates on which stocked lake trout spawn (reviewed by Marsden *et al.* 1995, Marsden *et al.* 2005). Important site characteristics are presence of cobble-rubble substrates with deep interstitial spaces, adjacency to steep drop-offs, and absence of organic material or fines. However, these features also vary in importance; lake trout have been found spawning on a shale slope at 15 m in Keuka Lake, and on a flat shale substrate with virtually no interstices at < 1 m depth in Otsego Lake (Fitzsimons *et al.* 2005; J. E. Marsden, unpublished observations). Commercial fishermen reported spawning by lake trout in deep water on a variety of substrates, including gravel and clay (Coberly and Horrall 1980); however, these reports are based on substrate clinging to anchors and tangled in gill nets in areas where ripe lake trout were captured, and may not represent substrates on which lake trout deposited their eggs. More recent observations via submersible at Lake Michigan's deep reefs indicate

clay is present, but there is also considerable bedrock and cobble (Edsall and Kennedy 1995, Marsden and Janssen 1997, Janssen *et al.* 2006).

Interstices are presumed to protect eggs from predators and movement by wave action. Interstitial space may not be as important on deep reefs where there is no wave surge and predators are likely less abundant than on shallow reefs (see below). A recent problem at deep reefs, particularly in Lake Michigan, is the dense colonization of hard substrates by quagga mussels (Jude *et al.* 2005). The presence of zebra mussels on shallow reefs appeared to reduce egg deposition and egg survival, as eggs cannot become entrained in the spaces between mussels and tend to be damaged as they wash across mussel shells (Marsden and Chotkowski 2001). On deep reefs, the damage may be less important because wave action is not present. Deposition of feces and pseudofeces by mussels produces high levels of organic material that may negatively affect egg incubation and evaluation of substrates as "clean."

Shallow spawning lake trout concentrate near contour breaks along the edge of a drop-off (Marsden *et al.* 1995). These areas have strong, pulsating, wave-generated currents that tend to keep the area clean of silt that can suffocate eggs. Wave pulses and turbulence will erode boundary layers that permit silt to settle (Vogel 1994). Martin and Olver (1980) noted that wave surge may even stimulate spawning in lake trout. However, shallow sites are also exposed to wind-generated turbulence that may dislodge or damage eggs (Eshenroder *et al.* 1995); windrows of eggs have been found downslope and at the base of shallow spawning reefs (Marsden *et al.* 2005). In deep water, currents can be strong, but they oscillate on a period of hours rather than the wave period of seconds in shallow water (Gottlieb *et al.* 1989, Mortimer 2004). This may restrict the area of clean substrate to being very near drop-offs and ridge tops where the "edge effect" produces little boundary layer (Vogel 1994).

The physical break in bottom topography at the upper edge of reefs may also serve to concentrate spawning fish. Initial work on Sheboygan Reef, using a remotely operated vehicle (ROV)-based suction sampling in fall, 2005, found evidence of egg deposition on a ridge with about 2–3 m relief above the reef's plateau (Janssen *et al.* 2006), and highest egg densities were found near the top of the ridge (Fig. 4). However, eggs (fall 2005) and sac fry (spring 2005) were also found at East Reef at 60 m, about 10 m from its summit and 40 m above its base. These eggs may have been dislodged and
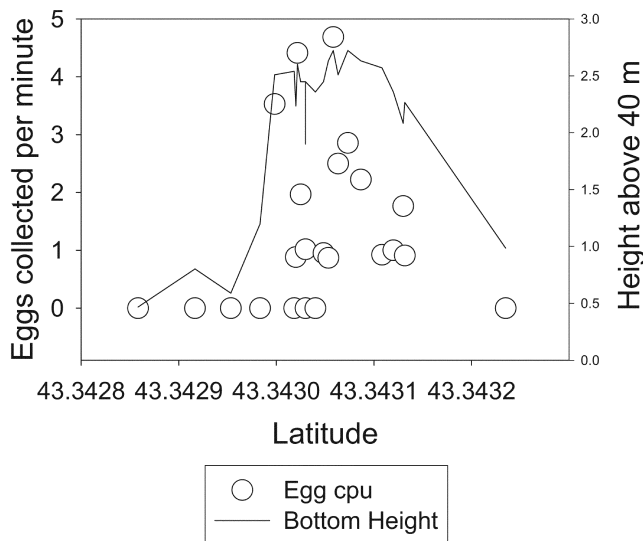
FIG. 4. *Plot of egg CPU (No. of lake trout eggs collected per min of suction sampling from an unmanned submersible) vs. bottom profile for a transect across Edsall Ridge, Sheboygan Reef, Lake Michigan. Lines show the Edsall Ridge bottom profile as determined by the submersible. The plateau surrounding Edsall Ridge is approximately 40 m deep. Details regarding the unmanned submersible are in Janssen* **et al. 2006.**

transported to depths below where they were deposited.

Because stocked lake trout did not evolve on these reefs, the possibility of egg deposition on unusual substrate cannot be eliminated without study of egg deposition by extant, deep-water lake trout strains. Additional habitat mapping and searching for eggs in areas without contour are needed to better elucidate where deepwater lake trout focus their spawning.

Egg Development and Incubation

Differences in thermal regimes in deep and shallow water will have substantial consequences for timing of egg deposition, incubation, hatch, and fry survival.

The rate of lake trout egg development, as measured in the laboratory, appears to be related to the number of thermal units, or degree days (= [days since deposition] × [temperature (C)]), to which the eggs are exposed during incubation. Survival to the fry stage in shallow strains is inversely related to total thermal units to which the eggs are exposed,

and is higher when eggs are deposited later in fall at lower temperatures (Casselman 1995). Whether this is true for deep strains such as humper and siscowet is unknown. The relationship between development and temperature is not necessarily linear (Allen *et al.* 2005), and varies among strains, such that development times vary by nearly 50 degree days (Horns 1985). However, the degree-day concept is useful as a model, at least for heuristic purposes, such as searching for potential differences in expected emergence date due to variation in incubation temperature regimes. Given the different thermal regimes on deep and shallow reefs (Fig. 2), these differences may have profound consequences for development and later survival of fry. For example in the hatchery, the Green Lake strain, which represents residual Lake Michigan genetic material, spawns 2 wk earlier than the Apostle Island (Lake Superior) strain (Brown *et al.* 1981). Hence incubation temperatures during development will differ for eggs deposited by the two strains.

Thermal regimes at offshore reefs also have implications for development. For example, the temperature at Sheboygan Reef initially warms during fall in contrast to shallow reefs at which there is only cooling in the fall. (Fig. 2). At shallow reefs, water temperatures peak in late summer and decrease thereafter. At Sheboygan Reef there is a warming in late October or November as the thermocline descends and erodes (Fig. 2). The thermal regimes at Gull Island Shoal (Lake Superior, Bronte *et al.* 1995) and Six-Fathom Bank Lake Huron (Savino *et al.* 1999) are similar to that for northern Lake Michigan, except they are somewhat cooler in September. Winter incubation periods at shallow reefs have temperatures around 0°C, while the Sheboygan Reef temperature record of the winter of 1982–1983 indicated a minimum in March of about 2.5°C. A deep enough reef will likely have a minimum temperature of about 4°C and, if it is deep enough that the effect of the descending thermocline is negligible, then there may not be any annual temperature cycle.

The differences in thermal regime with depth are likely to have an impact on timing of lake trout hatching of sac fry and swim-up stages of post-sac fry. To support this argument and assuming that it takes 700 degree-days to swim-up (from Horns 1985), the effect of early spawning (e.g., 1 Oct. to 15 Oct. about half a month's period) at both Gull Island Shoal and Sheboygan Reef expands the range of swim-up dates to about a month (Table 1). This is due to earlier spawned eggs incubating in warmer

TABLE 1.   *Estimation of time to hatch for lake trout for three locations, assuming 700 degree-days to swim-up. Dates listed as "NA" were ignored for northern Lake Michigan because water temperatures do not drop below 10°C before early November. LS = Lake Superior, LM = Lake Michigan.*

	Fertilization Date				
	1 Oct	15 Oct	1 Nov	15 Nov	1 Dec
Gull Is. Shoal, LS	17 May	17 June	10 Jul	22 Jul	2 Aug.
Sheboygan Reef, LM	7 Mar	2 Apr	30 Apr	22 May	9 June
N. Lake Michigan, LM	NA	NA	NA	10 Jun	18 Jun

water so that they develop through their early stages relatively quickly compared with eggs spawned a half a month later into relatively cool water. The effect of late spawning (e.g., 15 Nov. to 1 Dec.) on a Lake Michigan shallow reef is to temporally concentrate the swim-up dates in spring. A half-month difference in fall spawning date yields about an 8-day difference in spring. This range is somewhat longer for Gull Island Shoal, but is still less than half a month. For Sheboygan Reef the swim-up period is extended beyond the half-month deposition period. The difference between reefs is due to the rapid spring warm-up in shallow water and the lack of much warm-up for Sheboygan Reef. In addition, Casselman (1995) suggested that survival to the fry stage should be higher on deep reefs, as eggs will be spawned at lower temperatures.

Egg and Fry Predation

Differences in predator communities and water temperature regimes on deep and shallow reefs are important for predicting fry production.

Egg predators on shallow reefs are diverse and likely include any fish able to feed on the bottom and swallow a lake trout egg (Prevost 1957, Martin and Olver 1980). In deep water, the community of potential predators is more limited, and consists mostly of deepwater sculpins (*Myoxocephalus thompsoni*) and slimy sculpins (*Cottus cognatus*) (Hudson *et al.* 1995, Janssen *et al.* 2006) and burbot (*Lota lota*). Adult burbot collected with gill nets at East Reef in late October 2002 contained mainly lake trout eggs (from 0 to 47 eggs and 0 to 5 slimy sculpins; D. Janssen, unpublished data). Several stomachs had both eggs and slimy sculpins with digested body walls so these eggs may have originally been eaten by slimy sculpins, but the burbot with the most eggs had no sculpins in their stomachs. Burbot with stomachs filled with lake trout eggs have also been collected in fall on Julian's

Reef, southwestern Lake Michigan (J. E. Marsden, unpublished data). One unknown is the potential impact of deepwater sculpins (*Myoxocephalus thompsoni*). As yet, there have been no studies on lake trout spawning deep enough for these to be more than occasionally found. Slimy sculpins consume lake trout eggs at depths as great as 50 m on the Mid-lake Reef in Lake Michigan and this egg predation is the deepest yet reported (Janssen *et al.* 2006). This depth is still shallower than where deepwater sculpins become common. Two deepwater sculpin were collected in that study and these contained no lake trout eggs (Janssen *et al.* 2006).

Lake trout co-existed with the native deepwater fish community in the Great Lakes and smaller inland lakes. This community has been altered by the declines of coregonines and spoonhead sculpin (*Cottus ricei*) (Madenjian *et al.* 2002). The shallow-water community has become more complex with the introduction of exotic fishes, bivalves, and plankton (e.g., Mills *et al.* 1993), hence predators are likely to be more abundant and diverse in shallow than deep water. Round goby (*Neogobius melanostomus*) consume lake trout eggs in the laboratory (Fitzsimons *et al.* 2006), and emergent fry have been found in the stomachs of alewife (*Alosa pseudoharengus)* and white perch (*Morone americana*: Krueger *et al.* 1995; J. E. Marsden, unpublished data). These changes suggest that the potential for restoration may be higher in deep water that lacks these predators.

If predation on lake trout swim-up fry is a substantial bottleneck to recruitment then hatching and emergence that occurs in a short period of time may be best. As shown for mayfly emergence, a high density of animals can lead to predator satiation, making this strategy useful when predation pressure is high (Sweeney and Vannote 1982).

In lake trout, late emergence may be an advantage, with some risk that early spring warming may subject the fry to lethal temperatures before they

can seek cooler, deeper water. It is likely that swim-up depends on both adequate development and an environmental cue such as a triggering temperature. Conversely, if predation on eggs is a relatively significant source of predation, then a late spawn over a short period may enhance survival because predator metabolic rate is slowed and eggs are dense enough that predators are satiated.

The different temperature regimes on deep and shallow reefs may have important consequences for predation. Egg consumption, and likely fry predation, by sculpins and round gobies declines with temperature, although the relationship with temperature does not also hold for native crayfish (Fitzsimons *et al.* 2006, Ellrott *et al.* in press). On shallow reefs, eggs spawned later would therefore be less vulnerable to predators in fall and early winter. Because deep reefs are warmer in midwinter than shallow reefs, predation pressure may be more severe on lake trout eggs throughout the winter than on shallow reefs. Clearly, how this varies among genetic strains is important.

If food limitation is an important bottleneck then a protracted period of swim-up and first feeding may be an advantage as some individuals would be more likely to emerge with suitable prey diversity and densities. Also exposure to and losses from predation may change with time, therefore the chances of substantial year class failure from these sources are minimized. Rice *et al.* (1987) demonstrated that bloater, *Coregonus hoyi*, a fish that spawns during winter in deep water, have an extended period of swim-up, a characteristic of most coastal marine fishes for which it is argued that the strategy enhances survival in unpredictable environments. Temporal changes in catches of lake trout fry and hatching dates have been demonstrated for lean lake trout in Lake Superior (Bronte *et al.* 1995), and may be common for other morphotypes as well. While lake trout fry are relatively tolerant of starvation (Edsall *et al.* 2003), it is likely that, unless there is a suitable local food resource, fry will disperse.

First Feeding

In deep water local primary production and diversity of prey to support a local food web is less than in shallow water. However, strong currents at reefs can concentrate pelagic prey that derive their food from the photic zone, which would be advantageous to lake trout fry on these locations.

Diet of fishes is determined by a combination of available prey, prey behavior, encounter probability of predator with prey, and the morphological, sensory, and physiological constraints of the predator. Lake trout begin to feed at a relatively large size for fishes, about 25-27 mm total length (TL), while there is still some yolk remaining (Swedberg and Peck 1984).

In water deeper than where local primary production occurs, the ultimate source of energy must come from material physically transported from the photic zone, either by sinking and hydrodynamic processes, the behavior of the prey, or some combination of the two. The constraint of no local primary production should greatly limit the diversity of prey available, and likely their abundance, in deep water. On the other hand, in deep water there is likely to be less competition for food with exotic planktivores, such as alewife and rainbow smelt (*Osmerus mordax*).

If lake trout move into deeper water after hatching, food available to lake trout fry hatched on deep vs. shallow reefs may be similar (Eschmeyer 1956). Bronte *et al.* (1995) found movement of fry from a shallow reef to a deep nursery area (50 m) occurred over a 3-month period, but diet became less diverse at the nursery area (Hudson *et al.* 1995). Whether this is a general pattern for shallow Great Lakes strains of lake trout is unknown, but their results may indicate that shallow waters are not viable nursery areas either because of prey type and abundance or temperature or some other factor.

Diets from young lake trout in shallow water may yield some clues about what types of prey can be captured and consumed. At Presque Isle Harbor (Lake Superior) Swedberg and Peck (1984) found the diet consisted primarily of midge (Diptera: Chironominae) larvae and pupae, with about 2 to 10 times as many pupae as larvae in the diet. Because the pupal stage is very transient, it appears that chironomids are most vulnerable to predation as the pupae ascend to the surface. This is consistent with the observation that other early prey consisted of pelagic Cladocera (*Daphnia, Bosmina*) and copepods. Some ability to capture benthic prey is indicated by the presence of *Chydorus* and chironomid larvae in the diet. DeRoche's (1969) study in inland lakes indicated a diet that was mostly Cladocera, copepods, and chironomid pupae.

Prey diversity is less on deep reefs and at offshore locations. Microcrustaceans at deep reefs are primarily copepods, which peak during spring in Lakes Superior and Michigan (Torke 1975, Lehman and Cacares 1993, Link *et al.* 2004). Cladocerans, which are important in inland lakes and Great

Lakes bays, are absent during spring as they peak in abundance in August and September (Torke 1975, Lehman and Cacares 1993, Link *et al.* 2004). Chironomid pupae are present in the diet of slimy sculpins at Lake Michigan's Mid-Lake Reef Complex, so should be available for small lake trout. Of potentially great importance is the presence of *Mysis relicta (*Crustacea: Mysidacea) in the diets of slimy sculpins at the Mid-Lake Reef Complex at depths (40 m) less than their preferred diurnal depth of about 100 m (Gal *et al.* 1999). Despite the preferred depth, *Mysis* are frequently common at shallower depths, but are generally less abundant than in deeper water. For example, Pothoven *et al.* (2000) found a nearly perfect pattern of greater densities at a 110 m station vs. a 40–45 m station (one exception for 19 sampling days) in southeastern Lake Michigan, an area without many reefs (Janssen *et al.* 2005). The *Mysis* density at the shallower station was extremely variable over time with a range from 6 to 255 individuals/m^2 compared with a range of 51 to 458 individuals/ m^2 for the deeper station. It would be interesting to know whether the apparent increased variation at the shallow site was due to hydrodynamic phenomena, such as upwelling and downwelling, which are primarily nearshore phenomena (Mortimer 2004). During such upwellings *Mysis* can be found as shallow as 7 m in Lake Michigan (Janssen, unpublished observations). At the Mid-Lake Reef Complex and other deep reefs it is likely that currents carry *Mysis* over reefs during their nocturnal vertical migration and they become stranded on the reefs as they descend at dawn. At Sheboygan Reef the current strength and direction is extremely variable (Gottlieb *et al.* 1989), which would explain the great temporal and spatial variation in *Mysis* density and consumption by slimy sculpins at Sheboygan Reef, Lake Michigan (Houghton 2006). This phenomenon has also been suggested for oceanic sea mounts (Fock *et al.* 2002).

Strictly benthic prey may not be very vulnerable to predation by lake trout fry. Slimy sculpin collected in the same beam trawl tows as lake trout fry in Lake Superior (Hudson *et al.* 1995) contained mysids, as did the small lake trout, but also consumed *Diporeia* spp. (Crustacea: Amphipoda), isopods, benthic copepods, and snails. The difference in diet indicates prey selectivity by both species, and reflects a difference in the morphological/sensory/physiological constraints of the two species.

At present our only data on early diet of lake trout at deep reefs is a 28-mm fry with some yolk, captured by beam trawl (as in Hudson *et al.* 1995) in about 50 m in mid-June 2006. The individual had consumed one calanoid copepod and one cyclopoid copepod.

Swim Bladder Inflation and Neutral Buoyancy

Hatching in deep water may require alternative physiological or behavioral adaptations for filling the gas bladder and coping with buoyancy.

There are two challenges regarding swim bladder inflation for a fish that lives in deep water. The first challenge is initial inflation of the swim bladder, which requires, as far as is known, ascent to the surface to swallow a bubble of air. The second is regulation of the amount of air in the swim bladder to keep the fish neutrally buoyant.

Lake trout and other salmonines have an unusual combination of plesiomorphic and derived swim-bladder attributes. The plesiomorphic attribute is that lake trout are physostomes (Berinbrink *et al.* 2005) and the derived attribute is that they lack a gas-generating *rete mirabile*. The physiological mechanism by which a *rete mirabile* deposits gas in the swim bladder is by release of oxygen from hemoglobin by the Root effect. Some carbon dioxide is also generated, but is quickly absorbed and limited nitrogen gas is released by "salting out" (Pelster 1998). The *rete mirabile* is retained in *Coregonus* and *Thymallus,* but lost in *Oncorhynchus.* This is consistent with earlier observations that brown trout, *Salmo trutta*, rainbow trout *Oncorhynchus mykiss*, and lake trout cannot generate gas to fill their swim bladders while lake whitefish (*Coregonus clupeaformis*) and lake herring (*C. artedii*) can (Tait 1959). Tait (1959) found that lake whitefish and lake herring, when placed under increased pressure, can secrete oxygen-rich gas. He also determined that salmonine gas bladders lacked oxygen so the gas must be derived from some source other than a *rete mirabile.*

Lake trout have evolved a thick-walled swim bladder for maintaining neutral buoyancy at great depths. The thick wall resists gas loss by reducing dissolution into the blood under hydrostatic pressure (Tait 1960). There is a genetic basis for this adaptation (Ihssen and Tait 1974) and we expect that deepwater forms are particularly resistant to gas loss by dissolution.

Even without a *rete mirabile*, Tait (1959) found that lake trout captured from about 36 m had suffi-

cient gas in their swim bladders to maintain neutral buoyancy, so presumably these fish obtained gas at that depth. Experiments to determine whether lake trout under pressure could capture gas from the swim bladders of prey (i.e., fishes with swim bladders and *Chaoborus* larvae, a dipteran with gas vesicles) indicated that lake trout lost swim bladder gas and buoyancy during these experiments through dissolution (Tait 1959).

Initial inflation of the swim bladder is relatively simple for most salmonines that emerge in streams, but more difficult for lake trout emerging from deep water as they must swim great vertical distances to the surface. Lake trout fry with an unfilled swim bladder require less than an hour to swim 100 m upward and can swim vertically upward 270 m without a noticeable change in speed (Tait 1960). A second challenge is that fry may gain little advantage when it returns to the bottom because the swim bladder will be compressed as the fry descends. If the fry has neutral buoyancy at the surface and descends to 50 m (about 600 kpa or 6 total atmospheres pressure) the volume of air is approximately 1/6 that at the surface according to Boyles Law. It may be that fry remain pelagic for some time, but this only delays the problem of maintaining buoyancy at depth using the swim bladder. A third challenge is that the fry would be subject to predation by pelagic fishes during this phase as has been demonstrated for the non-indigenous alewife (Krueger *et al.* 1995). Whether native pelagic fishes such as *Coregonus* spp. are important predators on swim-up fry of deepwater forms of lake trout is unknown.

Unlike physoclistous fishes, initial filling of the swim badder can be delayed in salmonines. The seven species of salmonines studied by Tait (1960) all retained the ability to inflate the swim bladder apparently indefinitely. Thus it is possible for the ascent to the surface to be delayed until the fish is larger and perhaps a more competent swimmer. However, the fry must then be able to feed competently and escape predators without the use of the swim bladder.

The lack of swim bladder inflation can have serious consequences for survival. Larval yellow perch that had failed to fill their swim bladders had slower growth rate, were less able to capture evasive prey such as copepods, used more energy when swimming, and were more vulnerable to predation (Czesny *et al.* 2005). Lake trout fry are considerably larger than yellow perch fry, but an under-filled swim bladder increases the energetic cost of

swimming for salmonines much larger than their fry. Swimming efforts of adult chum salmon (*Oncorhynchus keta*) were greater as depth increased, which was attributed to loss of buoyancy from a compressed swim bladder (Tanaka *et al.* 2001). Thus the costs of not being neutrally buoyant extends from small (yellow perch larva; about 5–6 mm) to large fish (chum salmon; about 500 mm TL), so presumably there are costs to lake trout fry which are about 25–30 mm at swim-up.

However, lack of swim bladder inflation is not necessarily lethal as some populations of Eurasian perch (*Perca fluviatilis*) include individuals with uninflated swim bladders (Egloff 1996). These populations occur where there is little fish species diversity so the biotic selective forces of competition and predation may be diminished.

At present the mechanism by which deepwater lake trout obtain and maintain swimbladder gas is unknown. Tait (1959) tested whether lake trout could attain initial inflation by "piracy" of gas from other fishes with swim bladders consumed. Such piracy would require that the prey's swim bladder gas bubble move anterior from the stomach to the esophagus, then enter the swim bladder duct. While Tait obtained no positive result using a shallow strain of lake trout, fry from a deep water strain may produce different results. For the Great Lakes the likely native prey sources for gas piracy would be the physostomus deepwater coregonines (*Coregonus* spp.) and the physoclistous burbot.

We propose that future research focus on swim bladder inflation of fry of deep water lake trout to determine whether they can initiate swim bladder inflation by use of gas in prey. One possibility not considered by Tait (1959) is the gas bubble present in emerging chironomid pupae. Chironomid pupae generate a gas bubble to aid their ascent to the surface for emergence; these prey pupae are important in the diet of lake trout fry (Hudson *et al.* 1995) and are in the diet of slimy sculpin at Lake Michigan's deep reefs (Houghton 2006). The gas in a chironomid pupa's bubble is probably more available than that of *Chaoborus* because it is a transient feature rather than contained in a structure used for buoyancy regulation.

Interactions between First Feeding, Initial Swim-bladder Filling, and Homing

Imprinting on spawning sites has been suggested for lake trout but has never been demonstrated (see Eshenroder *et al.* 1995). Natal spawning site hom-

ing has been clearly shown for salmonines (Hasler and Scholz 1983) and Horrall (1981) discussed in detail the evidence for homing in lake trout. He felt that the critical imprinting stage was from hatching to at least the yolk-sac stage and probably to the swim-up stage. There is evidence of many different strains of lake trout in Lake Michigan historically, which suggests homing behavior to maintain genetic isolation of these stocks (Brown *et al.* 1981) and there is documented repeat spawning at the same site by lake trout (MacLean *et al.* 1981, Swanson and Swedberg 1980). Spawning lake trout and Arctic char (*Salvelinus alpinus*) also seem to be attracted to characteristic odors at sites (Doving *et al.* 1980).

Some evidence for imprinting is suggested by Bronte *et al.* (2002), when a spawning population was restored by incubating eggs in Astroturf bundles on a small offshore reef. If imprinting to natal spawning sites occurs during or shortly after incubation in deep water lake trout, then this feature would be important for restoration. However if deepwater lake trout ascend to the surface to fill their swim bladders then there is a risk that they will be displaced by currents from natal areas at descent. This risk may not be important if imprinting has already occurred. Current speeds of 15 cm sec^{-1} are common at Sheboygan Reef, Lake Michigan (Gottlieb *et al.* 1989) so a 1-hr time to ascend and descend would place the fry about 0.5 km from where it originated. On small deep reefs, such as Julian's reef, Lake Michigan, fry would be moved off of the reef. Displacement off the reef could also occur on East Reef, Lake Michigan, where eggs, embryos, and fry have been collected on the eastern edge, where depths descend rapidly from about 50 m to 100 m over a horizontal distance of about 500 m. If the risk of displacement is substantial, imprinting should occur in lake trout as sac fry prior to emergence. However, because lake trout stocked as yearlings seem to have a modest ability to return to stocking locations as adults (Bronte *et al.* in press), it suggests that some imprinting may occur later in life.

A nursery area near where lake trout emerge would facilitate imprinting by allowing a longer exposure period. It may be important that the nursery area for Gull Island Shoal is adjacent to the spawning shoal so the lake trout fry remain exposed to the chemical cues responsible for imprinting (Bronte *et al.* 1995, Hudson *et al.* 1995).

Implications for Future Research

The questions we raised about deepwater spawning by stocked lake trout highlight the need for further research on reproduction of wild deep water lake trout. In particular, advances in technology are needed to quantitatively sample spawners, eggs, and fry so that densities of these life stages on deep reefs can be compared with data for shallow reefs. This work presents unique challenges not just due to depth (50–100 m), but because the sites of interest are farther offshore (30–50 km) and logistics are more complicated by weather. Effects of storms are greater in open water, and transit times are long and limit working time particularly when severe weather is imminent. Deployment of gear is more difficult at these depths and must rely more on remote sensing than on traditional, direct-sampling methods used in shallow water. Using divers to set or retrieve gear in some habitats (e.g., deep reefs) may be limited to mixed-gas scuba or may be impossible. For these reasons, research time during the lake trout spawning season is limited; it is unlikely that detailed data on egg deposition and fry emergence over time acquired on shallow reefs, which requires weekly or more frequent visits to sites, will be practicable. Testing of new methodologies on shallow reefs is recommended before expending valuable offshore time in deployment.

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