

LAKE TROUT HABITAT SELECTION AT DRUMMOND ISLAND SPAWNING REEFS:
PARADIGM OR PARADOX?

By

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ABSTRACT

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Progress towards restoration of self-sustaining populations of lake trout in the Laurentian Great Lakes has been slow. Adequate survival of stocked yearlings to maturity suggests potential recruitment bottlenecks exist between spawning and the yearling life stage, possibly related to an inability to select spawning habitats suitable for egg incubation. However, little is known about the fundamental features of lake trout spawning habitats or the criteria by which it is selected. This information gap was addressed using a novel acoustic telemetry-based approach whereby sampling effort was apportioned among habitats known to have been encountered during the spawning period based on behavioral data from tagged adult lake trout. Among sites encountered by lake trout on three spawning reefs in northern Lake Huron, physical characteristics and egg survival were compared between habitats positive and negative for egg deposition. Widespread egg deposition was confirmed on all three reefs, but variables measured (substrate diameter, homogeneity, interstitial depth, and slope) were unable to fully explain the habitat selection observed, suggesting other variables may have been important. Based on an *in situ* habitat bioassay, egg survival did not differ between habitats that received egg deposition and those that did not, suggesting the supply of spawning habitat may exceed demand in this area. Further, lake trout spawned in habitats inconsistent with the commonly-accepted lake trout spawning habitat paradigm, including previously undescribed boulder-associated habitats. These unconventional habitats not only received egg deposition, but also produced viable juveniles, forcing us to rethink, adapt, and expand our conceptual understanding of suitable trout spawning habitat.

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Cheers!

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KEY TO ABBREVIATIONS

The following table describes abbreviations commonly referenced throughout this thesis and provides the page on which each abbreviation is first defined.

Abbreviation	Meaning	Page
AICc	Akaike's information criterion, corrected for small sample size	29
ANOVA	Analysis of variance	32
BLD	Boulder Alley	8
$\hat{\beta}$	Model-averaged parameter estimate	29
$\hat{\beta}^*$	Standardized model-averaged parameter estimate	29
$\frac{\hat{\beta}_j^*}{\widehat{\beta_{max}}^*}$	Standardized evidence ratio	29
CI	Confidence interval	29
CON	Control	32
CPUE	Catch per unit effort	73
CV	Coefficient of variation	84
DI	Detection interval	23
DIR	Drummond Island Refuge	6
F	Unique fish	23
HSD	Tukey's honest significant difference	32
HSR	Horseshoe Reef	7
HUI	Habitat use index	23
IS	Interstitial depth	25
μ_{diff}	Mean difference	46
ROV	Remotely operated vehicle	72
SCS	Scammon Shoal	7
SCUBA	Self-contained underwater breathing apparatus	7
w	Akaike weight	29

Chapter 1 : Introduction

Until the mid-20th century, lake trout, *Salvelinus namaycush*, was the dominant native keystone predator within the Laurentian Great Lakes, occurring in great abundance in Lake Superior, Lake Huron, Lake Michigan, Lake Ontario, and the eastern basin of Lake Erie. Early explorers of these vast inland seas, including Jacques Marquette, Louis Jolliet, and Louis Agassiz recounted the immense size and productivity of lake trout and commented on the dependence of aboriginal peoples on them for sustenance and trade (Agassiz and Cabot, 1850; Cleland, 1982). While lake trout were relatively inaccessible for much of the year due to their preference for great depths, they were available in almost limitless quantities throughout the spawning season ranging from August to December, supporting a crucial late season subsistence fishery (Zedeño et al., 2001). European colonization in the late 1800's developed a productive commercial fishery for lake trout with sustained combined annual harvests well over 6 million kg in lakes Michigan, Huron and Superior from 1900 to 1940 (Baldwin and Saalfeld, 1962; Berst and Spangler, 1973). Coastal communities and their economies flourished, driven largely by the seemingly limitless lake trout abundance and successive generations of immigrant-origin commercial fisherman (Bogue, 2001).

With European colonization came drastic environmental changes at scales never before experienced in the Great Lakes basin. Timber harvest and agriculture that supported rapid population growth drastically altered Great Lakes watersheds (Berst and Spangler, 1973; Bogue, 2001). To satisfy the nation's growing demand for iron ore, navigational locks were constructed to allow shipping from the rich Vermillion, Gogebic, and Menominee ranges in Minnesota, Wisconsin, and Michigan to eastern steel mills in Ohio, Pennsylvania, and New York. This increased navigational connectivity opened a migratory corridor around Niagara Falls to the

upper Great Lakes for invasion by non-native species, such as sea lamprey, *Petromyzon marinus*, and alewife, *Alosa pseudoharengus*, causing sweeping ecological changes to the trophic structure of the Great Lakes food web. In particular, the predatory and parasitic activity of sea lamprey, following their invasion in the 1920s, drastically altered growth and condition of lake trout, decimating native stocks (e.g., Smith and Tibbles, 1980; Coble et al., 1990; Eshenroder, 1992). At the same time, increased manufacturing capacity resulting from rapid industrialization altered water quality and caused widespread near-shore habitat degradation that potentially hindered lake trout reproductive capacity (e.g., Zint et al., 1995; Tillitt et al., 2008; Marsden et al., 2016). In combination with expanding commercial fisheries, these anthropogenic stressors led to a catastrophic crash of lake trout populations in the Great Lakes throughout the 1940s. By 1950, total lake trout yield had declined from 2.7 million to 0.18 million kg in Lake Huron, from 3.1 million to 0.16 million kg in Lake Michigan, and from 2.1 million to 0.23 million kg in Lake Superior (Hansen, 1999).

Today, rehabilitation of lake trout in the Laurentian Great Lakes represents one of North America's largest-scaled native species recovery endeavors. The task of reestablishing naturally reproducing populations of the keystone piscivore from near extinction in one of the world's largest freshwater ecosystems is unparalleled in ecological and socio-political complexity (Krueger and Ebener, 2004; Muir et al., 2012b). As a comparison of spatial scale among ecological restoration sites in the U.S., Lake Huron (59,600 km²) alone is over six times the area of Yellowstone National Park (8,982 km²), and nearly 30 times the area of the Florida Everglades (1,901 km²), where the recovery of native predators, the grey wolf, *Canis lupis*, and Florida panther, *Puma concolor coryi*, are national priorities (e.g., Johnson et al., 2010; Ripple and Beschta, 2012). Moreover, the watershed of the Laurentian Great Lakes includes the borders

of two Canadian provinces (Ontario and Quebec), eight US states (New York, Pennsylvania, Ohio, Michigan, Indiana, Illinois, Wisconsin, and Minnesota), and three tribal authorities (Chippewa-Ottawa Resource Authority, 1854 Treaty Authority, Great Lakes Indian Fish and Wildlife Authority). When combined with federal authorities of Canada and U.S., lake trout management is greatly complicated due to multiple jurisdictions and the possibility of conflicting interests. Remarkably, inter-jurisdictional management has been effectively conducted voluntarily by subnational governments, as opposed to using legislated federal jurisdictional authority (e.g., Gaden et al., 2008, 2009). To facilitate coordination among various entities, the binational Great Lakes Fishery Commission (GLFC) was formed by convention in 1955, with emphasis on guidance of research to support fishery rehabilitation and coordination of sea lamprey control efforts (Gaden et al., 2009). Initial management efforts aimed at restoring self-sustaining populations of lake trout in the Great Lakes were focused on reducing total mortality through fishery regulation, control of the invasive sea lamprey, and the re-introduction of lake trout through supplemental stocking (Hansen, 1999; Muir et al., 2012b).

Despite average annual stockings of over 4 million lake trout in each of the upper lakes from 1970 to 2000, progress towards the establishment of self-sustaining, naturally-reproducing populations of lake trout in the Great Lakes has been slow (e.g., Krueger and Ebener, 2004; Muir et al., 2012b). Numerous impediments to successful rehabilitation have been hypothesized, including continued excessive predation from sea lamprey, low genetic diversity, habitat degradation, low survival of early life stages, and poor spawning habitat selection caused by maladaptive hatchery propagation and stocking practices (e.g., Bronte et al., 2003, 2008). Furthermore, continued invasions of non-native species (e.g., Dreissenid mussels, *Dreissenia* spp.; round goby, *Neogobius melanostomus*; Spiny water flea, *Bythotrephes* spp.) have resulted

in profound ecological changes that greatly complicated rehabilitation efforts from the 1960s to present (Muir et al., 2012b). Today, after nearly 60 years of stocking and sea lamprey control, evidence of recovery (i.e., recruitment of wild origin adults) has been limited to Lake Superior, portions of Lake Huron and, most recently, a few isolated regions in Lake Michigan (Hansen, 1999; Riley et al., 2007; Hanson et al., 2013). Only Lake Superior has been declared restored. While these successes have been encouraging, basin-wide restoration has remained elusive as many areas continue to rely heavily on stocking of hatchery-reared lake trout, typically yearling age fish.

Because survival of stocked yearlings appears to be sufficient to establish spawning stocks, mortality affecting natural recruitment most likely occurs between spawning (deposition of eggs) and the yearling life stage (Selgeby et al., 1995; Krueger and Ebener, 2004; Muir et al., 2012b). As a result, the reproductive ecology of lake trout has long been identified as a critical research priority for their recovery in the Great Lakes (Eshenroder et al., 1984, 1999; Bronte et al., 2003). Hypothesized recruitment bottlenecks include low egg viability due to contaminant loading (e.g., Zint et al., 1995) and thiamine deficiency (e.g., Fitzsimons et al., 2010; Riley et al., 2011), excessive early mortality due to early life-stage predation, particularly by non-native species (e.g., Krueger et al., 1995; Claramunt et al., 2005; Jonas et al., 2005), asynchrony between free embryo emergence and feeding and food availability (e.g., Casselman, 1995; Edsall and Cleland, 2000; Houde, 2008), and egg and free embryo mortality due to low quality and quantity of suitable incubation habitats (e.g., Marsden et al., 1995; Muir et al., 2012a). In the absence of appropriate cues (e.g., geographic imprinting, olfactory homing, or pheromones), hatchery origin lake trout may be unable to successfully locate spawning reefs, find spawning aggregations, or select appropriate locations for spawning where eggs can successfully incubate

and hatch. Unfortunately, understanding of the fundamental characteristics of spawning habitat and the criteria by which lake trout evaluate sites for spawning is limited.

Previous research aimed at understanding critical features of lake trout spawning habitat has generated an evolving conceptual framework describing spawning habitat suitability (e.g., Marsden et al., 1995, 2016; Muir et al., 2012a), recently termed the ‘cobble-contour’ model (Simard 2017). In this model, lake trout spawn on multi-layered, rounded to sub-angular rubble-cobble (8 cm – 3 m diameter) substrates with clean interstitial spaces (typically > 30 cm) that are associated with sharp bathymetric features, such as a steeply sloped lake bottom (reported slope = 8 - 100%; e.g., Marsden and Krueger, 1991; Casselman, 1995; Fitzsimons, 1996). Interactions among rubble-cobble substrates with deep interstitial spaces with lake currents and bathymetric relief (i.e., slope) have been thought to provide ideal incubation conditions that entrain eggs, provide refuge from predation, and buffer physical forces associated with wave action and ice scour, while allowing adequate flow to prevent siltation and provide oxygen for incubation (e.g., Marsden and Chotkowski, 2001; Callaghan et al., 2016; Riley et al., 2017). This model has received support from studies conducted in several North American systems (e.g., Fitzsimons, 1995; Marsden et al., 1995; Muir et al., 2012a), but not all reported lake trout spawning sites conform to this model (e.g., Beauchamp et al., 1992; Callaghan et al., 2016).

Refinement of the ‘cobble-contour’ model has largely been limited by the lack of studies that examine habitat selection at fine spatial scales (m’s). Rarely has verification of spawning occurred through direct observation of spawning behaviors or egg deposition. Even when direct observation has occurred, most sampling for eggs, free embryos, and alevins has been targeted at spawning habitats that match those predicted to be used based on the existing model rather than at sites elsewhere (e.g., Gunn, 1995; Marsden et al., 1995). As a result, the model fails to explain

why some habitats are selected for egg deposition while other adjacent habitats with seemingly suitable characteristics are not. Consequently, little is known about how habitats selected for egg deposition differ from those that were encountered but not selected for egg deposition, nor is it known to what degree suitable habitats may not be used simply because they are not encountered by lake trout (Binder et al., 2018). Further, egg deposition by lake trout in spawning sites that do not fit model predictions is unexplained.

Decades of stocking of hatchery reared lake trout and sea lamprey control in Lake Huron have established spawning stocks of sufficient size to sustain natural reproduction (Selgeby et al., 1995; Ebener, 1998; He et al., 2012) and recent declines in alewife throughout Lake Huron have lessened predatory pressure and reduced the incidence of thiamine deficiency (Krueger et al., 1995; Madenjian et al., 2008b; Fitzsimons et al., 2010; Riley et al., 2011). As a result, survival and recruitment of early life stages of wild-spawned lake trout has greatly improved in Lake Huron, such that by 2013, greater than 50% of main basin lake trout age-7 or younger were naturally produced fish (Riley et al., 2007; He et al., 2012; Johnson et al., 2015). Successful natural reproduction by lake trout has recently been reported in Lake Huron (He et al., 2012; Johnson et al., 2015), particularly near the Drummond Island Refuge (DIR; Ebener 1998; Riley et al., 2007; Madenjian et al., 2008a). Created in 1985, the DIR covers 55,000 ha following the southern shore of Drummond Island eastward to the US-Canada border at False Detour Channel and extending southward to 45° 40' N latitude. Commercial and sport fishing of lake trout has been restricted within the DIR in support of efforts to reestablish self-sustaining populations in the Great Lakes. As such, this area provides a unique opportunity to better understand the spawning behavior and habitat use of a recovering population of successfully reproducing lake trout.

Recent acoustic-telemetry based research conducted within a $\sim 25 \text{ km}^2$ portion of the DIR monitored the spawning behavior of ~ 390 tagged wild (likely primarily F1 generation) and hatchery-reared lake trout over five consecutive spawning periods (Binder et al., 2016a, 2016b, 2018; Grimm et al., 2016). From 2010-2014, at least five discrete spawning sites in which lake trout consistently congregated were identified, including several that did not conform to the commonly-accepted conceptual model (e.g., Binder et al., 2018). Subsequent SCUBA-based surveys revealed egg deposition on each of the previously identified reefs in all years of the study, but no detailed analysis was done on the physical characteristics of habitats selected for spawning nor how they differ from habitats at sites that were encountered by lake trout, but not selected for egg deposition. This thesis builds upon the acoustic telemetry-based work conducted at the DIR from 2010-2014 to explore fine-scale spawning habitat selection on three of the six previously identified spawning sites.

In chapter one, fine-scale habitat selection was investigated on the two most popular spawning reefs within in the telemetry receiver array, Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*), to determine whether habitats selected for egg deposition differed in either physical characteristics or incubation success (egg survival) from habitats on the same reefs that were known to be encountered by spawning lake trout, but not selected for egg deposition. Specifically, the objectives of chapter one were to compare: 1) the physical characteristics of sites selected for egg deposition vs. those encountered but not selected, and (2) the relative survival of fertilized eggs incubated over winter at these same sites. I hypothesized that: 1) lake trout select spawning habitats based on specific measurable physical substrate characteristics (e.g., substrate diameter, interstitial depth, substrate homogeneity, and slope), and 2) lake trout select spawning habitats that maximize egg incubation success relative to other nearby available

habitats. Improving understanding of the relative quality of spawning habitats being used by lake trout and the criteria by which they are selected is a fundamental component of identifying and addressing possible limitations to recruitment.

In chapter two, spawning habitat selection by lake trout and physical description of sites chosen was studied within previously unreported ‘atypical’ (inconsistent with the ‘cobble-contour’ model) spawning habitats associated with giant (2 - 7 m diameter) boulders found at a third site, Boulder Alley (*BLD*). Congregations of lake trout were consistently observed between 2010 and 2014 within this 0.63 km² area located to the west of *HSR*, but the area appeared to lack any classic reef structure in terms of depth contours or cobble substrate in comparison to other spawning sites (Binder et al., 2018). Preliminary observations revealed the area was comprised of numerous broadly-spaced boulders greater than 1 m in diameter, with some as great as 3 - 4 m in diameter. Further surveys prior to my research confirmed that egg deposition occurred in clean gravel-rubble substrate under a handful of these boulders, and a single larva was caught adjacent to one of the boulders. However, the full extent to which boulder-associated spawning occurs within the array was unknown. Multi-beam bathymetry of *BLD* indicated that likely hundreds of these large boulders occurred in this area, so the combined contribution of this habitat type to lake trout recruitment in northern Lake Huron could be substantial. To better understand the potential for boulder-associated spawning to contribute to lake trout recruitment in northern Lake Huron, the specific objectives of chapter two were to: 1) describe the spatial extent of lake trout spawning in association with boulders at Drummond Island, 2) determine whether use of boulder-associated substrates for egg deposition by lake trout could be predicted by measurable physical characteristics of boulders or their adjacent substrates, and 3) compare the abundance of free embryos and alevins located in boulder-associated spawning habitats to

those in other highly-used nearby spawning habitats within the acoustic telemetry array. An accurate accounting of the total amount of suitable spawning habitat available to recovering populations improves understanding of the variability in recruitment and thus, limitations imposed by the carrying capacity of a system.

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Chapter 2 : Evaluation of lake trout habitat selection at Drummond Island spawning reefs

Abstract

In the Laurentian Great Lakes, slow recovery of lake trout, *Salvelinus namaycush*, suggests potential recruitment bottlenecks exist between spawning and the yearling life stage. Determining the critical features and quality of sites selected for embryo incubation may help understand limitations to larval recruitment. I used a novel acoustic-telemetry based sampling approach to compare physical characteristics and egg survival between sites receiving egg deposition and those that did not on two reefs in northern Lake Huron. Egg deposition was confirmed at 25 of 58 sites (20m x 20m), but the physical characteristics of sites receiving egg deposition varied between reefs. Slope magnitude was associated with habitat selection on one reef but not the other. No evidence existed to support a relationship between other substrate characteristics (i.e., substrate size, interstitial depth, and substrate homogeneity) and egg deposition on either reef. Based on an *in situ* habitat bioassay, no difference in survival to hatch was observed between sites selected for egg deposition and nearby sites that were not. However, some sites with adequate survival to hatch were not used, suggesting supply of suitable spawning habitat may exceed demand in this area.

Introduction

Lake trout, *Salvelinus namaycush*, were once the dominant native predator in the Laurentian Great Lakes, supporting a large and valuable fishery. These fish were diverse in diet and habitat use, and existed in several morphotypes, representing alternative life history strategies (e.g., Hansen et al., 2016). Populations collapsed in the late 1940s due to a combination of commercial exploitation and predation from invasive sea lamprey, *Petromyzon marinus* (e.g., Hile, 1949; Coble et al., 1990; Eshenroder, 1992). Since their decline, restoration of self-sustaining populations of lake trout in the Great Lakes has been the focus of one of the largest native species recovery endeavors in North America (Hansen, 1999; Krueger and Ebener, 2004; Muir et al., 2012b). However, after nearly 60 years of stocking and sea lamprey control, evidence of recovery (i.e., recruitment of wild origin adults) has been limited to Lake Superior, portions of Lake Huron and, most recently, a few isolated regions in Lake Michigan (Hansen, 1999; Krueger and Ebener, 2004; Muir et al., 2012b; Hanson et al., 2013). While these successes are encouraging, basin-wide restoration has remained elusive as many areas continue to rely heavily on stocking of hatchery-reared lake trout, typically yearling age fish.

Numerous possible impediments to lake trout recovery have been identified since rehabilitation efforts began, though none solely explain the slow recovery experienced over the last 60 years (Krueger and Ebener, 2004). Lack of success has occurred even though survival to maturity by hatchery-reared lake trout has yielded sufficient spawning stock abundances to sustain natural reproduction and year-class recruitment in some areas (Selgeby et al., 1995; Bronte et al., 2007; He et al., 2012). Because substantial survival occurs from when yearlings are stocked to adult life stages, limitations to natural recruitment most likely occur between

spawning and the yearling life stage (Bronte et al., 2003; Krueger and Ebener, 2004; Muir et al., 2012b). As a result, the reproductive ecology of lake trout has long been identified as a critical research priority (Eshenroder et al., 1984, 1999; Bronte et al., 2003). Hypothesized recruitment bottlenecks include low egg viability due to contaminant loading (e.g., Zint et al., 1995) or thiamine deficiency (e.g., Madenjian et al., 2008b; Fitzsimons et al., 2010; Riley et al., 2011), excessive mortality due to early life stage predation, particularly by non-native species (e.g., Krueger et al., 1995; Claramunt et al., 2005; Jonas et al., 2005), asynchrony between commencement of exogenous feeding and food availability (e.g., Casselman, 1995; Edsall and Cleland, 2000; Houde, 2008), and excessive mortality of eggs, free embryos and alevins due to low quality or quantity of suitable incubation habitats (e.g., Marsden et al., 1995; Muir et al., 2012a). The ability of hatchery origin adults to select spawning habitats where early life stages can develop successfully could also affect egg survival, including predation vulnerability and food asynchrony.

Optimum lake trout spawning habitat is thought to have two critical components; suitable habitat must 1) facilitate aggregation and mate selection by spawning fish, and 2) provide adequate protection and interstitial water quality for successful incubation of eggs from the autumn spawning period through hatch and alevin dispersal the following spring (e.g., Marsden et al., 1995). The interaction of broad-scale physical characteristics such as water depth, distance to shore, lake bathymetry, and reef orientation with fine-scale habitat characteristics such as substrate size, shape, and abundance must provide adequate flow conditions to oxygenate eggs, protect them from physical forces such as waves and ice, and reduce their vulnerability to predation (Dorr III et al., 1981; Sly, 1988; Fitzsimons, 1994). In the absence of appropriate cues (e.g., geographic imprinting, olfactory homing, or pheromones), hatchery origin lake trout may

be unable to successfully locate spawning reefs, find aggregations of adults, or select appropriate locations for spawning where eggs can successfully incubate and hatch.

Decades of research focused on lake trout spawning habitat has yielded a conceptual framework for spawning habitat suitability (e.g., Marsden et al., 1995, 2016; Muir et al., 2012a), recently termed the ‘cobble-contour’ model (Simard, 2017). In this model, lake trout spawn on multi-layered, rounded to sub-angular rubble-cobble (8 cm – 3 m diameter) substrates with clean interstitial spaces (typically > 30 cm in depth) that are associated with sharply changing bathymetric features often linked with a steeply sloped lake bottom (reported slope = 8 - 100%; e.g., Marsden and Krueger, 1991; Casselman, 1995; Fitzsimons, 1996). The model has received support from studies conducted in several North American systems (e.g., Fitzsimons, 1995; Marsden et al., 1995; Muir et al., 2012a), but not all reported lake trout spawning habitat conforms to this model, including spawning on aquatic vegetation and in rivers (e.g., Beauchamp et al., 1992; Callaghan et al., 2016, Jones et al., *in press*). Furthermore, the model fails to explain why some habitats are selected by lake trout for egg deposition while other seemingly similar habitats are not. Verification of spawning through direct observation of spawning behaviors or egg deposition has been rare and most sampling for early life stages has been limited to spawning habitats that fit this model (e.g., Gunn, 1995; Marsden et al., 1995), creating a potential bias in support of the model. As a result, little is known about how the characteristics of habitats selected for egg deposition differ from those that are not selected for egg deposition, nor is it known to what degree suitable habitats may not be used because they are not encountered by lake trout.

The goal of this study was to determine if habitats selected for egg deposition differed from those that were encountered by lake trout but not selected for egg deposition. The specific

objectives were to compare: 1) the physical characteristics of sites selected for egg deposition vs. those known to be encountered by lake trout but were not selected, and (2) the relative survival of fertilized eggs incubated over winter deployed at these same sites. I hypothesized that: 1) lake trout select spawning habitats based on specific measurable physical habitat characteristics (substrate diameter, interstitial depth, substrate homogeneity, and slope), and 2) lake trout select spawning habitats that maximize egg incubation success relative to other available habitats. For hypothesis one, physical habitat measurements were compared between sites that received egg deposition and those that were encountered by lake trout but did not. Logistic regression, model selection and multimodel inference were then used to estimate the relative importance of physical characteristics to predicting egg deposition. For hypothesis two, a habitat bioassay that included seeding incubators with hatchery fertilized eggs to compare the relative *in situ* survival of fertilized eggs overwinter to hatching between habitats that received egg deposition and those that were encountered by lake trout but did not.

Methods

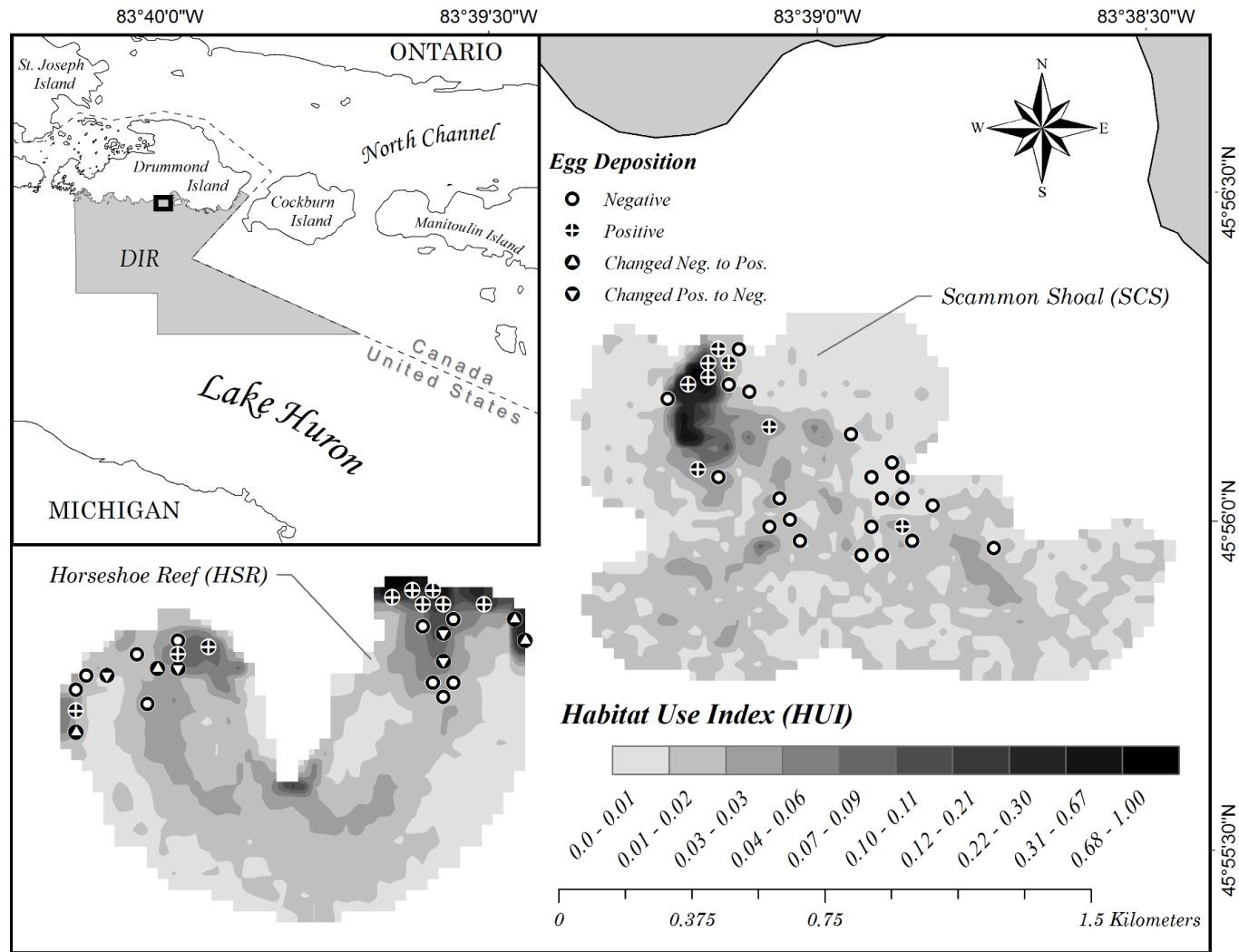
Study Area

The Drummond Island Refuge (DIR) is located in northern Lake Huron, covering 55,000 ha along the south shore of Drummond Island eastward to the USA-Canada border at False Detour Channel and extending southward to 45° 40' N latitude (Figure 2.1). Created in 1985, the DIR restricts commercial and sport fishing of lake trout in support of efforts to reestablish and rehabilitate self-sustaining populations in northern Lake Huron. Successful natural reproduction by lake trout in Lake Huron has recently been reported (Johnson and VanAmberg, 1995; He et

al., 2012; Johnson et al., 2015), particularly near the DIR (Ebener, 1998; Riley et al., 2007; Madenjian et al., 2008a).

A large-scale study of lake trout movements associated with spawning was conducted within the DIR from 2010 to 2014, using fine-scale, 2D positional acoustic telemetry within a $\sim 25\text{km}^2$ region along the southern shore of Drummond Island (Riley et al. 2014; Binder et al. 2016a, 2016b, 2018). This multi-agency collaborative effort used a VEMCO (Halifax, NS, Canada) positioning system (VPS) array consisting of between 108 and 152 autonomous acoustic telemetry receivers (VR2W receivers) to monitor the fine-scale movements (i.e., 5 - 10 m accuracy) of 390 acoustically-tagged (V16 transmitters) adult lake trout during late summer and autumn (see Binder et al. 2016a, 2016b, 2018 for complete tagging and acoustic array details). Throughout the course of the Drummond Island telemetry study, lake trout were concentrated consistently in six areas (Binder et al. 2018). Spawning at these areas was confirmed by diver-based egg surveys; however, spawning activity was greatest at two locations, Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*), located adjacent to one another approximately 1.0 to 1.85 km away from the southern shore of Drummond Island in the northwest corner of the array (Figure 2.1).

Figure 2.1: Lake Huron study site (grey box in map inset) adjacent to Drummond Island with primary spawning reefs, Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*). Habitat Use Index (*HUI*), an index of relative amount of time tagged lake trout spent in various habitats over the 2012 autumn spawning period, was calculated across 20 m x 20 m cells within reef polygons and was used to select sampling sites. Egg deposition was observed at 17 sites on *HSR* and eight sites on *SCS*. However, eight cells on *HSR* changed status between 2013 and 2014.



Habitat Use Index

The Drummond Island acoustic telemetry study provided a unique opportunity to advance understanding of lake trout spawning habitat characteristics by evaluating habitat selection using behavior of the fish. Fine-scale acoustic telemetry position data were used to concentrate sampling effort at *HSR* and *SCS* on habitats known to have been encountered by lake trout and, ultimately, to compare the physical characteristics (*Objective 1*) and relative survival of fertilized eggs to hatch (*Objective 2*) between specific locations that received egg deposition and those that did not. To accomplish this comparison, an index of the amount of time lake trout spent in various habitats on each reef (*Habitat Use Index: HUI*) was developed based on telemetry data collected in 2012 and was subsequently used to select sampling sites. Polygons surrounding the boundaries of each reef were demarcated along contour lines based on high-resolution bathymetric survey data (1 m² resolution) collected via multi-beam sonar in 2010 and 2011 (See Riley et al., 2014 for complete bathymetric survey details). Reef polygons then were divided into a grid of 20 m x 20 m cells and a HUI value was calculated for each cell (*HSR* = 1449 cells; *SCS* = 2038 cells).

HUI was calculated as the sum of the number of 1-h intervals in which a fish was detected at least once within cell q on reef r , termed detection intervals ($DI_{q,r}$), divided by the total number of unique fish (F) that were detected on reef r over the spawning period (*Eq. 1*). In 2012, 144 unique fish were detected within the telemetry array and the spawning period ranged from October 6 to November 18 (Binder et al., 2016b). Of these, 104 fish were detected on *HSR* and 93 were detected on *SCS*. Detection intervals were used in place of raw number of positions as an estimate of habitat use to limit potential bias associated with positioning probabilities that

varied both spatially (e.g., across reefs) and temporally (e.g., between years; See Binder et al., 2016a).

$$\text{Equation 1)} \quad \text{HUI}_q = \frac{\sum DI_{q,r}}{F_r}$$

The fundamental sampling units in this study were the 20 m x 20 m cells selected for sampling based on 2012 HUI rankings; hereafter referred to as ‘site’. To select sites for sampling, cells on each reef were ranked in descending order by their HUI and the 40 highest-ranking non-adjacent cells were identified. From these, the top 20 ranked non-adjacent cells and 10 random non-adjacent cells from rank 21-40 were selected (totaling 30 cells) as sampling sites for each reef. No two adjacent cells were selected to ensure that sampling sites were at least 40m apart and thus, reduce the potential for spatial autocorrelation.

Surveys for Egg Deposition

SCUBA diver-based egg surveys were conducted within a portion of all 30 sites on each reef during 2013 and 2014 to assign sites as having eggs present (*positive* = 1) or absent (*negative* = 0). Egg surveys were conducted within a 10 m diameter circle at the center of each site so that they corresponded with substrate photographs (see *Physical Characterization* below). Two divers searched independently for a minimum of 10 minutes or until both divers independently confirmed egg deposition by flipping rocks and flushing water into the substrate by hand to suspend eggs. Surveys commenced after peak spawning was estimated to have occurred. All sites identified as negative during the first survey were surveyed a second time later in the season to confirm egg absence. In both years, egg surveys began by Nov. 1, and all secondary surveys were complete by Nov. 18.

For statistical analyses, egg survey results from 2013 and 2014 were pooled such that sites in which eggs were observed in either year were considered positive for egg deposition (1), while sites in which eggs were not observed in both years were considered negative for egg deposition (0). Additionally, two sites on *HSR* were excluded from the analyses due to logistical issues in the field that prevented complete sampling, resulting in a final count of 28 sites on *HSR* and 30 sites on *SCS*.

Physical Characterization (Objective 1)

To determine the relative importance of physical characteristics on selection of spawning habitats (Objective 1), bathymetric features (e.g., water depth and slope) and measurements of the bottom substrate (e.g., diameter, homogeneity, and interstitial depth) were characterized at each site. Estimates of slope and water depth at each site were calculated using the multi-beam bathymetry by dividing each site into a grid of 400 - 1 m² sub-cells and then calculating the mean of 20 deepest sub-cells and 20 shallowest sub-cells as an estimate of the maximum and minimum water depth within each site. The predominant slope (%) for each site was calculated as the difference between the maximum and minimum mean water depth divided by the distance between the single shallowest and deepest sub-cell within the site, multiplied by 100.

Substrate at each site was characterized using a combination of underwater photographs and direct measurement by divers in 2013. A colored brick was placed at the center of each site and coordinates were confirmed using a taut surface line and Trimble® GeoXH differential GPS unit with sub-meter accuracy. Substrate was photographed by divers using an 8.1 megapixel digital camera (Panasonic Lumix DMC-FX55) mounted on an aluminum frame set 1.5 m above the lake bottom. Five ~1 m² images were collected within each site, one centered at the central

identifier brick and four others centered ~5 m from the center in each cardinal direction. Divers made three independent measurements as a surrogate of interstitial depth (*IS*) within each of the five imaged areas by inserting a 25.4 mm wide x 3 mm thick aluminum ruler into the spaces between substrates to its maximum depth (i.e., until bedrock was reached, or substrate did not permit further penetration). Interstitial depth for a site was estimated as the mean of fifteen interstitial depth measurements.

To estimate substrate size, shape, and homogeneity at each site, substrate photos were processed using a semi-automated segmentation macro developed using the *FIJI* package of *ImageJ* (Rasband, 1997; Schindelin et al., 2012). Images were calibrated using a 173 mm measure on a portion of the camera frame that was visible in each photo such that the total imaged area was 0.816 m² per photo for a total of 4.08 m² per site. To standardize for light differences between photos due to varying water depths and times of collection, images were altered using preprocessing filters and an iterative auto-thresholding technique was applied prior to segmentation. Segmentation results were reviewed individually by a single reader. Over-segmented regions were deleted, and poorly segmented or misaligned particles were manually outlined using a free-hand edge tool. All substrates near the border of the image in which at least 50% of its surface area was estimated to be included in the image were segmented and measured. Estimates of the maximum Feret diameter (i.e., the diameter along the particles longest axis; Merkus, 2009) and surface area were calculated for all visible substrates in each photo.

The predominant surficial substrate for each site was classified using a categorical classification scheme based on the proportion of the total measured surface area within various substrate size categories using a modified Wentworth scale (e.g., Marsden et al., 1995; Table 2.1, *bottom*). Measured substrate at each site was first assigned to a size category (i.e., gravel, rubble,

cobble) based on its maximum Feret diameter. The surface area of all substrate within each size category was then summed and expressed as a percentage of total measured area for each site. Usually, the substrate category with the highest percentage of total measured area was selected as the predominant substrate category for a given site. However, any site with greater than 33.3% of measured substrate in more than one category was given a ‘mixed’ substrate type that combined substrate categories (e.g., gravel-rubble mix, rubble-cobble mix, or gravel-cobble mix). Sites with > 50% of the imaged area not measurable were classified ‘uncharacterized’. Collectively, this category represented spaces between individual substrates which included fines such as sand or silt and bedrock or were indistinguishable substrates that could not be reliably segmented from the remainder of the image due to image quality. Using this classification scheme, all sites were assigned to one of seven possible predominant substrate categories (Table 2.1, *bottom*).

Relative substrate homogeneity was expressed as a continuous variable representing the maximum proportion of the total imaged area that occurred in a running 15 cm substrate diameter size bin. First, measured substrates in each image were assigned to 5 cm bins from 0 cm to 100 cm based on maximum Feret diameter. Next, the surface areas of all substrates in each 5 cm bin were summed and expressed as the percentage of the total imaged area (4.08 m²) within a site. Finally, the 5 cm diameter bin comprising the greatest proportion of the total imaged area was identified and summed with the proportions in the two adjacent 5 cm size bins. In this manner, the higher the proportion of imaged area in this 15 cm range of substrate diameters, the more homogeneous the substrate.

Relative Importance of Physical Characteristics (Objective 1)

While *HSR* and *SCS* were only located ~1 km apart from one other, the range and variance of measured variables differed substantially between reefs (Figure 2.2; Binder et al., 2018). As such, model selection procedures were run on each reef independently and multimodel inference was used to compare the relative importance of measured physical habitat characteristics within and between reefs. Initial data exploration revealed minor negative correlation between substrate homogeneity and interstitial depth on *SCS* (Pearson product-moment correlation: Homogeneity-IS; $r = -0.36$, $p = 0.01$). Furthermore, slope and interstitial depth estimates were spatially autocorrelated on *HSR* (Moran's I, slope; $I = -0.09$, $p < 0.01$, IS; $I = -0.14$, $p < 0.01$) and egg deposition and slope estimates were spatially autocorrelated on *SCS* (Moran's I, eggs; $I = -0.12$, $p < 0.01$, slope; $I = -0.15$, $p < 0.01$). As such, an autocorrelation parameter, 'distance', was included in all models to address the possible effects of adjacency in habitat selection (e.g., Dormann et al., 2007). The 'distance' parameter was calculated as the geospatial distance of each site from the highest ranked cell by HUI on that reef using the *distMeeus* function in the *geosphere* package in the *R* programming environment (Hijmans et al., 2014; R Core Team, 2015). This method assumes spatial stationarity, i.e., the effect of proximity is constant across sites within a reef. Therefore, due to the unique shape of *HSR* and the presence of two distinct areas of condensed activity, the *distance* parameter for sites on *HSR* was calculated as the geospatial distance of each site from the nearest of the top-ranked cells on each arm (East and West) of the reef (Figure 2.1).

A set of 16 competing additive fixed effect logistic regression models was used to relate egg deposition in 2013 and 2014 to measured habitat characteristics on each reef (*Objective 1*; Table 2.1). For each reef, models containing all possible combinations of measured physical

characteristics were evaluated, including the global model (all variables) and null model ('distance' variable only; Table 2.1). To simplify interpretation of the model outputs, an intercept term was not estimated, resulting in separate coefficients for each level of surficial substrate classification. Logistic regression models were fit using the *glm* function (*family* = 'binomial') in the base *stats* package in *R* (R Core Team 2015). Akaike's information criterion corrected for small sample sizes (*AICc*) was used to rank competing models on each reef by the maximum log likelihood, including a penalty for model complexity (e.g., Burnham and Anderson, 2002; Anderson, 2007). Multimodel inference and model averaging were then used to estimate the relative importance of measured physical habitat characteristics to predicting egg deposition among sites encountered by tagged lake trout on each reef (e.g., Burnham and Anderson, 2002; Grueber et al., 2011). Model-averaged parameter estimates ($\hat{\beta}$) were calculated for each reef using a weighted average across all models, substituting zero for models in which the parameter did not appear, and standardized ($\hat{\beta}^*$) relative to their partial standard deviation (adjusted for multiple correlations of input variables; See Grueber et al., 2011) to aide interpretation between parameters with differing scales and compensate for potential correlations among predictors. Because cumulative Akaike weights (w_i) were difficult to interpret among parameters with differing units, the relative importance of each physical characteristic was also expressed as an evidence ratio of the j th standardized model-averaged parameter estimate to the maximum standardized parameter estimate $\left(\frac{\hat{\beta}_j^*}{\hat{\beta}_{max}^*}\right)$ for comparison between reefs. An unconditional variance estimator, including both within and between model uncertainty estimates (e.g., Burnham and Anderson, 2002), was used to calculate 95% confidence intervals (CI) on the model-averaged parameter coefficients and parameters in which this 95% CI included zero were considered uninformative to habitat selection. All *AICc*-based analyses were conducted

following procedures described by Burnham and Anderson (2002) and Grueber et al. (2011) using the *MuMIN* package in *R* (Bartoń, 2013; R Core Team, 2015).

Incubation Success (Objective 2)

Relative *in situ* incubation success was compared between sites positive for egg deposition and those that were not using plexiglass incubators (e.g., Manny et al., 1989; Eshenroder et al., 1995) seeded with Seneca Lake wild (SLW) strain embryos stripped and fertilized at the Sullivan Creek National Fish Hatchery (U.S. Fish and Wildlife Service; Brimley, MI). Incubation success was assessed at 10 sites on each reef that were previously surveyed for egg deposition; five sites positive for egg deposition, including the highest ranked site by *HUI*, and five sites negative for egg deposition. Three incubators were attached along a 7.6m chain bisecting the central identifier and buried in substrate near the end of the 2013 and 2014 spawning seasons at each of the 10 sites (a total of 30 incubators per reef). Incubators were buried vertically such that the uppermost long edge of the incubator was approximately flush with the substrate surface. In this configuration, incubators consisted of five layered rows of cells ranging in depth from 1 - 2 cm to 10 - 12 cm beneath the surface. Each incubator was inspected immediately prior to deployment and eggs that had died since loading were recorded. Incubators were recovered the following spring and the proportion of live eggs at the time of deployment that were found to have developed to free embryos at the time of retrieval was used as an estimate of relative *in situ* incubation success.

To establish a baseline for comparisons of egg incubation success between reefs, a minimum of 18 incubators were retained as laboratory controls each year. Control incubators underwent identical handling procedures as the treatment groups but were subsequently

transferred to the USGS - Hammond Bay Biological Station (HBBS; Millersburg, MI) where incubators were placed in Heath incubation trays and supplied with ambient water from Lake Huron at 9-12 L/min throughout the incubation period. The temperature profile experienced by all control and *in situ* incubators was monitored over the incubation period using tethered Onset HOBO Pendant (UA-002) temperature loggers.

Upon recovery in the spring, each string of incubators was photographed to record its orientation prior to transport to the surface. The orientation of each incubator was assigned one of two classifications; those that '*stayed*' buried in the substrate (maintained vertical orientation), and those that '*moved*' (either tipped over or completely dislodged from substrate). Recovered incubators were transported to the lab in coolers filled with ambient lake water and were examined within 24 - 48 hours of retrieval. The contents of each incubation chamber were classified as either 'egg' or 'free embryo' and 'live' or 'dead' based on whether identifiable eggs or free embryos were present and their condition at the time of inspection.

Incubation success for a given site was calculated as the mean proportion of eggs surviving to hatch (i.e., sum of live eggs, live free embryos, and dead free embryos) among incubators that '*stayed*' buried in substrate at time of recovery at that site (i.e., each site was considered a replicate). On *HSR*, 26 of 30 (86.7%) incubators deployed in 2013 and 30 of 30 (100%) of incubators deployed in 2014 remained buried in substrate until recovery. Of the four incubators on *HSR* that moved, three were from sites positive for egg deposition, including one incubator from the highest ranked site by HUI. On *SCS*, 18 of 30 (60%) incubators deployed in 2013 and 24 of 30 (80%) incubators deployed in 2014 remained buried in the substrate. Of the 18 incubators on *SCS* that moved, 10 were from sites positive for egg deposition, including two incubators from the highest ranked site by HUI. *In situ* incubators that '*moved*' had significantly

lower mean incubation success than those that ‘*stayed*’ buried in substrate and were therefore excluded from subsequent analyses (*stayed* = 68.9%, *moved* = 39.0%; Welch two-sample t-test, $t = 5.49, p < 0.01$).

Comparisons of mean *in situ* incubation success between reefs and egg present/absent sites were made using two-way repeated measures Analysis of Variance (ANOVA). In this model, egg deposition (*present/absent*) and reef (*HSR, SCS*) were fixed effects, and site ID was a random effect to account for repeated measures between years. Comparison of mean incubation success of controls between years was conducted using Welch’s unequal variances *t*-test in *R* (R Core Team 2015). Comparisons of mean incubation success between *in situ* and control (*CON*) incubators were made using a one-way repeated measures ANOVA, and Tukey’s HSD (honest significant difference) test. In this model, reef (*HSR, SCS*) and eggs (*present* = +, *absent* = -) were combined as a categorical grouping factor (*HSR+*, *HSR-*, *SCS+*, *SCS-*, and *CON*) with fixed effect, and Site ID was a random effect to handle repeated measures between years. In all cases, the response variable, mean proportion hatch, was arcsine (square root) transformed to improve normality and control heteroscedasticity of the model residuals (e.g., Sokal and Rohlf, 1995). All repeated measures models were evaluated using the *lme4* package in *R* (Bates et al., 2015; R Core Team, 2015).

Results

Egg Deposition

Over 2013 and 2014, egg deposition was observed at 17 of 28 (60.7%) surveyed sites on *HSR* and 8 of 30 (26.6%) surveyed sites on *SCS* (Figure 2.1). However, egg deposition at some sites on *HSR* was not consistent between years; four sites near the shallowest ridge of the reef

switched from positive in 2013 to negative in 2014, while four sites on the outside boundary of the reef switched from negative in 2013 to positive in 2014 (Figure 2.1). Most sites selected for egg deposition by lake trout occurred in three distinct clusters; one on each arm of *HSR* and a third within a single area in the northwest corner of *SCS* (Figure 2.1).

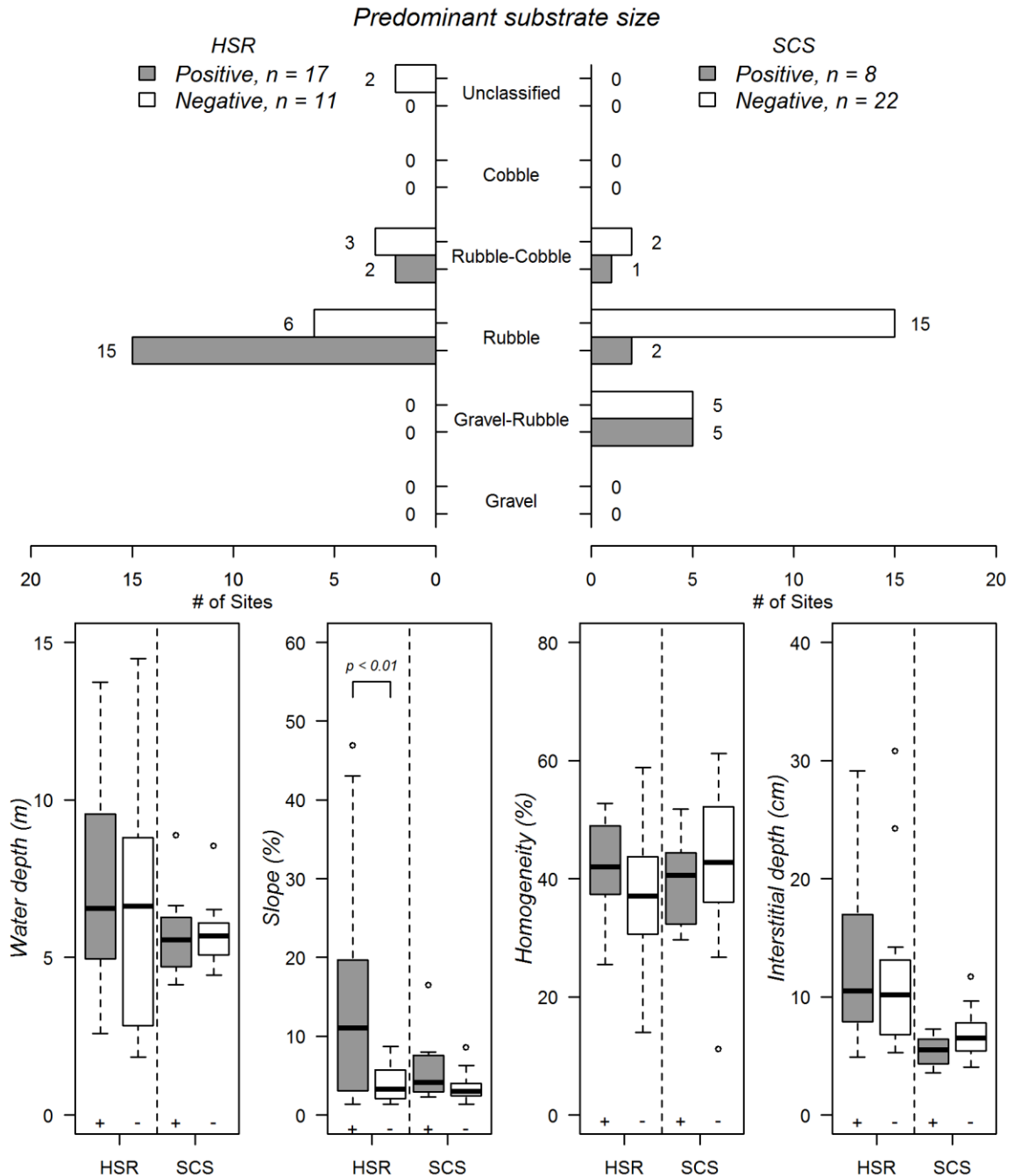
General Spawning Reef Characteristics

Overall physical characteristics differed substantially between *HSR* and *SCS* (Figure 2.2). In general, *HSR* was a 0.535 km² ‘U’ shaped rocky ridge comprised of numerous layers of sorted sediments ranging in size from silt to boulders. The reef was distinct from the surrounding bathymetry, rising abruptly from fine sediments at its base at 16 m depth to a small 0.038 km² portion of the eastern arm that rose above the water surface. *HSR* had steep slopes around its outer edges, particularly on the northern tip of the eastern arm. By comparison, *SCS* was a broad, relatively flat 0.758 km² shoal comprised of layers of sorted sediments ranging in size from silt to boulders lying atop bedrock that was exposed in some places. *SCS* was less distinct from its surrounding bathymetry than *HSR*, rising gradually from its base at 11 m depth to a small 0.003 km² portion lying just beneath the water surface (~0.5 m depth). While this lack of steep slopes at *SCS* was the most striking difference between the two reefs in this study, predominant substrates at sampled sites on *SCS* were also classified in smaller size classes (especially gravel-rubble class) than those on *HSR* (Figure 2.2; Fishers exact test; 2000 replicates, $p < 0.01$).

The three distinct clusters of egg deposition noted above aligned closely with the areas of highest activity as estimated by HUI using acoustic telemetry data (Figure 2.1; Binder et al., 2018). However, the physical characteristics of these three areas differed from each other (Figure 2.2). The predominant spawning area located at the tip of the east arm of *HSR* had features that

most closely aligned with the commonly-accepted conceptual model of lake trout spawning habitat. This area had steep slopes around its northern edge and was composed of rubble-cobble substrates with deep (> 15 cm) interstitial spaces. By contrast, the predominant spawning area on *SCS* had little to no slope and was composed of predominantly gravel-rubble substrates with shallow (< 10 cm) interstitial space. The predominant spawning area on the west arm of *HSR*, was between these two extremes, with more gradual slope than the east arm of *HSR*, and rubble substrates that were larger than those at *SCS*, but smaller than those on the east arm of *HSR*.

Figure 2.2: Physical characteristics of sites that were surveyed to be positive for egg deposition vs. those that were negative at Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*), Lake Huron. Dark shading represents habitats in which lake trout spawned, light shading represents habitats in which no eggs were found. Numbers beside bars in top panel indicate number of sites characterized in a given predominant substrate size class. On *HSR*, slope magnitude was the only measured parameter that differed between habitats positive for egg deposition and those that were negative (Welch two-sample t-test; $df = 26.1$, $t = 4.13$, $p < 0.01$). On *SCS*, no difference between physical characteristics of habitats selected for egg deposition and those that were not was detected.



Relative Importance of Physical Characteristics (Objective 1)

Among the 16 habitat models tested to predict egg deposition, no single ‘best’ model (i.e., $w_i > 0.90$) was observed on either reef (Table 2.1). On *HSR*, 10 of 15 habitat models evaluated ranked higher than the null model, indicating that physical parameters other than mere proximity to the highest ranked site by *HUI* were important for predicting egg deposition (Table 2.1). However, on *SCS*, the null model ranked highest (Table 2.1), indicating that the addition of measured habitat characteristics could not predict egg deposition any better than adjacency alone. As a result, measured physical characteristics were not deemed to be important to predicting egg deposition on *SCS* and no additional model inference was conducted on this reef.

On *HSR*, the highest-ranked habitat model only included *slope*, and carried 54.1% of the weight of evidence as expressed by Akaike weights (w_i ; Table 2.1). Two other habitat models, both including the *slope* parameter, were ranked above the information theoretic cutoff ($\Delta AICc < 5$) and thus were moderately supported by the data. Collectively, these top three models accounted for 85.4% of the weight of evidence. However, the 2nd and 3rd ranked models were hierarchically more-complex versions of the top-ranked model, and thus inclusion of additional parameters did not improve model fit enough to overcome the parametrization penalty inherent to *AICc*. As such, these additional parameters were also considered uninformative to habitat selection (e.g., Arnold, 2010). Model-averaged parameter estimates further supported *slope* being the only important measured characteristic for predicting egg deposition on *HSR* (Table 2.2). The standardized, model-averaged parameter estimate for ‘*slope*’ was 1.90, nearly six times greater than that of the next highest ranked parameter, the spatial autocorrelation term ‘*distance*’ ($\hat{\beta}_i^* = -0.34$), and was the only parameter estimate, whose 95% confidence interval did not include zero (Table 2.2).

Table 2.1: Models and parameter definitions used to predict egg deposition on Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*) ranked by AIC corrected for small sample sizes (*AICc*). All models include a spatial autocorrelation term (distance) that was omitted from this table to aid in clarity. Dashed line represents the information theoretic cutoff for models with moderate support ($\Delta AICc < 5.0$). Categorical substrate classifications were based on a Modified Wentworth scale (Marsden et al., 1995) including ‘mixed’ substrate categories for sites with >33.3% of measured substrates in more than one category.

<i>Horseshoe Reef (HSR)</i>							<i>Scammon Shoal (SCS)</i>					
<i>Model</i>	<i>K^a</i>	<i>log(L)^b</i>	<i>AICc^c</i>	$\Delta AICc^d$	<i>w_i^e</i>	<i>Rank</i>	<i>Model</i>	<i>K^a</i>	<i>log(L)^b</i>	<i>AICc^c</i>	$\Delta AICc^d$	<i>w_i^e</i>
~ Slope	2	-12.93	30.36	-	0.541	1	NULL	1	-13.60	29.34	-	0.227
~ IS + Slope	3	-12.90	32.83	2.48	0.157	2	~ Slope	2	-12.45	29.35	0.01	0.225
~ Homogeneity + Slope	3	-12.90	32.84	2.49	0.156	3	~ Homogeneity + Slope	3	-11.90	30.73	1.39	0.113
~ Homogeneity + IS + Slope	4	-12.89	35.59	5.24	0.040	4	~ IS	2	-13.27	30.98	1.64	0.100
~ Diameter + Slope	5	-11.74	36.33	5.97	0.027	5	~ Homogeneity	2	-13.49	31.43	2.09	0.080
~ IS	2	-16.14	36.77	6.41	0.022	6	~ IS + Slope	3	-12.27	31.46	2.12	0.079
~ Homogeneity	2	-16.35	37.21	6.85	0.018	7	~ Diameter	4	-11.75	33.09	3.75	0.035
~ Homogeneity + IS	3	-15.84	38.73	8.37	0.008	8	~ Homogeneity + IS	3	-13.17	33.27	3.93	0.032
~ Homogeneity + Diameter + Slope	6	-11.27	38.74	8.38	0.008	9	~ Homogeneity + Diameter	5	-10.43	33.36	4.02	0.030
~ IS + Diameter + Slope	6	-11.56	39.32	8.96	0.006	10	~ Homogeneity + IS + Slope	4	-11.90	33.40	4.06	0.030
NULL	1	-18.60	39.35	8.99	0.006	11	~ IS + Diameter	5	-11.31	35.12	5.78	0.013
~ Diameter	4	-15.02	39.86	9.50	0.005	12	~ Diameter + Slope	5	-11.52	35.54	6.20	0.010
~ IS + Diameter	5	-13.91	40.68	10.32	0.003	13	~ Homogeneity + IS + Diameter	6	-9.97	35.59	6.24	0.010
~ Homogeneity + IS + Diameter + Slope	7	-11.20	42.29	11.93	0.001	14	~ Homogeneity + Diameter + Slope	6	-10.19	36.04	6.70	0.008
~ Homogeneity + Diameter	5	-15.02	42.89	12.53	0.001	15	~ IS + Diameter + Slope	6	-10.54	36.73	7.39	0.006
~ Homogeneity + IS + Diameter	6	-13.70	43.60	13.24	0.001	16	~ Homogeneity + IS + Diameter + Slope	7	-9.13	37.35	8.01	0.004

Parameter Definitions

<i>Variables</i>	<i>Type</i>	<i>Description</i>	
<i>Eggs</i>	Binary Response	Egg deposition (<i>Eggs</i> +/-)	
<i>Distance</i>	Continuous	Distance to #1 ranked site by HUI to account for spatial autocorrelation (m)	
<i>Slope</i>	Continuous	Slope magnitude (%)	
<i>Homogeneity</i>	Continuous	Substrate homogeneity (%)	
<i>IS</i>	Continuous	Interstitial depth (cm)	
<i>Diameter</i>	Categorical	Predominant substrate diameter classification	<i>Gravel</i>
			<i>Gravel-Rubble</i>
			<i>Rubble</i>
			<i>Rubble-Cobble</i>
			<i>Cobble</i>
			<i>Gravel-Cobble</i>
			<i>Uncharacterized</i>
			Majority of measured substrate ranging from 0.2 - 6.4cm in diameter.
			Mixture of gravel and rubble substrates (>33.3% of measured area in each category).
			Majority of measured substrate ranging from 6.5 - 25.6cm in diameter.
			Mixture of rubble and cobble substrates (>33.3% of measured area in each category).
			Majority of measured substrate ranging from 25.7 - 99.9cm in diameter.
			Mixture of gravel and cobble substrates (>33.3% of measured area in each category).
			Greater than 50% of imaged area was unmeasured or composed of fines or bedrock.

^aNumber of parameters within the model, including spatial autocorrelation term (*distance*). ^bNatural logarithm of the model likelihood. ^cAkaike's Information Criterion corrected for small sample size.

^dDifference in the *AICc* value between each model and the top-ranked model. ^eAkaike weight of evidence in support of model.

Table 2.2: Unstandardized and standardized (denoted by an *) model-averaged parameter estimates ($\hat{\beta}_i$) and relative importance of physical characteristics for the selection of habitats for egg deposition by lake trout on Horseshoe Reef (*HSR*). An unconditional variance estimator ($\widehat{SE}(\hat{\beta}_i|g_i)$) was used to calculate 95% confidence intervals on model-averaged parameter estimates. Furthermore, the relative importance of each physical characteristic was expressed in two ways; first, as a ratio of the *i*th parameter Akaike weight to the maximum Akaike weight ($\frac{w_i}{w_{max}}$), and second, as an evidence ratio of the *i*th standardized model-averaged parameter estimate to the maximum standardized parameter estimate ($\frac{\hat{\beta}_i^*}{\hat{\beta}_{max}^*}$). Based on these criteria, slope magnitude was the only measured characteristic found to be important for the selection of spawning habitats on *HSR*.

<i>Parameter</i>	<i>Unstandardized Estimates</i>				<i>Standardized Estimates</i>				<i>Relative Importance</i>	
	$\hat{\beta}_i$	$\widehat{SE}(\hat{\beta}_i g_i)$	95% Confidence Interval		$\hat{\beta}_i^*$	$\widehat{SE}(\hat{\beta}_i g_i)^*$	95% Confidence Interval		$\frac{w_i}{w_{max}}$	$\frac{\hat{\beta}_i^*}{\hat{\beta}_{max}^*}$
<i>Distance (m)</i>	-0.006	0.005	-0.015	0.003	-0.339	0.254	-0.836	0.158	1.00	0.178
<i>Physical Habitat Characteristics</i>										
<i>Slope Magnitude (%)</i>	0.218	0.106	0.011	0.426	1.904	0.911	0.118	3.690	0.937	1.00
<i>Substrate Homogeneity (%)</i>	0.001	0.016	-0.307	0.033	0.008	0.071	-0.131	0.148	0.238	0.003
<i>Interstitial Depth (cm)</i>	0.008	0.059	-0.108	0.124	0.025	0.166	-0.301	0.351	0.233	0.010
<i>Predominant Substrate Category</i>										
<i>Rubble</i>	0.045	0.527	-0.988	1.077	0.006	0.071	-0.132	0.144	0.053	0.002
<i>Rubble-Cobble</i>	0.031	0.724	-1.388	1.450	0.005	0.127	-0.244	0.253	0.053	0.002
<i>Uncharacterized</i>	-0.897	671.41	-947.14	945.34	-0.262	195.95	-384.56	384.04	0.053	0.103

Incubation Success (Objective 2)

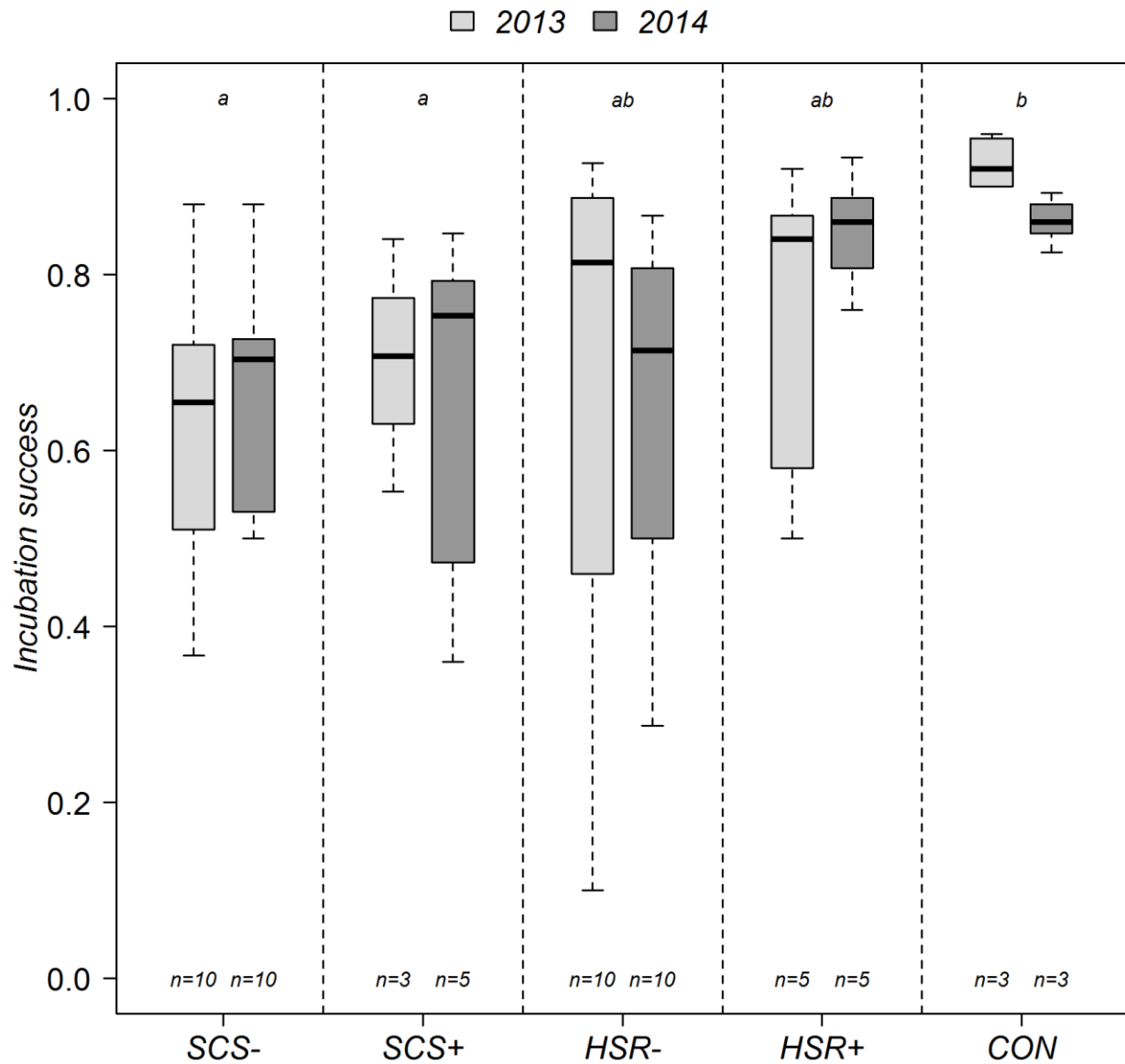
No evidence of a significant difference in mean proportion of eggs surviving to hatch (*in situ* incubation success) was observed between sites selected for egg deposition and those that were not ($POS = 73.8\%$, $NEG = 69.8\%$; two-way repeated measures ANOVA, $f = 0.06$, $p = 0.81$; Figure 2.3). However, mean incubation success differed significantly between reefs ($HSR: 78.2\%$, $SCS: 64.4\%$; two-way repeated measures ANOVA, $f = 5.65$, $p = 0.03$). No evidence occurred for an interaction between egg deposition and reef (two-way repeated measures ANOVA, $f = 0.32$, $p = 0.58$). Site ID was a significant random effect in this model (i.e., variance different from 0), suggesting intra-annual variability between sites was high, but overall *in situ* estimates of incubation success appeared to be consistent between years at the reef scale.

Incubation success on *HSR* ranged from 46.0 – 92.7% ($\bar{x} = 76.7\%$, $s = 18.2\%$) in 2013 and from 65.3 – 93.3% ($\bar{x} = 79.7\%$, $s = 9.0\%$) in 2014. Similarly, incubation success on *SCS* ranged from 36.7 – 84.0% ($\bar{x} = 65.3\%$, $s = 14.6\%$) in 2013 and 36.0 – 84.7% ($\bar{x} = 63.7\%$, $s = 16.3\%$) in 2014.

Control incubators held at Hammond Bay Biological Station (HBBS) showed lower survival of hatchery-reared eggs in 2014 than in 2013 ($CON; 2013 = 92.6\%$, $2014 = 86.1\%$; Welch's unequal variance t-test, $t = 4.24$, $p < 0.01$). After accounting for this variability, mean *in situ* incubation success differed from that of control incubators (one-way repeated measures ANOVA, $f = 4.71$, $p < 0.01$). Mean incubation success of sites negative for egg deposition on *SCS* (SCS^-) and sites positive for egg deposition on *SCS* (SCS^+) were both significantly lower than that of control incubators (Tukey HSD, SCS^- vs. CON , $t\text{-ratio} = 3.80$, $p < 0.01$, SCS^+ vs. CON , $t\text{-ratio} = 3.36$, $p = 0.02$). In contrast, no difference in mean incubation success between HSR^+ or HSR^- sites and controls (HSR^- vs. CON , $t\text{-ratio} = 1.56$, $p = 0.54$, HSR^+ vs. CON , $t\text{-ratio}$

$= 1.93, p = 0.33$) was observed, nor were any differences observed among *in situ* incubators (Figure 2.3).

Figure 2.3: Relative *in situ* incubation success (proportion survival to hatch) of sites positive (+) and negative (-) for egg deposition on Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*) vs. control incubators (*CON*) in 2013 (light bars) and 2014 (dark bars). No evidence was observed for a difference in mean incubation success of habitats positive for egg deposition vs. those that were negative (+ = 73.8%, - = 69.8%; two-way repeated measures ANOVA, $f = 0.06$, $p = 0.81$), but mean incubation success differed between reefs (*HSR*: 78.2%, *SCS*: 64.4%; two-way repeated measures ANOVA, $f = 5.65$, $p = 0.03$). Furthermore, mean *in situ* incubation success of positive and negative sites at *SCS* were both significantly lower than control incubators (letters, one-way repeated measures ANOVA, $f = 4.71$, $p < 0.01$; Tukey HSD, *SCS*- vs. *CON*, t -ratio = 3.80, $p < 0.01$, *SCS*+ vs. *CON*, t -ratio = 3.36, $p = 0.02$).



Discussion

Physical characteristics of spawning substrates on two adjacent spawning reefs in the Drummond Island Refuge varied considerably from one another, yet both were used for spawning by lake trout. On *HSR*, bathymetric slope was greater in habitats in which lake trout deposited eggs than on those that they did not. However, on *SCS*, habitats in which eggs were observed were indistinguishable from those where no eggs were found based on the habitat characteristics measured. While slope appears to have been an important predictor of spawning habitats on *HSR*, it was not a feature of every site chosen for spawning and some sites not receiving egg deposition also occurred on slopes greater than 8%. Moreover, inter-annual variability in sites selected for egg deposition on *HSR* suggested that some variables used by lake trout to select spawning habitats may vary over time. Due to environmental stochasticity, optimal conditions for egg incubation on a given spawning reef likely vary in both space and time (e.g., Fitzsimons and Marsden, 2014). Indeed, inter-annual variability in *in situ* incubation success appeared greater at the site scale than at the reef scale, so it is possible lake trout may respond to these changes by shifting their spawning locations within reefs between years. Alternatively, in environments with an abundance of suitable habitat, lake trout may spawn over a variety of physical conditions as a bet-hedging strategy to overcome this variability in incubation suitability (e.g., Fitzsimons and Marsden, 2014; Callaghan et al., 2016). Nonetheless, the physical characteristics measured in this study were unable to completely explain the spawning habitat selection observed, so other unmeasured variables may have been important.

No evidence was found to support a relationship between egg deposition and predominant substrate diameter. In both years of the study, egg deposition was observed on habitats in each of the predominant substrate categories measured, including small gravel

substrates (0.2 - 6.4 cm diameter) not typically included in the commonly-accepted conceptual model of lake trout spawning habitat suitability (e.g., Marsden et al., 1995). Admittedly, I found accurate characterization of substrates to be challenging. While surveys for egg deposition occurred in the same areas as were physically characterized, mean and median diameter estimates were likely biased due to spatial limitations inherent in using an image-based characterization method. Therefore, the use of categorical classifications for predominant substrate diameter required estimation of additional parameters ($K+3$), while parameters on a bounded continuous scale, such as slope, interstitial depth, and homogeneity only required a single parameter estimate. As such, the parameterization penalty inherent to AIC may have been exaggerated for models including substrate diameter. Furthermore, analyses were limited by small sample sizes and an unbalanced design between habitats positive and negative for egg deposition. Sites were intentionally selected to avoid use of adjacent cells within reefs, but portions of the reefs were broadly similar enough that not all combinations of habitat parameters were available at all levels of egg deposition. For example, because most sites were classified as predominantly rubble substrate (*HSR*: 21/28 sites, *SCS*: 17/30 sites), the three remaining sites classified as predominantly rubble-cobble substrate on *SCS* did not exist in both high and low levels of homogeneity or interstitial depth to determine if these parameters influenced the odds of egg deposition while accounting for other characteristics. Nonetheless, this study suggests that the specific size and shape of substrates are likely less critical for lake trout spawning habitat selection than previously thought (e.g., Sly, 1988). Rather, when placed on the same scale with other parameters, a single unit (%) change in slope increased the odds of selection for egg deposition on *HSR* by 12.8 (CI = [1.9, 63.4]) times. In contrast, slope did not appear to be important for predicting egg deposition on *SCS*. However, nearly all estimates of slope were

below that thought to be required (8%) for spawning described in the commonly-accepted conceptual model (e.g., Marsden et al., 1995). Therefore, slopes greater than 8% may not be required for spawning in all locations. Alternatively, slope may have an indirect relationship with other unmeasured correlated variables that influence habitat selection, such as current.

Slope or bathymetric contour has consistently been associated with lake trout spawning habitat (Marsden and Krueger, 1991; Bronte et al., 1995; Casselman, 1995; Marsden et al., 1995). While bathymetric contour may play a physical role in guiding and congregating spawning fish, the association of spawning habitats with areas of pronounced slope also may be related to the currents experienced above and through these habitats rather than the slopes themselves. Currents flowing interstitially benefit egg incubation by preventing siltation of eggs while ensuring eggs remain in oxygenated water (Gunn and Keller, 1984; Sly, 1988). Consistent water currents are critical to maintaining suitable interstitial water quality for successful development of incubating eggs and early life stages. Currents may also transport emergent lake trout from spawning to nursery habitats (Bronte et al., 1995; Casselman, 1995). However, incubating eggs are susceptible to mechanical stresses and therefore experience decreased survival when exposed to strong wave action (Eshenroder et al., 1995). Based on the Bernoulli principle and its corollary the Venturi effect, as velocity increases in an area of constriction, the static pressure exerted must decrease to maintain equilibrium (Vogel, 1994). Therefore, as strong, potentially damaging waves and currents course around reefs and through the interstices of the substrate that forms them, low pressure eddies of swirling water are formed, thus reducing the mechanical energy of this flow to a level that supports successful incubation (e.g., Thibodeaux and Boyle, 1987; Tonina and Buffington, 2007). In this study, many sites receiving egg deposition, including the most highly-used sites on *HSR* and *SCS* appeared to be on the

leeward (NW) side of the reefs, on slopes facing opposite the predominant current direction (SE to NW). In this manner, I hypothesize that water currents, bathymetric contour, shoreline shape, and substrate characteristics interact to buffer the physical forces of strong currents, providing reliable, consistent interstitial flow to oxygenate incubating eggs without damaging them.

Consistent interstitial flow during egg incubation is a common requirement for all salmonids (Chapman, 1988). The hyporheic exchange of groundwater and surface waters has been found to be a primary source of interstitial flow for the selection of spawning habitats in several closely related salmonid species (e.g., Power et al., 1999). For example, in brook trout, *Salvelinus fontinalis*, spawning occurs almost exclusively in close association with groundwater upwellings both in stream (e.g., Curry and Noakes, 1995) and lacustrine habitats (e.g., Ridgway and Blanchfield, 1998). In bull trout, *Salvelinus confluentus*, spawning habitats are strongly associated both with areas of upwelling and areas of downwelling within the same stream (e.g., Baxter and Hauer, 2000). Arctic char, *Salvelinus alpinus*, and chum salmon, *Oncorhynchus keta*, appear to favor groundwater upwellings for redd construction (e.g., Cunjak et al., 1986; Burril et al., 2010), while brown trout, *Salmo trutta*, and Atlantic salmon, *Salmo salar*, have been shown to preferentially select areas of downwelling for spawning (e.g., Zimmer and Power, 2006; Louhi et al., 2008). Nonetheless, lacustrine groundwater exchange has yet to have been implicated as a characteristic of lake trout spawning habitats. Given the potential overlap of areas of groundwater discharge and nearshore spawning habitats, the chemistry and predictable flow regimes associated with groundwater upwellings may be attractive to spawning lake trout (e.g., Gunn and Keller, 1984). Alternatively, hyporheic exchange of water as lake currents are forced through substrates due to sharp changes in bathymetric contour may resemble the flow regimes caused by groundwater upwellings (e.g., Gunn, 1995). While the degree to which lacustrine

groundwater discharge may influence lake trout spawning habitat selection is currently speculative, observations in this study suggest that factors other than those measured may be important. Therefore, I hypothesize that localized flow characteristics in close proximity to the lake bottom are likely to be an important component influencing the selection of habitats for egg deposition. Consequently, future studies seeking to identify the critical physical habitat requirements for successful lake trout spawning should focus on fine-scale hydrology and characterization of interstitial flow dynamics rather than characteristics of substrate alone.

I found no evidence to support a difference between the mean *in situ* incubation success of habitats on which lake trout deposited eggs and those that did not receive egg deposition. However, small sample sizes and high variability within reefs meant that power for detecting a significant difference was low. For example, assuming an $\alpha = 0.05$ and a mean difference of 10% ($\mu_{diff} \geq 0.10$) in incubation success between habitats selected for egg deposition and those that were not, a simulation-based power analysis using the *powerSim* function of the *simr* package in *R* (1000 simulations; R Core Team, 2015; Green and MacLeod, 2016) estimated power ($1-\beta$) at 42.5% (95% CI = [39.41, 45.63]). To achieve reasonable power (i.e., $1-\beta \geq 0.80$) using this analysis, the mean difference in incubation success between habitats selected for egg deposition and those that were not would have had to exceed 18% ($\mu_{diff} \geq 0.18$).

While no mean difference in incubation success was observed between habitats selected for egg deposition and those that were not, the fact that 12 of 18 (66%) sites selected for egg deposition had estimates of mean incubation success >75% suggests lake trout are capable of finding habitats with suitable chemical and physical properties to support incubation on both reefs. Conversely, some sites that were not selected for spawning had survival estimates greater than those that did receive egg deposition and therefore may be equally suitable from this

perspective. For example, some habitats where eggs were not observed had survival rates as high as 90%, while survival estimates as low as 40% were observed in habitats that did receive egg deposition. These survival estimates do not include all potential sources of mortality such as predation (e.g., Claramunt et al., 2005), dislodgement (e.g., Marsden and Krueger, 1991), or physical shock (e.g., Fitzsimons, 1994). Nonetheless, based on this information and the variable egg deposition observed on *HSR*, I conclude that the supply of suitable spawning habitat may exceed demand at Drummond Island. However, the precise explanation as to why some habitats were chosen for egg deposition while other seemingly suitable habitats were not remains unclear.

Despite similar deployment and handling methodologies, the mean *in situ* incubation success reported in this study for habitats in which lake trout deposited eggs (73.8% survival to hatch; 95% CI = [65.9%, 81.7%]) was greater than the 10 to 55% reported in five previous studies using the same habitat bio-assay throughout the Great Lakes (Casselman, 1995; Edsall et al., 1995; Eshenroder et al. 1995; Manny et al., 1995; Perkins and Krueger, 1995). Differences in survival to hatch between this study and previous studies may partially be explained by intrinsic characteristics such as the genetic makeup of the eggs used in this study, or extrinsic factors such as improved water quality could have also contributed. Non-native Dreissenid mussels (*Dreissena bugensis* and *D. polymorpha*) have been hypothesized to threaten egg incubation by altering interstitial flow regimes and smothering incubating eggs with feces and pseudofeces (Ackerman, 1999; Marsden and Chotkowski, 2001; Barbiero et al., 2011). However, lakewide oligotrophication associated with their rapid spread has greatly increased water clarity, particularly in nearshore benthic environments (Noonburg et al., 2003; Hecky et al., 2004; Evans et al., 2011). As a result, the overall incubation success of reef habitats in Lake Huron may have

improved over the last decade, lending further support to the idea that lake trout recruitment at Drummond Island does not appear to be limited by availability of suitable habitat.

The underlying architecture and features that distinguishes this study from previous studies of lake trout spawning habitat selection is the use of acoustic telemetry to guide sampling of habitats known to be encountered by lake trout. Selecting sampling sites based on behavior of the fish freed this study from biases associated with the *apriori* broad characterization of spawning shoals based on the capture of ripe fish, or from the sampling of habitats presumed to have adequate suitability. As a result, this study approached habitat selection at a scale not previously possible, allowing me to distinguish habitat use among closely-located sites based on whether habitats were deemed less preferable by fish known to have encountered them. Moreover, this methodology identified novel spawning habitats not typically included in the current conceptual model and therefore, accommodated behavioral plasticity as a possible explanation for spawning habitat selection. While the use of acoustic telemetry has considerable start-up costs associated with labor and equipment, behavior-based methods for habitat assessment probably hold the greatest promise for advancing conceptual understanding of the mechanisms underlying spawning behavior and habitat selection.

In this study, I observed widespread egg deposition in habitats with a wide range of physical characteristics and found no difference in mean relative incubation success between habitats in which lake trout deposited eggs and those they did not. Based on the inability of the measured substrate characteristics to fully explain habitat selection, I concluded substrate size was not a critical attribute and other, unmeasured, possibly correlated characteristics may influence selection of lake trout spawning habitats. Further, localized flow characteristics in close proximity to the lake bottom may be a critical variable influencing habitat selection in lake

trout. Based on *in situ* estimates of incubation success, I concluded that lake trout spawning at Drummond Island were capable of locating habitats that support successful incubation, and that habitat suitability does not appear to be limiting. Therefore, the greatest limitation to natural recruitment of lake trout in Lake Huron was probably the combination of low abundance of adult lake trout and poor survival of early life stages due to predation (e.g., Krueger et al., 1995; Chotkowski and Marsden, 1999; Jonas et al., 2005). The implications of these findings to management of lake trout in the Great Lakes are at least three-fold. First, lake trout are highly plastic in terms of spawning habitat requirements and in variables used to select habitats for egg deposition. Thus, lake trout are adaptive to a variety of spawning habitats and these habitats are not likely to restrain successful restoration efforts in the Great Lakes but could impede control efforts where lake trout have become invasive (Crossman, 1995; Hansen et al., 2008; Martinez et al., 2009). Second, interstitial flow dynamics represent a substantial knowledge gap in understanding of the critical characteristics of lake trout spawning habitat. With a better understanding of interstitial flow, whether due to lake currents, upwellings, or both, and its influence on habitat selection, managers can better understand recruitment dynamics and increase the efficiency of recovery or control efforts by matching stocking or fishing efforts to specific habitat requirements. Third, lake trout recruitment at Drummond Island does not appear to be limited by habitat availability or restricted by selection of poor incubation habitats. Therefore, I predict that recruitment from this location may continue to increase as the abundance of spawning adults increases.

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Chapter 3 : Atypical spawning habitat selection by lake trout in the Drummond Island Refuge, Lake Huron: spawning in substrates at the base of giant boulders

Abstract

Evidence of widespread lake trout spawning was observed in close association with large (>1 m diameter) boulders deposited by glaciers. In 2013, telemetry-based behavioral data and high-resolution multi-beam bathymetric survey data identified congregations of tagged lake trout in a 0.63 km² area consisting of numerous (>100) large boulders (2 - 7 m diameter) laying on top of glacial till within the Drummond Island Refuge, Lake Huron. Key features of habitat associated with these boulders were areas of clean gravel, most often located in undercut areas beneath overhanging edges of the boulders and in narrow spaces between adjacent (< 1 m separation) boulders, which were likely zones of scour by wind-driven currents. Diver-based surveys for egg deposition adjacent to these boulders revealed widespread egg deposition (40 out of 40 boulders surveyed) in gravel-rubble substrates ranging in diameter from 0.8 to 21.9 cm with interstitial depth from 2.8 to 21.1 cm. Presence of free embryos and alevins were confirmed in these habitats using specialized traps and surveys with a modified ROV-based electroshocker, though they appeared to occur at lower densities than in more typical nearby shoal habitats. Free embryos and alevins were also caught in locations where eggs were not observed previously on top of boulders and along the lake bottom away from boulders. Possibly, these early life stages may have the capability to move more than previously thought. These observations of extensive use of boulder-associated habitats for spawning, egg incubation, and early life history growth suggests that this previously undescribed habitat may provide an important contribution to total available lake trout spawning habitat and recruitment in northern Lake Huron, and possibly elsewhere in the Great Lakes.

Introduction

Lake trout, *Salvelinus namaycush*, of the Laurentian Great Lakes once supported a large and valuable freshwater fishery (Smith, 1968; Cleland, 1982; Eshenroder et al., 1995). By the 1950s, however, mortality resulting from extensive commercial exploitation and predation from non-native sea lamprey, *Petromyzon marinus*, outpaced the reproductive capacity of lake trout and caused widespread population collapse throughout the Great Lakes (Coble et al., 1990; Eshenroder, 1992; Muir et al., 2012b). Rehabilitation efforts have focused on reestablishing self-sustaining populations of lake trout in each of the Great Lakes (Hansen, 1999; Krueger and Ebener, 2004; Muir et al., 2012b); however, after nearly 60 years of supplemental stocking, sea lamprey control, and fishery regulation, full recovery has only been achieved in Lake Superior (Hansen, 1999; Krueger and Ebener, 2004; Muir et al., 2012b; Hansen and Bronte, *in press*). Recently, widespread reproduction has been observed in Lake Huron and portions of Lake Michigan (Riley et al., 2007; He et al., 2012; Hanson et al., 2013), but these systems are not yet fully restored.

Decades of stocking of hatchery-reared lake trout and sea lamprey control in Lake Huron have established spawning-stocks of sufficient size to sustain natural reproduction (Madenjian et al., 2008a; He et al., 2012), and recent declines in alewife, *Alosa pseudoharengus*, populations throughout Lake Huron have lessened predatory pressure on juvenile lake trout and reduced the incidence of thiamine deficiency (Krueger et al., 1995; Madenjian et al., 2008b; Fitzsimons et al., 2010; Riley et al., 2011). As a result, survival and recruitment of early life stages of wild-spawned lake trout has greatly improved in Lake Huron, such that by 2013, greater than 50% of main basin lake trout age-7 or younger were naturally produced fish (He et al., 2012; Johnson et al., 2015). Further, increased capture rates of wild juvenile lake trout in northern Lake Huron

adjacent to the Drummond Island Refuge suggests substantial natural reproduction is occurring nearby (DIR; Ebener 1998; Riley et al., 2007; Madenjian et al., 2008a). Consequently, this area provides an opportunity to identify spawning habitats being successfully used by lake trout.

The reproductive ecology of lake trout is a critical research priority (e.g., Eshenroder et al., 1984, 1999; Muir et al., 2012b). Previous research aimed at identifying the fundamental physical characteristics of lake trout spawning habitat has yielded a conceptual model for spawning habitat suitability (e.g., Marsden et al., 1995a, 2016; Muir et al., 2012a), recently termed the ‘cobble-contour’ model (Simard, 2017). This model states that lake trout spawn non-randomly on habitats consisting of multi-layered, rounded to sub-angular rubble-cobble (8 – 99 cm diameter) substrates with clean interstitial spaces (usually >30 cm) typically associated with a strong bathymetric feature, such as a rapid change in depth contour or pronounced ridge on the lake bottom (typically >8% slope; e.g., Marsden and Krueger, 1991; Marsden et al., 1995a). Rubble-cobble substrates are thought to increase egg survival by providing deep interstitial spaces that entrain developing eggs, buffer physical forces associated with wave action and ice scour and provide refuge from predation. Furthermore, currents directed by steeply sloped lake beds may interact with this three-dimensional structure to provide flow to prevent siltation and provide oxygen for incubation (Marsden and Chotkowski, 2001; Callaghan et al., 2016; Riley et al., 2017; Farha, Ch. 1, *this volume*).

The ‘cobble-contour’ model has provided a framework for considering spawning habitat suitability but fails to explain why some habitats are chosen for egg deposition while other adjacent habitats with seemingly suitable characteristics are not (Johnson et al., 2017; Binder et al., 2018; Farha, Ch. 1, *this volume*). Further refinement of this conceptual model has largely been limited by the scale at which habitat selection has been evaluated. While numerous putative

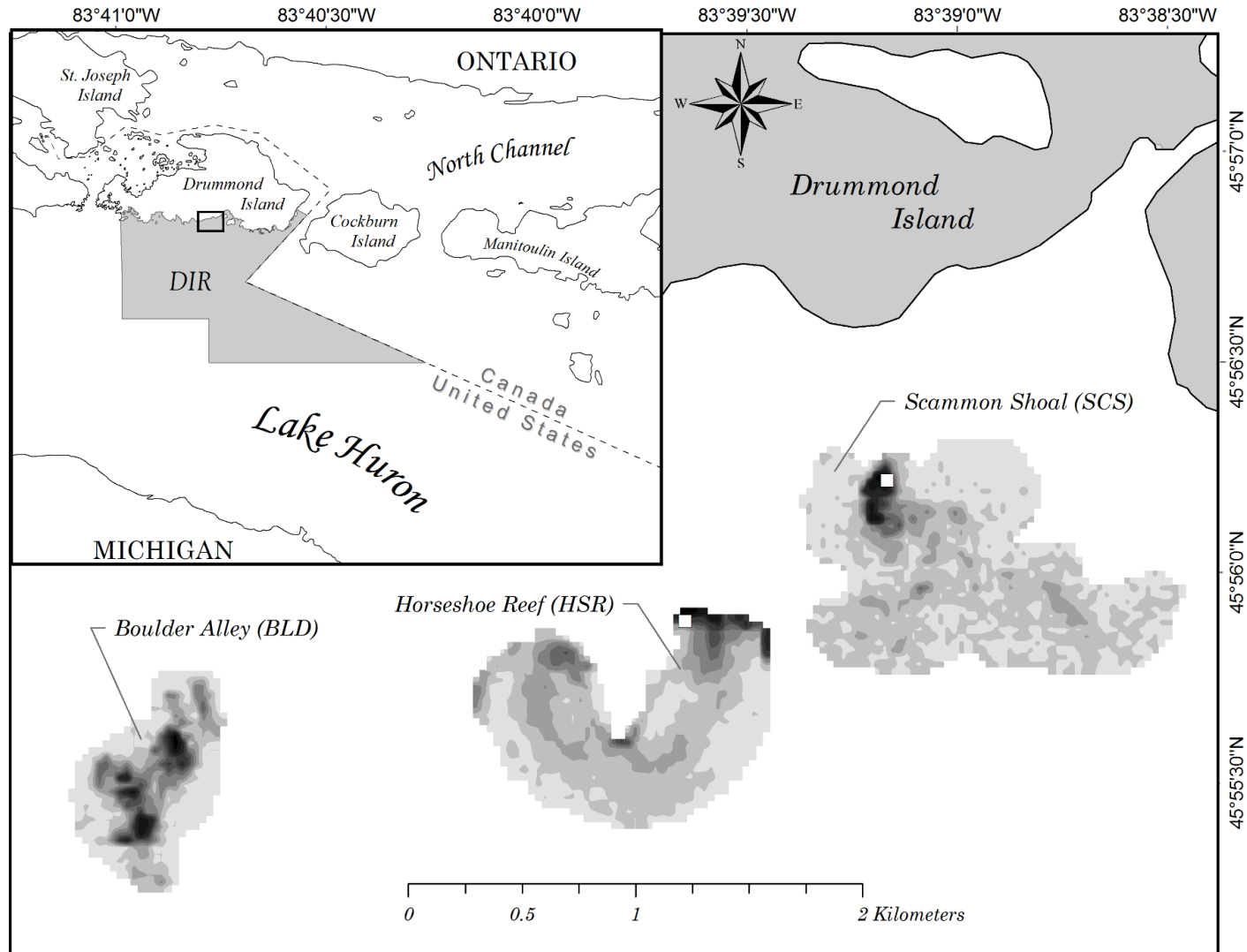
historical lake trout spawning sites have been reported based on capture of sexually mature adults in the area, few studies have identified specific spawning habitats by the presence of reproductive end-products such as eggs, free embryos, or alevins (Thibodeau and Kelso, 1990; Edsall and Kennedy, 1995). In addition, most sampling for eggs, free embryos, and alevins has been limited to habitats that match those predicted to be suitable based on the ‘cobble-contour’ model (Marsden et al., 1995a; Ellrott & Marsden, 2004; Claramunt et al., 2005). Furthermore, because observations of spawning in habitats that do not match the model are assumed to be rare occurrences, the current model does not accommodate the potential for behavioral plasticity as an explanation for the selection of alternative spawning habitats (Beauchamp et al., 1992; Simard, 2017; Jones et al. *in press*).

A recent positional acoustic telemetry study of lake trout spawning behavior and habitat use in the Drummond Island Refuge, a region of Lake Huron that now has extensive wild lake trout recruitment (Ebener, 1998; Riley et al., 2007), identified several consistently-used spawning locations that do not fit the commonly-accepted lake trout spawning habitat model (Binder et al., 2018; Farha, Ch. 1, *this volume*). Within the ~25 km² portion of the refuge encompassed by the positional acoustic telemetry array, activity during the spawning season was most concentrated at two sites, Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*), located adjacent to one another, approximately 1.5 km south of the Drummond Island shoreline (Figure 3.1). However, congregations of lake trout were also consistently observed in other areas of the array, including a 0.63 km² area to the west of *HSR* that appeared to lack any typical reef characteristics in terms of substrate or depth contours in comparison to other spawning sites (Binder et al., 2018). Brief visual scouting via a drop camera found that the area, subsequently named Boulder Alley (*BLD*; Figure 3.1), was comprised of numerous broadly-spaced boulders

greater than 1 m in diameter, with some as large as 3 - 4 m in diameter. Beyond their size, key features of these boulder sites were areas of clean gravel-rubble substrate located at their bases. Egg deposition was confirmed in autumn 2012 in the clean substrate under a handful of these boulders at the north end of the boulder field and a single alevin was caught adjacent to the boulders in spring 2013. The full extent to which boulder-associated spawning occurs within the array was unknown, but multi-beam bathymetry of *BLD* indicated that likely hundreds of these large boulders may exist in this area, so the contribution of this habitat to lake trout recruitment in northern Lake Huron could be substantial.

To better understand the potential for boulder-associated spawning to contribute to lake trout recruitment in northern Lake Huron, I sought to: 1) describe the spatial extent of lake trout spawning in association with boulders at Drummond Island, 2) determine whether egg deposition in boulder-associated habitats by lake trout could be predicted by measurable physical characteristics of the boulders or their adjacent substrates, and 3) compare the abundance of free embryos and alevins located in boulder-associated spawning habitats to those in other highly-used nearby spawning habitats within the acoustic telemetry array. To accomplish these objectives, 14 sampling locations on *BLD* were physically characterized, surveyed for egg deposition, assessed for free embryo and alevin abundance, and compared to the most highly used sites, based on telemetry detections, on nearby *HSR* and *SCS*.

Figure 3.1: Study site located within Drummond Island Refuge (*DIR*; grey polygon; inset) with primary spawning reefs: Horseshoe Reef (*HSR*), Scammon Shoal (*SCS*), and Boulder Alley (*BLD*). Grey shading represents the relative activity by lake trout as estimated by acoustic telemetry standardized to the reef-specific maximum. White squares indicate sites with the highest activity on *HSR* and *SCS*, as estimated by acoustic telemetry detections.



Methods

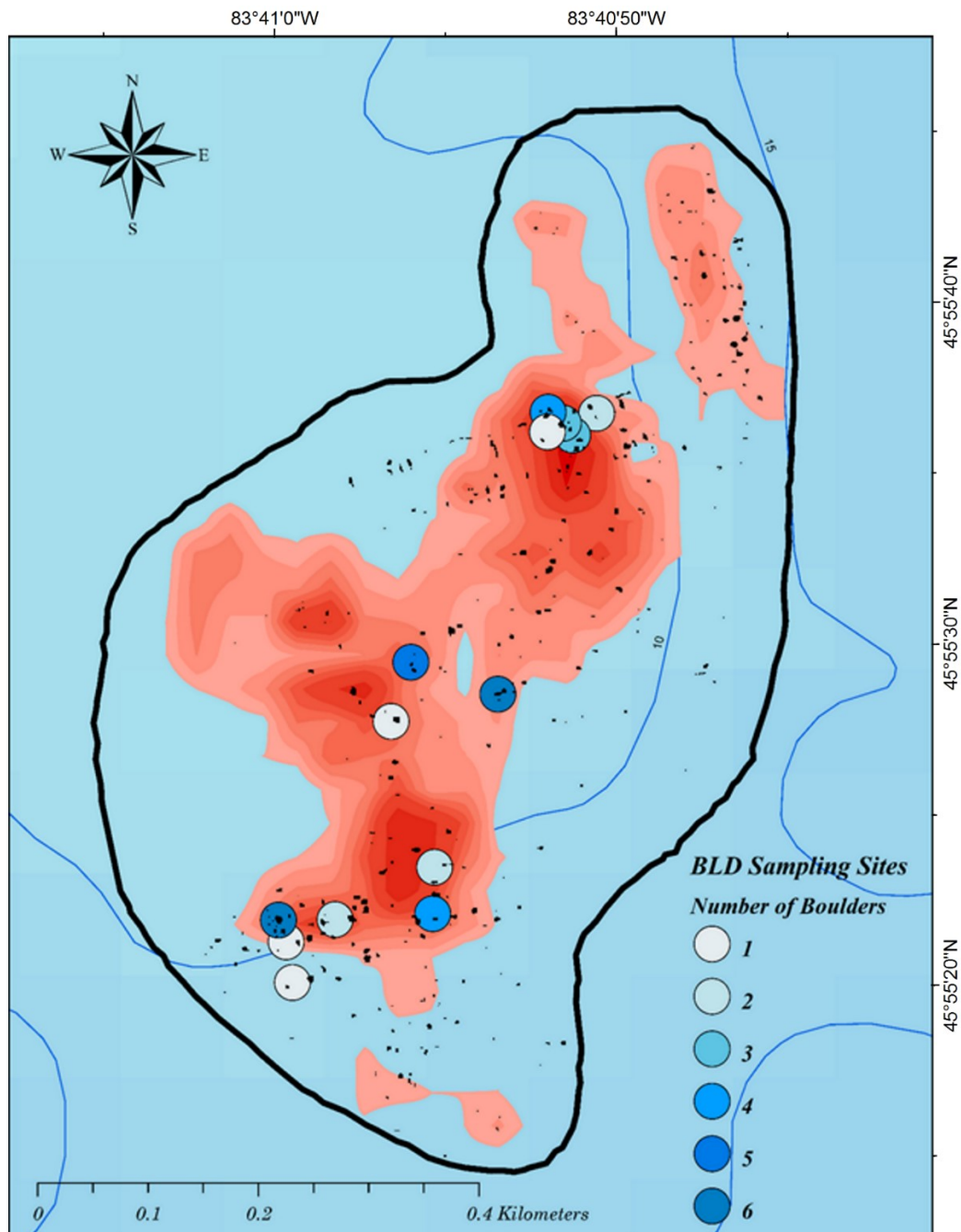
Site Selection

Selection of sampling locations at *BLD* was accomplished in two steps; 1) identification of potential boulders based on high-resolution bathymetry, and 2) selection of a subset of boulders to sample from among all potential boulders. Potential boulders located within the previously defined 0.63 km² study area were identified using high resolution (1 m²) bathymetric survey data collected via multi-beam sonar in 2010 and 2011 (see Riley et al., 2014 for complete bathymetric survey details). The mean depth of each 1 m² cell in the study area was compared against the 75th percentile depth of the surrounding 100 m²; all cells in which the mean depth was at least 0.5 m greater (depths were negative) than the surrounding 75th percentile depth were considered potential boulders. Potential boulders located in adjacent cells were merged, and remaining pixels were quantified using binary image analysis (Rasband, 1997; Schindelin et al., 2012). Using this methodology, I estimated that at least 269 potential boulders were present within the 0.63 km² study area (Figure 3.2).

Diver surveys were used to ground truth the bathymetric analysis and revealed that many potential ‘boulders’ identified using the previously described protocol were actually collections of several boulders in close proximity to one another, often with overhanging edges around their perimeter and between adjacent boulders. Therefore, final sampling locations, termed ‘boulder sites’, were intentionally selected to include a varying number of boulders at each site, ranging from sites with a single boulder to complexes consisting of five or more boulders. Boulder sites on *BLD* were also selected to include areas with relative lake trout activity categorized as high, medium, and low activity based on acoustic telemetry detection data collected in 2013 (see Binder et al., 2018, 2016 and Farha, Ch. 1, *this volume* for complete tagging and acoustic array

details). Additionally, some boulder sites were selected that visually appeared unsuitable for egg deposition based on boulder embeddedness or the size (e.g., fine gravel) or interstitial depth (e.g., minimal interstitial depth or occluded with fine materials) of boulder-associated substrates. In total, 14 discrete boulder sites, encompassing 40 total boulders, were selected for physical characterization and surveyed for egg deposition on *BLD* for comparison to the most highly used 20 m x 20 m site on each *HSR* and *SCS* (one site on each *HSR* and *SCS*, 16 total sites among *BLD*, *HSR*, and *SCS*; Figure 3.2). Lastly, to determine whether it was the substrates beneath boulders, or the boulders themselves that attracted lake trout, at least one 3-5 m diameter area with similar substrate characteristics (e.g., predominant substrate diameter, interstitial depth) was selected for comparison purposes near each boulder site (i.e., located at least 2x the diameter of the boulder away; min. = 4 m, max. = 12 m).

Figure 3.2: Boulder sites selected for sampling at Boulder Alley (*BLD*) on the south shore of Drummond Island, Lake Huron. Potential boulders were identified within the 0.63 km² study area (*black polygon*) based on comparison of the depth of 1m cells to the 75th percentile depth of the surrounding 100 m². Cells in which the mean depth was least 0.5 m greater (depths were negative) than the 75th percentile depth were identified as potential boulders (*black pixels*). Boulder sites (*blue shaded circles*; enlarged for clarity) were selected for sampling to include sites containing varying number of boulders and differing levels of activity by lake trout. Red shading represents the relative activity by lake trout as estimated by acoustic telemetry such that the darkest areas are those with the highest activity. Blue lines with black digits represent 5m depth contours (10 m and 15 m pictured).



Surveys for Egg Deposition (Objective 1)

To describe the extent of boulder-associated spawning at Drummond Island, egg deposition (*presence* or *absence*) was assessed at each of 14 boulder sites at *BLD* as well as the most highly used sites on two nearby lake trout spawning reefs, *HSR* and *SCS*, during the weeks of October 27 and November 9, 2014. Egg surveys were conducted via independent visual inspection by paired divers after peak spawning occurred. Within each boulder site, egg surveys were conducted around the perimeter of each boulder, including substrates beneath overhanging edges of boulders and in adjacent selected habitats paired with boulder sites. For the most highly used sites on *HSR* and *SCS*, egg surveys were conducted within a 10 m diameter circle at the center of each 20 m x 20 m site. In both cases, divers searched independently, turning rocks over and moving water into the substrate by hand to suspend eggs. Egg surveys determined presence/absence only, but specific locations of eggs within each boulder site were recorded on site maps during each dive.

Physical Characterization (Objective 2)

To determine whether egg deposition by lake trout could be predicted based on measurable physical characteristics of a boulder or its associated substrates, the 40 boulders at *BLD* were physically characterized using a combination of direct measurement by divers and video-based image processing. Overall diameter, height, relative compass orientation of the primary axis of each boulder, and number, location, and size of overhanging edges were recorded by divers and used to generate site maps. Overhanging edges were defined as areas extending beneath the boulder judged accessible to adult lake trout (minimum height of 10 cm). The relative area of available substrate present around the perimeter and beneath overhanging

edges of boulders was estimated using a combination of manual measurements and digital measurements using still images taken from video collected with a GoPro Hero III camera mounted on an extension pole with parallel reference lasers separated by a distance of 10 cm (Figure 3.4). In instances where the substrate spilled out beyond the overhanging edge of a boulder, the area was measured following the boundary of clean substrate that was usually visible where an overhanging edge stopped. However, the depth of areas beneath overhanging edges was difficult to measure effectively due to low lighting and the shallow angle of the camera required to access beneath the boulders. As a result, total area estimates of available substrate beneath overhanging edges were likely biased low.

Characterization of substrates beneath and adjacent to boulders on *BLD* also used a combination of direct measurement by divers and still images taken from the GoPro footage. For sites on *HSR* and *SCS*, substrate was characterized using five $\sim 1 \text{ m}^2$ images/site taken by divers using an 8.1-megapixel digital camera (Panasonic Lumix DMC-FX55) mounted on an aluminum frame set 1.5 m above the lake bottom (See Farha, Ch. 1, *this volume* for complete details). Substrates were classified based on the modified Wentworth scale described by Marsden et al. (1995a) using scaled video imagery and image analysis tools in the *FIJI* package of *ImageJ* (Rasband, 1997; Schindelin et al., 2012). A categorical classification representing the predominant surficial substrate was assigned for each site based on the maximum proportion of the total surface area comprised of measured substrates categorized as gravel (0.2 - 6.4 cm), rubble (6.5 - 25.6 cm) and cobble (25.7 - 99.9 cm). Furthermore, any site with greater than 33.3% of measured substrate in more than one category was given a ‘mixed’ substrate type that combined substrate categories (e.g., *gravel-rubble mix*, *rubble-cobble mix*, or *gravel-cobble mix*; See Farha, Ch. 1, *this volume*). As estimates of interstitial depth, three independent

measurements were taken in overhanging areas and in areas of substrate adjacent to boulders on *BLD*, as well as in each area photographed on *HSR* and *SCS* using a thin, flexible, aluminum meter rule to penetrate the substrate until bedrock was reached or substrate was too tight to permit passage. In cases where the height of an overhanging edge prevented access for direct measurement, interstitial depth was visually estimated by excavating loose substrates until maximum depth was reached.

Abundance of Free Embryos and Alevins (Objective 3)

To determine whether the relative abundance of free embryos and alevins at *BLD* differed from spawning habitats at *HSR* and *SCS*, a subset of sites on *BLD* and the sites with the highest amount of activity on *HSR* and *SCS* were sampled through a combination of targeted trapping using specialized custom-built traps and electroshocker surveys conducted via a remotely-operated vehicle (ROV; Janssen et al., 2006; Olson and Janssen, 2017) during spring 2015. Not all sites on *BLD* were sampled with both traps and the ROV. Instead, 10 sites were randomly selected for each sampling method, such that six of the 10 boulder sites sampled with traps were also sampled via ROV, ensuring each site was sampled using at least one method. For this study, juvenile lake trout caught via traps or ROV were classified as either free embryos, fish having an externally visible yolk-sac, or alevins, fish in which the yolk-sac had been fully adsorbed (Marsden et al., *in review*).

Custom 100.5 cm by 30 cm rectangular traps (Figure 3.3) constructed specifically to fit under boulders were deployed beneath overhanging edges of boulders and their surrounding substrates at 10 randomly-selected boulder sites. Four traps were deployed at each site, on three classes of habitat; 1) habitats associated with overhanging edges of boulders (i.e., *beneath*

boulder; 2 traps), 2) habitats immediately adjacent to a boulder but not associated with an overhanging edge (i.e., *beside* boulder; 1 trap), and 3) habitats with similar substrate not associated with boulders (i.e., *away* from boulder; 1 trap). For comparison to *HSR* and *SCS*, a combination of 10 rectangular traps and 10 more typical 62 cm diameter by 20 cm tall conical traps (e.g., Stauffer, 1981; Marsden et al., 1988) were deployed on each of these reefs. Both trap types covered an area of $\sim 0.3015 \text{ m}^2$ and had collection cups mounted as described by Marsden et al. (1988).

Traps on all three reefs were deployed on May 20, 2015 and checked by divers weekly until they were recovered on June 24, 2015. Divers changed collection cups for each trap on the lake bottom without dislodging traps. Therefore, within reefs, individual traps remained in their original location, and catches were tracked using site specific location IDs throughout the entirety of sampling to account for spatial variability in comparisons between trap types (See *Statistical comparisons* below). The relative abundance of free embryos and alevins (CPUE) was calculated as the total number of fish caught per trap per day (CPUE: $\text{fish} \cdot \text{trap}^{-1} \cdot \text{d}^{-1}$) and summarized by habitat class and reef for comparisons.

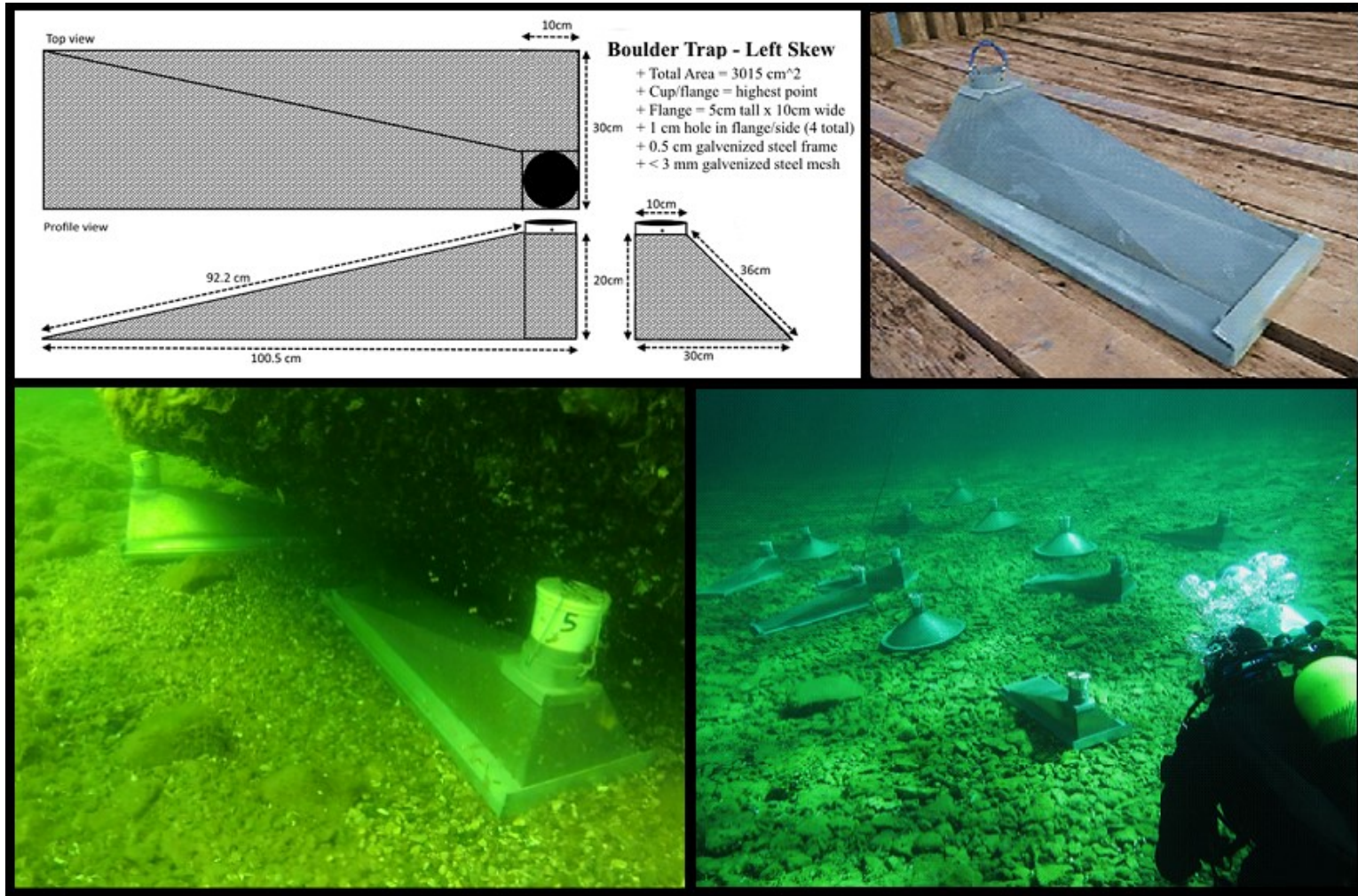
As a complement to trapping efforts, 10 randomly-selected boulder sites and the sites on *HSR* and *SCS* were surveyed with a modified VideoRay Pro 3 GTO ROV outfitted with an ETS ABP-3 electrofishing backpack unit (pulsed DC; 1-1000 Hz and up to 250v) and suction sampler consisting of a MiniRover thruster attached to a 50mm diameter clear acrylic collection tube that protruded ~ 10 cm from the bottom of the ROV (e.g., Janssen et al., 2006; Olson & Janssen, 2017). To access undercut spaces beneath boulders, twin cathodes were mounted on semi-rigid poles on each side of the ROV (0.3 m wide) and extended ~ 1 m into the viewing space of the ROV from a single anode mounted on the collection tube, near the main body of the ROV. In

this configuration, the general fishing area between cathodes and anode consisted of a 0.15 m^2 triangle (1 m high x 0.3 m base).

All ROV sampling was recorded digitally for visual quantification of stunned fish that were not collected. Relative abundance (CPUE) of free embryos and alevins via ROV was estimated as the mean number of fish observed from recorded video footage per electrofishing event, termed a 'run' (i.e., each time electrofishing unit was triggered was considered a 'run'; $\text{CPUE} = \text{fish} \cdot \text{run}^{-1}$) and was summarized by site (*HSR*, *SCS*, 10 boulder sites within *BLD*) and sampling location (*base* or *top* of boulder). A small led visible in the frame of the video indicated when the electrofishing unit was triggered. Each run was limited to 1-2 seconds, during which the ROV would hold as still a position as possible, usually resting on the bottom briefly. The ROV would then quickly maneuver to attempt to collect stunned fish, before conducting another run in a new location.

ROV-based sampling occurred from June 1 - 4, 2015. At sites on *BLD*, the ROV moved around the perimeter of all boulders and across habitats located away from the boulder, electrofishing the substrate at random intervals and attempting to collect any stunned fish. At the beginning of each dive, the ROV would stop briefly at the top of each boulder to conduct pre-survey systems checks. Free embryos and alevins were observed responding to these checks on top of the boulders, and therefore the tops of all boulders at sites selected for ROV sampling were also electrofished. At *HSR* and *SCS*, the ROV sampled each $20 \text{ m} \times 20 \text{ m}$ (400 m^2) area, intermittently electrofishing the substrate at random intervals and collecting stunned free embryos and alevins. ROV configuration and electroshocker settings used on *HSR* and *SCS* were identical to those used at *BLD* but sampling was limited to 20 min for each site. In comparison, mean sampling time at *BLD* was 35 min due to habitat complexity.

Figure 3.3: Schematic drawing and pictures of custom rectangular traps for the collection of early life stages of lake trout from beneath large boulders. Rectangular traps were deployed to estimate the abundance of early life stages of lake trout beneath boulders at Boulder Alley (*bottom-left*) and adjacent to round traps at Horseshoe Reef and Scammon Shoal for trap comparisons (*bottom-right*). Rectangular traps were constructed from the same 3 mm galvanized mesh and had the same coverage area ($\sim 0.30 \text{ m}^2$) as round traps but had a long shallow slope for accessing boulder-associated habitats (*bottom-left*). Collection cups were fastened to trap flange using elastic cords.



Statistical Comparisons

Substrate size classification among boulder sites for comparison purposes was challenging. The angle divers used to photograph substrate and the number of photographs at each site were not consistent due to the confined spaces associated with overhanging edges. Thus, the total area photographed differed based on the specific conditions at each site. Further, more small substrates fit in a given image than large substrates, causing low mean and median diameter estimates, a consistent low bias. Therefore, substrates adjacent to boulders and beneath overhanging edges were characterized using a categorical classification scheme based on the predominant substrate diameter. Statistical comparisons of substrate size among reefs and between substrates found at the base and away from boulders were conducted using a two-way contingency table and a chi-square test of independence with a simulated p-value (2000 simulations) in the *R* programming environment. Statistical comparisons of mean interstitial depth among boulder sites at *BLD* and the two spawning reefs (*HSR* and *SCS*) were done using a one-way ANOVA and Tukey's Honest Significant Difference (HSD) post-hoc test in *R* (R Core Team, 2015; Wickham, 2015).

For trap-based CPUE estimates, three distinct statistical comparisons using linear mixed models fit with restricted maximum likelihood were performed using the *lme4* and *lmerTest* packages in *R* (Bates et al., 2015; Kuznetsova et al., 2015; R Core Team, 2015). First, to determine whether CPUE differed by trap shape (*round* vs. *square*) for traps deployed on *HSR* and *SCS*, trap *shape* was treated as a fixed effect, *reef* and *week* were treated as simple, scalar random effects to account for repeat measures and *location ID:reef* as a multilevel random effect with *location ID* nested within *reef* to account for spatial variability. Second, to determine whether CPUE differed by habitat class (*under* boulder, *beside* boulder, vs. *away* from boulder)

for traps deployed on *BLD*, *class* was treated as a fixed effect, while boulder *site* and *week* were treated as simple, scalar random effects to account for repeat measures. Lastly, to determine whether CPUE differed by reef (*BLD* vs. *HSR* vs. *SCS*), *reef* was treated as a fixed effect while *week* was treated as a simple, scalar random effect to account for repeat measures. For all cases, random effects were assessed as random intercepts only and the response variable, CPUE, was log transformed to improve normality and control heteroscedasticity of the model residuals. To handle this transformation, which cannot accommodate zeros, a small value ($1.0e-15$) was added to all trap-based CPUE estimates.

Statistical comparisons of ROV sampling among *BLD*, *HSR* and *SCS* were prevented by single sampling events on *HSR* and *SCS*. To determine whether ROV CPUE differed between the base and top of boulders within *BLD*, a linear mixed model predicting CPUE with *Location* (i.e., *top* or *base*) as a fixed effect and *SiteID* as a simple, scalar random effect was fit with restricted maximum likelihood and evaluated using the *lme4* and *lmerTest* packages in the *R* programming environment (Bates et al., 2015; Kuznetsova et al., 2015; R Core Team, 2015).

Results

Surveys for Egg Deposition (Objective 1)

Across 14 sites at *BLD*, egg deposition was confirmed beneath or adjacent to all 40 boulders surveyed, and always occurred in association with overhanging edges of boulders. In total, eggs were found in substrates beneath all 86 discrete overhanging edges among the 40 boulders surveyed. While eggs were not observed in any of the areas not associated with overhanging edges, they were often observed in continuous patches that extended up to 1m away from an overhanging edge, as though ‘spilling’ out of the covered space. A single egg was also

observed on top of one boulder ~1.6 m above the lake bottom during the week of November 9, 2014. Surveys on *HSR* and *SCS* confirmed widespread egg deposition at each of the most highly used sites, extending well beyond the arbitrary 20 m x 20 m site boundaries. While surveys for egg deposition were not formally quantitative, egg densities in boulder-associated substrates visually appeared to rival or exceed those at sites on *HSR* and *SCS*. However, because boulder-associated habitats on *BLD* were discontinuous, egg deposition appeared to occur in small patches under the boulders vs. the spatially broad egg deposition observed at *HSR* and *SCS*.

Physical Characterization (Objective 2)

Boulders at the 14 sites on *BLD* varied from large pieces of angular bedrock with sharp edges to round boulders with smooth edges and ranged from 0.9 - 7.3 m in diameter and 0.5 – 2.2 m in height (Table 3.1). Mean water depth of the 14 boulder sites ranged from 8.5 - 10.9 m, with a mean of 9.6 m. Among 40 boulders characterized, 86 discrete overhanging edges were observed and classified as one of three distinct types (Figure 3.4). At single boulders, the interface between the substrate and the edges of the boulder appeared to have been eroded away such that the boulder resembled a ‘mushroom’ with a central supporting pillar and a complete undercut perimeter (Figure 3.4a). In some instances, a boulder edge appeared embedded in the substrate on the lake bottom creating a tunnel, while the opposite edge jutted out of the substrate, as though the ‘mushroom’ had tipped over. In other cases, boulders in close proximity (< 1 m) to one another appeared to have the space between them eroded, creating overhanging edges on one or both boulders (Figure 3.4b). Instances in which the overhanging edges of two adjacent boulders faced one another were generally considered a single overhang. Finally, boulders were also observed atop one another, creating space between the bottom of the upper boulder and the

lake bottom (Figure 3.4c). Overhanging edges in these ‘stacked’ boulders were often difficult to define, as portions of an undercut area were sometimes visible from multiple edges of the boulder. To determine whether a single continuous overhanging edge or separate spaces occurred, a diver would shine a flashlight in one side, while the other diver filmed with an extension pole to determine if light shined through from the opposite side. In each type of overhanging edge, the boulder itself provided cover for the substrate beneath it, and the substrate within was visibly cleaner (i.e., little to no algae growth, minimal *Dreissena spp.* colonization, light siltation) than the surrounding substrate.

The space beneath overhanging edges ranged from 59 – 300 cm in length (distance along perimeter of boulder), 21 – 191 cm in width (depth extending beneath boulder), and 9.4 - 97.4 cm in height (Table 3.1). The area of available substrate beneath overhanging edges ranged from 0.25 – 2.38 m² and summed to a total estimate of 73.38 m² over the 40 boulders surveyed. Overhanging edges of boulders were not consistent in their compass orientation between boulders, and thus did not appear to be oriented facing the predominant current. However, algae growth appeared to be minimal on northern faces of boulders, likely due to reduced sunlight due to shading by the boulder (at latitude 46° N). As a result, clean substrate generally extended farther out from the boulder when overhanging edges faced north vs. other directions.

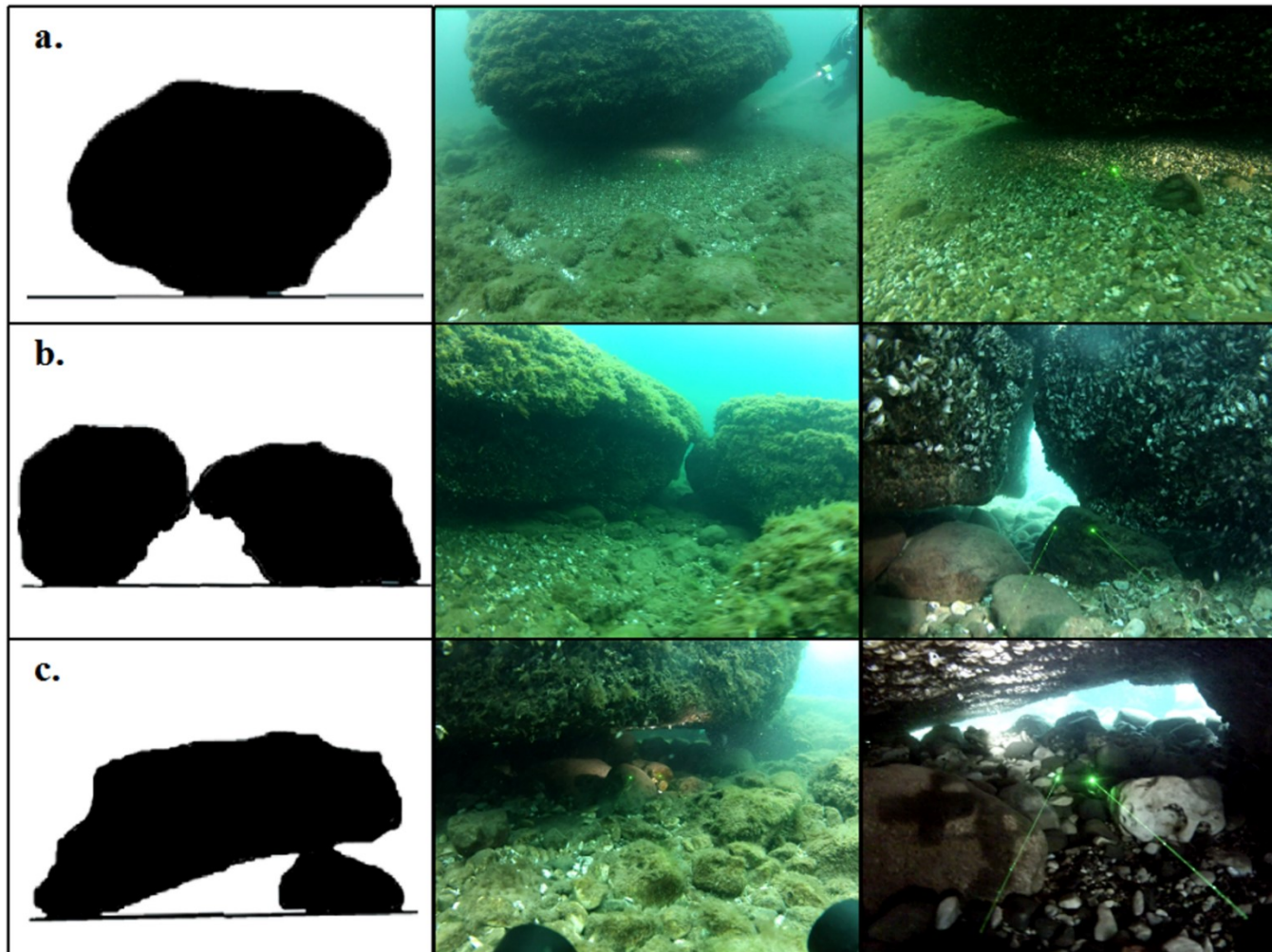
In general, boulder-associated substrates within and around overhanging edges visually appeared smaller in diameter and had less interstitial depth than those found on the most highly used sites on *HSR* and *SCS* (Table 3.1). Substrate located beneath overhanging edges and around the perimeter of boulders was predominantly gravel-rubble mix and ranged in diameter from 0.8 - 21.9 cm. Substrates located in boulder-associated habitats at *BLD* were significantly smaller than those on *HSR* and *SCS*, but no clear differentiation in physical characteristics was observed

between substrates found around the edges of boulders vs. those beneath overhanging edges (Table 3.1; Chi-square test of independence; 2000 simulations, $\chi^2 = 22.8$, $df = 6$, $p < 0.01$). By design, substrates selected for characterization at *BLD* that were not associated with a boulder were similar in size and composition (gravel-rubble mix, 1.3 - 24.1 cm diameter) to boulder-associated substrates. In contrast, substrates at sites on *HSR* and *SCS* were larger than those at *BLD*, being predominantly rubble, and ranged in diameter from 1.3 - 39.5 cm on *HSR*, and 1.2 - 36.8 cm on *SCS*. Mean interstitial depth of substrates was greatest at *HSR* (24.6 cm), followed by boulder-associated substrates at *BLD* (12.8 cm), and finally *SCS* (5.9 cm; One-way ANOVA, $f_{(2, 113)} = 41.8$, $p < 0.01$; Tukey HSD, $p < 0.01$ for all comparisons).

Table 3.1: Summary of boulder, overhang, and substrate characteristics. Substrates were characterized using a categorical classification based on the percentage of measured substrate within size bins using a modified Wentworth scale (*Marsden et al., 1995a, Farha, Ch. 1, this volume*). The size bin with the largest proportion of measured substrate was usually considered the predominant substrate size, but sites with multiple categories having greater than 33.3% of measured substrates were given a mixed classification. Substrates at Boulder Alley (*BLD*) located around the base and away from boulders were smaller (gravel-rubble mix; 0.2 - 25.6 cm) than substrates on Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*) (rubble; 6.5 – 25.6 cm; Chi-square test of independence; 2000 simulations, $\chi^2 = 22.8$, $df = 6$, $p < 0.01$, expected frequencies in parentheses). Boulder-associated substrates on *BLD* also had less interstitial depth than substrates at *HSR*, but greater than those at *SCS* (One-way ANOVA, $f_{(2, 113)} = 41.8$, $p < 0.01$; Tukey HSD, $p < 0.01$ for all comparisons). Variability was expressed as the coefficient of variation (CV) for comparison among parameters with differing units.

Boulder Measurements (m)	Minimum	Maximum	Median	Mean	CV	
Long-axis diameter	1.4	7.3	4.1	4.0	29.5%	
Short-axis diameter	0.9	6.8	3.9	3.7	32.7%	
Boulder height	0.5	2.2	1.3	1.4	28.0%	
Water depth	8.5	10.9	9.3	9.6	7.4%	
Overhang Measurements (cm)						
Length	59.0	300.0	154.5	155.7	30.1%	
Width	21.0	191.0	68.0	74.6	45.2%	
Area (cm ²)	2520	23794	7229	8534	58.1%	
Height	9.4	97.4	35.2	39.7	51.9%	
Substrate Measurements						
	—— Percent Measured ——			Size	– Interstitial Depth –	
	Gravel	Rubble	Cobble	Classification	Mean (cm)	CV
BLD - Base	35.7 (27.9)	53.6 (63.1)	10.7 (8.9)	Gravel-Rubble	11.4	47.6%
BLD - Away	34.1 (27.9)	57.6 (63.1)	8.3 (8.9)	Gravel-Rubble	10.1	31.3%
HSR	12.9 (27.9)	82.2 (63.1)	4.9 (8.9)	Rubble	25.4	24.6%
SCS	28.9 (27.9)	59.1 (63.1)	11.9 (8.9)	Rubble	5.9	21.0%

Figure 3.4: Representation of three types of overhanging edges observed in boulder-associated spawning habitats: a) '*mushroom*' boulders, b) '*adjacent*' boulders, and c) '*stacked*' boulders. Sample photographs of each type of overhang are ordered by row, increasing in zoom from left to right (i.e., picture farthest to the right depicts habitat located beneath an overhanging edge of the boulder pictured in a given row). Parallel reference lasers (*green dots*) were used to indicate 10 cm in the image regardless of focal length. All habitats pictured were positive for egg deposition by lake trout.



Abundance of Free Embryos and Alevins (Objective 3)

Most free embryos and alevins caught at *BLD* were collected from traps deployed in undercut habitats; however, free embryos and alevins were caught from each of the three habitat classes, including traps placed away from the boulder where egg deposition was never observed (Table 3.2). Boulder *site* and *week* were both significant random effects (i.e., variance different from 0) in the model (*site*: $R^2 = 0.069$, *week*: $R^2 = 0.073$), but no significant difference in mean CPUE (fish·trap⁻¹·d⁻¹) was found among habitat classes (Table 3.2; Linear mixed model; $f_{(2, 134)} = 2.04$, $p = 0.135$). Trap catches on *BLD* were low and highly variable, which limited statistical power to detect a significant difference among habitat classes.

At *HSR* and *SCS*, trap-based CPUE estimates varied by *week* and *reef* (*week*: $R^2 = 0.063$, *reef*: $R^2 = 0.057$). More free embryos and alevins were caught in total in rectangular traps (1930 fish caught) than round traps (1224 fish caught; Table 3.2), but catches were highly variable based on trap location (*locationID:reef*: $R^2 = 0.467$). As a result, mean CPUE did not differ significantly between rectangular and traditional round traps deployed on *HSR* and *SCS* (Table 3.2; Linear mixed model; $f_{(1, 39.6)} = 0.18$, $p = 0.672$), and no evidence occurred for an interaction between *reef* and trap *shape* (Linear mixed model; $f_{(1, 38.6)} = 0.21$, $p = 0.652$). Therefore, data from the two trap types were pooled for comparison against CPUE at *BLD*.

Trap-based CPUE estimates of lake trout free embryos and alevins varied from 0 - 17.47 fish·trap⁻¹·d⁻¹ and peaked near the week of June 9 on all reefs. Prior to the week of June 9, fish captured in traps were almost exclusively free embryos as evidenced by visible yolk sacs. In contrast, all fish captured in the final week of sampling (June 24) lacked a visible yolk sac and were therefore considered alevins. Mean CPUE differed significantly among the three reefs (*BLD*, *HSR*, and *SCS*; Table 3.2; Linear mixed model; $f_{(2, 380.4)} = 197.28$, $p < 0.001$). Mean

CPUE was highest on *SCS* ($2.74 \text{ fish} \cdot \text{trap}^{-1} \cdot \text{d}^{-1}$), followed by *HSR* ($2.59 \text{ fish} \cdot \text{trap}^{-1} \cdot \text{d}^{-1}$), and lastly *BLD* ($0.02 \text{ fish} \cdot \text{trap}^{-1} \cdot \text{d}^{-1}$). Comparatively few free embryos and alevins were caught on *BLD* (27 caught) relative to habitats at *HSR* (1570 caught) and *SCS* (1584 caught). However, catch was highly variable on all reefs. Catches were most variable among traps deployed on *BLD* (*Coefficient of Variation*, $CV = 304.1$), followed by *SCS* ($CV = 152.4$), and *HSR* ($CV = 115.8$).

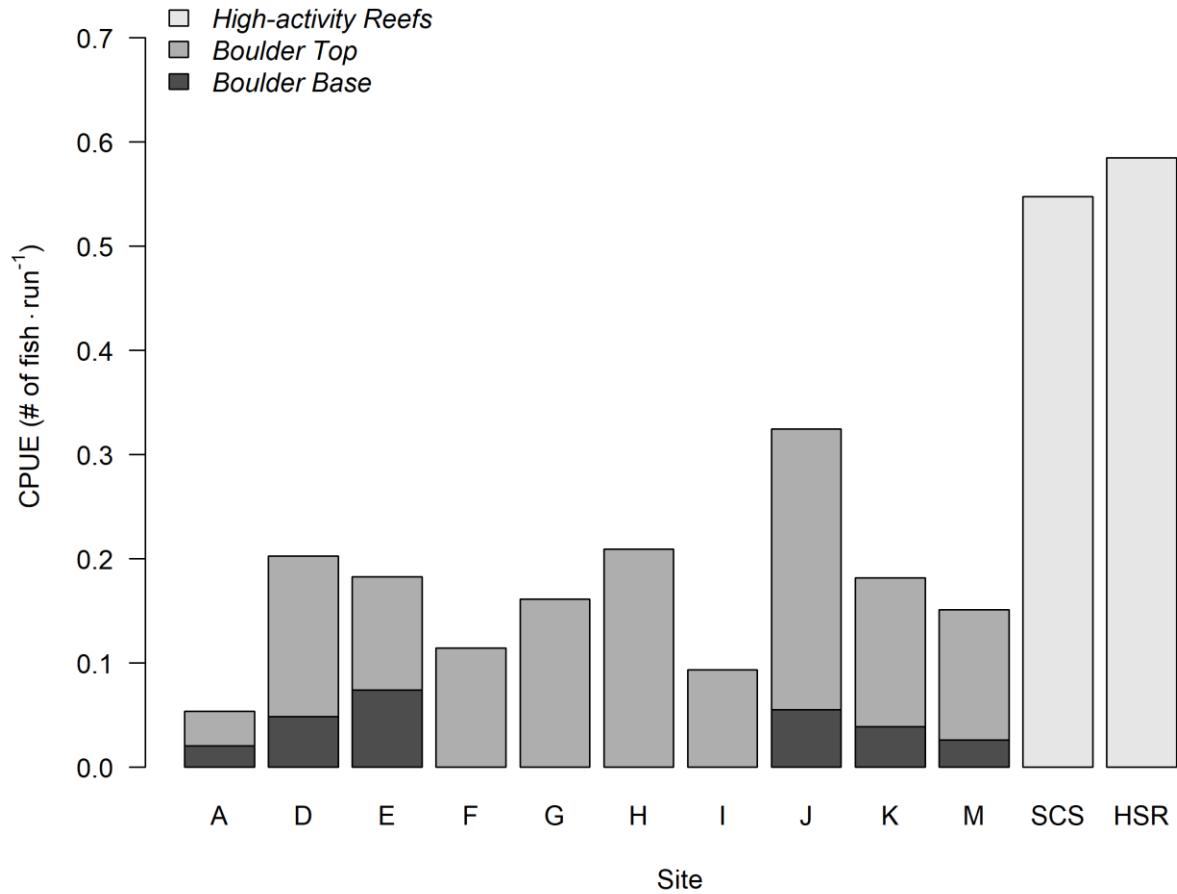
Results from ROV-based electrofishing for free embryos and alevins (Figure 3.5) were consistent with the results from trapping. While no formal statistical comparisons were possible due to single sampling events at *HSR* and *SCS*, the relative abundance of free embryos and alevins at these sites was double that of the single highest boulder site and over seven times greater than the mean CPUE at *BLD* (Figure 3.5). In total, 55 fish were observed over 717 runs at *BLD* ($\text{CPUE} = 0.077 \text{ fish} \cdot \text{run}^{-1}$), while 31 fish were observed over 53 runs at *HSR* ($\text{CPUE} = 0.585 \text{ fish} \cdot \text{run}^{-1}$) and 23 fish were observed over 42 runs at *SCS* ($\text{CPUE} = 0.548 \text{ fish} \cdot \text{run}^{-1}$). Nonetheless, ROV-based sampling provided secondary confirmation of natural production of wild-spawned free embryos and alevins at all boulders sampled. Notably, mean CPUE by electrofishing on the tops of boulders was significantly greater than that at the base of boulders where eggs were observed ($\text{Top} = 0.134 \text{ fish} \cdot \text{run}^{-1}$, $\text{Base} = 0.024 \text{ fish} \cdot \text{run}^{-1}$, Figure 3.5; Linear mixed model; $f_{(1,10)} = 10.01$, $p = 0.01$). Moreover, juvenile lake trout were observed around the base of boulders at only six of 10 boulder sites while at least one juvenile lake trout was observed on the top of every boulder sampled (Figure 3.5). Over the 10 sites sampled, 10 juvenile lake trout were observed (six caught) over 396 discrete electrofishing runs around the base of boulders and 45 juvenile lake trout were observed (19 caught) over 321 runs on the tops of boulders. Four of the six juvenile lake trout caught around the base of boulders and 11 of the 19 caught on the top of boulders were free embryos and the remaining were alevins. Of the 10

juvenile lake trout observed at the base of boulders, six were from undercut habitats, three were in habitats adjacent to boulders, and one was observed responding to the electrical field ~2-3 m away from a boulder. Juvenile lake trout were primarily observed in gravel (0.2 - 6.4 cm) and rubble (6.5 - 25.6 cm) substrates, including areas where interstitial depth was minimal, but no discernable preference for substrate size was identified.

Table 3.2: Weekly relative abundance (CPUE: fish·trap⁻¹·d⁻¹) of lake trout free embryos and alevins caught in three habitat classes using custom rectangular traps at Boulder Alley (*BLD*) and traditional round and custom rectangular traps on more typical habitats on Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*) from May 28 – June 24, 2015. Habitat classes for *BLD* included: habitats beneath overhanging edges of boulders (*beneath* boulder), habitats adjacent to a boulder (*beside* boulder), and nearby habitats at least 2x the diameter of a boulder away (*away* from boulder). N indicates the weekly number of traps of each type deployed at each site. CV represents the coefficient of variation (%) for comparing weekly variability among reefs.

		Date					
Site		May 28	June 3	June 9	June 17	June 24	Total
<i>BLD</i> Beneath boulder	N	20	20	20	20	20	100
	Total Catch	1	2	7	8	0	18
	CPUE	0.01	0.02	0.07	0.05	0.0	0.03
	CV	316.3	211.7	202.0	162.9	--	102.7
<i>BLD</i> Beside boulder	N	10	10	10	10	10	50
	Total Catch	1	1	2	1	0	5
	CPUE	0.02	0.02	0.04	0.01	0.0	0.02
	CV	316.2	316.3	214.8	316.3	--	87.5
<i>BLD</i> Away from boulder	N	10	10	10	10	10	50
	Total Catch	0	1	3	0	0	4
	CPUE	0.0	0.01	0.06	0.0	0.0	0.01
	CV	--	316.3	164.4	--	--	172.7
<i>HSR</i> Round traps	N	9	10	10	10	10	49
	Total Catch	31	247	283	118	10	689
	CPUE	0.57	4.25	4.68	1.47	0.14	2.26
	CV	60.0	39.0	41.5	37.2	132.6	98.6
<i>HSR</i> Square traps	N	10	9	10	10	10	49
	Total Catch	29	300	429	117	6	881
	CPUE	0.48	5.74	7.10	1.46	0.08	2.92
	CV	80.5	46.5	56.8	74.7	141.7	123.5
<i>SCS</i> Round traps	N	10	10	10	9	10	49
	Total Catch	17	198	244	76	0	535
	CPUE	0.29	3.23	4.74	0.96	0.00	1.86
	CV	100.4	79.3	93.1	78.5	--	156.6
<i>SCS</i> Square traps	N	10	10	10	10	10	50
	Total Catch	19	462	457	110	1	1049
	CPUE	0.32	7.54	8.87	1.25	0.01	3.60
	CV	208.4	59.3	65.9	73.8	314.3	138.9

Figure 3.5: Relative abundance (CPUE: # of fish·run⁻¹) of lake trout free embryos and alevins caught via SeaRay ROV modified for electroshocker sampling in boulder-associated habitats at Boulder Alley (*BLD*) and typical habitats with the most activity at Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*). CPUE was calculated as the number of fish observed on recorded video per electroshocking event ('run', i.e., each time electroshocker was triggered). Boulder sites are represented by single letters (*A-M*) and include fish collected around the base (*dark shading*) and top (*medium shading*) of boulders, while single sampling events were conducted in 20 m x 20 m cells on each *HSR* and *SCS* (*light shading*).



Discussion

In this study, widespread egg deposition by lake trout was observed in boulder-associated habitats, inconsistent with the commonly-accepted conceptual model of habitat suitability. Notably, eggs were observed in substrates at the bases of all 40 boulders surveyed in this study. Egg deposition occurred exclusively in association with overhanging edges of the boulders and occurred at all 86 discrete overhangs identified. To my knowledge, this observation is the first report of widespread spawning by lake trout in substrates associated with overhanging edges of boulders >1 m in diameter. Further, this observation is also the first report of free embryos and alevins captured from the tops of large boulders. Possibly, boulder-associated spawning is common in lake trout, but had been previously overlooked due to non-conformity of this habitat type to the commonly-accepted ‘cobble-contour’ model of habitat suitability (e.g., Marsden et al., 2016, 1995a; Muir et al., 2012a). Alternatively, boulder-associated spawning may be a local adaptation shown only by lake trout at the Drummond Island reefs and shoals in northern Lake Huron, similar to reports of atypical spawning habitat use in other populations (Peck, 1986; Beauchamp et al., 1992; Marsden et al., 1995b). Regardless, over the 40 boulders surveyed, the mean area of available substrate associated with overhanging edges was 1.8 m² per boulder (95% CI = [1.5, 2.3]). Extrapolated to the 269 potential boulders identified by bathymetric analysis, I estimated the existence of about 488 m² (95% CI = [403.5, 618.7]) of potential boulder-associated spawning habitat in the 0.63 km² study area at *BLD*. However, because many of the potential boulders identified from bathymetric analysis were in fact collections of multiple boulders in close proximity, this estimate was biased low. Nonetheless, the above observations suggest a potentially important areal contribution to habitat being successfully used for spawning

by lake trout not currently accounted for by the commonly-accepted conceptual model of habitat suitability.

Although widespread egg deposition was observed in boulder-associated habitats, no consistent pattern in the diameter or interstitial depth of the substrates in which eggs were deposited was discernable. Habitats selected for egg deposition varied in substrate size and interstitial depth, including gravel substrates with minimal interstitial depth that appeared to be unsuitable for successful egg incubation. Furthermore, none of the surveyed areas that were away from a boulder received egg deposition, despite having similar substrate composition to habitats beneath overhanging edges that were selected for egg deposition. Large boulders may serve as physical features for aggregating lake trout in spawning condition similar to the role proposed for steep contours in bathymetry (Marsden & Krueger, 1991; Marsden et al., 1995a). However, the observation that egg deposition at *BLD* only occurred in close proximity to distinct overhanging edges suggests that these undercut features were critical for the selection of boulder-associated habitats for spawning.

While the characteristics that makes boulders attractive to spawning lake trout remain uncertain, I hypothesize that the selection of boulder-associated habitats for spawning was most likely driven by flow dynamics present in these habitats rather than the specific physical characteristics of the boulder or its associated substrates. Further, I posit that the undercut spaces beneath boulders were most likely formed through mechanical erosion resulting from the interaction of lake currents and the boulders, possibly in association with storm events and surface waves. Though the flow characteristics of boulder-associated habitats were not directly measured in this study, divers reported feeling stronger currents while sampling at *BLD* than on adjacent reefs and marked concrete blocks (20 cm x 20 cm x 41 cm; ~14 kg) that were placed on

top of boulders for site identification were often swept off the tops of boulders after storm events. Based on the Bernoulli principle and its corollary the Venturi effect, lake currents would be accelerated as they are forced under and around boulders, potentially eroding under the boulder and cleaning fine sediments from the associated substrates over time (Thibodeaux & Boyle, 1987; Vogel, 1994). Local circulations around obstructions, such as differing bed topography in stream channels, can induce hyporheic exchange (Buffington & Tonina, 2009) which also may be attractive to spawning lake trout (Farha, Ch. 1, *this volume*). Furthermore, these same flow dynamics probably prevent siltation and help oxygenate developing embryos during incubation, and therefore satisfy two common requirements for all salmonid spawning habitats (Gunn & Keller, 1984; Chapman, 1988; Sly, 1988).

Successful incubation of wild-spawned embryos to the free embryo and alevin stages was confirmed in boulder-associated habitats using two complimentary methods. However, despite the appearance of similar egg densities in the substrate, the abundance of early life stages in boulder-associated habitats was low compared to those in habitats at *HSR* and *SCS*. This result could be explained at least partially by the inability of the sampling techniques I used to access complex boulder-associated habitats as efficiently as more typical spawning habitats. However, given the combination of current acceleration and small gravel-rubble substrates with minimal interstitial space, eggs deposited in boulder-associated habitats may also experience higher rates of dislodgement and predation (e.g., Claramunt et al., 2005; Marsden & Krueger, 1991). Small-bodied interstitial predators such as crayfish (*Cambrus spp.* and *Orconectes spp.*), round goby (*Neogobius melanostomus*), and sculpin (*Cottus cognattus* and *Cottus bairdi*) appeared to be abundant in boulder-associated habitats and are known to prey on early life stages of lake trout (Jonas et al., 2005; Fitzsimons et al., 2007). In early November, stationary underwater cameras

used to monitor lake trout spawning behaviors around boulders recorded bufflehead ducks (*Bucephala albeola*) diving and feeding on unprotected eggs lying atop gravel substrates with minimal interstitial depth beneath overhanging edges of boulders in 10 m of water depth. Alternatively, the productivity of boulder-associated habitats may be higher than I estimated due to high rates of emigration of exposed free embryos and alevins that quickly move from these habitats to find refuge from predation. These observations of both free embryos and alevins caught in habitats where eggs had not been observed previously, such as on top of boulders and in habitats away from boulders, suggests that these early life stages may have the capability to move more than previously thought.

Spawning in association with boulders was consistent with recent linkages between lake trout spawning habitats and glacially-derived bedforms, such as drumlins, eskers, and moraines (Riley et al., 2014, 2017). The boulders described herein appear to have been most densely located in a 300m wide by 500m long band oriented in a northeast-southwest direction, consistent with the adjacent submerged drumlin field described by Riley et al. (2014). These boulders were likely to have been deposited along with fine glacial till following a junction line between lobes of the Laurentide Ice Sheet during the Wisconsinan glaciation (Karrow, 1987; Eyles & Doughty, 2016). Likely, additional boulders were deposited throughout the drumlin fields at Drummond Island and west following along the mainland Upper Peninsula of Michigan, including the Les Cheneaux Islands (Eschman & Mickelson, 1986; Karrow, 1987). Indeed, lake trout eggs were observed in gravel substrate (0.5 - 3 cm diameter) at the base of a single boulder (1.5 m diameter) located near the center of SCS during surveys related to a separate study (See Farha, Ch. 1, *this volume*). If boulder fields exist throughout the Great Lakes and spawning in

boulder-associated habitats is widespread, these habitats may make an important contribution to total lake trout recruitment, even if net production per boulder of juvenile lake trout is low.

In this study, the use of acoustic telemetry to inform sampling led to the identification of spawning habitats not previously included in the commonly-accepted conceptual model of spawning habitat suitability. Furthermore, the discovery of widespread boulder-associated spawning suggested that flow dynamics was likely to be an important variable governing spawning habitat selection by lake trout. The implications of these findings to management of lake trout are at least three-fold. First, an accurate accounting of the total amount of spawning habitat available to recovering populations allows for better understanding of variability in recruitment, and thus, the speed of a given populations recovery. Combined with population modelling, this information could be used to adjust stocking numbers to increase the likelihood of successful rehabilitation efforts and minimize wasted effort. Second, identification of the critical features of lake trout spawning habitat could be used to identify prime habitats elsewhere for protection or restoration, as well as help specify construction features to incorporate into new artificial habitats (e.g., Marsden et al., 2016). Finally, where lake trout are an invasive species and have caused negative interactions with native salmonids, this information could be helpful in designing control efforts in areas that include boulder-associated habitats (e.g., Crossman, 1995; Hansen et al., 2008). Based on the potential contribution of boulder-associated habitats to total recruitment in the Great Lakes, I advocate for high resolution bathymetric mapping to determine locations of boulder fields and for additional comparisons of juvenile lake trout production and relative incubation success of boulder-associated and traditional habitats. Moreover, to further improve conceptual understanding of lake trout spawning habitat selection, future studies seeking to identify critical habitat requirements should focus on characterizing fine-scale flow

regimes within and immediately adjacent to substrates in both traditional and boulder-associated habitats.

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Chapter 4 : Conclusion

From 2013 – 2014, lake trout spawning in the Drummond Island refuge deposited eggs in a wide variety of habitats, including several habitats with physical characteristics that did not match those described in the commonly-accepted ‘cobble-contour’ conceptual model of spawning habitat suitability. In chapter one, habitats in which lake trout deposited eggs on two adjacent reefs were described. Slope magnitude was found to be an important predictor of egg deposition at one reef, but not the other. Differences in substrate composition did not differentiate between habitats positive for egg deposition and those negative on either reef. Further, a few of the habitats selected for egg deposition varied between years on one reef but remained consistent between years on the other. In chapter two, widespread egg deposition was detected in association with boulder-associated habitats at a third location within the Drummond Island refuge and this site differed substantially in physical characteristics from the most highly used habitats at the other two reefs examined in this thesis. Collectively, these observations of variable spawning habitat use at several locations in close proximity (< 3 km apart) suggested that a wide variety of habitats fit the requirements for successful spawning, and therefore, lake trout were not highly specific in terms of substrate requirements for spawning habitat. Additionally, the variables used to select spawning habitats can vary both temporally and spatially. Common characteristics among all sites was the use of clean stony substrates and the likelihood that water current was an important variable. These observations are consistent with previous studies that suggest lake trout are highly adaptive to shifting conditions in both their native range and areas where they have been introduced (Evans and Olver, 1995; McAughey and Gunn, 1995; Simard, 2017).

Based on three of the most-commonly referenced physical characteristics in the ‘cobble-contour’ model of lake trout spawning habitat suitability, nearly all habitats characterized in this study were outside of the intersection of ranges thought to be suitable (Figure 4.1). In general, habitats surveyed at Drummond Island were associated with substrates that were smaller in diameter and had less interstitial depth than those generally considered appropriate for lake trout spawning, particularly in the Great Lakes (Figure 4.1). As such, the ‘cobble-contour’ conceptual model of habitat suitability, as currently described, did not sufficiently encompass the range of habitats being successfully used by lake trout spawning in the DIR. Further, the physical habitat characteristics measured in this study did little to advance and modify the conceptual model of spawning habitat suitability, and therefore, other unmeasured, possibly correlated variables, are likely involved in habitat selection. Therefore, I hypothesize that water flow is likely to be a primary variable governing spawning habitat selection. Moreover, because optimum conditions for egg incubation are variable spatially both within and between reefs and temporally season to season (e.g., Fitzsimons and Marsden, 2014; Callaghan et al., 2016), physical habitat characteristics for spawning likely also vary in both space and time, such that nearly all combinations of stony substrates, slope, and interstitial depth can be suitable for egg deposition, depending on the site-specific flow characteristics. For example, in conditions with a predictable strong current that may damage incubating eggs, a sharp break in bathymetry with large substrate and deep interstitial spaces may be required to buffer the physical forces involved to a level suitable for incubation. In contrast, small substrates with minimal interstitial depth may also be suitable for incubation in areas where currents are less likely to damage eggs, such as around the base of boulders in water deeper than waves and ice penetrate.

Interstitial flow is a common requirement of all salmonid spawning habitats (Chapman, 1988). Currents flowing interstitially benefit egg incubation by preventing suffocation of eggs through siltation while ensuring eggs remain well-oxygenated (Gunn and Keller, 1984; Sly, 1988). Consistent water currents are critical in maintaining suitable interstitial water quality for successful development of early life stages and currents may also transport emergent lake trout from spawning to nursery habitats (Bronte et al., 1995; Casselman, 1995). In chapter one, four sites near the shallowest ridge of the reef switched from positive for egg deposition in 2013 to negative in 2014, while four sites on the outside boundary of the reef switched from negative in 2013 to positive in 2014 (Figure 2.1). This variability in habitats selected for egg deposition on *HSR* between years may be explained by an abrupt change in water levels. The water level in northern Lake Huron fluctuated from 0.43 m below the long-term average for October (1918 – 2012; 176.43 m above sea level) in 2013 to 0.10 m above the long-term average for October in 2014. Possibly, this change in water levels altered the interaction of lake currents and the slope present on *HSR*, shifting the flow dynamics such that some sites on the shallowest central portion of the reef that were previously attractive to lake trout for spawning became less attractive, and others around the outer edges of the reef, where prominent slopes existed, became more attractive. In contrast, egg deposition on *SCS* was consistent between years and did not appear to be influenced by possible changes in flow conditions due to differing water levels, likely due to the limited slope present on that reef. Collectively, these observations highlight the importance of flow, its possible interaction with bathymetric features, and their collective influence on spawning habitat selection.

While the current ‘cobble-contour’ model of lake trout spawning habitat suitability has been instrumental in identifying habitats important to lake trout rehabilitation in the Great Lakes,

an accurate accounting of the quality and quantity of habitat available is critical to understanding the limitations affecting the speed of population restoration (Marsden et al., 1995; Bronte et al., 2007; Muir et al., 2012). Therefore, further improvement of the model is a key component of ensuring the success of rehabilitation efforts and could also be useful in developing methods to control populations in systems where lake trout are invasive. As currently defined, at least two limitations to advancing the conceptual model of lake trout spawning habitat suitability exist and should be addressed in future studies of lake trout spawning habitat selection. The next two paragraphs will explore these limitations in turn.

First, I propose that an overemphasis on substrate size has occurred in the past. Historically, much of the work characterizing lake trout spawning habitats has focused on substrate size and shape, but the size of substrates in which lake trout spawned was often variable, leading to uncertainty regarding its influence on habitat selection (e.g., Dorr III et al., 1981; Wagner, 1982; Fitzsimons, 1995; Schreiner et al., 1995). Substrates, particularly those in the rubble size class (6.5 – 25.6 cm), were thought to be important for habitat selection based on their ability to buffer potentially damaging lake currents, while excluding egg predators and preventing dislodgement of early life stages (Gunn, 1995; Marsden et al., 1995; Sly and Evans, 1996). However, the characterization of substrate is challenging and often not consistent between studies (Edsall et al., 1992; Marsden et al., 1995). Further, surprisingly little information about structure at the lake bottom exists for the Great Lakes, and that which does exist is generally limited to high traffic near-shore areas and often only describes hardness (i.e., rock vs. sand or silt). High-resolution characterization is labor-intensive and typically requires specialized equipment and, therefore, can be cost-prohibitive. As such, researchers often only broadly characterize surficial substrates, and the actual terminology used to describe them frequently

differs between studies. Broad classification of substrates typically assumes some degree of uniformity, but egg deposition by lake trout, including that described in this thesis, is generally patchily distributed and the total area used for spawning is commonly $< 10\%$ of the total available habitat on a given reef (e.g., Marsden and Krueger, 1991; Gunn, 1995; Kelso et al., 1995; Binder et al., 2018). In reality, the lake bottom is composed of variable patches of an intricate mix of multiple substrate sizes in 3D space that interact with water currents to provide suitable incubation conditions. Broad characterization focused on the diameter of surficial substrate alone greatly oversimplifies this complex relationship. Moreover, this issue is further complicated because the size ranges of substrate classes are not equal (e.g., gravel: 2 - 6.4 cm vs. cobble: 25.7 - 99.9 cm), and therefore habitats are more likely to be classified in the larger size categories, potentially over-inflating the relative-importance of these sizes. Improvements in the resolution of remote characterization technologies, such as multibeam sonar and 3-d stereoscopic imaging, along with enhanced processing capabilities, such as machine learning, hold great promise for improving understanding of the 3-d structure of the lake bottom, and lowering the costs of doing so. Nonetheless, this study suggests that substrate size alone was not informative to predicting egg deposition. Therefore, future efforts to improve understanding of the role of substrate size on the selection of spawning habitats should focus on the interaction of various size substrates and their influence on flow conditions at fine spatial scales, using these enhanced methodologies as they become more accessible, rather than the broad characterization of surficial substrate alone.

Second, several parameters in the 'cobble-contour' model tend to be correlated and are therefore difficult to assess independent from one another. Substrate size and shape, interstitial depth, and substrate homogeneity are all attempts to quantify the interstitial volume between

substrates and are therefore, correlated. In this study, I observed positive correlation between interstitial depth and mean diameter (Pearson product-moment correlation; $r = 0.78$, $p < 0.01$) and negative correlation between substrate homogeneity and interstitial depth (Pearson product-moment correlation; $r = -0.43$, $p = 0.01$). Moreover, this issue is often further compounded by spatial autocorrelation. In this study, model residuals did not appear to be spatially autocorrelated, but the degree of spatial autocorrelation among predictors varied between reefs such that interstitial depth was autocorrelated on one reef but not the other. With little information on the area evaluated by spawning lake trout or the degree to which lake trout spawn in multiple locations in a single season, the spatial extent of a 'site' becomes difficult to define and statistical methods to account for spatial autocorrelation are limited (e.g., Dormann et al., 2007). Lastly, the degree to which these parameters influence the selection of spawning habitats is likely dependent on site-specific flow conditions and therefore difficult to generalize. As such, future studies should focus on characterization of flow dynamics and their interaction with the complete interstitial volume, rather than on these parameters independently.

Successful spawning at Drummond Island does not appear to be limited by availability of suitable incubation habitats or by lake trout selecting unsuitable habitats for egg deposition. In chapter one, mean *in situ* incubation success of habitats in which lake trout deposited eggs was estimated to be 73.8% (95% CI = [65.9%, 81.7%]), which was higher than the 10 to 55% reported in five previous studies using the same habitat bio-assay throughout the Great Lakes (Casselman, 1995; Edsall et al., 1995; Eshenroder et al., 1995; Manny et al., 1995; Perkins and Krueger, 1995). While these estimates did not include all possible sources of mortality, such as predation or dislodgment, habitats at Drummond Island appear to support successful egg incubation, and lake trout appeared to be capable of finding suitable spawning habitats.

Moreover, overlap in incubation success between habitats positive for egg deposition and those that were negative indicated that some habitats not being used may be equally suitable for incubation based on interstitial water quality and the physicochemical conditions experienced. Therefore, from this perspective suitable habitats did not appear to be saturated. In chapter two, natural production of wild-spawned juvenile lake trout was confirmed within boulder-associated habitats using two methods, albeit at lower abundance than the most highly used sites on *HSR* and *SCS*. Because boulder-associated substrates were generally smaller in diameter and had minimal interstitial depth, eggs deposited beneath boulders were hypothesized to have experienced greater rates of predation and dislodgement than eggs deposited on nearby *HSR* and *SCS*. Lake trout may diversify egg deposition in differing habitats as a bet-hedging strategy to optimize the probability of success in the face of environmental uncertainty (Fitzsimons and Marsden, 2014). Unfortunately, little is known about the extent to which a single fish may evaluate or spawn on multiple reefs in the same season (Pinheiro et al., 2017). As such, the precise explanation as to why some habitats were chosen for egg deposition while other seemingly suitable habitats were not remains unclear. Nonetheless, recruitment at Drummond Island does not appear to be limited by habitat availability or the selection of inappropriate habitats, and therefore, spawning activity in this area and year-class recruitment contribution is likely to increase as the abundance of spawning adults increases.

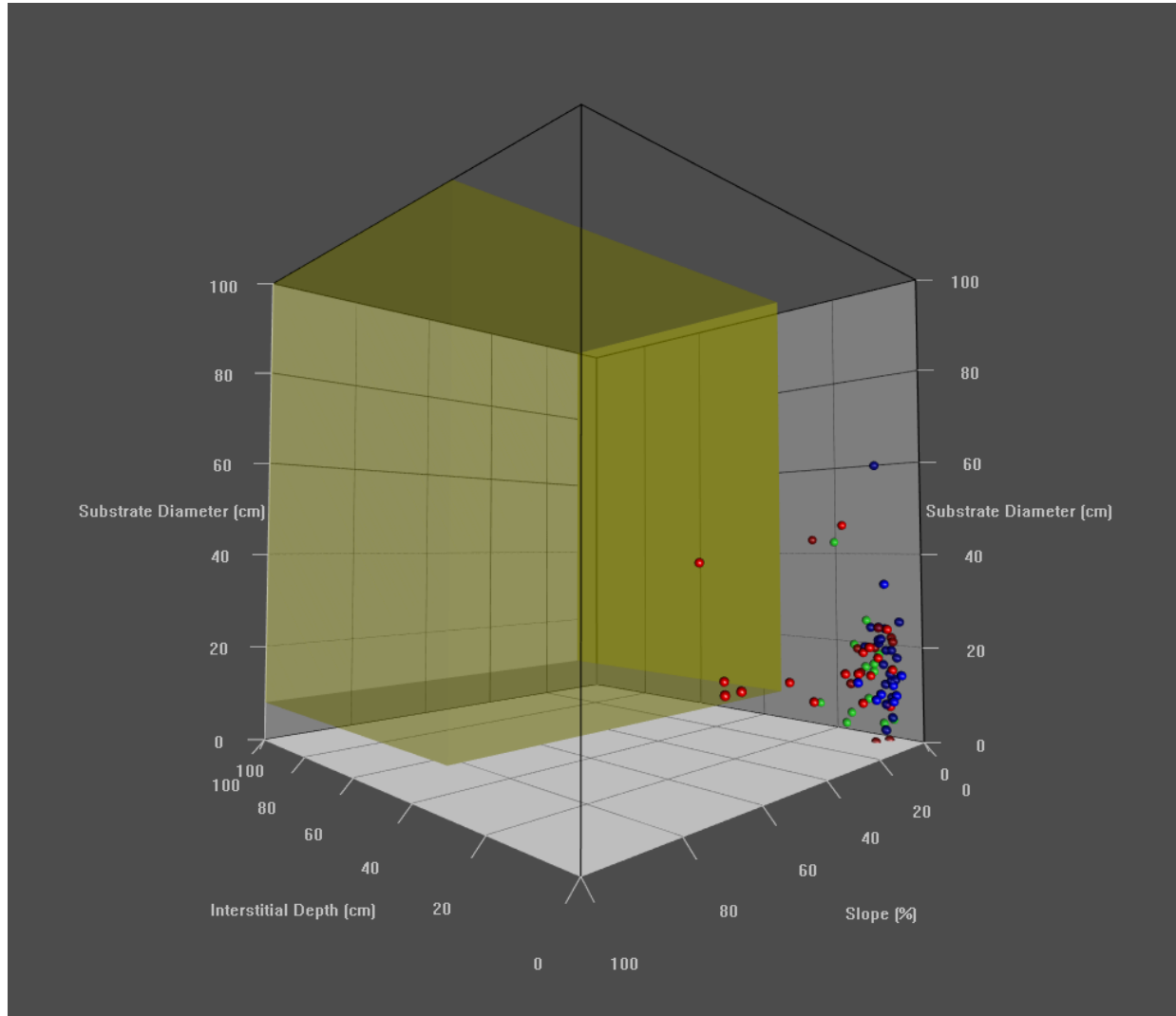
The underlying architecture and feature that distinguishes this study from others was the use of acoustic telemetry to evaluate habitat selection from the perspective of the fish. Selecting sampling sites based on the behavior of the fish freed this study from biases associated with the *a priori* broad characterization of spawning shoals based on the capture of ripe fish. As a result, this study evaluated habitat selection at a scale not previously possible and identified use of

habitats not suspected to be important that may have been overlooked otherwise. Perhaps most interesting, not only was egg deposition observed in these ‘atypical’ habitats, they produced viable naturally spawned juvenile lake trout each year, forcing us to rethink, adapt, and expand our conceptual understanding of lake trout spawning habitat suitability. Whether or not spawning observed within the DIR represents the new paradigm for recovering populations in Lake Huron or if behaviors observed here were single, potentially inconsistent observations (paradox) is uncertain; more research is needed. Further investigations should be focused on areas being successfully used by spawning lake trout, such as the DIR, using technologies such as high-resolution bathymetric mapping and acoustic telemetry as these methods likely hold the greatest promise for advancing conceptual understanding of the mechanisms underlying habitat selection by lake trout.

Improvement in understanding the fundamental features of spawning habitats and the criteria by which habitats are selected may benefit the rehabilitation of lake trout in the Great Lakes in at least three ways. First, with better knowledge of the features of habitats being successfully used by recovering populations, limitations imposed by the carrying capacity of a system can be better identified, and the ability of recovering fish to select suitable habitats can be better evaluated. Second, improved understanding of the habitat requirements of spawning lake trout may enhance the effectiveness of stocking programs through targeted stocking of early life stages on high-quality substrates for imprinting. Third, a better understanding of the habitat requirements of lake trout will help to identify prime habitats on which to focus conservation and rehabilitation efforts. Further, remediation of historic spawning reefs or the construction of artificial reefs in areas where habitat is limited can be enhanced to match habitat characteristics that increase the probability of use and therefore, extend population recovery to areas that may

not have experienced it otherwise. Finally, while broadening conceptual understanding of lake trout spawning behavior will support rehabilitation efforts in the species native range, this information also will benefit control efforts where lake trout have become invasive (e.g., Crossman, 1995; Hansen et al., 2008; Martinez et al., 2009), by identifying potential habitats that previously may have been deemed unsuitable.

Figure 4.1: Conceptual diagram of primary physical characteristics, slope magnitude (%), interstitial depth (cm), and substrate diameter (cm), of habitats selected for egg deposition on Horseshoe Reef (*red dots*), Scammon Shoal (*blue dots*) and Boulder Alley (*green dots*) vs. the ‘cobble-contour’ conceptual model of spawning habitat suitability (*yellow box*). This model states habitats suitable for spawning have substrates between 8-100 cm in diameter, with interstitial depth greater than 30cm, and slopes between 8-100% (5-45°; *yellow box*). Nearly all habitats selected for egg deposition at Drummond Island were outside of the intersection of characteristics described in the conceptual model. In general, Drummond Island habitats had smaller diameter substrates with less interstitial depth than that described in the model.



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APPENDICES

APPENDIX A

Chapter 2: Supplementary Material

The following section contains supplementary materials related to analyses presented in Chapter 2 but are not immediately essential to understanding of the main text. As presented, Chapter 2 is intended for submission to the Canadian Journal of Fisheries and Aquatic Sciences, and these materials will not be included in the submission. They are included here as an archival record for the sake of posterity.

Table A.1: Unstandardized and standardized (denoted by an *) model-averaged parameter estimates ($\hat{\beta}_i$) and relative importance of physical characteristics for the selection of habitats for egg deposition by lake trout on Scammon Shoal (SCS). An unconditional variance estimator ($\widehat{SE}(\hat{\beta}_i|g_i)$) was used to calculate 95% confidence intervals on model-averaged parameter estimates. Furthermore, the relative importance of each physical characteristic was expressed in two ways; first, as a ratio of the i th parameter Akaike weight to the maximum Akaike weight ($\frac{w_i}{w_{max}}$), and second, as an evidence ratio of the i th standardized model-averaged parameter estimate to the maximum standardized parameter estimate ($\frac{\hat{\beta}_i^*}{\hat{\beta}_{max}^*}$). Based on these criteria, none of the measured characteristics were found to be important for the selection of spawning habitats on SCS.

<i>Parameter</i>	<i>Unstandardized Estimates</i>				<i>Standardized Estimates</i>				<i>Relative Importance</i>	
	$\hat{\beta}_i$	$\widehat{SE}(\hat{\beta}_i g_i)$	95% Confidence Interval		$\hat{\beta}_i^*$	$\widehat{SE}_*(\hat{\beta}_i g_i)$	95% Confidence Interval		$\frac{w_i}{w_{max}}$	$\frac{\hat{\beta}_i^*}{\hat{\beta}_{max}^*}$
<i>Distance (m)</i>	-0.006	0.003	-0.011	-0.0001	-0.896	0.428	-1.73	-0.058	0.475	1.00
<i>Physical Habitat Characteristics</i>										
<i>Slope Magnitude (%)</i>	0.104	0.174	-0.237	0.444	0.194	0.307	-0.408	0.796	1.00	0.216
<i>Substrate Homogeneity (%)</i>	-0.010	0.035	-0.079	0.060	-0.028	0.103	-0.230	0.174	0.272	0.031
<i>Interstitial Depth (cm)</i>	-0.012	0.201	-0.406	0.382	0.002	0.106	-0.206	0.210	0.307	0.002
<i>Predominant Substrate Category</i>										
<i>Gravel-Rubble</i>	0.508	2.07	-3.55	4.57	0.075	0.272	-0.459	0.609	0.116	0.084
<i>Rubble</i>	0.365	1.90	-3.35	4.08	0.037	0.231	-0.415	0.490	0.116	0.042
<i>Rubble-Cobble</i>	0.496	2.03	-3.49	4.48	0.062	0.234	-0.397	0.520	0.116	0.069

Table A.2: Complete dataset used for analyses on Horseshoe Reef (*HSR*). *Logistic* and *incubators* columns are binary dummy variables indicating whether site data was used (1) or not (0) in the respective analyses presented in Chapter 1. On *HSR*, site 37 was excluded due to technical issues that prevented complete analysis and all sites not-encountered by lake trout (i.e., site ID's >100) were excluded from analyses for clarity.

Site	Logistic	Incubators	Depth	Eggs	Eggs	Combined	Relative			Slope	Substrate class	Homogeneity	IS	Survival	
				2013	2014	Eggs	HUI	HUI	Distance	magnitude				2013	2014
1	1	1	-11.2	1	1	1	25.56	1.00	20.0	37.2	Rubble	48.9	24.6	0.92	0.93
2	1	0	-6.9	1	1	1	15.53	0.61	39.6	46.9	Rubble	38.7	17.1		
3	1	0	-1.8	0	0	0	0.78	0.03	271.0	1.4	Rubble	40.4	10.2		
4	1	1	-9.1	1	1	1	20.28	0.79	79.9	39.2	Rubble-Cobble	51.8	29.1	0.87	0.89
5	1	1	-9.5	0	1	1	7.21	0.28	253.4	18.4	Rubble	50.4	15.2	0.93	0.86
6	1	0	-5.0	1	1	1	9.97	0.39	184.3	43.1	Rubble	37.3	16.1		
7	1	1	-2.1	0	0	0	0.97	0.04	315.3	1.4	Rubble-Cobble	30.0	14.2	0.46	0.69
8	1	1	-6.6	0	0	0	2.40	0.09	89.0	2.8	Rubble	58.8	5.3	0.80	0.77
9	1	1	-5.0	1	1	1	5.71	0.22	28.0	11.1	Rubble	52.0	6.4	0.58	0.81
10	1	0	-5.3	1	0	1	1.81	0.07	89.0	2.2	Rubble	41.9	9.0		
11	1	0	-5.0	1	1	1	12.46	0.49	107.8	13.2	Rubble	42.0	7.9		
12	1	1	-14.5	0	0	0	1.29	0.05	298.0	7.0	Bedrock	14.0	7.3	0.93	0.74
13	1	1	-9.5	0	0	0	1.72	0.07	80.0	26.0	Bedrock	25.0	5.8	0.85	0.87
14	1	0	-6.7	0	0	0	1.19	0.05	198.0	6.5	Rubble	47.3	10.9		
15	1	0	-9.7	0	1	1	7.71	0.30	295.9	6.7	Rubble	43.5	10.2		
16	1	1	-13.2	1	1	1	1.00	0.04	323.0	19.7	Rubble	52.7	20.3	0.84	0.76
17	1	0	-8.2	0	0	0	1.21	0.05	161.0	5.0	Rubble	34.4	7.4		
18	1	0	-5.8	1	1	1	2.79	0.11	80.0	3.1	Rubble	43.5	5.9		
19	1	0	-6.6	0	1	1	1.59	0.06	127.0	3.0	Rubble	48.0	6.4		
20	1	0	-3.8	0	0	0	3.59	0.14	144.4	1.4	Rubble	30.8	6.3		
21	1	0	-13.3	0	0	0	1.25	0.05	267.0	3.2	Bedrock	30.4	6.1		
22	1	0	-13.7	0	1	1	0.63	0.03	357.0	14.4	Rubble	37.8	10.2		
23	1	0	-9.6	1	0	1	0.56	0.02	228.0	4.0	Rubble	25.5	4.9		
24	1	0	-2.6	1	0	1	4.19	0.16	156.3	1.4	Rubble	34.3	11.2		
27	1	1	-3.1	1	0	1	2.16	0.09	222.7	2.7	Rubble-Cobble	28.3	16.9	0.50	0.65
31	1	0	-3.2	0	0	0	1.65	0.07	116.5	8.7	Rubble	37.1	12.0		
37	0	0	-13.8	0	0	0	11.54	0.45	20.0	1.0	Gravel-Rubble	2.2	0.0		
38	1	0	-2.4	0	0	0	1.65	0.07	285.5	3.3	Rubble-Cobble	47.0	24.2		
40	1	0	-3.2	1	1	1	4.04	0.16	71.9	6.3	Rubble	34.6	10.5		
223	0	0	-9.4	0	0	0	0.25	0.01	327.3	4.5	Rubble-Cobble	39.7	30.8	0.89	0.85
225	0	0	-3.6	0	0	0	0.93	0.04	432.0	1.9	Rubble-Cobble	24.2	14.7		
227	0	0	-12.1	0	0	0	0.10	0.00	558.0	6.4	Cobble	29.5	20.3		
230	0	0	-12.2	0	0	0	0.09	0.00	681.0	7.8	Rubble-Cobble	28.7	18.6		
234	0	0	-6.0	0	0	0	1.93	0.08	368.0	6.2	Rubble	44.9	6.6		
236	0	0	-3.4	0	0	0	0.59	0.02	181.0	3.8	Rubble	36.5	10.5		
237	0	0	-9.1	0	0	0	0.24	0.01	474.5	5.1	Cobble	35.1	29.3		
240	0	0	-10.1	0	0	0	0.09	0.00	673.9	3.5	Rubble-Cobble	35.8	26.9		
243	0	0	-3.9	0	0	0	1.19	0.05	183.3	9.0	Rubble	32.2	11.0	0.10	0.29
246	0	0	-0.6	0	0	0	0.46	0.02	469.0	19.8	Rubble-Cobble	26.5	20.0		
252	0	0	-2.8	0	0	0	0.49	0.02	365.0	5.5	Rubble	38.9	10.5	0.25	0.35
253	0	0	-10.3	0	0	0	0.09	0.00	620.2	4.1	Rubble-Cobble	32.8	19.1		
255	0	0	-6.0	0	0	0	0.65	0.03	305.1	9.1	Rubble	47.8	6.1		
260	0	0	-2.2	0	0	0	0.26	0.01	474.0	10.4	Rubble-Cobble	24.0	13.9		
262	0	0	-10.8	0	0	0	0.03	0.00	568.3	4.3	Rubble	31.0	13.5		
266	0	0	-1.7	0	0	0	0.12	0.01	261.0	2.7	Rubble-Cobble	34.2	14.9		
272	0	0	-1.8	0	0	0	0.35	0.01	304.9	1.9	Rubble	40.4	9.1		
278	0	0	-3.9	0	0	0	0.18	0.01	323.0	12.8	Rubble	49.5	7.3		
281	0	0	-0.6	0	0	0	0.29	0.01	283.0	17.4	Rubble-Cobble	33.9	16.3		
499	0	0	-5.0	0	0	0	0.94	0.04	583.0	2.8	Rubble-Cobble	17.9	17.5		
586	0	0	-10.1	0	0	0	0.16	0.01	326.0	3.4	Rubble	30.4	9.0	0.83	0.81
611	0	0	-11.0	0	0	0	0.16	0.01	565.0	3.7	Rubble-Cobble	32.3	17.1		
719	0	0	-4.3	0	0	0	1.15	0.05	545.0	2.5	Cobble	37.3	19.6		
763	0	0	-5.9	0	0	0	0.44	0.02	628.0	3.4	Cobble	17.2	24.4		
788	0	0	-6.5	0	0	0	0.46	0.02	671.0	5.7	Rubble-Cobble	13.6	13.2	0.59	0.50

Table A.3: Complete dataset used for analyses on Scammon Shoal (SCS). *Logistic* and *incubators* columns are binary dummy variables indicating whether site data was used (1) or not (0) in the respective analyses presented in Chapter 1. On SCS, all sites not-encountered by lake trout (i.e., site ID's >100) were excluded from analyses for clarity.

Site	Logistic	Incubators	Depth	Eggs		Combined Eggs	Relative HUI		Distance	Slope magnitude	Substrate class	Homogeneity	KS	Survival	
				2013	2014		HUI	HUI						2013	2014
1	1	1	-4.1	1	1	1	3.87	0.99	0.0	7.1	Rubble	47.3	5.9	0.69	0.75
2	1	1	-6.1	0	0	0	0.05	0.01	90.0	2.2	Rubble	58.3	4.1	0.37	0.51
3	1	0	-6.7	1	1	1	2.30	0.59	40.0	8.0	Gravel-Rubble	33.3	6.6		
4	1	1	-4.9	1	1	1	0.83	0.21	184.6	2.5	Rubble	40.9	3.6	0.55	0.47
5	1	0	-8.9	1	1	1	1.78	0.45	82.5	16.4	Gravel-Rubble	51.8	6.3		
6	1	1	-5.8	1	1	1	3.92	1.00	44.3	3.6	Gravel-Rubble	40.3	4.2	0.71	0.79
7	1	0	-4.8	0	0	0	0.10	0.03	605.5	2.2	Rubble-Cobble	11.1	7.1		
8	1	1	-5.3	1	1	1	0.24	0.06	260.9	2.3	Rubble-Cobble	31.4	7.3	0.00	0.36
9	1	1	-5.3	0	0	0	0.06	0.02	272.4	2.4	Rubble	53.2	6.8	0.68	0.62
10	1	0	-6.5	0	0	0	0.75	0.19	99.9	3.2	Rubble	61.2	5.4		
11	1	0	-5.1	0	0	0	0.57	0.15	45.0	4.1	Gravel-Rubble	50.4	4.9		
12	1	0	-6.0	0	0	0	0.08	0.02	511.2	3.4	Rubble	45.5	5.4		
13	1	0	-5.7	0	0	0	0.05	0.01	323.2	3.0	Rubble	40.2	6.9		
14	1	0	-5.9	1	1	1	0.30	0.08	56.8	3.3	Gravel-Rubble	29.7	5.1		
15	1	1	-4.5	1	1	1	0.33	0.08	567.6	4.6	Gravel-Rubble	41.3	4.4	0.84	0.85
16	1	1	-6.1	0	0	0	0.10	0.03	426.1	2.9	Gravel-Rubble	50.1	4.8	0.76	0.71
17	1	0	-6.2	0	0	0	0.10	0.03	738.8	2.8	Rubble	26.7	11.7		
18	1	1	-5.0	0	0	0	0.25	0.06	280.8	3.0	Rubble-Cobble	35.5	8.8	0.72	0.53
19	1	0	-8.5	0	0	0	0.21	0.05	100.3	8.5	Gravel-Rubble	42.1	4.2		
20	1	0	-4.4	0	0	0	0.49	0.13	610.3	3.4	Rubble	36.0	8.1		
22	1	0	-6.3	0	0	0	0.06	0.02	433.9	5.3	Rubble	35.2	7.3		
23	1	0	-4.8	0	0	0	0.06	0.02	583.7	2.5	Rubble	38.2	8.6		
24	1	0	-6.2	0	0	0	0.10	0.03	473.3	6.3	Rubble	35.9	6.3		
25	1	1	-6.0	0	0	0	0.05	0.01	569.6	4.5	Gravel-Rubble	52.2	6.1	0.60	0.78
26	1	0	-5.1	0	0	0	0.03	0.01	481.8	4.0	Rubble	37.2	9.7		
31	1	0	-5.2	0	0	0	0.17	0.04	368.0	1.9	Rubble	59.5	7.4		
32	1	0	-5.8	0	0	0	0.08	0.02	437.0	1.4	Rubble	53.6	5.1		
35	1	0	-5.7	0	0	0	0.08	0.02	528.8	4.0	Gravel-Rubble	45.7	5.4		
36	1	0	-5.1	0	0	0	0.05	0.01	431.2	2.4	Rubble	43.4	5.8		
39	1	0	-4.6	0	0	0	0.16	0.04	494.4	2.1	Rubble	36.9	7.8		
156	0	0	-5.8	0	0	0	0.06	0.02	882.1	2.5	Rubble-Cobble	10.9	13.7		
178	0	0	-7.6	0	0	0	0.08	0.02	205.9	3.0	Bedrock	35.6	5.9		
187	0	0	-7.3	0	0	0	0.03	0.01	311.4	2.2	Rubble	28.4	9.0		
189	0	0	-5.3	0	0	0	0.08	0.02	695.4	0.9	Rubble	38.0	7.3	0.63	0.73
201	0	0	-6.8	0	0	0	0.02	0.01	323.5	2.3	Rubble	30.7	9.0		
203	0	0	-5.7	0	0	0	0.13	0.03	673.1	3.5	Rubble-Cobble	18.6	12.4		
204	0	0	-4.6	0	0	0	1.43	0.37	184.4	4.8	Bedrock	11.7	4.1		
236	0	0	-6.9	0	0	0	0.02	0.01	460.6	1.6	Gravel-Rubble	48.3	5.3		
259	0	0	-11.7	0	0	0	0.02	0.01	354.2	2.8	Rubble	1.1	1.0		
260	0	0	-9.1	0	0	0	0.02	0.01	204.0	14.7	Bedrock	40.5	5.9		
262	0	0	-9.3	0	0	0	0.02	0.01	971.3	2.4	Bedrock	27.1	7.1		
282	0	0	-5.9	0	0	0	0.02	0.01	354.3	1.0	Bedrock	39.0	4.1		
303	0	0	-5.9	0	0	0	0.03	0.01	349.6	2.8	Gravel-Rubble	36.2	6.1	0.68	0.71
309	0	0	-11.4	0	0	0	0.00	0.00	636.7	2.6	Gravel-Rubble	3.0	0.5		
329	0	0	-8.6	0	0	0	0.02	0.01	216.9	4.7	Rubble	47.5	11.2	0.88	0.88
351	0	0	-6.4	0	0	0	0.03	0.01	344.7	3.8	Rubble	57.6	4.4	0.46	0.50
353	0	0	-7.0	0	0	0	0.02	0.01	221.0	2.0	Bedrock	21.9	2.2		
363	0	0	-9.7	0	0	0	0.03	0.01	753.4	2.3	Bedrock	23.2	5.6		
369	0	0	-10.6	0	0	0	0.06	0.02	272.6	0.9	Gravel-Rubble	1.0	0.0		
388	0	0	-5.9	0	0	0	0.17	0.04	300.8	5.9	Rubble-Cobble	33.7	6.6	0.51	0.70

APPENDIX B

Chapter 3: Supplementary Material

The following section contains supplementary materials related to analyses presented in Chapter 3 but are not immediately essential to understanding of the main text. As presented, Chapter 3 is intended for submission to the Journal of Great Lakes Research, and these materials will not be included in the submission. They are included here as an archival record for the sake of posterity.

Table B.4: Complete boulder characterization data for all boulders characterized on Boulder Alley (*BLD*). In total, 40 boulders were surveyed consisting of 86 discrete overhangs.

Site ID	Latitude	Longitude	Boulder (<i>n</i>)	Minimum diameter (m)	Maximum diameter (m)	Boulder height (m)	Overhangs (<i>n</i>)	Average length (cm)	Average depth (cm)	Average height (cm)	Average Area (cm ²)
A	45.92687	-83.68071	1	4.7	5.6	1.3	2	144	107	37	7748
A	45.92686	-83.68077	2	4.5	5.3	1.5	3	172	83	86	11282
B	45.92670	-83.68091	1	4.1	4.4	1.1	3	151	70	41	9169
B	45.92667	-83.68090	2	1.3	1.6	0.5	1	125	40	21	3656
B	45.92666	-83.68094	3	0.9	1.3	0.6	2	110	41	18	5189
C	45.92679	-83.68098	1	4.5	5.1	1.7	3	185	89	100	8741
C	45.92675	-83.68097	2	1.3	1.7	0.8	2	119	55	28	4375
C	45.92678	-83.68106	3	1.7	2.3	1.3	3	169	66	109	6572
D	45.92688	-83.68111	1	4.0	5.1	1.6	3	164	71	133	8038
D	45.92692	-83.68111	2	4.1	4.5	1.2	2	77	45	85	4788
D	45.92689	-83.68105	3	3.1	3.2	1.0	1	181	61	24	8026
D	45.92683	-83.68109	4	2.9	3.9	0.9	1	101	48	41	6137
E	45.92458	-83.68152	1	4.2	4.5	0.7	1	114	25	26	8899
E	45.92460	-83.68146	2	4.3	4.4	1.2	2	216	56	65	7190
E	45.92454	-83.68151	3	2.9	3.1	0.8	2	148	30	34	4654
E	45.92456	-83.68138	4	3.0	5.0	0.9	1	170	82	25	11102
E	45.92459	-83.68141	5	3.4	3.6	0.9	2	143	57	59	4622
F	45.92257	-83.68324	1	4.6	5.2	1.1	3	163	102	78	8253
G	45.92274	-83.68331	1	3.6	4.7	1.4	3	137	88	112	8234
G	45.92270	-83.68330	2	3.9	4.1	1.2	1	187	96	55	13126
G	45.92270	-83.68333	3	3.3	4.5	1.1	1	100	69	15	5587
G	45.92279	-83.68332	4	3.3	5.0	1.0	3	185	125	69	15403
G	45.92279	-83.68338	5	4.2	5.9	1.3	4	188	84	42	10649
H	45.92275	-83.68284	1	3.9	4.7	1.7	3	224	100	22	16717
H	45.92284	-83.68271	2	4.3	4.4	1.1	2	177	125	61	13944
H	45.92277	-83.68280	3	2.1	3.3	1.0	1	213	58	84	9351
I	45.92280	-83.68205	1	6.8	7.3	0.8	2	157	77	54	6500
I	45.92281	-83.68211	2	2.6	3.6	1.2	1	116	95	91	6973
I	45.92285	-83.68205	3	3.6	3.8	0.9	2	140	68	33	4064
I	45.92284	-83.68200	4	2.3	3.3	0.5	2	153	90	15	7752
J	45.92317	-83.68203	1	3.7	4.4	0.8	2	124	62	27	5110
J	45.92315	-83.68185	2	3.4	3.9	1.5	3	97	53	85	4104
K	45.92484	-83.68222	1	4.1	5.5	1.0	3	228	87	30	15722
K	45.92485	-83.68215	2	3.7	4.6	0.6	2	110	53	35	4312
K	45.92489	-83.68215	3	3.5	3.9	0.9	2	116	43	37	6523
K	45.92488	-83.68221	4	3.4	3.9	0.8	2	151	54	65	6718
K	45.92484	-83.68218	5	2.1	3.5	0.8	2	159	88	50	6783
L	45.92436	-83.68239	1	4.5	5.0	1.3	4	147	63	107	8278
M	45.92223	-83.68319	1	4.4	5.7	1.3	3	135	74	78	8466
N	45.92672	-83.68111	1	3.3	4.3	1.2	2	167	89	45	10410
<i>Total</i>			40	3.5	4.2	1.1	86	151	72	55	8079

Table B.5: Complete substrate characterization data for boulder-associated substrates adjacent to boulders at Boulder Alley (*BLD*) and beneath overhangs vs. the most popular sites on Horseshoe Reef (*HSR*) and Scammon Shoal (*SCS*). Substrate was classified based on the proportion of measured substrate in size bins using a modified Wentworth scale (*Marsden et al., 1995a, Farha et al. Ch. 1*). The size bin with the largest proportion of measured substrate was usually considered the predominant substrate size, but sites with multiple categories having greater than 33.3% of measured substrates were given a mixed classification.

Reef	Site ID	Substrate	Gravel (%)	Rubble (%)	Cobble (%)	Unclassified (%)	Average Diameter (cm)	Interstitial depth (cm)	Slope magnitude (%)
HSR	1	Rubble	12.9	82.1	5.0	40.9	7.1	24.6	37.16
SCS	1	Rubble	29.0	59.1	12.0	30.2	5.7	5.9	7.1
BLD	A	Gravel-Rubble	34.0	66.1	0.0	40.0	5.3	12.3	<i>n/a</i>
BLD	B	Gravel	45.3	32.6	22.1	36.9	3.1	6.6	<i>n/a</i>
BLD	C	Rubble	19.4	72.4	8.1	34.7	6.8	9.8	<i>n/a</i>
BLD	D	Gravel-Rubble	35.2	64.8	0.0	34.4	5.5	11.0	<i>n/a</i>
BLD	E	Gravel	54.2	32.1	13.7	35.7	3.8	8.8	<i>n/a</i>
BLD	F	Gravel-Rubble	34.7	65.3	0.0	42.4	5.2	6.6	<i>n/a</i>
BLD	G	Rubble	29.4	66.9	3.7	35.1	6.4	13.0	<i>n/a</i>
BLD	H	Gravel	51.1	31.9	17.0	37.9	3.3	17.8	<i>n/a</i>
BLD	I	Rubble-Cobble	5.6	59.8	34.6	42.7	11.3	15.7	<i>n/a</i>
BLD	J	Rubble-Cobble	10.4	56.2	33.4	32.0	14.0	20.4	<i>n/a</i>
BLD	K	Rubble	29.0	71.0	0.0	35.0	7.0	11.0	<i>n/a</i>
BLD	L	Gravel	63.6	32.3	4.2	30.8	3.7	24.4	<i>n/a</i>
BLD	M	Gravel	59.6	32.8	7.6	34.2	3.3	16.5	<i>n/a</i>
BLD	N	Rubble	28.3	71.7	0.0	37.0	6.9	12.7	<i>n/a</i>

Table B.6: Relative survival to hatch for incubators deployed at Boulder Alley (*BLD*) and controls (*CON*) using methodology described in Chapter 1 (See *Chapter 1 – Methods – Incubation Success (Objective 2)* for complete details). This analysis was removed from Chapter 3 for the sake of clarity. Habitat classes were (1) areas of clean gravel (< 6 cm diameter) associated with an overhang, (2) areas of gravel (< 6 cm diam.) not associated with boulders ($\geq 2x$ boulder diameter away), (3) areas of clean rubble (6 - 25 cm diam.) associated with an overhang, and (4) areas of rubble (6 - 25 cm diam.) not associated with boulders. At recovery, incubators were classified either as those that ‘*stayed*’ buried in the substrate (*Orientation* = 1; maintained vertical orientation), and those that ‘*moved*’ (*Orientation* = 2; either tipped over or completely dislodged from substrate).

Site	Class	Orientation	Fry (<i>n</i>)	Egg (<i>n</i>)	Empty (<i>n</i>)	Survival (%)	Standard Deviation
A	CON	1	40	10	0	0.79	0.06
D	CON	1	42	8	0	0.84	0.04
H	CON	1	45	5	0	0.91	0.09
K	CON	1	42	8	0	0.83	0.08
L	CON	1	46	4	0	0.92	0.02
M	CON	1	43	7	0	0.87	0.08
A	1	2	29	15	6	0.58	<i>n/a</i>
A	2	1	35	6	9	0.70	0.03
A	3	1	25	20	6	0.49	0.16
A	4	2	17	28	6	0.34	0.03
D	1	2	8	9	34	0.15	0.01
D	2	2	27	10	13	0.54	<i>n/a</i>
D	3	1	29	16	6	0.57	0.16
D	4	2	20	25	6	0.40	0.06
H	1	2	2	42	7	0.04	0.06
H	2	1	17	22	11	0.34	0.42
H	3	1	22	17	12	0.44	0.06
H	4	2	11	24	15	0.22	0.09
K	1	1	19	12	19	0.38	<i>n/a</i>
K	2	1	13	9	29	0.25	0.07
K	3	1	29	10	12	0.58	0.03
K	4	2	27	20	4	0.53	0.16
L	1	2	13	27	11	0.26	0.20
L	2	1	43	5	3	0.85	0.18
L	3	1	27	11	13	0.53	0.07
L	4	2	11	25	15	0.21	0.01
M	1	2	29	10	12	0.57	0.27
M	2	2	7	19	25	0.14	0.11
M	3	2	14	21	15	0.28	<i>n/a</i>
M	4	2	22	23	6	0.43	0.24

Figure B.1: Weekly relative abundance (CPUE: fish·trap⁻¹·d⁻¹) of lake trout free embryos and alevins caught in three habitat classes using custom rectangular traps at Boulder Alley (*BLD*; *Left*) vs. traditional round and custom rectangular traps on typical habitats on Horseshoe Reef (*HSR*; *Right*) and Scammon Shoal (*SCS*; *Right*) from May 28 – June 24, 2015. Habitat classes for *BLD* included: habitats beneath overhanging edges of boulders (*beneath* boulder), habitats adjacent to a boulder (*beside* boulder), and nearby habitats at least 2x the diameter of a boulder away (*away* from boulder).

