

An Investigation of Lake Whitefish Spawning and Early Life History in the Allagash Watershed: Preliminary Results

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SUMMARY

Many of Maine's Lake Whitefish populations have experienced significant declines, including extirpations following the establishment of invasive Rainbow Smelt (hereafter smelt). Smelt are believed to influence early whitefish survival and recruitment. Several large waterbodies within the Allagash watershed are considered the last remaining stronghold of northern Maine whitefish, however, whitefish in many of these waters are at historically low numbers since smelt establishment. The objective of this research is to investigate lake whitefish spawning habitat use and availability, food availability for post hatch larval whitefish, and predation of larval whitefish by smelt in the Allagash watershed. We conducted spawning ground surveys on six whitefish waters to investigate spawning habitat availability, used artificial egg collection mats to document the use of previously identified spawning habitat, conducted larval trawls (500 μ mesh) to monitor post hatch larval whitefish and zooplankton assemblages in the spring, and collected smelt via gillnets during the spring to assess their stomach contents for larval fish remains.

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 one Round Whitefish spawning location in a third lake. Lake Whitefish used both tributary streams and windswept rocky shoals to spawn. Our findings suggest that the availability of spawning habitat and use of different spawning life history strategies may be factors affecting recruitment success.

Four of our study lakes were trawled during the spring of 2019. Larval whitefish were captured in trawl tows in two of four lakes, confirming egg survival to hatch. The lack of larval whitefish in the other two waters was likely reflective of low whitefish densities. Zooplankton densities varied widely among study waters, which 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 whitefish survival, were nearly absent in the three 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 whitefish recruitment failure observed in these lakes.

A small sample of smelt (n=21) was obtained through intensive gillnetting efforts, with no larval whitefish remains identified in their stomachs. 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 whitefish numbers and may not be as prevalent as it was when whitefish were more abundant.

Our initial findings have broadened the scope and understanding of the mechanisms influencing whitefish declines in the Allagash watershed. This project is ongoing, and additional research is necessary to help better understand whitefish declines and inform future whitefish recovery efforts.

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 fishery to a small, passionate angling community in northern Maine. Over the past century, whitefish populations have experienced significant declines, including extirpation in a number of waters. 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. 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 collapsed by the 1950s. Lakes in the Allagash watershed, prized by avid anglers, are considered the last remaining stronghold of northern Maine whitefish. In recent decades, these too have begun to see drastic declines.

Routine survey data in many of the lakes across the Allagash watershed reveal an absence of young 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 whitefish populations in lakes within both drainages. There are currently 21 waters containing whitefish in the Allagash watershed. Eighteen of which now have smelt populations. Many of these waters have historically low whitefish densities (Wood 2016).

The association between smelt establishment and 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 whitefish recruitment failure. 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 upwards of 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 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 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 whitefish declines (J. Wood unpublished data).

Understanding the mechanisms responsible for 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 watershed is widely unknown. We suspect that the availability of spawning habitat and the use of different 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. Finally, 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 waters remains an important information need. The objectives of the research are to: 1) document whitefish spawning activity in various waters to assess how spawning habitat use and availability may influence recruitment; 2) document whitefish survival to hatch through larval trawls; 3) collect stomach data from adult smelt to assess predation on larval whitefish; and 4) monitor zooplankton community assemblages to assess how their abundance may influence larval whitefish survival.

STUDY AREA

The Allagash watershed lies within the North Maine Woods, a largely 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. Six 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 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 fisherman year-round. Anglers report catching whitefish in both the open water and ice fishing season, and current winter creel surveys reveal a healthy whitefish fishery (Wood 2018). Understanding the biological and environmental factors that have allowed these whitefish to persist in the presence of smelt may help us 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. Early MDIFW reports describe seemingly endless quantities of spawning whitefish being dipnetted by fisherman in the inlet stream. Since the establishment of smelt in the 1970's, whitefish numbers have declined dramatically, and no longer support a popular fishery. Anglers frequently ice fish the lake for Lake Trout (*Salvelinus namaycush*) and very 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 it 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 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") is a 1,222-acre lake in T7R12, Piscataquis County, with a maximum depth of 52 feet. 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. Recent gillnetting efforts reveal that adult whitefish exist at relatively high numbers in comparison to surrounding lakes. Recent recruitment has not been documented however, 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 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 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.



Figure 1. Study waters in the Allagash watershed.

METHODS

Spawning Habitat Surveys:

Spawning habitat surveys were conducted in each of the six study waters to identify potential whitefish spawning sites and to assess the availability of habitat in each water. Spawning habitat selection by 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/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.

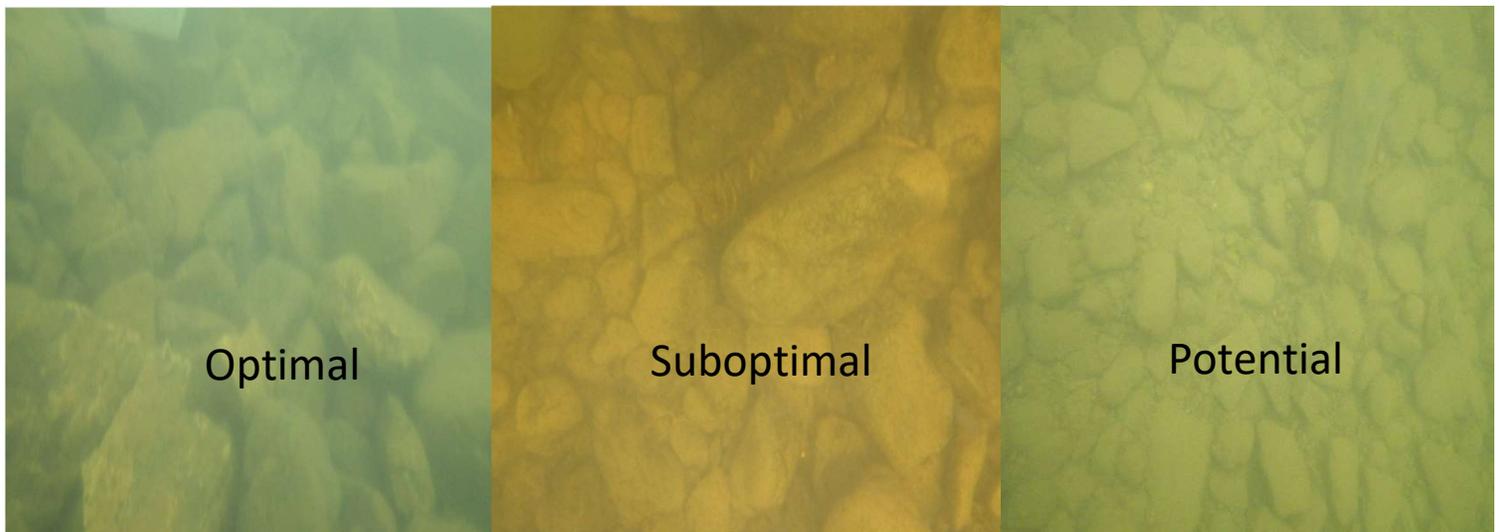


Figure 2. Examples of the three classes of whitefish spawning habitat.

Egg Mat Study:

Artificial egg collection mats were used to assess whitefish spawning habitat. Egg mats were constructed based on 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 Indian Pond; where mats were placed on habitats representing each of the three categories. Mats were set starting the week of October 26, 2019, prior to whitefish spawning. Mats were checked weekly

for the presence of whitefish eggs on Ross Lake, Second Musquacook Lake, Clear Lake, and Indian Pond until November 12, when an abnormally early ice cover prevented further sampling in the lake environment. Stream egg mats were monitored until December 5, 2019. 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 whitefish spawning had concluded in the other lakes.

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. 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, with a gang of 3 egg mats at each site. 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. Indian Pond had 18 egg mats placed on two optimal shoals, two suboptimal shoals, and two potential shoals.

Larval/Zooplankton Trawls

Whitefish survival to hatch and zooplankton community assemblages were monitored on Crescent Pond, Ross Lake, Second Musquacook, and Clear Lake using a larval trawl (1 m² mouth opening, 500 μ mesh). Trawling began in early May immediately after ice off, when whitefish typically hatch from their eggs (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, and Clear lake had 8, 11, 10, and 10 sites respectively. Sampling locations in each lake were trawled once a week for four weeks from May 9, 2019 to June 1, 2019. The trawl was towed 50 feet behind an outboard motor at approximately 2-2.5mph 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, we trawled each site 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, larval fish and zooplankton were transferred from the bucket to a 250 or 500 ml sample bottle, labeled, and preserved in 90% ethanol to be counted and identified in the lab. Larval fish and zooplankton were identified under a dissecting microscope. Larval fish were

measured to the nearest millimeter. Zooplankton were identified and grouped into Cladocerans (primarily *Bosmina*, *Daphnia*, *Sida*, *Holopedidae*, *Polyphemidae*), and Copepods (*Calanoid* and *Cyclopoid*). Zooplankton from each sample were transferred into a 10 mm graduated cylinder. Total counts of zooplankton were recorded if the sample had less than 6 mm of zooplankton. For samples with greater than 6 mm of zooplankton, two 1 mm subsamples were taken using a Hensen-Stempel one-millimeter pipet. The average zooplankton counts of these subsamples were extrapolated to get an estimate of total zooplankton in the sample.

Volume of water filtered was quantified using readings from a flow meter (General Oceanics, model 2030R) mounted in the trawl opening. This value was used to calculate larval fish densities (fish/1000m³) and mean zooplankton densities (m³) (data pooled for all trawl locations for each week sampled). Relative abundance of larval whitefish (data pooled over the four-week sampling period) was evaluated at each trawling location to assess horizontal distribution of larval fish throughout the lake. Relative abundances of larval fish were expressed as percentages and rounded to the nearest whole number. Zooplankton counts were pooled from each trawling site to assess zooplankton relative abundance for each weekly sampling period.

Smelt Predation on Larval Whitefish:

Experimental gillnetting surveys were conducted in conjunction with trawling to collect adult smelt for diet analysis. 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. Three smelt nets were used during the surveys, two 5'x100' nets, and one 5'x50' net. Net mesh size ranged from ½" to ¾". After the larval trawling study was finished (June 1) MDIFW received reports of invasive smelt in Haymock Lake. Haymock Lake was gillnetted during the first week of June to follow up on angler reports and document the smelt introduction. Seven smelt were captured, and their stomach contents were inspected for larval whitefish remains.

RESULTS

Spawning Habitat Surveys

Ross Lake

A total of 16 possible spawning sites were identified in Ross Lake; 4 optimal, 10 suboptimal, and 2 potential (Figure 3). 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 20 yds of the bank. This section of the shoreline is adjacent to prevailing northwesterly winds, providing sufficient wave action to keep the substrate clean. The spawning area stretches for close to a kilometer presenting an abundance of suitable spawning habitat for whitefish to utilize (Figure 3). Three other optimal spawning sites were identified along the eastern shoreline of the lake (Figure 3). 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 bank. A notable section of suboptimal spawning habitat exists at the north end of the lake by the outlet stream (Figure 3). There is good cobble here, and the current from the outlet keeps

these rocks relatively clean; however, sand from the beach shoreline appears to settle out between the rocks which presents less than optimal spawning conditions for whitefish.

Ross Lake has an inlet and outlet stream and an additional five tributary streams. No spawning habitat was identified in any of the tributary streams or inlet stream. 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. Boucher Brook, on the northeastern side of the lake, had no dam impediments, but flows in this stream appeared inadequate for spawning whitefish. Sweeney Brook, at the northwest end of the lake, had stagnant water with high levels of silt deposits. 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. Ross Lake outlet was the only stream with spawning habitat, which was identified within 150 yds of the mouth of the outlet (Figure 3).

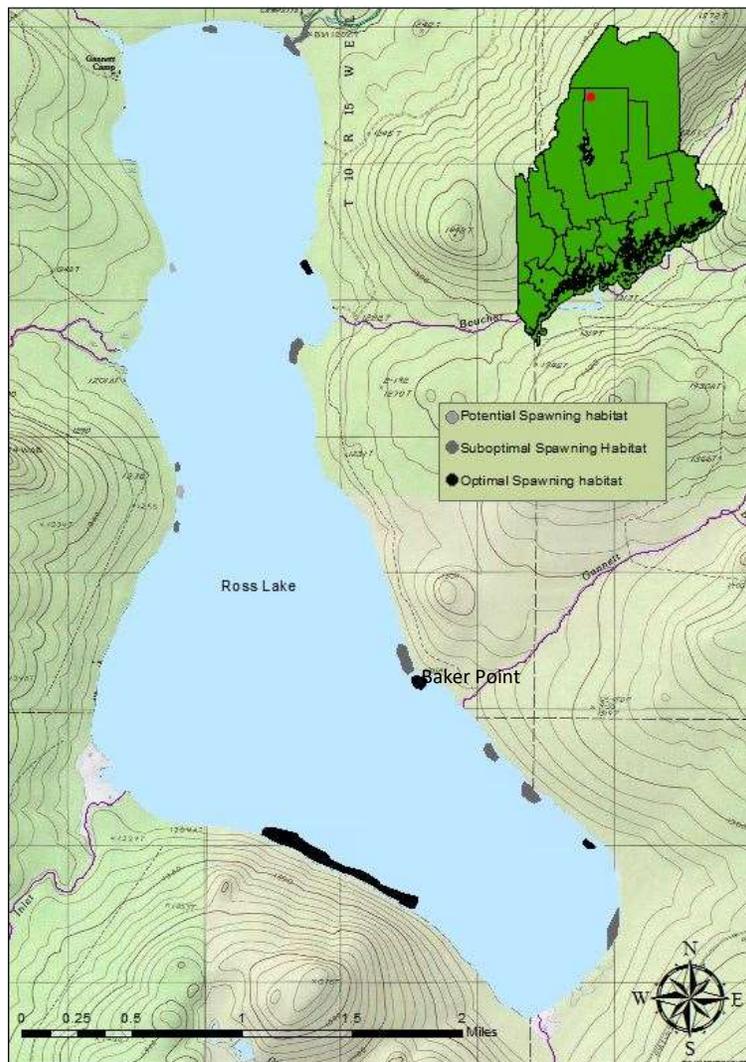


Figure 3. Locations of possible whitefish spawning habitat in Ross lake, T10R15, Piscataquis County, ME.

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 grounds 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 (Figure 4). Four other potential spawning sites were identified around the lake (Figure 4).

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 4). Additionally, water levels in the stream were 1-2 feet deep, providing enough water for whitefish to navigate during the spawning season.

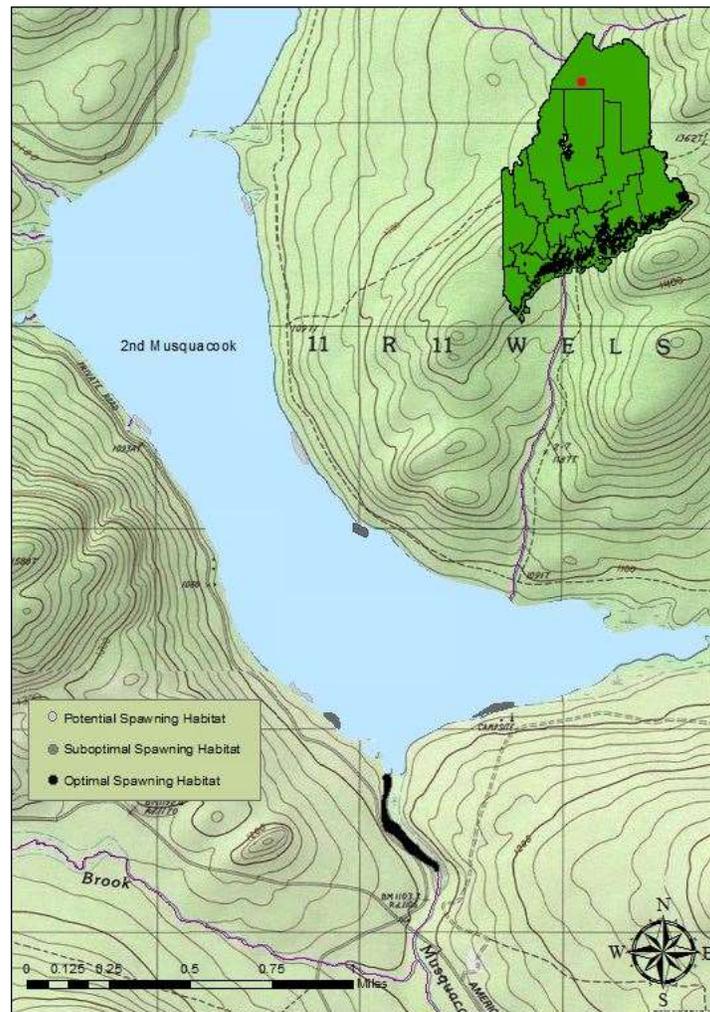


Figure 4. Locations of possible whitefish spawning habitat in Second Musquacook Lake, T11R11, Aroostook County, ME.

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 5). 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 ground 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 whitefish.

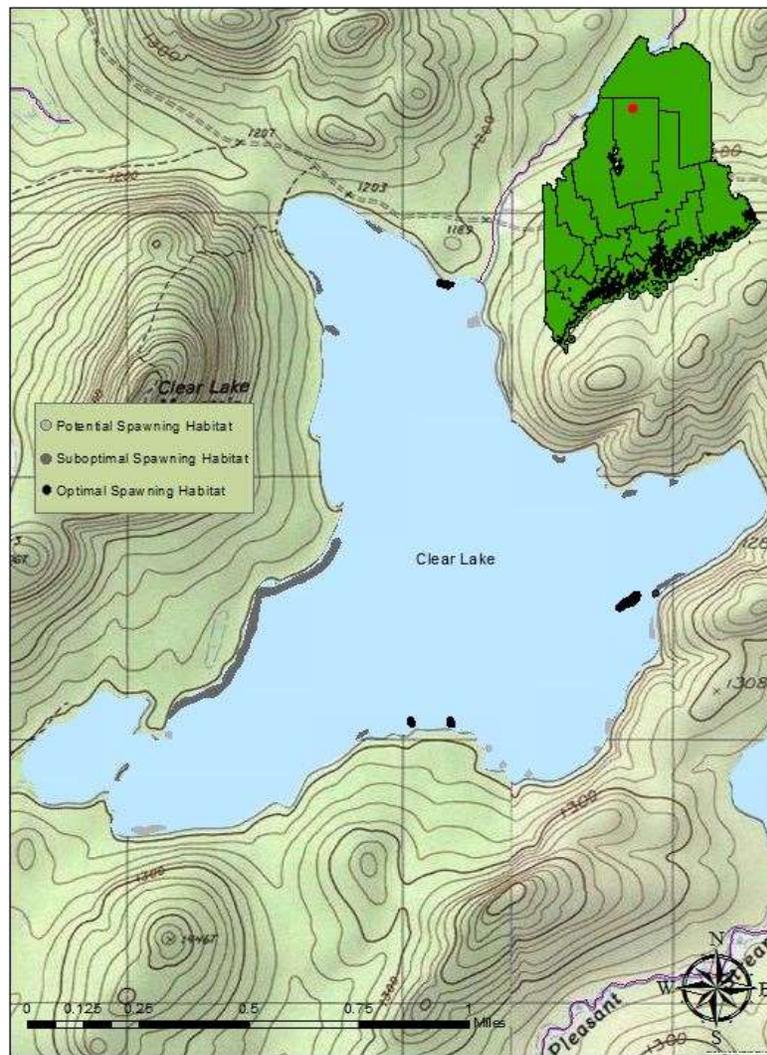


Figure 5. Locations of possible whitefish spawning habitat in Clear Lake, T10R11, Piscataquis County, ME.

Crescent Pond

Crescent Pond's shoreline is predominately mud and silt and provides less than optimal spawning habitat for whitefish. Eight possible spawning ground 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 6). They both consisted of small uniform cobble, with little silt deposition. The remaining six sites were identified as potential spawning grounds.

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 50 yds upstream of its mouth. Stagnant, silty water above and below the dam provide no suitable spawning substrate.

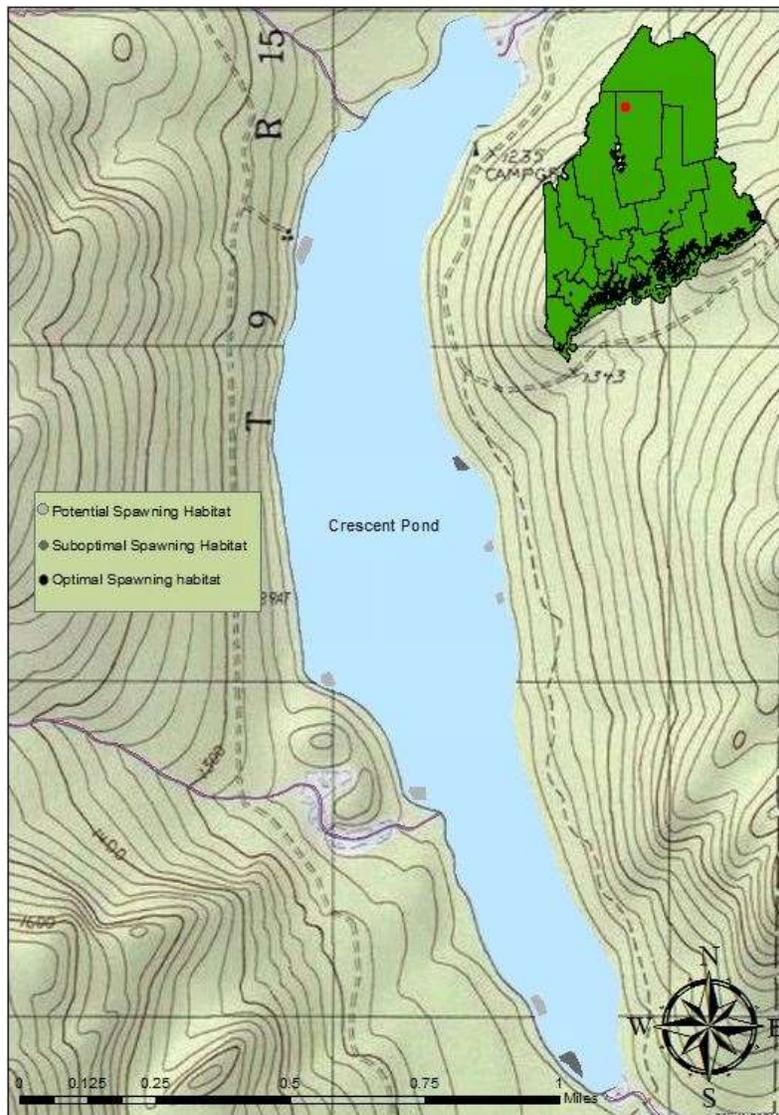


Figure 6. Locations of possible whitefish spawning habitat in Crescent Pond, T9R15, Piscataquis County, ME.

Haymock Lake

Haymock Lake's shoreline is predominately silt and mud which provides less than optimal spawning habitat for whitefish. Seven spawning ground 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 7).

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.

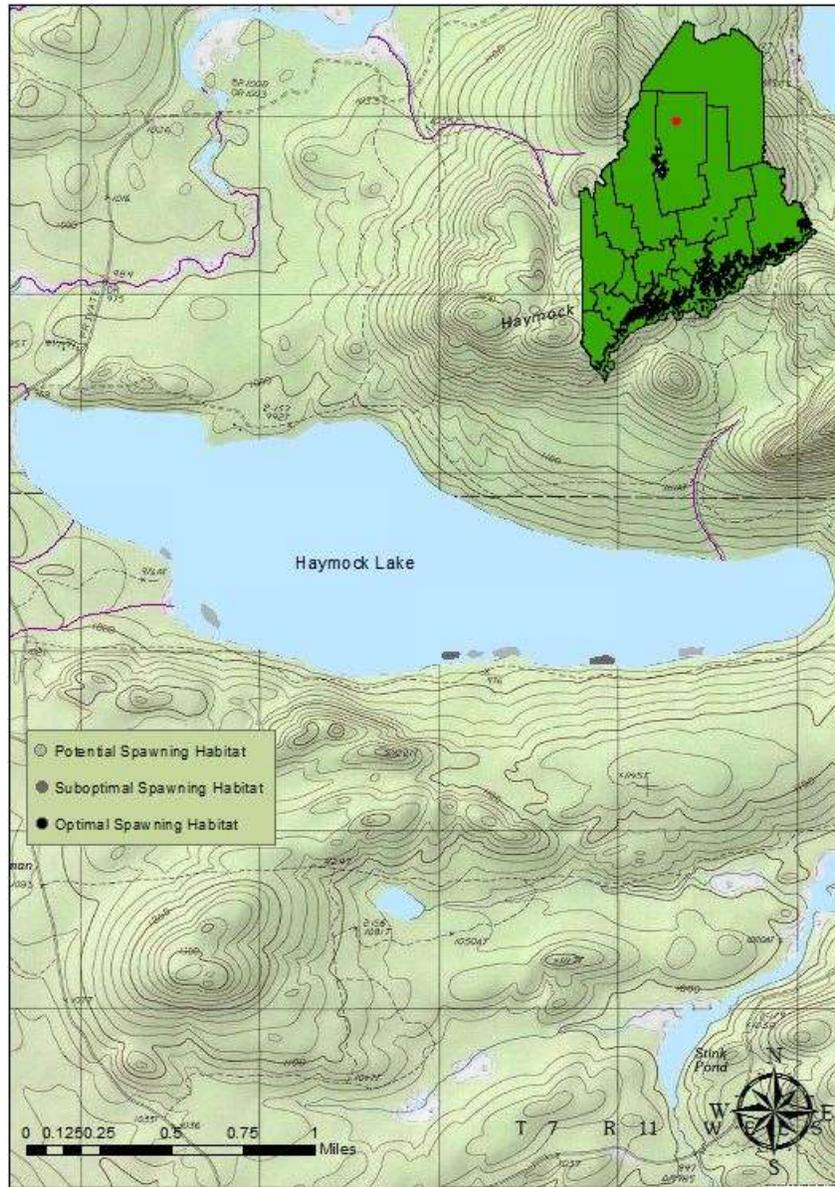


Figure 7. Locations of possible whitefish spawning habitat in Haymock Lake, T7R11, Piscataquis County, ME.

Indian Pond

Indian Pond spawning ground surveys revealed a wide array of possible whitefish spawning sites. A total of 14 sites were identified. Four optimal shoals were identified along the southwestern arm of the lake. A notable optimal shoal with exceptional cobble exists on the far western shoreline of the lake and begins about 30 yds from the point (Figure 7). Seven other suboptimal shoals and three potential shoals were identified throughout the rest of the lake (Figure 8).

Indian Pond has two tributary streams and one outlet stream that flows into the lake. No whitefish spawning habitat was identified in any of the tributary streams or outlet stream. Low water levels this past summer and fall may have presented less than adequate spawning habitat in these tributaries.

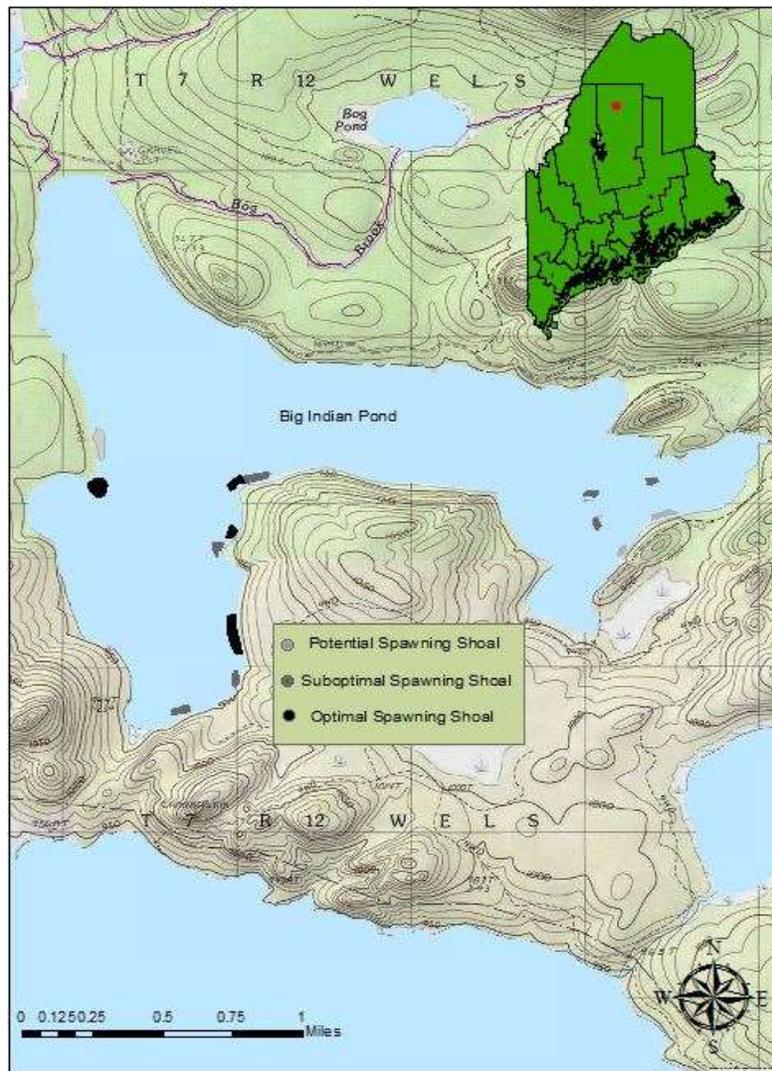


Figure 8. Locations of possible whitefish spawning habitat in Indian Pond, T7R12, Piscataquis County, ME.

Egg Mat Surveys

No eggs were collected during the spawning season on any of the in-lake spawning sites in Ross Lake (Figure 9). Egg mats were collected through the ice in mid-January 2019 and no eggs were identified on any of the mats. Six eggs were collected in the outlet stream on November 20, 2019. Genetic testing conducted by Laval University determined these eggs came from Round Whitefish eggs. Ultimately, no whitefish spawning was documented in Ross Lake.

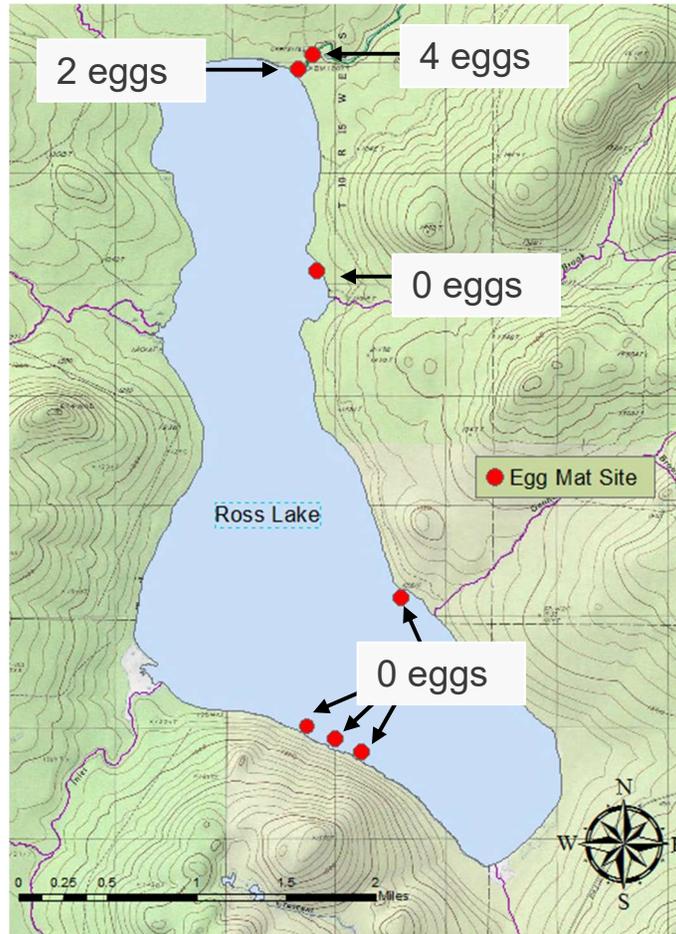


Figure 9. Egg mat locations and number of eggs collected at each site in Ross Lake T10R15, Piscataquis County, ME.

Whitefish spawning was confirmed in the inlet to Second Musquacook Lake. A total of 22 whitefish eggs were collected at the downstream site near the mouth of the inlet, and 41 eggs were collected at the upstream site (Figure 10). Whitefish eggs were collected in the inlet stream starting November 12, 2019. 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 10).

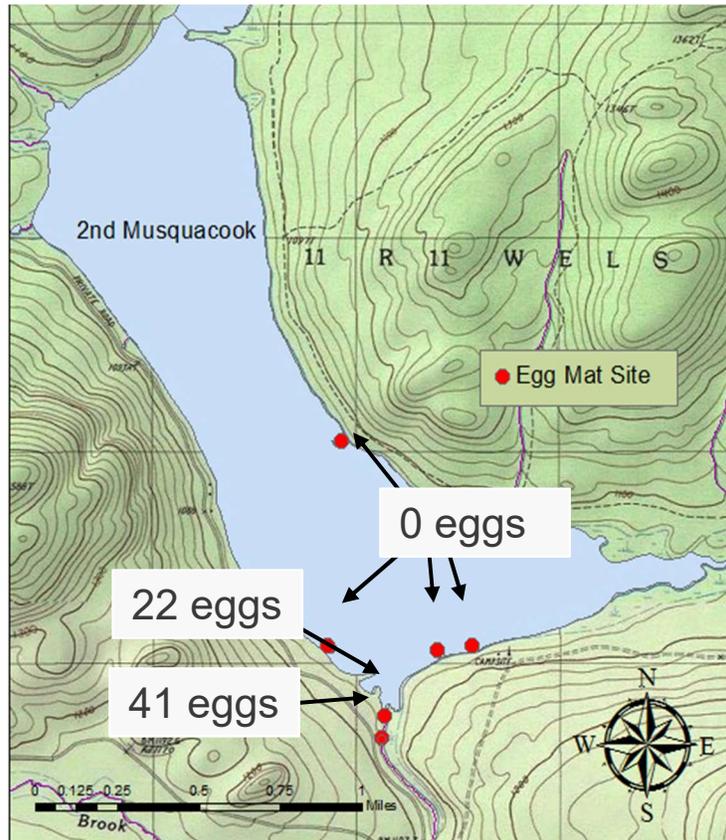


Figure 10. Egg mat locations and number of eggs collected at each site in Second Musquacook Lake T11R11, Piscataquis County, ME.

Egg mats confirmed two spawning 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 11). Eggs were collected at both sites on November 5 and 12, 2018 (Table 1). 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 1). The eastern shoal egg mats were not found through the ice, therefore no additional eggs were observed at this site.

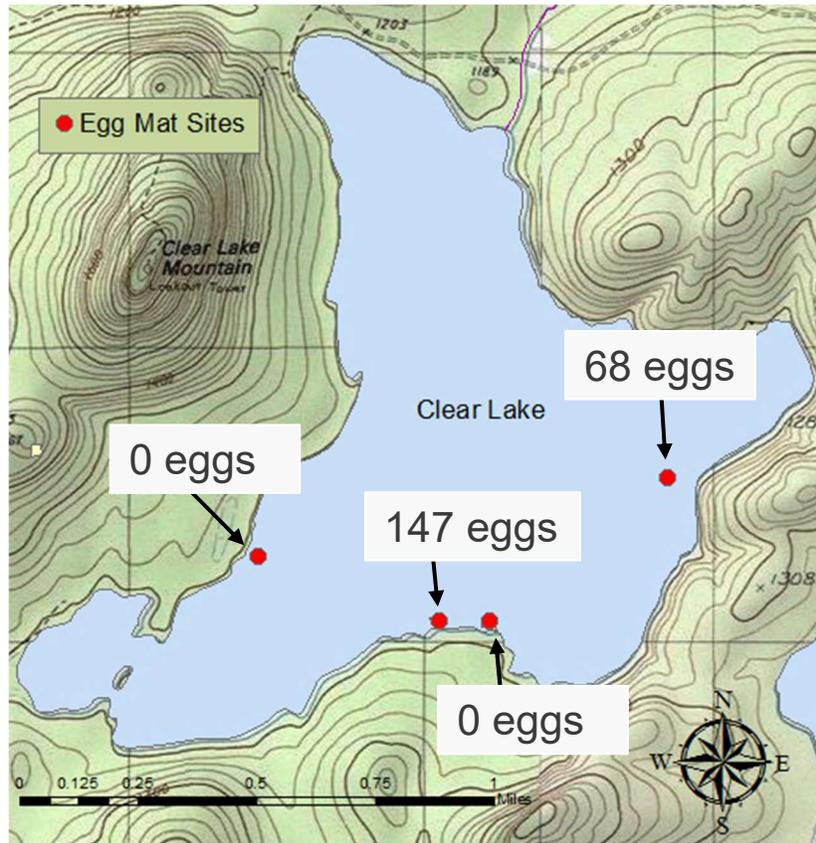


Figure 11. Egg mat locations and number of eggs collected at each site in Clear Lake T10R11, Piscataquis County, ME.

No eggs were collected on any of the spawning sites in 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 whitefish spawning sites were identified in Indian Pond (Figure 12).

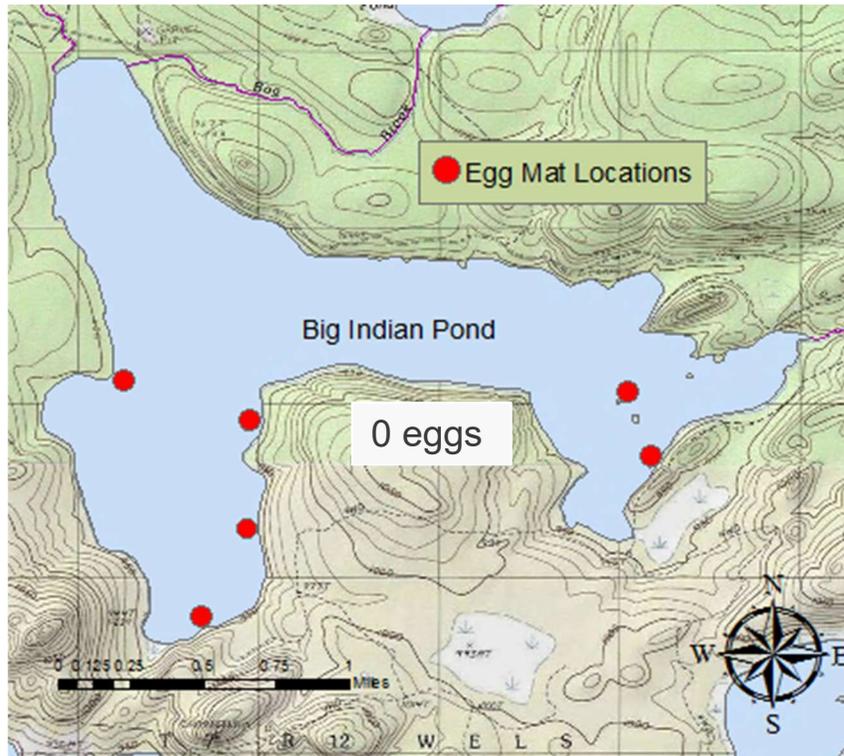


Figure 12. Egg mat locations and number of eggs collected at each site in Indian Pond T7R12, Piscataquis County, ME.

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

Table 1. 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 Downstream	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

Haymcock 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.

Trawling- Larval Whitefish

Larval whitefish were captured in two of the four study waters: Ross Lake and Clear Lake. A total of 35 larval whitefish were caught in Ross Lake over the 4-week sampling period, 19 during the first week and 5 each week during the next 3 consecutive trawling events (Table 2). Larval densities were at a high of 8.51 fish/1000m³ trawled during week 1 and dropped to 1.38, 1.46, and 1.39 fish/1000m³ during weeks 2, 3, and 4 respectively (Table 2). The highest congregations of whitefish were at sites F, I, and K, representing ~70% of total larval whitefish caught (Figure 13). There was no discernable difference in larval whitefish length. All larval whitefish caught were between 10 and 14 mm in length.

Two larval whitefish were caught in Clear Lake during the first week of trawling, and none thereafter (Table 2). Larval fish densities in Clear Lake were 0.68 fish/1000m³ during the first week.

Table 2. Larval whitefish counts and densities (1000 m³) in each lake during each week of trawling from May 10, 2019 to June 1, 2019.

	Ross Lake		Crescent Pond		2nd Musquacook		Clear Lake	
	Larval Counts	Larval Density	Larval Counts	Larval Density	Larval Counts	Larval Density	Larval Counts	Larval Density
week 1	19	8.51	0	0	0	0	2	0.68
week 2	5	1.38	0	0	0	0	0	0
week 3	5	1.46	0	0	0	0	0	0
week 4	5	1.39	0	0	0	0	0	0

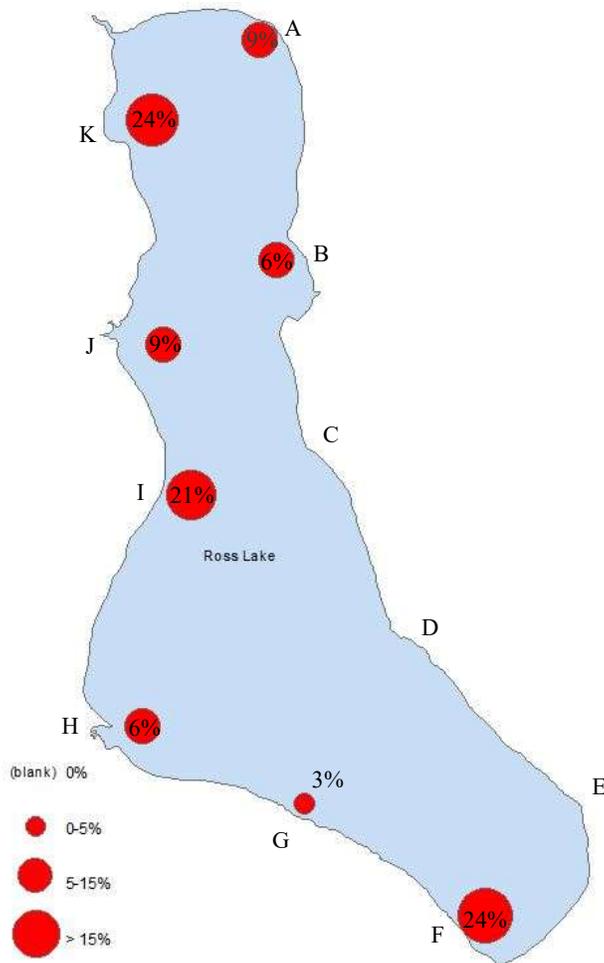


Figure 13. Larval whitefish relative abundance over the 4-week sampling period in Ross Lake T10R15, Piscataquis County, ME. Letters are used to label each fixed trawling site.

Zooplankton Trawls

Zooplankton abundance and community assemblages varied widely across the four study waters. All zooplankton in each lake fell under the order Cladocera (predominately *Daphnia* and *Holopedium*) or class Copepoda (*Cyclopoidea* and *Calanoida*) and were counted and identified accordingly. Cladocerans made up a large proportion of the overall zooplankton abundances in all of the study waters. The relative abundance of Cladocera ranged from 85.8% to 99.9% throughout the study period (Table 3). Conversely, copepods made up a small percentage of overall zooplankton abundances each week ranging from 0.1% to 14.2% (Table 3). Cladoceran abundances dominated the zooplankton assemblages during the first three weeks of trawling in Clear Lake and Second Musquacook Lake, ranging from 99.7% to 99.9% of total abundance in both lakes. During the fourth week the relative abundance of Cladocerans at Second Musquacook remained at 99.8%, but Clear lake shifted to 89.8%, with the remaining 10.2% of zooplankton consisting of copepods (predominantly calanoids). Cladocerans dominated the zooplankton samples taken from Crescent Pond (relative abundance 96.2% - 99.5%). Cladoceran relative abundances dominated the zooplankton assemblages in Ross Lake but were

noticeably lower than any of the other sampled lakes. Cladoceran abundances in Ross ranged from 85.8% to 96.9%. Copepods (predominately cyclopoids) made up the rest of the zooplankton assemblage in Ross Lake and ranged from a low of 3.1% during the second week to a high of 14.2% during the fourth week (Table 3).

Zooplankton densities varied between lakes but increased over time in all lakes. Zooplankton densities in Crescent Pond, Ross Lake, Second Musquacook Lake, and Clear lake started at ~26, 3, 1, and 1 zooplankton/m³ respectively (Figure 14). At the end of the study zooplankton densities increased to ~91, 8, 28, and 16 zooplankton/m³ respectively. Ross Lake zooplankton densities remained around 3-4 zooplankton/m³ during the first three sampling periods and rose to ~8 zooplankton/ m³ during the fourth week. Crescent Pond had high zooplankton densities during the first week at ~26 zooplankton/m³, and then dropped to 9 zooplankton/m³, during the second week, and increased to ~37 and ~91 zooplankton/m³ during the third and fourth week, respectively. Clear Lake zooplankton densities increased every sampling period, but zooplankton densities increased from ~2 zooplankton/m³ during the first and second week to ~15 zooplankton/m³ during the third and fourth weeks. Second Musquacook zooplankton densities were relatively low at ~1, ~2, ~4 zooplankton/m³ during the first, second, and third weeks respectively, but spiked to ~28 zooplankton/m³ during the fourth week. Surface water temperatures varied between the lakes, but zooplankton productivity increased with water temperature in all lakes (Figure 14).

Although copepods made up a very small percentage of the overall abundance in each water, there was an important distinction in the number of cyclopoid copepods observed in each lake. Second Musquacook Lake and Clear Lake had nearly absent cyclopoid densities (< 0.03 cyclopoids/m³) during the first three weeks of trawling (Figure 14). Crescent Pond had slightly higher cyclopoid densities (0.02 to 0.09 cyclopoids/m³). Ross lake had the highest cyclopoid densities at 0.32, 0.13, and 0.51 cyclopoid/m³ during weeks one, two, and three respectively (Figure 15).

Table 3. Mean zooplankton densities (m³) and percent abundance of cladocerans and copepods in Clear Lake, Ross Lake, 2nd Musquacook Lake, and Crescent Pond over each sampling week from May 10 to June 1, 2019.

		Clear Lake		Ross Lake		2nd Musquacook		Crescent Pond	
		Density	Percentage	Density	Percentage	Density	Percentage	Density	Percentage
week 1	Cladocerans	1.223	99.6%	2.958	95.4%	0.854	99.9%	25.730	98.3%
	Copepods	0.005	0.4%	0.143	4.6%	0.001	0.1%	0.453	1.7%
	Combined	1.228		3.101		0.855		26.183	
week 2	Cladocerans	1.914	99.7%	4.087	96.9%	2.342	99.8%	8.636	96.2%
	Copepods	0.006	0.3%	0.132	3.1%	0.005	0.2%	0.344	3.8%
	Combined	1.920		4.220		2.347		8.980	
week 3	Cladocerans	15.408	99.8%	3.138	85.8%	4.170	99.8%	36.809	99.5%
	Copepods	0.038	0.2%	0.520	14.2%	0.007	0.2%	0.191	0.5%
	Combined	15.446		3.659		4.177		37.000	
week 4	Cladocerans	14.167	89.8%	7.399	95.6%	27.520	99.8%	88.837	97.7%
	Copepods	1.612	10.2%	0.341	4.4%	0.049	0.2%	2.151	2.4%
	Combined	15.779		7.739		27.569		90.888	

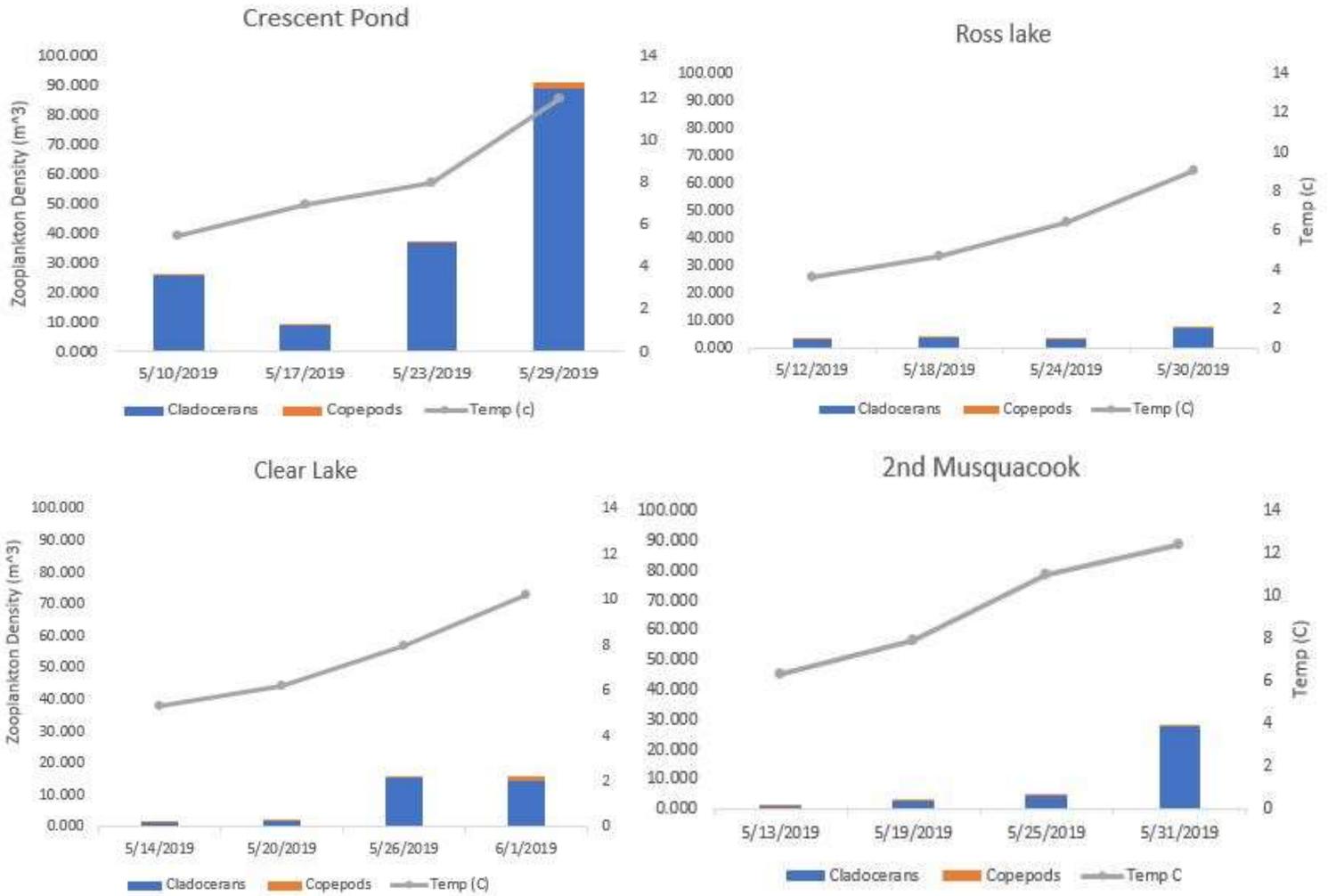


Figure 14. Mean Zooplankton Densities and measured water temperature during each week of trawling on Crescent Pond, Ross Lake, Second Musquacook Lake and Clear Lake, 2019.

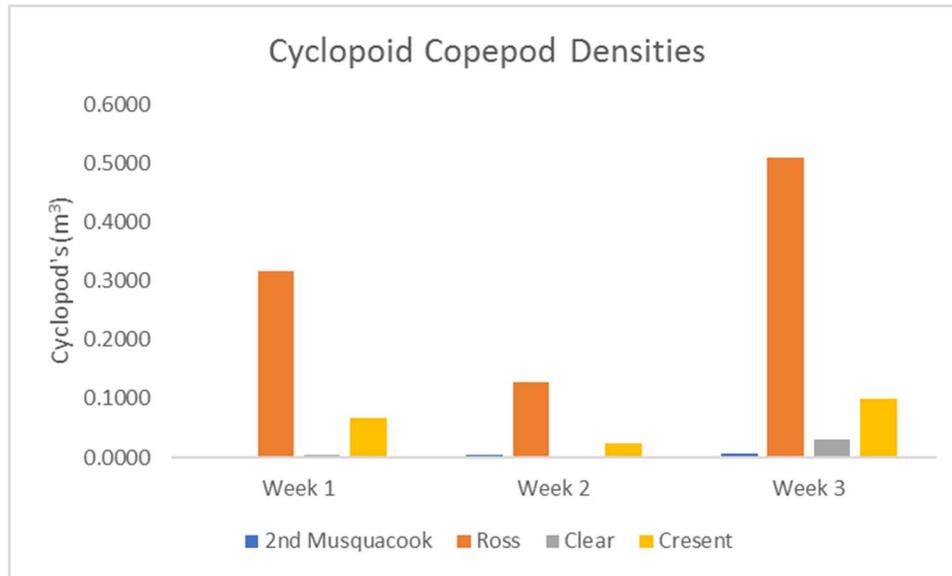


Figure 15. Mean cyclopoid copepod densities during the first three weeks of trawling on Crescent Pond, Ross Lake, Second Musquacook Lake, and Clear Lake, 2019.

Experimental Gillnetting:

Forty-four gillnet sets were conducted in the five study waters from May 10 to June 7, 2019. Gillnets were fished for a total of 567.5 hours and resulted in the capture of 21 smelt. The highest catch rates were in Clear Lake (0.08 smelt/hr), followed by Haymock Lake (0.03 smelt/hr), and Crescent Pond (0.02 smelt/hr; Table 4). No smelt were caught in gillnetting surveys in Second Musquacook or Ross Lake. Smelt lengths ranged from 78 to 107mm and nearly all smelt were caught in the ½” mesh size. No fish remains were identified in smelt stomachs.

Table 4. Number of smelt caught in gillnetting surveys for each sample lake. Gillnetting surveys took place between May 10 and June 7, 2019.

Lake	#Sets		Depth range (ft)	Mesh Size	Total Net Length (ft)	Hours Fished	Smelt Caught	Min/Max Length (mm)	Fish/hr
	Floating	Sinking							
Haymock	10	11	8-45	1/2"-3/4"	1520	222	7	90-107	0.03
Clear	9	1	6-35	1/2"-3/4"	800	173	13	81-99	0.08
Ross	5	2	6-28	1/2"-3/4"	600	93	0	-	0.00
Crescent	3	2	6-30	1/2"-3/4"	450	63	1	78	0.02
2nd Musquacook Lake	1	0	7-10	1/2"-3/4"	100	16.5	0	-	0.00

DISCUSSION

Early whitefish survival and recruitment is influenced by a number of different factors, including quality of spawning habitat, food availability for post hatch larval fish, and predation by adult smelt on larval fish. The research we conducted in 2018-2019 was focused on investigating how these mechanisms influence northern Maine whitefish populations. We documented available spawning habitat on six waters and attempted to document spawning use through artificial egg mats, monitored food availability for larval whitefish via larval trawling in the spring, and collected adult smelt via gillnetting to analyze their diets.

We assessed whitefish spawning habitat availability in six waters. The quality and availability of spawning habitat varied among our study waters. For instance, spawning ground surveys in Ross Lake revealed a high abundance of optimal spawning habitat. In contrast, Crescent Pond contained a low abundance of spawning habitat, all of which was classified as suboptimal or potential. The recruitment success in whitefish populations may be linked to the quality and abundance of spawning habitat. Substrate type is known to influence egg retention and survival (Freeberg et al. 1990; Begout et al. 1999; Fudge and Bodaly 2011), and high egg survival rates as a result of optimal spawning habitat may lessen the impacts smelt have on whitefish recruitment. Furthermore, the stressors associated with smelt interactions may be exacerbated when spawning ground limitations are present (e.g. Crescent Pond). The fact that Ross Lake whitefish have persisted in the presence of smelt may be an example of the influence spawning habitat has on whitefish recruitment success. However, more information on spawning habitat use and recruitment in many of these waters is needed to make a stronger correlation between the two. Recognizing these spawning limitations, or lack thereof, should be an important consideration for management and research efforts moving forward.

We confirmed three whitefish spawning locations in two of our study lakes. Whitefish spawned in tributary streams and on windswept rocky shoals. Utilizing these different spawning life history strategies may influence early whitefish survival. Larval whitefish that use tributary streams as rearing habitat for a period after hatch may be better protected from predation by smelt. In contrast, whitefish hatching in the lake are suspended in the water column and are potentially more vulnerable to predation post-hatch. Egg mats were also noticeably more effective in stream locations. Whitefish eggs were collected at all four stream spawning sites (despite Ross Lake eggs being from Round Whitefish) which may illustrate the importance of stream spawning habitat. Additionally, flows from the stream can transfer eggs onto the mats and mat location may not be as important in the stream as it is on shoal locations. The low occurrence of eggs collected on shoals may be a product of inaccurate spawning ground surveys, low whitefish densities, or the low percentage of shoal coverage by egg mats. Future egg mat studies should focus on covering a higher percentage of spawning shoals to more accurately determine their use.

Larval fish were caught in two of our study waters confirming egg survival to hatch. Based on our sampling, larval whitefish were low in abundance or undetectable in three of the four study lakes trawled in 2019. The absence of larval fish in two of the waters we sampled is likely directly related to the low number of adult whitefish in these waters and brings an added perspective on the severity of declines in these waters. In Ross Lake, larval whitefish were captured throughout the trawling period, a testament to its whitefish productivity, even in the presence of smelt. However, whitefish waters where smelt have not been introduced appear to have higher larval densities than Ross Lake (J. Wood unpublished data). More information on smelt and whitefish interactions is needed to understand how these interactions are affecting larval whitefish densities. Low larval densities may be attributed to poor spawning/incubation habitat, low food availability post hatch, and predation by adult smelt on larval whitefish.

Overall zooplankton densities varied among our study waters. While variations in zooplankton densities within a water is likely linked to temperature, length of growing season, and the type

of zooplankton present (Shuter and Ing 1997), variations in zooplankton densities between waters is likely more closely related to differences in fish assemblages. Smelt are an important predator of zooplankton and can drastically alter zooplankton assemblages. Larval whitefish require a specific diet of zooplankton, feeding almost exclusively on cyclopoid copepods (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. Larval whitefish exposed to food limitations in a laboratory setting experienced 100% mortality within one to three weeks of the onset of exogenous (post yolk sac) feeding (Taylor and Freeberg 1984; Brown and Taylor 1992). Cyclopoid copepod abundances were nearly absent in Crescent Pond, Second Musquacook Lake, and Clear lake during the first three weeks of our trawling study. We suspect the lack of available Cyclopoid copepods in these waters is linked to smelt interactions and may explain the absence of larval fish, and the subsequent lack of recruitment in these lakes. Conversely, Ross Lake had the highest number of cyclopoid densities, and larval fish were caught throughout the trawling study. One explanation for the difference in zooplankton assemblages among our study waters may be tied to Lake Trout abundances. Ross Lake has a naturally abundant Lake Trout population, which prey upon smelt in the lake and may mediate smelt impacts on zooplankton. Waters such as Clear Lake and Second Musquacook Lake have historically depended on MDIFW Lake Trout stocking programs to support their sport fisheries. Over the past two decades, the Lake Trout stocking program in these lakes have been scaled back, with the goal of managing for higher size quality with a more robust forage base of smelt. Early indications are that this may have resulted in lower levels of Lake Whitefish recruitment in these waters. Future work should continue to investigate the interaction between Lake Trout, smelt, and whitefish recruitment. In the fall of 2018, 200 Lake Trout were transferred from Allagash Lake to Crescent Pond in an attempt to reduce smelt numbers and potentially allow for whitefish recruitment. Future research will continue to monitor zooplankton assemblages in Crescent Pond to investigate zooplankton community changes in response to higher Lake Trout densities.

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 especially 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. 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. Smelt have been recently established in Haymock Lake, and predation on larval whitefish may be more easily identified here through future research.

Whitefish populations continue to decline in northern Maine waters following the establishment of Rainbow Smelt, but the mechanisms driving these declines may be far more

complex than previously thought. The preliminary results of our work suggest a wide variety of spawning habitat use and availability among waters, as well as a broad range in zooplankton community assemblages. While zooplankton communities and sources of larval whitefish mortality appear directly linked to the presence of smelt, other factors such as the type and amount of spawning habitat may mediate these impacts. Future work to improve our understanding of whitefish early life history is needed to help direct management efforts moving forward and increase our ability to sustain lake whitefish as a species in Maine.

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