An Investigation of Lake Whitefish Recruitment, Spawning, and Early Life History in Northern Maine: Final Report

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SUMMARY

Many of Maine's Lake Whitefish (*Coregonus clupeaformis*) populations have experienced significant declines, including local extirpations following the establishment of invasive Rainbow Smelt (*Osmerus mordax*). Several lakes within the Allagash River watershed are considered the last remaining stronghold of northern Maine Lake Whitefish, however, whitefish in many of these waters are at historically low numbers since smelt establishment. Recruitment failure appears to occur at early life stages among Lake Whitefish populations and is likely tied to high smelt densities. Spawning habitat quality and abundance, predation by smelt on larval whitefish, and food availability for juvenile whitefish have been identified as factors important to early Lake Whitefish survival (Fudge and Bodaly 1984, Taylor and Freeberg 1984, Loftus and Hulsman 1986). The objective of this research was to investigate Lake Whitefish spawning habitat use and availability, larval whitefish abundance, food availability for post hatch larval whitefish, predation of larval whitefish by smelt, and collect sagittal otoliths to assess the age structure and recruitment of Lake Whitefish populations in northern Maine. We conducted spawning ground surveys on six Lake Whitefish waters to investigate spawning habitat availability, used artificial egg collection mats to document the use of previously identified spawning habitat, tracked Lake Whitefish via radio telemetry during the spawning season in one study lake, conducted larval trawls to monitor post hatch larval whitefish and zooplankton assemblages in the spring, collected smelt via gillnets during the spring to assess their stomach contents for larval fish remains, and collected sagittal otoliths via gillnetting and creel census to assess the age structure of northern Maine Lake Whitefish populations.

Habitat mapping revealed that spawning habitat abundance and quality varied widely among study waters. Through our egg mat study, we identified three Lake Whitefish spawning locations in two study lakes and two Round Whitefish (*Prosopium cylindraceum*) spawning locations in a third lake. Lake Whitefish in northern Maine spawned during early November when water temperatures dropped below 6°C and continued to spawn as water temperatures approached freezing. Lake Whitefish used clean well layered cobble in both tributary streams and on windswept rocky shoals. Our findings suggest that the availability of spawning habitat and use of different spawning life history strategies may be factors affecting recruitment success.

Lake Whitefish were tracked via radio telemetry in Ross Lake in early November 2019. Peak in-shore movements occurred between November 4 and November 6, 2019 when water temperatures were 6-7°C. Radio tagged Lake Whitefish movements towards previously identified shoals through habitat mapping suggest whitefish used at least three different spawning sites within Ross Lake, though more work is needed to characterize the level of spawning use on these shoals. Ross Lake may be one example of a lake where abundant spawning habitat has positively influenced Lake Whitefish recruitment.

Six lakes were trawled during early spring for larval whitefish and larval smelt from 2015-2020. Larval whitefish were captured in trawl tows in five of these lakes, confirming egg survival to hatch providing evidence of successfully spawning Lake Whitefish in waters where it was not identified through egg mat surveys. Larval whitefish and smelt abundances varied among waters and years. High larval whitefish abundances were observed when larval smelt

abundances were low; conversely, high larval smelt abundances corresponded to low or in some instances absent larval whitefish. Given larval smelt hatch later than larval whitefish and at a much smaller size, competition between the two species at the larval stage is not believed to influence observed patterns in larval fish abundances. We suspect larval fish numbers are early indications of what biological conditions are like for these two species and may provide insight into whitefish recruitment failure particularly during years of high larval smelt densities and low larval whitefish densities.

Zooplankton densities varied widely among study waters and was likely related to variations in abiotic and biotic factors specific to these lakes. In addition, there was a clear distinction in the type of zooplankton present in these lakes. Cyclopoid copepods, a food resource critical to early Lake Whitefish survival (Teska and Behmer 1981; Freeberg et al. 1990; Chouinard and Bernatchez 1998; Johnson et al 2009), appeared to be absent in lakes where low/absent larval whitefish densities were observed. We suspect that limitations on larval whitefish food resources is tied to smelt interactions and may explain Lake Whitefish recruitment failure observed in study lakes.

A small sample of smelt (n=126) was obtained through intensive gillnetting efforts, with no larval whitefish remains identified in their stomachs. Post spawned smelt have proven difficult to capture during early spring, and future research will consider experimental sampling efforts to increase capture efficiency. Furthermore, predation by smelt has likely decreased with declining Lake Whitefish numbers and may not be as prevalent as it was when Lake Whitefish were more abundant.

Three hundred seventy-one Lake Whitefish otoliths were collected for age analysis from 15 lakes in northern Maine. Lake Whitefish ages ranged from 1 to 45 years old. Of these 15 lakes, 13 have invasive smelt and age structure data suggests 10 have experienced some degree of recruitment failure in the past decade. Three populations appear to have sustainable levels of recruitment in the presence of smelt. Year classes where recruitment is observed appears to coincide with high Lake Trout densities. Lake trout likely play an important role in regulating smelt abundance and mediating smelt-whitefish interactions among Allagash River drainage lakes. Abundant spawning habitat, food availability, and low predation rates by adult smelt are believed to influence successful recruitment where it is observed.

Lake Whitefish age and growth trajectories from Ross Lake demonstrated a general pattern seen in many fish populations whereby rapid growth early in life results in early maturity, followed by a steep decline in growth rate. Ross Lake length-at-age data was similar to other unexploited and lightly exploited Lake Whitefish populations. The whitefish population in Ross Lake is considered to be abundant (Wood 2018). Ross Lake is among a few waters that maintains an intact Lake Whitefish population in the presence of smelt. Abundant spawning habitat, food availability, and a naturally productive Lake Trout population are believed to mediate smelt-whitefish interactions in this lake. Recognizing conditions that are favorable for whitefish in Ross Lake is important for the persistence and conservation of this at-risk species.

Lake whitefish populations continue to experience declines across their native range. Increasing anthropogenic manipulation through habitat degradation and invasive species introductions are commonly cited factors driving Lake Whitefish declines throughout their range, though the impacts of smelt appear to be the ultimate driver of declines in Northern Maine. Besides the introduction of invasive smelt, the fish assemblages in most of our study waters remain biologically intact. These waters present a unique opportunity for research, management and conservation of this at-risk species. This report is meant to inform future conservation efforts of Maine Lake Whitefish populations and serve as a reference for other regions experiencing similar declines.

Key Words: Lake Whitefish, Allagash Watershed, Recruitment, Spawning habitat, Zooplankton, Larval Trawl, Rainbow Smelt.

INTRODUCTION

Lake Whitefish (*Coregonus clupeaformis;* also referred to as "whitefish" in this document) provide a unique and desirable recreational fishery to a small, passionate angling community in northern Maine. Over the past century, Maine's Lake Whitefish populations have experienced significant declines, including extirpation in a number of waters throughout the state. Lake Whitefish are designated as a Species of Greatest Conservation Need in Maine and understanding the factors that are influencing their population-level declines is of growing importance (MDIFW 2015). Whitefish populations experienced initial declines in many waters at the turn of the 20th century, most notably in the Fish River Chain of lakes, where they had collapsed by the 1950s (Wood 2016). Lakes in the Allagash River watershed, prized by avid whitefish anglers, are considered the last remaining stronghold of northern Maine Lake Whitefish. In recent decades, these too have begun to see drastic declines.

Routine survey data in many of the lakes across the Allagash River watershed reveal an absence of young Lake Whitefish, suggesting recruitment failure as the driving force behind population declines. This failure has been closely linked to the establishment of invasive Rainbow Smelt (*Osmerus mordax*). Smelt, which are not indigenous to northern Maine, were introduced into the Fish River Chain in 1894 and in Allagash lakes from the 1940's to 1980's. These smelt introductions coincide with the onset of declining Lake Whitefish populations in lakes within both drainages. There are currently 21 waters containing Lake Whitefish in the Allagash watershed, 18 of which now have smelt populations, many of these waters support historically low numbers of whitefish since smelt establishment (Wood 2016).

The association between smelt establishment and Lake Whitefish declines has been widely documented across North American inland lakes (Loftus and Hulsman 1986; Evans and Loftus 1987; Evans and Waring 1987; Crowler 1980; Gorsky 2011). Predation by adult smelt on larval whitefish, and competition (both direct and indirect) between smelt and whitefish are indicated as the primary mechanisms causing declines. Predation by adult smelt on larval whitefish led to the extirpation of whitefish in Twelve Mile Lake, Ontario, and is believed to be an important factor causing recruitment failure in Lake Simcoe, Ontario (Loftus and Hulsman 1986; Evans and Waring 1987). Additionally, Gorsky and Zydlewski (2013) demonstrated 100% predation efficiency on larval whitefish by adult smelt in a laboratory setting, though such evidence has proven difficult to document in the field.

Smelt are also important predators of zooplankton, to the point where they can drastically change zooplankton assemblages (Johnson and Goettl 1999; Beisner et al 2003). Direct competition for food between smelt and Lake Whitefish is sometimes mentioned as a reason for whitefish declines, but evidence of this is lacking (Gorsky 2011). Given the large size of larval whitefish compared to larval smelt and the difference in hatch timing between them, direct competition from larval smelt is not likely to be a driving factor behind Lake Whitefish declines. However, recent work by Maine Department of Inland Fisheries and Wildlife (MDIFW) indicates that changes in zooplankton communities, and corresponding lack of food for larval whitefish, may be responsible for recruitment failure and Lake Whitefish declines (J. Wood personal communication).

Gorman (2008) illustrated the importance top predators like Lake Trout (*Salvelinus namaycush*) have on regulating smelt and coregonid (whitefish) populations. High Lake Trout densities following intense stocking in Lake Superior marked a decrease in smelt abundance as smelt were the predominant prey of Lake Trout. Following the reestablishment of Lake Trout and subsequent declines of smelt, coregonid populations rebounded from historic low numbers. The high abundance of smelt prior to Lake Trout reestablishment appears to be the only factor linked to recruitment failure of whitefish in Lake Superior (Gorman 2008). Other studies have relied on food web alterations that promote native piscivore species through restrictive bag regulations or supplemental stocking to control smelt and recover native coregonid populations (Krueger and Hrabik 2005, Gaeta et al. 2014). Lake Trout are native to most Lake Whitefish waters in Maine and are the predominant predator of smelt in Allagash waters, it is hypothesized that fluctuations in Lake Trout abundance may influence factors important to whitefish survival.

Understanding the mechanisms responsible for Lake Whitefish population declines, or lack thereof, has become a critical information need for MDIFW fisheries managers. Since recruitment failure appears to be occurring in early life stages, whitefish spawning ecology and early survival is a focal point of our current research. Spawning habitat use and reproductive success of whitefish populations in the Allagash River watershed is largely unknown. We suspect that the availability of spawning habitat and varying spawning life history strategies may influence recruitment success in some waters. Food availability during critical early life stages of whitefish is another important information need. Zooplankton community assemblages in Allagash waters are largely unknown and have likely changed since smelt establishment. Investigating zooplankton assemblages among different waters where smelt have become established may provide some insight into observed patterns in recruitment. Direct predation of larval whitefish by adult smelt is known to cause whitefish population extirpation (Loftus and Hulsman 1986) but is very difficult to document in the field. Determining whether adult smelt are feeding on larval whitefish in Allagash River drainage lakes remains an important information need. Finally, age and growth data are lacking among most Lake Whitefish populations in Maine. A better understanding of population age structure is critical in identifying waters experiencing recruitment failure and interpreting how factors described above may influence observed patterns in recruitment.

The objectives of the research were to: 1) document the availability and use of whitefish spawning habitat in various waters and assess how this may influence recruitment; 2) monitor larval whitefish and smelt abundance through larval trawls; 3) collect stomach content data from adult smelt to assess predation on larval whitefish; 4) monitor zooplankton community assemblages to assess their potential influence on larval whitefish survival; and 5) collect otoliths to characterize the age structure and assess recruitment of northern Maine Lake Whitefish populations.

STUDY AREA

The Allagash watershed lies within the North Maine Woods, an unpopulated area, covering ~3.5 million acres of privately-owned industrial forest land. Landowners manage the area primarily for timber production but allow fee-based public use for recreational activity, including fishing. Many of the lakes in this area contain small campsites and primitive boat launches.

Most lakes within the Allagash River watershed remain biologically intact, with low anthropogenic influences. Lakes are characterized as oligotrophic, comprised of cold-water fish assemblages, with relatively low species composition. Fish community assemblages are commonly composed of Lake Trout (*Salvelinus namaycush*), Brook Trout (*Salvelinus fontinalis*), Lake Whitefish (*Coregonus clupeaformis*), Round Whitefish (*Prosopium clindraceum*), Brown Bullhead (*Ameiurus nebulosus*), Burbot (*Lota lota*), Slimy Sculpin (*Cottus cognatus*), White Sucker (*Catostomus commersonii*) Blacknose Dace (*Rhinichthys atratulus*), Northern Red Belly Dace (*Chrosomus eos*), Creek Chub (*Semotilus atromaculatus*), Lake Chub (*Couesius plumbeus*), Rainbow Smelt (*Osmerus mordax*) and Three-spine Sticklebacks (*Gasterosteus aculeatus*).

Six Lake Whitefish lakes in the Allagash drainage were selected for this study (Figure 1). Ross Lake is a 2,982-acre lake in T10R15, Piscataquis County, with a maximum depth of 105 feet. Smelt have been established in Ross Lake since 1941. Despite this, the Lake Whitefish population in the lake is currently robust. The lake has several privately-owned camps with a primitive boat launch located at the northern end of the lake by the outlet stream. Ross Lake Camps, a small hunting and fishing lodge on the southwestern shoreline of the lake attracts and accommodates anglers throughout the year, with a primary focus on the ice fishing season. Most recent winter creel survey data reveal a healthy fishery for Lake Whitefish in Ross lake (Wood 2018). Understanding the biological and environmental factors that have allowed these whitefish to persist in the presence of smelt may help identify solutions to better manage waters where whitefish are in decline.

Crescent Pond is a 320-acre lake in T9R15, Piscataquis County, with a maximum depth of 68 feet. Crescent Pond is closed to ice fishing; however, anglers have reported catching whitefish in the open water in past decades. Periodic survey data collected from the lake reveal a dramatic decline in whitefish numbers since the establishment of smelt in 1980. A small cohort of whitefish still exist in the lake, but their long-term persistence is in question.

Second Musquacook Lake is a 762-acre lake in T11R11, Aroostook County, with a maximum depth of 62 feet. Historically, Second Musquacook supported a thriving whitefish fishery. In the early 1970's, regional MDIFW fisheries biologists described "seemingly endless" quantities of spawning whitefish in Second Musquacooks inlet stream. Since the establishment of smelt in the late 1970's, whitefish numbers have declined dramatically in the lake and no longer support a popular fishery. Anglers frequently ice fish Second Musquacook Lake for Lake Trout (*Salvelinus namaycush*) and rarely report catching whitefish.

Clear Lake is a 614-acre lake in T10R11, Piscataquis County, with a maximum depth of 86 feet. The lake supported a popular whitefish fishery for many decades. Smelt became established in Clear Lake in the 1990's, and whitefish numbers have declined to the point where the lake no longer supports a sport fishery. Because of the relatively recent establishment of smelt and the decline of the whitefish population, Clear Lake has been the focus of several previous whitefish studies. An experimental MDIFW Lake Whitefish hatchery program relied on whitefish eggs taken from Clear Lake in the early 2000's. The hatchery program continued for several years and was halted to await follow-up monitoring and future studies.

Indian Pond (also referred to as "Big Indian Pond") is a 1,222-acre lake in T7R12, Piscataquis County, with a maximum depth of 52 feet. Big Indian Pond, like Crescent Pond, is closed to ice fishing. Anglers have reported whitefish being caught in the open water season. The pond has a large population of smelt which are believed to have been established in the 1990's. Past gillnetting efforts revealed a relatively abundant cohort of adult Lake Whitefish in Big Indian Pond but evidence of recent recruitment has not been documented, and whitefish persistence in the presence of smelt is in question.

Haymock Lake is a 928-acre lake in T7R11, Piscataquis County with a maximum depth of 61 feet. The Haymock Lake whitefish population is a result of an experimental transfer of dwarf whitefish from Second Musquacook in the autumn of 1962 and 1963. The transfer was successful and Haymock continues to support a dwarfed Lake Whitefish population today. These dwarfed fish are generally too small for anglers to catch and do not support a fishery though they serve as a forage base for the Lake Trout population. Haymock was one of four remaining Lake Whitefish populations in the Allagash watershed without smelt; however, smelt were discovered here in the spring of 2019, and pose a serious threat to the whitefish population in Haymock Lake.

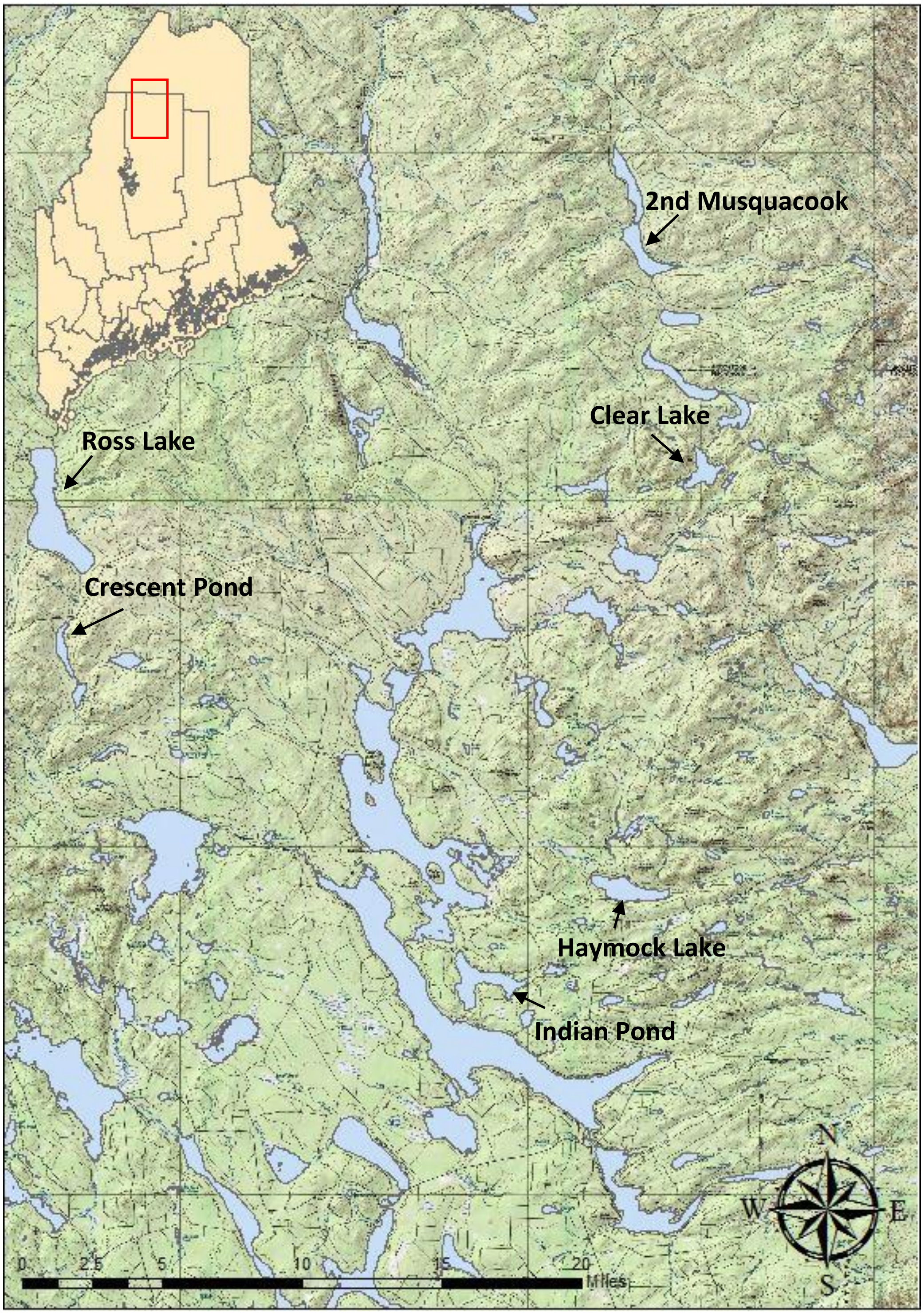


Figure 1. Whitefish study waters in the Allagash watershed.

METHODS

Spawning Habitat Surveys:

Spawning habitat surveys were conducted in each of the six study lakes to identify potential Lake Whitefish spawning sites and to assess the availability of habitat in each water. Spawning habitat selection by Lake Whitefish can vary greatly among lakes, depending on the quality and quantity of available habitat. To ensure low quality spawning habitat wasn't overlooked in our surveys, habitat was separated by three classifications: optimal, suboptimal, and potential. Optimal habitat consisted of unfragmented, deeply layered substrate, with a combination of large, medium, and small cobble/gravel that constituted deep crevices for adequate egg cover (Figure 2). Suboptimal habitat consisted of unfragmented, not deeply layered substrate with a combination of large, medium, and small cobble/gravel that was relatively uniform and provided some cover for eggs. Lastly, potential spawning habitat consisted of some combination of small, medium, and large substrate that was not deeply layered and had very little interstitial space. The entire perimeter of the lake shoreline was visually scanned by boat and inlet and outlet streams were surveyed on foot. All observed spawning grounds were marked in a GPS and later mapped in ArcMap 10.6.1.

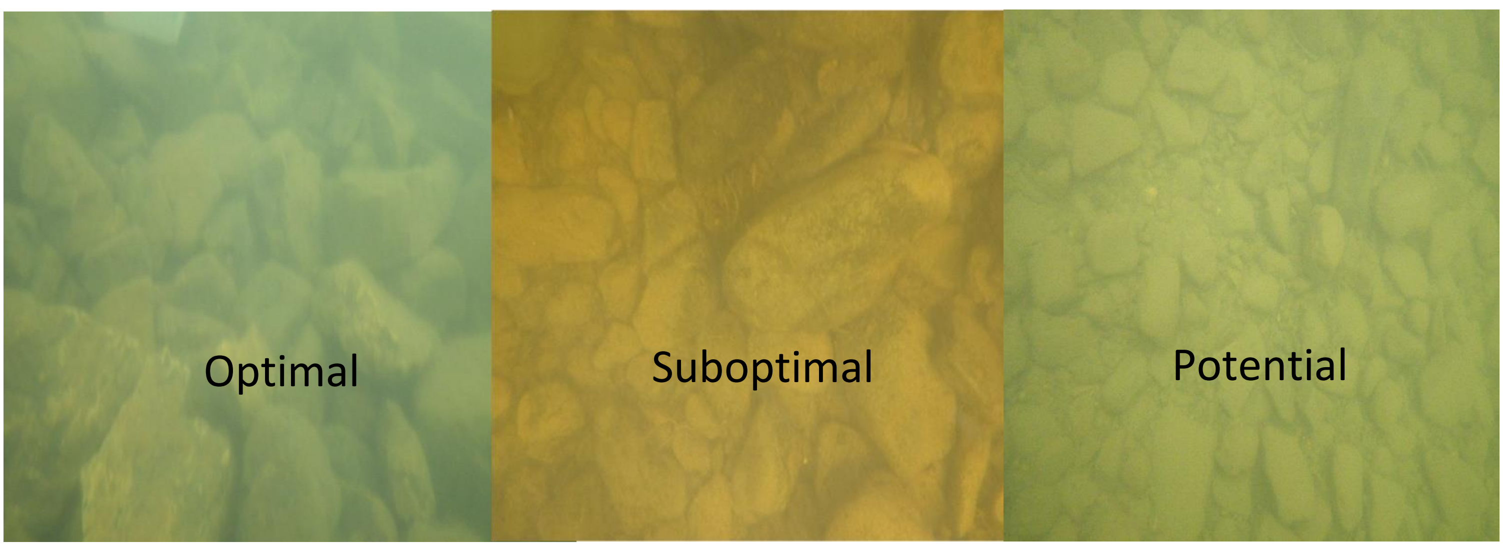


Figure 2. Examples of the three classes of Lake Whitefish spawning habitat.

Egg Mat Study:

Artificial egg collection mats were used to assess Lake Whitefish spawning habitat and confirm successful egg deposition. Egg mats were modified from the techniques described in Roseman et al. (2011). Our mats were made using a standard cored concrete block (16x8x4") with a 1" thick natural hog hair furnace filter sheet that was glued to the top to capture falling eggs. Mats were tied together ~15 feet apart in gangs of three to get a broader coverage of the spawning site. Mats were placed on the best available spawning sites identified during spawning ground surveys, except on Big Indian Pond; where mats were placed on habitats representing each of the three categories. Mats were set starting the week of October 26, 2018, prior to Lake

Whitefish spawning. Mats were checked weekly for the presence of whitefish eggs on Ross Lake, Second Musquacook Lake, Clear Lake, and Big Indian Pond until November 12, when newly formed ice prevented further sampling. Stream egg mats were monitored until December 5, 2018. Egg mats were collected through the ice (when ice conditions were safe) and checked for eggs in December and January. Due to the remoteness of the study waters and time restrictions, Crescent Pond and Haymock Lake egg mats were not monitored weekly. Instead, they were checked after Lake Whitefish spawning had concluded in the other lakes.

Lake Whitefish eggs were identified visually during each egg mat check. If eggs were present, a subsample of eggs was taken, and egg diameters were measured to the nearest millimeter. Lake Whitefish eggs have a unique egg size (~3mm diameter) and based on egg size and spawn timing can only be confused with Round Whitefish (*Prosopium cylindraceum*), which are far less common or absent from most study waters. Eggs collected from waters that harbored both Round and Lake Whitefish populations were sent to Laval University, Quebec for genetic sampling to distinguish the two species.

A total of 87 egg mats were deployed over 29 possible spawning sites during the fall of 2018. Each spawning site had a gang of three egg mats. Ross Lake had 15 egg mats placed over five shoals and 6 mats at 2 sites in the outlet stream. Second Musquacook Lake had 12 egg mats placed over four shoals and 6 egg mats placed at 2 sites in the inlet stream. Clear Lake had 12 egg mats over four shoals in the lake. Haymock and Crescent had 9 egg mats that were placed over three shoals each. Big Indian Pond had 18 egg mats placed on two optimal shoals, two suboptimal shoals, and two potential shoals.

We continued the egg mat study in 2019 on Ross Lake. Fourty-eight egg mats were deployed in Ross Lake over 6 potential spawning shoals and 4 potential spawning streams during the fall of 2019 following the methods described above.

Radio Telemetry

Fifteen Lake Whitefish in Ross Lake were outfitted with radio tags in the fall of 2019. Ten fish were caught through short gill net sets (20-30 minutes) in 30-45ft of water, the remaining five fish were caught via rod and reel. Fish lengths ranged from 338-525mm (13.5-20.5 in) weights were not recorded to limit excess handling of fish. Each fish was placed in an anesthetic bath (Aqui-S, ~6mL/L) then transferred to a v-shaped surgical table outfitted with a ¾" PVC tube that fed lake water over the fish's gills (Figure 3). A small incision was made along the abdomen and a radio transmitter (ATS F1580) was inserted into the body cavity. The tag's antenna was run through a hole in the body cavity that was pierced with a needle. The incision was closed with two to three sutures and washed with an antiseptic. Fish were placed in a live-well to recover before being released back into Ross Lake.

Figure 3. Lake Whitefish radio tag surgery.

Each tag was programmed with a unique transmission signal between 150.000-150.999 MHz (Table 1) so individual fish could be tracked and located. Whitefish were tracked by boat 1-2 times a week with an ATS R2000 radio receiver from October 9 to October 31, 2019 during daylight hours from 10am to 4pm. Fish were tracked along concentric rings around the lake at the 20 ft, 35 ft, 50 ft, and 65 ft depth contours. Daytime and evening tracking began on November 4, 2019 when surface water temperatures dropped to 8°C. Whitefish were tracked 7 evenings between November 4th and November 13th from 6pm to 10:30pm. Ice conditions prevented tracking beyond November 13th. All whitefish locations were marked with a GPS.

Table 1. Lake Whitefish length at capture and radio tag frequency.

Length (mm)	Length (in)	Radio Tag MHz
423	16.7	150.131
525	20.7	150.100
344	13.5	150.091
483	19.0	150.121
368	14.5	150.110
398	15.7	150.031
338	13.3	150.151
343	13.5	150.071
416	16.4	150.142
434	17.1	150.040
378	14.9	150.010
377	14.8	150.082
365	14.4	150.062
371	14.6	150.020
345	13.6	150.049

Larval/Zooplankton Trawling

Lake Whitefish survival to hatch and zooplankton community assemblages were monitored on Crescent Pond, Ross Lake, Second Musquacook Lake, Clear Lake, and Haymock Lake during the spring of 2015-2020 using a larval trawl (1 m^2 mouth opening, 500 µ mesh). Trawling began in early May immediately after ice off, when Lake Whitefish typically hatch (Chouinard and Bernatchez 1998). Each lake had a fixed number of shoreline sampling locations that were systematically chosen and equally spaced based on the size of the lake and feasibility to sample each location within a given sampling period. Crescent Pond, Ross Lake, Second Musquacook Lake, Clear Lake and Haymock Lake had 8, 11, 10, 10, and 9 sites respectively. Sampling locations in each lake were trawled once a week for four weeks following ice off. The trawl was towed 50 feet behind a Yamaha 9.9hp outboard motor at approximately 2.5mph for five minutes at each site. High congregations of larval whitefish have been observed near shore and near the surface of the water column during daylight hours (Chouinard and Bernatchez 1998; McKenna and Johnson 2009). Therefore, trawling at each site took place along the shoreline, in the top meter of the water column, during peak daylight hours (1000am to 200pm). The trawl was towed over a minimum 10 ft of water to avoid hitting the bottom and damaging the trawl or collecting unwanted silt/debris.

Larval fish and zooplankton caught in the trawl were collected in a 150 µ mesh sample bucket. After each trawl tow, larval fish and zooplankton were washed from the bucket and transferred to a 250 or 500 ml sample bottle and preserved in 90% ethanol to be counted and identified in the lab. Larval fish and zooplankton were identified using a dissecting microscope. Larval fish were measured to the nearest millimeter. Zooplankton were identified and grouped into

Cladocerans (primarily *Bosmina, Daphnia, Sididae, Holopedidae, Polyphemidae*) and Copepods (*Calanoid* and *Cyclopoid*). Zooplankton from each sample were transferred into a 10 mm graduated cylinder. If the sample contained less than 10 mm of zooplankton, the entire contents were identified and counted in a Bogorov counting tray. For samples containing more than 10 mm of zooplankton, two 1 mm subsamples were taken using a Hensen-Stempel one-millimeter pipet. The average zooplankton counts of these subsamples were applied to the overall sample volume to obtain an estimate of total zooplankton in the sample.

Volume of water filtered during trawl tows was quantified using readings from a flow meter (General Oceanics, model 2030R) mounted in the trawl opening. This value was used to calculate mean zooplankton densities (1000m^3) (data pooled from all trawl locations for each sampling date). No statistical analysis was performed on these data for this report, they are simply presented to compare zooplankton densities and relative abundances between study lakes.

Mean cyclopoid copepod densities were calculated using methods described above. Cyclopoid densities were not normally distributed and were log transformed to compare trends in cyclopoid abundances between waters.

The entire contents of each sample were viewed under a dissecting microscope to identify and count all larval fish caught during each trawl tow. Larval fish were identified to species based on appearance and length measurements. Total catch of larval fish during spring sampling are presented to compare general patterns in larval fish abundances for each water.

Smelt Predation on Larval Whitefish:

Experimental gillnetting surveys were conducted in conjunction with trawling to collect adult smelt for diet analysis during the spring of 2019 and 2020. Weather and time permitting, gillnets were set in each lake after trawling was finished for the day. The gillnets were collected the following morning and smelt were measured, weighed, and their stomachs were dissected to search for larval fish remains. Six smelt nets were used during the surveys, two 5’x100’ nets, one 5’x50’ and three 5’x200’ net. Net mesh size ranged from ½” to 1”.

Age estimation:

Lake Whitefish were captured in various waters via gillnetting, angler creel surveys, and experimental angling from 2014 to 2020 for age analysis. Sagittal otoliths, a calcified bone in the inner ear, were used to determine the age of each individual Lake Whitefish to assess the age structure of these populations. Total length (mm) and weight (g) of fish were recorded and otoliths were extracted by flipping the fish on its back and cutting the gill arches away from the lower jaw exposing the underside of the fish’s cranium. A second incision on the underside of the cranium was made so otoliths could be extracted from the brain cavity using a pair of tweezers. Otoliths were mounted in a Ted Pella 110 silicone mold and embedded in epoxy resin to form a small block for sectioning. Each otolith was given an ID number for future identification. The nucleus of each otolith was visually identified and marked prior to sectioning. A 0.75 mm transverse section was taken using a diamond bladed saw, each section was glued to a microscope slide using crystal bond, dried, then wetted and polished with 600-

1500 grit sandpaper. Otolith sections were photographed using Image Pro Premier 9.2 software and a digital imaging microscope. Age estimates were determined by counting annuli, the transitional zone between winter slow growth (opaque zone) and summer fast growth (translucent zone). Annuli were counted by two staff biologists independently of each other using ImageJ software. Afterwards, individual fish ages were assessed by the biologists to evaluate any discrepancies between ages. If there was a discrepancy between age estimations the biologists would study the discrepancies and come to an agreement on the best age estimate for that fish.

Back calculated length-at-age was assessed for Ross Lake's Lake Whitefish population. Length-at-age was assigned to each identifiable annulus by measuring the proportional distance between the focus and the annulus and the focus and outer edge of the otolith. This ratio was multiplied by the known length at capture to estimate length-at-age for each annulus. These data were used to calculate average and 95% confidence intervals for each age.

RESULTS

Spawning Habitat Surveys

Ross Lake

A total of 18 possible spawning sites were identified in Ross Lake; 4 optimal, 13 suboptimal, and 2 potential (Figure 4). The majority of the spawning habitat was located on the southern end of the lake where the shoreline drops off moderately, reaching depths of 4 to 5 ft within 100 ft of the shore. This section of shoreline is adjacent to prevailing northwesterly winds, providing sufficient wave action to keep substrate clean. The spawning area stretches for close to a kilometer presenting an abundance of suitable spawning habitat for Lake Whitefish to utilize (Figure 4). Three other optimal spawning sites were identified along the eastern shoreline of the lake (Figure 4). The most notable of these three shoals was identified off Baker point (Figure 3). The shoreline drops off steeply here, and optimal spawning habitat is within close proximity to the shore. A few notable sections of suboptimal spawning habitat exist at the north end of the lake by the outlet stream (Figure 4) and along the eastern shoreline in the "Narrows" or the neck of the lake. There is good cobble in these locations, and rocks are relatively clean of silt; however, shoals are intermittent suggesting less than optimal spawning conditions for Lake Whitefish.

Ross Lake has an inlet and outlet stream and five additional tributaries. No spawning habitat was identified in any of the tributary streams or inlet stream during 2018 spawning ground surveys. Beaver dams at the mouth of many of the tributaries and the inlet stream, in combination with low water conditions, resulted in no suitable spawning habitat in the tributaries. It is important to note that abnormally low rainfall in the Summer and Fall months prior to spawning ground surveys may have presented inadequate spawning conditions in tributary streams. Suitable spawning habitat may present itself in these streams with higher water levels and should not be overlooked in future spawning ground studies, particularly in the inlet stream and Fools Brook which have some small cobble upstream of the mouth. Ross

Lake outlet was the only stream with enough water and quality spawning habitat for Lake Whitefish and was identified within 150 yds of the mouth of the outlet (Figure 4).

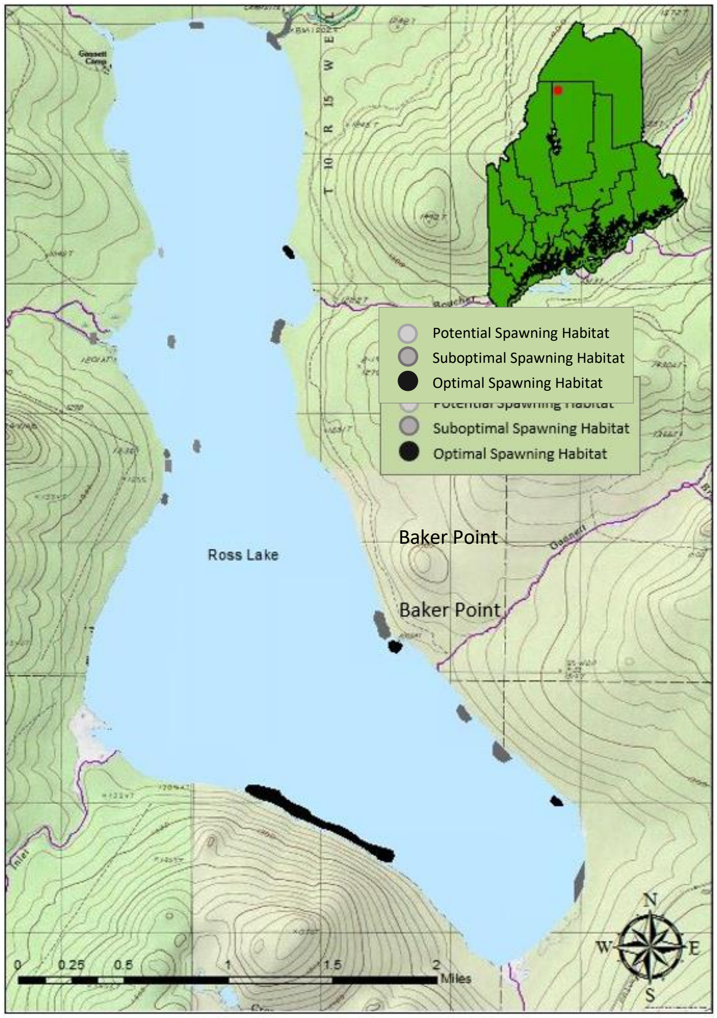


Figure 4. Locations of possible Lake Whitefish spawning habitat in Ross Lake, T10R15, Piscataquis County, ME.

Second Musquacook Lake

The shoreline of Second Musquacook Lake was predominantly mud and silt and contained very limited spawning habitat. Seven sites were identified as possible spawning areas in the lake. No optimal spawning habitat was identified along the lake shoreline. Two suboptimal shoals were identified on the southern end of the lake and one small suboptimal shoal was identified on the eastern shoreline. Four other potential spawning sites were identified around the lake (Figure 5).

There are three small tributaries and one inlet stream that flow into Second Musquacook. No suitable spawning habitat was identified in any of the tributary streams, though some optimal habitat was identified in the large inlet stream. The current from the inlet stream was adequate to clean substrate along the river bottom and helped to create a patchwork of optimal habitat that stretched a few hundred yards upstream from the mouth (Figure 5). Additionally, water levels in the stream were 1-2 feet deep, providing enough water for Lake Whitefish to navigate during the spawning season.

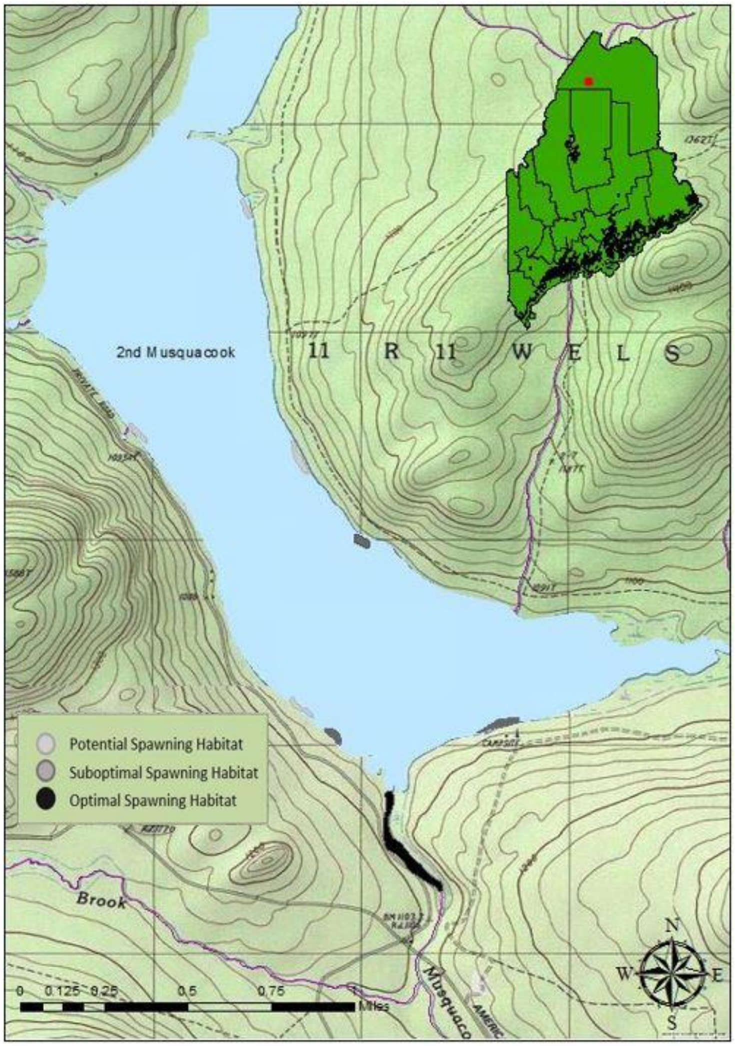


Figure 5. Locations of possible Lake Whitefish spawning habitat in Second Musquacook Lake, T11R11, Aroostook County, ME.

Clear Lake

Twenty-two possible spawning shoals were identified along the shoreline of Clear Lake. Spawning habitat ranged from optimal to potential. Four optimal spawning shoals were identified within the lake. Two of these sites were on the southern shoreline, one was on the southeastern shoreline, and the last was identified towards the north end of the lake near the outlet stream (Figure 6). These shoals were small in size but had exceptional spawning substrate. Notable suboptimal habitat exists throughout a network of islands along the southwestern shoreline. This area presents a patchwork of suitable substrate for spawning whitefish, but the islands face southeast, away from prevailing northwest winds and much of the spawning substrate in this area had levels of sedimentation that made the site less than optimal. Ten other suboptimal and six potential spawning sites were identified in spawning habitat surveys. Substrate appeared suitable on these, but sedimentation made many of them less than optimal. Clear Lake has no inlet streams and the outlet stream is too small to accommodate spawning Lake Whitefish.

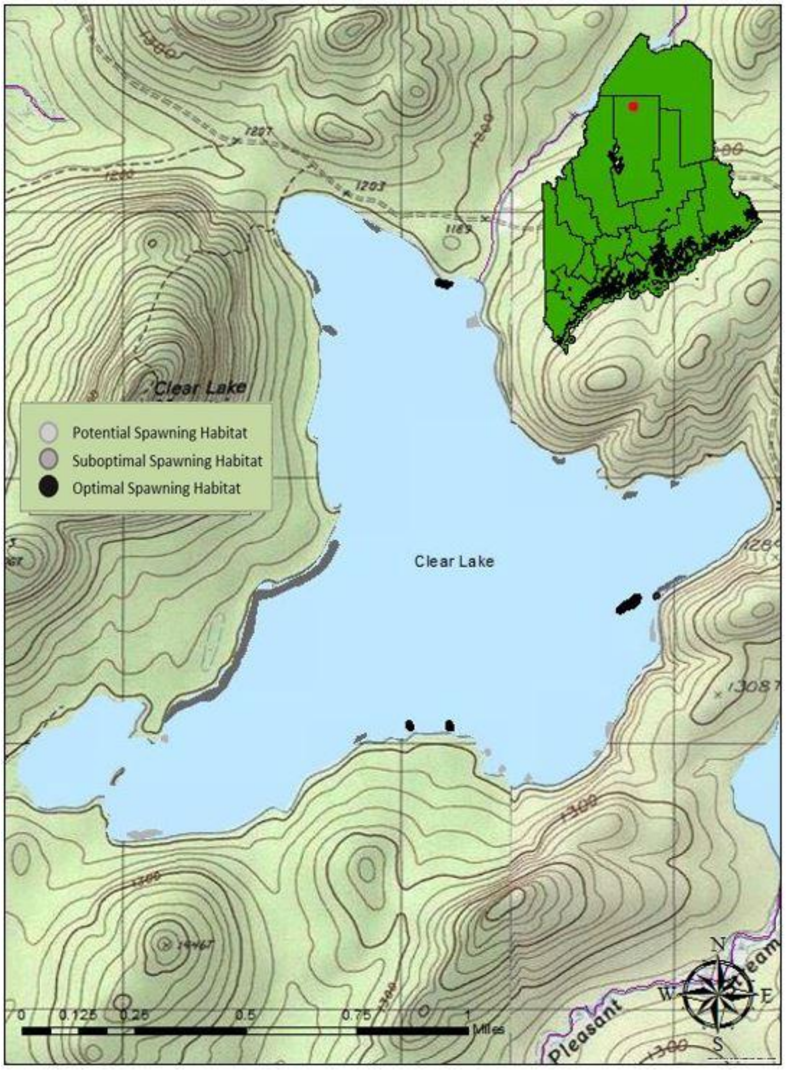


Figure 6. Locations of possible whitefish spawning habitat in Clear Lake, T10R11, Piscataquis County, ME.

Crescent Pond

Crescent Pond's shoreline is predominately mud and silt and provides less than optimal spawning habitat for Lake Whitefish. Eight possible spawning sites were identified. Two sites were identified as suboptimal, one site was located on the southern tip of the pond and the other along the eastern shoreline (Figure 7). They both consisted of small uniform cobble, with little silt deposition. The remaining six sites were identified as potential spawning areas.

Crescent Pond has a northern inlet and southern outlet, and two small tributaries on the western shoreline. No suitable spawning habitat was identified in the inlet, outlet, or tributary streams. The outlet is heavily jammed with logs and there is no suitable habitat downstream of the log jam. The inlet stream has a large beaver dam ~100 ft upstream of its mouth. Stagnant, silty water above and below the dam provide no suitable spawning substrate.

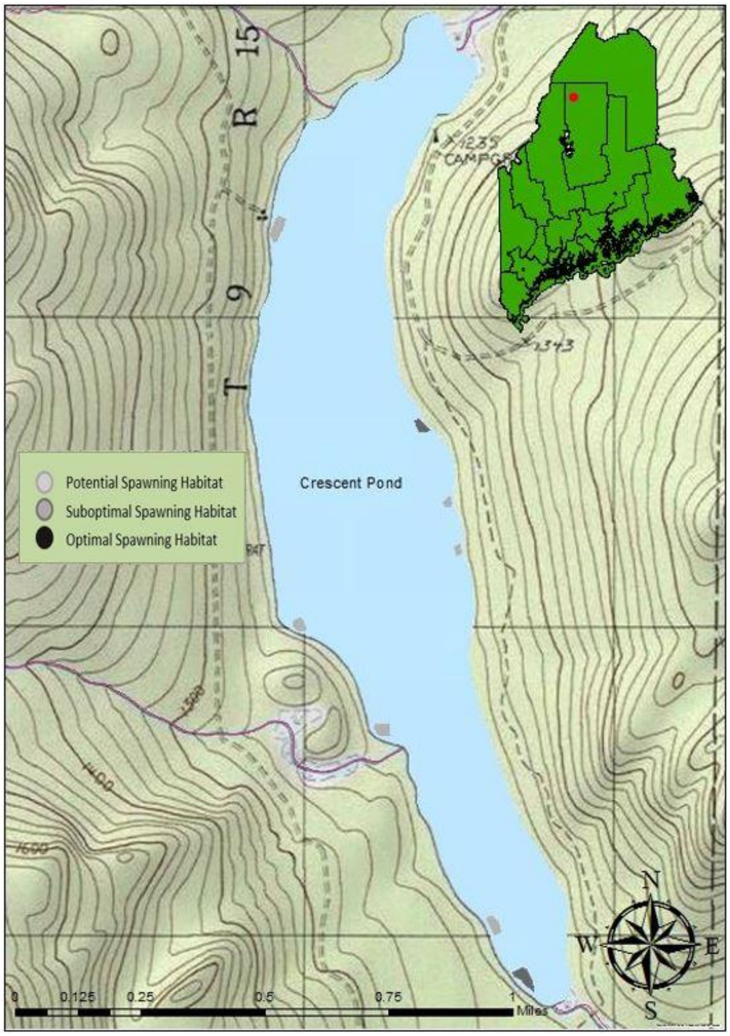


Figure 7. Locations of possible Lake Whitefish spawning habitat in Crescent Pond, T9R15, Piscataquis County, ME.

Haymock Lake

Haymock Lake's shoreline is predominately silt and mud which provides less than optimal spawning habitat for Lake Whitefish. Seven potential spawning sites were identified in the survey. Two suboptimal shoals with small uniform cobble were identified on the southeastern end of the lake. This substrate might be suitable for the dwarf form of whitefish present in the lake. The remaining five sites were identified as potential spawning sites (Figure 8).

There are three tributary streams that flow into Haymock Lake and one outlet stream. No suitable spawning habitat was observed in any of the tributary streams or the outlet stream.

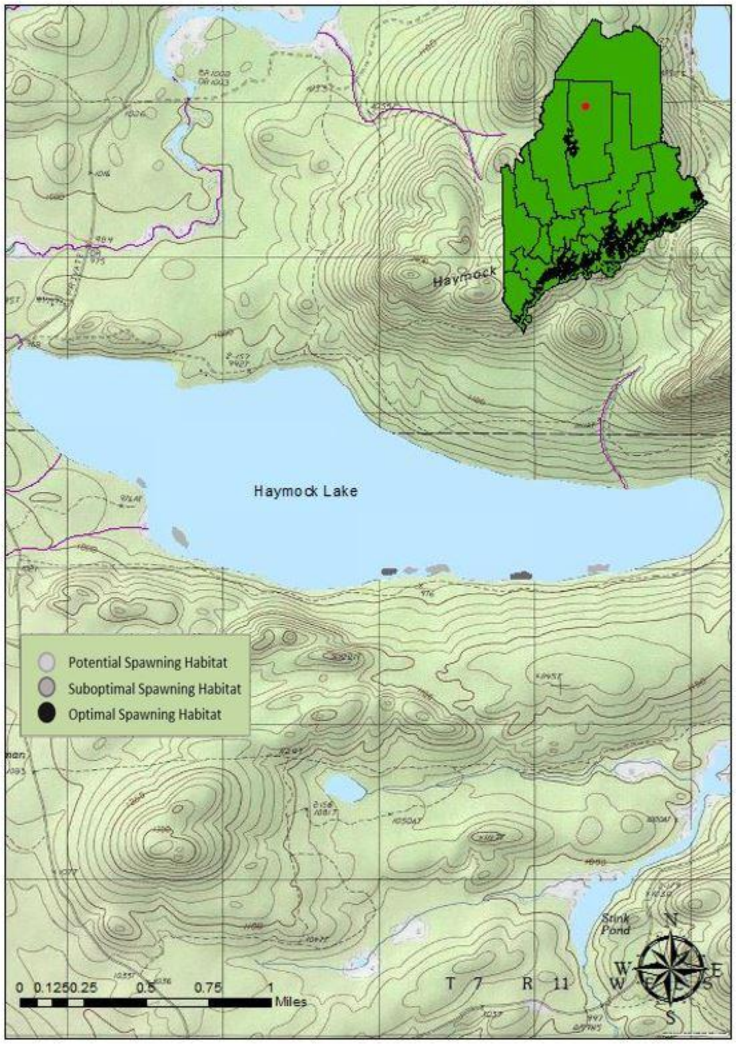


Figure 8. Locations of possible Lake Whitefish spawning habitat in Haymock Lake, T7R11, Piscataquis County, ME.

Big Indian Pond

Big Indian Pond spawning ground surveys revealed a wide array of possible Lake Whitefish spawning sites. A total of 14 sites were identified. Four optimal shoals were identified along the southwestern arm of the lake, all were relatively small in size. A notable optimal shoal with exceptional cobble exists on the far western shoreline of the lake and begins about ~75 ft from the point (Figure 9). Seven other suboptimal shoals and three potential shoals were identified throughout the rest of the lake (Figure 9).

Indian Pond has two tributary streams and one outlet stream that flows into the lake. No suitable Lake Whitefish spawning habitat was identified in any of the tributary streams or outlet stream. Low water levels during the Summer and Fall of 2018 may have presented less than adequate spawning habitat in these tributaries.

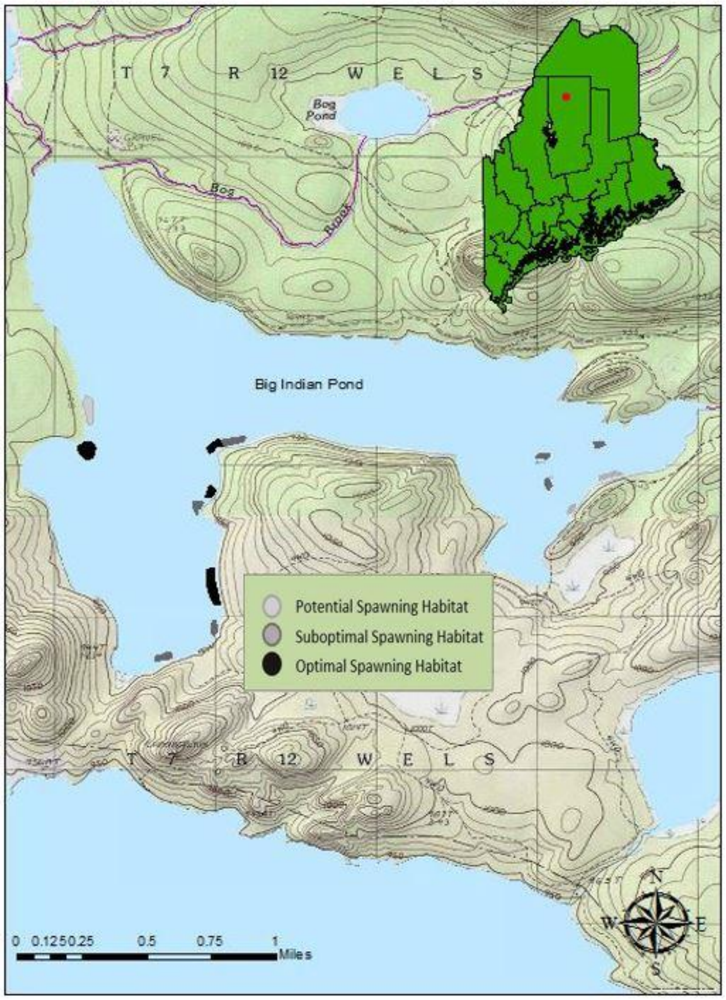


Figure 9. Locations of possible whitefish spawning habitat in Indian Pond, T7R12, Piscataquis County, ME.

Egg Mat Surveys

No eggs were collected during the spawning season on any of the shoreline spawning sites in Ross Lake during the fall of 2018 and 2019 (Figure 10). Six eggs were collected in the outlet stream on November 20, 2018 and 2 eggs were collected in the inlet stream on November 13, 2019. Genetic testing conducted by Laval University determined these eggs came from Round Whitefish. Ultimately, no Lake Whitefish spawning was documented via egg mat surveys in Ross Lake in the fall of 2018 and 2019.

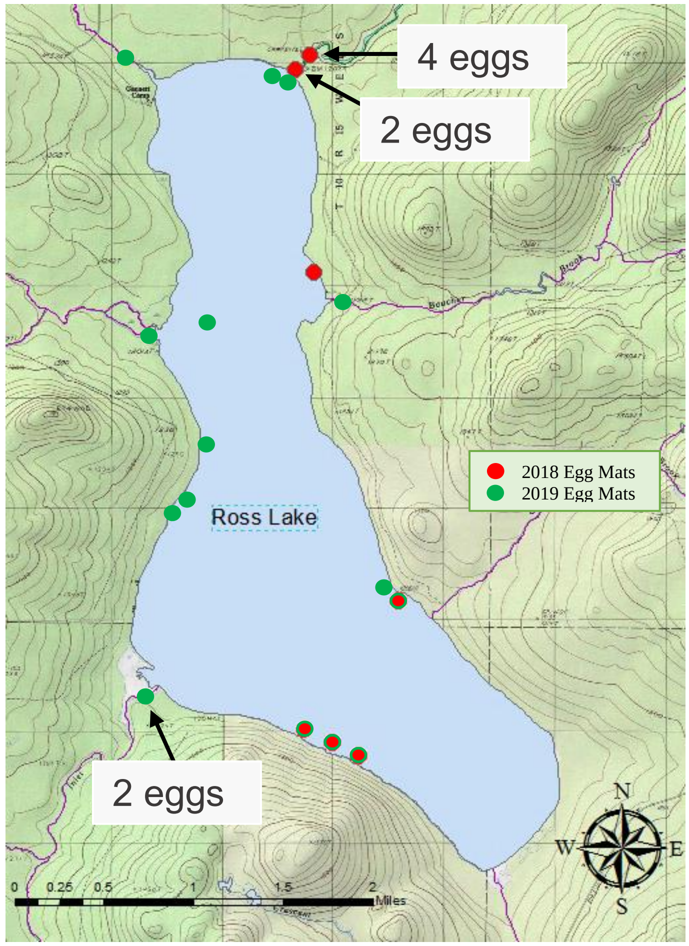


Figure 10. Egg mat locations and number of eggs collected at each site in Ross Lake T10R15, Piscataquis County, ME.

Lake Whitefish spawning was confirmed in the inlet to Second Musquacook Lake. A total of 22 Lake Whitefish eggs were collected at the downstream site near the mouth of the inlet, and 41 eggs were collected at the upstream site (Figure 11). Lake Whitefish eggs were collected in the inlet stream starting November 12, 2019 when water temperatures were 3°C. Eggs were collected on two other occasions up to December 5, when mats were pulled (Table 1). No eggs were collected on any of the in-lake spawning shoals in Second Musquacook Lake (Figure 11).

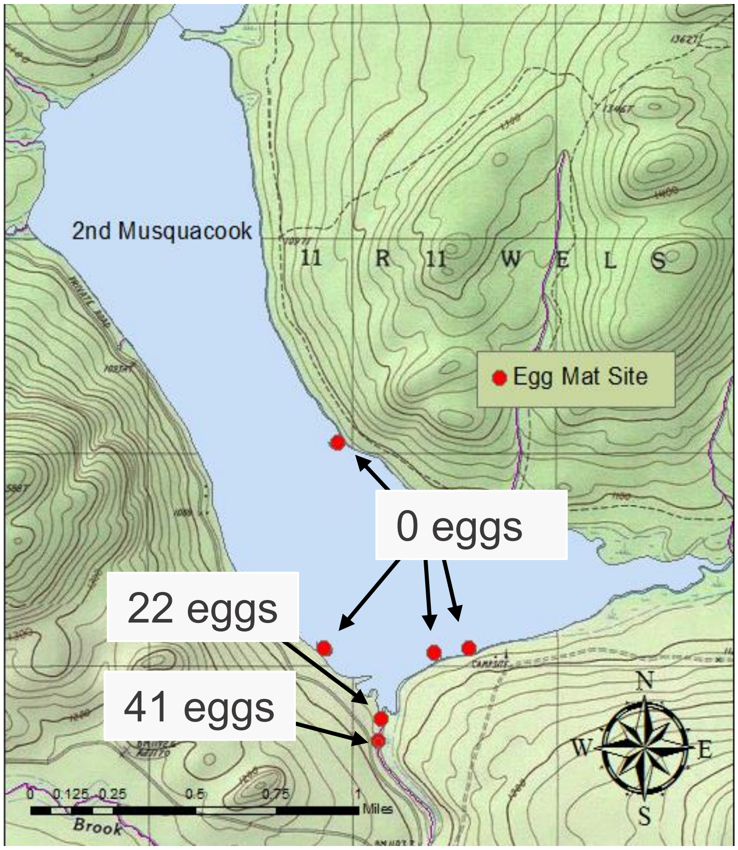


Figure 11. Egg mat locations and number of eggs collected at each site in Second Musquacook Lake T11R11, Piscataquis County, ME.

Egg mats confirmed Lake Whitefish spawning activity on two shoals in Clear Lake. One hundred forty-seven eggs were collected on the southern shoal and 68 eggs were collected on the eastern shoal (Figure 12). Eggs were collected at both sites on November 5 and 12, 2018 when water temperatures were 5°C (Table 2). Mats were collected through the ice in Clear Lake on December 11, 2018. Twenty-eight additional eggs were collected on the southern shoal at this time (Table 2). The eastern shoal egg mats were not found through the ice, therefore no additional eggs were observed at this site.

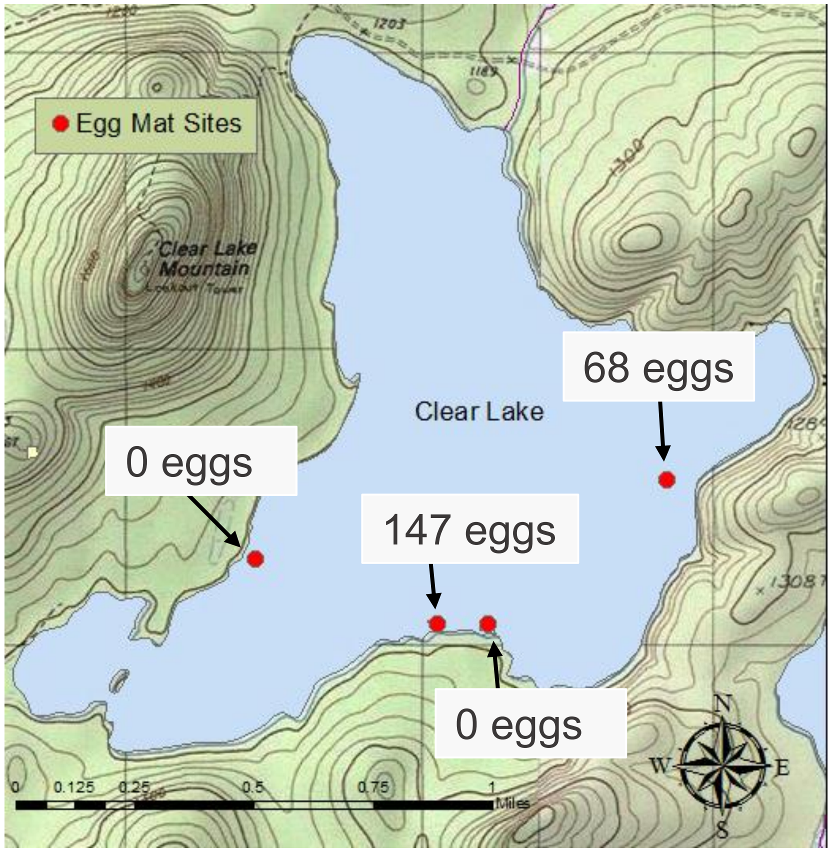


Figure 12. Egg mat locations and number of eggs collected at each site in Clear Lake T10R11, Piscataquis County, ME.

Big Indian Pond, Haymock Lake and Crescent Pond

No eggs were collected on any of the spawning sites in Big Indian Pond through the spawning season. All egg mats were collected through the ice in January and no eggs were collected on any of the mats at this time. Ultimately, no Lake whitefish spawning sites were identified in Big Indian Pond (Figure 13).

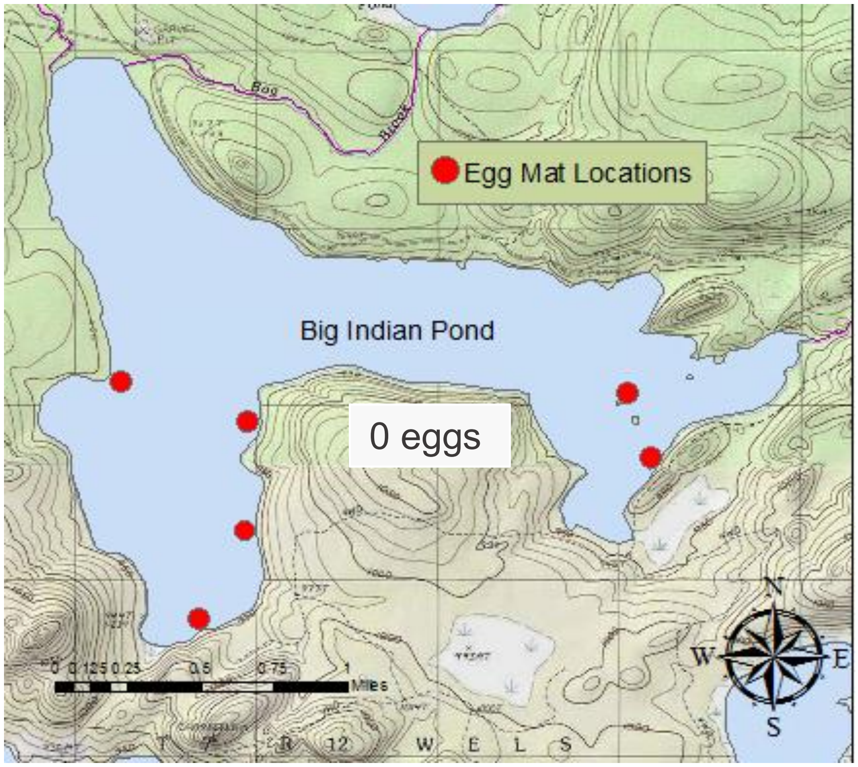


Figure 13. Egg mat locations and number of eggs collected at each site in Indian Pond T7R12, Piscataquis County, ME.

Early ice conditions made collecting egg mats through the ice on Haymock Lake and Crescent Pond nearly impossible. No eggs were collected, and no Lake Whitefish spawning grounds were identified in these two lakes.

Table 2. Whitefish egg counts by site in Second Musquacook Lake, Clear Lake, Ross Lake, and Indian Pond, 2018.

Waterbody	Egg Mat Site	Oct 26 - Nov 1	Nov 2 - Nov 8	Nov 9- Nov 16	Nov 17 - Nov 24	Nov 25 - Dec 5	Dec 6 - Jan 16
2nd Musquacook							
	Inlet Mouth	0	0	2	2	3	-
	Inlet Upstream	0	0	10	13	18	-
	Shoal 1	0	0	0	-	-	0
	Shoal 2	0	0	0	-	-	0
	Shoal 3	0	0	0	-	-	0
	Shoal 4	0	0	0	-	-	0
Clear Lake							
	Shoal 1	0	0	0	0	0	0
	Shoal 2	0	48	20	-	-	-
	Shoal 3	0	98	21	-	-	28
	Shoal 4	0	0	0	0	0	0
Ross Lake							
	Outlet Mouth	0	0	0	4*	-	0
	Outlet Downstrean	0	0	0	2*	-	0
	Shoal 1	0	0	0	-	-	0
	Shoal 2	0	0	0	-	-	0
	Shoal 3	0	0	0	-	-	0
	Shoal 4	0	0	0	-	-	-
	Shoal 5	0	0	0	-	-	-
Big Indian Pond							
	Shoal 1	0	0	0	-	-	0
	Shoal 2	0	0	0	-	-	0
	Shoal 3	0	0	0	-	-	0
	Shoal 4	0	0	0	-	-	0
	Shoal 5	0	0	0	-	-	0
	Shoal 6	0	0	0	-	-	0

Haymock Lake and Crescent Pond egg mats were unable to be checked due to winter/ice conditions and are excluded from the table
(-) egg mats were not checked due to ice cover or high water events.
(*) indicates round whitefish eggs.

Radio Telemetry

Fifteen Lake Whitefish were outfitted with radio receivers on October 9, 2019 in Ross Lake. Each fish was tracked and located within two weeks of surgeries to assess tag retention and survival. Fish 031 was found dead on October 21, 2019 a few hundred feet north of Ross Lake Camps where surgeries were conducted, the cause of death was likely surgery related. Tag numbers 091, 151, 121, 049, 071, and 062 moved to separate deep-water holes (30-60ft) after surgeries but did not move from these holes throughout the tracking study (Figure 15). These fish either died post-surgery, expelled their tags, or were alive but did not spawn. Fish 010 and 020, were only found twice during this tracking study. They were found in water deeper than 60 ft and were never found in the evening along the shoreline.

Tag numbers 040, 082, 100, 142, 131, and 110 were found regularly throughout the tracking study period. During the day these fish were found in 30-45 ft of water in the “narrows” or the “neck” of the lake, east of Ross Lake Camps, or north of the inlet (Figure 14) with the exception of fish 040 which was found in 15-25ft of water near the north end of the lake during daylight hours (Fig 16). Beginning November 4, 2019 all fish moved from their deep-water habitat during the day to shallower waters at night (Figure 14). At night these fish were typically found within 10-30 ft of water but were also found as shallow as 5 ft and as deep as 40 ft. Fish moved to shallower water every evening.

No fish were observed spawning during the course of this tracking study, but evening movements towards four previously mapped shoals suggest these fish may spawn on or near these locations. Fish 082 and 110 were found near Shoal 1 between November 4 and November 7 (Figure 17 & 19). Fish 142 and 131 were found near Shoal 2 between November 5 and November 13 (Figure 20 & 21). Fish 100 and 040 were found on Shoal 3 between November 4 and November 5 (Figure 16 & 18). Fish 100 was found near Shoal 4 on November 5 and 6 before it was found dead in the outlet stream on November 7.

The largest fish movements occurred between November 4 and November 6 when surface water temperatures dropped to 6-7°C and is likely when these fish spawned. Fish movements towards previously identified spawning habitat suggest fish spawn on or near these shoal locations and use multiple different spawning sites within Ross Lake.

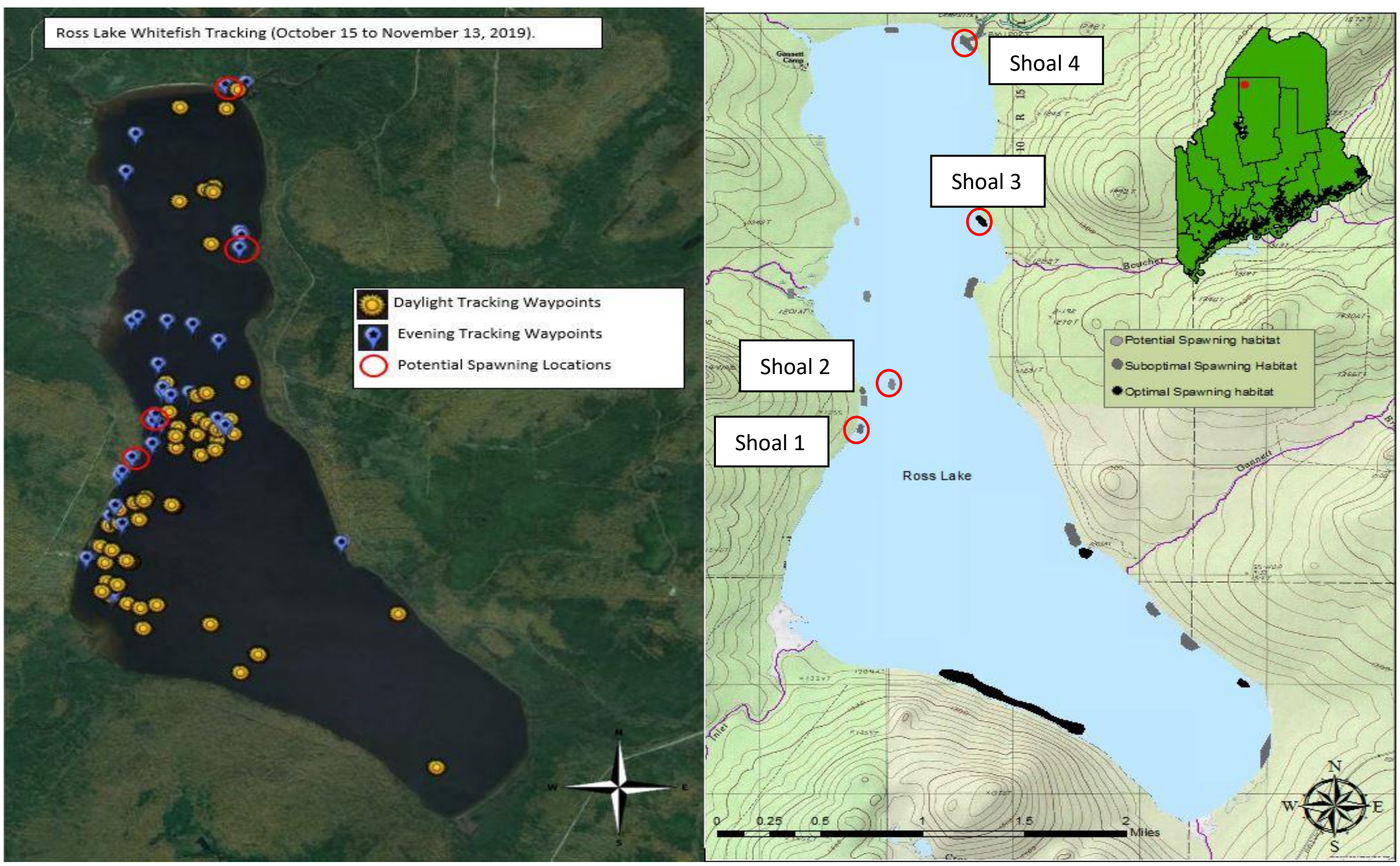


Figure 14. Day light and evening tracking locations of six Lake Whitefish in Ross Lake from October 15 to November 13, 2019 (Left) and potential spawning shoals based on previously mapped spawning habitat and fish proximity to this habitat (right).

Figure 15. Fish 049, 062, 071, 091, 121, and 151 moved to their respective locations post-surgery and did not move from these locations for the remainder of the tracking study.

Figure 16. Fish 040 tracking locations. This fish was found at the North end of Ross Lake in 25 ft of water during daylight tracking. Its largest movements occurred between 11/5 – 11/6. It was found in the evening near shoal 3 in 7 ft of water on 11/5, it moved across the lake to 15ft of water on 11/6. It was not found again until 11/11 in 30 ft of water towards the Neck of the lake where it remained for 2 days/evenings.

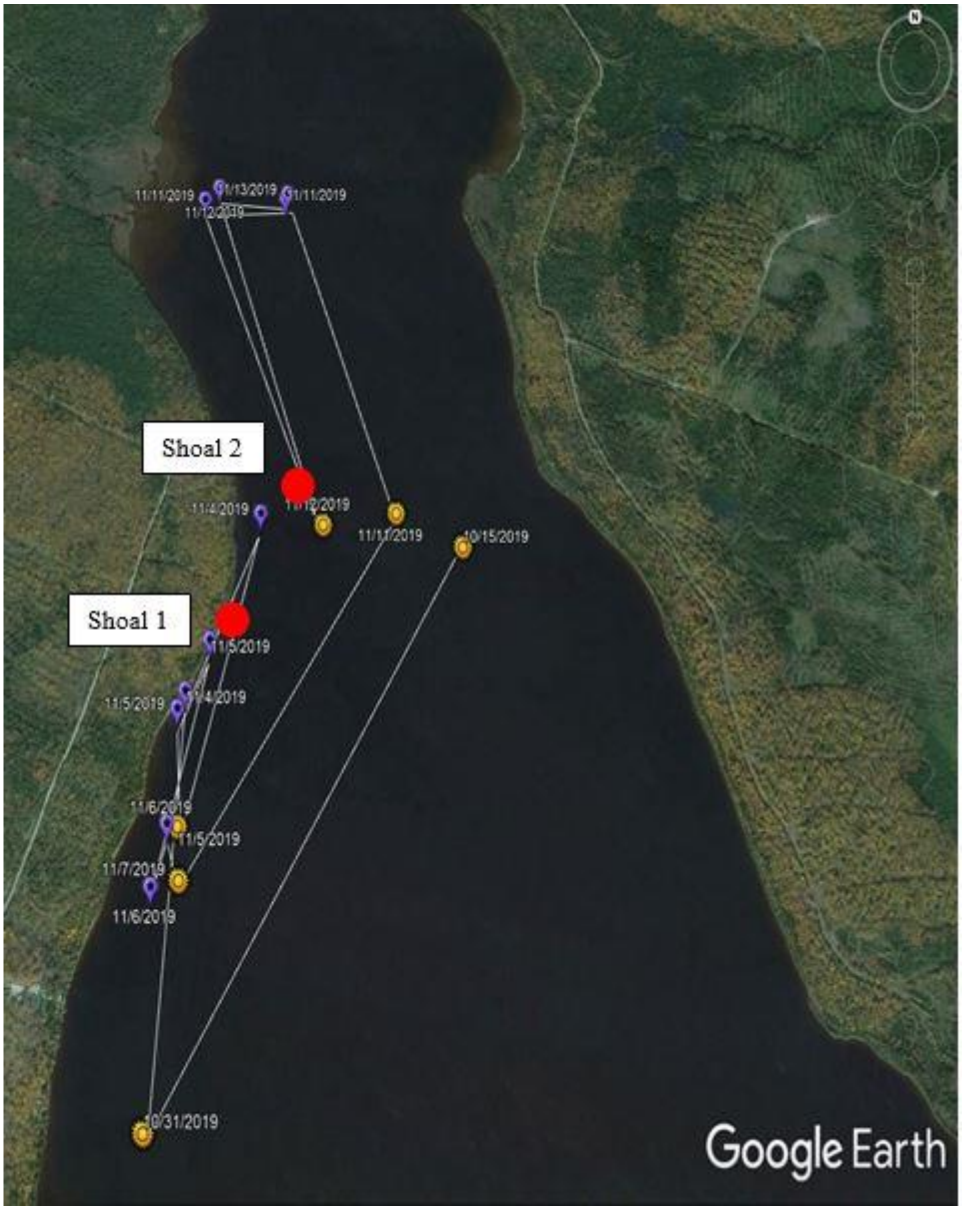


Figure 17. Fish 082 tracking movements. This fish was found in 30-45 ft of water near the Narrows or in front of Ross Lake Camps during daylight tracking. On the evening of 11/4 and 11/5 it was found in 5 to 10 ft of water south of shoal 1. On 11/6 and 11/7 it moved a few hundred feet south of this location in 20 ft of water. Between 11/11 and 11/13 it moved north towards Fools brook and was found in 8-15ft of water.

Figure 18. Fish 100 tracking locations. Fish 100 was found in 30-45 ft of water in the narrows of the lake during day light tracking. On 11/4 it moved to 10 ft of water north of shoal 3. on 11/5 – 11/6 it was found near shoal 4 at the mouth of Ross Lake outlet before it was found dead in the outlet stream on 11/7.

Figure 19. Fish 110 tracking locations. Fish 110 was found offshore of Ross Lake Camps in 20-45ft of water during daylight tracking. On 11/4 it was found north of shoal 1 in 15 ft of water. On 11/5 it moved to 10 ft of water in front of Ross Lake Camps. Between 11/7 – 11/13 it was found offshore of Ross Lake Camps in 20-40 ft of water during day/evening tracking.

Figure 20. Fish 131 tracking movements. Fish 131 was found in the narrows of Ross Lake during daytime and evening tracking until 11/6. It moved north of shoal 1 on 11/6 to 15 ft of water. On 11/12 it moved to 30 ft of water offshore of Ross Lake Camps, then to 15 ft of water southeast of Fools Brook on 11/13.

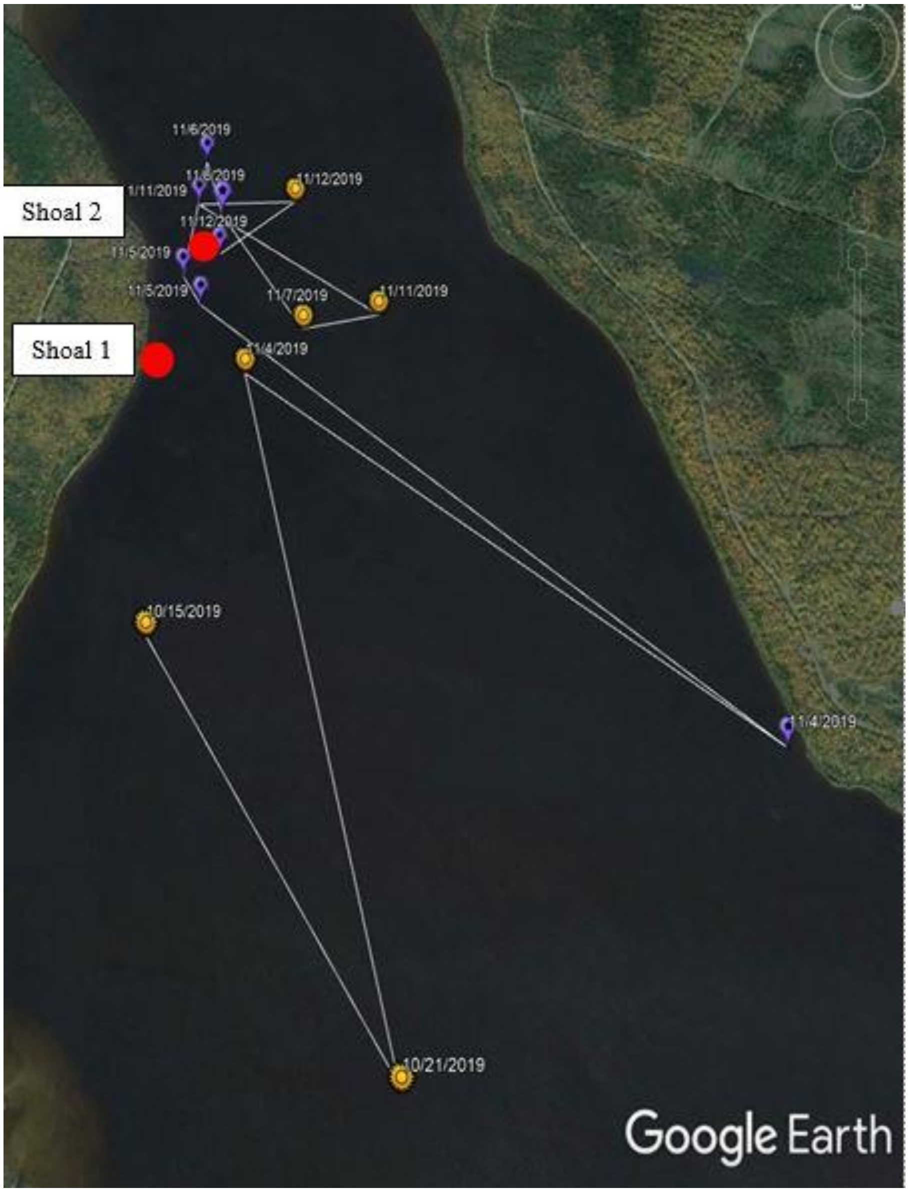


Figure 21. Fish 142 tracking locations. Fish 142 was in 40- 50 ft of water during daylight tracking east of Ross Lake, North of the Inlet stream and in the Narrows of the lake during daylight tracking. Largest movements occurred on 11/4 – 11/5. It was found north of Baker point on 11/4 in 8 ft of water. On 11/5 It moved to 15 ft of water near shoal 1. It remained near shoal 1 and the Narrows of the lake between 11/6-11/13.

Trawling- Larval Lake Whitefish

128 Larval whitefish and 1855 larval smelt were captured in Ross Lake, Haymock Lake, Clear Lake, Crescent Pond, and Second Musquacook Lake during spring larval trawling from 2015 to 2020. Ross Lake had the highest larval whitefish numbers in larval trawls of all lakes with 25 larval whitefish caught in 2017, 34 larval whitefish caught in 2019, and 30 larval whitefish in 2020 (Table 3). Haymock Lake had the second highest total catch of larval whitefish in 2018

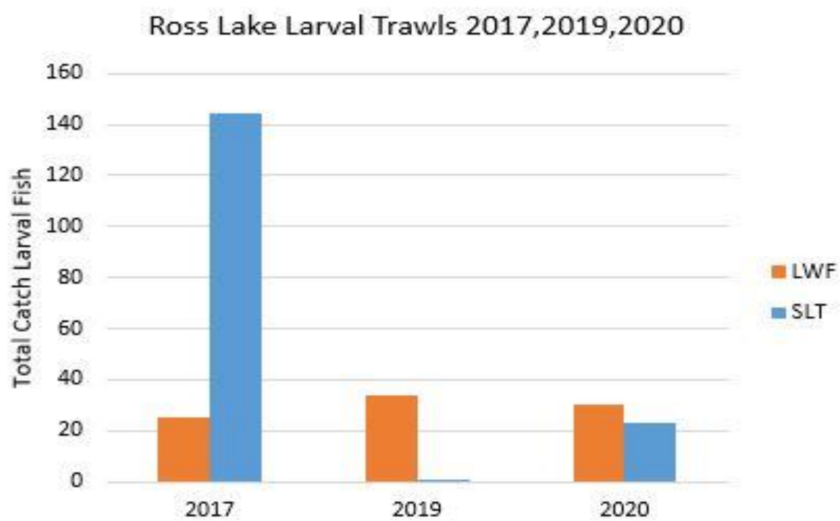
with 17 larval whitefish, however total catch dropped in Haymock Lake to 2 larval whitefish in 2020. Clear lake had the third highest total catch of larval whitefish with 16 larval whitefish caught in 2016. Larval whitefish total catch in Clear lake dropped dramatically in 2019 and 2020 to 2 and 0 larval whitefish caught respectively. Total catch of larval whitefish in Second Musquacook Lake was low in 2016 and 2019 with only 2 and 0 larval whitefish caught in respective sampling years. No larval whitefish were caught in Crescent Pond during spring sampling in 2017, 2019, or 2020. In each lake where larval whitefish were captured, larval whitefish catch rates were the highest immediately following ice off (likely the time fish hatched) and declined in following sampling events (Table 3).

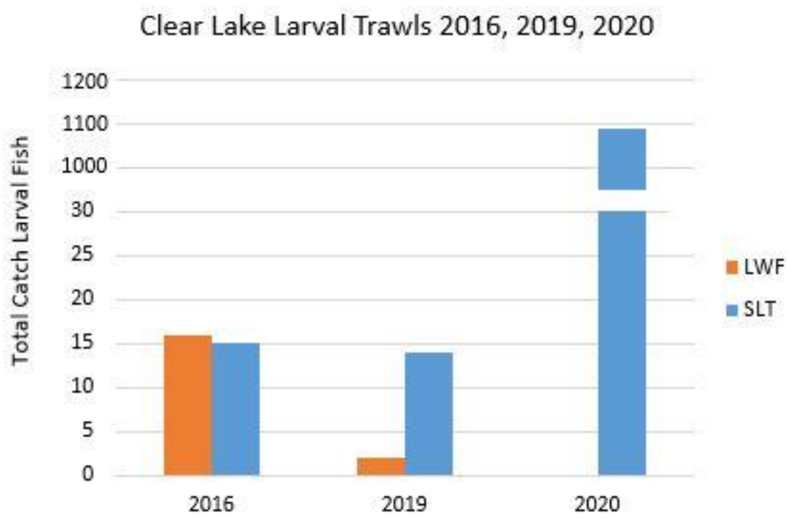
Larval smelt total catch was high in Crescent Pond and Ross Lake during the spring of 2017 with 304 and 145 larval smelt caught in trawl tows respectively (Table 3). In 2019, smelt total catch dropped dramatically in both lakes to 6 and 0 larval smelt respectively. In 2020 smelt densities remained low but rose slightly to 9 and 23 larval smelt respectively. Two hundred 18+ inch Lake Trout were translocated from Allagash Lake to Crescent Pond in the fall of 2018 and may partially explain the recent decrease in larval smelt abundance in Crescent Pond. An inverse trend in smelt abundance occurred in Second Musquacook and Clear Lake. Larval smelt total catch was low in Second Musquacook Lake with 10 larval smelt caught during trawl tows in 2015. Smelt total catch in Second Musquacook Lake increased in 2019 to 113 larval smelt. A similar trend was observed in Clear Lake, larval smelt total catch was low at 15 and 14 larval smelt caught during spring tows in 2016 and 2019 respectively. In 2020 larval smelt abundance increased dramatically in Clear Lake with 1093 larval smelt caught during spring larval tows. Of the 1855 larval smelt caught throughout this study, 1093 were caught in Clear Lake during 2020 spring sampling. In 2018 zero larval smelt were caught in trawl tows in Haymock Lake. In 2020 120 larval smelt were caught in Haymock Lake. These larval smelt along with numerous angler reports confirm the invasion and establishment of smelt into Haymock Lake around 2018-2019. If spawning smelt were present in Haymock Lake during 2018 they were undetected in larval trawls.

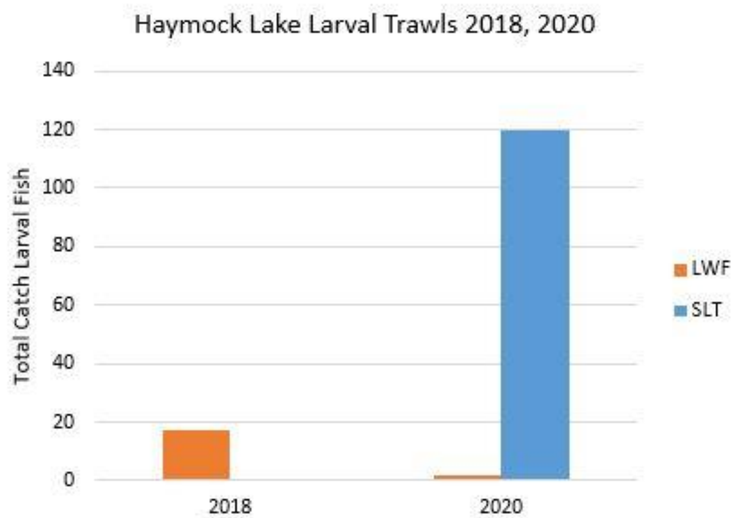
When we compare larval fish catches there appears to be an interesting pattern between larval whitefish and larval smelt abundance. Years with the highest larval whitefish densities coincide with years with the lowest smelt densities (Figure 22). As larval smelt densities increase, larval whitefish densities decrease. In some instances, like Clear Lake and Second Musquacook Lake, extremely high larval smelt densities coincide with absent larval whitefish numbers.

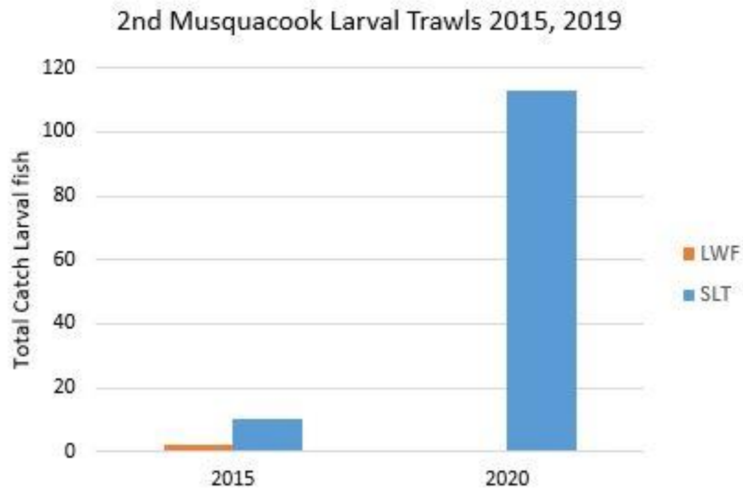
Table 3. Larval witefish and smelt (total catch) in Clear Lake, Crescent Pond, Haymock Lake, Ross Lake, and Second Musquacook Lake from 2016-2020. A hyphen (-) indicates the water was not trawled that spring.

		Clear Lake		Crescent Pond		Haymock Lake		Ross Lake		Second Musquacook Lake	
Year	Week	LWF	SLT	LWF	SLT	LWF	SLT	LWF	SLT	LWF	SLT
2015	1	-	-	-	-	-	-	-	-	1	0
	2	-	-	-	-	-	-	-	-	1	0
	3	-	-	-	-	-	-	-	-	0	10
	4	-	-	-	-	-	-	-	-	-	-
	total									2	10
2016	1	3	0	-	-	-	-	-	-	-	-
	2	6	0	-	-	-	-	-	-	-	-
	3	7	14	-	-	-	-	-	-	-	-
	4	0	1	-	-	-	-	-	-	-	-
	Total	16	15								
2017	1	-	-	0	0	-	-	5	0	-	-
	2	-	-	0	26	-	-	13	0	-	-
	3	-	-	0	6	-	-	6	35	-	-
	4	-	-	0	272	-	-	1	110	-	-
	Total			0	304			25	145		
2018	1	-	-	-	-	15	0	-	-	-	-
	2	-	-	-	-	2	0	-	-	-	-
	3	-	-	-	-	0	0	-	-	-	-
	4	-	-	-	-	0	0	-	-	-	-
	total					17	9				
2019	1	2	0	0	0	-	-	19	0	0	0
	2	0	0	0	0	-	-	5	0	0	0
	3	0	0	0	3	-	-	5	1	0	0
	4	0	14	0	3	-	-	5	0	0	113
	total	2	14	0	6			34	1	0	113
2020	1	0	0	0	0	2	0	17	0	-	-
	2	0	46	0	0	0	0	10	1	-	-
	3	0	946	0	0	0	54	1	19	-	-
	4	0	101	0	9	0	66	2	3	-	-
	total	0	1093	0	9	2	120	30	23		




Clear Lake Larval Trawls 2016, 2019, 2020
Total Catch Larval Fish
1200
1100
1000
30
25
20
15
10
5
0
2016
2019
2020
LWF
SLT


Haymock Lake Larval Trawls 2018, 2020
Total Catch Larval Fish
140
120
100
80
60
40
20
0
2018
2020
LWF
SLT



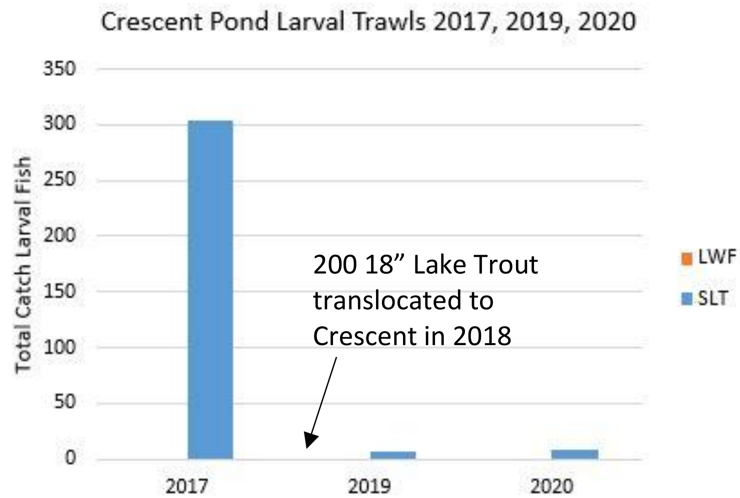


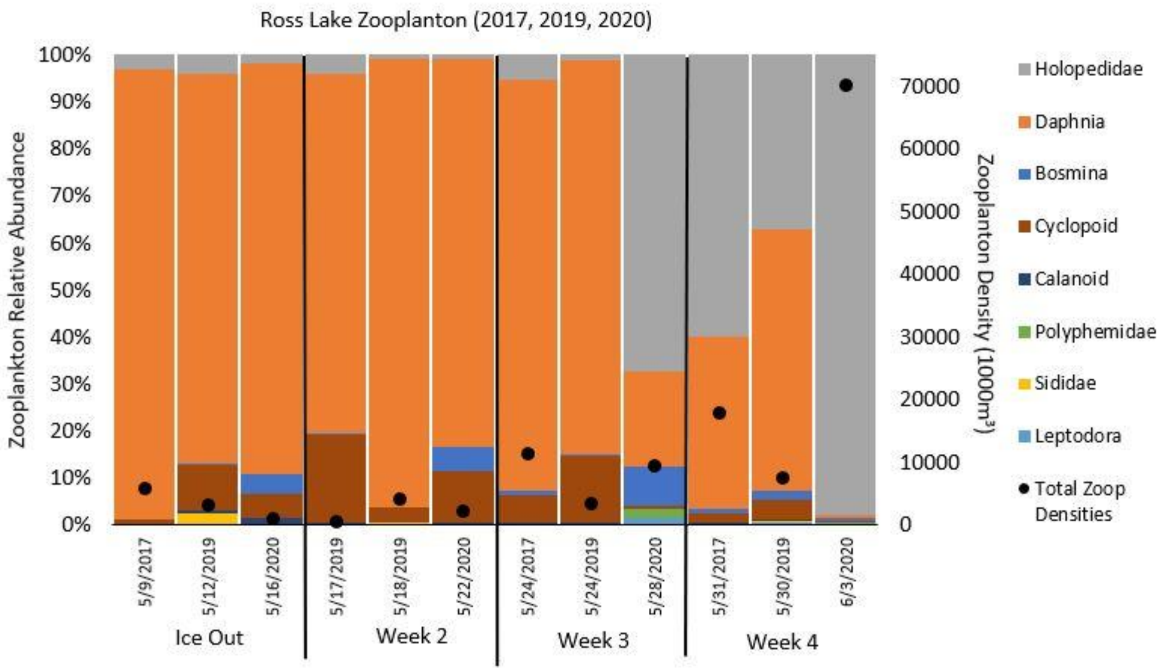
Figure 22. Larval whitefish and smelt total catch during spring trawling in Ross Lake, Clear Lake, Haymock Lake, Second Musquacook Lake, and Crescent Pond from 2015-2020. Values on the x-axis are not standardized for all graphs.

Trawling - Zooplankton Trawls

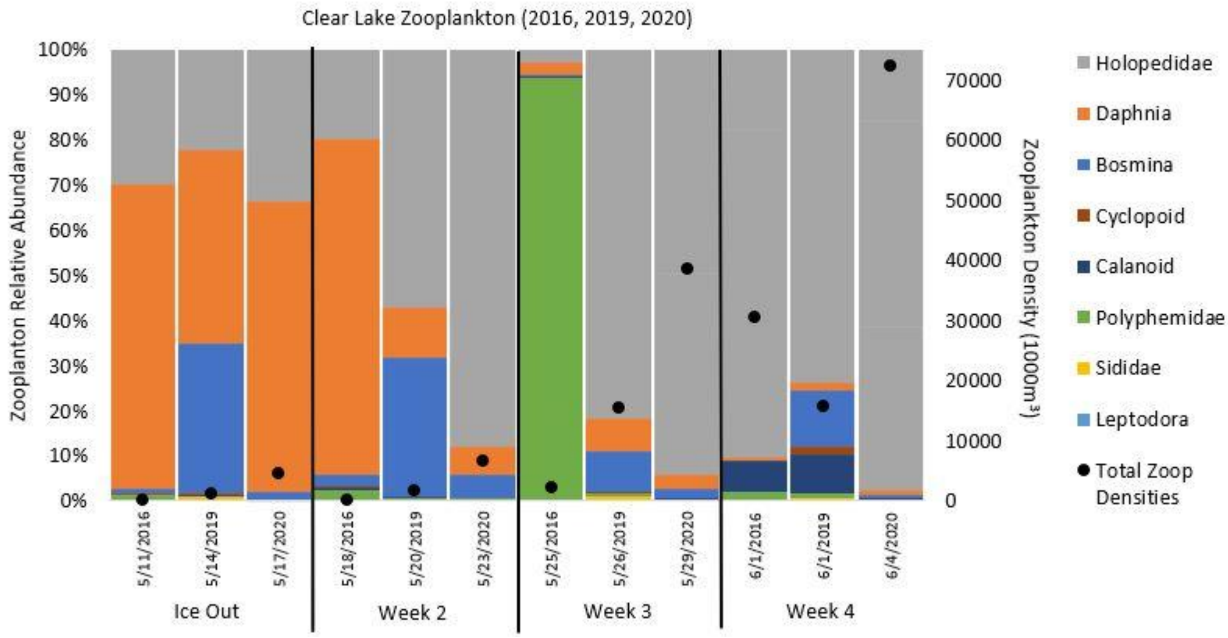
Zooplankton relative abundance and community assemblages varied across study waters. All zooplankton in each lake fell under the order Cladocera (*Daphnia*, *Holpedidae, Bosmina*, *Polyphemidae*, *Sididae*, *Leptodora*) or class Copepoda (*Cyclopoida* and *Calanoida*) and were counted and identified accordingly. Cladoceran’s, particularly Daphnia, Holopedidae, and Bosmina, made up 65-100% of the overall zooplankton abundances in all study waters (Figure 23). Conversely, copepods made up a small percentage of overall zooplankton abundances each week ranging from 0% to 35%. There was a noticeable shift in the dominant Cladocera group during the fourth sampling event (~May 25) in Ross Lake, Crescent Pond, and Clear Lake, and zooplankton abundances typically changed from predominately Daphnia to Holopedidae. Ross Lake copepod relative abundance was the highest among all study waters during the first three weeks of trawl tows and ranged from 1-20% relative abundance, cyclopoids were the dominant copepod in Ross Lake. Crescent Pond had the second highest copepod abundances during the first three weeks of trawling and ranged from 1-5% relative abundance and were predominately calanoids. Clear Lake, Second Musquacook Lake, and Haymock Lake had nearly absent copepod numbers during the first three weeks of trawling and ranged from 0-4% relative abundance. Copepod abundance increased in all waters except Ross Lake during the fourth trawling event (~June 1) but still only made up a fraction of the overall zooplankton abundance in most waters with the exception of Haymock Lake which had 35% copepod relative abundance by the fourth week of trawling in 2018 and 2020.

Zooplankton densities varied between and within study waters from 2015 to 2020 (Figure 23). Variations in zooplankton densities were likely influenced by differences in increasing water temperatures. Zooplankton densities were lowest during the first two weeks of trawling in all lakes when water temperatures were below 10°C and increased in density during the third and fourth week when water temperatures rose above 10°C. Crescent Pond had the highest zooplankton densities among study waters and ranged from 5,000 to 250,000 zooplankton/1000m^3. In comparison, Clear Lake, Haymock Lake, Ross Lake, and Second Musquacook Lake zooplankton densities ranged from 1,000 to 75,000 zooplankton/1000m^3.

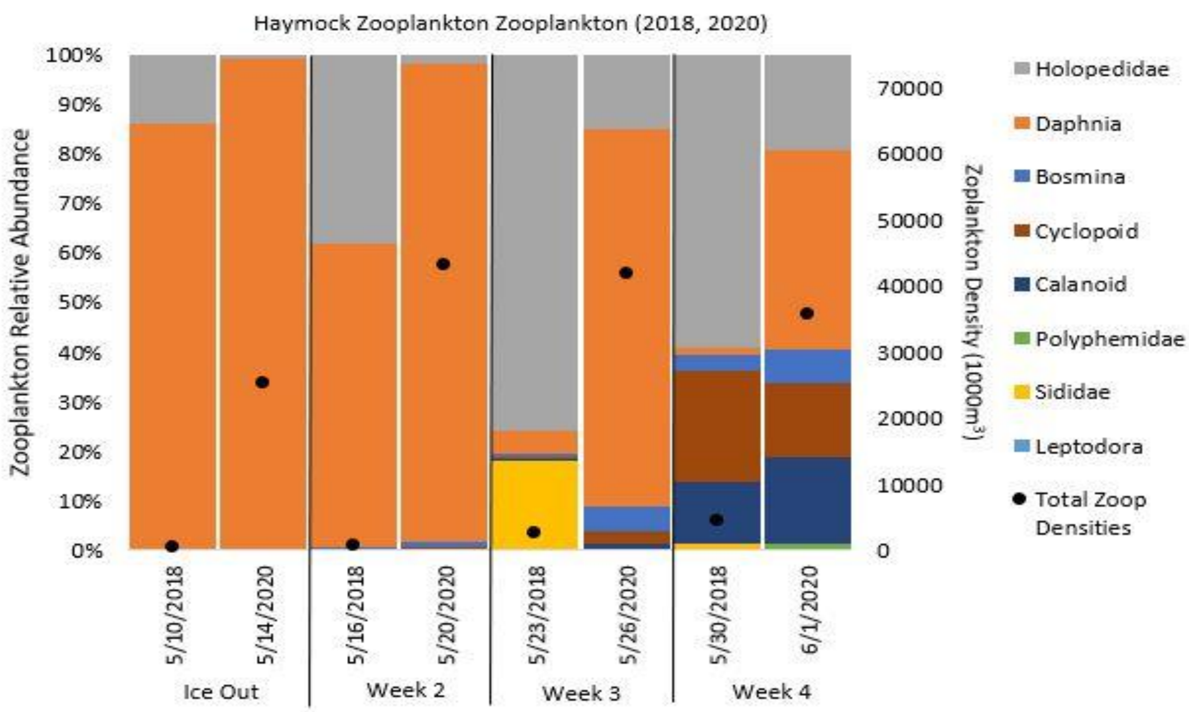
Although copepods made up a small percentage of the overall abundance in each water, there was an important distinction in the number of cyclopoid copepods observed in each lake (Table 4). Ross Lake consistently had high cyclopoid densities compared to other study waters, it also had the highest average cyclopoid densities within the first two weeks of trawling (Figure 24). Crescent Pond and Haymock Lake had low cyclopoid densities within the first two weeks of trawling in most years but increased dramatically in the third and fourth week of trawling. It is important to note that cycloploid densities were abnormally high in Crescent Pond during the spring of 2020 (Table 4). Two hundred Lake Trout were transferred from Allagash Lake to Crescent Pond in 2018 and changing fish community assemblages within Crescent Pond may partly explain a recent increase in observed cyclopoid densities. Cyclopoid copepods were nearly absent from Clear Lake and Second Musquacook Lake during the entirety of this trawling study.



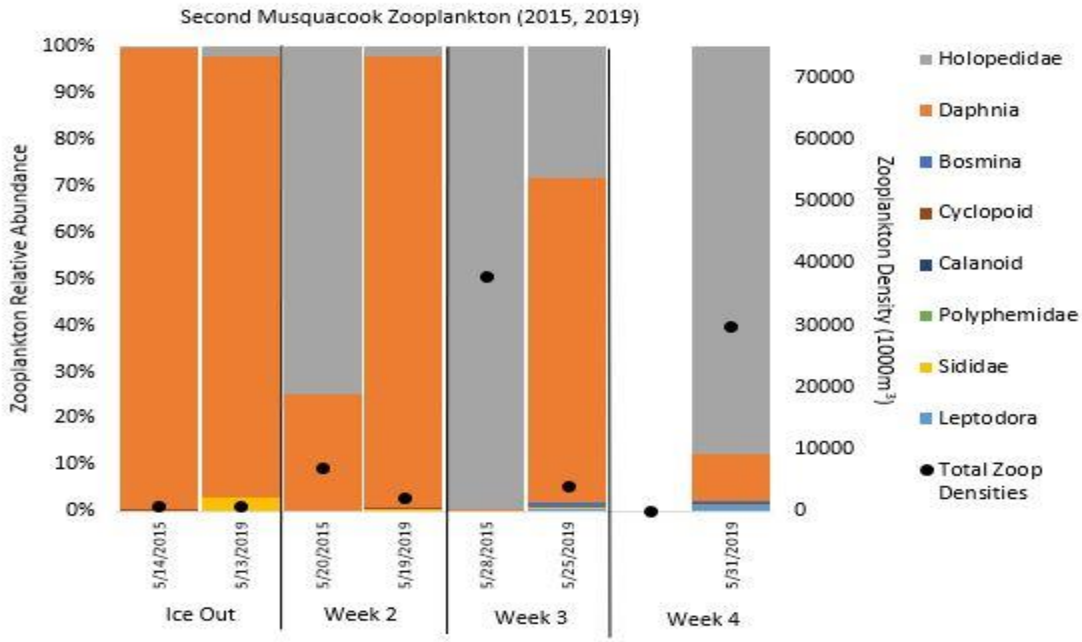
Ross Lake Zooplanton (2017, 2019, 2020)
Zooplankton Relative Abundance
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Zooplanton Density (1000m³)
70000
60000
50000
40000
30000
20000
10000
0
5/9/2017
5/12/2019
5/16/2020
5/17/2019
5/18/2019
5/22/2020
5/24/2017
5/24/2019
5/28/2020
5/31/2017
5/30/2019
6/3/2020
Ice Out
Week 2
Week 3
Week 4
Holopedidae
Daphnia
Bosmina
Cyclopoid
Calanoid
Polyphemidae
Sididae
Leptodora
Total Zoop Densities



Clear Lake Zooplankton (2016, 2019, 2020)
Zooplanton Relative Abundance
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
70000
60000
50000
40000
30000
20000
10000
0
Zooplankton Density (1000m³)
5/11/2016
5/14/2019
5/17/2020
5/18/2016
5/20/2019
5/23/2020
5/25/2016
5/26/2019
5/29/2020
6/1/2016
6/1/2019
6/4/2020
Ice Out
Week 2
Week 3
Week 4
Holopedidae
Daphnia
Bosmina
Cyclopoid
Calanoid
Polyphemidae
Sididae
Leptodora
Total Zoop Densities



Haymock Zooplankton Zooplankton (2018, 2020)
Zooplankton Relative Abundance
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
70000
60000
50000
40000
30000
20000
10000
0
Zoplankton Density (1000m³)
5/10/2018
5/14/2020
5/16/2018
5/20/2020
5/23/2018
5/26/2020
5/30/2018
6/1/2020
Ice Out
Week 2
Week 3
Week 4
Holopedidae
Daphnia
Bosmina
Cyclopoid
Calanoid
Polyphemidae
Sididae
Leptodora
Total Zoop Densities



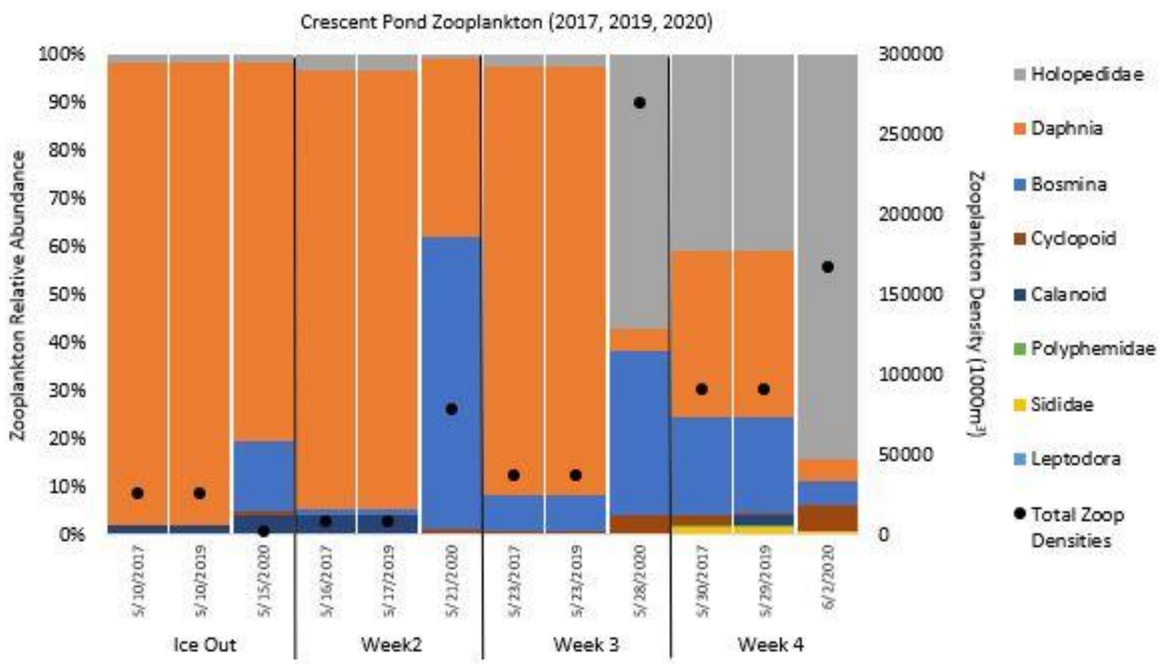


Figure 23. Zooplankton relative abundance and densities (zooplankton/1000m^3) during each week of trawling after ice off on Ross Lake, Clear Lake, Haymock Lake, Second Musquacook Lake, and Crescent Pond from 2015-2020.

Table 4. Cyclopoid Densities (1000m^3) each week following ice off in five Allagash drainage Lakes 2015-2020

	Year	Week 1	Week 2	Week 3	Week 4
	2017	74.6	109.6	657.1	319.1
Ross Lake	2019	316.7	129.0	508.7	333.0
	2020	63.0	272.3	44.8	174.3
	2016	0.6	0.9	1.0	0.6
Clear Lake	2019	3.2	3.5	32.3	267.0
	2020	6.8	13.3	54.3	53.8
	2017	67.8	23.9	99.5	2406.3
Crescent Pond	2019	67.8	23.9	99.5	664.6
	2020	12.0	484.5	10890.0	8806.5
	2018	0.0	1.1	11.0	985.4
Haymock Lake	2020	23.5	153.7	1049.4	5439.8
	2015	1.1	0.8	0.0	-
2nd Musquacook	2019	1.1	4.4	6.0	40.6

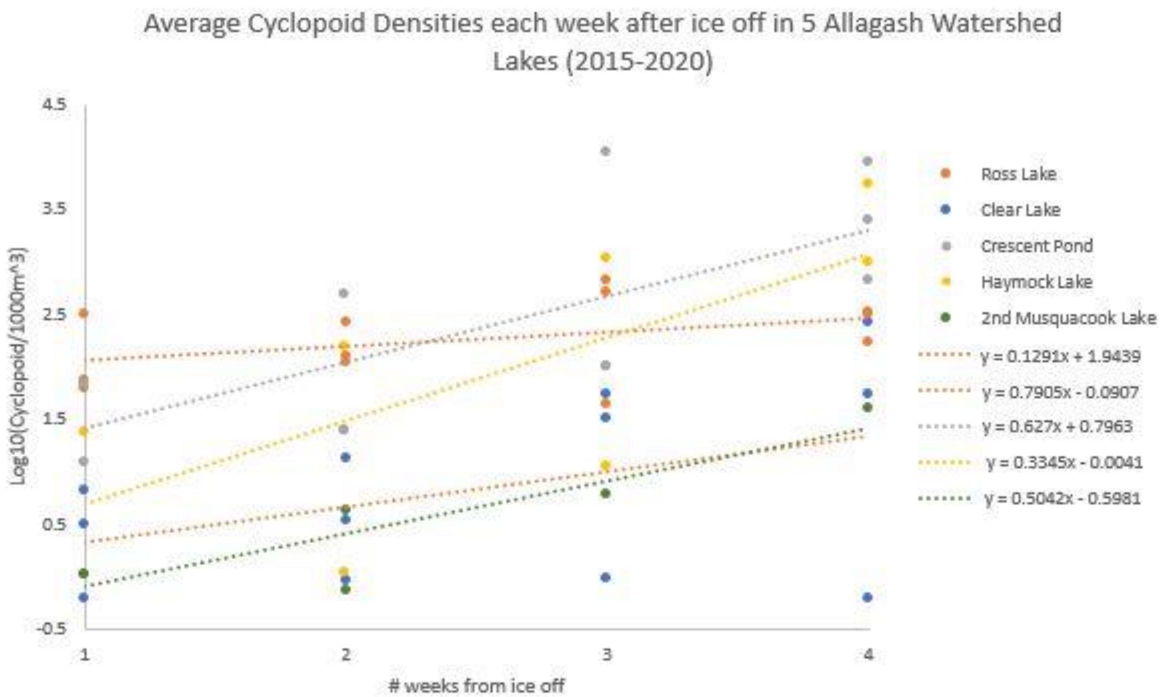


Figure 24. Log_{10}(Cyclopoid/1000m^3) each week after ice off in Ross Lake, Clear Lake, Crescent Pond, Haymock Lake and Second Musquacook Lake (2015-2020). This graph illustrates that cyclopoid densities are low following ice off but increase through time with the exception of Ross Lake (orange trendline) which appears to maintain relatively high cyclopoid densities throughout early spring.

Experimental Gillnetting:

Ninety-one gillnets were set in five study waters through the month of May in 2019 and 2020. Gillnets were fished for a total of 795.6 hours and resulted in the capture of 126 smelt. The highest catch rates in 2019 were in Clear Lake (0.08 smelt/hr), followed by Haymock Lake (0.03

smelt/hr), and Crescent Pond (0.02 smelt/hr; Table 5). No smelt were caught in gillnetting surveys in Second Musquacook or Ross Lake in 2019. Smelt lengths ranged from 78 to 107mm (3 to 4.2 inches) and nearly all smelt were caught in the ½” mesh size. No fish remains were identified in smelt stomachs in 2019.

We changed gear types in the 2020 season following the low catch rates of 2019 (Table 6). In 2020 we used three 200’x5’ 1” stretch mesh sinking gillnets. These nets were more effective at catching large smelt, which are known to be more effective larval predators (Gorsky and Zydlewski 2013), however, smelt catch rates via gillnets remained extremely low and no fish remains were identified in any smelt stomachs in 2020. Crescent Pond had the highest catch rates (1.2 smelt/hr), followed by Ross Lake (0.1 smelt/hr), only one smelt was caught in gillnets in Haymock lake (<0.1 smelt/hr), no smelt were captured in Clear Lake in 2020. High catch of smelt in Crescent Pond occurred on one evening near the mouth of a tributary where smelt were actively spawning, explaining the higher than normal catch rates in this lake.

To supplement catch rates of smelt in the spring of 2020 we used side-scan sonar to locate schools of baitfish. These concentrations of baitfish were typically found mid water column. We suspect low catch rates of smelt in gillnets is likely a product of smelt actively feeding higher in the water during early spring when waters are well mixed, and a thermocline has not been established. Additionally, smelt in these waters may not have been susceptible to our gillnet mesh sizes.

Table 5. Number of smelt caught in gillnetting surveys for each sample lake. Gillnetting surveys took place between May 10 and June 7, 2019.

	#Sets								
Lake	Floating	Sinking	Depth range (ft)	Mesh Size	'otal Net Length (ft	Hours Fished	Smelt Caught	Min/Max Length (mm	Fish/hr
Haymock	10	11	8-45	1/2"-3/4"	1520	222	7	90-107	0.0
Clear	9	1	6-35	1/2"-3/4"	800	173	13	81-99	0.1
Ross	5	2	6-28	1/2"-3/4"	600	93	0	-	0.0
Cresent	3	2	6-30	1/2"-3/4"	450	63	1	78	0.0
2nd Musquacook Lake	1	0	7-10	1/2"-3/4"	100	16.5	0	-	0.0

Table 6. Number of smelt caught in gillnetting surveys for each sample lake 2020. Gillnetting surveys took place between May 14 and June 4, 2020.

	#Sets								
Lake	Floating	Sinking	Depth range (ft)	Mesh Size	'otal Net Length (ft	Hours Fished	Smelt Caught	Min/Max Length (mm	Fish/hr
Haymock	0	12	10-45	1"	1520	96	1	109	0.0
Clear	0	10	20-60	1"	800	40	0	-	0.0
Ross	0	15	10-50	1"	600	120	6	130-165	0.1
Cresent	0	10	10-45	1"	450	80	98	125-155	1.2

Lake Whitefish Age Structure

A total of 371 Lake Whitefish were captured from 15 waters in northern Maine from 2014 to 2020 for age analysis. Lake Whitefish total lengths ranged from 5 to 23 inches. A list of these waters with their respective age data was constructed to inventory age information among Lake Whitefish waters and to assess population age structure and whitefish recruitment (Table 7).

A small sample size (n=<20) of Lake Whitefish were captured from 11 of these waters. First, Second, Third Musquacook Lake, Big Indian Pond, Crescent Pond, Haymock Lake, and Spider

Lake were extensively sampled for Lake Whitefish age analysis. A low sample of individuals collected in these lakes is likely a result of low Lake Whitefish densities. Ages from these waters ranged from 1+ to 45+ year old fish. Most of these low-density populations were represented by stocks of older age fish (10+ years) with large gaps between age classes suggesting recruitment failure between years. Lake Whitefish in Upper Sysladobsis were collected through routine gillnetting, only six Lake Whitefish were caught. Given the low sample of whitefish caught and their relatively old age (10+) whitefish are presumed to be in low abundance in Upper Sysladobsis and are likely experiencing some degree of recruitment failure, although more information is needed from this population to make a stronger case.

Lake Whitefish were incidentally caught through routine gillnetting or experimental angling in East Grand Lake, Big Pleasant Lake, and Harrow Lake. Low sample size of whitefish collected from these lakes (n=13, 12, 2 respectively) is likely related to low sampling efforts and not directly related to Lake Whitefish abundance among these waters. Harrow Lake and Big Pleasant Lake are two of four remaining Lake Whitefish populations in the state of Maine that do not harbor smelt. East Grand Lake supports a small Lake Whitefish fishery in the presence of smelt and age classes from our sample of fish suggest recruitment is occurring with fish representing ages classes from 2 to 15 years old.

Ross Lake, Clear Lake, West Grand Lake, and Lower Jo Mary Lake had sample sizes of fish greater than 20 and ranged from 23 to 68 fish among sampling years. Ross Lake and West Grand Lake had the highest sample of Lake Whitefish among waters. Fish from these populations represented most year classes with little evidence of recruitment failure between years and are presumed healthy in the presence of smelt. Clear Lake and Lower Jo Mary Lake samples were represented of strong age classes with gaps of recruitment between years suggesting recruitment failure in these waters.

124 otoliths collected from Ross Lake from 2016-2020 were used for back calculated length at age measurements. Age frequency data show a decreasing number of whitefish with increased age, except for 9 and 10-year-old fish (Figure 25). At this age Lake Whitefish are more susceptible to creel census as they approach the 18-inch minimum length limit on Ross Lake which explains the spike in 9-10-year-old fish. Lake Whitefish in Ross Lake exhibit fast growth rates early on reaching 11 inches by age 3 (Figure 26). Growth rates decreased around age 4 likely coinciding with sexual maturity. Whitefish grew roughly 1 inch a year from age 4 to 9 until they reached approximately 17.5 inches. After age 9, growth rates continue to decrease with increasing age, but variability in length-at-age increased dramatically with increasing age.

Table 7. List of Lake Whitefish waters where otolith age data exists and individual age data for each fish.

				AGE																																								
n	Lake	Water Code	Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
4	1st Musquacook	1914	2020											1		1					1	1																										
9			2014						1	1				3							1	3																										
-			2015	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	2nd Musquacook	1916	2017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12			2019											1	3			1	2	4	1																											
4			2020															1	1		1							1																				
4			2014											1	3																																	
-			2015	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	3rd Musquacook	1918	2016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13			2019							1						1	2	4	2	2																												1
4	Big Indian Pond	2866	2020							1		1				1													1																			
15	Big Pleasant	2756	2015										1		2	1	3	5	2	1																												
25			2014				1	3				1	5	4			1	2	1	3	2	1													1													
-			2015	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2016	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	Clear Lake	1938	2017	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
-			2019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29			2020			12	14			2													1																									
4			2017																											1					1		1	1										
-			2018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0	Crescent Pond	2964	2019	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
0			2020	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	East Grand Lake	1070	2019		2		1			1																																						
9			2020						1		1		2	1		1	1	1											1																			
2	Harrow Lake	1934	2016		2																																											
11			1994									1	2	1	1	1	1						1			1		1			1																	
5	Haymock Lake	2814	2019			3	2																																									
8			2020				2	2	2	1	1																																					
23	Lower Jo Mary Lake	984	2019					1		2	8	2	3				5	1		1																												
25			2016	3	6	8	2		1	1	1		1				1					1																										
18			2017							2	3	6	5	2																																		
0	Ross Lake	1888	2018	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
49			2019		1	2	12	6	8	3	5	1	4	4		1				1	1																											
56			2020	10		6	5	2	3	5	3	9	3	1	1	4	1	1							1	1																						
12	Spider Lake	2758	2020	9		1		1													1																											
6	Upper Sysladobsis Lake	4688	2019										4	1							1																											
33	West Grand Lake	1150	2019			2	10	2		1	1	2	5	4	1	3		1		1																												

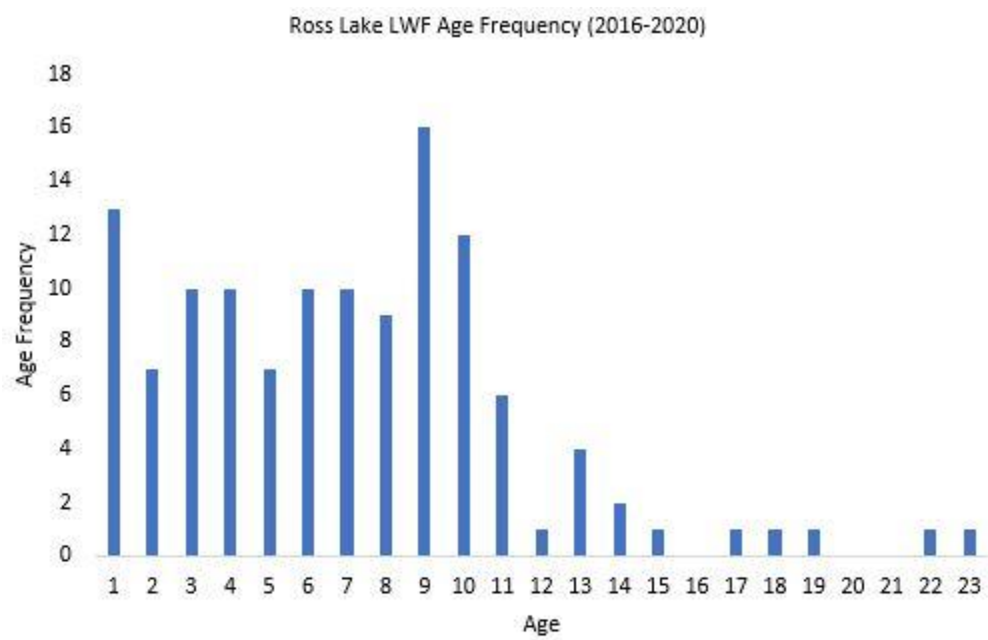


Figure 25. Lake Whitefish age frequency, Ross Lake, 2016-2020.

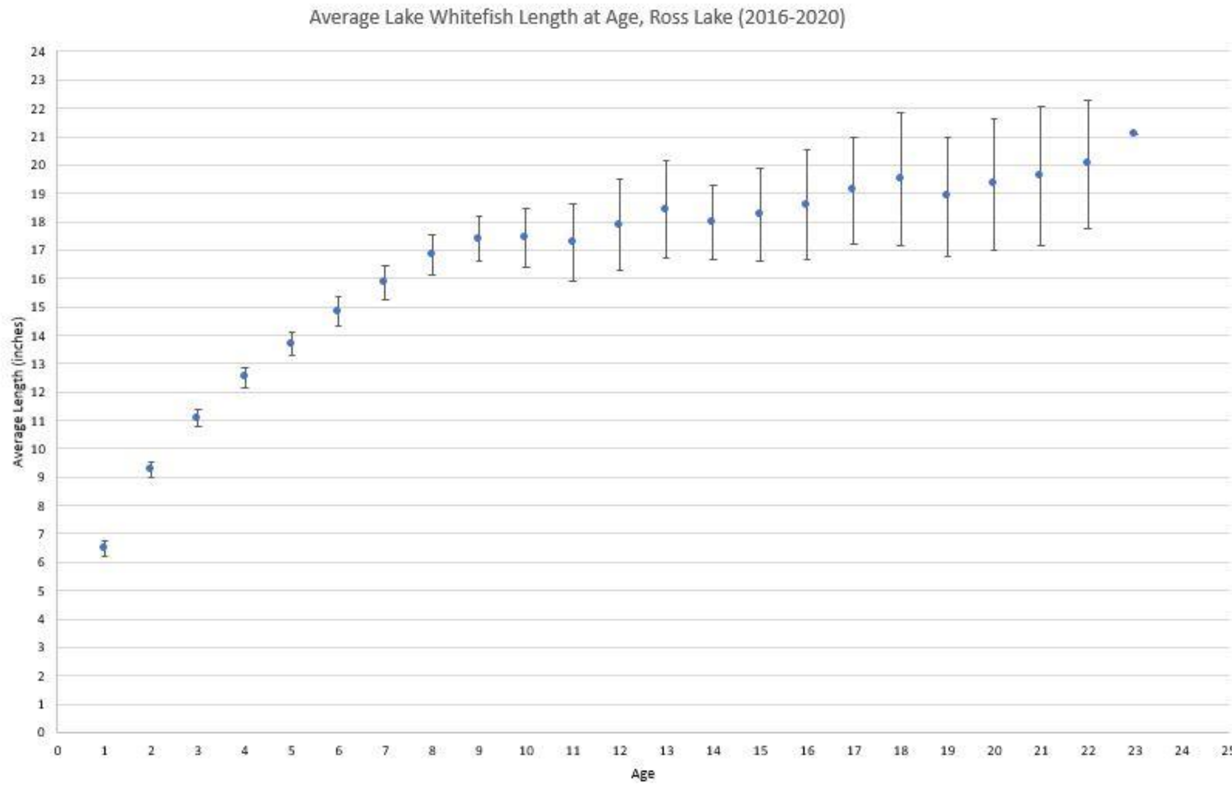


Figure 26. Average length-at-age for Ross Lake whitefish based on back-calculated otolith aging (2016-2019).

DISCUSSION

Early Lake Whitefish survival and recruitment is influenced by several different factors, including quality of spawning habitat, food availability for post hatch larval fish, and predation by adult smelt on larval fish (Fudge and Bodaly 1984, Taylor and Freeberg 1984, Loftus and Hulsman 1986). Our research focused on investigating how these mechanisms influence northern Maine Lake Whitefish populations. We documented available spawning habitat on six Lake Whitefish waters and attempted to document spawning use through artificial egg mats, used radio telemetry in Ross Lake to document fish movements during the spawning season, monitored larval whitefish abundances and food availability via larval trawling in the spring, collected adult smelt via gillnetting to analyze their diets, and collected sagittal otoliths to investigate whitefish age structure and recruitment failure among Northern Maine Lake Whitefish populations.

We found that Lake Whitefish recruitment varied widely among northern Maine whitefish populations. Age data revealed several whitefish populations that exhibited prolonged recruitment failure spanning 10 years or longer while other populations displayed marginal or no recruitment failure. Evidence suggests smelt abundance influences whitefish recruitment in these waters. We suspect that smelt contribute to observed variations in zooplankton densities in larval trawls and may explain the lack of food availability for post hatch whitefish and the subsequent lack of recruitment in many of these waters. Predation by adult smelt on larval whitefish was not documented in this study suggesting that predation by smelt may be lower than initially thought. Although predation by smelt was not observed it remains to be a potential threat to Lake Whitefish populations in Maine. Spawning ground surveys revealed variations in the amount of spawning habitat between study waters. Lake Whitefish populations that have access to abundant spawning habitat appear to exhibit more frequent recruitment than those waters with limited spawning habitat. Our results suggest that spawning habitat abundance likely plays an important role in mitigating whitefish-smelt interactions.

The quality and abundance of available spawning habitat varied among study waters. For instance, spawning ground surveys in Ross Lake revealed a high abundance of optimal spawning habitat around the lake shoreline. In contrast, Crescent Pond and Haymock Lake contained a low abundance of spawning habitat, all of which was classified as suboptimal or potential. Second Musquacook Lake, Clear Lake, and Big Indian Pond had quality spawning habitat, but it was confined to a few small areas. The recruitment success, or lack thereof, among these whitefish populations may be linked to the quality and abundance of observed spawning habitat. Substrate type is known to influence egg retention and survival (Freeberg et al. 1990; Begout et al. 1999; Fudge and Bodaly 1984), and high egg survival rates as a result of optimal spawning habitat may lessen the impacts smelt have on whitefish recruitment, particularly during years of low smelt abundance. Furthermore, the stressors associated with smelt interactions may be exacerbated when spawning ground limitations are present. Studies have shown that predation risk by smelt on larval fish is high when there is an overlap in spawning habitat between the two species (Loftus and Hulsman 1985; Myers et al. 2009). Given the low availability of spawning habitat in many of our study lakes, coupled with their relatively small waterbody size, it is likely that whitefish and smelt use the same spawning sites or are close in proximity to one another increasing predation risk or competition and may partly explain recruitment failure among many Lake Whitefish populations in northern Maine.

Spawning ground limitations may also have impacts on other species important to whitefish recruitment. Lake Trout use similar spawning habitat as Lake Whitefish and evidence suggests that high Lake Trout densities positively impact whitefish recruitment by regulating smelt abundance. Limited spawning habitat may influence Lake Trout recruitment impeding their ability to regulate smelt-whitefish interactions. Many of our study waters with limited spawning habitat have historically relied on supplemental stocking of Lake Trout to support their trout populations and increase angler harvest opportunity. Larval trout, like whitefish, are subject to predation by smelt which has been identified as one factor leading to low Lake Trout recruitment in Lake Champlain (Riley and Marsden 2009). Recognizing these spawning ground limitations should be an important consideration when interpreting whitefish recruitment failure and can be useful when prioritizing at risk populations.

While egg mat surveys were not effective in characterizing total spawning ground use among study waters, we did identify key spawning sites used by Lake Whitefish in two lakes, and documented spawn timing. Lake Whitefish eggs were collected on two windswept rocky shoals in Clear Lake, and in Second Musquacook's inlet stream. The onset of spawning began on November 5, 2018 in Clear Lake when water temperatures dropped to 5°C, and on November 12, 2018 in Second Musquacook inlet when water temperatures reached 3°C. Our results are similar to other findings, whitefish have been observed spawning between 0.5°C and 10 °C but typically spawn when temperatures drop below 6°C (Dunford 1980). Eggs collected under the ice in Clear Lake suggest that whitefish continue to spawn as water temperatures approach freezing.

The results of our egg mat study shed light on variations in spawning life history strategies between Lake Whitefish populations in Northern Maine. Whitefish were documented using clean well layered cobble in both tributary streams and windswept rocky shoals, a common finding among Lake Whitefish populations (Basely 2018, Begout et al 2011, Fischer et al 2018). Utilizing multiple spawning life history strategies may be another factor important to whitefish recruitment in the presence of smelt. Similar to an abundance of spawning habitat, having access to a diversity of different spawning life history strategies within a lake may buffer larval whitefish and smelt interactions and increase recruitment among whitefish populations that have access to a variety of spawning habitat. This may partly explain why some whitefish populations, such as Ross Lake fare better than others in the presence of smelt. However, more information on spawning ground use and recruitment in many waters is needed to make a stronger case between the two. The low occurrence of eggs collected on shoals in most lakes may be a product of low Lake Whitefish densities, inaccurate spawning habitat surveys, low percentage of shoal coverage by egg mats, or a combination of the three. In order to answer the question surrounding spawning ground use and its impacts on whitefish recruitment, future studies should consider covering a higher percentage of spawning shoals (if feasible) to more accurately determine their use. Where spawning habitat is abundant, egg mats should be used in combination with other sampling methods such as trap nets, electrofishing, acoustic telemetry, and scuba diving.

Radio telemetry data from Ross Lake suggests Lake Whitefish use multiple different spawning locations in the lake. Given Ross Lake's healthy whitefish population, this may be one example of a lake that illustrates the influence abundant spawning habitat has on whitefish recruitment. Vertical movements from deep to shallow water during evening hours suggest whitefish in our study were spawning between November 4 and November 13, 2019. Thermal conditions in Ross Lake during this time were appropriate for whitefish spawning. Lake whitefish typically spawn in Allagash waters in early November when water temperatures drop below 6°C (Basely 2001, Whitaker and Wood 2019). Additionally, whitefish spawning movements in a small boreal lake in Canada found near-shore movements to occur during a short 15-day window with peak spawn movements occurring 5-6 days immediately before ice covered the lake (Begout et al. 2011). This is in accordance with other studies and aligns with our tracking study as peak in-shore movements occurred between November 4 and 6 prior to ice cover on November 14, 2019. Whitefish were also tracked near or on four spawning sites identified through spawning ground surveys in 2018, suggesting they use multiple spawning sites in Ross Lake.

Behavioral differences in fish movements also occur between sexes of whitefish. Studies have shown swimming depth discrimination between male and female spawning whitefish. Male spawners typically arrive early and remain on shoals longer, whereas females only visit spawning shoals to deposit eggs and retire to deeper water (Beagout et al. 2011, Dabrowski 1981, Luczynski 1986). Sexes were not identified during radio tag surgeries in our study to limit stress on whitefish, however sex discriminant movements may explain differences in near-shore movements among our whitefish. For instance, fish 040, and 131 were on or near shallow spawning habitat during one evening of tracking (November 4 and November 6, respectively) before returning to their deep-water habitat. Conversely, fish 082, 142, and 100 were found on or near shoal habitat for a minimum of 2 consecutive evenings, with fish 142 remaining near shoal habitat for 7 consecutive evenings.

This radio telemetry study was subject to a few limitations. Lake Whitefish are extremely sensitive to capture, and surgeries likely resulted in high mortality of fish limiting the number of trackable fish to 6 whitefish. Despite these limitations, whitefish movements during our radio tracking study provide valuable information on spawning movements in Ross Lake. Spawn timing appears to occur during a short window when temperatures in the lake approach freezing and likely occurs at a similar time to other populations in the region (Whitaker and Wood 2019). High congregation of fish towards the eastern shoreline in the neck of the lake, towards the mouth of the outlet, and on the western point of the lake north of Bouchey Brook, suggest whitefish spawn in close proximity to these locations. Future work should focus on identifying whitefish spawning use at these different sites through trap netting, scuba diving, or egg collection mats.

Larval fish were captured via larval trawls in Ross Lake, Clear Lake, Haymock Lake, Second Musquacook Lake, and Crescent Pond from 2015-2020. Larval whitefish were captured in each lake except Crescent Pond during this time providing evidence of successfully spawning whitefish in waters where it wasn’t documented by egg collection mats. In all lakes where larval whitefish were captured, high larval whitefish abundance coincided with low larval smelt abundance. When smelt abundance increased, larval whitefish abundance decreased or were absent in trawl samples. Given the large size of larval whitefish compared to larval smelt and the difference in hatch timing between them, direct competition from larval smelt is not likely to be a driving factor behind low larval whitefish densities. Rather, larval fish abundances may provide an index of biological conditions favoring either of the two species and their potential impacts on whitefish recruitment. Prolonged years of high larval smelt abundances and low larval whitefish abundance may be a signal of recruitment failure.

Smelt are an important predator of zooplankton and high smelt densities can drastically change zooplankton abundances and subsequent food availability for larval fish (Evans and Loftus 1987). Larval whitefish require a specific diet of zooplankton, feeding almost exclusively on cyclopoid copepods during the first month of growth until they are large enough to transition to other sources of food (Teska and Behmer 1981; Freeberg et al. 1990; Chouinard and Bernatchez 1998; Johnson et al 2009). Chouinard and Bernatchez found that 98% of larval whitefish diets in Cliff Lake, Maine (smelt are absent from this lake) consisted of these cyclopoids. Other studies have shown the importance this food resource has on larval whitefish survival. For instance, larval whitefish exposed to food limitations in a laboratory setting experienced 100% mortality within one week of the onset of exogenous (post yolk sac) feeding (Taylor and Freeberg 1984; Brown and Taylor 1992). Cyclopoid copepod abundances were nearly absent in Second Musquacook Lake, Clear lake, Crescent Pond, and Haymock Lake during the first two weeks of trawling in most sampling years. We suspect the lack of available Cyclopoid copepods in these waters in early spring is linked to smelt interactions and may explain the absence of larval whitefish, and the subsequent lack of recruitment in these lakes. Conversely, Ross Lake had the highest number of cyclopoid densities early on, and larval whitefish were caught throughout the trawling study. In the spring of 2020, Crescent Ponds cyclopoid densities increased exponentially in comparison to previous sampling years. Two hundred 18+ inch Lake Trout were transferred to Crescent Pond in the fall of 2018 in an effort to reduce smelt numbers. Larval smelt densities have declined in Crescent Pond since this transfer. Although no larval whitefish have been captured in Crescent Pond the recent increase in cyclopoid copepods and decline in larval smelt suggest conditions are becoming more favorable for early life history stages of whitefish and provides evidence to explain how Lake Trout may positively impact whitefish recruitment.

It is important to mention that zooplankton densities and community assemblages are also strongly influenced by temperature, growing season, wind, sun exposure, and the type of zooplankton present (Shuter and Ing 1997) and likely contributed to variations in overall zooplankton densities observed in our study. For instance, Crescent Pond, our smallest lake by water volume warmed quickly and zooplankton densities increased more rapidly with increasing water temperatures. Wind and sun exposure likely influenced zooplankton densities within waters as well. Zooplankton densities were typically the highest on sunny days or windy days. Although these environmental factors are important for explaining zooplankton production and can certainly influence larval whitefish survival and recruitment, fish community assemblages particularly smelt abundances are believed to be more impactful to zooplankton important to early whitefish survival.

Lake Trout abundance and their influence on smelt and whitefish densities may play an important role in other study waters as well. In 2016, Clear Lake's Lake Trout densities were considered to be very high based on catch rates and poor Lake Trout body condition, likely a result of low smelt abundance (Wood, MDIFW, personal communication). At this time, larval whitefish densities in larval trawls were the highest among sampling years in Clear Lake, and larval smelt densities were the lowest. MDIFW liberalized Lake Trout size and bag limits in Clear Lake in 2016 to manage for better size quality and provide angler harvest opportunity. Since this regulation change, larval smelt densities in Clear Lake have increased dramatically in larval tows as Lake Trout densities may have decreased. Subsequently, larval whitefish densities in Clear Lake have decreased to zero. Additionally, a sample of 33 whitefish were collected in Clear Lake for age analysis in 2020. This sample was almost entirely comprised of 3 to 4-year-old fish providing evidence of successful recruitment in 2016 and 2017 when Lake Trout and larval whitefish densities were high, and smelt densities were low. Similar trends in smelt, Lake Trout, and coregonid population dynamics have been observed in other systems (Gorman 2008, Krueger and Krabik 2005).

Lake Trout and smelt interactions may have important implications on lake whitefish recruitment in other study waters as well. Ross Lake, with its abundant spawning habitat and abundant forage base, has an abundant Lake Trout population which likely mediates smelt densities and may partly explain the abundance of larval whitefish and recruitment observed in this lake. Second Musquacook Lake has been supplemented with hatchery stocked Lake Trout for decades to support its sport fishery, but in recent years Lake Trout stocking has been drawn back to manage for higher size quality and a more robust smelt forage base. High smelt densities in Second Musquacook Lake in recent years may be another example where increasing larval smelt densities resulted in low to absent larval whitefish densities in 2015 and 2019. Smelt have recently invaded Haymock Lake, since smelt establishment larval whitefish densities have decreased illustrating the negative relationship smelt have on larval whitefish in this lake.

Predation by adult smelt on larval whitefish was not documented in this study. Given the low larval densities in many of these lakes, a large sample size of smelt would be needed to document predation. Smelt sampling via gillnets has proven to be a difficult endeavor particularly in early spring when predation on larval whitefish would be expected to occur. The window of predation is short, and typically occurs as smelt transition from their spawning grounds in early spring and resume active feeding. Catching smelt during this transitional window makes documenting predation even more challenging. Waters are well mixed in early spring before a thermocline is established and smelt are likely higher in the water column and less susceptible to sinking/floating gillnets used in this study. Additionally, in most of our study waters the impact of smelt predation may have occurred at a much higher rate decades ago, when whitefish were more abundant. Due to the low densities of whitefish, larval fish likely make up a very small percentage of smelt diets today, though smelt predation on larval whitefish is still believed to be a factor that influenced recruitment failure among these lakes.

Age information is important to monitoring fish population trends and provides valuable information on recruitment. Whitefish recruitment failure has been identified as the driving force behind declines across the state of Maine. However, limited information on the age and growth of many whitefish populations in Maine has made it difficult to accurately assess current recruitment levels. This study provides the first look at age data among 15 northern Maine Lake Whitefish Populations. Thirteen of these waters have invasive smelt and age data suggest that only three of the fifteen have sustainable levels of recruitment. In some of these waters, a more robust dataset will be necessary to better determine whether adequate recruitment is taking place.

The extent of recruitment failure varies among waters where it has been identified, but there appears to be a relationship between Lake Trout densities and whitefish recruitment in waters where both species occur. Samples collected from First, Second, and Third Musquacook Lakes were almost entirely composed of 10 to 19-year-old whitefish. The youngest fish observed in the Musquacook lakes was a 7-year-old fish caught in Third Musquacook Lake, and the oldest was a 45-year-old fish, also caught in Third Musquacook Lake. Fish < 10 years old were nearly absent from these populations, suggesting recruitment failure throughout the past decade. Lake Trout stocking rates were the highest in these lakes in the 1990's to early 2000's which coincides with age classes observed in our sample. Based on our findings elsewhere in this report the lack of recruitment in the Musquacooks Lakes may be related to the reduction in Lake Trout stocking.

Similar trends in Lake Trout densities and recruitment are observed in Clear Lake and Spider Lake. Recent angler creel census data from Spider Lake show a marked increase in Lake Trout catch rates, similar to what was observed in Clear lake prior to 2016. Age 1+ whitefish were captured via gillnetting in Spider Lake in 2020 marking the first evidence of whitefish recruitment here in decades. The suggested relationship between lake trout density and whitefish recruitment is certainly deserving of additional investigation.

Age data from Upper Sysladobsis Lake, Big Indian Pond, and Lower Jo Mary Lake suggest recruitment failure is taking place in these waters. More information is needed on fish community assemblages and their interactions with whitefish to better understand the cause of whitefish recruitment failure in these waters. Continued close monitoring will be necessary to develop conservation efforts for these whitefish populations.

Ross Lake, West Grand Lake, and East Grand Lake age structure data provide evidence of whitefish recruitment in recent years with little evidence of recruitment failure. These waters are large, contain an abundance of spawning habitat, and support healthy whitefish, Lake Trout, and smelt populations. Unlike Allagash waters, West Grand and East Grand Lake also support popular landlocked salmon fisheries, another important predator of smelt. Whitefish populations where age data confirms recruitment likely do not need any immediate management or conservation actions, rather these whitefish populations should continue to be monitored via age structure analysis to insure they remain healthy in the presence of smelt.

Age and growth trajectories from Ross Lake demonstrated a general pattern seen in many fish populations whereby rapid growth early in life results in early maturity, followed by a steep decline in growth rate. Ross Lake whitefish grow rapidly early on, reaching ~11 inches by age 3 before growth slows, likely with the onset of sexual maturity. Ross Lake whitefish typically reach ~18 inches between 10-12 years of age, the largest individual in our sample was 21 inches long and 23 years old. Ross Lake length-at-age data was almost identical to an unexploited Lake Whitefish population in Lake Pend Orielle, Idaho (Hosack and Hansen 2014) and similar to other lightly exploited populations in its region (Weaver et al 2018). Unexploited whitefish populations often occur at high densities with slow growth rates based on the common observation that such populations respond strongly to exploitation through increased growth, recruitment, and fecundity (Healey 1975, 1978, 1980). Additionally, commercially exploited populations, such as those in the Great Lakes experience some of the highest growth rates among whitefish populations. Ross Lake is lightly exploited and has a 1 fish bag limit with a minimum length limit of 18 inches which may partly explain its high whitefish density and relatively slow growth rates. Unlike unexploited whitefish populations but similar to exploited populations, Ross Lakes whitefish population had few older individuals (20+ years) which is most likely a product of these older individuals being harvested by recreational anglers once they reach legal length requirements. In theory, whitefish growth rates in Ross Lake would benefit from increased exploitation. However, little is known about the impacts invasive smelt have on growth and survival of whitefish in Ross Lake. Given the negative interactions smelt have on early life stages of whitefish in surrounding Allagash waters it is possible that increased exploitation of Ross Lake's whitefish population could have compounding effects on whitefish-smelt interactions, especially if conditions become more favorable for smelt and less favorable for whitefish. Rather, recognizing that conditions currently favor whitefish in Ross Lake is important for the persistence and conservation of this at-risk species and the population should continue to be managed conservatively and monitored routinely to protect and learn about this valuable resource.

Whitefish populations across their native range have been subject to numerous conservation efforts such as habitat improvement via artificially constructed spawning shoals, supplementation of whitefish stocking, and through invasive species suppression by manipulation of predatory fish abundances (Fischer et al 2018, McMurtry et al 1997, Gorman 2008, Kruegar and Hrabik 2005). Northern Maine whitefish populations present a unique opportunity for management and conservation of the species. With the exception of rainbow smelt introductions, northern Maine fish assemblages remain relatively intact, and many of these waters are relatively small in size and habitat complexity, allowing them to better respond to species and habitat related management activities.

Through this research we have identified smelt abundance as the predominant mechanism influencing whitefish recruitment and survival in northern Maine Lakes. Recent evidence suggests that Lake Trout densities may play an important role in smelt-whitefish interactions where populations overlap. Experimental manipulation of wild Lake Trout populations may be beneficial to select whitefish waters and warrants further investigation. Other management strategies, including a whitefish hatchery program or opportunities for manual smelt suppression or removal, may also be necessary to conserve and recover native Lake Whitefish populations in Maine.

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