BEHAVIOR, ECOLOGY, AND RESTORATION OF LAKE WHITEFISH

(Coregonus clupeaformis) AND ARCTIC CHARR

(Salvelinus alpinus) IN MAINE LAKES.

By

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Artic charr (*Salvelinus alpinus*) and lake whitefish populations located in the contiguous United States lie at the southernmost limit of the species range, and can be found in a select few number of Maine lakes. These populations are under considerable stress for a variety of reasons and some have suffered extirpation. A number of strategies have been utilized to promote and enhance these vulnerable populations including chemical reclamation and stocking practices. It is unknown how these populations of these native fish species will function once reintroduced.

This study assesses the seasonal vertical and thermal habitats of both reintroduced fish species in their respective waters using acoustic telemetry. In addition, I utilized
otolith aging and back calculation methods to describe growth of the reintroduced lake whitefish population in relation to a source population.

Arctic charr utilized deep and cold water habitats during daylight hours, during periods of stratification and inhabited shallower warmer waters at night. I discuss the bioenergetic implications of these movement patterns. Lake whitefish demonstrated reduced levels of activity during ice cover (December-March), while fish in the summer months (June-September) fish displayed the highest levels of activity. During periods of thermal stratification fish displayed diel vertical migrations, actively selecting depths and temperatures that may be more energetically profitable. During late season stratification, fish routinely utilized areas of warmer (>15°C) than optimal temperatures for growth. Arctic charr and lake whitefish seasonal activity and depth use were driven by periods of ice cover during the winter months and thermal stratification during the summer months. To describe growth of a reintroduced lake whitefish population in relation to a source population age at length data were incorporated into a von Bertalanffy growth function and used to model lifetime growth in two lakes; additionally, growth trajectories from individual fish were examined to evaluate length at age variability within and among lake whitefish populations. Ages for lake whitefish from Clear Lake ranged from 8-30 years, and the oldest individuals demonstrate the slowest incremental growth when compared to younger cohorts. Lake whitefish from St. Froid Lake ranged from 2-9 years. Von Bertalanffy models suggest reduced growth in lake whitefish from St. Froid Lake when compared with Clear Lake. Findings suggest complex early life history interactions may limit the scope for growth in reintroduced populations from hatchery stocks.
DEDICATION

I would like to dedicate this work to my father, Lloyd Ratten, who has always urged me to pursue a higher level of education. He is a strong and at times stubborn individual, who refuses to let others define who he is. I will always admire him for these and many other characteristics and strive to be a man of his caliber. He has sacrificed a great deal throughout his life for his children and finds his greatest happiness in their success.
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CHAPTER ONE:

USING ACOUSTIC TELEMETRY TO IDENTIFY SEASONAL VERTICAL AND THERMAL HABITAT USE OF REINTRODUCED ARCTIC CHARR IN BIG REED POND, MAINE

Abstract

Artic charr (*Salvelinus alpinus*) populations located in the contiguous United States lie at the southernmost limit of the specie’s range, and can be found in a select few of Maine’s lakes. These populations are under considerable environmental stress and some have suffered extirpation. Chemical reclamation is a commonly used fisheries management tool that may aid to facilitate reestablishment of Arctic charr, were they are threatened by invasive species. A total of 10 Arctic charr were tagged with acoustic transmitters and monitored to understand seasonal movements of reintroduced Arctic charr in a chemically reclaimed water body. Seasonal and diel patterns of Arctic charr movement along with depth use and temperature information were collected. Depth and temperature use varied as a function of season and time of day. In general, during periods of thermal stratification, Arctic charr utilized deep and cold water habitats during daylight hours, and inhabited shallower warmer waters at night. I discuss the bioenergetic implications of these movement patterns.
**Introduction**

Artic charr (*Salvelinus alpinus*) populations located in the contiguous United States are at the southernmost limit of the species range. Currently, twelve Arctic charr populations persist in the lakes of Maine (Michaud 2008). Arctic charr require thermally stable, cold-water environments for persistence (3 to 15°C) and are highly vulnerable to anthropogenic disturbance (Lehtonen 1998; Klemensten et al. 2003). Arctic charr have suffered extirpation worldwide due to the introduction of non-native species and climate change impacts (Maitland 2007; Winfield 2010). Arctic charr evolved in oligotrophic lake environments with characteristically low species diversity (Bernatchez et al. 2002), a life history characteristic that contributes to the present day vulnerability to invasive species establishment. Several Arctic charr populations in the contiguous United States have suffered extirpation, including those in Sunapee Lake (New Hampshire) and Rangeley Lake (Maine) (Everhart and Waters 1965; Kircheis 1985; Maitland 2007). The population level responses to environmental disturbance have been predicted for Arctic charr in the northern portion of their species range (Lehtonnen 1998) yet few have discussed the immediate implications of population decline in the southern portion of the species range (Gerdeaux et al. 2011).

Currently Arctic charr populations in Maine are under severe threat of extirpation due to the illegal introduction of nonnative species, including rainbow smelt. Rainbow smelt (*Osmerus mordax*) are native to several coastal drainages in Maine, but have been introduced as a popular forage fish by anglers to target game fish species such as landlocked salmon (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) (Warner and Fenderson 1963). Rainbow smelt are implicated for contributing to Arctic charr
population declines in Maine as their establishment has coincided with subsequent negative population trends. Fishery biologists with Maine Department of Inland Fisheries and Wildlife (MDIFW) documented such declines in Arctic charr abundance following smelt introduction in Big Reed Pond, Piscataquis County, Maine (Frost 2001). Gill net catches of Arctic charr declined in abundance from the 1990s to 2006, and consequently management actions were set in place to preserve one of the last extant Arctic charr populations in the contiguous United States. In fall 2010 Big Reed Pond was chemically reclaimed with rotenone (Pro-Noxfish® powder and Prentox® liquid) to eradicate nonnative fish species (namely rainbow smelt). Due to the remote location of Big Reed Pond, most equipment was flown in via float plane. In addition to chemical treatment in Big Reed Pond, both outlet and inlet streams required treatment as well. Prior to reclamation, rescue efforts were employed to capture the remaining Arctic charr within the system. Subsequently a captive breeding program was established from surviving charr.

Currently there is a lack of information regarding the potential for reintroduction or restoration of Arctic charr in the lake systems of Maine. The objectives of this research were to 1) provide insight into Arctic charr survivorship and behavior following reintroduction, and 2) obtain insights in charr habitat use at the southern range limit for the species. In combination these objectives would serve to guide future risk assessment, conservation and restoration efforts.
Methods

Study system: Big Reed Pond is a 37 hectare pond located in unorganized township T8 R10, northern Piscataquis County, Maine (Figure 1.1). Big Reed Pond harbors one of 12 remaining Arctic charr populations in Maine. Land immediately surrounding Big Reed Pond is owned by The Nature Conservancy (TNC), embedded within the larger tract of commercial forest lands (1.41 million hectares) known as the North Maine Woods (NMW).

Figure 1.1. Location map of Big Reed Pond, Maine. Closed circles represent receiver locations and open circles indicate the location of a temperature logger array. The bolded square indicates Big Reed Pond’s location in Maine, USA.
**Fish capture:** Between the years of 2007-2009 Arctic charr were captured with trapnet and gillnet methods to initiate a captive breeding program at Mountain Springs Trout Farm in Frenchville, Maine. Subsequently, chemical reclamation (approximately 3750 kg rotenone) was implemented in Big Reed Pond and tributaries from late September to early October 2010 to eliminate nonnative species. Rotenone is a commonly utilized biocide in fisheries management that allows for the reclamation of freshwater systems negatively impacted by invasive fish species (Finlayson et al. 2000).

**Fish tagging and telemetry:** Ten Arctic charr were selected from the Mountain Springs Trout Farm for tagging in the fall of 2011. Tagged fish were progeny from wild fish captured from Big Reed Pond, and manually spawned and reared in captivity. Fish were anesthetized using a buffered solution of tricaine methanesulfonate (MS-222); 100 mg/L; 0.20-mM NaCO$_3$ pH = 7.0. Fish total length was measured to the nearest millimeter and mass to the nearest gram. A small incision with a sterile scalpel was made posterior to the pectoral girdle. Subsequently, a Vemco V9TP (Vemco, Halifax Nova Scotia) acoustic tag (42mm, 2.7g in water) was then inserted into the abdomen. Three sterile sutures were used to enclose the incision and the tag within. The percentage body burden (tag mass (g)/fish mass(g)) ranged from 0.010-0.013 among tagged fish. Surgery time was approximately two minutes. All fish were allowed to recover for 5 days within an isolated hatchery tank. During this time no mortality was observed. On November 9, 2011 fish were transferred into oxygen infused bags of water and transported to Big Reed Pond by float plane for stocking.

Vemco V9TP tags transmit unique fish identification, temperature, and depth information to receivers submerged within Big Reed Pond. For the first 11 months of the
study tags were programmed to ping randomly at a rate between 460 and 500 seconds. This increased ping rate was used to obtain detailed movement information during a likely spawning period. Tags were programmed to have an increased ping rate between October 23 2012 and November 1, 2012. During this time period, an increase in acoustic ping collisions resulted in decreased detection efficiency by passive receivers, due to detection interference (collisions). Tags continued with a 460 to 500 second delay on November 2, 2012.

**Passive telemetry:** Three Vemco VR2 receiver units were deployed within Big Reed Pond in November 2011 for year round detection of tagged Arctic charr (Figure 1.1). Acoustic receivers were downloaded triennially until May 2013. Data exclusion from tagged fish occur under three circumstances. First, mortality was inferred from prolonged periods with absence of vertical movement or when an individual was no longer detected in the system; the second assumption is reasonable given lack of connectivity from Big Reed Pond to adjacent water bodies. Mortality was assigned by inspecting raw detection data from individual Arctic charr. Second, if fish occupied depths or experienced temperatures that were clearly extralimital they were removed from the dataset. A total of three fish survived for greater than one year and provided reliable vertical and thermal habitat use data (Table 1.1). As a result these fish provided information for vertical and thermal habitat descriptions.
Table 1.1. Length (mm), mass(g), observation time (days) and percent body burden of Arctic charr tagged on 8 November 2011. Arctic charr tracked between November 2011 and May 2013 by means of acoustic transmitters. Bolded individuals are those utilized in analysis. Means are given as ±1SD.

<table>
<thead>
<tr>
<th>Fish</th>
<th>Total Length (mm)</th>
<th>Mass (g)</th>
<th>Observation Time (d)</th>
<th>Percent Body Burden</th>
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<td>1</td>
<td>275</td>
<td>212.3</td>
<td>184</td>
<td>0.013</td>
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<tr>
<td>2</td>
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<td>233.1</td>
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</tr>
<tr>
<td>3</td>
<td>293</td>
<td>250.4</td>
<td>113</td>
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</tr>
<tr>
<td>4</td>
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<td>294</td>
<td>247.6</td>
<td>411</td>
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<td>301</td>
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<td>293</td>
<td>247.2</td>
<td>188</td>
<td>0.011</td>
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293 ± 9mm   255.2 ± 22.2g

**Temperature monitoring:** Throughout the study water temperature in Big Reed Pond was monitored throughout the water column using HOBO temperature loggers (Onset Computer Corp., Bourne, Massachusetts). Six HOBO loggers, positioned at 1, 3, 5, 7, 9, and 11 meters in depth made up an array within Big Reed Pond. The array was placed in approximately 15 meters of water to provide year round temperature information (Figure 1.1).

**Seasonal vertical and thermal habitat use:** Acoustic detection data were examined for surviving Arctic charr. Vertical detection data was binned by Julian week (e.g. January 1 to January 7). Due to lake size, individual pings from a tagged fish were frequently
detected by multiple receivers. We used a minimum time differential of 8 minutes between detections from the same fish to ensure duplicate depth and temperature data were not used. Mean weekly depth and temperature data were used to describe seasonal vertical and thermal habitat use.

**Daily vertical and thermal habitat use:** Detections from individual fish were examined to determine seasonal patterns of daily vertical and thermal habitat use. Sunset and sunrise times were used to designate day and night detections. Again, an 8 minute time differential was utilized to separate depth and thermal detections.

**Results**

**Seasonal vertical habitat use:** Individual Arctic charr displayed seasonal shifts in depth use throughout the investigation (Figure 1.2). Immediately after release in November 2011 and through December 2011 fish occupied depths from 1.38-18.08m, nearly the entire range of vertical habitats available in Big Reed Pond.
Figure 1.2. Center panel demonstrates seasonal depth and temperature use by one tagged Arctic charr in Big Reed Pond from January 2012 to January 2013. Points represent mean weekly depths (Depth ±1S.D.). The single line represents mean weekly temperature use. (A-D) Representative five day detection series from Arctic charr depicting seasonal trends in daily depth and temperature use. Dots indicate individual depth detections and lines indicate individual temperature detections. Bottom shaded bars denote night time, and unshaded bars denote day time hours.
By late December 2011 into January 2012 Arctic charr occupied greater depths (8-10m) for approximately two weeks, coincident with ice formation on Big Reed Pond (Figure 1.2 center panel). Throughout February, March, and much of April 2012 Arctic charr frequented a narrow range of depths near 5m. In late April into early May, fish utilized the uppermost portions of the water column. At this time movements into the upper portions of the water column correspond with ice out events on Big Reed Pond. By mid-May and in through June and July two Arctic charr show little variation in depth use, centering around 7m (Figure 1.3C). In contrast, a third fish demonstrated prolonged variability in depths used, and occupied the greatest depths available in Big Reed Pond through July 2012 (Figure 1.3). Throughout August and into late September 2012 Arctic charr occupied a narrow range of depths, regardless of their early summer depth use (Figure 1.3A). At this time, depth use appears to be tightly coupled to thermocline (Figure 1.2C). In late September and through October 2012 fish again occupied a wide range of depths in conjunction with fall turnover in Big Reed Pond. Depths used in December 2012 (1.38-15.88m) were similar with depth use from the previous year (Figure 1.3A).
Figure 1.3. (A) Seasonal vertical distribution of three tagged Arctic charr (lines represent mean weekly depths); (B) Seasonal thermal habitat use of three tagged Arctic charr (Lines represent mean weekly temperatures). (C) Isopleth depicting the seasonal thermal habitats available (3-11m) in Big Reed Pond between 11/25/2011 and 5/20/2012. Data compiled from temperature logger location (Figure 1).
Diel vertical habitat use: Arctic charr displayed diel patterns of depth use that are seasonally dependent. Under ice cover in January, February, and March of 2012 Arctic charr show an increase in use depth variability during the daylight hours. In contrast, during these same months, Arctic charr remain constant depth during night time periods (Figure 1.2A). Ice out occurred in early April, at which time Arctic charr occupied the upper 2-3 meters of the water column for approximately 2 weeks. During this time, day and night depth uses were similar.

In late April and into May Arctic charr utilize a variety of vertical habitats, occupying greater depths (15-17m) during daytime periods with movements higher in the water column, approximately 13 m at night. Movements into the upper 5 meters of the water column were also noted at this time, though typically brief in duration and occurring near dusk and dawn. In June, July, and August 2012 Arctic charr continue to utilize deeper habitats during the daytime hours while moving higher into the water column at night. From June to late September the magnitude of these movements decreases until day and night depth use is nearly identical, approximately 7m (Figure 1.2C).

In late September, prior to fall turnover, artic charr occasionally move into vertical habitats of less than 2m for short periods of time. These movements occur exclusively during the night. After fall turnover occurs Arctic charr resume a depth pattern whereby fish utilize greater depths during the daylight hours (8-10m) and ascend to shallower depths (5m) at night. This daily pattern of depth use continues through October, November, and December though the magnitude of vertical movements decreases once again with ice cover on Big Reed Pond.
**Seasonal thermal habitat use:** Arctic charr utilized a variety of temperatures in conjunction with seasonal changes in the thermal environment (Figure 1.3B & 1.3C). Arctic charr utilized similar thermal habitat from January to March (Figure 1.3B), during which thermal variability throughout the lake was at a minimum (Figure 1.3°C). Thermal habitat use was variable among individual fish between April and August. In April and May, Fish 5 and Fish 8 utilized lower water temperatures when compared to fish 7. From June until late September Fish 7 and Fish 8 utilized consistently warmer temperatures on average than fish 5. Also in late September, fish 8, 7, and 5 experienced the highest weekly average temperatures observed in the study 12.44 °C, 12.89°C, and 13.11°C respectively. Fall turnover occurred in early October on Big Reed Pond at which time thermal habitat use for all fish remained similar for the remainder of calendar year (Figure 1.3B).

**Diel thermal habitat use:** Arctic charr showed seasonal differences in diel temperature use. In general, under periods of stratification fish utilized colder temperatures during the daylight hours and warmer temperatures during the nighttime (Figure 1.2B). During late season thermal stratification this pattern was not apparent, with slight variation in day and night temperature use (Figure 1.2C), despite the availability of a wide variety of temperatures in Big Reed Pond. From January to March 2012, day and night temperature use was nearly identical, which results from the lack of variability in thermal habitat throughout the water column (Figure 1.3C).
**Discussion**

Diel vertical movements by tagged individuals indicate fish occupy greater depths during the daylight hours and move higher in the water column at night. A number of studies have documented similar vertical movement patterns for freshwater fish (Brett 1971; Scherer and Harrison 1988; Gorsky et al. 2012). Reasons for the observed diel vertical migration patterns may include a means predator avoidance, feeding opportunities, and bioenergetic efficiency. Arctic charr may utilize the greatest depths during the day to avoid would be predators during the anti-predation window (Clark and Levy 1988), and inhabit shallow depths at dusk for opportunistic feeding opportunities. However, predator avoidance is an unlikely explanation as Arctic charr function as one of the main predators in Big Reed Pond after reclamation. During lake stratification Arctic charr utilize deeper and colder waters during the day, a behavior that may maximize bioenergetic efficiency. Toward dusk Arctic charr ascend in the water column likely feeding on zooplankton. Zooplankton ascend in the water column to feed on phytoplankton during a time where they are less vulnerable to predation (Clark and Levy 1988). Interestingly, during the nighttime ascent Arctic charr also utilize water temperatures 3-4 °C higher than during the daylight hours, and maintain this thermal use throughout the night. This behavior may be energetically beneficial, as it would elevate digestion, food conversion and potentially increase growth rates (Wurtsbaugh and Neverman 1988).

Laboratory investigations have indicated an *optimum* temperature for adult Arctic charr growth was reported to be 16°C ±0.24 S.E. (Larsson and Berglund 1998), while field studies routinely document lower utilized temperatures, (Lehtonen 1998; Larsson
Although these optimum temperatures are readily available in Big Reed Pond from June to September, all fish were rarely observed utilizing such temperatures. When temperatures upwards of 17˚C were in fact utilized, events were brief in duration.

Differences between observed and the optimal growth temperatures are likely a result of tradeoffs between food availability and optimum thermal habitat. By definition, oligotrophic waters have reduced primary productivity, and thus food is likely a limiting factor. If fish are feeding at a rate less than optimum, they would utilize colder temperatures to decrease metabolic activities. In recent studies by Elliot (2011) there is also evidence to suggest Arctic charr have evolved the ability feed in colder temperatures and under lower light conditions when compared to other salmonids. Furthermore, Arctic charr in Big Reed Pond may be optimizing their growth efficiency and not growth rate (Larsson 2005). The frequency, at which Arctic charr utilized these colder water habitats, particularly during periods of lake stratification, indicates the of importance cold water habitats for Arctic charr in Big Reed Pond.

Understanding where thermal habitats exist in the water column and the frequency at which they are utilized is fundamental in monitoring Big Reed Pond’s Arctic charr population. It is equally important for fishery managers to understand the seasonal and annual variability of cold water habitat and how it may change under predicted climatic conditions (Gerdeaux 2011).
Interactions between thermal habitat use and thermal habitat availability may indicate future success of Arctic charr in fulfilling their biological requirements. In newly reclaimed waters, such as Big Reed Pond, understanding these interactions is critical to understanding the relative health of the Arctic charr populations.
CHAPTER TWO:
COMPARISON OF AGE AND GROWTH FROM STOCKED AND WILD LAKE
WHITEFISH POPULATIONS IN MAINE

Abstract

Annual growth of lake whitefish from a stocked population in St. Froid Lake and a wild population in Clear Lake was assessed with observed and back calculated length at age data. We captured a total of 255 fish from St. Froid Lake and 62 fish from Clear Lake via trap netting, gill netting, and ice angling. Age at length data were incorporated into a von Bertalanffy growth function and used to model lifetime growth in the respective lakes; additionally, growth trajectories from individual fish were examined to evaluate length at age variability within and among lake whitefish populations. Ages for Clear Lake whitefish ranged from 8-30 years, and the oldest individuals demonstrate the slowest incremental growth when compared to younger cohorts. Lake whitefish from St. Froid Lake ranged from 2-9 years. Von Bertalanffy models suggest reduced growth in lake whitefish from St. Froid Lake when compared with Clear Lake. Findings suggest complex early life history interactions may limit the scope for growth in reintroduced populations from hatchery stocks.

Introduction

In continental North America lake whitefish (*Coregonus clupeaformis*) are distributed from areas of Northern Maine to the Great Lakes region, north into interior Canada and northwest to Alaska (Evans et al 1988). In the Great Lakes region lake whitefish are a valuable economic resource (Spangler 1970; Fleischer 1992) and in some cases exploitation has had negative consequences on lake whitefish populations.
In contrast to populations in the Great Lakes region, lake whitefish in Maine are not subject to commercial harvest and experience minimal impact from recreational fisheries. Despite low levels of fishery induced mortality, lake whitefish populations in Maine have still suffered extirpation and declines (Basley 2001).

Stocking is a common strategy for the rehabilitation of lake whitefish populations (McMurty 1989; Amtstaetter 2002; Amtstaetter and Willox 2004). In lake systems with extirpated populations, the stocking of hatchery reared lake whitefish may be the only practical means by which to reestablish self-sustaining populations.

St. Froid Lake located in Winterville, Maine, lies within the Fish River Chain of Lakes, a waterway consisting of numerous lakes and rivers, in a region that is regarded for its cold water fisheries. St. Froid Lake supported a native lake whitefish population, but sometime around the late 1920’s this population was extirpated. In efforts to restore the once present lake whitefish, St. Froid Lake received variable levels of stocking from an extant population of lake whitefish in nearby Clear Lake. Stocking occurred between the years of 2003 and 2010, at which time individuals received cohort specific marks for future year class identification (Table 2.1).
Table 2. Lake whitefish stocked in St. Froid Lake between 2003-2010. Prior to stocking fish received cohort specific marks including adipose (AD), mixed, right ventral (RV), left ventral (LV), right pectoral (RP), left pectoral (LP), and both ventral (BV) clips. (Mixed = 11 combinations of marks).

<table>
<thead>
<tr>
<th>Year</th>
<th>Quantity</th>
<th>Mark</th>
</tr>
</thead>
<tbody>
<tr>
<td>2003</td>
<td>2400</td>
<td>AD</td>
</tr>
<tr>
<td>2004</td>
<td>229</td>
<td>MIXED</td>
</tr>
<tr>
<td>2005</td>
<td>4800</td>
<td>RV</td>
</tr>
<tr>
<td>2007</td>
<td>4800</td>
<td>LV</td>
</tr>
<tr>
<td>2008</td>
<td>2400</td>
<td>RP</td>
</tr>
<tr>
<td>2009</td>
<td>2400</td>
<td>LP</td>
</tr>
<tr>
<td>2010</td>
<td>1214</td>
<td>BV</td>
</tr>
</tbody>
</table>

We perform retrospective increment analysis on otoliths to reconstruct growth histories of individual fish and characterize differences in growth and age structure between two lake whitefish populations. Using the von Bertalanffy model we describe growth of the source and reintroduced lake whitefish populations. Objectives of this study were to document the growth potential of St. Froid Lakes reintroduced lake whitefish population. Growth of lake whitefish from the donor lake, Clear Lake served as a reference to investigate the growth of reintroduced lake whitefish in St. Froid Lake. Findings provide baseline growth information for a reintroduced population of lake whitefish in relation to its donor population.

**Methods**

**Study sites:** St. Froid Lake is (971 ha) located in Winterville, Aroostook County, Maine (46°57'46.75" N and 68°37'07.25" W) (Figure 1). St. Froid Lake is an oligotrophic lake with a mean depth of 14.5m and a maximum depth of 34.7m (Lakes of Maine). The St. Froid Lake fish assemblage is made up of 24 species (Table 2.2).
Figure 2.1. Location maps of St. Froid Lake (A) and Clear Lake (B). Black boxes indicate the region in which each lake is located in Maine, U.S.A.

Clear Lake is (253 ha) located in the unorganized township T10 R11 WELS, Piscataquis Count, Maine (46°31′16.02″N, 69°7′33.97″W) (Figure 1). Clear Lake is an oligotrophic lake with a mean depth of 8.8 m and a maximum depth of 26.2m (Lakes of Maine). The Clear Lake fish assemblage is comprised of 13 species (Table 2.2).
Table 2.2. Species present in St. Froid and Clear Lakes, Maine. Common and scientific names are listed below.

<table>
<thead>
<tr>
<th>St. Froid Lake</th>
<th>Clear Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>banded killifish (<em>Fundulus diaphanus</em>)</td>
<td>blacknose dace (<em>Rhinichthys atratulus</em>)</td>
</tr>
<tr>
<td>blacknose dace (<em>Rhinichthys atratulus</em>)</td>
<td>brook trout (<em>Salvelinus fontinalis</em>)</td>
</tr>
<tr>
<td>brook trout (<em>Salvelinus fontinalis</em>)</td>
<td>brown bullhead (<em>Ameiurus nebulosus</em>)</td>
</tr>
<tr>
<td>brown bullhead (<em>Ameiurus nebulosus</em>)</td>
<td>burbot (<em>Lota lota L.</em>)</td>
</tr>
<tr>
<td>burbot (<em>Lota lota L.</em>)</td>
<td>creek chub (<em>Semotilus atromaculatus</em>)</td>
</tr>
<tr>
<td>creek chub (<em>Semotilus atromaculatus</em>)</td>
<td>lake chub (<em>Couesius plumbeus</em>)</td>
</tr>
<tr>
<td>common shiner (<em>Luxilus cornutus</em>)</td>
<td>lake trout (<em>Salvelinus namaycush</em>)</td>
</tr>
<tr>
<td>fallfish (<em>Semotilus corporalis</em>)</td>
<td>lake whitefish (<em>Coregonus clupeaformis</em>)</td>
</tr>
<tr>
<td>finescale dace (<em>Phoxinus neogaeus</em>)</td>
<td>northern red belly dace (<em>Phoxinus eos</em>)</td>
</tr>
<tr>
<td>golden shiner (<em>Notemigonus crysoleucas</em>)</td>
<td>rainbow smelt (<em>Osmerus mordax</em>)</td>
</tr>
<tr>
<td>lake chub (<em>Couesius plumbeus</em>)</td>
<td>slimy sculpin (<em>Cottus cognatus</em>)</td>
</tr>
<tr>
<td>lake trout (<em>Salvelinus namaycush</em>)</td>
<td>white sucker (<em>Catostomus Commersoni</em>)</td>
</tr>
<tr>
<td>lake whitefish (<em>Coregonus clupeaformis</em>)</td>
<td>three spine stickleback (<em>Gasterosteus aculeatus</em>)</td>
</tr>
<tr>
<td>landlocked salmon (<em>Salmo salar</em>)</td>
<td></td>
</tr>
<tr>
<td>long nose sucker (<em>Catostomus catostomus</em>)</td>
<td></td>
</tr>
<tr>
<td>nine spine stickleback (<em>Pungitius pungitius</em>)</td>
<td></td>
</tr>
<tr>
<td>northern red belly dace (<em>Phoxinus eos</em>)</td>
<td></td>
</tr>
<tr>
<td>rainbow smelt (<em>Osmerus mordax</em>)</td>
<td></td>
</tr>
<tr>
<td>round whitefish (<em>Prosopium cylindraceum</em>)</td>
<td></td>
</tr>
<tr>
<td>slimy sculpin (<em>Cottus cognatus</em>)</td>
<td></td>
</tr>
<tr>
<td>three spine stickleback (<em>Gasterosteus aculeatus</em>)</td>
<td></td>
</tr>
<tr>
<td>white sucker (<em>Catostomus Commersoni</em>)</td>
<td></td>
</tr>
<tr>
<td>yellow perch (<em>Perca flavescens</em>)</td>
<td></td>
</tr>
</tbody>
</table>

**Fish rearing and stocking:** In 2001, Maine Department of Inland Fisheries and Wildlife (MDIFW) established a hatchery program for the reintroduction of lake whitefish into selected waters that (a) had severely reduced population levels or (b) had suffered extirpation. Lake whitefish broodstock for this program originated from Clear Lake, Maine. In fall 2002 and between 2004-2009 lake whitefish from Clear Lake were captured by trapnet, spawned manually, and released. Subsequently, fertilized eggs were transported to a hatchery facility in Enfield, Maine. Subsequently, in fall 2003-2005 and 2007-2010 lake whitefish were stocked as fall fingerlings and spring yearlings (only in
2004), in varying quantities into St. Froid Lake (Table 2.1). All stocked fish were released from the same location, boat launch on the eastern shore of St. Froid Lake.

**Fish capture:** Lake whitefish were collected from St. Froid Lake with a combination of experimental gillnet, trapnet, and ice angling gear from 2010 to 2012. All gillnet sampling occurred during periods of thermal stratification. Additional gill net sampling from 2006 to 2009 provided 137 fish. Although otoliths from these samples were not available for back calculation, length at age data were utilized. Additional gillnet sampling on St. Froid Lake occurred in the summers of 2006-2011. All lake whitefish were captured using 122m experimental gill nets (3.81-8.89cm mesh size). Trap netting (30m lead line) occurred in the fall of 2010-2012. Ice angling occurred in the winter of 2012.

Clear Lake was sampled in the summer of 2011 with two identical 122m experimental gill nets. Additional capture information can be found in Table 2.3. For all captured lake whitefish total length was measured to the nearest millimeter, mass was measured to the nearest 0.1g, a scale sample was taken, fin clips (when present) were recorded, sex was determined and sagittal otoliths were removed. Otoliths were then wiped clean and allowed to air dry in an individually labeled vial.
Table 2.3. Numbers of lake whitefish capture in St. Froid and Clear lakes (2006 to 2012). Capture methods include gill net, trap net, and ice angling. Values indicate capture quantity for a given lake and year and values in parentheses indicate the number of otoliths used.

<table>
<thead>
<tr>
<th>Year</th>
<th>St. Froid Lake</th>
<th>Clear Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>2006</td>
<td>46 (0)</td>
<td>0</td>
</tr>
<tr>
<td>2007</td>
<td>27 (0)</td>
<td>0</td>
</tr>
<tr>
<td>2008</td>
<td>7 (0)</td>
<td>0</td>
</tr>
<tr>
<td>2009</td>
<td>57 (0)</td>
<td>0</td>
</tr>
<tr>
<td>2010</td>
<td>25 (24)</td>
<td>0</td>
</tr>
<tr>
<td>2011</td>
<td>86 (75)</td>
<td>62 (57)</td>
</tr>
<tr>
<td>2012</td>
<td>4 (4)</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>255 (103)</td>
<td>62 (57)</td>
</tr>
</tbody>
</table>

Otolith removal and preparation: The largest of the three otolith pairs, sagittal otoliths were located and removed from individual fish with forceps, wiped clean, and air dried. To section, small rubber molds were half filled with a mixture of epothin™ resin and hardener and allowed to set for approximately 12 hours. A release agent was applied to the rubber mold surface prior to pouring to avoid adhesion of epoxy to the mold. Next the core of the otolith was marked lightly for reference and then positioned into rubber molds distal side down. A small amount of Henkel Loctite® super glue was used to fasten the otolith in place. Molds were backfilled once again with epothin™ resin and hardener and allowed to set up for an additional 12 hours. Otoliths were sectioned with an IsoMet® low speed saw. One millimeter otolith sections were cut transversely through the otolith core. Otolith sections were then positioned on glass microscope slides with crystal bond™ adhesive. Individual otoliths were sanded and polished to improve visual clarity of the otolith.
**Otolith analysis:** Otoliths were imaged using a microscope equipped with Alicona – TEX – Basic imaging software (version 1.4.2). Ages of St. Froid Lake whitefish were assigned using knowledge of “known age” fish from fin clips of stocked fish, but this was not possible for Clear Lake fish, so we relied on a previously reported annulus validation for lake whitefish (Mills and Chalanchuk 2004). A subset of otoliths form St. Froid Lake and Clear Lake were aged by Michigan Department of Natural Resources, Charlevoux Research Station. Otolith measurements were performed with Image J software (ImageJ 1.46r). First growth transects were created at approximately a 45 degree angle towards the dorsal surface of the otolith. A light (hyaline) and dark (opaque) growth zone constituted one year of fish growth. The distance between opaque zones (annulus to annulus) was measured as a predictor of annual growth in millimeters. Fraser-Lee methods (including a standard intercept correction factor) were used to back calculate lengths at age for individual fish and provide individual growth trajectories throughout the lifetime of the fish.

**Growth models:** Starting parameter estimates were obtained by constructing Ford-Walford plots (Walford 1946) and final parameter estimation was performed in R software (R Development Core Team 2012). The von Bertalanffy growth function (von Bertalanffy 1938) is described as follows.

\[ L_t = L_\infty [1 - e^{-K(t-t_0)}], \]

Where \( L_t \) is the mean length of fish at age \( t \), \( L_\infty \) is the asymptotic length of fish in the population, \( K \) is the Brody growth coefficient, and \( t_0 \) is a constant (origin of the equation). Variations of the von Bertalanffy growth function have been used to predict
size at first reproduction (Jensen 1996) and stage explicit growth (He and Stewart 2002) among other life history characteristics. Here we incorporate back-calculated and observed lengths at age into a von Bertalanffy growth model for each respective lake whitefish population.

To describe the variation in growth parameters among individuals, von Bertalanffy models were run, and parameters were estimated for each fish. To compare von Bertalanffy growth parameters between populations and within Clear Lake, fish were separated into three groups based on age. These groups were ages 4-9 which allowed for a direct comparison with lake whitefish from St. Froid Lake, 10-15, and all fish older than 20. Mean asymptotic lengths and growth coefficients for each age group were calculated. Differences in parameters between overlapping age groups (4-9) were assessed between populations using a student t-test. Differences in mean growth parameters between age groups in Clear Lake were assessed using a one way analysis of variance (ANOVA) with a Tukey post hoc comparison. The relationship between the asymptotic length ($L_\infty$) and growth coefficient (k) was analyzed for lake whitefish in Clear Lake using east squares regression.

**Results**

**Fish capture:** A total of 255 fish from St. Froid lake were utilized for the growth analysis. In 2010, gill net samples yielded 28 fish. In 2011, trapnet and gill net sampling provided 46 and 40 fish respectively. Ice angling in the winter 2012 provided an additional 4 lake whitefish. Additional gill net sampling between 2006 -2009 accounted for 137 total fish, although these otoliths were not available for back calculation.
procedures, lengths at age were utilized. In addition, for a subset of otoliths utilized, annuli along the predetermined measurement transect were not readable and only age at capture could be assigned from fin clips. In both circumstances, length at age data was still utilized in growth models.

In total, otolith back calculation procedures provided 602 lengths at age with all stocked cohorts being represented in the St. Froid Lake sample. Fish ranged from 2 to 9 years of age, and from 218mm to 404mm in total length.

Lake whitefish from Clear Lake were collected by gillnet in the summer of 2011. Three experimental gill nets were used to collect a total of 62 fish; from these captures, 57 otoliths were used for analysis. Lake whitefish ranged in age from 8 to 30 years in Clear Lake with total length at capture ranging from 370mm to 514mm. All ages less than 8 and many intermediate age classes were not represented in the Clear Lake sample. Back calculation methods provided 822 lengths for the Clear Lake analysis.
Table 2.4. Captured size at age and calculated size at age of lake whitefish from Clear (A) and St. Froid Lakes (B). Bolded values indicate the mean length for a given age.

Growth trajectories: Few (6) old age fish (>20 years) were captured in Clear Lake as they are most likely a small component of this wild population (Table 2.4). Individual growth trajectories based on back calculated lengths at age show a wide range (nearly 100mm) in age one total length for Clear Lake (Figure 2.2 A.). Variability in length at age increased with increasing age. Back calculated lengths at age demonstrate that older fish are also the slowest growing individuals, thus exhibit small lengths at age in comparison to younger cohorts from Clear Lake (Figure 2.2A).
Figure 2.2. Individual growth trajectories from lake whitefish from Clear Lake (A) and St. Froid Lake (B) using Fraser-Lee back calculation procedures.

Back calculated lengths from St. Froid Lake fish also reveal a large degree of variability in year one growth (Figure 2.2B) despite experiencing hatchery conditions. Although older cohorts were not present in St. Froid Lake at time of sampling, it appears that the older fish in this population (maximum of age 9) also display a slower growth rate over their lifetime.
**Growth models:** For the St. Froid Lake population, predicted lake whitefish total length was described by the von Bertalanffy growth model as

\[ L_t = 357[1 - e^{-0.429(t+0.323)}] \]

For the Clear Lake population, predicted lake whitefish total length (mm) was described by the von Bertalanffy growth model as

\[ L_t = 431[1 - e^{-0.197(t+1.310)}] \]

When both observed and back calculated lengths at age are plotted along with the von Bertalanffy growth curve, the influence of older and slower growing fish is evident. When von Bertalanffy growth curves are plotted jointly, an intersection of growth trajectories is apparent near age seven (Figure 2.3C). From this point on, von Bertalanffy length at age estimates are consistently lower than Clear Lake length estimates for the same age.
Figure 2.3. A) Individual lengths age at age and von Bertalanffy growth curve for lake whitefish from St. Froid Lake, B) Individual lengths at age and von Bertalanffy growth curve for lake whitefish from Clear Lake, C) Von Bertalanffy growth curves from St. Froid and Clear Lakes with associated parameters.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Clear Lake</th>
<th>St. Froid Lake</th>
</tr>
</thead>
<tbody>
<tr>
<td>$L_\infty$</td>
<td>431</td>
<td>357</td>
</tr>
<tr>
<td>$K$</td>
<td>0.197</td>
<td>0.429</td>
</tr>
<tr>
<td>$t_0$</td>
<td>-1.31</td>
<td>-0.323</td>
</tr>
</tbody>
</table>
Mean asymptotic lengths of the 4-9 age groups significantly differed between St. Froid and Clear Lakes ($p = <0.001$). In Clear Lake, mean asymptotic lengths differed across the three age groups ($p = <0.001$) (Table 2.5). Tukey post hoc comparisons of the three groups indicate that the 4-9 age range group ($M = 453\pm 36$) had a lower asymptotic lengths when compared to the 10-15 range age group ($M = 498\pm 36$) and the greater than 15 age group ($M = 501\pm 27$). Mean growth coefficients also differed across the three age groups ($p = <0.001$). Tukey post hoc comparisons indicate that all age range groups differed from one another in growth coefficients. A strong negative relationship exists between Age and growth coefficient (K) in the Clear Lake sample (n=57, $R^2 = 0.72$, $p=<0.001$).

Table 2.5. Mean growth parameters of three age range groups in St. Froid and Clear Lakes. * indicate parameter differences between populations. Population parameter differences are shown (a,b).

<table>
<thead>
<tr>
<th>Age Group</th>
<th>n</th>
<th>$L_\infty$</th>
<th>K</th>
<th>n</th>
<th>$L_\infty$</th>
<th>K</th>
</tr>
</thead>
<tbody>
<tr>
<td>(4 - 9)</td>
<td>64</td>
<td>367 ± 40*</td>
<td>0.405 ± 0.238*</td>
<td>18</td>
<td>453 ± 36a</td>
<td>0.221 ± 0.033a</td>
</tr>
<tr>
<td>(10 -15)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>32</td>
<td>498 ± 32b</td>
<td>0.138 ± 0.030b</td>
</tr>
<tr>
<td>(&lt; 15)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>7</td>
<td>501 ± 29b</td>
<td>0.070 ± 0.015c</td>
</tr>
</tbody>
</table>

**Discussion**

Individual back calculated trajectories suggest that older fish in Clear Lake grew slower at a given age than did young fish (Figure 2.2C). Brown and Taylor (1992) describe the positive relation between growth and prey density and prey density and increased survival in larval lake whitefish. Lake whitefish from St. Froid Lake were hatchery reared individuals that did not encounter the same food limitations experienced.
by Clear Lake juvenile lake whitefish in the wild. A size advantage by juvenile lake whitefish in St. Froid Lake is evident by predicted lengths at age (Figure 2.3C). These larger predicted lengths from St. Froid Lake may dictate important life history characteristics such as size at maturity, adult growth trajectories, and theoretical maximum length (He and Stewart 2002). Specifically, fish would reach sexual maturity at a smaller size, when compared to wild fish under food resource limitations. Both male and female lake whitefish in St. Froid Lake display sexual maturity by age 3, but because fish of similar age were not captured in Clear Lake we cannot make this comparison. However, lake whitefish do have the ability to display a rapid reproductive response with changing conditions of growth (Jensen 1985).

Adult growth trajectories in the St. Froid Lake population are consistent with early maturation, as growth is reduced after age 8. Conversely, lake whitefish from Clear Lake may mature later, live longer, and defer growth to later stages of life, evident by a smaller growth coefficient ($K$) (Figure 2.3C).

Differences in feeding opportunity may explain the slower growth of older fish in St. Froid Lake. These differences may arise from reduced prey quality or a lack of prey availability, both of which can prohibit fish from undergoing a diet shift to larger more energetically profitable prey items (Pazzia et al. 2002). Similar instances have been reported in populations of yellow perch whereby the energy efficiency of prey switching is interrupted (Sherwood et al. 2002). Although a failure to make an ontogenic diet shift is conceivable, knowledge regarding diet overlap between lake whitefish and other fish species in St. Froid Lake is lacking.
Harvest alone has the potential to shape the size structure of a fishery (Amtstaetter 2002). If harvest of the fastest growing and largest individuals in St. Froid Lake was occurring, one might expect a lake whitefish population dominated by slow growing lake whitefish. However, anecdotal evidence suggests the fish angled in St. Froid Lake are of legal size. Stocking practices can provide a number of desired outcomes for fisheries managers, and afford a logical means by which lake systems with extirpated populations can be restored. However, the stocked lake whitefish in St. Froid Lake have experienced unintended, and from a management perspective, undesirable growth. Our findings thus indicate lake whitefish restoration in St. Froid Lake may entail a long term evaluation, and it remains to be seen whether lake whitefish will successfully reproduce in St. Froid Lake.
CHAPTER THREE:

SEASONAL VERTICAL, THERMAL, AND SPATIAL HABITAT USE BY A REINTRODUCED POPULATION OF LAKE WHITEFISH IN ST. FROID LAKE, MAINE.

Abstract

Spatial, vertical, and thermal habitat use was examined for a reintroduced population of lake whitefish in St. Froid Lake, Maine using acoustic telemetry. Tagged individuals were observed from October 2011 to June 2013. Tags provided year round vertical and thermal habitat use information. Data from 23 tagged lake whitefish were used in analyses. During periods of thermal stratification fish were localized in areas of St. Froid Lake providing deep cold water habitat. Seasonal activity and depth use were driven by periods of ice cover during the winter months and thermal stratification during the summer months. Under periods of ice cover (December-March) fish demonstrated reduced levels of activity while fish in the summer months (June-September) fish displayed the highest levels of activity. During periods of thermal stratification fish displayed diel vertical migrations, actively selecting depths and temperatures that may be more energetically profitable. During late season stratification, fish routinely utilized areas of warmer (>15°C) than optimal temperatures for growth.
**Introduction**

In continental North America lake whitefish (*Coregonus clupeaformis*) are distributed from areas of Northern Maine to the Great Lakes region, north into interior Canada and northwest to Alaska (Evans et al. 1988). In the Great Lakes region, lake whitefish serve as a valuable economic resource (Spangler 1970; Fleischer 1992) but over exploitation in some populations has led to negative population trends (Pothoven et al. 2001; Rennie et al., 2009). In contrast, lake whitefish populations in Maine are not commercially harvested and receive minimal impact from recreational fisheries. Fishery induced mortality is low for many of Maine’s lake whitefish populations, still some have suffered extirpation (Basley 2001).

Stocking is a common strategy for the rehabilitation of lake whitefish populations in the Great Lakes (McMurty 1989; Amstaetter 2002; Amtstaetter and Willox 2004) and has recently been utilized in selected waters throughout Maine. In lake systems that were extirpated, stocking of hatchery reared lake whitefish has potential to rebuild a historic fisheries resource. Integral to the success of these reintroduced fish is the ability to utilize energetically beneficially vertical, thermal, and spatial habitats.

In the fall lake whitefish occupy shallow littoral habitats in conjunction with spawning activity. Anras et al. (1999) documented intense lake whitefish spawning activity over a 5-6 day period in late October, when surface water temperatures became less that 6°C. However, Wanzenboeck et al. (2012) documented prolonged spawning activity in a whitefish population responding to trigger factors that are likely genetic rather than environmental. Regardless of temporal variability in spawning activity, lake whitefish rely on adequate shallow water habitats during this critical life history stage.
Adult lake whitefish perform diel vertical migrations under prolonged periods of thermal stratification in lake systems (Busch et al. 2011; Gorsky et al. 2012). However, stimuli for these behaviors appear to be system dependent (Busch et al. 2011). Gorsky et al. (2012) described summer diel vertical migration activity patterns with changes in lake surface temperature, though other factors including food availability (Wurtsbaugh and Neverman 1988), metabolic cost, (Brett 1971), and predation risk (Lampert 1989) are certain to influence the timing and duration these vertical movements. To add further complexity, many of Maine’s lakes now contain a fish community that differs from the historic cold-water assemblage (Table 3.1) (Mercado-Silva et al. 2006). The ability of lake whitefish to perform basic life history functions within these altered lake systems is unknown.

We use acoustic telemetry and environmental data to describe spatial, temperature, and depth use by reintroduced lake whitefish in a Maine lake which undergoes thermal stratification. Using the previous findings by Gorsky et al. (2012) in which seasonal habitat and diel vertical activity was examined for an extant lake whitefish population, we aim to expand knowledge of seasonal and diel patterns for reintroduced lake whitefish in St. Froid Lake.
Table 3.1. Listed below are native and non-native species found within St. Froid Lake.

<table>
<thead>
<tr>
<th>St. Froid Lake</th>
<th>Clear Lake</th>
</tr>
</thead>
<tbody>
<tr>
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</tr>
<tr>
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</tr>
<tr>
<td>creek chub (<em>Semotilus atromaculatus</em>)</td>
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<td>slimy sculpin (<em>Cottus cognatus</em>)</td>
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<td>lake trout (<em>Salvelinus namaycush</em>)</td>
<td>white sucker (<em>Catostomus Commersoni</em>)</td>
</tr>
<tr>
<td>lake whitefish (<em>Coregonus clupeaformis</em>)</td>
<td>three spine stickleback (<em>Gasterosteus aculeatus</em>)</td>
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<td>landlocked salmon (<em>Salmo salar</em>)</td>
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<td>long nose sucker (<em>Catostomus catostomus</em>)</td>
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<td>round whitefish (<em>Prosopium cylindraceum</em>)</td>
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<tr>
<td>three spine stickleback (<em>Gasterosteus aculeatus</em>)</td>
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<tr>
<td>white sucker (<em>Catostomus Commersoni</em>)</td>
<td></td>
</tr>
<tr>
<td>yellow perch (<em>Perca flavescens</em>)</td>
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</tbody>
</table>

**Methods**

**Stocking:** In 2001, Maine established a hatchery program for the reintroduction of lake whitefish into waters with severely reduced abundance or those that had experienced extirpation. Lake whitefish broodstock for this program originated from Clear Lake, Piscataquis County, Maine. During the 2002-2009 spawning seasons, lake whitefish from Clear Lake were captured by trapnet, manually spawned, and released. Subsequently, fertilized eggs were transported to a hatchery facility in Enfield, Maine, where they were reared until the fall fingerling stage. During the fall season, juvenile lake whitefish were
then distributed to selected lakes. One of these lakes was St. Froid Lake in Winterville, Maine. St. Froid Lake received variable levels of reintroduction stockings between the years of 2003 and 2010.

**Study Site:** St. Froid Lake is 971 ha located in Winterville, Aroostook County, Maine (46°57′46.75″ N and 68°37′07.25″ W) (Figure 3.1). St. Froid Lake is an oligotrophic lake with a mean depth of 14.5m and a maximum depth of 34.7m (Lakes of Maine 2012). The St. Froid Lake fish assemblage consists of four top predators, a robust benthic community, as well as a number of forage fish species (Table 3.1). St. Froid Lake is just one of a number of lakes in the Fish River Chain of Lakes, which are regarded as a historic region for cold-water fisheries (Warner and Fenderson 1963).
Figure 3.1. Location map of St. Froid Lake, Winterville, Maine. Open circles indicate locations of acoustic receivers. The closed circle within the inset map indicates the approximate location of St. Froid Lake in Maine.
Environmental monitoring: Throughout the study, we monitored surface light intensity (lux) and water temperatures (°C) in St. Froid Lake with HOBO light and temperature loggers (model: Onset Computer Corp., Bourne, Massachusetts). Six HOBO loggers, positioned at 2, 8, 14, 20, 26, and 32 meters in depth made up a vertical array within St. Froid Lake. The Hobo logger at 2 meters depth was equipped with both temperature and light measuring capabilities. The entire array was placed in approximately 32 meters of water to provide year round surface light intensity and water temperature information.

Fish capture, tagging, and telemetry: A total of 23 adult fish were tagged between February 2011 and March 2012 to provide telemetry data for analysis (Table 3.2). All study fish were captured by ice angling methods. Subsequent to capture fish were anesthetized using a buffered tricaine methanesulfonate (MS-222); 100 mg/L; 0.20-mM NaCO₃ pH = 7.0) solution. Fish total length was measured to the nearest millimeter and when possible mass was measured to the nearest gram. To tag lake whitefish a small incision was made posterior to the pectoral girdle using a sterile scalpel blade. Next, a Vemco V9 Temperature and Pressure (V9TP) (Vemco, Halifax Nova Scotia) acoustic tag (42mm, 5.2g) was inserted into the incision. Three sterile sutures were used to enclose the incision and the tag within. The percentage body burden of the tag ranged from 0.15 to 2.8% among tagged fish (Table 3.2). Surgery time was approximately 2 minutes and fish were allowed to recover in source water. Fish typically regained equilibrium within 2-3 minutes of the surgery and were released in close proximity to the capture location.
Table 3.2. Lake whitefish tagged and utilized for data analysis in 2011 and 2012.

<table>
<thead>
<tr>
<th>Fish ID</th>
<th>Total Length (mm)</th>
<th>Mass (g)</th>
<th>Time Observed (d)</th>
<th>% Body Burden</th>
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<tr>
<td>7</td>
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<td>301.6</td>
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<td>0.017</td>
</tr>
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</table>

**Passive telemetry:** Vemco V9TP tags transmit unique fish identification, temperature (°C), and depth (meters) information with alternate pings to receivers submerged throughout St. Froid Lake (Figure 3.1). Tags were programmed to randomly ping between 180 and 270 seconds and were decoded by stationary acoustic receivers. Twelve Vemco VR2 receivers were deployed within St. Froid Lake for year round detection of tagged lake whitefish (Figure 3.1). VR2 receivers were downloaded bi-annually.
Initial data exclusion was performed at the individual level to assure fish status and data quality. Data exclusion occurred in three circumstances. First, mortality was inferred by an absence of vertical movement for prolonged periods of time (>3 months) or if detection data became non-existent for the duration of the study. Second, if depth or temperature data was nonsensical (beyond the range for depths or temperatures) for St. Froid Lake, these detections were removed from the dataset.

**Spatial habitat use:** Spatial habitat use of tagged fish was assessed from May 2012 to June 2013. Acoustic detections were pooled by tagged individual and the associated receiver. Using the data exclusion methods previously described, the time span of fish observation was determined. Subsequently, quantities of daily detections were recorded for each fish, at each individual receiver station. Fish with one or greater detections for a given receiver, for a given day were assigned a “1”, conversely days having no detections were assigned a “0”. Assignments were compiled into binary matrices that described detections of an individual fish, at a given receiver, for the lifetime of the fish. Daily “1” and “0” assignments were further separated into eight different seasonal time periods. For each fish, the proportional number of detection days was tabulated and mean proportional detection across all fish at each receiver station was calculated. We report the mean percentage of detections in proximity to each receiver for seasonal time periods. These periods include May-June 2012, July 2012, August 2012, September 2012, October-November 2012, December-January 2013, February-April 2013, and May-June 2013.
Seasonal activity and habitat use: To assess seasonal habitat use patterns, acoustic depth and temperature detection data from individual fish were compiled between October 2011 and October 2012. Exclusion of data occurred when individual fish had fewer than 20 detections (depth and temperature respectively) for a given week, to avoid bias of underrepresented fish. We report mean weekly depths and temperatures for lake whitefish in St. Froid Lake (depth/temperature±1S.D.).

To evaluate seasonal activity levels we analyze depth ranges from compiled acoustics data for individual fish using acoustic telemetry from May 2012 to April 2013. For seasonal photoperiod adjustment, all depth detection times were converted to a decimal time system that ranged from 0.00-0.99. Decimal time values between 0.00 and 0.49 represent “day” periods (between sunrise and sunset). Conversely decimal values between 0.50 and .99 are “night” detections (after sunset and before sunrise). Each day and night period was then further divided into five segments that represent a diel interval index. In order to be included in analysis a threshold of three detections or greater for individual fish, per diel interval, was implemented for inclusion. Individual fish depth by diel interval by month was tabulated. Mean depth for diel segments are reported (depth ± 1 S.E.). All diel intervals were represented by 11 or more fish throughout the observation period.

Diel vertical and thermal habitat use: Individual fish detection data was assessed for diel patterns in thermal and vertical habitat use. Diel patterns were monitored between October 2011 and October 2012. Individual measurements were again characterized by the decimal time system. For this analysis crepuscular time periods were eliminated to reduce known variability in habitat use during these times. Day detections were
represented in the decimal time system by 0.05 to 0.45 and detections falling between 0.55 and 0.95 in decimal time were classified as Night detections. If individual fish had 10 or fewer detections for a given standard week, these data were excluded from analysis. Weekly means for day and night depths and temperatures are presented (depth/temperature±1S.D.).

**Results**

**Spatial habitat use:** During May and June 2012 fish were primarily located in the southern portions of St. Froid Lake at which time fish utilized the upper portions of the water column (3.1m±1.1). The highest mean detection proportion was recorded at receivers 8, 9, and 12 (0.41, 0.37, and 0.50 respectively) (Figure 3.2). Thermal stratification occurred in St. Froid Lake in late June. At this time all receivers had relatively low proportion of detection values (<0.250). In July lake whitefish utilized some of the deepest habitats observed (5.48m± 2.2) and (12.52m±4.33) respectively. Fall turnover (Figure 3.4D) occurred by late September and detection proportions increased overall at all receivers with fish beginning to inhabit northern portions of St. Froid Lake and becoming more surface oriented (6.58m±4.66). During the spawning season in October and November fish were surface oriented (4.63m ± 2.66m) and detection percentages increased in the northern portion of the lake, with uniform proportion of detection throughout. Under ice cover conditions in December 2012 and January 2013 detection proportions were highest at receivers 7 and 10 (0.384 and 0.440 respectively). During this time period, mean depth use was 5.48m ±4.96m. Between February and April proportion of detection values were highest at receivers 7, 10, and 12 (0.370, 0.526, and 0.381) and fish utilized deeper waters when compared to early winter. After ice out
in the spring months of May and June the greatest detection proportions were found in
the southern portion of lake at receiver 12 (0.410). In conjunction with the previous May
and June 2012 fish in 2013 again inhabited the upper portions of the water column
(2.56m±1.55).

Figure 3.2. Mean proportion of detection for each receiver from May 2012 to June 2013.
Bar graphs in lower left of each panels indicate the mean depth in meters (±1 S.D.)
during the given time period.
**Seasonal activity and habitat use:** Lake whitefish utilized a variety of vertical and thermal habitats seasonality (Figure 3.4B). From October to December 2012, lake whitefish use progressively deeper water to approximately 7-meters. Ice cover on St. Froid lake occurs by late December 2012 and remains until mid-March (Figure 3.4C) at which time fish ascend to roughly 4 meters, and remain near this depth until ice out occurs. When ice out begins in mid-March to late April, average weekly depth use decreases to approximately 7 meters, while at the same time depth use variability increases. Between May and early June fish exclusively utilize the upper 2 meters of the water column and exhibit little variability in vertical habitat use. Lake stratification occurs in June and remains through mid-August. At this time fish descend to approximately 13 meters (Figure 3.4B). During the stratification period in September fish demonstrate variability in vertical habitat use. With fall turnover events in mid-September, fish gradually ascend in the water column to approximately 4 meters, and maintain this depth from late September into October.

Mean weekly temperature use by lake whitefish ranged from 1°C to nearly 20°C throughout the study (Figure 3.4A). From October 2011 to late May 2012 St. Froid Lake was not thermally stratified, therefore fish demonstrate only slight variation in weekly temperature use. In June, waters begin to thermally stratify and there was greater variability in weekly temperature use (Figure 3.4A). This pattern persists through mid-September at which time fall turnover again produces a thermally uniform water column.

The greatest mean depth ranges occurred predominately during *day* periods regardless of season. During periods of thermal stratification (June-September 2012) the greatest depth ranges carried over into crepuscular periods (Figure 3.3). During
stratification in August 2012, fish show the greatest mean depth ranges during mid-day, although relatively high crepuscular activity is also evident. During the spawning season in October and November 2012 fish demonstrate similar mean depth ranges during *day* and *night* periods. When ice cover occurs in December 2012 through March 2011, virtually all vertical movement has ceased prior to dusk. Similarly, *day* mean depth ranges have diminished to near 1m for most diel segments in all winter months.
Figure 3. Mean diel depth ranges of tagged lake whitefish in 2012 and 2013 by month. Within plot segments represent diel interval indices. Closed circles represent mean depth range values for all fish alive during the given time period. Surrounding dashed lines represent ±1 S.E. All diel segments incorporate at least 11 fish (n=11).

**Diel vertical and thermal habitat use**: Lake whitefish in St. Froid Lake demonstrate differences in diel vertical habitat use across seasons. In October 2011 day and night fish depth did not differ greatly (Figure 3.4B). However, during the height of spawning season in November, fish were higher in the water column during the day than at night. With the onset of ice and snow cover in December (Figure 3.4C) fish in general used similar vertical habitat during both day and night periods (Figure 3.4B). This pattern persists during the period of ice cover which extended to mid-March, based on light intensity measurements (Figure 3.4C). Ice out began by mid-March at which time fish
utilized greater daytime depths coinciding with an increase in lake surface light intensity (Figure 3.4C). A similar diel depth pattern persists until late May 2012 at which time weekly day and night time depths are similar for three weeks. During thermal stratification in June and July, fish show the greatest differences in mean day and night depth use, as fish in the later of these periods occupy vertical habitats higher in the water column. In August fish utilize similar depths during day and night and greatest depths observed throughout the study (Figure 3.4B). June, July, and August were months with the greatest levels of light intensity and warmest surface temperatures (Figure 3.4C and 3.4D). In September 2012 fish utilized slightly greater depths in the water column during the day when compared to night time use. By late September fall turnover occurs day and night depth use patterns are similar to those described in the previous October.

Thermal habitat use by lake whitefish in St. Froid Lake was driven by seasonal changes in thermal habitat availability. From October 2011 to June 2012 day and night time temperature use was similar as available temperatures within the water column were nearly uniform (Figure 3.4A). The onset of thermal stratification begins in June at which time fish utilized consistently higher temperatures during the day than at night. The greatest differences between weekly mean day and night temperatures occurred in July. This pattern of diel temperature utilization persisted until late September, when waters were no longer thermally stratified (Figure 3.4A). By late September fall turnover occurred in St. Froid Lake and fish again utilized similar day and night time temperatures as the previous fall.
Figure 3.4. (A) Mean weekly temperature use (°C ±1S.D.) by tagged fish (n=23) in St. Froid Lake; (B) Mean weekly depth (m ±1S.D.) use by tagged fish in St. Froid Lake; (C) Light intensity measured from St. Froid Lake; (D) Isopleth created from mean weekly temperatures from loggers at 2, 8, 14, 20, and 26m depth in St. Froid Lake. All data shown from October 2011 to October 2012.
Discussion

Regardless of season, the percentage of detection remained the greatest in the southern portions of St. Froid Lake. During late season periods of thermal stratification this pattern of spatial habitat use coincides with fish presence in a part of the lake with some of the greatest depths available in St. Froid Lake. Tagged individuals were associated with areas of the lake with the deep water habitats during the height of summer. As summer progressed, thermocline depth increased, with the warming of surface waters (Figure 4D). Thermal dynamics coupled with the physical characteristics of St. Froid Lake, namely depth, may limit the areas in St. Froid Lake where whitefish will or can inhabit. When lake whitefish are seasonally localized in regions with deeper waters they may be isolated from preferred food resources by biological constraints (Vanderploeg et al. 2009). In this study, we had the lowest level of detection during the summer months when fish were the deepest in the water column and surface waters were the warmest. This suggests use of deep water habitat.

Seasonal patterns of vertical and thermal habitat use are driven by periods of lake ice cover and thermal habitat availability during stratification periods. Diel vertical migratory behavior is well documented for a number of coregonids (Busch et al. 2011; Mehner and Kasprzak 2011) and is ultimately controlled by a host of physical, chemical, and biological variables. Lake whitefish in St. Froid Lake demonstrate temporal variability in the magnitude of these behaviors.

In the fall (October and November) fish showed a clear pattern of surface oriented movement consistent with spawning behavior (Anras et al. 1999, Gorsky et al. 2012). Field observations indicate lake whitefish in St. Froid Lake are reproductively mature and
these vertical behaviors indicate fish are able to utilize near lake surface habitats, ideal for spawning.

Daily changes in depth use and activity observed in the summer are consistent with a visual predator that is reliant on time periods where prey is most vulnerable (e.g. dusk and dawn). Similar depth use patterns have been noted for zooplankton (McLaren 1963), which can make up a large portion of lake whitefish diet (Pothoven et al. 2001). However, lake whitefish diet and the vertical migration patterns of the zooplankton community in St. Froid Lake have not yet been investigated.

Daily temperature use patterns show lake whitefish in St. Froid Lake predominately moved into colder waters during dawn and dusk (crepuscular) time periods, a tactic that may be energetically beneficial in food limited environments (Brett 1971; Clark and Levy 1988; Wurtsbaugh and Neverman 1988). Interestingly, lake whitefish in St. Froid Lake used noticeably higher summer temperatures than were previously reported in Maine lakes Gorsky et al. (2012) and what has been reported for both thermal preference and thermal optimum in a number of lake whitefish studies (Christie and Regier 1988). Prolonged thermal habitat use outside of the preferred range requires fulfillment of increased metabolic costs and oxygen consumption (Bernatchez and Dodson 1985) and thus can be detrimental to overall fish condition.

Understanding the use of important thermal habitats and where they exist within the water column seasonally, provides important baseline information for fisheries managers tasked with restoring lake whitefish populations. However, lake whitefish are only one of host of fish species, both native and nonnative, that inhabit St. Froid Lake. In
the oligotrophic lakes of northern Maine, food resources are often a limiting factor and
habitat use may reflect real biological tradeoffs encountered by lake whitefish in
reintroduced lake systems, such as St. Froid Lake.
BIBLIOGRAPHY


BIOGRAPHY OF THE AUTHOR

Silas Ratten was born in Rockport, Maine on September 28th, 1985. He was raised in Searsmont, Maine by the most loving and supportive parents. He graduated from Belfast Area High School in 2004. He attended the University of Maine and graduated in 2008 with a Bachelors of Science degree in Forest Ecosystem Science. He never ventured far, working as a technician for a number of fisheries research laboratories at the University of Maine, as a technician for NOAA fisheries, and as a contract worker for Maine Department of Inland Fisheries and Wildlife (MDIFW). He has gained perspective and appreciation for the important aspects of life through this experience and will strive for humble simplicity in whatever he decides to pursue next. Silas is a candidate for the Master of Science degree, in Wildlife Ecology from the University of Maine in December 2013.