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Effectiveness of Spawning Substrate Enhancement for Adfluvial Fish in a Regulated Sub-Arctic River

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Abstract

This study was conducted to meet regulatory requirements under the Fisheries Act in Canada, specifically for a hydroelectric facility on the Yellowknife River in the Northwest Territories. The research focused on annual snorkel surveys of adfluvial fish and their spawning habitat below the facility. Initial observations of egg mortality, potentially due to overcrowding, prompted the investigation of natural and enhanced habitat for spawning Lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedi*) from 2016 to 2019. The design and composition of the installed habitat were based on fish utilization of the natural channel below the hydro facility and design principles from previous habitat rehabilitation projects for anadromous fishes. Pre- and post-enhancement data on egg density and survival were collected using 1 m ^{2} plots on both natural and artificially enhanced substrates. Three years of post-enhancement monitoring indicated higher egg densities and a greater proportion of live eggs in the artificially enhanced habitat compared to the natural habitat, with more pronounced trends observed for coregonids (lake whitefish and cisco) compared to lake trout. These findings suggest that habitat enhancement has the potential to enhance juvenile recruitment for adfluvial fish. A critical factor in the design was the substrate composition, providing adequate interstitial spaces for egg development and protection. This study represents the first documented attempt at habitat improvement in a regulated sub-Arctic river in Canada. The findings offer valuable guidance for stakeholders involved in new or existing development projects that require conservation actions to maintain fisheries productivity.

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ABSTRACT

This study was conducted to meet regulatory requirements under the Fisheries Act in Canada, specifically for a hydroelectric facility on the Yellowknife River in the Northwest Territories. The research focused on annual snorkel surveys of adfluvial fish and their spawning habitat below the facility. Initial observations of egg mortality, potentially due to overcrowding, prompted the investigation of natural and enhanced habitat for spawning Lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*) and cisco (*Coregonus artedi*) from 2016 to 2019. The design and composition of the installed habitat were based on fish utilization of the natural channel below the hydro facility and design principles from previous habitat rehabilitation projects for anadromous fishes. Pre- and post-enhancement data on egg density and survival were collected using 1 m^2 plots on both natural and artificially enhanced substrates. Three years of post-enhancement monitoring indicated higher egg densities and a greater proportion of live eggs in the artificially enhanced habitat compared to the natural habitat, with more pronounced trends observed for coregonids (lake whitefish and cisco) compared to lake trout. These findings suggest that habitat enhancement has the potential to enhance juvenile recruitment for adfluvial fish. A critical factor in the design was the substrate composition, providing adequate interstitial spaces for egg development and protection. This study represents the first documented attempt at habitat improvement in a regulated sub-Arctic river in Canada. The findings offer valuable guidance for stakeholders involved in new or existing development projects that require conservation actions to maintain fisheries productivity.

INTRODUCTION

Habitat enhancements in freshwater ecosystems have the potential to be a viable tool for fisheries conservation and management in northern regions of Canada where effects of climate change, overfishing, and industrial works have the potential to limit or impair the productivity of fisheries (McPherson, Cott, Lewis, Swanson, & Poesch, 2023). Habitat enhancement can also be a legal requirement in many countries, including Canada, where proponents are responsible to implement project mitigation or conservation offsets for new developments or existing operating facilities (DCCEEW, 2012; DFO, 2019; Favaro & Olszynski, 2017; zu Ermgassen et al., 2019). Indeed, habitat enhancement is a widely practiced restoration method in many developed regions around the world where high valued recreational fisheries are in decline, however, designing and implementing suitable habitat enhancements in northern (e.g., Arctic and sub-Arctic regions) ecosystems is challenging due to their remote nature, the difficulty in monitoring the effectiveness of outcomes, and the paucity of available information and documented records on past successes or failures in habitat enhancement approaches.

Lake trout (*Salvelinus namaycush*), lake whitefish (*Coregonus clupeaformis*), and cisco or lake herring (*Coregonus artedi*) are widely distributed salmonid species found in the northern regions of North America. They inhabit areas that were previously glaciated, ranging from the Atlantic watersheds westward throughout the Canadian provinces to British Columbia. They can also be found in the Arctic watersheds across the Northwest Territories and Nunavut (Evans, Reist, & Minns, 2002; Richardson, Reist, & Minns, 2001; Scott &

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Crossman, 1998). These three species are found in water bodies of various sizes, ranging from smaller inland lakes (McAughey & Gunn, 1995) to the largest lakes in North America, including the Laurentian Great Lakes (Lake Superior, Huron, Michigan, Erie, and Ontario) and the Mackenzie Great Lakes (Great Bear and Great Slave Lake) (Evans et al., 2002; MacKenzie, Fortin, & E., 2021). They hold significant biological, cultural, commercial, and recreational importance throughout their distribution range (MacKenzie et al., 2021; Mohr & Nalepa, 2005).

Habitat enhancements in northern ecosystems often focus on general principles of improving habitat characteristics (Theis, Ruppert, & Poesch, 2023; Theis, Ruppert, Shirton, & Poesch, 2022), but with a specific focus on improving spawning substrates habitat (Gatch, Höök, Roseman, & Koenigbauer, 2020; Selgeby et al., 1995), based on the assumption that it will improve egg survivorship and ultimately increase fish abundance. However, the success of enhancing spawning substrate is heavily dependent on the life history types of the targeted species, and there is a significant disparity in available research between lacustrine (lake) and adfluvial (river) spawning life history types. For example, there is a substantial body of research on the life history, spawning behavior, and spawning habitat requirements of lacustrine lake trout (Callaghan, Blanchfield, & Cott, 2016; Fitzsimons, 1995; Gunn, 1995; Richardson et al., 2001). Similarly, extensive literature exists on the spawning behavior and habitat of lacustrine lake whitefish and cisco, mainly in relation to fisheries management objectives for commercial fisheries in the Laurentian Great Lakes (Fischer et al., 2018; Gatch et al., 2020; George, 2019). Although lake trout, lake whitefish, and cisco can be found in northern adfluvial systems, our understanding of the extent to which they use riverine habitats for spawning is limited. There is a lack of information regarding the frequency and characteristics of watercourse utilization for spawning, highlighting the need for further research on the utilization of riverine areas by these three adfluvial species (Evans et al., 2002; Jones, Parna, Parna, & Chong, 2018; Richardson et al., 2001).

The development of habitat enhancements to improve spawning substrate based on life history characteristics of multiple adfluvial species provides the potential to help prioritize conservation measures for the benefit of multiple species. To do this, we require an understanding of life history types and similarities and differences of these advluvial species, their habitat use, and spawning characteristics, based on empirical information. Lake trout, lake whitefish, and cisco have unique life histories and spawning behaviors, but they also share certain similarities, which may allow for some synergism in developing habitat enhancements. For example, all three species are members of the Salmonidae family with lake trout belonging to the Salmoninae sub-family and lake whitefish and cisco belonging to the Coregoninae sub-family (Evans et al., 2002; Richardson et al., 2001; Roberge, Hume, Minns, & Slaney, 2002). Secondly, all three species are fall-spawning, lithophilic broadcast spawners, meaning they deposit their eggs in granular substrates (Roberge et al., 2002; Scott & Crossman, 1998; Stewart, 1997). Thirdly, while their lacustrine and/or anadromous populations have been extensively studied, the adfluvial populations of these species, which migrate to rivers for spawning, have received less research attention regarding their life history, spawning behavior, and habitat requirements (Evans et al., 2002; Richardson et al., 2001). Finally, all three species play significant roles in commercial, Indigenous subsistence, and recreational sport fisheries in Canada (MacKenzie et al., 2021; Mohr & Nalepa, 2005), which make them highly suitable candidates for habitat enhancements measures and offsetting in general.

The availability of suitable spawning habitat plays a crucial role in the recruitment of spawning salmonid populations. Numerous studies have highlighted the significance of spawning habitat availability for freshwater fishes and its impact on year class strength and population variability (Fitzsimons, 1995; Gunn, 1995; Milner et al., 2003). Unfortunately, anthropogenic activities have significantly impacted the spawning habitat of anadromous salmonids (McPherson et al., 2023; Poesch, Chavarie, Chu, Pandit, & Tonn, 2016), resulting in degradation and fragmentation. Factors such as habitat degradation, hydroelectric dams, and overfishing have contributed to these impacts (Cowx & Welcomme, 1998; Whiteway, Biron, Zimmermann, Venter, & Grant, 2010; Zeug et al., 2014). To address these challenges and restore or enhance fisheries production, government agencies and non-profit organizations have dedicated substantial resources to the restoration of degraded spawning habitat. Efforts have included the installation or creation of artificial spawning habitat and the evaluation of different designs and approaches for rehabilitating anadromous salmonid populations

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(Murchie et al., 2008; Pulg, Vollset, & Lennox, 2019; Roni, Hanson, & Beechie, 2008). Various rivers and waterways along the Pacific coast of North America, as well as the Atlantic coast of North America and Europe, have seen the construction and assessment of artificial spawning habitat for anadromous salmonid species, including chinook salmon, steelhead trout, Atlantic salmon, and brown trout (Barlaup, Gabrielsen, Skoglund, & Wiers, 2008; Pedersen, Kristensen, Kronvang, & Thodsen, 2009; Whiteway et al., 2010). Overall, these efforts highlight the importance of addressing the impacts on spawning habitat and the implementation of restoration measures to support the sustainability of salmonid populations.

The Great Slave Lake fishery is home to adfluvial species such as lake trout, lake whitefish, and cisco. It heavily relies on the major tributaries surrounding the lake for essential flows, nutrients, and energy for food webs. These tributaries also serve as critical spawning and egg incubation locations for fall-spawning adfluvial salmonids (MacKenzie et al., 2021; Rawson, 1951; Stewart, 1997). Located at the outlet of Bluefish Lake on the Yellowknife River, approximately 18 km upstream from where the Yellowknife River meets Great Slave Lake, is the Bluefish Hydroelectric Facility (hereafter 'Bluefish') (KCB, 2017). In 2011, the Northwest Territories Power Corporation (NTPC) received a Fisheries Act Authorization (FAA) from Fisheries and Oceans Canada (DFO) for the construction of a new primary impoundment dam and spillway for the facility (Golder, 2019). The FAA mandated monitoring, including confirming the spawning of fall-spawning salmonid species (lake trout and coregonids), in the lower spillway of the historical Yellowknife River channel and downstream of Bluefish. Observations of spawning adults and fertilized eggs in the area provided direct evidence of adfluvial lake trout, lake whitefish, and cisco spawning in the Yellowknife River below Bluefish (Golder, 2019) (Figure 1).

The main goal of this study was to provide a comprehensive summary of the collected data on spawning activity at Bluefish and contribute to the limited existing research on adfluvial lake trout, lake whitefish, and cisco spawning behavior and habitat requirements, both for natural and artificially enhanced substrates in northern freshwater ecosystems.

STUDY AREA

The study area is located on the Yellowknife River, situated downstream of Bluefish Lake and upstream of Prosperous Lake, in the northern region of Yellowknife, Northwest Territories (refer to Figure 1). The Yellowknife River drainage area, just downstream of the study area at the entrance to Prosperous Lake, spans approximately 11,300 km^2 (ECCC, 2020). Further downstream, at the outlet where the Yellowknife River meets Great Slave Lake, the total drainage area expands to around 16,000 km^2 (Spence, 2001). The Yellowknife River basin falls within the sub-Arctic Canadian Shield physiographic region, specifically within the Taiga Shield Ecozone. This basin is characterized by shallow and exposed Precambrian bedrock, an open black spruce forest, and a multitude of lakes, with surface water covering approximately 25% of the basin area (Spence, 2001).

The study area encompasses the lower portion of the historic Yellowknife River channel, situated downstream of the Bluefish Lake Dam, which serves as a natural spillway for Bluefish. The construction of the Bluefish Lake Dam took place in 1940 at the Yellowknife River's outlet, primarily to facilitate storage for the G1 generating plant (KCB, 2017). Subsequently, in 1994, a second generating plant (G2) was constructed approximately 20 meters west of the G1 plant. In 2012, a new dam and spillway were built around 400 meters downstream from the original dam (KCB, 2017). The discharge of flow from the G1 and G2 plants occurs into the main Yellowknife River channel, situated 80 meters east of the spillway outlet, within a section known as the Tailrace Area (Golder, 2019). The Tailrace Area spans approximately 110 meters in width and exhibits depths reaching around 4 meters.

The spillway, which carries water not utilized by the generating plants, incorporates the historic Yellowknife River channel (Golder, 2019). Within this channel, the Instream Flow Gate was installed in 2012 to ensure minimum flows for fall-spawning fish, with a regulated minimum flow of 0.75 mˆ3/s. Prior to the installation of the gate, flow in the spillway was maintained through leakage from the old dam, spanning from 1942 to 2010 (Golder, 2019). The downstream section of the spillway, providing habitat for fall-spawning salmonids, is referred to as Reach 1. It is characterized by a natural waterfall at the upstream end and extends to the confluence with the Tailrace Area, where the flow enters the main Yellowknife River channel at the downstream end. Reach 1 measures 178 meters in length and exhibits water depths of up to 1.5 meters. The substrate composition is predominantly boulders and cobbles, with exposed bedrock areas interspersed (Golder, 2019). Adfluvial fall-spawning fish species, such as lake trout, lake whitefish, and cisco, migrate annually from either Prosperous Lake or Great Slave Lake to spawn in Reach 1 and the Tailrace Area (Golder, 2019; MacKenzie et al., 2021; Stewart, 1997).

METHODS

The study was conducted over a 4-year period, including Pre-Habitat Enhancement Construction Monitoring (2016), Habitat Enhancement Construction (2017 & 2018) and Post-Habitat Enhancement Construction (2017-2019) during the months of September through October. Annual monitoring of spawning fish abundance and distribution was conducted in the Yellowknife River below Bluefish as part of the regulatory requirements for Bluefish operations under the FAA for the new impoundment dam since 2013 (Golder, 2019). Spawning fish counts were made during six to eight snorkel surveys conducted from September to early November, timed to coincide with suitable temperatures for the spawning of lake trout, lake whitefish, and cisco (Scott & Crossman, 1998). During the surveys, one observer was in the water enumerating spawning, while a recorder on the shore documented the observations. It is important to note that surveys in 2019 began in early October, missing the peak arrival of lake trout, and therefore, the snorkel data for lake trout in that year are not included in the analysis.

To assist with the interpretation of trends across study years, we summarized supporting environmental data on daily water temperature and river flow discharge, from the Water Survey of Canada (WSC) hydrometric gauges in the Yellowknife River (ECCC, 2020). Daily discharge data were obtained from station no. 07SB003, located below the Tailrace Area (Figure 1), while daily water temperature data were obtained from station no. 07SB015 in Bluefish Lake, upstream of the dam. Historical "baselines" were defined on data collected from 1991 to 2020.

Pre-Habitat Enhancement Construction Monitoring (2016)

In 2016, the pre-habitat enhancement construction monitoring efforts focused on characterizing the spawning habitat and the use of different substrate types for egg incubation by adfluvial lake trout, lake whitefish, and cisco in the study area. Seven sampling events took place from September 15 to November 2, 2016, to coincide with the spawning phenology of the three species (Supplementary Information Photo 1). This timeframe corresponds to the period when water temperatures for spawning ranged from approximately 1°C to 14° C. Egg deposition areas were identified by conducting surveys while wading or floating across various hydraulic conditions and areas, including depths and velocities. The presence and relative abundance of eggs were determined through underwater snorkel observations of the substrate. The snorkeler gently agitated the substrate with their hand or foot to facilitate the detection of eggs. However, to avoid disturbing the egg incubation areas, some eggs embedded in the substrate may have been missed without thorough agitation. While lake trout eggs are noticeably larger in size, allowing them to be differentiated from coregonid eggs (cisco and lake whitefish), cisco and lake whitefish eggs could not be distinguished based on size alone. Therefore, the results of this study collectively refer to cisco and lake whitefish eggs as coregonid eggs.

A detailed assessment of habitat characteristics was conducted at specific locations where eggs were observed (14 egg plots) and where no eggs were observed (15 non-egg plots) in Reach 1 and the Tailrace Area (Figure 1). Within each egg and non-egg plot, habitat characteristics were evaluated within a 1 m^2 frame. To ensure representative sampling, survey plot locations were selected within the approximate spatial extent of the egg deposition area. First, locations where eggs were present were identified, and then additional plots were randomly positioned nearby without eggs. These non-egg plots were typically within a short throwing distance of the plot frame, landing within 2 to 8 m of the plots with eggs. During each survey plot, the following information was recorded: GPS coordinates to accurately locate the plot, total depth of the water column, midwater column velocity, and the proportion of different substrate types. Substrate type proportions were

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determined based on particle size diameter, with clay/silt defined as < 0.06 mm, sand as 0.06-2 mm, gravel as 2-63 mm, cobble as 64-256 mm, and boulder as > 256 mm (Figure 2A).

Initial snorkel surveys revealed significant mortality of eggs deposited in clumps on boulder and bedrock habitats in the study reach of the Yellowknife River. This was attributed to the absence of suitable interstitial spaces for egg development and the presence of a cotton-like white substance, likely caused by the water mold Saprolegnia sp (Univ. of Saskatchewan, 1996; Brown & Bruno, 2002; Van Den Berg et al., 2013). To mitigate the high egg mortality in the study reach, the construction of artificially enhanced spawning habitat was initiated. The design principles drew inspiration from habitat installation and rehabilitation projects for anadromous salmonids in rivers, as well as artificial spawning reefs constructed in lakes for lacustrine populations of lake trout and lake whitefish (Claramunt, Jonas, Fitzsimons, & Marsden, 2005; Eshenroder, Bronte, & Peck, 1995; Evans et al., 2002; Fitzsimons, 2014; Gatch et al., 2020). Three site-specific actions were considered: structural placement, gravel injection, and designed gravel placement (Bunte, 2004). A crucial aspect of the design was the inclusion of substrates that aligned with the documented spawning shoals of lacustrine lake trout and whitefish. These substrates provided interstitial spaces for egg anchorage and protection from predation and strong currents that could otherwise dislodge the eggs (Marsden et al., 2016; Marsden, Casselman, et al., 1995; Sly, 1988).

Habitat Enhancement Construction (2017 & 2018)

The design principles for the artificially enhanced spawning habitat combined parameters used for anadromous salmonid habitat installations with characteristics of rehabilitation projects in rivers and artificial spawning reefs constructed in lakes for lacustrine populations of lake trout and lake whitefish (Bronte, Schram, Selgeby, & Swanson, 2002; Fitzsimons, 1995; Manny, Edsall, Peck, Kennedy, & Frank, 1995; Mohr & Nalepa, 2005). Key design factors included substrates that matched documented lacustrine lake trout and coregonid spawning shoals, which incorporated interstitial spaces for egg protection (Claramunt et al., 2005; Gatch et al., 2020; Marsden et al., 2016; Marsden, Perkins, & Krueger, 1995; Sly, 1988). Design criteria encompassed a minimum spawning bed thickness of 0.3 m, substrate sizes ranging from approximately 5 to 30 cm, a preference for angular cobble and gravel to maximize interstitial spaces, and ensuring final spawning elevations remained ice-free during winter (at least 1.0 m depths during fall flow conditions).

In the summer of 2017, the first phase of the habitat enhancement project commenced, targeting a 40 m^2 area of moderately deep run habitat in lower Reach 1. The selected location predominantly consisted of bedrock with some patches of boulder, and the measured mean depth was 1.8 m prior to installation. The initial step involved adding a base layer of boulders sourced from the shoreline to provide stability and heterogeneity of cover for fish. The area was then filled with crushed gravel and cobble, which was thoroughly washed on the shoreline to remove fines before being transferred by boat to the spawning bed location. Upon completion of the first phase in 2017, the total surface area of bedrock covered by the placed substrate measured approximately 9 m^2 (see Supplementary Information Photo 2). The composition of the substrate on the completed spawning bed was visually estimated as 50% cobble, 35% gravel, and 15% boulder.

In the subsequent summer of 2018, using the same methods and materials, the area of the artificially enhanced spawning bed within Reach 1 was expanded approximately four times its original size. This expansion aimed to cover all exposed bedrock in the area, resulting in a total installed habitat area of 40 m^2 in the study reach (Figure 1).

Post-Habitat Enhancement Construction Monitoring (2017-2019)

After the installation of the spawning habitat enhancements, we conducted regular monitoring visits from 2017 to 2019 to assess habitat use by deploying randomly positioned plots in Reach 1 Natural (non-modified area) (52 plots), Reach 1 Enhanced (modified area) (97 plots), and the Tailrace Area (77 plots). Egg survival was determined based on the proportion of live eggs compared to the total, including dead or non-fertilized eggs, during the early stages of development. During the monitoring visits, we estimated egg density, calculated the egg survival index, and recorded habitat characteristics per randomly positioned plot. The same habitat characteristics used in 2016 were assessed in Reach 1 Natural, Reach 1 Enhanced, and within known

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egg deposition areas of the Tailrace Area. The surveys began in early September, and each reach was sampled with a minimum of 15 survey plots per year, except for 2019 when a tighter schedule led to the start of surveys in early October and only four survey plots were deployed in Reach 1 Natural. All surveys were completed by early November, just prior to freeze-up each year.

Statistical Analysis

We first present a descriptive statistical summary of the spawning fish count data for lake whitefish and cisco from 2016 to 2019, and for lake trout from 2016 to 2018, to provide a context for interpreting egg densities and survival rates pre- and post-habitat enhancement. For the habitat data, we calculated the mean proportion of substrate types, mean mid-water column velocity, and mean depth using the data collected in 2016. We compared the habitat characteristics between survey plots with eggs and those without eggs, as well as between survey plots in Reach 1 and the Tailrace Area. To determine distinguishable habitat features for plots with eggs, we conducted Analysis of Variance (ANOVA) and tested for statistical differences between the independent habitat factors and their interaction effect. Prior to the tests, the habitat data were transformed (square root of proportions and logarithm of depths and velocities) to meet the assumption that residuals are normally distributed. Using the egg data collected from 2017 to 2019, we calculated the means and standard errors (SEs) for egg densities per species. We tested the effect of habitat type (Reach 1 Natural, Reach 1 Enhanced, and Tailrace Area), year (2017, 2018, and 2019), and the interaction effect of habitat type and year on egg densities using a two-factor permutational ANOVA (Anderson, 2001). Permutational analysis of variance often provides more power in situations where independence of variance may be an issue and assessing multiple factors (Anderson, 2001). In cases where the interaction term was significant, post hoc tests were conducted for each study year and habitat type, with p-values adjusted using the Holm method to correct for multiple comparisons (Holm, 1979). Chi-squared tests were also performed to analyze the differences in the proportion of live eggs between habitat types and years, with p-values adjusted using the Holm method (Holm, 1979). Statistical significance was determined using an alpha level of 0.05. All statistical summaries and analyses were conducted in R.

RESULTS

During the period of September through October, the mean temperature at Bluefish Lake was 8.6°C, slightly below the long-term average of 8.8°C, which was calculated based on data recorded over a 30-year period from 1991 to 2020. Among the four study years, 2018 had the lowest mean fall temperature, measuring 6.1°C. On the other hand, 2017 had the highest mean fall temperature of 10.4°C. Both 2016 and 2019 had an average fall daily temperature of 9.0°C. The mean daily discharge was recorded as 21.5 m^3/s. It is worth noting that these flows were below the long-term average of 30.8 m^3/s, which was calculated based on the daily fall flows summarized over a 30-year period from 1991 to 2020. Among the four study years, 2016 had the lowest mean daily discharge, measuring 15.1 m^3/s. Subsequently, there was a gradual increase in mean daily discharge, with values of 18.1 m^3/s in 2017, 23.4 m^3/s in 2018, and 29.2 m^3/s in 2019.

Pre-Habitat Enhancement Construction Monitoring (2016)

Habitat characteristics for egg incubation indicated statistically significant differences in substrate composition, with a higher use of hard substrates observed at locations with eggs than without (Table I). We observed substantial variations in substrate composition in the Tailrace Area, where egg plots had a mean percentage of fines of 0.8% compared to non-egg plots with 77.5% fines (Figure 2A). Similarly, the mean percentage of gravel in the Tailrace Area was 58.3% in egg plots and 4.2% in non-egg plots (Figure 2A). Similar trends were observed in Reach 1, although the magnitude of the effect was less pronounced compared to the Tailrace Area, with an interacting effect of fines and study reach (Table I). Within Reach 1, the largest absolute difference in substrate composition was observed for cobble, with a mean percentage of 58.1% in egg plots compared to 37.8% in non-egg plots. The dominant habitat types differed between the two study reaches, with gravel cover (31%) and fines (39.2%) being more prevalent in the Tailrace Area, while boulder cover (37.9%) and cobble cover (34.5%) dominated in Reach 1 (Table I). Additionally, the survey data indicated that plots in the Tailrace Area were significantly deeper, with a mean depth of 0.74 m, compared to plots in

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Reach 1, which had a mean depth of 0.59 m (Table I).

Post-Habitat Enhancement Construction Monitoring (2017-2019)

Following the enhancement of riverbed substrate in Reach 1, we conducted surveys covering a total of 226 survey plots. These plots were distributed among three areas: Reach 1 Enhanced (n = 97), Reach 1 Natural (n = 52), and known spawning locations in the Tailrace Area (n = 77). In Reach 1 Enhanced, the substrate cover in the habitat enhancement area consisted of 69% gravel, 24% cobble, and 7% boulder (Figure 2B). In comparison, Reach 1 Natural had a higher proportion of cobble (41%), boulder (31%), and bedrock (12%) cover (Figure 3). When comparing Reach 1 Natural to the Tailrace Area, the substrate cover in Reach 1 Natural showed similar levels of cobble and boulder cover, but slightly more gravel and no fines. In the Tailrace Area's known spawning locations, the sampled area was primarily composed of gravel (61%) and cobble (24%), with smaller amounts of boulder (7%) and fines (6%) (Figure 3).

The maximum number of adult lake trout observed during a complete survey of Reach 1 and the Tailrace Area showed a steady increase over the years. In 2016, the maximum count was 42 fish, which rose to 54 fish in 2017 and further increased to 60 fish in 2018. In contrast to lake trout, the numbers of lake whitefish and cisco generally declined over time. The highest count of lake whitefish was observed in 2016, with a maximum of approximately 1,343 fish, slightly surpassing the maximum count of 1,000 fish recorded in 2017. In 2018, the maximum count of lake whitefish decreased to 411 fish, and in 2019 it further reduced to 683 fish. As for cisco, they were most abundant in 2017, with a maximum count of approximately 5,200 fish during one survey, slightly higher than the maximum count of 4,420 cisco recorded in 2016. However, the maximum count of cisco declined in the subsequent years. In 2018, the maximum count was 670 cisco, and in 2019 it dropped to 93 cisco during one survey. Overall, the snorkel surveys provided valuable data on the abundance of spawning schools of lake trout, lake whitefish, and cisco, showing different patterns of change over the years.

Overall lake trout egg densities were, on average, 50.9 eggs per m^2 ± 11.9 SE. Across study years, mean egg densities for Lake trout ranged from a high of 56.5 eggs per m^2in 2018 to a low of 42.8 eggs per m^2 in 2019. When pooling the data across three study years, the mean density of lake trout eggs was highest in Reach 1 Enhanced (68.5 eggs per m^2 ± 10.2 SE), followed by non-modified areas of Reach 1 (51.6 eggs per m^2 ± 11.9 SE) and the Tailrace Area (28.1 eggs per m^2 ± 6.2 SE) (Figure 3). Habitat type and year were not statistically significant for lake trout egg densities for the permutational ANOVA; however, the interaction of habitat type and year was statistically significant (Table II, Figure 3). Post hoc test of mean lake trout egg densities in Reach 1 Enhanced identified statistically significant differences between years, including higher densities in 2018 versus 2017, and in 2019 versus 2017. Lake trout egg densities in Reach 1 Enhanced were similar between 2019 and 2018. Densities in Reach 1 Natural and Tailrace Area were also similar between years. Post hoc tests of mean lake trout egg densities identified significant effects of habitat type during each study year (Table II). Lake trout egg density in Reach 1 Enhanced was statistically lower than the density in Reach 1 Natural during 2017, but higher than the density in the Tailrace Area during 2018 and 2019 (Figure 3). Pooling 2018 and 2019 data combined (n = 180 plots), mean egg density for lake trout was 2.4-times higher in Reach 1 Enhanced versus Reach 1 Natural, and 3.0-times higher in Reach 1 Enhanced versus Tailrace Area.

Overall, coregonid egg densities were, on average, 413.6 eggs per m^2 ± 38.9 SE. Across study years, mean egg density for coregonids was more variable than that recorded for lake trout with a high of 613.8 eggs per m^2 in 2018, 3.4-times greater than densities in 2017, and 3.5-times greater than densities in 2019. Similar to lake trout, the mean density of coregonid eggs was highest in Reach 1 Enhanced across habitat types when pooling data collected across study years (n = 226 plots): Reach 1 Enhanced = 725.7 eggs per m^2 (± 71.7 SE), Reach 1 Natural = 288.1 eggs per m^2 (± 57.5 SE), and Tailrace Area = 105.3 eggs per m^2 (± 21.2 SE). Overall mean egg density was 2.5-times greater in Reach 1 Enhanced versus Reach 1 Natural, and 7.0-times greater in Reach 1 Enhanced versus Tailrace Area. Habitat type and year were statistically significant for coregonid egg densities for the permutational ANOVA and the interaction of habitat type and year was also statistically significant (Table II, Figure 4). Post hoc tests of mean coregonid egg densities

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identified significantly higher densities in 2018, versus 2017 and 2019 for both the Tailrace Area and Reach 1 Enhanced (Figure 4). Mean coregonid egg densities in Reach 1 Natural were similar between study years. Post hoc tests of mean coregonid egg densities identified statistically significant effects of habitat type during 2018 and 2019, with non-significant effects in 2017 (Table II). In 2018, densities were significantly higher in Reach 1 Enhanced versus Reach 1 Natural and Tailrace Area, and were similar between Reach 1 Natural and Tailrace Area. In 2019, densities were significantly higher in Reach 1 Enhanced and Reach 1 Natural, versus the Tailrace Area, and were similar between Reach 1 Enhanced and Reach 1 Natural.

Total lake trout egg count across all plots was 191 eggs in 2017, 620 eggs in 2018, and 273 eggs in 2019. The annual range of the survival rate metric was 0.424 to 0.542, with the highest survival rate metric in 2019 (0.542 $\pm$ 0.03 SE), followed by 2017 (0.515 $\pm$ 0.02 SE), and 2018 (0.424 $\pm$ 0.03 SE). Annual trends for Lake Trout within a specific habitat type included a higher egg survival metric in Reach 1 Enhanced in 2019 versus 2018 (Chi-squared = 34.5, $p < 0.001$) (Figure 5). The egg survival metric for Reach 1 Natural was also statistically higher in 2018 versus 2017 (Chi-squared = 8.17, $p = 0.012$). Of note, relatively few lake trout eggs were recorded in Reach 1 Enhanced during 2017 (n = 8 eggs) and in Reach 1 Natural during 2019 (n = 4 eggs) to provide a reliable comparison with other years and habitat types. The egg survival metric for the Tailrace Area was statistically similar ($p > 0.05$) for comparisons of 2017 versus 2018, and 2017 versus 2019; however, the metric was statistically higher in 2018 versus 2019 in the Tailrace Area (Chi-squared = 6.91, $p = 0.026$) (Figure 5).

For the period from 2017 to 2019, egg count for lake trout was 626 eggs in Reach 1 Enhanced, followed by 242 eggs in non-modified Reach 1, and 216 eggs in Tailrace Area. When pooling the data across three study years, the proportion of surviving eggs within a plot as a metric for egg survival for lake trout was highest in Reach 1 Enhanced (0.558 $\pm$ 0.02 SE), followed by non-modified Reach 1 Natural (0.545 $\pm$ 0.03 SE), and Tailrace Area (0.31 $\pm$ 003 SE). Within years, the egg survival metric for lake trout was statistically similar between Reach 1 Natural and Tailrace Area during 2017 ($p > 0.05$). During 2018, the egg survival metric was higher in Reach 1 Natural versus Reach 1 Enhanced (Chi-squared = 7.96, $p = 0.014$), and higher in Reach 1 Natural versus Tailrace Area (Chi-squared = 8.07, $p = 0.014$), but was statistically similar between Reach 1 Enhanced and Tailrace Area ($p > 0.05$). In 2019, the egg survival metric was higher in Reach 1 Enhanced versus Tailrace Area (Chi-squared = 74.86, $p < 0.001$).

Total egg count for coregonids across all plots was 756 eggs in 2017, 6740 eggs in 2018, and 1121 eggs in 2019. The annual range of survival rate metric was 0.558 to 0.707, with the highest survival rate metric in 2019 (0.707 $\pm$ 0.01 SE), followed by 2017 (0.577 $\pm$ 0.02 SE), and 2018 (0.558 $\pm$ 0.01 SE). Annual trends for coregonids within a habitat type included year-over-year increases in the egg survival metric for Reach 1 Enhanced in 2018 versus 2017 (Chi-squared = 128.25, $p < 0.001$), and in 2019 versus 2018 (Chi-squared = 218.33, $p < 0.001$) (Figure 5). The egg survival metric was similar across years for Reach 1 Natural ($p > 0.05$). For the Tailrace Area, the egg survival metric was similar between 2017 and 2019 ($p > 0.05$) but was statistically higher in 2018 versus 2017 (Chi-squared = 32.99, $p < 0.001$) and in 2018 versus 2019 (Chi-squared = 145.42, $p < 0.001$).

For the period from 2017 to 2019, egg count for coregonids was 6478 eggs in Reach 1 Enhanced, followed by 1377 eggs in non-modified Reach 1, and 762 eggs in Tailrace Area. Based on all data collected across the three study years, the overall egg survival rate metric for coregonids was highest in the Tailrace Area (0.719 $\pm$ 0.02 SE), followed by Reach 1 Enhanced (0.611 $\pm$ 0.01 SE) and non-modified Reach 1 Natural (0.351 $\pm$ 0.01 SE). For 2017, the egg survival metric for coregonids was statistically similar between Reach 1 Natural and Tailrace Area ($p > 0.05$) and was higher in Reach 1 Enhanced versus Reach 1 Natural (Chi-squared = 211.28, $p < 0.001$), and Tailrace Area (Chi-squared = 42.36, $p < 0.001$). As observed in 2017, the egg survival metric was higher in Reach 1 Enhanced versus Reach 1 Natural during 2018 (Chi-squared = 142.66, $p < 0.001$) and 2019 (Chi-squared = 122.30, $p < 0.001$). The egg survival metric for coregonids in the Tailrace Area peaked in 2018, statistically higher than Reach 1 Enhanced (Chi-squared = 167.72, $p < 0.001$) and Reach 1 Natural (Chi-squared = 142.66, $p < 0.001$) for that study year. In 2019, the egg survival metric for the Tailrace Area was lower than Reach 1 Enhanced (Chi-squared = 169.95, $p < 0.001$), and statistically similar with that observed in Reach 1 Natural ($p > 0.05$).

DISCUSSION

The upper Yellowknife River in Northern Canada is a unique location for the application of a habitat enhancement project as it supports spawning adfluvial populations of lake trout, lake whitefish, and cisco. This study focused on the reach below the Bluefish facility, which provides suitable spawning substrates and regulated flows to sustain populations of lake trout and coregonids. The area is part of the Great Slave Lake ecosystem and has a history of unregulated harvests that lasted for several decades through the mid 20^{th} century (Evans et al., 2002; Golder, 2019; Stewart, 1997). The opportunity to monitor and research the spawning behavior and habitat requirements of adfluvial lake trout and coregonids in this study area was made possible by the long-term resilience of fish populations and the presence of important spawning areas near an active hydroelectric facility. The regulatory requirement to study fisheries in proximity to the facility and offset any adverse impacts also contributed to the research efforts. The field sampling conducted for this study, as well as the installation of artificially constructed spawning habitat, were carried out to comply with federal and territorial environmental legislation. The accessibility of the study site, in comparison to other remote locations in Northern Canada where adfluvial lake trout and coregonids may be found, facilitated the research and monitoring activities.

A robust dataset on egg incubation densities and survival were provided by the 226 egg survey plots that were sampled within the gravel augmented Reach 1 Enhanced area, Reach 1 Natural, and known spawning locations for the Tailrace Area. Key findings were observations of overall higher densities of coregonid eggs (> 2x) on the installed spawning habitat in the Reach 1 in comparison to other naturally occurring spawning habitats below the facility, with statistically significant effects in 2018. Lake Trout egg density was trending higher in the installed habitat in comparison to other naturally occurring spawning habitats below the facility in 2018 and 2019, with annual year over year increases in mean egg densities.

Although the methods and scope of this study did not look to evaluate the specific mechanisms that resulted in the increase in egg density, only to document and analyze densities of eggs and survivability across different natural and enhanced habitats, we can make some conjecture based on our data and previous studies. Lake trout, lake whitefish and cisco are lithophilic broadcast spawners, as they do not create a nest but deposit fertilized eggs over suitable substrates which drift and settle into the interstitial spaces within those substrates (Bégout Anras, Cooley, Bodaly, Anras, & Fudge, 1999; Evans et al., 2002; Richardson et al., 2001; Roberge et al., 2002). Prior to the installation of the artificially enhanced habitat, existing conditions in Reach 1 were largely dominated by boulder and bedrock, where there was no anchorage and a lack of suitable interstitial spaces for egg development (Golder, 2019). Two potential mechanisms that likely interacted to result in the increase in egg densities are habitat selection and the suitability of the installed substrate to hold eggs. An increase in egg density due to habitat selection would occur through the fish actively seeking out the best spawning habitats and substrates, which based on the egg density results, is the installed habitat, and spawning directly in or above these locations. An increase in egg density due to the suitability of the installed substrate to hold eggs would occur when the fish continue to spawn where they have always historically spawned but the newly installed substrates, of gravel and cobble, have more interstitial spaces and are better at holding eggs in place therefor increasing egg densities. Given the broadcast spawning nature of these three species and the associated variability further study would be required to define precisely which mechanism was the driving force behind the increase in egg density. Further study into the mechanisms behind the increases in egg density would contribute to the body of knowledge for spawning site selection for these species for which there are still many unknowns (Bégout Anras et al., 1999; Evans et al., 2002; Sawatzky et al., 2007; Stewart, 1997).

The two potential mechanisms may also explain why the response to the installed habitat for egg densities for both lake trout and coregonids was delayed, specifically why the 2017 results showed no obvious increase in density on the installed habitat. The first year post-installation in 2017 included a relatively small area of only 9 m^2, and that area increased to 40 $m^2$the following year. As such, the smaller area of installed habitat in 2017 in comparison to 2018 and 2019 may have had an impact on the delayed response in egg

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densities for both lake trout and coregonids. Possible explanations include that the small area was inefficient at capturing and holder drifting eggs from nearby spawning fish or failed to elicit a habitat selection response by spawning fish. Related to the latter mechanism, the new rock installed within the study reach in 2017 may have altered environmental and olfactory cues for spawning, deterring fish that arrived later that fall to spawn. Environmental and olfactory cues can be important factors in the choice of spawning location (Bett & Hinch, 2016; Keefer & Caudill, 2014), and such cues were potentially adequate or better during 2018 and 2019, particularly for Lake Trout. The potential preference for the artificially enhanced spawning habitat, and use of augmented substrates for egg incubation in the Reach 1 Enhanced steadily increased year over year while the preference for the natural spawning habitat, and use of natural substrates for egg incubation in Reach 1 Natural, decreased over time. Although the mean egg density statistic for coregonids was variable across years, coregonids may have spawned in higher numbers over the enhanced spawning habitat, compared to surrounding natural substrate during the second and potentially third year of post-installation monitoring, suggesting that spawning cues were also adequate for spawning fish.

The installed habitat had mixed results on the survival rate of developing embryos, with no obvious benefit for lake trout. However, lake trout egg survival rates in R1 Enhanced did trend higher over time. Furthermore, overall numbers of lake trout eggs were lower than coregonid eggs with an average egg plot density of $51/m^2$ for lake trout eggs and $414/m^2$for coregonids across all egg survey plots, and as such, the lower amount of eggs for lake trout may have precluded a fulsome study of survivability of eggs. Importantly, the survival rate metic of coregonid eggs was statistically higher on the installed habitat each year of post-installation monitoring in comparison to the natural substrates in Reach 1 Natural. Overall, the proportion of live coregonid eggs was 1.7-times higher on enhanced substrate versus natural substrate in Reach 1. The consistent results across year and overall magnitude of effects suggests that the artificially installed substrates were effective at providing better interstitial spaces and protection for the eggs to survive than that of the naturally occurring substrates in the Reach 1 area. Of note, the proportion of live coregonids eggs on the installed habitat dipped during 2018 when coregonid egg densities were highest. Therefore, it is possible that the benefits of the augmented spawning substrate in mitigating the effects of overcrowding on survival were reduced when densities of eggs were highest. It is also possible that the cooler water temperatures in 2018 may have also limited the spread of the water mould such that the benefit of the augment substrate for improving survival was limited under cooler temperatures.

The results of this study suggest that the enhanced habitat installed in the Reach 1 area of the Yellowknife River employed successful design principles and that the installation methods have the potential to increase recruitment and ultimately benefit the overall population abundance for adfluvial coregonids, and possible lake trout). The results of our study are also generally consistent with other studies on lacustrine lake trout and whitefish and anadromous salmonines spawning habitat where gravel and cobble substrates are more productive for egg incubation than fine substrates as the gravel and cobble provide sufficient interstitial spaces for egg survival (Barlaup et al., 2008; Bégout Anras et al., 1999; Evans et al., 2002; Pedersen et al., 2009). Given the previous characterizations for the importance of interstitial spaces for lacustrine fish eggs for protection from predation, water flow, currents and wave action (Gatch et al., 2020; Marsden et al., 2016; Marsden, Casselman, et al., 1995; Sly, 1988), the egg density results from 2016 and the mass mortality of deposits of eggs in clumps on the unsuitable bedrock and boulder substrates throughout Reach 1 before the habitat installation (Golder, 2019) a key factor in the design was ensuring a proper substrate composition of the installed habitat and integration of pre-installation data on substrate in 2016.

Indeed, the substrate composition for the installed habitat was very close to the design parameters (i.e., 70% gravel, 25% cobble, and 5% boulder), with the mean substrate composition recorded through egg survey plots in the Reach 1 Enhanced area being 69% gravel, 24% cobble and 7% boulder (Figure 3). The substrate composition for the installed habitat was also very similar to the substrate composition for egg plots at known spawning locations in the Tailrace Area where the mean substrate was 62% gravel, 24% cobble, 6% fines and 7% boulder. This design may have been critical in providing suitable interstitial spaces for egg development to avoid the effects of overcrowding and transmission of pathogenic water moulds (e.g., *Saprolegnia* spp.) (Brown & Bruno, 2002). The results and findings of this study works towards filling the gap in published data

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for spawning behavior and habitat characteristics for adfluvial lake trout, lake whitefish and cisco populations and can be used by fisheries managers to identify spawning habitat locations in other river systems across the northern portion of the ranges for these three species where adfluvial life history types are more common (Evans et al., 2002).

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Table I. Analysis of variance (ANOVA) results for mean differences in habitat variables between Reach 1 and Tailrace Area and for sampling locations with eggs versus without eggs (lake trout and coregonid species) in the Yellowknife River, fall 2016.

One-Way ANOVA	**Factor**$^{+}$	**F**	p-value
Boulder	Reach	9.73	**0.0044**
	Egg presence	0.26	0.6129
Cobble	Reach	11.29	**0.0024**
	Egg presence	3.89	0.0592
Gravel	Reach	9.96	**0.0040**
	Egg presence	7.04	**0.0134**
Fines	Reach	71.38	**<0.0001**
	Egg presence	100.51	**<0.0001**
	Reach *x* Egg	68	**<0.0001**
Depth	Reach	5.57	**0.0260**
	Egg presence	0.39	0.5355
Velocity	Reach	0.04	0.8402
	Egg presence	3.81	0.0617

$^{+}$degrees of freedom for F = 1, 26 (or 1, 25 for model with interaction); interaction term removed if non-significant; bold values are statistically significant.

Table II. Permutational analysis of variance results for differences in egg densities across habitat types: Reach 1 (R1) Natural, R1 Enhanced, and known spawning locations in the Tailrace Area, 2017-2019.

Analysis of Variance			Lake Trout	Lake Trout	Coregonid	Coregonid	Coregonid	
Model	Factor	Df	F	*p-value* [(a)]	*p-value* [(a)]	F	*p-value* [(a)]	*p-valu*
Full Model	Year	2, 217	0.09	1	1	7.02	**0.002**	**0.002**
	Habitat Type	2, 217	1.65	0.194	0.194	11.80	**<0.001**	**<0.00**
	Year *x* Habitat	4, 217	3.76	**0.009**	**0.009**	2.79	**0.028**	**0.028**
Post-Hoc Tests [(a)]								
Tailrace (Tail)	2017 vs. 2018	1, 37	0.33	1	1	5.30	**0.048**	**0.048**
	2017 vs. 2019	1, 47	0.18	1	1	0.14	0.687	0.687
	2018 vs. 2019	1, 64	0.05	1	1	16.33	**<0.001**	**<0.00**
R1 Natural (R1N)	2017 vs. 2018	1, 46	3.25	0.231	0.231	0.56	1	1
	2017 vs. 2019	1, 22	1.56	0.414	0.414	0.52	1	1

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Analysis of Variance			Lake Trout	Lake Trout	Coregonid	Coregonid	Coregonid	
	2018 vs. 2019	1, 30	0.80	0.414	0.414	0.03	1	1
R1 Enhanced (R1E)	2017 vs. 2018	1, 79	7.16	**0.017**	**0.017**	11.56	**0.003**	**0.003**
	2017 vs. 2019	1, 29	7.63	**0.006**	**0.006**	1.78	0.208	0.208
	2018 vs. 2019	1, 80	0.07	0.789	0.789	5.67	**0.042**	**0.042**
2017	Tail vs. R1N	1, 29	1.43	0.260	0.260	2.97	0.268	0.268
	Tail vs. R1E	1, 24	2.79	0.231	0.231	2.27	0.268	0.268
	R1N vs. R1E	1, 33	6.51	**0.015**	**0.015**	<0.01	0.956	0.956
2018	Tail vs. R1N	1, 54	6.51	0.467	0.467	0.99	0.338	0.338
	Tail vs. R1E	1, 92	6.70	**0.033**	**0.033**	23.02	**<0.001**	**<0.00**
	R1N vs. R1E	1, 92	4.04	0.106	0.106	14.96	**<0.001**	**<0.00**
2019	Tail vs. R1N	1, 40	0.46	0.651	0.651	83.36	**<0.001**	**<0.00**
	Tail vs. R1E	1, 52	6.65	**0.032**	**0.032**	28.23	<**0.001**	<**0.00**
	R1N vs. R1E	1, 18	1.83	0.336	0.336	0.89	0.689	0.689

[(a)] P-values adjusted for post-hoc tests using the Holm method; bold values indicate statistical significance.

Figure Legends

Figure 1 - Reach 1 in the lower spillway of the historical reach of the Yellowknife River, installed spawning beds, Tailrace Area below Bluefish and regional location for the study area.

Figure 2 - (A) Mean substrate composition for survey plots with eggs versus without eggs in non-modified Reach 1 and Tailrace Area, surveyed fall 2016 before any enhanced habitat was installed. (B) Mean substrate composition for survey plots in non-modified Reach 1 Natural, Reach 1 Enhanced, and known spawning locations of the Tailrace Area (2016-2019).

Figure 3 - Mean egg densities per m^2 (with confidence intervals) in survey plots for lake trout (upper panel) and coregonids (lower panel) in Reach 1 Natural, Reach 1 Enhanced, and known spawning location of the Tailrace Area (2017-19).

Figure 4 - Proportion of live eggs in all survey plots combined for lake trout (upper panel) and coregonids (lower panel) in Reach 1 Natural, Reach 1 Enhanced, and known spawning locations of the Tailrace Area (2017-1019).

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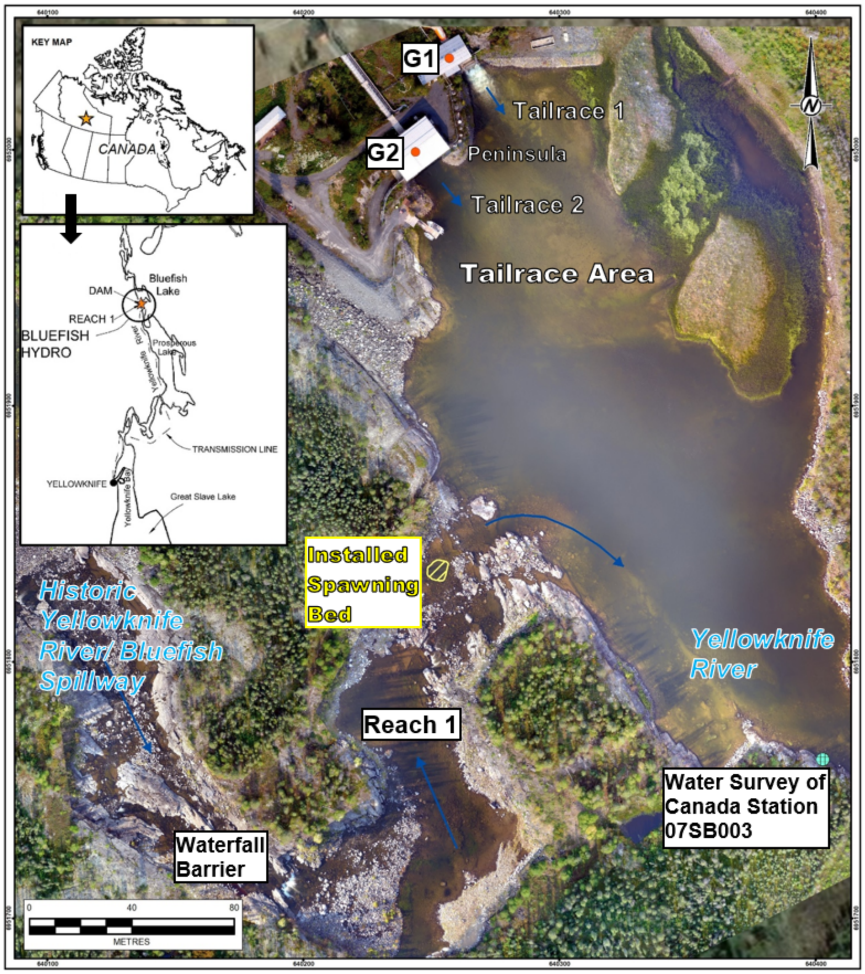

Figure 1.

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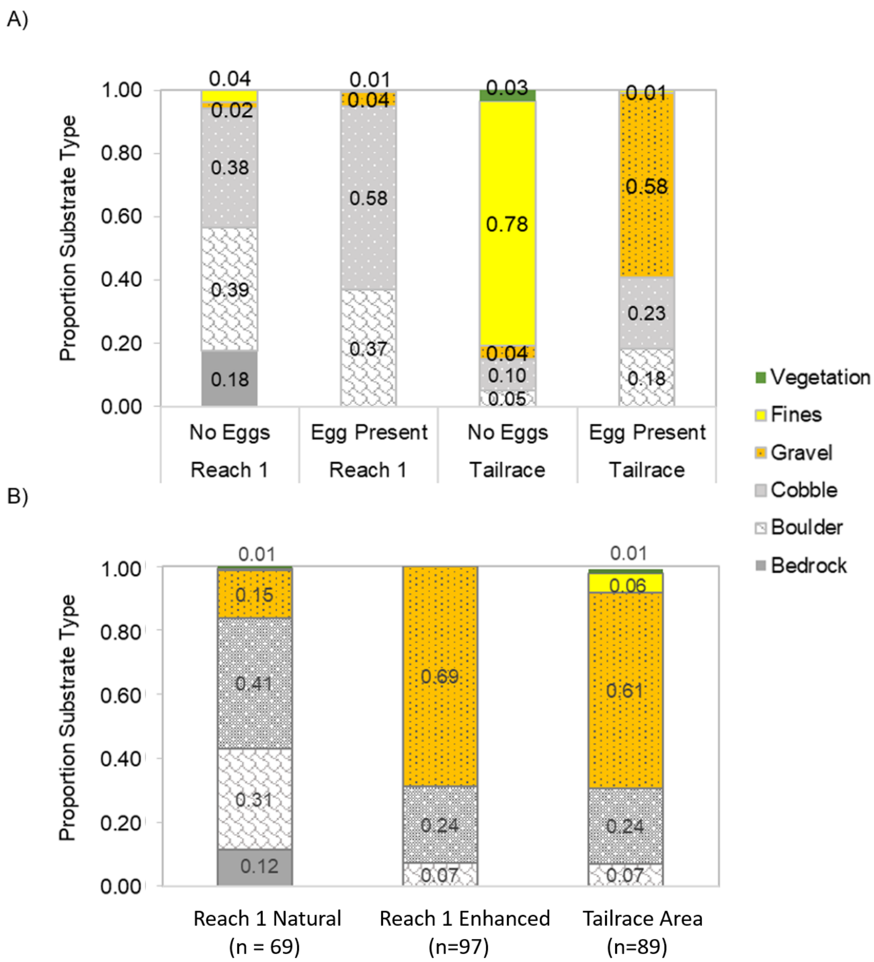
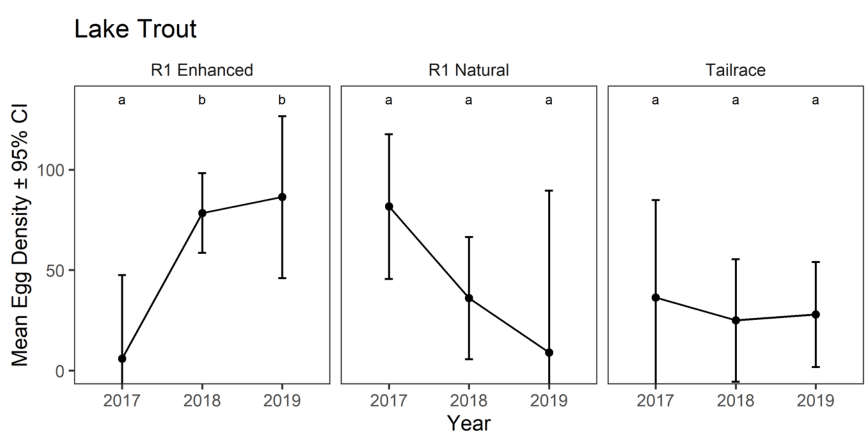


Figure 2.



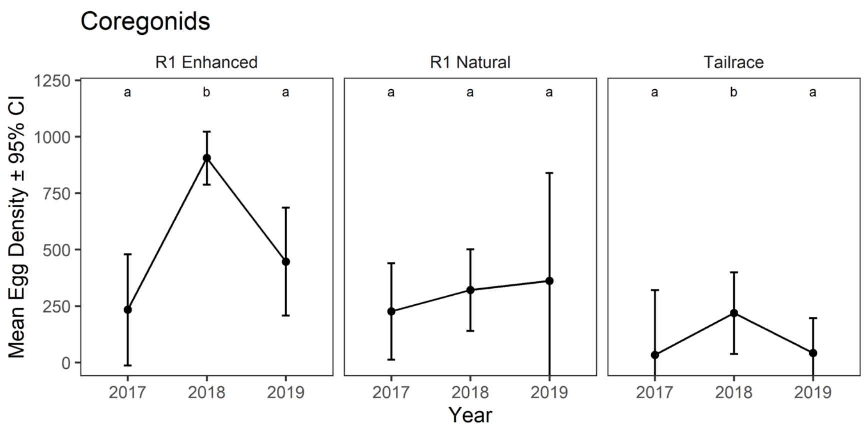


Figure 3.

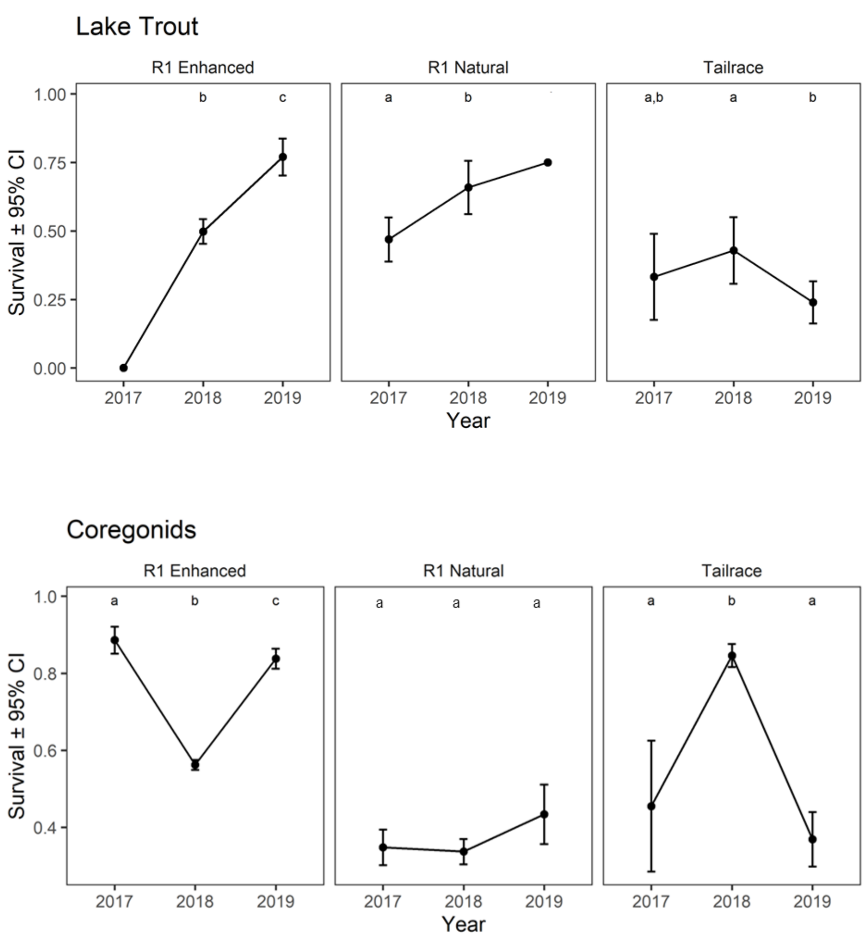


Figure 4.

REFERENCES

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Anderson, M. J. (2001). Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences, 58* (3), 626-639.

Barlaup, B. T., Gabrielsen, S. E., Skoglund, H., & Wiers, T. (2008). Addition of spawning gravel - a means to restore spawning habitat of atlantic salmon (Salmo salar L.), and anadromous and resident brown trout (Salmo trutta L.) in regulated rivers. *River Research and Applications, 24* , 543-550.

Bégout Anras, M. L., Cooley, P. M., Bodaly, R. A., Anras, L., & Fudge, R. J. P. (1999). Movement and habitat use by lake whitefish during spawning in a boreal lake: integrating acoustic telemetry and geographic information systems. *Transactions of the American Fisheries Society, 128* , 939-952.

Bett, N. N., & Hinch, S. G. (2016). Olfactory navigation during spawning migrations: a review and introduction of the Hierarchical Navigation Hypothesis. *Biological Reviews, 91* , 728-759.

Bronte, C., Schram, S., Selgeby, J., & Swanson, B. (2002). Reestablishing a spawning population of Lake Trout in Lake Superior with fertilized eggs in artificial turf incubators. *North American Journal of Fisheries Management, 22* , 796-805.

Brown, L. L., & Bruno, D. W. (2002). Infectious diseases of coldwater fish in fresh water. In *Diseases and disorders of finfish in cage culture* (pp. 107-169). Wallingford, UK: CAB International.

Bunte, K. (2004). *State of the science review gravel mitigation and augmentation below hydroelectric dams: A geomorphological perspective* . Retrieved from US Department of Agriculture, Forest Service, Rocky Mountain Research Station. Report submitted to the Stream Systems Technology Center, Fort Collins, CO.:

Callaghan, D., Blanchfield, P., & Cott, P. (2016). Lake trout (Salvelinus namaycush) spawning habitat in a northern lake: The role of wind and physical characteristics on habitat quality. *Journal of Great Lakes Research, 42* , 299-307.

Claramunt, R. M., Jonas, J. L., Fitzsimons, J. D., & Marsden, J. E. (2005). Influences of spawning habitat characteristics and interstitial predators on lake trout egg deposition and mortality. *Transactions of the American Fisheries Society, 134* , 1048-1057.

Cowx, I. G., & Welcomme, R. L. (1998). *Rehabilitation of rivers for fish: a study undertaken by the European Inland Fisheries Advisory Commission of FAO* . Retrieved from

DCCEEW. (2012). Department of Climate Change, Energy, the Environment and Water (DCCEEW). (2012). EPBC Act environmental offsets policy. Available at: https://www.dcceew.gov.au/environment/.

DFO. (2019). Measures to protect fish and fish habitat. Available at: https://www.dfo-mpo.gc.ca/pnw-ppe/measures-mesures-eng.html.

ECCC. (2020). Environment and Climate Change Canada. Station Information, Real-Time and Historic Data for Station 07SB003 and Station 07SB015. Available at: http://wateroffice.ec.gc.ca/.

Eshenroder, R. L., Bronte, C. R., & Peck, J. W. (1995). Comparison of lake trout-egg survival at inshore and offshore and shallow-water and deepwater sites in Lake Superior. *Journal of Great Lakes Research, 21* , 313-322.

Evans, C. E., Reist, J. D., & Minns, C. K. (2002). *Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on riverine habitat requirements* . Retrieved from Ottawa, Canada:

Favaro, B., & Olszynski, M. (2017). Authorized net losses of fish habitat demonstrate need for improved habitat protection in Canada.*Canadian Journal of Fisheries and Aquatic Sciences, 74* (3), 285-291.

Fischer, J. L., Pritt, J. J., Roseman, E. F., Prichard, C. G., Craig, J. M., Kennedy, G. W., & Manny, B. A. (2018). Lake sturgeon, lake whitefish, and walleye egg deposition patterns with response to fish spawning

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substrate restoration in the St. Clair-Detroit River system. *Transactions of the American Fisheries Society, 147* , 79-93.

Fitzsimons, J. D. (1995). Assessment of lake trout spawning habitat and egg deposition and survival in Lake Ontario. *Journal of Great Lakes Research, 21* , 337-347.

Fitzsimons, J. D. (2014). *Assessment of measures to assess compensation and mitigation as related to the creation, rehabilitation, or restoration of spawning habitat for fluvial or lacustrine spawning salmonines* . Retrieved from Ottawa, Canada:

Gatch, A., Höök, T., Roseman, E., & Koenigbauer, S. (2020). Assessment of two techniques for remediation of lacustrine rocky reef spawning habitat. *North American Journal of Fisheries Management, 41* , 484-497.

George, E. M. (2019). The history and ecology of cisco Coregonus artedi in the Laurentian Great Lakes. *Aquatic Ecosystem Health and Management, 22* , 280-293.

Golder. (2019). *Bluefish Hydroelectric Plant 2018 fisheries and flow monitoring report* . Retrieved from

Gunn, J. M. (1995). Spawning behavior of lake trout: effects on colonization ability. *Journal of Great Lakes Research, 21* , 323-329.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics, 6* (2), 65-70.

Jones, N. E., Parna, M., Parna, S., & Chong, S. (2018). Evidence of lake trout (Salvelinus namaycush) spawning and spawning habitat use in the Dog River, Lake Superior. *Journal of Great Lakes Research, 44* , 1117-1122.

KCB. (2017). *Klohn Crippen Berger Ltd - Northwest Territories Power Corporation – Bluefish Dam: operations, maintenance, and surveillance (OMS) manual* .

Keefer, M. L., & Caudill, C. C. (2014). Homing and straying by anadromous salmonids: a review of mechanisms and rates. *Reviews in Fish Biology and Fisheries, 24* , 333-368.

MacKenzie, C. J. A., Fortin, B. L., & E., S. C. (2021). *Summary of ecological information relevant to Great Slave Lake fisheries* . Retrieved from Ottawa, Canada:

Manny, B. A., Edsall, T. A., Peck, J. W., Kennedy, G. W., & Frank, A. M. (1995). Survival of lake trout eggs on reputed spawning grounds in Lakes Huron and Superior: in situ incubation, 1987–1988. *Journal of Great Lakes Research, 21* , 302-312.

Marsden, J. E., Binder, T. R., Johnson, J., He, J., Dingledine, N., Adams, J., . . . Krueger, C. C. (2016). Five-year evaluation of habitat remediation in Thunder Bay, Lake Huron: comparison of constructed reef characteristics that attract spawning lake trout. *Fisheries Research, 183* , 275-286.

Marsden, J. E., Casselman, J. M., Edsall, T. A., Elliott, R. F., Fitzsimons, J. D., Horns, W. H., . . . Swanson, B. L. (1995). Lake trout spawning habitat in the Great Lakes — a review of current knowledge. *Journal of Great Lakes Research, 21* , 487-497.

Marsden, J. E., Perkins, D. L., & Krueger, C. (1995). Recognition of spawning areas by lake trout: deposition and survival of eggs on small, man-made rock piles. *Journal of Great Lakes Research, 21* , 330-336.

McAughey, S. C., & Gunn, J. M. (1995). The behavioral response of lake trout to a loss of traditional spawning sites. *Journal of Great Lakes Research, 21* , 375-383.

McPherson, M., Cott, P. B., Lewis, J. B., Swanson, H. K., & Poesch, M. S. (2023). Habitat use by fluvial Arctic Grayling (Thymallus arcticus) across life stages in northern mountain streams. *Environmental Biology of Fishes, 106* , 1001-1020.

Milner, N. J., Elliott, J. M., Armstrong, J. D., Gardiner, R., Welton, J. S., & Ladle, M. (2003). The natural control of salmon and trout populations in streams. *Fisheries Research, 62* , 111-125.

Mohr, L. C., & Nalepa, T. F. (2005). Proceedings of a workshop on the dynamics of lake whitefish (Coregonus clupeaformis) and the amphipod Diporeia spp. in the Great Lakes. *Great Lakes Fisheries Commission Technical Report, 66* .

Murchie, K., Hair, K., Pullen, C., Redpath, T., Stephens, H., & Cooke, S. (2008). Fish response to modified flow regimes in regulated rivers: research methods, effects and opportunities. *River Research and Applications, 24* , 197-217.

Pedersen, M. L., Kristensen, E., Kronvang, B., & Thodsen, H. (2009). Ecological effects of re-introduction of salmonid spawning gravel in lowland Danish streams. *River Research and Applications, 25* , 626-638.

Poesch, M. S., Chavarie, L., Chu, C., Pandit, S. N., & Tonn, W. (2016). Climate change impacts on freshwater fishes: A Canadian perspective.*Fisheries, 41* (7), 385-391.

Pulg, U., Vollset, K., & Lennox, R. (2019). Linking habitat to density-dependent population regulation: How spawning gravel availability effects abundance of juvenile salmonids (Salmo trutta and Salmo salar) in small streams. *Hydrobiologia, 841* , 13-29.

Rawson, D. S. (1951). Studies of the fish of Great Slave Lake.*Journal of Fisheries Research Board of Canada, 8* , 207-240.

Richardson, E. S., Reist, J. D., & Minns, C. K. (2001). *Life history characteristics of freshwater fishes occurring in the Northwest Territories and Nunavut, with major emphasis on lake habitat requirements* . Retrieved from Ottawa, Canada:

Roberge, M., Hume, J. M. B., Minns, C. K., & Slaney, T. (2002).*Life history characteristics of freshwater fishes occurring in British Columbia and the Yukon, with major emphasis on stream habitat characteristics* . Retrieved from Ottawa, Canada:

Roni, P., Hanson, K., & Beechie, T. (2008). Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North American Journal of Fisheries Management, 28* , 856-890.

Sawatzky, C. D., Michalak, D., Reist, J. D., Carmichael, T. J., Mandrak, N. E., & Hunting, L. G. (2007). *Distributions of freshwater and anadromous fishes from the mainland Northwest Territories, Canada* . Retrieved from Ottawa, Canada:

Scott, W. B., & Crossman, E. J. (1998). *The freshwater fishes of Canada* . Oakville, Canada: Galt House Publications Ltd.

Selgeby, J. H., Bronte, C. R., Brown Jr, E. H., Hansen, M. J., Holey, M. E., VanAmberg, J. P., . . . Ferreri, C. P. (1995). Lake trout restoration in the Great Lakes: stock-size criteria for natural reproduction. *Journal of Fisheries Research Board of Canada, 21* , 498-504.

Sly, P. G. (1988). Interstitial water quality of lake trout spawning habitat. *Journal of Great Lakes Research, 14* , 301-315.

Spence, C. (2001, 18 to 27 July 2001). *Sub-grid runoff processes and hydrological. In soil-vegetation-atmosphere transfer schemes and large-scale hydrological models.* Paper presented at the Proceedings of an International Symposium (Symposium S5) Held During the Sixth Scientific Assembly of the International Association of Hydrological Sciences (IAHS) Maastricht, The Netherlands.

Stewart, D. B. (1997). *A review of the status and harvests of fish stocks in the North Slave area, Northwest Territories* . Retrieved from Ottawa, Canada:

Theis, S., Ruppert, J. L. W., & Poesch, M. S. (2023). Coarse woody habitat use and structural integrity of enhancements over time in a shallow northern boreal lake assessed in a Bayesian modeling approach.*Ecological*

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Solutions and Evidence, 4 (2), e12200.

Theis, S., Ruppert, J. L. W., Shirton, J., & Poesch, M. S. (2022). Measuring beta diversity components and beneficial effects of coarse woody habitat introduction on invertebrate and macrophyte communities in a shallow northern boreal lake: implications for offsetting. *Aquatic Ecology, 56* , 793-814.

Whiteway, S., Biron, P., Zimmermann, A., Venter, O., & Grant, J. (2010). Do in-stream restoration structures enhance salmonid abundance? A meta-analysis. *Canadian Journal of Fisheries and Aquatic Sciences, 67* , 831-841.

Zeug, S., Sellheim, K., Watry, C., Rook, B., Hannon, J., Zimmerman, J., . . . Merz, J. (2014). Gravel augmentation increases spawning utilization by anadromous salmonids: A case study from California, USA. *River Research and Applications, 30* , 707-718.

zu Ermgassen, S. O., Baker, J., Griffiths, R. A., Strange, N., Struebig, M. J., & Bull, J. W. (2019). The ecological outcomes of biodiversity offsets under "no net loss" policies: A global review. *Conservation Letters, 12* (6), e12664.

Supporting Information

Photo 1. Lake whitefish staging for spawning in Reach 1 photographed during snorkel surveys in 2016.

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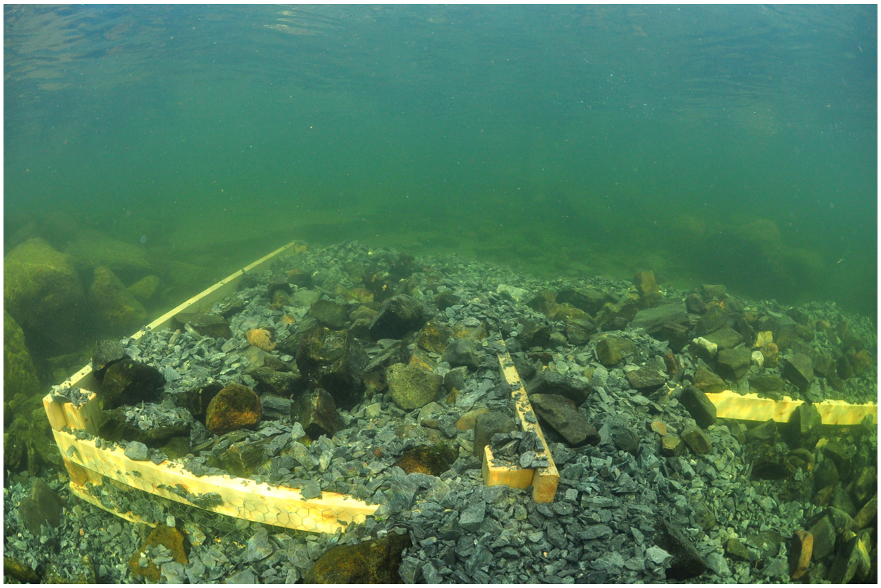

Photo 2. The installed spawning bed in Reach 1 after the completion of the first phase of installations in 2017.