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Spawning Site Selection and Fry Development of Invasive Lake Trout in Yellowstone Lake, Yellowstone National Park, Wyoming

Lee Simard
University of Vermont

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SPAWNING SITE SELECTION AND FRY DEVELOPMENT OF INVASIVE LAKE TROUT IN YELLOWSTONE LAKE, YELLOWSTONE NATIONAL PARK, WYOMING

A Thesis Presented

by

Lee Gregory Simard

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of

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Thesis Examination Committee:

J. Ellen Marsden, Ph.D., Advisor
Charles J. Goodnight, Ph.D., Chairperson
Jason D. Stockwell, Ph.D.
Cynthia J. Forehand, Ph.D., Dean of the Graduate College
ABSTRACT

Since their discovery in Yellowstone Lake in 1994, Lake Trout (*Salvelinus namaycush*) have been the object of an intensive gillnet suppression program due to their predation on native Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*). Managers are also interested in targeting early life stages to augment suppression. A benthic sled was used to sample for Lake Trout eggs at 24 locations, hypothesized to be spawning sites, that encompassed a range of depths, slopes, and substrate composition to determine the location and characteristics of spawning sites in Yellowstone Lake. Lake Trout eggs were collected at seven sites, five of which had not been previously confirmed as spawning sites. Habitat characterization at these sites indicate Lake Trout spawning in Yellowstone Lake is limited to areas with rocky substrate, but is not constrained to areas with interstitial spaces or contour breaks as is seen within the species’ native range. Lake Trout fry were captured around Carrington Island, an additional spawning site in Yellowstone Lake, in 2014 and 2015. These fry were significantly larger at each developmental stage, consumed more food beginning at earlier stages, and were captured much later into the summer than fry captured at a spawning site in Lake Champlain. The lack of potential egg and fry predators in Yellowstone Lake could be driving these differences in spawning site selection and fry behavior. This information will allow managers to identify additional spawning locations for suppression and evaluate the impact their efforts might have on the Lake Trout population in Yellowstone Lake.
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CHAPTER 1: LITERATURE REVIEW

Introduction

Lake Trout (*Salvelinus namaycush*) are a large-bodied species of fish in the Salmonidae family that is highly sought after throughout the northeastern United States, Great Lakes region, and most of Canada. Both recreational and commercial fishermen target this species, which is praised for its high quality as a food resource. Large commercial fisheries existed in all of the Great Lakes until habitat degradation, overfishing, and the invasion of invasive Sea Lamprey (*Petromyzon marinus*) collapsed nearly all Lake Trout stocks (Scott and Crossman 1973). Lake Trout have since been at the center of an intensive restoration effort; Sea Lamprey control and the stocking of millions of yearling Lake Trout has successfully restored large adult populations in each lake (Hansen 1999). While survival of stocked yearlings is high, natural recruitment has only been successful in Lake Superior and, in recent years, portions of lakes Huron and Michigan (Hansen et al. 1995, Riley et al. 2007, Hanson et al. 2013). This slow recovery spurred extensive research evaluating Lake Trout spawning and egg and fry survival throughout the Great Lakes in an attempt to understand the factors limiting recruitment.

While scientists and managers are working hard to restore Lake Trout in portions of its native range, others are trying to reduce populations of invasive Lake Trout in many systems beyond its native range. Lake Trout were introduced by state and federal agencies into many systems in the western United States to create new sport fisheries, but have also expanded into new areas through illegal introductions or by traveling through connected waterways (Martinez et al. 2009). Lake Trout are a
phenotypically plastic species and have been very successful in colonizing many of these ecologically different systems (Eshenroder et al. 1995b, Martinez et al. 2009). Although highly popular Lake Trout sport fisheries have been created, Lake Trout are also dramatically disrupting the natural communities of many systems primarily through the predation of native trout species. In Yellowstone Lake, for example, Lake Trout predation on native Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*) is having impacts on the entire Greater Yellowstone ecosystem (Koel et al. 2005). Suppression efforts integrating many techniques that target multiple life stages are being implemented in Yellowstone Lake and other systems in an attempt to reduce the Lake Trout population sizes and limit their impacts (Gresswell et al. 2015).

**Range and diversity**

Lake Trout are naturally distributed throughout all Canadian provinces except Prince Edward Island and insular Newfoundland and exist in northern states from Maine to Minnesota plus parts of Montana and Alaska (Martin and Olver 1980, Crossman 1995). The current native range of Lake Trout occurs almost completely within the extent of Pleistocene glaciation indicating most of its dispersal has occurred since the recession of the Wisconsin ice sheet (Lindsey 1964). Lake Trout are believed to have found refugia during glacial periods north of the glacial extent in portions of Alaska and south in portions of the upper Mississippi drainage, the upper Missouri River, and along the Atlantic coast (Lindsey 1964, Khan and Qadri 1971). From these refugia, Lake Trout likely used temporary pondings, large glacial lakes, and interconnected waterways created as the glacial boundary retreated to establish its present range (Lindsey 1964, Khan and Qadri 1971).
Lake Trout are a phenotypically plastic species that has the ability to adapt to a wide range of environmental conditions (Eshenroder et al. 1995b). The species is commonly associated with large, deep lakes, but can also be found in small, shallow bodies of water in alpine, subalpine, and arctic areas where water temperatures remain cold throughout the year (Martin and Olver 1980). They are also able to inhabit great depths and have been caught as deep as 426 m in Great Bear Lake (Martin and Olver 1980). Lake Trout are also found in large, clear arctic rivers for either part or all of the year (Ellis 1962, Martin and Olver 1980). Lake Trout usually shift from planktivory to piscivory as they become larger (Martin and Olver 1980); however, diet can vary dramatically between systems. In habitats where forage fish are absent, Lake Trout remain planktivorous throughout their life (Scott and Crossman 1973, Martin and Olver 1980). Lake Trout are second only to Chinook salmon (*Oncorhynchus tshawystcha*) in terms of maximum size among North American salmonids (Donald and Alger 1986), but can vary widely in length and weight depending on the food resources available (Martin 1966, Plosila 1977, Martin and Olver 1980). Maximum sizes range from 500g in otherwise fishless lakes (Donald and Alger 1986) to the world record caught in Lake Athabasca, Saskatchewan, Canada that weighed 46.3kg (Scott and Crossman 1973). Lake Trout also have long lifespans and can likely live over 50 years (Power 1978, Schram and Fabrizio 1998). The plasticity of these traits has allowed the species to originally colonize a wide range of systems, including the cold, harsh environments of glacial meltwater systems, prior to most other species (Balon 1980, Evans and Olver 1995).
Considerable genetic diversity exists among Lake Trout populations (Krueger et al. 1989, Marsden et al. 1993, Krueger and Ihssen 1995) and many of the larger differences in characteristics are a result of genetic differentiation. The differences in fat content in Lake Superior leans and siscowets, two of four distinct morphotypes that are commonly seen in Lake Superior (Muir et al. 2014, Hansen et al. 2016), are genetically based as both types have been shown to breed true to their form on the same diet in a hatchery and have intermediate fat contents when hybridized (Eschmeyer and Phillips 1965, Stauffer and Peck 1981, Goetz et al. 2010). Variability in spawning depth and timing also has a genetic basis (Krueger et al. 1983, Elrod and Schneider 1987); however, a genetic basis has not been found for many other characteristics. For example, two morphologically distinct groups living at discrete depths in Flathead Lake, Montana were shown to be genetically similar and separated instead by food resource partitioning (Stafford et al. 2013).

**Lake trout spawning**

*Spawning behavior aspects*

Many facets of spawning are notably plastic between different Lake Trout populations. Lake Trout are iteroparous spawners that produce relatively few (880-2640/kg), large eggs, approximately 5 mm in diameter (Scott and Crossman 1973, Auer 1982, Evans and Olver 1995). Spawning occurs once a year generally between August and December (Milner 1874, Koelz 1926, Miller and Kennedy 1948, Royce 1951, Eschmeyer 1955, Rahrer 1965, Goodier 1981), although ripe males and females have been captured into January in Lake Tahoe (Martin and Olver 1980) and throughout the summer beginning as early as late-April in Lake Superior (Eschmeyer 1955, Bronte
Once fish begin to appear on a site, the spawning period can range from less than a week to upwards of two months (Martin and Olver 1980). Both the timing and duration of a spawning season can vary in response to environmental conditions (Martin and Olver 1980). Temperature appears to be a primary driver with the start of spawning occurring as temperatures drop to 10-12°C and the lake turns over (Royce 1951, DeRoche and Bond 1957, McCrimmon 1958, Rawson 1961, DeRoche 1969, Martin and Olver 1980, Casselman 1995). Strong shoreward winds may also drive spawning, either by accelerating lake turn-over, clearing sediment from spawning substrate, or by acting as a general cue for movement toward spawning reefs (Royce 1951, Martin 1957, McCrimmon 1958, DeRoche 1969, Martin and Olver 1980, Esteve et al. 2008, Muir et al. 2012). A decreased photoperiod may also be an environmental cue, especially at deep spawning sites where temperature and turbulence remain constant year-round (Bronte 1993). Royce (1951) and McCrimmon (1958) found evidence that suggested increased cloudiness and cooler temperatures during the months prior to spawning could advance the spawning date and reduce the duration of the spawning period.

Sampling has provided demographic information about assemblages of Lake Trout at spawning sites, but detailed spawning behavior has only recently begun to be described. Males tend to appear at spawning sites earlier in the season than females, remain at the site longer, and are present in higher numbers (Royce 1951, Eschmeyer 1955, Martin 1957, DeRoche 1969, Noakes and Curry 1995, Bronte et al. 2007, Muir et al. 2012). Spawning primarily occurs nocturnally, but has been documented during the day (Gunn 1995, Esteve et al. 2008, Binder et al. 2015). The majority of Lake Trout will begin to move onto the site during the evening and begin a courtship process
consisting of a series distinct behaviors described by Esteve et al. (2008) and further detailed by Binder et al. (2015). Small groups of males, between two and six individuals, will hover with a female for a period of time above the bottom and then begin traveling together with the males swimming tightly beside the female. The group will then stop, sink to the bottom, and the males and female will quiver and release gametes together. This process is likely repeated with individual males and females spawning multiple times. Competition among males during spawning is common among other members of the Salmonidae family, especially during instances with a male-skewed sex-ratio (Clutton-Brock and Parker 1992, Kvarnemo and Ahnesjo 1996); however, very little aggression has been seen between Lake Trout males. Males will commonly jockey amongst themselves for the position nearest the female, but otherwise no other mate selection process is apparent (Gunn 1995, Esteve et al. 2008, Binder et al. 2015).

Unlike other members of the Salmonidae family, Lake Trout do not construct redds; eggs are deposited over existing substrate where they settle into interstitial spaces (Cuerrier and Schultz 1950, Royce et al. 1951, Eschmeyer 1964, DeRoche 1969, Martin and Olver 1980, Marsden et al. 1995a). As eggs settle, they water harden and entrain into spaces where they are protected from dislodgement and predation (Stauffer and Wagner 1979, Balon 1980, Marsden et al. 1995a). River spawning historically occurred in several Lake Superior tributaries and rivers within the arctic and Lake Nipigon (Dymond 1926, Loftus 1958, Martin and Olver 1980, Goodier 1981). This reproductive strategy was likely a primitive characteristic held over from periods of glaciation when riverine systems were used as refugia (Eshenroder et al. 1995b). In some instances,
Lake Trout appear to actively clean the spawning area of loose sediment to clear interstitial spaces by rapidly swimming over or fanning the substrate (Royce 1951, Martin 1957, DeRoche and Bond 1957, Eschmeyer 1964, Foster 1985). However, any cleaning may be a passive result of many fish swimming over the area (DeRoche 1969, Esteve et al. 2008) or simply a means of detecting infilling that is not readily apparent from the surface (Marsden and Krueger 1991). While silt and other fine sediment may temporarily be removed from a site by this perceived cleaning action, eggs deposited at sites prone to heavy siltation may be suffocated overwinter as new material is deposited (Royce 1951, Sly and Widmer 1984, Sly 1988, Marsden and Krueger 1991).

*Spawning site selection*

Lake Trout spawning is primarily associated with sites with multi-layered rocky substrate; however, specific characteristics such as area, rock size, amount of interstitial space, depth, and slope can vary substantially (Marsden et al. 1995a). The area of Lake Trout spawning sites varies from as small as rock piles less than 5 m in diameter (Marsden et al. 1995a, Marsden et al. 1995b) to the Lake Michigan Mid-Lake Reef Complex that is 2,859 km², although only small areas of the reef may be suitable for spawning (Holey et al. 1995, Janssen et al. 2006).

Particle size influences the amount of interstitial space available, and thus the depth that eggs can penetrate into the substrate (Marsden and Krueger 1991). The actual depth eggs need to permeate to be protected is site-specific; variability in predator composition and environmental factors such as fetch, wave energy, and underwater currents between sites will change the forces that act upon eggs (Marsden et al. 1995a, Fitzsimons and Marsden 2014). Substrate size has been characterized by various terms,
frequently without any reference scale, creating challenges when comparing among studies. Marsden et al. (1995a) suggested using a modified scale based on Wentworth (1922) that splits particle size into six categories ranging from fines to boulders. Using this scale, spawning typically occurs over areas with cobble (257-999 mm) to boulder (>999 mm) sized substrate which provides ample interstitial space for eggs to settle into (Royce 1951, DeRoche 1969, Fitzsimons 1995, Marsden et al. 1995a, Janssen et al. 2006); small gravel or mixed sized substrate is also utilized (Tibbits 2007), but does not allow eggs to permeate as deeply (Marsden et al. 1995a). Although eggs that settle deeper are more protected from predation and physical forces, those that settle to basal substrate will likely encounter accumulated organic material that could suffocate eggs through an elevated biological oxygen demand (Sly 1988).

Historical records from commercial fishermen in the Great Lakes suggest that Lake Trout also spawned at sites with sand, clay, or bedrock bottoms (Coverly and Horral 1980, Goodyear et al. 1982, Holey et al. 1995); however, few spawned eggs have been found at sites with these characteristics. Lake Trout eggs were found entrained in pitted or honeycomb rocks brought up in gillnets in Lake Superior (Milner 1874). In Lake Tahoe, Lake Trout spawn over beds of the macrophytes Chara delicatula 15-30 cm tall rather than over rocky substrate (Beauchamp et al. 1992). Eggs spawned over these macrophytes settled into the lower third of the plant’s strands and were provided a similar level of protection from predators and dislodgement as eggs spawned over multi-layered cobble (Beauchamp et al. 1992). The lack of additional evidence for spawning at sites without multi-layered rock substrate may be a result of limited sampling effort at alternate sites rather than an actual representation of Lake
Trout spawning site selection. Most Lake Trout egg sampling has been focused on sites with characteristics that match those where spawning is usually confirmed, rather than searching across a broader range of substrate types; areas without interstitial spaces are usually assumed to be inadequate for Lake Trout spawning and not assessed for egg deposition after initial evaluation (Nester and Poe 1987, Horns et al. 1989, Marsden 1994, Fitzsimons 1995, Marsden et al. 1995a, Ellrott and Marsden 2004, Claramunt et al. 2005). Although spawning may occur at locations that provide limited protection for eggs, the proportion of eggs that survive is unknown and may be considerably lower than at sites where eggs are more protected (Marsden et al. 1995b).

Lake Trout spawning depths are also highly variable, likely as a result of geomorphological shifts across the species’ native range. In many lakes, spawning sites are usually located in shallow, shoreline areas (Eshenroder et al. 1995a); however, deep-water sites are often used in larger systems, especially throughout the Great Lakes (Holey et al. 1995; Janssen et al. 2006; Riley et al. 2011). Lake Trout spawning has been confirmed at sites ranging from <1 m (Martin 1957, McCrimmon 1958, DeRoche 1969) to as deep as 50 m in Lake Michigan (Marsden and Janssen 1997, Janssen et al. 2006, Riley et al. 2011) and 60 m in Lake Tahoe (Beauchamp et al. 1992). Historic maps of suspected spawning sites in the Great Lakes and the capture of ripe male and female Lake Trout at sites up to 182 m deep suggest spawning likely occurs at even greater depths (Goodier 1981, Hansen et al. 1995). Nearshore spawning may have been an evolutionary advantage for Lake Trout when glaciers retreated and shoreline erosion was the primary source for rocky substrate (Eshenroder et al. 1995b). The development of deep-water strains in the Great Lakes may have then occurred as water levels
increased and shallow spawning sites were further submerged (Hough 1963, Eshenroder et al. 1995b). Lake Trout populations that utilized previously shallow locations could have evolved with the changing water levels into separate strains that inhabited and spawned in deeper water (Eshenroder et al. 1995b). Although Lake Trout eggs have been found at several deep spawning sites, the extent to which most historically identified deep sites are currently used is unknown. The abundance of adult Lake Trout captured during the spawning season at offshore sites in Lake Michigan suspected of being spawning locations was higher at locations where stocking had occurred than at areas that had not been stocked (Bronte et al. 2007). This suggests site-specific stocking may be increasing the usage of deep, offshore sites; however, logistical challenges associated with surveying deep, offshore sites during difficult fall weather has limited the amount of egg sampling at most of these locations (Marsden et al. 1995a, Janssen et al. 2006).

Lake Trout spawning sites are often characterized as having steep slopes or edges (Marsden and Krueger 1991, Marsden 1994, Casselman 1995, Fitzsimmons 1995, Kelso et al. 1995). Slopes may direct stronger currents that would improve water quality and clear sediment from interstitial spaces (Marsden et al. 1995a). Slopes could also provide a structure for fish to congregate around (Marsden and Krueger 1991). The highest egg and hatched fry densities are usually found along the upper edges of slopes, although many eggs that do not become entrained are commonly found aggregated along the bottom edge (Dorr III et al. 1981, Marsden and Krueger 1991). Historical records suggest spawning also occurred across areas of flat lake bed (Coberly and
Horrall 1980, Goodyear et al. 1982), but has only infrequently been confirmed through the detection of eggs (Marsden 1994).

**Lake Trout in the Great Lakes**

Stock recovery efforts

Given the economic and ecological importance of Lake Trout to the Great Lakes region, there was a strong motivation from all stakeholders to coordinate and implement Lake Trout restoration plans. The Great Lakes Fishery Commission was formed in 1955 with the authority to direct Sea Lamprey control and Lake Trout restoration efforts, and coordinate fisheries research among managers from the United States and Canada for each lake (Hansen 1999, GLFC 2012). Restoration plans were established for each lake that involved setting stocking levels, fishery regulations, and Sea Lamprey control objectives (Schneider et al. 1983, LSLTTC 1986, Hansen 1996, Ebner 1998, Hansen 1999, Bronte et al. 2008, Markham et al. 2008). Sea Lamprey control first began in the early 1950s in lakes Huron, Michigan, and Superior using physical barriers to block and capture Sea Lampreys in tributary streams; however, the greatest impacts to Sea Lamprey populations came after the discovery of selective chemical lampricides (Smith and Tibbles 1980, Hansen 1999). These treatments began as early as 1958 in Lake Superior and allowed Lake Trout stocking to begin (Smith and Tibbles 1980).

Juvenile Lake Trout stocking began in the early 1950s in Lake Superior to prevent the complete collapse of the remaining wild populations, but little improvement was seen until the final commercial fisheries were closed in 1962 (Pycha and King 1975, Hansen et al. 1995, Hansen 1999). Stocking was intensified in Lake Superior at the onset of chemical lampricide treatments, and then began in Lake Michigan in 1965,
Lake Huron in 1969, Lake Erie in 1978, and Lake Ontario in 1972 once Sea Lamprey populations were substantially reduced and other environmental factors were addressed (Cornelius et al. 1995, Elrod et al. 1995, Eshenroder et al. 1995c, Holey et al. 1995). Spring-stocked yearling Lake Trout made up the vast majority of stocked fish in each lake as they were shown to have four to ten times the survival rate of fall fingerling stocked fish (Buettner 1961, Pycha and King 1967). The number of Lake Trout stocked varied between years, but was generally between 2-3 million fish per year in Lake Superior (Hansen et al. 1995), around 2.4 million fish per year in Lake Michigan (Holey et al. 1995), 2 million fish per year in Lake Huron (Eshenroder et al. 1995c), between 1.5-2.5 million fish per year in Lake Ontario (Elrod et al. 1995), and generally a little over 200,000 fish per year in Lake Erie (Cornelius et al. 1995). Many different Lake Trout strains have been stocked into the Great Lakes to maximize genetic diversity; however, the survival, growth rate, spawning success, and adaptability to different environments in the Great Lakes of these strains has been highly variable (Schneider et al. 1983, Krueger et al. 1989, Marsden et al. 1989, Burnham-Curtis et al. 1995, Krueger and Ihssen 1995, Page et al. 2003, Bronte et al. 2007). Despite high survival of stocked yearling Lake Trout and the establishment of adult populations in each of the lakes, recruitment of wild fish was initially only detected in Lake Superior (Cornelius et al. 1995, Eshenroder et al. 1995c, Hansen et al. 1995, Holey et al. 1995, Elrod et al. 1995, Hansen 1999). Insufficient spawning habitat due to physical and chemical degradation of historic sites was suspected as a factor limiting recruitment (Dorr III et al. 1981, Sly and Widmer 1984); however, surveys confirmed an abundance of sites with high quality substrate in each of the lakes, including many where successful spawning was occurring.
(Jude et al. 1981, Nester and Poe 1984, Peck 1986, Marsden et al. 1988, Kelso et al. 1995, Marsden and Janssen 1997, Fitzsimons and Williston 2000, Ellrott and Marsden 2004). Density of spawning adults could also have been a limiting factor. Other than in Lake Erie, hatchery limitations kept the annual stocking levels below restoration targets (Hansen 1999). Additionally, mortality due to Sea Lamprey and commercial fishing, although reduced, remained high (Selgeby et al. 1995). When combined, these factors kept adult Lake Trout densities below levels considered sufficient for successful wild recruitment in many areas of the lakes (Selgeby et al. 1995). Even in areas where densities were sufficient, wild Lake Trout were not being recruited into the population, suggesting bottlenecks affecting early-life stages were resulting in failed recruitment (Selgeby et al. 1995).

*Potential recruitment bottlenecks*

The high survival of stocked fingerling Lake Trout suggested that a bottleneck between spawning and the end of the first year of life was contributing to this lack of recruitment. This bottleneck could have occurred due to high mortality during a number of different critical phases including egg incubation or fry development, or it could also have been a result of Lake Trout stocking practices in the Great Lakes.

Factors affecting egg survival have been extensively evaluated as potential contributors to the recruitment bottleneck. Eggs may die due to intrinsic problems (lack of fertilization, developmental issues), overwinter egg mortality can be caused by poor water quality, siltation that smothers and suffocates eggs, predation, and physical disturbance from water movement (Casselman 1995, Claramunt et al. 2005, Fitzsimons et al. 2007). Egg mortality due to poor water quality and siltation has frequently been
measured using egg incubators (Casselman 1995, Edsall et al. 1995, Eshenroder et al. 1995a, Manny et al. 1995, Marsden et al. 1995b) and has been shown to range widely from 1% at a site in Lake Superior (Eshenroder et al. 1995a) to 49% at sites in Lake Michigan (Edsall et al. 1995) depending on site conditions and incubator placement (Eshenroder et al. 1995a, Marsden et al. 1995b). Predation can be a significant factor reducing egg survival (Fitzsimons et al. 2007). The impact of interstitial predators on overwintering eggs is dependent upon predator density and size, egg density, substrate size, and factors, such as temperature, that affect metabolism (Chotkowski and Marsden 1999, Savino et al. 1999, Claramunt et al. 2005). Epibenthic predators will eat eggs before they settle into the substrate; however, their impact is likely limited as only a small proportion of eggs remain on the surface of the substrate (Savino et al. 1999). Interstitial predators such as Sculpin (Cottus spp.) and crayfish (Orconectes spp.) have a greater impact than epibenthic predators, as they are able to access eggs that have settled deep into the substrate (Stauffer and Wagner 1979, Jones et al. 1995, Chotkowski and Marsden 1999, Fitzsimons et al. 2002, Marsden and Tobi 2014). Savino et al. (1999) modeled the cumulative effects of epibenthic and interstitial egg predators and fry predators on the percent of spawned eggs that survive to swim up and estimated between 0% and 80% survival for starting densities of 100 eggs*m$^{-2}$ and 1,000 eggs*m$^{-2}$, respectively. Physical disturbance also plays a factor in egg survival as wind-driven waves and currents can cause mortality by displacing eggs out of the substrate (Ventling-Schwank and Livingstone 1994, Roseman et al. 2001, Fitzsimons et al. 2007, Fitzsimons and Marsden 2014) or by damaging them through direct physical shock (Fitzsimons 1994). The impact of these forces is influenced by depth and the
fetch associated with prevailing winds and can potentially have a greater impact than predation (Fitzsimons et al. 2007). Sites in Lake Michigan with an average fetch of 26.3 ± 4.5 km lost, on average, 75.6 ± 2.4% of seeded eggs in egg bags left out for an average of 25 days (Fitzsimons et al. 2007). However, egg bags in Parry Sound, Lake Huron with an average fetch of 1.9 ± 0.64 km only lost, on average, 47.8 ± 3.1% of seeded eggs over 19 days (Fitzsimons et al. 2007). Claramunt et al. (2005) seeded egg bags that were retrieved at different time intervals and found egg loss was greatest immediately after seeding. After two weeks, losses were minimal as the eggs that were most vulnerable to loss from physical disturbance were removed soon after they were seeded, leaving only those eggs that were protected within the substrate.

High fry mortality may also have contributed to lack of Lake Trout recruitment. Lake Trout fry generally remain on spawning reefs until they have utilized most of their yolk sac and then move off the reef into deeper water (Miller and Kennedy 1948, Eschmeyer 1955, Eschmeyer 1956, DeRoche 1969, Jude et al. 1981, Bronte et al. 1995), although Peck (1982) demonstrated that fry may remain in shallow water near the spawning site for several months if water temperatures remain low. While fry are resident on spawning reefs, they are vulnerable to predation from both interstitial and epibenthic predators such as sculpin, round gobies, yellow perch (Perca flavescens), burbot (Lota lota), suckers (Catostomus spp), and rainbow smelt (Osmerus mordax), many of which are common in high densities around rocky sites where Lake Trout spawn (Stauffer and Wagner 1979, Jones et al. 1995, Chotkowski and Marsden 1999, Riley and Marsden 2009). Krueger et al. (1995) demonstrated that non-native alewife (Alosa pseudoharengus) were present around Lake Trout spawning reefs in Lake
Ontario during the spring period when Lake Trout fry were most vulnerable, and consumed fry (Baird and Krueger 2000). Using these data, Jones et al. (1995) concluded that alewife predation was capable of eliminating entire fry year classes in Lake Ontario when inshore alewife densities were high in the spring. Fry mortality is also caused by Early Mortality Syndrome (EMS), a condition where Lake Trout fry die early in development due to thiamine deficiency (Fisher et al. 1996, Fitzsimons et al. 2001). Although adult Lake Trout accrue sufficient thiamine from their prey items, consumption of prey that contain thiaminase, a thiamine-degrading enzyme results in reduced thiamine levels in eggs (Honeyfield et al. 2002, Honeyfield et al. 2005, Tillitt et al. 2005, Richter et al. 2012). Once eggs hatch, thiamine-deficient fry suffer from reduced visual acuity, foraging ability, predator avoidance, and growth rates (Carvalho et al. 2009, Fitzsimons et al. 2009). EMS symptoms also include loss of equilibrium, hyperexcitability, anorexia, and eventual death (Fisher et al. 1996, Fitzsimons et al. 2001, Jaroszewska et al. 2009). The effects of EMS have only been documented in hatchery or laboratory settings (Fisher et al. 1996, Jaroszewska et al. 2009). Feeding by Lake Trout fry in the wild prior to yolk sac absorption may increase thiamine levels and reduce mortality due to EMS (Ladago et al. 2016, Carrie Kozel, University of Vermont, personal communication) thus the impact of this condition on wild Lake Trout populations may be minimal.

Lake Trout stocking practices in the Great Lakes may also be contributing to the lengthy population recovery process. Although Lake Trout are able to find and spawn over new locations (Binder et al. 2016, Marsden et al. 2016), evidence suggests they often will return to a natal spawning reef (Loftus 1958, Horrall 1981, Foster 1985,
Lake Trout are usually stocked as yearlings to minimize mortality during their first year; however, individuals hatched and reared in a hatchery are unable to imprint on a spawning location and may not utilize the best quality spawning habitat later in life (Horrell 1981, Binkowski 1984, Foster 1984). Stocking methods that place yearlings directly over spawning sites, especially those in deep water, or incubate eggs directly on spawning reefs, are more likely to result in higher return rates than previous stocking which broadly distributed fish throughout the lakes (Horrell 1981, Swanson 1982, Binkowski 1984, Bronte et al. 2002). In general, stocked Lake Trout have lower viability and are less fit than wild counterparts, as they are likely not adapted to local conditions (Haskell et al. 1952, Plosila 1977, Maclean et al. 1981). This is an issue in lakes such as Lake Superior or Lake Huron where native, self-sustaining populations are beginning to recover. Supplemental stocking in these areas may negatively impact native stocks through gene introgression and numerical displacement resulting in a population of less fit individuals (Evans and Willcox 1991).

Current status of Lake Trout in the Great Lakes

All of the challenges outlined above are potential reasons why Lake Trout recovery has proceeded slowly since restoration efforts began. Following the collapse of Lake Trout in the 1940s and 1950s across each lake, managers expected fishery regulations, lamprey control, and stocking to lead to rapid recovery of Lake Trout stocks (e.g., Dryer and King 1968). While this clearly was not the case in the lower four Great Lakes, positive signs have begun to appear in recent years.
Indications of natural recruitment have been most prominent in Lake Huron. Although adult mortality was still high, wild young-of-the-year Lake Trout were regularly captured in bottom trawls in Thunder Bay, Lake Huron by the late 1980s and the proportion of unclipped adults captured in assessment netting increased, indicating the population was being partially supported by natural reproduction (Johnson and VanAmberg 1995). Lake Trout were considered restored in Parry Sound, Lake Huron by 1997 following extensive Sea Lamprey control, harvest restrictions, and stocking efforts that utilized fish from the remnant population in Parry Sound as broodstock (Reid et al. 2001). Between 2002 and 2004, Alewife stocks crashed in Lake Huron (Schaeffer et al. 2005, Warner et al. 2005), potentially reducing the effects of thiamine deficiency throughout the lake (Fitzsimons et al. 2010). As a result, by 2004 high numbers of wild juvenile Lake Trout began to be caught throughout the main basin of Lake Huron, indicating widespread natural recruitment was occurring (Riley et al. 2007). Although wild Lake Trout stocks are beginning to recover in Lake Huron, uncertainty regarding recruitment success on an annual basis suggests that the population needs to still be regularly assessed and managed appropriately as it transitions from hatchery stocks (He et al. 2012).

Recent evidence suggests natural recruitment is also occurring in Lake Michigan. Sporadic year-classes in the late 1970s and early 1980s were comprised of a substantial number of unclipped and presumably wild Lake Trout (Rybicki 1991), but no evidence of natural recruitment was seen in the following years (Holey et al. 1995, Bronte et al. 2007, Bronte et al. 2008). However, in 2011 and 2012, nearly 20% of the Lake Trout captured in gillnets and bottom trawls targeting Bloater (Coregonus hoyi) in
the northwestern and southern offshore regions of Lake Michigan were unclipped (Hanson et al. 2013). Unclipped Lake Trout came from the 2007-2010 year classes, indicating several consecutive years of natural recruitment had occurred (Hanson et al. 2013).

**Lake Trout introductions beyond their native range**

Lake Trout have been introduced into many lakes within their native range that were not naturally colonized and into lakes in four Canadian provinces, 15 US states, and 13 other countries around the world outside their native range (Crossman 1995). Many Lake Trout introductions were conducted by federal and state governments in an effort to create popular recreational fisheries to capitalize on the species’ large size and high quality as a food source (Scott and Crossman 1973, Crossman 1995, Martinez et al. 2009). However, once they are in a system, Lake Trout are able to move through connected waterways and colonize additional areas. For example, Lake Trout stocked in Flathead Lake, MT, in 1905 dispersed throughout nearly all lakes in the Flathead River basin (Spencer et al. 1991, Muhlfeld et al. 2000, Fredenberg 2002, Fredenberg et al. 2007, Meeuwig 2008).

The success of agency-sponsored Lake Trout introductions has been variable and is influenced by many factors (Crossman 1995). Lake Trout were more likely to establish self-sustaining populations in small Ontario lakes that had lower species richness, a condition similar to the original meltwater systems in which Lake Trout were believed to have become initially established (Evans and Olver 1995); however, once established they are able to tolerate colonization of additional species that increase the species richness (Evans and Olver 1995). Oligotrophic systems tend to have lower
species richness and are more vulnerable to introductions due to fewer competitive interactions between introduced and existing species (Li and Moyle 1981, Evans et al. 1987, Evans and Olver 1995). Lake Trout are usually more likely to become successfully established in large lakes despite the fact that larger lakes tend to have greater species diversity (Evans and Olver 1995). Lakes with greater surface area and depth typically have a greater diversity of habitat available for different life stages, decreasing the incidences of negative interactions with other species (Evans and Olver 1995). Individual Lake Trout can spawn at multiple locations within a single season (Deroche 1969, MacLean et al. 1981, Peck 1986, Bronte et al. 2002, Binder et al. 2016); as lake size increases, the number of shoreline spawning sites is likely to increase as well, allowing for greater reproductive potential (Evans and Olver 1995). Greater depth ensures suitable thermal conditions are present and provides an area of refuge from littoral species for juvenile Lake Trout after they leave spawning sites (DeRoche 1969, Jude et al. 1981, Bronte et al. 1995, Evans and Olver 1995).

Impacts of invasion

The impacts of Lake Trout colonization outside its native range, especially in western lakes and reservoirs in the United States, have been widely documented and researched (Martinez et al. 2009). Lake Trout have become established in over 200 waterbodies in Wyoming, Colorado, Montana, California, Washington, Idaho, and Utah following authorized and unauthorized introductions and dispersal through connected waterways from these locations (Martinez et al. 2009). Lake Trout are an ecologically dominant species that, once established, can prey on and reduce existing fish assemblages, reducing the influence that other species can have on the Lake Trout
population (Johnson 1994, Eshenroder et al. 1995b). Individual Lake Trout in systems with a forage fish base can reach large sizes, further increasing their foraging potential (Keeley and Grant 2001, Ruzycki et al. 2003, Beauchamp et al. 2007). Many of the species preyed upon in the western United States are native salmonids, including subspecies of Cutthroat Trout (*Oncorhynchus clarkii* subsp.) and Bull Trout (*Salvelinus confluentus*), of which many are imperiled or endangered (Gresswell and Varley 1988). Native Lahontan Cutthroat Trout (*O. c. henshawi*) were extirpated from Lake Tahoe, California in the 1930s due to several factors including competition from introduced Lake Trout (Vander Zanden et al. 2003). Bull Trout were nearly extirpated from Priest Lake, Idaho by the late 1990s (Venard and Scarnecchia 2005) and experienced a rapid decline in Flathead Lake, Montana in the 1980s as a result of Lake Trout predation (Beauchamp et al. 2006). In addition to the predatory pressure Lake Trout place on Bull Trout, the two species also compete for similar resources, putting Bull Trout at an even further disadvantage (Donald and Alger 1993, Fredenberg 2002).

As a result of these rapid declines, especially in Flathead Lake, bull Trout were listed as threatened range-wide by the Endangered Species Act in 1998 (Martinez et al. 2009). In addition to the decline of native species, many other non-native species present in systems where Lake Trout have invaded have also declined. Kokanee (*Oncorhyncus nerka*) are a popular sport fish that has also been introduced widely throughout western lakes and reservoirs (Martinez et al. 2009). Although non-native, the species is often seen as innocuous due to its planktivorous diet and inability to hybridize with native species (Scott and Crossman 1973). Kokanee make up a large portion of the diet of Lake Trout in systems where the species coexist, leading to declines in Kokanee

Lake Trout can also impact aspects of the ecosystems they invade beyond the forage fish they consume. In Lake Tahoe, Lake Trout occupy a similar trophic niche as the extirpated Lahontan cutthroat Trout (Oncorhynchus clarkii henshawii), but have eliminated much of the pelagic forage base on which Lahontan Cutthroat Trout previously relied (Vander Zanden et al. 2003). In Yellowstone Lake, the reduction in planktivorous Yellowstone Cutthroat Trout due to Lake Trout predation resulted in a shift in the zooplankton assemblage from smaller copepods to larger cladocerans (Tronstad et al. 2010). The increased foraging ability of the larger zooplankton has dramatically increased water clarity in Yellowstone Lake due to a three to sevenfold decrease in phytoplankton biomass (Tronstad et al. 2010). The decrease in Yellowstone Cutthroat Trout in Yellowstone Lake has also resulted in smaller spawning runs into the lake’s tributaries (Koel et al. 2005). This has had cascading effects as there are at least 42 species known to use Cutthroat Trout in the Yellowstone area as a food source, including grizzly bears (Ursus horribilus), otters (Lutra canadensis), osprey (Pandion haliaetus), and bald eagles (Haliaeetus leucocephalus) (Varley and Schullery 1995, Haroldson et al. 2005, Koel et al. 2005, Wengeler et al. 2010). Many bears that previously relied on Cutthroat Trout as a primary food resource in the spring now target migrating elk calves and have reduced population growth of elk in Yellowstone National Park by 2-11% (Middleton et al. 2013). A similar effect is being seen in Flathead Lake, Montana, where a collapse of the Kokanee population due to Lake Trout predation reduced spawning runs that provided a food source for many species,
including large wintering congregations of bald eagles around the lake (Spencer et al. 1991). The reduction of spawning Cutthroat Trout from Yellowstone Lake has also resulted in a shift in the nutrient exchange between Yellowstone Lake and its tributaries (Tronstad et al. 2015). Excretions from Cutthroat Trout were likely an integral part of nitrogen cycling when spawning trout were abundant, but now only make up 6.1% of the NH$_4^+$ utilized by stream microbes (Tronstad et al. 2015).

**Management of invasive lake trout**

The presence of non-native Lake Trout in a system can present many management challenges that should be considered on a case-by-case basis. Despite the negative impacts commonly associated with Lake Trout, the species is often the focus of sustainable sport fisheries that draw considerable fishing effort (Martinez et al. 2009). As in systems where Lake Trout are native, managers employ common fisheries management practices to maintain healthy Lake Trout populations (Martinez et al. 2009). However, other systems that are managed for Lake Trout, often with the focus of creating populations of trophy-sized individuals, are unsustainable (Johnson and Martinez 2000, Martinez et al. 2009, Schoen et al. 2012, Ng et al. 2016). For example, Blue Mesa Reservoir, Lake Granby, Taylor Park Reservoir, and Twin Lakes in Colorado are all managed for trophy-sized Lake Trout through selective harvest regulations and annual stocking of Kokanee and Rainbow Trout (*Oncorhynchus mykiss*), the primary prey species for Lake Trout in these systems (Johnson and Martinez 2000). Although stocking and harvest restrictions have created excellent Lake Trout fisheries, these management actions have also created a major imbalance in the lake’s food web. Piscivorous fish biomass is, on average, 60% of the total pelagic fish.
biomass, and has led to a sharp decline in Kokanee abundance (Martinez and Bergersen 1991, Johnson and Martinez 2000). The stocking program required to maintain the Lake Trout fishery was primarily funded by angler license sales, very few of whom actually target Lake Trout, creating a situation where the majority of anglers are supporting a system in which only a minority actually participate (Johnson and Martinez 2000).

Managers have utilized a number of different strategies to try to reduce Lake Trout populations in invaded systems. The first method utilized in most systems, regardless of the final management goal, is to eliminate stocking (Martinez et al. 2009). Following this, fishing regulations that relax or remove bag limits can be put in place to increase angler exploitation of the population. Although slot limits continue to be used in some areas to maintain populations of trophy-sized Lake Trout, their use has begun to be eliminated as prey populations often cannot support the increased number of large individuals (Martinez et al. 2009). Angler pressure can be further increased beyond a level that would normally be supported by using raffles, bounties, or other rewards to encourage anglers to target and remove Lake Trout (Hansen et al. 2008, Martinez et al. 2009). Mechanical removal techniques such as gill nets and trap nets deployed by local managers or contracted fishing firms can increase removal levels even further (Hansen et al. 2008, Gresswell 2009, Syslo et al. 2011). Research is now being conducted to explore strategies to target early life stages as a means of accelerating control (Martinez et al. 2009, Cox et al. 2012, P. Bigelow, Fisheries and Aquatic Sciences Program, Yellowstone National Park, personal communication). Use of sterile triploid Lake Trout has also been considered as a method to reduce spawning success (Kozfkay et al. 2005).
Work with other invasive species has shown that the most successful control strategies are often ones that integrate a number of different strategies together so they work in conjunction with one another to suppress the target species. This strategy, termed integrated pest management (IPM), was first developed for insect suppression in agricultural settings, but has since been applied to a range of other pest species (Sawyer 1980, Luckmann and Metcalf 1994). Unilateral approaches where various alternatives are independently applied are often ineffective over time (Stern et al. 1959). Instead, IPM follows a set of principles, summarized by Sawyer (1980), that are designed to coordinate multiple control methods together to control the target species in the most effective manner. Prior to the implementation of any additional control methods, managers must approach the problem ecologically and manage for any naturally occurring factors that would limit the target species’ growth or survival. Detailed, quantitative models derived from sampling must be used to predict population trends and economic thresholds and guide any additional control efforts. These models should be designed to work toward a specific goal, such as minimizing pest numbers or maximizing yield of a crop or another affected species. Control methods should be designed to maintain pest populations at a predetermined economic injury level (EIL), the population density at which the cost of additional control outweighs benefits obtained by additional suppression (Stern et al. 1959, Sawyer 1980). Chemical pesticides should only be used as a last resort in a management plan as there are often disruptive side effects associated with their use. Finally, eradication of the target species and preventative treatments are antithetical to IPM theory and should not be part of a management strategy.
Invasion and management of Lake Trout in Yellowstone Lake

Lake Trout were discovered in Yellowstone Lake (Figure 1) in 1994 (Kaeding et al. 1996). Otolith microchemistry analysis showed that Lake Trout from Lewis Lake, located on the opposite side of the continental divide, were intentionally introduced multiple times during the late 1980s and early 1990s (Munro et al. 2005). Yellowstone Lake is at an elevation of 2,357 m, has a surface area of 34,020 ha, a maximum depth of 133 m, and 239 km of shoreline, making it the largest lake above 2,000 m in North America (Kaplinski 1991, Morgan et al. 2003). The lake is generally ice covered between mid-December and late May or early June, and develops a thermocline around 15 m; surface temperatures can reach 17°C in July and August (Koel et al. 2007). Prevailing winds are generally from the south and southwest (Benson 1961). The fish assemblage in the lake is limited to native Yellowstone Cutthroat Trout and Longnose Dace (*Rhinichthys cataractae*); non-native Longnose Sucker (*Catostomus catostomus*), Redside Shiner (*Richardsonius balteatus*), and Lake Chub (*Couesius plumbeus*) are present in the lake in addition to Lake Trout, although in relatively low numbers (Gresswell and Varley 1988).

National Park Service officials immediately recognized the ecological threat Lake Trout posed to Yellowstone Lake (Varley and Schullery 1995). Yellowstone Lake is home to the largest remaining population of non-hybridized Yellowstone Cutthroat Trout and makes up 80% of the remaining lacustrine habitat for the species (Gresswell and Varley 1988, Gresswell et al. 1994). Adult Lake Trout in Yellowstone Lake were found to consume an average of 41 Yellowstone Cutthroat Trout per year (Ruzycki et al. 2003); this level of predation was estimated to cause the cutthroat Trout population
in Yellowstone Lake to decline by 60% over 100 years if Lake Trout were not controlled (Stapp and Hayward 2002, Ruzycki et al. 2003). In contrast to Yellowstone Cutthroat Trout, Lake Trout tend to stay in deep water and do not migrate upstream to spawn, making them inaccessible as a prey item for terrestrial species (Stapp and Hayward 2002, Koel et al. 2005). Yellowstone Cutthroat Trout are also the focus of a large recreational fishery, and more than a third of a million people visit LeHardy Rapids and Fishing Bridge to view the migrating fish during the spawning season (Gresswell and Liss 1995, Varley and Schullery 1995); thus, the loss of the species would have social and economic impacts as well.

Aspects of IPM have been utilized throughout the development and implementation of the Lake Trout suppression program in Yellowstone Lake. The primary goal of the suppression program has been to reduce the Lake Trout population to a size where its impact on Yellowstone Cutthroat Trout was minimized while considering the social, ecological, and economic impacts of any control method (Varley and Schullery 1995). Although gillnetting has been used as the primary control method in Yellowstone Lake, many alternatives have been evaluated (McIntyre 1995, Gresswell et al. 2013). Some alternatives, such as using chemical toxicants or releasing sterile male Sea Lamprey, have been eliminated from consideration due to their potential to negatively impact Cutthroat Trout and the broader ecological system (McIntyre 1995). Other alternatives, such as trap nets or boat electroshocking over spawning grounds, have been utilized but later discontinued after evaluation indicated their efficacy, in terms of time and cost, was lower than is seen with gillnets (P. Bigelow, Fisheries and Aquatic Sciences Program, Yellowstone National Park, personal communication).
Optimum strategies would exploit Lake Trout characteristics that make the vulnerable to exploitation, including their slow growth rate, late maturity, and low reproductive potential (Keleher 1972, Healey 1978, Martin and Olver 1980, McIntyre 1995, Shuter et al. 1998, Syslo et al. 2011, Syslo et al. 2013). Gillnets are positioned throughout Yellowstone Lake during the entire fishing season in areas designed to target both juvenile and adult Lake Trout while minimizing Cutthroat Trout bycatch. Additionally, nets are placed around spawning sites during fall months (Dux et al. 2011, Syslo et al. 2011, Syslo et al. 2013). This strategy is especially beneficial as it removes many of the largest and most fecund individuals that consume many Cutthroat Trout and contribute the most to future recruitment (Ruzycki et al. 2003, Syslo et al. 2011). Lake Trout distribution and population characteristics were not fully understood before suppression techniques were first implemented in Yellowstone Lake, so the efficiency of the suppression program was likely low in early years (Dux et al. 2011, Syslo et al. 2011). Although over 100,000 Lake Trout were removed between 1994 and 2004 (Koel et al. 2005) and nearly 450,000 had been removed by 2009, modeling conducted by Syslo et al. (2011) indicated the Lake Trout population was continuing to grow. The National Park Service responded by hiring a commercial fishing firm from Lake Michigan to supplement their own efforts (Gresswell 2009). Models have since been used successfully to decide the amount of fishing effort needed, monitor the response of the Lake Trout population to control, and readjust effort as needed (Ruzycki et al. 2003, Syslo et al. 2011). Catches have increased dramatically, with almost 302,000 Lake Trout being removed in 2012 alone (Gresswell et al. 2013). Multiple metrics currently
indicate the Lake Trout population is beginning to decline as a direct result of these elevated catch rates (Gresswell et al. 2015).

A key component of IPM that has not been a part of the Lake Trout suppression program on Yellowstone Lake is the development of an EIL. While salmonid eradication has been shown to be feasible in small, mountain lakes (Knapp and Matthews 1998), managers have recognized that complete eradication of Lake Trout from Yellowstone Lake is highly unlikely. Instead, managers are focused on reducing the population to a stable level that has minimal impact on Yellowstone Cutthroat Trout (McIntyre 1995). However, this target level has yet to be established. To determine the actual EIL, managers must compare the costs associated with reducing and maintaining the Lake Trout population size at a given level against the value of the benefits and services lost as a result of Lake Trout being present in the system; this valuation must include the value of the individual Cutthroat Trout lost to Lake Trout predation as well as the value of the lost ecological and social services they provide as well (Sawyer 1980). This EIL is clearly very difficult to obtain, especially given the complexity and interconnectedness of the greater Yellowstone ecosystem (Tronstad et al. 2010, Middleton et al. 2013, Tronstad et al. 2015); however, as suppression efforts continue and the Lake Trout population is reduced, an estimate will need to be determined to continue to justify suppression efforts that will likely need to continue in perpetuity.

*Lake Trout early life stage suppression in Yellowstone Lake*

As part of an IPM strategy, Yellowstone Lake managers are also considering targeting Lake Trout at early life stages, specifically eggs and fry on spawning reefs, in addition to targeting adults. Although this method was originally estimated to have less
than a 30% chance of working on its own when first proposed (McIntyre 1995), if done in conjunction with other control methods it may improve suppression (Kogan 1998, Hansen et al. 2008). The Lake Trout population growth rate in Yellowstone Lake was found to be most sensitive to age-0 survival (Syslo et al. 2011). Supplementing existing gillnetting efforts with methods that target developing embryos or fry may reduce the population more efficiently. A number of different methods including seismic air guns, suction dredges, electric grids placed on sites, and tarps designed to cover and suffocate eggs are all currently being evaluated as potential ways of aiding suppression (Cox et al. 2012, Gresswell et al. 2015).

Identifying Lake Trout spawning sites in Yellowstone Lake has been repeatedly identified as a research priority (McIntyre 1995, Kaeding et al. 1996, Gresswell et al. 2012). To effectively suppress Lake Trout early life stages in Yellowstone Lake, the extent and location of spawning must be identified so managers can determine the feasibility of accessing the majority of spawning sites and the potential level of impact that suppression techniques could have on the overall population. An early substrate survey conducted around the shoreline of Yellowstone Lake in 2 m – 7m of water revealed extensive areas of cobble, rubble, or boulder substrate (Kaeding et al. 1996). The area around Carrington Island was confirmed as a spawning site with the collection of eggs in 1996 (Figure 1; Ruzycki 2004, Bigelow 2009). This small island (379 m²) is located near the northwestern shore of the West Thumb of Yellowstone Lake and is surrounded by cobble substrate in water generally less than four meters deep. Areas near West Thumb Geyser Basin, Solution Creek, and Breeze Channel were inferred to be spawning sites based on consistent catches of gravid females (Figure 1; Ruzycki
2004, Bigelow 2009); more potential spawning sites have been identified in recent years (P. Doepke, Fisheries and Aquatic Sciences Program, Yellowstone National Park, personal communication). A habitat suitability model for Yellowstone Lake designed to predict areas suitable for spawning based on wave energy, fetch, and geomorphic data estimated only 4% of the lake area was suitable for spawning (Bigelow 2009). Transects across areas predicted to either be suitable or unsuitable for spawning based on this model were observed with a camera. Angular, sediment free, rock substrate was rarely found and occurred almost exclusively within areas predicted by the model to be suitable for spawning (Bigelow 2009). Starting in 2011, acoustic telemetry was used to track the movement of Lake Trout and identify potential spawning areas based on aggregations of adults in fall. Telemetry data have revealed several potential spawning sites (Gresswell et al. 2016), but spawning has not been directly confirmed by collections of eggs or fry at any of these locations except around Carrington Island.

Caution must be used when identifying spawning locations without direct evidence of eggs or fry; although telemetry and gillnets indicate the presence of fish in a specific area, they cannot confirm spawning actually occurred (Marsden et al. 1995a, Binder et al. 2014, Binder et al. 2016). Several techniques have been used in the Great Lakes to sample Lake Trout eggs and fry to confirm spawning locations (Collins 1975, Stauffer 1981, Marsden et al. 1988, Horns et al. 1989, Marsden et al. 1991, Perkins and Krueger 1994, Riley et al. 2011). Site selection for gear placement in systems where Lake Trout are native is usually based on historical evidence of spawning locations or on manmade rock structures such as breakwalls and water intake rip-rap mounds that are commonly used as spawning reefs (Marsden et al. 1995b). However, given the
plasticity of Lake Trout spawning site selection, Lake Trout may behave unpredictably in the face of environmental conditions different than those found in the Great Lakes and may spawn on sites with different characteristics in invaded lakes. For example, the species diversity of fish in Yellowstone Lake is very limited (Gresswell and Varley 1988) and none are known to be major predators or are capable of accessing eggs that have settled into rocky substrate. Without a strong predatory pressure, spawning may not be limited to areas with deep interstitial spaces and may be successful in areas deemed “sub-par” in other systems.

The duration and timing of the spawning and period of fry residence on spawning reefs are also critical pieces of information for managers to evaluate the potential efficacy of suppression efforts targeting Lake Trout eggs and fry. Managers must ensure that suppression is implemented at a time when sufficient eggs or fry are present that there will be an impact on the overall population. In Yellowstone Lake, spawning is known to begin in early September and continues into October. However, it is uncertain whether spawning continues beyond this time, as boats are removed from the lake before the end of October due to inclement weather. A study evaluating the gonadosomatic index of Lake Trout in Yellowstone Lake showed that a number of females were still ripe in the middle of October; however, these fish may not have spawned that season, as signs of egg resorption have been seen in the spring (Gresswell et al. 2015). Prior to the current study, no fry sampling had been conducted and no information was available on fry hatching or their residence interval at spawning sites.

Prior to the implementation of any large-scale suppression program targeting Lake Trout early life stages in Yellowstone Lake, the shortcomings in our knowledge
about these stages must be addressed. Evidence of spawning should be sought at additional locations, including those suspected of being spawning sites, so that suppression efforts can be targeted appropriately. The physical characteristics of confirmed locations should be evaluated to determine whether Lake Trout spawning site selection is limited to specific substrate types, as in the Great Lakes, or if a more diverse range of substrate types are used instead. Egg densities should also be evaluated at multiple sites to determine the relative importance of each site for spawning Lake Trout. Overwinter survival of eggs should also be quantified at multiple sites to evaluate the proportion of eggs die naturally and thus the proportion that must be killed by suppression methods. Finally, the duration of fry residence on spawning sites during the spring should be determined. If most Lake Trout fry in Yellowstone Lake leave spawning sites either before or soon after ice-off occurs, suppression methods targeting this life stage would be of minimal use. Information about Lake Trout fry growth and feeding while they are still on spawning sites in Yellowstone Lake would also be useful as a comparison with similar data collected within the species’ native range. These data could provide a better understanding of factors that have led to the rapid population growth of Lake Trout in Yellowstone Lake and other invaded lakes.
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Figure 1: Locations within Yellowstone Lake, Yellowstone National Park, Wyoming.
CHAPTER 2: SPAWNING SITE PLASTICITY OF INVASIVE LAKE TROUT

*SALVELINUS NAMAYCUSH* IN A SPECIES DEPAUPERATE LAKE, YELLOWSTONE LAKE

Abstract

Lake Trout (*Salvelinus namaycush*) are the focus of restoration efforts across their range and suppression efforts outside their range. Since their discovery in Yellowstone Lake in 1994, Lake Trout have been the object of an intensive gillnet suppression program. In an attempt to augment suppression, managers are also interested in targeting early life stages. Prior to the implementation of any early life stage control, the location and physical characteristics of spawning sites must be determined. Confirmed Lake Trout spawning sites in their native range are generally limited to areas with multi-layered cobble substrate along a sharp contour break; however, the phenotypic plasticity of Lake Trout combined with low species diversity and the absence of interstitial egg predators in Yellowstone Lake may allow Lake Trout to utilize spawning sites that do not meet this classic cobble-contour model. A benthic sled was used to sample 24 sites hypothesized to be spawning sites for Lake Trout eggs, encompassing a range of depth, slope, and substrate composition. Lake Trout eggs were collected at seven sites, five of which had not been previously confirmed as spawning sites. Habitat characterization at these sites indicate Lake Trout spawning in Yellowstone Lake is limited to areas with rocky substrate, but is not constrained to areas with interstitial spaces or contour breaks. This new spawning site model information will help Yellowstone managers identify additional spawning sites for targeting suppression efforts.
Introduction

Phenotypic plasticity, or the change in expression of a genotype in response to new or changing environmental conditions, can promote a species’ ability to invade a broad range of new environments (Bradshaw 1965). Invasive plant species commonly demonstrate greater phenotypic plasticity than similar non-invasive species across a wide range of growth, morphological, physiological, and fitness-related traits allowing them to become established in new locations (Davidson et al. 2011). Round Gobies (*Neogobius melanostomus*) in Lake Michigan tributaries grow faster, have shorter lifespans, and lower age at 50% maturity compared with individuals collected from Lake Michigan, allowing the species to utilize both habitat types despite different temperature regimes and environmental forces (Kornis et al. 2016). Diet plasticity, especially across trophic levels, can allow invasive species to utilize alternate resources if their preferred prey is unavailable (e.g., Almeida et al. 2012).

Lake Trout (*Salvelinus namaycush*) are popular sportfish that are capable of utilizing a range of habitats and resources due to its phenotypic plasticity (Crossman 1995, Eshenroder et al. 1995). Lake Trout are commonly associated with large, deep lakes and have been captured as deep as 426 m in Great Bear Lake, but can also utilize large rivers or small, shallow bodies of water in alpine or arctic areas where water temperatures remain cold (Ellis 1962, Martin and Olver 1980). Lake Trout usually shift from planktivory to piscivory as they become larger, but are also capable of remaining planktivorous throughout their life in systems where forage fish are absent (Scott and Crossman 1973, Martin and Olver 1980). Lake Trout can reach very large sizes as demonstrated by the world record caught in Lake Athabasca, Saskatchewan, Canada
that weighed 46.3 kg (Scott and Crossman 1973), but maximum lengths and weights vary widely depending on the food resources available (Scott and Crossman 1973, Donald and Alger 1986). Spawning usually occurs once a year between August and December (Milner 1874, Koelz 1926, Miller and Kennedy 1948, Royce 1951, Eschmeyer 1955, Rahrer 1965, Goodier 1981), although ripe males and females have been captured into January in Lake Tahoe (Martin and Olver 1980) and throughout the summer as early as late April in Lake Superior (Eschmeyer 1955, Bronte 1993). Skip spawning has also been observed, with multiple years between spawning events (Goetz et al. 2011). Once fish begin to appear on a spawning site, the spawning period can range from less than a week to upwards of two months in response to differing environmental conditions (Martin and Olver 1980).

Lake Trout are the focus of a long-term restoration program in the Great Lakes, but are also considered invasive in portions of the western United States. Following the near extirpation of Lake Trout from the Great Lakes in the 1940s and 1950s, stocking and sea lamprey control have restored robust populations of adults (Hansen 1999). Although eggs and fry have been found on spawning reefs throughout the Great Lakes (e.g., Marsden et al. 2005), wild recruitment has been limited and self-sustaining populations currently only exist within Lake Superior and portions of lakes Huron and Michigan (Hansen et al. 1995, Riley et al. 2007, Hanson et al. 2013). In contrast, Lake Trout have been successfully introduced into many systems in the western United States, often to create new fisheries (Crossman 1995, Martinez et al. 2009). Many of these systems have very simple food-webs relative to the Great Lakes and contain only a few additional fish species (Crossman 1995). The high prey demand of Lake Trout
has caused populations of other sportfish such as native Cutthroat Trout (*Oncorhynchus clarkii*), Bull Trout (*Salvelinus confluentus*), and non-native Kokanee (*Oncorhynchus nerka*) to collapse (Martinez et al. 2009). From the systems where Lake Trout were legally introduced, they have continued to invade further via illegal introductions or by spreading through connected waterways (Crossman 1995, Martinez et al. 2009). In many systems, managers are altering management strategies, including actively suppressing Lake Trout, to allow other species to recover (Martinez et al. 2009).

The success of Lake Trout in invaded systems may be a result of their plastic spawning behavior response to different ecological constraints. Although the timing, duration, and frequency of Lake Trout spawning are already recognized as plastic traits, the plasticity of spawning site selection and its impact on Lake Trout restoration and suppression has not been evaluated. Unlike other members of the Salmonidae family, Lake Trout do not construct redds; eggs are deposited over existing substrate where they settle into interstitial spaces (Cuerrier and Schultz 1950, Royce 1951, Eschmeyer 1964, DeRoche 1969, Martin and Olver 1980, Marsden et al. 1995). Lake Trout are generally believed to non-randomly spawn over portions of sites with sharp contour breaks composed of large, multi-layered rocky substrate with clean interstitial spaces to increase egg survival; deep interstitial spaces provide protection from predation and dislodgement and currents directed by the slopes keep the substrate well oxygenated and clear of sediment (Marsden and Krueger 1991, Marsden et al. 1995). Most Lake Trout egg and fry sampling has been limited to areas that match this ‘cobble-contour’ spawning site model under the assumption that mortality would be very high at alternate sites and thus would not be utilized (Nester and Poe 1987, Horns et al. 1989, Fitzsimons...
1995, Marsden et al. 1995, Ellrott and Marsden 2004, Claramunt et al. 2005). However, many of the systems invaded by Lake Trout do not contain the epibenthic or interstitial egg predator species that may be limiting Lake Trout recruitment in the Great Lakes (Jones et al. 1995). If spawning site selection is a plastic behavior, alternate substrate types may be utilized in systems without this ecological constraint.

Lake Trout were illegally introduced in the late 1980s and early 1990s into Yellowstone Lake, a species-depauperate system in Yellowstone National Park, Wyoming (Kaeding et al. 1996, Munro et al. 2005). The Lake Trout population began to rapidly expand and prey on the native Yellowstone Cutthroat Trout (*Oncorhynchus clarkii bouvieri*), prompting the National Park Service to implement a suppression program in 1994 (Koel et al. 2005). Identifying Lake Trout spawning sites in Yellowstone Lake has been repeatedly highlighted as a research priority to enable integrating suppression techniques that target Lake Trout eggs and fry on spawning reefs into the gillnet suppression program (McIntyre 1995, Kaeding et al. 1996, Gresswell et al. 2016). Prior work used substrate surveys to identify areas with rocky substrate and habitat suitability models to predict where spawning might occur based on factors such as wave energy theory, geomorphology, and distance to potential nursery areas (Kaeding et al. 1996, Bigelow 2009). Consistently high catches of gravid females in gillnets (P. Doepke, Center for Resources, Yellowstone National Park, personal communication) and information from acoustic telemetry positioning arrays during spawning seasons (Gresswell et al. 2016) have indicated areas with dense aggregations of fish, but these techniques do not directly confirm spawning occurs at these locations (Marsden et al. 1995, Binder et al. 2014, Binder et al. 2016). Yellowstone Lake contains
very few fish species, none of which are major Lake Trout egg or fry predators that can access interstitial spaces (Gresswell and Varley 1988). I hypothesize that without interstitial egg predators and few epibenthic predators, Lake Trout spawning in Yellowstone Lake will not be limited to areas that match the cobble-contour spawning site model. I actively sampled sites suspected of being spawning locations, based on earlier work that indicated the presence of spawning, using a novel benthic sled design to directly confirm the presence of spawning and evaluate the physical characteristics of sites where eggs were both detected and not detected. I evaluate the plasticity of Lake Trout spawning site selection and assess its potential impact as managers consider the inclusion of suppression methods targeting Lake Trout eggs and fry on spawning sites into the suppression program in Yellowstone Lake.

**Methods**

**Study area**

Yellowstone Lake is located at an elevation of 2,357 m with a surface area of 36,017 ha (Koel et al. 2007), a mean depth of 48.5 m (Kaplinksy et al. 1991), and a maximum depth of 133 m (Morgan et al. 2003; Figure 1). The lake is dimictic with a maximum summer surface temperature of 17°C and is typically ice covered between mid-December and mid-May (Benson 1961). The lake is mesotrophic (Theriot et al. 1997) and contains only two native fish species, Yellowstone Cutthroat Trout and Longnose Dace (*Rhinichthys cataractae*; Simon 1962). In addition to Lake Trout, non-native species present in the lake include Redside Shiner (*Richardsonius balteatus*), Longnose Sucker (*Catostomus catostomus*), and Lake Chub (*Couesius plumbeus*; Gresswell and Varley 1988). Prior to this study, Lake Trout spawning had been
confirmed at three locations in Yellowstone Lake: Carrington Island, Snipe Point, and Olson Reef (Figure 1, Ruzycki 2004, Bigelow 2009, Dylan Olson, University of Wisconsin-Milwaukee, unpublished data).

Egg sampling

A benthic sled (Figure 2) modified from a design by Stauffer (1981) was used to sample areas of Yellowstone Lake for Lake Trout eggs during the spawning period in September and October, 2015. A manifold with three 40° high pressure jets directed at the lake bottom was attached to interior side of the leading edge of the sled. A pressure washer rated for 3000 psi (20,684 kPa) and 10.6 liters per minute on the tow boat sent water through a high-pressure hose to the jets and washed material off the benthos into the water column. A 1.6 m long net constructed of 1.6 mm knotless delta mesh attached to the sled captured the suspended material. Four parallel bars (9.5 mm diameter steel) welded between the runners prevented rocks from catching on the sled frame, allowing the sled to pass over rocky substrate.

Sampling was focused at sites where spawning was suspected to occur based on gill net catches of gravid females, acoustic telemetry data from tagged adult Lake Trout, and bathymetric contours; sites were primarily within the southern portion of the South Arm and the area between Snipe and Plover points (Figure 1). Additionally, shoreline areas were sampled where rocky substrate was visible from the surface.

Tows lasted 1-9.5 minutes at speeds between 0.5 and 1.0 m/s; duration was dictated by the fullness of the net after the first tow and the size of the site being sampled. Tow duration was measured as the length of time the pressure washer was running. Multiple tows were conducted at most sites. The sled was towed with at least a
3:1 scope relative to the greatest depth expected for each tow. All material collected was emptied through a 3 mm sieve and the number of Lake Trout eggs recorded. Two GoPro cameras (Hero 3+ Silver and Hero 4 Black editions) were attached to the leading edge of the sled, one facing forward and one backward to record the substrate and amount of material washed into the water column by the pressure washer during each tow. Depth, boat position, and speed were logged every two seconds during each tow using a sonar and handheld GPS onboard the tow boat.

Site and substrate analysis

The maximum fetch for each site was measured from the center of the sampled area assuming prevailing winds from the south-southwest (Benson 1961). The depth for each site was calculated as a weighted average across all tows.

Video footage from each tow was evaluated to determine substrate conditions for five parameters at all sampled sites (Table 1). Interstitial space quality, particle size, and macrophyte density were determined every two seconds for the area immediately in front of the sled as viewed by the forward-facing camera, and the degree of infilling was determined every two seconds using footage from the rear-facing camera. The interstitial space quality was classified as either “poor,” “moderate,” or “good” based on the amount of rock coverage and thus protection an egg would be provided from predators and physical displacement. Dominant particle sizes were qualitatively assessed from the video footage using the sled for scale and then described as either “gravel” (2-64 mm), “rubble” (65-256 mm), or “cobble and boulder” (>257 mm) based on the Wentworth scale as used by Marsden et al. (1995). Areas of bedrock were also noted. Macrophyte density was classified as either “sparse” or “dense”. Presence of fine
material in interstices (infilling) was determined by the amount of material suspended into the water column by the pressure washer and was classified as either “none to light” or “moderate to heavy”. The presence or absence of a slope or contour break was subsequently determined for portions of sites where rocky substrate was found (Table 1).

Substrate evaluations were used to determine whether sites contained areas that matched the cobble-contour spawning site model. Although I could not determine the specific location within a tow where eggs were collected, I assumed spawning occurred over the portion of the site that I observed that most closely matched the characteristics of the cobble-contour model and classified the site accordingly. Specifically, I determined a site matched the model if it contained an area with rubble or cobble and boulder sized rocks, good interstitial space quality, and no or light infilling occurring along a contour break (Marsden and Krueger 1991, Marsden et al. 1995; Table 2). If one or more of these factors were missing, the area was considered to have not met the model. To define a model that encompassed all spawning sites confirmed by the benthic sled in Yellowstone Lake, I considered variations on the cobble-contour model that excluded single or multiple parameters or included multiple alternatives of a parameter (Table 3).

Results

A total of 85 tows, between one and nine per site, was conducted across 24 sites (Figure 1). Between one and five eggs were found in 12 tows at seven different sites with as many as nine eggs being captured at a single site (Figure 1, Table 2). The
average depth of sampled sites ranged between 1.5 and 35.8 m while fetch ranged between 20 and 4170 m (Table 2).

Eggs were captured at Olson Reef and Snipe Point, where spawning had been previously confirmed, and five sites where eggs had not previously been found. Of the 17 additional sites where eggs were not found, nine contained areas with either moderate or high quality interstitial space while the remaining eight consisted of only sandy or muddy substrate, with scattered individual rocks that did not create any interstitial spaces (Table 2). None of the sites where eggs were not found fit the cobble-contour spawning site model (Table 2).

Two sites where eggs were found, the Elbow of Flat Mountain Arm and Olson Reef, met all components of the cobble-contour spawning site model (Figure 1, Table 2). The Elbow of Flat Mountain Arm is a shallow, shoreline site in the northeast corner of Flat Mountain Arm. Multiple layers of cobble and boulder sized rounded rocks gently slope out from shore and form a sharp edge that drops approximately 1 m down to a hard, sandy bottom (Figure 3). Dense macrophytes were present across much of the sandy area, but only sparse macrophytes were growing across rocky portions of the site. Olson Reef is a hump north of the entrance of Flat Mountain Arm that peaks at about 13 m depth and rapidly drops off to about 40 m. Most substrate on the hump and throughout the surrounding area is a fine sediment commonly seen throughout Yellowstone Lake, but a patch of single and multi-layered angular cobble and boulders was found on the steep northern slope of Olson Reef (Figure 3). The areas with multi-layered rock at both sites created high quality interstitial spaces that had minimal infilling.
Eggs were also found at Snipe Point and Mid Flat Mountain Arm; neither site was along a contour break or slope (Figure 1, Table 2). Both sites were situated along shorelines with an average depth around 2 m. Portions of both sites, especially Snipe Point, had areas with multiple layers of rubble or cobble and boulders creating high quality interstitial spaces without any infilling. These sites also had large areas of a mosaic of single-layered rocky substrate and patches of sand. Macrophytes were present across some areas of Snipe Point, but were not seen at Mid Flat Mountain Arm.

South Frank Hump, Breeze Channel Hump, and Outer Snipe Point also lacked any areas that matched the cobble-contour spawning site model (Figure 1, Table 2). South Frank Hump and Breeze Channel Hump are located offshore with average depths of 31 m and 26 m, respectively, although South Frank Hump was sampled to nearly 40 m (Table 2). Neither site had areas with high quality interstitial spaces, except for a very trace amount on South Frank Hump (Table 3). The majority of the rocky substrate at these sites was dominated by layered or crumbly bedrock with scattered rubble or cobble and boulders that created only moderate quality interstitial spaces (Figure 3, Table 3). South Frank Hump did have several mounds with slopes over 10°, but did not have any contour breaks (Figure 3). Breeze Channel Hump was largely flat except for outcroppings of bedrock that emerged gradually from the sandy bottom without creating any sharp contours (Figure 3). Outer Snipe Point is located along a slope approximately 170 m to the east of the center of the Snipe Point site. Both the front and rear cameras were blocked by vegetation for the majority of each tow. Dense macrophytes covered the bottom during the remainder of the tows with only sporadic moments of open sand.
and individual rocks scattered across the bottom (Figure 3). No areas with moderate or good quality interstitial spaces were observed.

The cobble-contour model includes rubble, cobble, or boulder sized rock, good quality interstitial spaces, no or little infilling, and an adjacent contour break as important site characteristics. As noted above, only two sites matched this model. I came up with four alternative models that incorporated different combinations of parameters (Table 3). Only one of these models, which included only the presence of rubble or cobble and boulder sized rock and good or moderate quality interstitial spaces, consistently predicted the presence of eggs at all but one site (Table 3).

Discussion

Lake Trout eggs were captured at sites with a broad range of substrate types, supporting our hypothesis that Lake Trout spawning is not limited to areas that match the cobble-contour spawning site model. Most confirmed Lake Trout spawning sites in the Great Lakes and other portions of the species’ native range are composed of multi-layered, cobble-sized rock with clean interstitial spaces situated along a sharp contour break (Marsden and Krueger 1991, Marsden et al. 1995). Lake Trout eggs have been collected in only a few instances at sites that do not match the slope-contour model (Milner 1874, Beauchamp et al. 1992, Tibbits 2007). Although I found eggs at two sites in Yellowstone Lake that match this description, eggs were also found at five other sites missing at least one of these characteristics. A simple model only requiring a minimum of 50% coverage by rubble or cobble and boulders describes nearly all areas where Lake Trout eggs were captured in Yellowstone Lake. I did not sample any sites that were dominated solely by gravel substrate, thus it is possible that areas with adequate
coverage of smaller rock would be suitable as well. Although Breeze Channel Hump and South Frank Hump had some areas with rubble or slightly larger rock, both sites were mostly comprised of bedrock. The presence of eggs at these two sites indicates bedrock may be suitable spawning substrate for Lake Trout in Yellowstone Lake. Fetch and depth do not appear to be predictive variables for the locations I sampled; however, I did not sample any locations with extremely long fetches, such as along the eastern shore of the lake, or at depths greater than 40 m. Given that eggs were found at several sites with only moderate quality interstitial spaces and were likely resting directly on the substrate, infilling may not be a limiting factor; however, sites where eggs were found tended to have sandy infilling rather than the finer silt commonly found elsewhere in the lake. Areas that are composed of or infilled by these finer sediments that are more likely to cover and suffocate an egg may be avoided by spawning Lake Trout.

Collecting a Lake Trout egg at a site is not necessarily proof that the site was selected as a spawning location; two alternative hypotheses could also explain why eggs were present. Prior to our study, Lake Trout fry were observed at both Snipe Point and Olson Reef (Bigelow 2009, D. Olson, unpublished data), confirming that these are spawning sites. Lake Trout are regularly targeted with gillnets at South Frank Hump and Breeze Channel Hump during the spawning season. Fish captured in nets set prior to our sampling could have expelled eggs that were subsequently captured. Eggs were captured in two separate tows covering somewhat different portions of South Frank Hump, thus the probability that I only collected eggs expelled by fish in gillnets may be low; however, this may be a reasonable explanation for the single egg collected at
Breeze Channel Hump. Alternatively, eggs could have drifted from another site where spawning does actually occur. Outer Snipe Point is within 170 m of Snipe Point, so the single captured egg could have originally been spawned there and swept downslope by underwater currents. This hypothesis appears logical given Outer Snipe Point only contained a few scattered rocks and did not fit our most inclusive spawning site model. Additionally, dense macrophytes were generally not present at other sites where eggs were found, further distinguishing Outer Snipe Point from all locations where eggs were found. I conclude that Outer Snipe Point was a false positive detection and spawning does not actually occur there. In contrast, gillnets are set deeper than the sites at Elbow of Flat Mountain Arm and Mid Flat Mountain Arm, and no other spawning sites have been confirmed near these sites, so I am confident that spawning likely did occur at these two locations.

Several factors could explain why Lake Trout might spawn on alternate substrate types in Yellowstone Lake. If the number of sites with high quality substrate that matches the cobble-contour model is limited in Yellowstone Lake and those that do exist are consistently surrounding by gillnets during the spawning season, Lake Trout may be forced to spawn at alternate and potentially inferior locations. Lake Trout in Whitepine Lake selected new spawning locations when historically used sites were covered with plastic tarpaulins (McAughey and Gunn 1995). Recently invaded Lake Trout populations expanding throughout a new system may also behave differently than populations that are already established. In the absence of known, traditional spawning areas, Lake Trout must explore an invaded lake to find sites. Exploratory behavior may not be limited to invading populations; Lake Trout in Thunder Bay, Lake Huron
explored newly constructed spawning reefs during the spawning season and spawned on them (Marsden et al. 2016). The lack of potential egg or fry predators in Yellowstone Lake may allow high survival of early life stages even at sites that do not offer much protection. Conversely, Lake Trout may regularly spawn at sites that do not match the cobble-contour model in all systems, but a lack of sampling effort at these locations may have prevented their detection. Historical records from commercial fishermen in the Great Lakes suggest that Lake Trout spawned at sites with sand, clay, or bedrock substrate (Coberly and Horral 1980, Goodyear et al. 1982, Holey et al. 1995); however, these records are based on the presence of adults at a given location rather than through the observation of eggs or fry. Small patches of undetected substrate matching the cobble-contour model could have been present within broad areas of otherwise poor substrate as has been shown at sites such as Julian’s Reef in Lake Michigan (Edsall et al. 1996).

The absence of egg detection at the remaining 17 sampled sites in Yellowstone Lake is not conclusive evidence that spawning does not occur at them. Nine sites where eggs were not captured matched our most inclusive spawning site model, but spawning could also be occurring at sites even more general than this model describes. I characterized sites based on the portion of the site that most closely matched the cobble-contour model; however, eggs may have been collected during any portion of a tow including over areas without any rocks. Alternatively, eggs that were present may have missed, especially if they were at low densities. The capture efficiency of our sled is likely low, as indicated by the small number of eggs recovered at any site. Eggs that are protected within interstitial spaces may be difficult to collect even with the use of a
pressure washer. Capture efficiency was likely reduced when the net was fouled with vegetation or filled with mud.

Our benthic sled design may be a useful tool for future efforts to identify spawning sites of Lake Trout or other fish species that spawn over rocky substrate. Many techniques have been developed to sample Lake Trout eggs (Stauffer 1981, Horns et al. 1989, Marsden et al. 1991, Perkins and Krueger 1994, Marsden and Janssen 1997, Riley et al. 2011), although most are passive methods and are inefficient for sampling across large areas. Our sled was able to actively sampling multiple sites within in a single day, allowing many areas to be assessed within a single spawning season. The sled was easily deployed and retrieved by two individuals with the aid of a winch and a separate boat operator. Although our sampling was limited to about 40 m depth, the addition of lights, high-pressure camera housings, and additional lengths of pressure hose would allow the sled to be used at substantially greater depths. The sled was most effective when targeting locations where rocky material was known to occur rather than broadly exploring large areas, as the cod end and net would quickly fill up with mud and debris; however, constructing a net out of a larger mesh size when possible would help alleviate some of this fouling. A live feed camera wired to the surface could also improve sampling efficiency by allowing more targeted sampling, although this bias would have to be accounted for in sampling protocols. Although the sled is efficient at determining the presence or absence of eggs, it does not provide a quantitative estimate of egg densities.

Our results suggest Lake Trout spawning site selection is a plastic trait and Lake Trout spawn at sites with a range of substrate compositions. This variability in
spawning site choice has not been extensively documented elsewhere and may contribute to the success of Lake Trout in Yellowstone Lake and other invaded systems. I found spawning at multiple sites that did not match the cobble-contour model, but our search was not exhaustive; additional spawning sites are likely present in other areas of the lake, or include additional substrate types. Consequently, suppression efforts targeting early life stages may need to be implemented at many sites to have a significant impact on the Lake Trout population. Future work should confirm that spawning regularly occurs at the sites I identified while also exploring and assessing new areas to better understand the extent of spawning and the impact site selection might have on the success of the Lake Trout population in Yellowstone Lake.

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**Literature Cited**


Table 1: Parameters used to evaluate sites sampled with a benthic sled for Lake Trout eggs in Yellowstone Lake.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Option</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Interstitial space quality</td>
<td>Poor</td>
<td>Sand or silt bottom OR &lt;50% coverage of single-layered rock</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Single-layered rock with coverage &gt;50% but &lt;100% OR Complete coverage of</td>
</tr>
<tr>
<td></td>
<td>Moderate</td>
<td>single or multi-layered rock visibly embedded OR Bedrock</td>
</tr>
<tr>
<td></td>
<td>Good</td>
<td>Complete coverage of single or multi-layered rock not visibly embedded</td>
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<tr>
<td>Particle size</td>
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<tr>
<td></td>
<td>Rubble</td>
<td>65 mm - 256 mm</td>
</tr>
<tr>
<td></td>
<td>Cobble-Boulder</td>
<td>&gt;257 mm</td>
</tr>
<tr>
<td></td>
<td>Bedrock</td>
<td>Contiguous areas of non-particulate rock</td>
</tr>
<tr>
<td>Level of infilling</td>
<td>No/light</td>
<td>No material washed up by sled, OR small, intermittent cloud of sediment</td>
</tr>
<tr>
<td></td>
<td>Moderate /Heavy</td>
<td>Moderate to thick cloud of sediment partially or completely obscuring</td>
</tr>
<tr>
<td></td>
<td></td>
<td>runners or sled</td>
</tr>
<tr>
<td>Vegetation density</td>
<td>Sparse</td>
<td>No macrophytes OR scattered pieces of macrophytes not forming dense clumps</td>
</tr>
<tr>
<td></td>
<td>Dense</td>
<td>Macrophytes forming dense clumps OR covers &gt;30% of bottom</td>
</tr>
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<td>Contour breaks or slope</td>
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<td>No slope or a slope less than 10 degrees</td>
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<td></td>
<td>Slope</td>
<td>Area with a grade greater than 10 degrees</td>
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<tr>
<td></td>
<td>Contour break</td>
<td>Area with an abrupt change of slope greater than 45 degrees</td>
</tr>
</tbody>
</table>
Table 2: Sampling effort, egg collections, site characteristics, and compatibility with the cobble-contour Lake Trout spawning site model at 24 sites in Yellowstone Lake sampled for Lake Trout eggs with a benthic sled. The cobble-contour model is defined as an area composed of rubble or cobble and boulder sized rocks with good quality interstitial spaces and no or light infilling along a contour break.

<table>
<thead>
<tr>
<th>Site</th>
<th># of Tows</th>
<th># of Tows with Eggs</th>
<th># of Eggs Captured</th>
<th>Average Depth (m)</th>
<th>Depth Range (m)</th>
<th>Fetch (m)</th>
<th>Match cobble-contour model?</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs found</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1: Breeze Channel Hump</td>
<td>4</td>
<td>1</td>
<td>1</td>
<td>26.4</td>
<td>24.5-29</td>
<td>990</td>
<td>No</td>
</tr>
<tr>
<td>2: Elbow Flat Mountain Arm</td>
<td>6</td>
<td>3</td>
<td>5</td>
<td>1.9</td>
<td>1.1-4.3</td>
<td>940</td>
<td>Yes</td>
</tr>
<tr>
<td>3: Mid Flat Mountain Arm</td>
<td>3</td>
<td>1</td>
<td>1</td>
<td>1.7</td>
<td>1.1-2.9</td>
<td>340</td>
<td>No</td>
</tr>
<tr>
<td>4: Olson Reef</td>
<td>4</td>
<td>1</td>
<td>4</td>
<td>17.9</td>
<td>13-20.7</td>
<td>2470</td>
<td>Yes</td>
</tr>
<tr>
<td>5: Outer Snipe Point</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>7.3</td>
<td>6.1-9.4</td>
<td>370</td>
<td>No</td>
</tr>
<tr>
<td>6: South Frank Hump</td>
<td>4</td>
<td>2</td>
<td>2</td>
<td>31.1</td>
<td>24.8-38.6</td>
<td>4170</td>
<td>No</td>
</tr>
<tr>
<td>7: Snipe Point</td>
<td>9</td>
<td>4</td>
<td>9</td>
<td>2.5</td>
<td>1.1-4.6</td>
<td>80</td>
<td>No</td>
</tr>
<tr>
<td>No eggs, moderate or good quality interstitial space present</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8: Inner Plover</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>1.5</td>
<td>1.1-3.2</td>
<td>20</td>
<td>No</td>
</tr>
<tr>
<td>9: NE FMA Entrance Knoll</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>11.9</td>
<td>6.3-18.5</td>
<td>1690</td>
<td>No</td>
</tr>
<tr>
<td>10: NW Frank</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>1.7</td>
<td>1.2-3.1</td>
<td>2870</td>
<td>No</td>
</tr>
<tr>
<td>11: Outer Elbow Slope</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>13.7</td>
<td>1.8-20.9</td>
<td>1190</td>
<td>No</td>
</tr>
<tr>
<td>12: Outer Plover</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>5.8</td>
<td>2.5-9.9</td>
<td>640</td>
<td>No</td>
</tr>
<tr>
<td>13: Peale Island</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>2.9</td>
<td>1.2-8.1</td>
<td>730</td>
<td>No</td>
</tr>
<tr>
<td>14: South Arm Hump</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>22.4</td>
<td>18.8-31.2</td>
<td>2540</td>
<td>No</td>
</tr>
<tr>
<td>15: Snipe Point West</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>2.3</td>
<td>3.2-2.0</td>
<td>50</td>
<td>No</td>
</tr>
<tr>
<td>16: South Elbow Shore</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>1.5</td>
<td>1.2-2.6</td>
<td>20</td>
<td>No</td>
</tr>
<tr>
<td>No eggs, poor quality interstitial space only</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>17: Eagle Bay Entrance</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>3.0</td>
<td>1.7-8.2</td>
<td>650</td>
<td>No</td>
</tr>
<tr>
<td>18: Flat Mountain Arm Entrance</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>7.1</td>
<td>6.6-7.8</td>
<td>400</td>
<td>No</td>
</tr>
<tr>
<td>19: NE Peale Island Slope</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>11.0</td>
<td>5.9-18.5</td>
<td>290</td>
<td>No</td>
</tr>
<tr>
<td>20: North Plover</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>16.4</td>
<td>14.0-19.1</td>
<td>700</td>
<td>No</td>
</tr>
<tr>
<td>21: South Arm Mid-Ridge</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>24.6</td>
<td>19.9-28.7</td>
<td>1350</td>
<td>No</td>
</tr>
<tr>
<td>22: South Arm West Ridge</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>35.8</td>
<td>34.6-37.1</td>
<td>1320</td>
<td>No</td>
</tr>
<tr>
<td>23: South Slope Flat Mountain Arm Entrance</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>24.5</td>
<td>22.3-28.3</td>
<td>1250</td>
<td>No</td>
</tr>
<tr>
<td>24: SW Corner of South Arm</td>
<td>4</td>
<td>0</td>
<td>0</td>
<td>6.6</td>
<td>1.5-16.8</td>
<td>790</td>
<td>No</td>
</tr>
</tbody>
</table>
Table 3: Evaluation of fit to the cobble-contour spawning site model, and variations to the model, for sites sampled for Lake Trout eggs in Yellowstone Lake. The cobble-contour spawning site model is defined as an area along a contour break composed of rubble or cobble and boulder sized rocks (referred to as “medium-large” rock within the table) with good quality interstitial spaces and no or light infilling. Alternate models varied by excluding one or more of these parameters from consideration or by allowing alternate options for a parameter. Only sampled sites that contained substrate with moderate or good quality interstitial spaces are included within the “eggs absent” category.

<table>
<thead>
<tr>
<th>Site</th>
<th>Good interstitial space, medium-large rock, no/light infilling</th>
<th>Good or moderate interstitial space, medium-large rock, slope or contour break</th>
<th>Good or moderate interstitial space, medium-large rock</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eggs found</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1: Breeze Channel Hump</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>2: Elbow Flat Mountain Arm</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>3: Mid Flat Mountain Arm</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>4: Olson Reef</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>5: Outer Snipe Point</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>6: South Frank Hump</td>
<td>Trace</td>
<td>Trace</td>
<td>Yes</td>
</tr>
<tr>
<td>7: Snipe Point</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>Eggs absent</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8: Inner Plover</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>9: NE FMA Entrance Knoll</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>10: NW Frank</td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td>11: Outer Elbow Slope</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>12: Outer Plover</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>13: Peale Island</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>14: South Arm Hump</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>15: Snipe Point West</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
<tr>
<td>16: South Elbow Shore</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
</tr>
</tbody>
</table>
Figure 1: Benthic sled sampling locations in Yellowstone Lake, Wyoming, fall 2015. Diamonds indicate areas where lake trout eggs were found, squares indicate areas where eggs were not found but quality rocky substrate was found, and circles indicate where eggs were not found, but only sandy or muddy substrate was observed. Contour lines indicate 20 m depth intervals on map (a) and 5 m intervals in inset maps (b) and (c).
Figure 2: Benthic sled used to sample for Lake Trout eggs at potential spawning sites. The black hose attached to the front of the frame leads to a pressure-washer.
Figure 3: Representative substrate of spawning sites in Yellowstone Lake, Yellowstone National Park, Wyoming confirmed by a benthic sled. (a) Snipe Point, (b) Elbow Flat Mountain Arm, (c) Mid Flat Mountain Arm, (d) Olson Reef, (e) South Frank Hump, (f) Breeze Channel Hump, (g) Outer Snake Point.
CHAPTER 3: COMPARISON OF AGE-0 DIET AND GROWTH BETWEEN A
NATIVE AND AN INVASIVE POPULATION OF LAKE TROUT

Abstract

The population of invasive Lake Trout (*Salvelinus namaycush*) in Yellowstone Lake, Yellowstone National Park grew nearly exponentially following their illegal introduction in the late 1980s. Yellowstone Lake is a species-depauperate system without any fish species known to be major Lake Trout egg or fry predators. Without this predation threat, Lake Trout fry feeding and growth in Yellowstone Lake may be greater than that of fry in the Great Lakes, potentially leading to increased survival of age-0 individuals and the rapid population growth observed in Yellowstone Lake. I compared the length, development, and feeding patterns of Lake Trout fry captured at a spawning site in Yellowstone Lake in 2014 and 2015 with fry captured in their native range at a spawning site in Lake Champlain in 2011. The majority of fry (96%) captured in Yellowstone Lake were feeding and had between 1 and 67 items in their stomachs, regardless of length or developmental stage; however, fry captured Lake Champlain were not consistently feeding until later stages. As a result of this higher rate of feeding early in life, the average length of Lake Trout fry captured each year in Yellowstone Lake was significantly greater than the average length of fry captured in Lake Champlain, both overall and within individual development stages. With an abundance of available food and no threat of predation, fry remained on the spawning site in Yellowstone Lake much later into the summer than in Lake Champlain, allowing them to achieve a greater maximum length.
before they left to avoid increasing water temperatures. This higher feeding and
growth likely leads to high survival of Lake Trout fry in Yellowstone Lake,
contributing to the population’s rapid growth.

**Introduction**

The first year of life is recognized as a critical period that can influence the
survival of a fish population (Hjort 1914, Houde 2008). The recruitment of a
particularly strong year class can have a long-lasting positive impact on the growth of a population (e.g., Yule et al. 2008), while conversely, the failure of one or many
subsequent year classes could potentially lead to major population declines (e.g.,
Watanabe et al. 1995). A number of theories have been proposed to explain recruitment
variability (e.g., Hjort 1914, Cushing 1990). Although these theories differ slightly, they
are all based on the influence of a number of key mechanisms, including temperature,
physical processes, prey and predator abundance, and growth, that either alone or in
combination can strongly influence the recruitment success of a population (Houde
2008).

A recruitment bottleneck during the early life stages of Lake Trout (*Salvelinus
namaycush*) has been identified as a likely factor limiting restoration of this species in
the Great Lakes (Selgeby et al. 1995). Lake Trout stocked as fingerlings or yearlings
have high survival and have established robust adult populations throughout the lakes.
While spawning has been confirmed through the capture of eggs and pre-emergent fry
on spawning reefs, the capture of wild recruits has only occurred in Lake Superior and
portions of lakes Huron and Michigan (Hansen et al. 1995, He et al. 2012, Hanson et al.
2013). The high survival of stocked yearlings suggests high mortality of wild post-
emergent individuals occurs prior to this stage (Elrod et al. 1988, Zimmerman and Krueger 2009). A number of factors may contribute to this bottleneck including predation on eggs and fry (Jones et al. 1995), nutrient deficiencies (Fisher et al. 1996), and reduced growth due to prey limitations (Edsall et al. 2003).

In contrast to the Great Lakes, invasive Lake Trout in Yellowstone Lake have experienced near exponential population growth (Kaeding et al. 1996, Munro et al. 2005, Syslo et al. 2011). Following the discovery of Lake Trout in Yellowstone Lake in 1994, managers expressed concern about the impact predatory Lake Trout would likely exert on the native Yellowstone cutthroat Trout (*Oncorhynchus clarkii bouvieri*) and implemented a gillnet suppression program in 1994 (Koel et al. 2005). Despite an increasing amount of gillnetting effort each year, modeling indicated the Lake Trout population was continuing to increase and suppression efforts needed to be increased further to reduce the population size (Syslo et al. 2011). Modeling also revealed the Lake Trout population was most sensitive to age-0 survival (Syslo et al. 2011) indicating high survival at this lifestage may have contributed to the rapid population growth in Yellowstone Lake.

Differences in age-0 survival contribute to exponential growth of the Lake Trout population in Yellowstone Lake and failure of restoration in the Great Lakes. A comparison of feeding and growth at age-0 in these systems could help explain the differences in recruitment success. Prior work on Lake Trout fry in the Great Lakes has focused on the relative abundance of fry (e.g., Stauffer 1981, Marsden et al. 1988, Riley and Marsden 2009), but high relative abundance is not a good indicator of survival or recruitment (Marsden et al. 2005). If fry are unable to find adequate food resources or
grow to sufficient size, overwinter mortality may be high. Lake Trout fry in the Great Lakes face competition and predation from a relatively diverse fish community (Edsall et al. 2003, Riley and Marsden 2009), whereas Yellowstone Lake is highly depauperate (Gresswell and Varley 1988); the absence of many competitors or predators may allow fry to consume more food and grow larger. I hypothesized Lake Trout fry captured in Yellowstone Lake would be longer for a given development stage and would consume more food than Lake Trout fry captured in their native range, thus contributing to the success of the Lake Trout population in Yellowstone Lake.

**Methods**

*Site descriptions*

Yellowstone Lake is located at an elevation of 2,357 m with a surface area of 34,020 ha, a mean depth of 48.5 m (Kaplinski et al. 1991), and a maximum depth of 133 m (Morgan et al. 2003; Figure 1). The lake is dimictic with a maximum summer surface temperature of 17°C and is typically ice covered between mid-December and mid-May (Benson 1961). Yellowstone Lake is a mesotrophic system (Theriot et al. 1997) with a plankton community composed of relatively few species. The phytoplankton community is generally dominated by diatoms (Interlandi et al. 1999) while the zooplankton community is limited to two species of cladocerans (*Daphnia schödleri* and *Daphnia pulecia*), two species of calanoid copepods (*Leptodiaptomus ashdandi* and *Hesperodiaptomus shoshone*), and one species of cyclopoid copepod (*Diacyclops bicuspidatus thomasi*; Tronstad et al. 2010). Amphipods (*Gammarus lacustris* and *Hyallela azteca*), oligochaetes, and aquatic insect larvae are also abundant benthos (Benson 1961). Yellowstone Lake contains only two native fish species, Yellowstone
Cutthroat Trout (*Onchorhyncus clarkii bouvieri*) and Longnose Dace (*Rhinichthys cataractae*; Simon 1962), and four non-native species, Lake Trout (*Salvelinus namaycush*), Redside Shiner (*Richardsonius balteatus*), Longnose Sucker (*Catostomus catostomus*), and Lake Chub (*Couesius plumbeus*; Gresswell and Varley 1988). Crayfish (*Orconectes spp.*), documented predators of lake trout eggs (Ellrott et al. 2007), are absent from the lake.

Lake Trout spawning in Yellowstone Lake was first confirmed in 1996 at Carrington Island, a small island near the western shore of the West Thumb basin (Ruzycki 2004; Figure 1). The area of exposed land on the island can vary substantially throughout the course of a year due to fluctuating water levels (Benson 1961). Approximately 5,000 m$^2$ of rocky substrate surrounds Carrington Island at depths less than 3 m during the fall spawning season. Peak spawning is estimated to occur in mid to late September (Gresswell et al. 2013).

Lake Trout populations in Lake Champlain were used as a native species comparison. Lake Trout were extirpated by 1900 and are currently supported by stocking (Marsden and Langdon 2012). Lake Champlain is situated between Vermont, New York, and Quebec at about 30 m above sea level (Figure 1). The lake, which is mostly meso-oligotrophic, has a surface area of 1,127 km$^2$, a mean depth of 19.5 m, and a maximum depth of 120 m (Ellrott and Marsden 2004). Lake Champlain does not consistently freeze over at its widest location (19 km), but will usually freeze within bays and narrower portions of the lake by mid-February (Lake Champlain Basin Program 2006). Lake Champlain has a diverse zooplankton community (Mihuc et al. 2012) and contains 87 fish species (Marsden and Langdon 2012), many of which have
been documented as predators of Lake Trout eggs and fry (Jones et al. 1995, Riley and Marsden 2009). Several species of crayfish are abundant in the lake (Fitzsimons et al. 2007).

Lake Trout egg and fry densities have been assessed at sites throughout Lake Champlain (Ellrott and Marsden 2004). Extremely high densities of Lake Trout eggs and fry have been consistently captured at Gordon Landing (identified as the “Grand Isle breakwall” in Ellrott and Marsden 2004; Figure 1). The site has approximately 570 m² of cobble and boulder substrate with water depths typically ranging from 2 to 5 m during the fall. Timing of spawning is variable between years, but generally peaks in late November (Ellrott and Marsden 2004).

Fry collections

Lake Trout fry were sampled with emergent fry traps, similar to those described by Marsden et al. (1988), at Gordon Landing in 2011 and at Carrington Island in 2014 and 2015 beginning as soon as possible after ice-off, which occurred on April 7 in 2011, May 31 in 2014, and May 6 in 2015. The traps were steel mesh cones with a 73 cm diameter base; 1 L bottles containing inverted funnels were mounted on top of the traps and captured fry rising from underneath. Thirteen traps were deployed at Gordon Landing on April 14 and checked seven times before they were removed on June 15 (Figure 2). In 2014, fry traps were set at Carrington Island on June 5 and checked 12 times before they were removed on July 22 (Figure 2). In 2015, fry traps were set at Carrington Island on May 13 and checked 14 times before they were removed on August 10 (Figure 2). Traps were checked by lifting from the surface about once a week until the number of fry captured approached or reached zero. All captured fry were
immediately preserved in 10% formalin. The catch-per-unit-effort (CPUE) calculated as number of fry*trap\(^{-1}\)*day\(^{-1}\) was determined for each date traps were checked. Water temperatures were recorded at Gordon Landing in 2011 and Carrington Island in 2015 on each day when traps were checked.

**Fry processing**

Total length and the length of any external yolk was measured to the nearest 0.1 mm for all fry captured at Carrington Island in 2014 and 2015 and a subsample of fry taken randomly from all sample dates at Gordon Landing in 2011 (Ladago et al. 2016). Individuals that had died and partially decomposed in fry traps at Carrington Island were excluded from these measurements and all further analysis. Measured fry were separated into four development stages as defined by Ladago et al. (2016). Fry with external yolk sacs were separated into those with a yolk sac length greater than 25% of the fry length or less than 25% of the fry length while fry without external yolk sacs were classified as either having internal yolk or no yolk. Herein I will refer to these stages, from youngest to oldest, as stages 1, 2, 3, and 4. All fry captured at Carrington Island in 2014, minus 33 captured on June 11, were dissected and the stomach contents quantified. Zooplankton were identified to the species level when possible. For the first 79 dissected fry, *H. shoshone* and *L. ashlandi* were not distinguished and were identified collectively as calanoid copepods; the two species were separated for all remaining fry. Diets of the subsample of measured fry captured at Gordon Landing were identified to family, or genus when possible, by Ladago et al. (2016). Diet composition was expressed as the percentage by number of each item type relative to the total number of diet items counted in each fry stage.
Statistical analysis

To test whether fry from Carrington Island were longer at a given developmental stage than those from Gordon Landing, average lengths were compared between sites among sampling years overall, at individual development stages, and among development stages within a single sampling year using one-way ANOVAs. Differences in average length among individual years and development stages were identified using a Tukey-Kramer HSD test.

To determine whether stage-specific diets different between lakes, the percentage of fry at each stage that contained food items within their stomach was calculated and compared between lakes overall and at each stage using a Pearson chi-square analysis. A linear regression was used to determine whether the number of diet items was related to fry length, and a one-way ANOVA was used to determine whether the number of diet items changed with development stage at Carrington Island. Differences between the average number of diet items found in fry captured at Carrington Island and at Gordon Landing overall and at individual development stages were evaluated with two-tailed t-tests. All statistical analyses were performed in JMP® Pro 12 (SAS Institute Inc., Cary, NC).

Results

A total of 1,296, 234, and 220 fry were captured at Gordon Landing in 2011 and Carrington Island in 2014 and 2015, respectively. CPUE peaked at 4.06, 0.75, and 0.725 fry*trap⁻¹*day⁻¹ in 2011, 2014, and 2015, respectively (Figure 2). Fry were captured as late as June 15 in Lake Champlain and July 22 in Yellowstone Lake in 2014, the dates traps were removed, and on June 30 in 2015, though traps were removed after that date
The number of traps checked on July 22, 2014 was not recorded, thus the CPUE value for that date is an estimate based on the maximum number of traps that could have been deployed. Water temperatures increased from 4.4°C when the traps were set to 16.7°C on June 30 at Carrington Island in 2015 and from 3.6°C on April 14 when traps were set to 17.1°C on June 15 when traps were removed at Gordon Landing in 2011 (Figure 2).

A subsample of 301 fry (18-31 mm total length) from Gordon Landing were evaluated for development stage and diet (Ladago et al. 2016; Figure 3); 34% (n=102) were stage 1, 33% (n=99) were stage 2, 17% (n=52) were stage 3, and 16% (n=48) were stage 4 (Figure 4). At Carrington Island, 213 (22-44 mm) fry in 2014 and 178 (24-35 mm) in 2015 were measured (Figure 3). In the two combined samples, 2% of fry (n=9) were stage 1, 46% (n=180) were stage 2, 35% (n=137) were stage 3, and 17% (n=65) were stage 4 (Figure 4). The lack of fry below 22 mm and the limited number of stage 1 fry at Carrington Island was likely a result of extended ice coverage on Yellowstone Lake that limited sampling of newly hatched fry.

On each sampling date at both sites, fry traps contained fry at a range of developmental stages, but the average length and stage tended to increase during the sampling season (Figures 2, 5). The average length of fry captured at Gordon Landing and at Carrington Island was significantly different among the three sampling years overall (F=205.8, p<0.0001, df=2) and within each development stage between lakes and years (stage 1 F=29.1475, p<0.0001, df=2; stage 2 F=109.9235, p<0.0001, df=2; stage 3 F=85.9329, p<0.0001, df=2; stage 4 F=10.6978, p<0.0001, df=2; Figures 3, 4). Fry captured at Gordon Landing were significantly shorter overall than those captured
at Carrington Island in both 2014 (p<0.0001) and 2015 (p<0.0001), and significantly shorter (p<0.0172) at each development stage (Figure 4).

Overall length and stage-specific length of fry from Carrington Island also differed significantly between years. Fry were significantly shorter overall in 2014 than 2015 (p=0.0019; Figure 3) and shorter at stage 2 (p=0.0004) and stage 3 (p<0.0001; Figure 4). The average length of stage 1 or 4 fry was not significantly different between years (Figure 4).

The average length of fry was significantly different among development stages within each sampling year at both sites (Gordon Landing 2011 F=144.7884, p<0.0001, df=3; Carrington Island 2014 F=15.7104, p<0.0001, df=3; Carrington Island 2015 F=13.4371, p<0.0001, df=3; Figure 4), and increased significantly with each development stage at Gordon Landing (p<0.0001; Figure 4). At Carrington Island in 2014, fry at stage 4 were larger compared to all other stages (p<0.0374), but not different among any other development stages (Figure 4). In 2015 fry were longer at stages 3 and 4 than at stages 1 and 2 (p<0.0039), but there was no difference between fry at stages 3 and 4 or between stages 1 and 2 (Figure 4).

A total of 179 fry captured at Carrington Island in 2014 and all 301 captured at Gordon Landing in 2011 that were evaluated for development stage were dissected for diet analysis (Figure 6). Dissections and diet composition of fry captured at Gordon Landing was detailed in Ladago et al. (2016). Briefly, 60% of dissected fry contained diet items in their stomachs with the proportion containing items increasing with development stage. Twenty-two percent of fry with stomach contents contained greater than five diet items with a maximum of 215 items found in a single fry. *Bosmina* were
the predominant diet item of fry at stages 2-4 with calanoid and cyclopoid copepods also present (Ladago et al. 2016). Food was found in stomachs of 96% dissected Lake Trout fry captured at Carrington Island; only eight fry, two in stage 1, three in stage 2, two in stage 3, and one in stage 4 did not have any food in their stomach. At Carrington Island, 60% of fry with stomach contents had over five diet items with a maximum of 67 items. Diet contents were limited to relatively few taxa; three species of copepods made up over 90% of the diet items of fry at each development stage, except for those at stage 1, which only contained unidentified material (Figure 6). The smaller copepod species, *Leptodiaptomus ashlandi* and *Diacyclops bicuspidatus thomasi*, made up between 26-42% and 21-34% of the diet items by number within each stage, respectively, while *Hesperodiaptomus shoshone* consisted of an additional 4-6% of the diet items (Figure 6). Unidentified calanoid copepods (either *L. ashlandi* or *H. shoshone*) from the first 79 dissected fry made up between 10-33% of the diet items within each stage while unidentified copepods made up an additional 7-8% (Figure 6). Chironomid larvae, other insects, and unidentified material made up the remaining 5-10% of total diet items (Figure 6). No cladocerans, oligochaetes, or amphipods were found in any stomachs.

Lake Trout fry captured at Carrington Island were significantly more likely to have fed than fry at Gordon Landing both overall ($\chi^2 = 68.97$, $p<0.0001$, df=1) and at stage 2 ($\chi^2 = 21.358$, $p<0.0001$, df=1). The proportion of fry feeding was not significantly different between the two locations at any other stage. There was no relationship between the length of fry and the number of diet items in their stomachs for fry from Carrington Island (Figure 7). The number of diet items found in the stomachs...
of fry from Carrington Island was not significantly different at different development stages. The average number of diet items across all fry was not significantly different between locations; however, fry captured at Carrington Island had significantly more diet items than those captured at Gordon Landing in stage 2 (p<0.0001, df=179) and stage 3 fry (p<0.0001, df=98), while stage 4 fry captured at Gordon Landing had significantly more diet items than fry captured at Carrington Island at the same stage (p=0.0019, df=91). The average number of diet items was not significantly different between stage 1 fry from the two locations, although the sample size of stage 1 fry from Carrington Island was low.

**Discussion:**

The timing, development, and feeding patterns of Lake Trout fry captured at Carrington Island in Yellowstone Lake were considerably different from those of fry captured at Gordon Landing in Lake Champlain. Lake Trout fry captured at Carrington Island remained resident on the spawning site longer into the year, were longer at each development stage, had a higher proportion feeding, and contained more diet items at stages 2 and 3 than fry captured at Gordon Landing. Taken together, these factors likely have a strong positive influence on the ability of Lake Trout to survive their first year in Yellowstone Lake and contribute to the success of the population (Houde 2008).

Lake Trout fry length was advanced at Carrington Island relative to Gordon Landing despite the extended duration of winter conditions on Yellowstone Lake. The average length of Lake Trout fry captured at Carrington Island on an individual sample date was greater than the average length of fry captured at Gordon Landing on equivalent calendar dates. Fry lengths averaged 25 mm on June 7 near the end of the
emergence period at Gordon Landing in 2011; on the comparable dates at Carrington Island, fry were 26 mm on June 6 in 2014, and 30 mm on June 4 in 2015. For comparison, Lake Trout that had left the spawning site and were captured by bottom trawl on June 17-19, 1991 near Gull Island Shoal in Lake Superior averaged 28 mm (Bronte et al. 1995). Despite being captured two weeks later in the year, the average length of these fry was either similar to or shorter than that of fry from Carrington Island. The fry at Carrington Island were either larger because they were older (i.e., hatched earlier), or because they grew faster either due to higher temperatures, earlier onset of feeding, access to more food, or spent less time avoiding predators. I do not know the hatch date at Carrington Island or have degree-day information to directly compare developmental rates between Yellowstone Lake and Lake Champlain; however, the temperature regime between spawning and ice cover and between ice-off and the deployment of fry traps was similar between the two systems. Peak spawning occurs at least two months earlier in Yellowstone Lake than in Lake Champlain which could be sufficient extra time for fry at Carrington Island to accrue the necessary number of degree days to match or surpass the length of fry at Gordon Landing by mid-June despite low water temperatures during that period.

I also do not know when fry began feeding at Carrington Island, but if they fed more than fry at Gordon Landing, they could reach equal or greater average lengths by the same date even if degree days were similar. Virtually all fry captured at Carrington Island contained many diet items, regardless of length or stage; however, fry captured at Gordon Landing were not consistently feeding until stages 3 or 4 (Ladago et al. 2016). Although fry at Gordon Landing were capable of feeding early in development, either
food availability was limited early in the season, there was either not a strong drive to feed until yolk material was nearly depleted, or the threat of predation prevented fry from consistently feeding until the necessity to do so outweighed potential risks. Not only were most fry from Carrington Island eating more items than fry at Gordon Landing, but the average size of the taxa consumed was larger as well; the size of the smaller copepod species in Yellowstone Lake (*Leptodiaptomus ashlandi* and *Diacyclops bicuspidatus thomasi*) are at least twice as large as the *Bosmina* that dominated the diets of fry at Gordon Landing (Ladago et al. 2016). A smaller range of taxa was consumed by fry at Carrington Island either due to lack of availability, as may have been the case for the cladoceran species (Benson 1961), or gape limitations in the case of oligochaetes or amphipods; amphipods are a major diet item for larger Lake Trout in Yellowstone Lake (Syslo et al. 2016). By eating a greater number of larger, and thus more energy rich, diet items, the fry around Carrington were likely able to increase their growth rate.

The increased length of fry at Carrington Island at a given development stage did not come at the expense of yolk storage. Fry were apparently able to hold yolk supplies in reserve by consuming sufficient exogenous food resources for survival and growth. Average length of fry at each stage was greater at Carrington Island than Gordon Landing indicating growth in length and yolk absorption were disconnected.

The availability of food as well as lack of potential predators likely allowed Lake Trout fry to remain at Carrington Island much later into the year than at Gordon Landing. In their native range, fry generally disperse from spawning sites into deeper water by the time external yolk material has been fully absorbed and external feeding
begins, generally at 25 mm (DeRoche 1969, Stauffer 1978, Jude et al. 1981). Dispersal may be driven by a lack of available food resources or the threat of predation by epibenthic or interstitial predators (Bronte et al. 1995, Jones et al. 1995). Normal (i.e., early) fry dispersal occurred at Gordon Landing in 2011, but at Carrington Island fry continued to be captured for several months after they reached 25 mm. The average length of fry at Carrington Island increased over the sampling period indicating fry were remaining and continuing to grow; i.e., I was not just capturing new groups of fry that were spawned later in the fall or that had hatched later in the spring. Without the threat of predation, and with food available, fry at Carrington Island had no stimulus to leave the reef (Brown et al. 1999).

Elevated water temperatures likely dictated when fry finally left Carrington Island. Water temperatures were above 15°C, the upper avoidance temperature for Lake Trout fry (Jude et al. 1981, Peck 1982), on the last day a fry was captured in 2015. Although the last date fry were captured at Gordon Landing in 2011 also coincided with increasing water temperatures, fry are generally no longer captured well before temperatures reach 15°C in other years (unpublished data) supporting the hypothesis that alternate pressures drive this departure. Several small Lake Trout were noted at the surface after electroshocking at Olson Reef, a 13-20 m deep spawning site in the main basin of Yellowstone Lake, on May 18, 2015; the single individual that was recovered was 120 mm, and likely age-1 based on size of spring yearlings in Lake Champlain (P. Doepke, Yellowstone National Park Center for Resources, personal communication). As much of this site remains below the thermocline throughout the summer, juvenile
Lake Trout may remain on or around the site for over a year if they are not forced to leave due to elevated water temperatures.

Slower growth, in general, will increase the potential for mortality by increasing the amount of time individuals are susceptible to size-selective predation (the stage-duration hypothesis, Anderson 1988). Under this theory, Lake Trout eggs and fry in Yellowstone Lake should experience higher mortality relative to Lake Champlain given its extended winter length, but the lack of potential egg and fry predators minimizes this risk. Egg loss due to predation in the Great Lakes is greatly reduced within a few weeks after spawning as eggs in accessible areas are either eaten or dislodged, leaving only those that had settled into more protected locations (Claramunt et al. 2005). Thus, even if substantial egg predation were occurring in Yellowstone Lake, the increased time spent at the egg stage may not actually lead to higher predation mortality. The extended period of cold water temperatures may also slow the metabolism and feeding rates of potential predators, limiting the risk of predation even further (Claramunt et al. 2005).

The availability of food and lack of predators experienced by fry at Carrington Island would allow rapid growth and high survival and recruitment (Houde 2008). In fact, Lake Trout population modelling for Yellowstone Lake has shown that survival from egg to age-2 is potentially more than double that of native populations (Gresswell et al. 2013). However, although I only documented feeding in one year and growth patterns in two years at one shallow-water spawning site in Yellowstone Lake, I saw significant inter-annual differences in growth. Many spawning sites have been documented in Yellowstone Lake that encompass a range of depths and substrate types (Simard 2016). Eggs and fry at these sites could be demonstrating dramatically different
patterns in feeding, growth and survival and thus could each be contributing to the growth of the Lake Trout population differently. Future work should investigate how growth and recruitment vary among sites and years to optimize suppression efforts targeting early life stages in Yellowstone Lake.

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Figure 1: Map of study sites in Yellowstone Lake and Lake Champlain.
Figure 2: CPUE (fry*trap⁻¹*day⁻¹) and average length (mm) of fry captured at (a) Gordon Landing, Lake Champlain in 2011, (b) Carrington Island, Yellowstone Lake, in 2014, and (c) Carrington Island in 2015 with associated water temperatures (°C) aligned by ice-off date. Total length is represented by solid black lines, CPUE by dashed black lines, and water temperature by solid gray lines. Reference lines indicating 25 mm and June 1 are indicated by horizontal and vertical dotted gray lines, respectively.
Figure 3: Length-frequency of Lake Trout fry captured at Carrington Island, Yellowstone Lake, in 2014 and 2015 and at Gordon Landing, Lake Champlain in 2011.
Figure 4: Length-frequency of Lake Trout fry captured at Carrington Island, Yellowstone Lake in 2014 and 2015 and at Gordon Landing, Lake Champlain in 2011 at different development stages. Black bars indicate fry captured in 2014, gray bars indicate fry captured in 2015, and patterned bars indicate fry captured in 2011.
Figure 5: Proportion of fry at different development stages captured at (a) Gordon Landing, Lake Champlain in 2011 and at Carrington Island, Yellowstone Lake in (b) 2014 and (c) 2015 on individual sample dates. Numbers above bars indicate the total number of fry evaluated for a given sample date.
Figure 6: Percent composition of diet items in Lake Trout fry stomachs at four different development stages collected at (a) Carrington Island, Yellowstone Lake in 2014 and (b) Gordon Landing, Lake Champlain in 2011. Numbers in parenthesis indicate the number of fry dissected. *H. shoshone* and *L. ashlandi* were not separately distinguished for the first 79 dissected fish from Carrington Island in 2014 and are collectively identified as “Unidentified calanoid copepods.” Figure (b) was modified from Ladago et al. (2016) with permission from the authors.
Figure 7: Number of diet items in 179 Lake Trout fry captured at Carrington Island in 2014 relative to their total length.
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