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Ecology of larval fishes and large zooplankton in the Keweenaw
Current region of Lake Superior, with special focus on lake herring,
Coregonus artedii

Jason K. Oyadomari
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**ECOLOGY OF LARVAL FISHES AND LARGE ZOOPLANKTON IN THE
KEWEENAW CURRENT REGION OF LAKE SUPERIOR, WITH SPECIAL
FOCUS ON LAKE HERRING, *COREGONUS ARTEDI***

by

Jason K. Oyadomari

A DISSERTATION

Submitted in partial fulfillment of the requirements

for the degree of

DOCTOR OF PHILOSOPHY

(Biological Sciences)

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ABSTRACT

I assessed the influence of the Keweenaw Current and spring thermal bar on the distribution of larval fishes and large zooplankton in Lake Superior. In 1998 and 1999, samples were collected from inshore (0.2 – 3.0 km from shore) and offshore (5.0 – 9.0 km from shore) locations on three transects off the western coast of the Keweenaw Peninsula, Michigan. For larval fishes, density and size distribution patterns of lake herring (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsoni*), and spoonhead sculpin (*Cottus ricei*) suggest a seasonal inshore to offshore movement. For zooplankton, seasonal warming appeared to be the major factor that limited planktonic catches of the primarily benthic *Mysis relicta* and *Diporeia* spp., while simultaneously stimulated growth and reproduction of the cladocerans *Daphnia* spp., *Holopedium gibberum*, and *Bythotrephes cederstroemi*. In contrast, calanoid copepods as a group were abundant throughout the entire sampling season. The greatest abundances of zooplankton were generally encountered offshore, even for the cladocerans, which apparently expanded from inshore to offshore locations with seasonal warming.

In 2000, sampling efforts focused on lake herring. Samples were collected from surface waters at 0.1 – 17.0 km from shore on two transects. Lake herring larvae were also reared in the laboratory from eggs in order to validate the use of otolith microstructure for aging. Increment deposition was not statistically different from a daily rate starting from 28 days after hatching, near the time of yolk-sac absorption, but larvae with lower growth rates could not be aged as accurately. In Lake Superior, lake herring tended to be slightly more abundant, larger, and older at inshore locations, but a dense patch of younger larvae was also encountered 7 – 13 km from shore. The distribution

patterns suggest that larvae were transported by prevailing currents into the study region, possibly from the more productive spawning regions in western Lake Superior. Growth rates were suppressed at offshore locations where temperatures were less than 8°C. These results indicate that lake herring larvae may be transported far distances from spawning concentrations by longshore currents, and water temperatures may largely control their growth.

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CHAPTER 1

Inshore-Offshore Distribution of Larval Fishes in Lake Superior off the Western Coast of the Keweenaw Peninsula, Michigan

ABSTRACT

I surveyed the larval fish community in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan, as a first component in understanding how the Keweenaw Current affects larval fish distribution and survival. From transects at Ontonagon, Houghton, and Eagle Harbor, I collected larval fishes with a 1-m diameter plankton net towed through surface and deep (below metalimnion) waters at an inshore location (1 km from shore) and an offshore location (5 – 9 km from shore) during daytime and nighttime in 1998 and 1999. The most abundant larvae caught were lake herring (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsoni*), and spoonhead sculpin (*Cottus ricei*). Lake herring were generally most abundant at the surface during daylight, while the other four species were abundant at the surface only at night. Overall, larval fish densities were greater inshore than offshore, with exceptions for particular locations and seasonal periods (1.24 times greater inshore for lake herring, 12.93 times greater inshore for rainbow smelt, 1.27 times greater inshore for burbot, 1.25 times greater inshore for deepwater sculpin, and 4.26 times greater inshore for spoonhead sculpin). Differences in the sizes of larvae between inshore and offshore locations, in conjunction with density patterns, suggest a seasonal inshore to offshore movement. Despite the presence of the Keweenaw Current, the overall distribution patterns of larval fishes followed those of previous studies conducted in the Great Lakes, but with lower densities, as might be expected for oligotrophic Lake Superior.

INTRODUCTION

Many native commercial fish stocks of the Laurentian Great Lakes declined drastically from overexploitation of fisheries, drainage modifications, and exotic species introductions following European settlement (Smith 1968, 1972). Accordingly, Lake Superior management efforts focus on restoring these stocks to historic levels (Busiahn, 1990). However, the size of fish stocks is largely dependent upon recruitment, which can vary drastically from year to year, resulting generally from highly variable survivorship during early life stages (Saville and Schnack 1981, Houde 1987). Understanding the dynamics of early life survival requires knowledge of the spatial and temporal distributions of larval fishes. Large-scale hydrological features such as currents (e.g., Houde and Forney 1970, Simpson 1987), upwelling (e.g., Heufelder et al. 1982), fronts (e.g., Sakamoto and Tanaka 1986, Sabatés and Olivar 1999), and river plumes (e.g., Govoni et al. 1989, Grimes and Finucane 1991) can readily alter the distribution of larval fishes, which generally have limited swimming abilities.

In Lake Superior, the Keweenaw Current flows northeasterly along the western coast of the Keweenaw Peninsula, Michigan (Lam 1978, Beletsky et al. 1999) with recorded velocities of over 60 cm/s near Eagle Harbor in September 1999 (Chen et al. 2004), and in conjunction with the spring thermal bar (Hubbard and Spain 1973), has the potential to influence larval fish distribution and survival. The spring thermal bar is the 4°C front that separates warmer inshore waters from colder offshore waters during the early spring warming of dimictic lakes. The 4°C water, the density maximum of freshwater, descends creating a downwelling that has been proposed to prevent inshore waters from directly mixing with offshore waters (Hubbard and Spain 1973). The Keweenaw Current and spring thermal bar can affect larval fishes indirectly as well, by

altering the distribution of zooplankton food resources, and by impeding the offshore transport of terrestrial-borne nutrients important for primary productivity.

The objective of this study was to document the distribution of larval fishes in the Keweenaw Current region of Lake Superior. Knowing the distribution of larval fishes is the first component in understanding how transport by the Keweenaw Current and local habitat characteristics within this region affect larval fish survival, and subsequently, recruitment. I hypothesized that fish larvae would be confined with inshore, warmer waters by the thermal bar, and that greater densities of larger larvae would be found near the base of the Keweenaw Peninsula, where the current is presumably wider and slower and waters are generally warmer. Elsewhere I expected that the current would quickly transport larvae along the coast and out of the area.

STUDY AREA

The study area included the region of Lake Superior located off the western coast of the Keweenaw Peninsula, Michigan (Figure 1-1). As part of the Keweenaw Interdisciplinary Transport Experiment in Superior (KITES) project, I utilized three transects within this region (Ontonagon, Houghton, and Eagle Harbor) that crossed the Keweenaw Current. Each transect differed in its physical characteristics. The bottom slope at Ontonagon is gradual with depths of 12 m at 1 km, 28 m at 5 km, and 63 m at 9 km offshore. The slope at Eagle Harbor is steep with depths of 161 m at 1 km, 246 m at 5 km, and 251 m at 9 km offshore. The slope at Houghton is intermediate with depths of 10 m at 1 km, 108 m at 5 km, and 114 m at 9 km offshore. Correspondingly, in spring and summer, warm, inshore waters extend offshore sooner and farther at Ontonagon than at Houghton or Eagle Harbor, with Eagle Harbor waters remaining cold for most of the

year, even at relatively close distances from shore (Ragotzkie and Bratnick 1966, Ullman et al. 1998). However, summer maximum temperatures were approximately 20 °C for all transects (Figure 1-2). The Keweenaw Current in summer is characterized by warm, inshore waters within a strong thermal front (Green and Terrell 1978). The width of the Keweenaw Current follows lake bathymetry, being narrowest at the steep slope at Eagle Harbor (extending approximately 5 – 10 km offshore in July) and wider where bottom slope is more gradual (Green and Terrell 1978).

METHODS

Field Sampling

Fish larvae were sampled from April – August in 1998 and 1999. Samples were collected along three transects, Ontonagon, Houghton, and Eagle Harbor (Figure 1-1), with a 1-m diameter, 500- μ m mesh, conical (3:1 length to diameter ratio) plankton net, equipped with a center-mounted digital flowmeter (General Oceanics Inc.; Model 2030). Flow meter recordings were used to calculate the volume of water filtered for each tow. In 1998, an initial survey was conducted by sampling from an “inshore” and an “offshore” location on each transect, whenever possible, where distances from shore of selected locations sometimes varied among cruises for the different transects. The distances from shore of “inshore” locations were 1.0 km for Ontonagon, 0.2, 0.5, 1.0, or 3.0 km for Houghton, and 0.5 or 1.0 km for Eagle Harbor. The distances from shore of “offshore” locations were 9.0 km for Ontonagon, 5.0 or 7.0 km for Houghton, and 5.0 for Eagle Harbor. In 1999, inshore and offshore locations were limited to only one distance from shore for each transect. The inshore location in 1999 was 1.0 km from shore on all

three transects, whereas the offshore location was 9.0 km from shore at Ontonagon and 5.0 km from shore at Houghton and Eagle Harbor.

At each station (i.e., a particular distance from shore on a particular transect) for both years, surface and deep tows were taken during daytime and nighttime. Surface tows were taken from the top 1 m of water. Deep tows were taken from immediately below the metalimnion at deeper, stratified stations and close to bottom at shallower, well-mixed stations. For deep tows, the angle and length of the towing cable were used in a cosine function to calculate towing depth. At a particular station, surface tows were alternately taken with deep tows following a trajectory parallel with shore, typically heading southwest, starting from the transect line. The net was towed horizontally through the water, typically for 10 minutes at a speed of 0.77 – 1.03 m/s (1.5-2.0 knots) and filtering an average (\pm SD) volume of 430 (\pm 165) m³ of water. Because it was possible to continue to catch larvae during net retrieval, the deepwater samples may have contained larvae caught from surface waters. However, the long towing duration should have reduced the relative contribution of incidental catch, especially at shallower inshore locations.

In 1998, whenever possible, two samples were collected from each offshore location for both depths during daytime and nighttime. In 1999, three samples were collected from the inshore location and two samples from the offshore location for both depths during daytime and nighttime. On occasion, surface tows were also collected from the North Entry of the Keweenaw Waterway and from immediately within the mouth of the Ontonagon River (Figure 1-1) to determine if different species occurred around riverine inflows. A total of 89 tows in 1998 (16 from Ontonagon, 41 from

Houghton, 23 from Eagle Harbor, and 9 from riverine areas) and 317 tows in 1999 (84 from Ontonagon, 165 from Houghton, 44 from Eagle Harbor, and 24 from riverine areas) were collected. A small amount of 10% formalin was added to each sample for preservation. A vertical water temperature profile was recorded before each tow with a Sea-Bird Electronics CTD (SBE-25) or a Hydrolab® MiniSonde®. Profiles were also taken at additional locations from shore along the three transects during cruises additional to those of larvae fish sampling to determine the location of the spring thermal bar.

Identification and Measurements

In the laboratory, I separated larval fishes from each sample and stored them in vials containing 4% formalin. Larval fishes were identified to species whenever possible following Auer (1982). Large fish were measured to the nearest 0.05 mm with a dial caliper while small fish were measured to the nearest 0.01 mm with a dissecting microscope equipped with an ocular micrometer and using 0.9 – 2.0 times magnification. The abundance of each species was converted to density as number of larvae per 1000 m³.

Data Analysis

The sampling design studied the following five factors that may influence larval fish abundance: transect, distance from shore, date, day period, and tow depth. Larval fish studies typically involve limited number of samples, low catches including many zero catches, and high variability among samples. This was true of this study as well, so I decided to narrow the data set in stages. Based on the study objective, I was primarily interested in differences among transects and distances from shore (i.e., gradients along the current and offshore). The other three factors were included to increase the chances

of catching various species, considering that each species likely has a different spatial and temporal pattern of occurrence.

I first identified the most abundant species and their seasonal periods of occurrence. On seven occasions in 1999, I happened to have started night sampling before the end of civil twilight. Because, twilight is possibly a transitional period with catches different from either daytime or nighttime catches, I then tested the validity of pooling twilight tows with post-twilight tows for each of the abundant species. I used daytime, twilight, and post-twilight tows taken during each of the seven occasions at a particular station as a block of data, omitting entire blocks for a given species when containing only zero catches. I did not catch spoonhead sculpin (*Cottus ricei*) in any of these blocks, thus no analysis was employed for this species. For the remaining species, I analyzed for differences in mean density with randomized-block ANOVA on square-root ($\sqrt{X + 0.5}$) transformed data (Zar 1999) for within-block factors, depth and day period, and their two-way interaction. Upon obtaining a significance result, I performed the Tukey multiple comparison test (Zar 1999) to determine which day periods in particular were statistically different from each other for each depth. I found a statistical difference only for lake herring (*Coregonus artedii*) where twilight tows were statistically greater than either daytime or nighttime tows (see Results). Because I did not collect twilight tows often enough to be well represented in the dataset, I omitted surface twilight tows from subsequent analyses for lake herring so that they would not bias any of the lake herring density estimates. For the remaining species, differences were not significant (see Results), so accordingly, I pooled twilight and post-twilight nighttime tows for subsequent analyses. For each abundant species, I also identified their most abundant

seasonal period in which I considered catches to be sufficiently abundant for subsequent analyses.

Next, I assessed the depth and diel dimensions of occurrence for each of the most abundant species by first balancing the sampling effort. I balanced the effort by using tows belonging to a set of an equal number of surface vs. depth tows and daytime vs. nighttime tows from a particular station during a particular cruise. Sampling in 1998 produced six complete sets, where each set contained 8 tows, while sampling in 1999 produced 23 complete sets, where each set contained 4, 8, or 12 tows. I then used the complete sets of tows that coincided with the most abundant seasonal period for each species to assess their depth and diel dimensions of occurrence. In addition, I did not include a complete set if it failed to capture larvae because a set of zero catches does not contribute to the determination of what depth and diel period a species occurs. This only occurred once, for spoonhead sculpin in 1999. Because of the numerous zeros still remaining in the dataset, I reduced the catches to presence/absence data and analyzed for differences with logistic regression (Tabachnick and Fidell 1996) for factors, depth and day period, and their two-way interaction. I performed the analysis on data pooled for both years to increase the sample size. For three of the five abundant species, I still did not have a sufficient sample size to estimate the log-likelihood in 15 iterations for the analysis. Thus, given that I had a balanced design, I estimated each factor separately for these three species.

Finally, I looked for differences in larval fish abundance and length among transects and distances from shore by employing data from only the depth and diel dimensions of occurrence for each particular species (as indicated on Table 1-4). I also

only present spatial data from 1999, because 1998 catches were generally too low to observe trends. Considering seasonal changes in density and length, and the inability to consistently sample all three transects during each cruise, I statistically analyzed the data separately by month and transect for each species, except for spoonhead sculpin for which I pooled June and July. I analyzed for differences between inshore and offshore densities with the Mann-Whitney test (Zar 1999), and differences between inshore and offshore lengths with the two-sample t -test on $\log(X + 1)$ transformed data (Zar 1999). For months in which it was possible to incorporate both transect and location for the length data analysis, I did so with a two-factor ANOVA on $\log(X + 1)$ transformed data (Zar 1999). Delimiting the data set in this manner eliminated many tows with zero captures, and thus allowed attention to be focused on the times and places at which larvae were caught.

I used surface (1-3 m depth) temperature measurements from all CTD and Hydrolab® profiles to determine the offshore location of the spring thermal bar. I estimated its location by linearly interpolating between adjacent surface temperature measurements that contained the 4°C isotherm. When the 4°C isotherm was not contained within the spatial extent of the temperature profiles, I simply noted the starting or ending sampling location beyond which I expected the thermal bar to exist and the temperature at that location. I used only the surface temperature measurements that were recorded during larval fish sampling cruises to directly relate temperature to larval fish distribution. All statistical analyses were performed with SYSTAT 10 (SPSS Inc.).

RESULTS

As expected, the spring thermal bar formed at Ontonagon first, probably sometime in April, and at Eagle Harbor last, sometime in May (Table 1–1). The thermal bar formed and advanced into Lake Superior earlier in 1998 compared to 1999, indicating that the lake warmed up earlier in 1998. However, surface temperatures were similar between years after June at all transects (Figure 1-2). In 1999, recorded drops in surface temperature in August at both inshore and offshore locations at Houghton indicated that a large upwelling event occurred (Figure 1-2). This upwelling event presumably spanned over most of the western coast, however I did not sample the other two transects during that period to actually record its spatial extent.

In 1998, a total of 152 fish larvae were caught with 89 larval net tows, while in 1999, 1,386 larvae were caught with 317 tows (Table 1–2). Three of the 17 genera or species I identified occurred exclusively or predominately around riverine inflows, while five additional scarce taxa occurred exclusively inshore near the Ontonagon River or the North Entry Canal (Table 1–2). The majority of the catches (91% in 1998 and 95% in 1999) belonged to the following five species: lake herring (*Coregonus artedii*), rainbow smelt (*Osmerus mordax*), burbot (*Lota lota*), deepwater sculpin (*Myoxocephalus thompsoni*), and spoonhead sculpin (*Cottus ricei*).

Seasonal Occurrence

These five species occurred during different periods of the sampling season (Figure 1-2). Larval lake herring were caught from the onset of sampling in mid to late April and, along with deepwater sculpin, peaked in abundance in early to mid May, at surface temperatures of 2.7 – 5.8 °C, and became rare by the end of June. Catches of

rainbow smelt and burbot displayed a peak in abundance in June, at 10.8 – 17.4 °C, while spoonhead sculpin larvae were caught only during a brief period from mid June to early July, at 12.7 – 16.9 °C.

Depth and Diel Distribution

For the seven occasions on which twilight tows were collected, lake herring densities were statistically greater at twilight compared to daytime or nighttime at the surface ($P < 0.001$), but not in deeper waters ($P > 0.50$) (Table 1–3). Because twilight tows were rarely taken, I omitted surface twilight tows from subsequent analyses for lake herring to prevent biasing the lake herring density estimates. There were no statistical differences in day period or depth densities for rainbow smelt, burbot, or deepwater sculpin (Table 1–3). Accordingly, I pooled twilight and post-twilight nighttime tows for these species for subsequent analyses. In addition, I truncated the seasonal periods of occurrences into the most abundant seasonal period (see Table 1–4) for each species for subsequent analyses.

Of the five most abundant species, only lake herring occurred in large numbers at the surface during daylight (Table 1–4). At night, lake herring were more abundant in deeper waters, suggesting that larvae migrated downward after sunset. However, the proportion of tows containing lake herring larvae did not differ statistically between day periods or depths (Table 1–5). Rainbow smelt, burbot, deepwater sculpin, and spoonhead sculpin were rare to nonexistent in surface samples during daylight (Table 1–4). In general at night, rainbow smelt, burbot, and deepwater sculpin were as abundant, and spoonhead sculpin was even more abundant, at the surface than in deeper waters. Therefore, these four species appeared to remain in deep waters during daylight and

ascend after sunset, reaching surface waters at night. The proportion of tows capturing larvae supports this trend for burbot with a significant depth by day period interaction, and for spoonhead sculpin, with a marginally significant interaction (Table 1–5). Rainbow smelt and deepwater sculpin densities were statistically different between depths, with a greater number of deep tows containing larvae compared to surface tows. Densities of deepwater sculpin additionally were statistically different between day periods, with a greater number of nighttime tows containing larvae compared to daytime tows. I used only the depth and diel combinations that resulted in abundant catches (Table 1–4) for subsequent analyses of each species.

Spatial Distribution

Lake herring was the most abundant species captured, with a peak density of 88 larvae per one tow (187.6 larvae/1000 m³) occurring inshore at Houghton in late April. However, the replicate tow to this high yielded no lake herring, attesting to the extreme patchiness of larval fish distribution. By early June, there was an inshore-to-offshore shift in abundance at Houghton (Table 1–6). Densities were (marginally) statistically greater inshore (9.4 times) than offshore in May (Mann-Whitney test, $n_{\text{inshore}} = 12$, $n_{\text{offshore}} = 6$, $P = 0.06$) while offshore was 7.2 times greater than inshore in June ($n_{\text{inshore}} = 14$, $n_{\text{offshore}} = 10$, $P = 0.04$). During this period, Houghton mean surface temperatures increased from 6.0 to 11.2 °C inshore and from 3.4 to 8.8 °C offshore. Densities at Ontonagon and Eagle Harbor did not peak as they did at Houghton, although these transects were not sampled as often. In May, inshore and offshore densities were not statistically different at Ontonagon (Mann-Whitney test, $n_{\text{inshore}} = 9$, $n_{\text{offshore}} = 6$, $P = 0.55$) nor at Eagle Harbor ($n_{\text{inshore}} = 4$, $n_{\text{offshore}} = 3$, $P = 0.72$). In May, at Ontonagon, mean

surface temperatures were 7.6 °C inshore and 4.5 °C offshore, and at Eagle Harbor, 2.9 °C inshore and 3.0 °C offshore. Overall, I saw no consistent inshore-offshore difference in densities among all three transects for lake herring. In addition, lake herring frequently occurred immediately off of North Entry, but along with burbot and deepwater sculpin, lake herring never occurred in samples from within the North Entry Canal.

Total length of lake herring larvae ranged from 8.2 – 21.8 mm, with mean lengths, in general, increasing only slightly with the season (Table 1–7). Mean length \pm SE by month, pooled for all stations, were 12.8 ± 0.1 mm in April, 12.4 ± 0.1 mm in May, 13.2 ± 0.4 mm in June, and 19.4 ± 2.4 mm in July. In May, lengths differed statistically for transect (two-factor ANOVA, $N = 144$, $P = 0.03$), location ($P < 0.0001$) and their interaction ($P < 0.0001$). Lake herring at Ontonagon were 1.2 times larger inshore compared to offshore (Tukey test, $P < 0.001$). At Houghton, inshore vs. offshore differences in length were not significant in May (Tukey test, $P > 0.05$) or June (two-sample t -test, $n_{\text{inshore}} = 9$, $n_{\text{offshore}} = 39$, $P = 0.14$). However, lengths at Houghton started off similar in early June, became 1.5 times greater inshore by mid June, and then were 1.2 times greater offshore by late June. At Eagle Harbor when I was able to sample in early May, the lake herring caught had nearly identical lengths between inshore and offshore locations (Tukey test, $P > 0.5$). Among inshore locations in May, similar-sized larvae at Ontonagon and Houghton (Tukey test, $P > 0.5$) were marginally larger (1.1 times) compared to Eagle Harbor (Ontonagon: Tukey test, $P > 0.05$; Houghton: Tukey test, $P < 0.05$). Among offshore locations, the reverse trend was observed—Eagle Harbor produced larger larvae (Tukey test, $P > 0.5$), and Ontonagon produced smaller larvae

(Tukey test, $P > 0.1$), than Houghton, where Eagle Harbor larvae were statistically larger (1.2 times) than Ontonagon larvae (Tukey test, $P < 0.001$).

Rainbow smelt reached a peak mean density of 46.5 larvae/1000 m³ inshore at Ontonagon in mid May at 8.4 °C, and yet none was ever caught offshore at Ontonagon (Table 1–6), resulting in a significant inshore vs. offshore difference (Mann-Whitney test, $n_{\text{inshore}} = 12$, $n_{\text{offshore}} = 8$, $P = 0.04$). Even greater densities (mean \pm SE of 141.5 ± 23.3 larvae/1000 m³) were observed for three tows taken from immediately within the North Entry Canal in late June (17.2 °C) at the surface at night. At Houghton, I caught rainbow smelt larvae from both inshore and offshore locations in June, but likewise, densities were greater inshore (13.0 times), at 11.6 °C, than offshore, at 3.3 °C (Mann-Whitney test, $n_{\text{inshore}} = 17$, $n_{\text{offshore}} = 10$, $P < 0.0007$). At Eagle Harbor, I did not sample during the seasonal period during which rainbow smelt peaked at the other transects, and thus only two larvae were caught there in early July.

Total length of rainbow smelt ranged from 4.0 - 31.6 mm, with a substantial seasonal increase in mean length (Table 1–7). Monthly mean lengths \pm SE were 6.2 ± 0.05 mm in May, 6.5 ± 0.1 mm in June, and 22.2 ± 1.4 mm in July. At Houghton in June, rainbow smelt larvae differed statistically in length among riverine, inshore, and offshore locations (single-factor ANOVA, $N = 385$, $P < 0.0001$). Larvae were 1.4 times larger inshore than riverine (Tukey test, $P < 0.0001$) and 1.3 times larger offshore than riverine (Tukey test, $P = 0.08$), but inshore and offshore lengths did not differ statistically (Tukey test, $P = 0.71$). As densities diminished by July, the largest larvae occurred inshore at Ontonagon and offshore at Houghton.

Burbot had similar peaks in mean density inshore at Ontonagon (8.4 °C) in mid May and inshore (6.6 °C) and offshore (3.3 °C) at Houghton in early June (Table 1–6). Burbot consistently was more abundant inshore than offshore at all transects. However the difference was not significant at Houghton in May (Mann-Whitney test, $n_{\text{inshore}} = 18$, $n_{\text{offshore}} = 11$, $P = 0.16$) or June ($n_{\text{inshore}} = 17$, $n_{\text{offshore}} = 10$, $P = 0.46$), and only marginally so at Ontonagon in May ($n_{\text{inshore}} = 12$, $n_{\text{offshore}} = 8$, $P = 0.08$). Eagle Harbor was not sampled during late May to late June when burbot was abundant elsewhere, however a few larvae were caught there at both inshore and offshore locations in early July.

Total length of burbot ranged from 3.3 - 17.3 mm, with a seasonal increase in mean lengths (Table 1–7). Monthly mean lengths \pm SE were 4.1 ± 0.1 mm in April, 4.3 ± 0.1 mm in May, 4.4 ± 0.1 mm in June, 10.1 ± 1.0 mm in July, and 11.6 ± 3.0 mm in August. At Houghton in June, inshore larvae were 1.2 times larger than offshore larvae (two-sample *t*-test, $n_{\text{inshore}} = 44$, $n_{\text{offshore}} = 28$, $P = 0.0002$), however, by early to mid July, the largest larvae were caught offshore from each transect.

Deepwater sculpin was the least abundant of these five species, with its highest mean density occurring inshore at Houghton during mid May, at 6.6 °C (Table 1–6). Densities were consistently greater offshore at Ontonagon, whereas at Houghton, they were generally greater inshore. However, differences were not significant in May for either Ontonagon (Mann-Whitney test, $n_{\text{inshore}} = 9$, $n_{\text{offshore}} = 6$, $P = 0.52$) or Houghton ($n_{\text{inshore}} = 12$, $n_{\text{offshore}} = 7$, $P = 0.25$). Of all species caught, only deepwater sculpin and burbot still occurred in the catches in August at temperatures of 9.9 – 19.4 °C, and yet also occurred early in the collecting season in April at temperatures near 4 °C.

Total length of deepwater sculpin ranged from 8.2 - 19.8 mm (Table 1–7). Lengths did not show a seasonal increasing trend as they did for the other species, and even in late August, some of the smallest larvae were caught at Eagle Harbor and Houghton. Monthly mean lengths \pm SE were 13.9 ± 0.9 mm in April, 14.2 ± 0.4 mm in May, 15.9 ± 0.9 mm in June, 17.4 ± 0.6 mm in July, and 10.7 ± 0.2 mm in August. Only at Houghton did there seem to be an inshore-offshore difference in length, with inshore larvae being slightly larger than offshore larvae. However, there were no statistical differences for transect (two-factor ANOVA, $N = 33$, $P = 0.66$), location ($P = 0.21$), or their interaction ($P = 0.38$).

Spoonhead sculpin had the shortest seasonal occurrence (~25 days) of these five species, with a peak mean density offshore at Houghton in mid June, at 11.4°C (Table 1–6), however, the other two transects were not sampled during this time. At Houghton with June and July data combined, inshore densities were 7.5 times greater than offshore densities (Mann-Whitney test, $P = 0.05$). Along with rainbow smelt, spoonhead sculpin were also caught within the North Entry Canal, but only on one occasion.

Total length of spoonhead sculpin ranged from 6.0 – 11.8 mm (Table 1–7). There was an increase in mean length \pm SE from 7.2 ± 0.2 mm in mid June to 9.7 ± 0.4 mm in early July. With June and June data combined for Ontonagon and Houghton, there was a statistical difference for location (two-factor ANOVA, $N = 30$, $P = 0.0008$), but not for transect ($P = 0.58$) nor their interaction ($P = 0.98$). Length was 1.3 times larger offshore at Houghton and 1.4 times larger offshore at Ontonagon.

DISCUSSION

I sampled further offshore than many larval fish surveys conducted in the other Great Lakes (e.g., Cooper et al. 1981, Mizera et al. 1981, O’Gorman 1983, Tin and Jude 1983, Cole and MacMillan 1984, Dunstall 1984). Thus, I was able to evaluate if distinct inshore and offshore larval fish communities exist in Lake Superior, especially in relation to the Keweenaw Current and spring thermal bar.

One factor that may differentially influence larval fish catches among stations is differences in water clarity, as turbidity can inhibit a fish’s ability to see and thus avoid the plankton net. However, the vertical attenuation coefficient (K_d) for 555 nm wavelength (green) light recorded during May – Aug 1999 and 2000 suggests that water clarity did not differ statistically (based on two-factor ANOVA on $\log[X + 1]$ transformed data; $N = 35$) among transects ($P = 0.12$) or offshore locations ($P = 0.07$), or their interaction ($P = 0.28$) (Sarah Green, Michigan Technological University, personal communication).

The capture of yellow perch (*Perca flavescens*) and other warm-water species (e.g., *Notropis* spp., *Promoxis* spp., rock bass, log perch) was restricted to riverine areas or inshore locations of Lake Superior adjacent to riverine discharges. These species, because of their very rare occurrences and limited distribution, probably drifted into nearshore regions of Lake Superior from inland waters, as previously suggested for yellow perch in Lake Superior (Hatch 1980) and Lake Michigan (Perrone et al. 1983). It is not known if these larvae are lost into Lake Superior or if they are able to recruit into protected embayment populations. In contrast, yellow perch was found to be among the dominant members of the nearshore larval community in Lake Erie (Cooper et al. 1981,

Mizera et al. 1981), Lake Michigan (Jude et al. 1981), and Lake Huron (O’Gorman 1983). In addition, Klumb et al. (2003) found that larvae of yellow perch and *Lepomis* spp. were much more abundant within embayments (1.8 – 24 m contour) compared to adjacent nearshore regions (2.5 – 25 m contour) of Lake Ontario.

Lake herring populations in the other Great Lakes crashed in the first half of the 1900s, and presently only Lake Superior, northern Lake Huron including Georgian Bay, and the St. Mary’s River support substantial stocks (Fleischer 1992). During late fall, lake herring spawn in shallow areas (Goodyear et al. 1982), 14 – 36 m deep in Lake Superior (Dryer and Beil 1964), and eggs hatch in early spring, just after ice breakup (Colby and Brooke 1973, Cucin and Faber 1985). The most productive lake herring spawning areas in Lake Superior are in the western region, from Black Bay to the Apostle Islands, although this study area did contain several historic spawning locations (Goodyear et al. 1982). Accordingly, densities of lake herring larvae were substantially lower than a recorded peak density of 1719 larvae/1000 m³ for Black Bay (Ontario) during 25-26 May 1974 (Selgeby et al. 1978), and peak densities of 1111 larvae/1000 m³ during 28 May 1981 and 1118 larvae/1000 m³ during 28 May 1982 for the Duluth (Minnesota) to Superior (Wisconsin) region (Hatch and Underhill 1988). In contrast, densities were comparable to a peak density of 17.2 larvae/1000 m³ for the Apostle Islands region (Wisconsin) during 28 – 30 May 1974 (Selgeby et al. 1978). However, my estimates, as well as those of previous studies, may not reflect true peak densities due to limitations in sampling frequency.

Based on lake herring life history, I expected to find greater densities of young, small larvae inshore, and, as they disperse, lower densities of older, larger larvae

offshore. In fact, I generally found greater densities inshore compared to offshore at Ontonagon and Houghton, but interestingly, not at Eagle Harbor. Because of greater depths and colder waters, both inshore and offshore locations at Eagle Harbor seem to be ecologically equivalent to the offshore regions at Ontonagon and Houghton. Contrary to my prediction, however, inshore caught larvae were larger at Ontonagon, and, from April to June, at Houghton. Perhaps many of the captured larvae were transported from the more productive western region of Lake Superior. The Keweenaw Current may transport younger, smaller larvae alongshore in the offshore region, while larvae that hatch within, or settle into, the inshore region are able to remain on the coast longer and grow at a faster rate in the warmer waters.

A different pattern arose in June at Houghton, in which the offshore location contained a greater density, and later in July, contained larger lake herring larvae, compared to the inshore location, suggesting a mid season migration into the lake. Hatch and Underhill (1988) observed a migration out of inshore waters of Lake Superior in June, although they noted that migration was not size-dependent. In addition, they did not catch larvae in their open water samples until mid June. Clady (1976) also found an inshore-to-offshore movement of lake herring larvae, with a slight shift in size, during May in Oneida Lake, NY. Because lake herring hatch at a relatively large size compared to the other species and to the size of the net mesh, it is unlikely that lake herring larvae were lost through net extrusion. However, larger larvae possibly escaped by net avoidance, especially larvae greater than 15 mm (Karjalainen and Viljanen 1992).

Rainbow smelt colonized the Great Lakes after having been successfully stocked into Crystal Lake, MI in 1912 (Van Oosten 1937), and since has become an important

inhabitant of the inshore waters of Lake Superior (Lawrie 1978). The greatest catches of rainbow smelt larvae occurred inshore near riverine discharges, as would be expected considering that adults typically migrate into streams to spawn in April to May (Auer 1982) and the larvae are washed into the lake upon hatching (Hatch 1980; Goodyear et al. 1982). Few larvae dispersed to offshore waters in Lake Superior in July when they were larger and the offshore region was well stratified. In Lake Michigan, Nash and Geffen (1991) also documented greater inshore densities in June with larvae not captured farther than 9.2 km offshore. Then in July and August, they observed concentrations of rainbow smelt as far as 23.9 km offshore.

The densities of rainbow smelt at water depths of 10 – 15 m are comparable to those at similar depths in Lake Michigan (Nash and Geffen 1991), however, in shallower waters (1 – 6 m), Tin and Jude (1983) recorded a greater mean density of 571 larvae/1000 m³ in Lake Michigan and O’Gorman (1984) recorded a peak mean density of 505 larvae/1000 m³ in Lake Huron. In addition, shallower waters of Lake Ontario produced similar densities at exposed stations, while stations with substantial variation in shoreline aspect and gradient produced considerably greater densities (Dunstall 1984). Thus, during this study, rainbow smelt larvae were probably concentrated closer to shore than the inshore sampling location until later in the season when they dispersed into the lake. In addition, selectivity of the net mesh size likely underestimated the abundance of smaller sizes (< 7 mm) of rainbow smelt larvae (Cole and MacMillan 1984; O’Gorman 1984), as well as other small-sized larvae, due to net extrusion.

Burbot spawn from January to March in Lake Superior (Bailey 1972) in shallow waters or in streams (Auer 1982). I observed greater densities inshore at Ontonagon in

mid May, as expected, but inshore and offshore at Houghton, densities were nearly identical in June and July. Mansfield et al. (1983) found a similar pattern in Lake Michigan in which burbot larvae were more abundant in shallow waters in April and May, and then became evenly distributed horizontally in June. Nash and Geffen (1991) also found burbot larvae as far as 13.1 km offshore in June, then as far as 23.9 km offshore in July in Lake Michigan.

In Lake Superior, deepwater sculpin spawn in mid winter, with a peak in January, but spawning might extend from late November through mid May (Hatch 1980; Selgeby 1988); most likely occurring in deep waters (Mansfield et al. 1983). In Lake Michigan, Nash and Geffen (1991) and Geffen and Nash (1992) found that in early spring (May – June) deepwater sculpin hatch in deep water (75 – 100 m contour; 13.1 – 23.9 km from shore), rise to the surface, and then are transported inshore (15 – 25 m contour; 1.7 – 5.0 km from shore). Then by late September they move out of inshore locations into bottom waters offshore. My catches were low and variable, making it difficult to identify trends, but I did observe greater densities inshore early in the season at Houghton. However, at Ontonagon, densities were slightly greater offshore, possibly because shallower waters limit inshore movement more than distance from shore.

Spoonhead sculpin spawn in early to mid May in Lake Superior, possibly on rough, rocky substrate in shallow protected areas (Selgeby 1988). Spoonhead sculpin are rare or absent in the other Great Lakes (Selgeby 1988, Potter and Fleischer 1992) and no information is available on their larval distribution. Spoonhead sculpin larvae seem to have originated inshore, as expected based on Selgeby (1988), and then disperse offshore, disappearing from the catches by August. They had a strikingly short season of

occurrence, despite having a peak mean density greater than that of burbot or deepwater sculpin. Differences between daytime and nighttime samples also indicate that spoonhead sculpin has a stronger tendency than rainbow smelt, burbot, and deepwater sculpin to migrate to the surface at night. Net avoidance is a possible explanation for daytime vs. nighttime differences, with larvae being more capable of seeing the net during daylight. Because larger larvae more easily avoid capture by plankton nets, I expected that lake herring, being larger, would be the most capable of the species I encountered to avoid net capture. However, lake herring actually exhibited greater surface densities during daylight in 1999, and comparable daytime vs. nighttime surface densities in 1998. Therefore, it is unlikely that the daytime vs. nighttime differences in the smaller-sized spoonhead sculpin resulted entirely from net avoidance.

Overall, I found that the inshore vs. offshore distribution of larval fishes were similar to that of other lakes despite the possible influence of the Keweenaw Current and spring thermal bar. Most of the larval fishes peaked in abundance, or occurred exclusively, after the thermal bar moved offshore. Only a few lake herring and deepwater sculpin larvae occurred early in the season at locations where surface temperatures were less than 4°C. The larvae of these species are larger than those of many other species, and thus are even more likely to out-swim the downward flow, estimated to be on the order of 0.01 cm/sec (Spain et al. 1976), at the 4°C margin. Larval walleye (*Stizostedion vitreum vitreum*) and yellow perch (*Perca flavescens*) (Houde 1969), and larval striped bass (*Morone saxatilis*) (Meng 1993) have been recorded to swim at sustained speeds of 3 – 4 body lengths per second, and thus larval lake herring (8.5 – 12.8 mm at hatching; Auer 1982) and deepwater sculpin (8 – 10 mm as yolk-sac

larvae; Auer 1982) are expected to easily be able to cross the inshore-offshore 4°C thermal barrier.

The Keweenaw Current, however, is such a strong current that it should readily be able to transport larval fishes far from their point of origin. It is still unclear how this current affects larval fish survivorship and recruitment by potentially transporting larvae into or away from nurseries areas. In addition, transported larvae will carry genes to different breeding stocks unless these fishes are later able to recruit back into their natal breeding population. Future work may determine if particular breeding stocks should be more closely managed because of their greater contribution to lake-wide recruitment, possibly resulting from larvae transport and subsequent growth and survival.

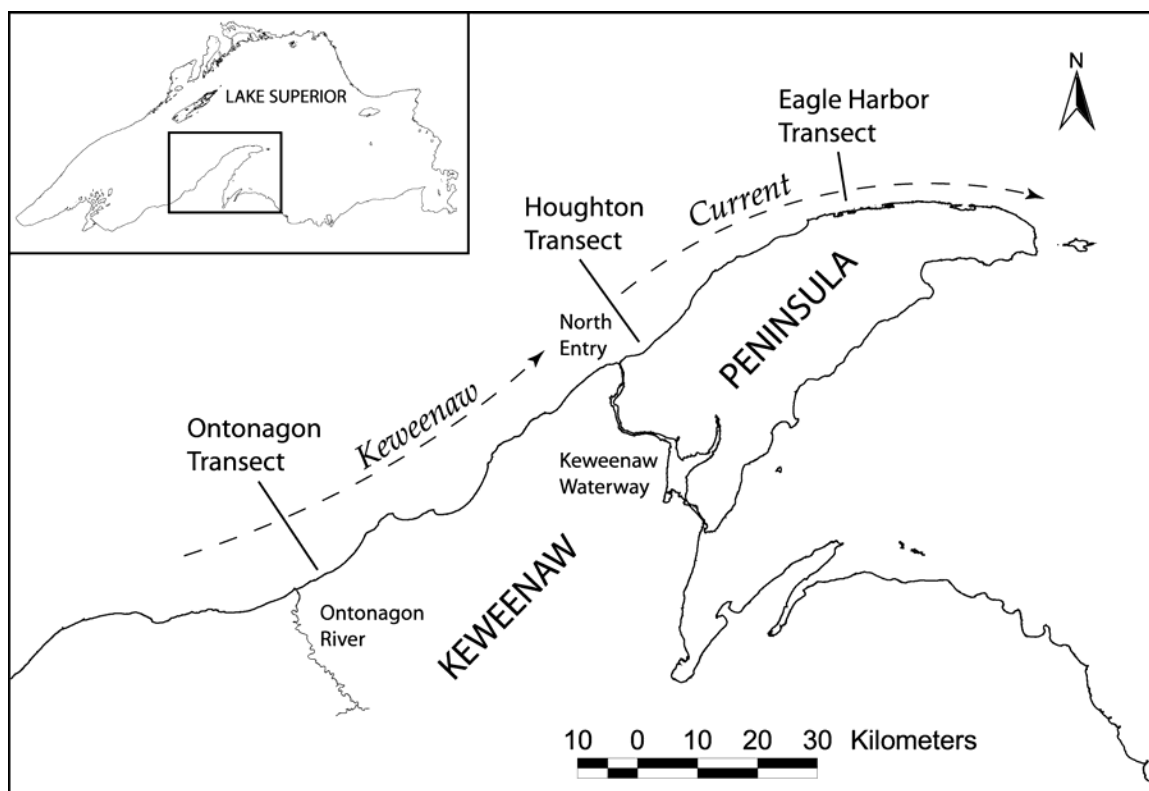


Figure 1-1. Map of Lake Superior showing the three larval fish sampling transects off the western coast of the Keweenaw Peninsula, Michigan.

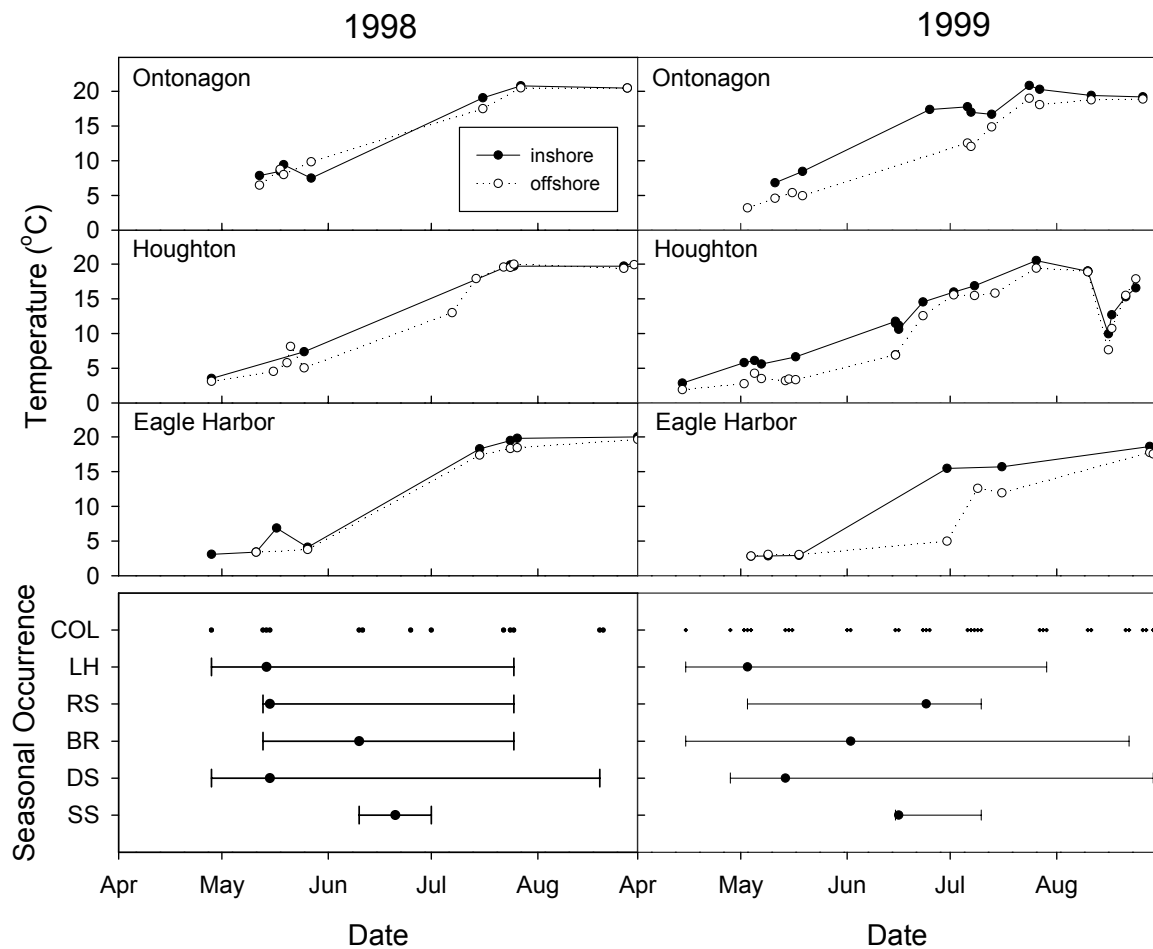


Figure 1-2. Surface water temperatures, sampling dates, and the seasonal occurrences of the five most abundant larval fishes caught in 1998 and 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. COL = sampling date; LH = lake herring; RS = rainbow smelt; BR = burbot; DS = deepwater sculpin; SS = spoonhead sculpin. For seasonal occurrences, dots represent medians and T-bars extend from the first to the last day of capture.

Table 1–1. Seasonal changes in the offshore location (in km) of the spring thermal bar (4°C isotherm) on the three sampling transects, Ontonagon (ON), Houghton (HN), and Eagle Harbor (EH), in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan 1998 and 1999. For cases when the thermal bar was not contained by the sampling locations, I note the starting or ending sampling location nearest to the thermal bar and, in parentheses, the temperature (°C) at that location.

1998	28 April	10-12 May	16-18 May	19-21 May	25-27 May	7-8 June
ON		17.4	> 21.0 (4.6)	24.0	> 30.0 (7.7)	
HN	0.6	1.7	8.0	14.8	17.0	> 18.0 (17.8)
EH	< 0.1 (3.2)	< 0.1 (3.6)	2.2		4.2	> 9.5 (14.9)
1999	2-4 May	7-11 May	16-18 May	19-21 May	30 June	2-7 July
ON	6.4	10.8	13.0	13.8		> 21.0 (9.0)
HN	3.3	3.3	4.5	7.2		> 21.0 (9.6)
EH	< 1.0 (2.8)	< 0.1 (2.9)	< 0.1 (3.0)		> 9.0 (4.8)	

Table 1–2. Types and numbers of larval fishes caught in 1998 and 1999 with plankton net tows (89 tows in 1998; 317 tows in 1999) from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Note that a few specimens could only be identified to family or genus. * indicates taxa that occurred exclusively or predominately around riverine inflows and ** indicates taxa that occurred exclusively inshore near riverine inflows.

Scientific Name	Common Name	1998			1999		
		Riverine <i>n</i> = 9	Inshore <i>n</i> = 48	Offshore <i>n</i> = 32	Riverine <i>n</i> = 24	Inshore <i>n</i> = 181	Offshore <i>n</i> = 112
Clupeidae							
<i>Alosa pseudoharengus</i> **	Alewife	0	0	0	2	1	0
Salmonidae							
<i>Coregonus artedi</i>	lake herring	19	29	9	7	316	226
<i>Coregonus clupeaformis</i> **	lake whitefish	0	1	0	0	0	0
Osmeridae							
<i>Osmerus mordax</i>	rainbow smelt	0	42	0	339	167	12
Cyprinidae							
<i>Notropis</i> spp.**	Shiner	0	0	0	0	2	0
Catostomidae							
<i>Catostomus commersoni</i>	white sucker	0	0	0	0	0	1
Percopsidae							
<i>Percopsis omiscomaycus</i>	trout perch	0	0	0	0	1	2
Gadidae							
<i>Lota lota</i>	Burbot	0	5	3	0	107	37
Gasterosteidae							
<i>Pungitius pungitius</i> **	ninespine stickleback	0	0	0	0	2	0
Centrarchidae							
<i>Pomoxis</i> spp.*	Crappie	0	0	0	8	2	0
<i>Ambloplites rupestris</i> **	rock bass	0	0	0	0	1	0
Percidae							
<i>Perca flavescens</i> *	yellow perch	0	1	0	14	5	0
<i>Percina caprodes</i> *	log perch	0	0	0	10	0	0
Cottidae							
<i>Myoxocephalus thompsoni</i>	Deepwater sculpin	4	17	5	0	35	21
<i>Cottus ricei</i>	Spoonhead sculpin	0	3	3	3	39	5
<i>Cottus cognatus</i>	slimy sculpin	0	3	0	1	8	0
<i>Cottus bairdi</i>	mottled sculpin	0	8	0	0	2	0
unknown		0	0	0	0	1	1
total		23	109	20	389	692	305

Table 1–3. Mean (SE) density (larvae/1000 m³) of larval fishes captured within blocks of daytime, twilight, and nighttime tows in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, and results of randomized block ANOVA. LH = lake herring, RS = rainbow smelt, BR = burbot, DS = deepwater sculpin, D = daytime, T = twilight, N = nighttime, Dep = depth factor, Per = day period factor, and Int = depth by day period interaction. * indicates the day period that was statistically different from the other day periods within a particular depth based on Tukey test ($P < 0.001$).

Species	Surface			Deep			<i>n</i>	<i>P</i> -value		
	D	T	N	D	T	N		Dep	Per	Int
LH	11.4 (3.8)	59.1(12.9)*	6.7 (2.1)	3.7 (1.6)	7.2 (4.0)	10.8 (8.5)	52	0.002	0.0003	0.006
RS	1.1 (1.1)	1.1 (1.1)	1.9 (1.9)	0.2 (0.2)	0.8 (0.8)	0.0 (0.0)	26	0.41	0.88	0.82
BR	0.3 (0.2)	4.9 (2.3)	2.1 (1.1)	1.4 (1.1)	1.1 (1.1)	0.0 (0.0)	46	0.11	0.10	0.06
DS	0.0 (0.0)	0.8 (0.8)	0.0 (0.0)	0.8 (0.6)	3.2 (1.7)	0.9 (0.5)	40	0.02	0.06	0.67

Table 1–4. Mean density (larvae/1000 m³) ± SE of larval fishes captured with daytime vs. nighttime and surface vs. deep tows in 1998 and 1999 from Lake Superior off the western coast of the Keweenaw Peninsula. The proportion of tows in each depth and diel combination that captured larvae is shown in parentheses. LH = lake herring, RS = rainbow smelt, BR = burbot, DS = deepwater sculpin, SS = spoonhead sculpin, Date = most abundant seasonal period from which I calculated these estimates, *n* = number of tows in each combination, and * indicate the depth and diel combinations of each species used for subsequent transect and offshore location analyses (shown on 1999 estimates).

Species	Date	<i>n</i>	Daytime		Nighttime	
			Surface	Deep	Surface	Deep
1998						
LH	5/13 – 6/11	10	2.1 ± 1.0 (0.40)	1.1 ± 0.4 (0.50)	2.3 ± 1.0 (0.40)	3.4 ± 1.9 (0.50)
RS	5/15	2	0.0 ± 0.0 (0.00)	34.0 ± 4.6 (1.00)	0.0 ± 0.0 (0.00)	18.0 ± 0.8 (1.00)
BR	5/15 – 6/10	4	0.0 ± 0.0 (0.00)	1.2 ± 0.8 (0.50)	0.9 ± 0.9 (0.25)	0.0 ± 0.0 (0.00)
DS	5/15 – 6/11	6	0.0 ± 0.0 (0.00)	0.3 ± 0.3 (0.17)	2.1 ± 2.1 (0.17)	2.0 ± 1.1 (0.50)
SS	6/10	2	0.0 ± 0.0 (0.00)	0.0 ± 0.0 (0.00)	1.7 ± 1.7 (0.50)	0.8 ± 0.8 (0.50)
1999						
LH	5/2 – 6/16	19	*6.4 ± 2.0 (0.74)	2.5 ± 0.8 (0.63)	3.0 ± 1.0 (0.53)	*7.2 ± 3.1 (0.53)
RS	6/1 – 6/16	5	0.0 ± 0.0 (0.00)	*3.2 ± 1.2 (0.80)	*5.5 ± 2.9 (0.60)	*5.2 ± 0.7 (1.00)
BR	6/1 – 6/16	6	0.3 ± 0.3 (0.17)	*3.7 ± 1.6 (0.83)	*3.8 ± 2.8 (0.67)	*3.1 ± 1.2 (0.67)
DS	5/2 – 5/14	13	0.0 ± 0.0 (0.00)	*1.3 ± 0.5 (0.46)	0.7 ± 0.4 (0.23)	*3.2 ± 0.9 (0.69)
SS	6/15 – 7/9	11	0.0 ± 0.0 (0.00)	0.2 ± 0.2 (0.09)	*6.0 ± 2.2 (0.82)	1.6 ± 0.8 (0.27)

Table 1–5. Results of logistic regression analysis for depth and diel differences in larval fish occurrences. LH = lake herring, RS = rainbow smelt, BR = burbot, DS = deepwater sculpin, SS = spoonhead sculpin, OR = odds ratio, B = bottom, S = surface, D = daytime, N= nighttime, *P* = *P*-value, and * indicate species for which parameters were estimated separately.

Species	Depth		Day Period		Interaction	
	OR (B/S)	<i>P</i>	OR (D/N)	<i>P</i>	OR (BD/SN)	<i>P</i>
LH	1.15	0.79	1.75	0.29	0.75	0.71
RS*	47.67	0.001	0.30	0.13	6.60	--
BR	0.66	0.65	0.11	0.07	31.50	0.03
DS*	8.50	0.0006	0.31	0.03	1.49	--
SS*	0.38	0.13	0.03	0.002	0.14	--

Table 1–6. Mean (SE) density (larvae/1000 m³) of larval fishes captured in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula. These estimates include the entire seasonal period of occurrence for each species.

Species	Cruise	Ontonagon			Houghton			Eagle Harbor	
		Riverine	Inshore	Offshore	Riverine	Inshore	Offshore	Inshore	Offshore
LH	15 Apr					1.3 (1.3)			
	28 Apr					93.8 (93.8)			
	2-4 May		7.6 (2.8)	11.0 (6.3)		22.4 (9.6)	1.1 (1.1)	9.6 (4.4)	7.8 (2.6)
	14-16 May		9.2 (1.4)	1.5 (1.5)		7.6 (5.7)	1.8 (1.3)		
	1 June					0.8 (0.5)	29.5 (4.5)		
	15 June				0.0 (0.0)	0.9 (0.6)	1.8 (0.8)		
	23-25 June	0.0 (0.0)	0.0 (0.0)			1.6 (1.6)	2.0 (0.4)		
	6-9 July		0.6 (0.6)	0.0 (0.0)		0.0 (0.0)	0.4 (0.4)	0.0 (0.0)	0.0 (0.0)
RS	2-4 May		1.1 (0.9)	0.0 (0.0)		0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	14-16 May		46.5 (7.7)	0.0 (0.0)		0.0 (0.0)	0.0 (0.0)		
	1 June					7.7 (2.6)	1.1 (0.8)		
	15 June				20.9 (–)	4.2 (1.0)	0.0 (0.0)		
	23-25 June				141.5 (23.3)				
	6-9 July		3.1 (1.4)	0.0 (0.0)		0.0 (0.0)	1.1 (0.9)	0.5 (0.5)	0.2 (0.2)
BR	15 Apr				0.0 (–)	1.1 (–)			
	28 Apr					2.9 (1.0)			
	2-4 May		0.3 (0.3)	0.0 (0.0)		1.8 (1.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
	14-16 May		7.6 (2.1)	0.0 (0.0)		0.0 (0.0)	0.0 (0.0)		
	1 June					7.4 (2.1)	7.1 (2.5)		
	15 June				0.0 (–)	2.4 (1.1)	1.5 (1.0)		
	23-25 June				0.0 (0.0)				
	6-9 July		1.8 (1.1)	0.4 (0.4)		0.0 (0.0)	0.0 (0.0)	1.6 (1.0)	0.2 (0.2)
	27-28 July				0.0 (–)	0.4 (0.4)	0.3 (0.3)		
	10-11 Aug				0.0 (0.0)	0.4 (0.4)	0.0 (0.0)		
	21 Aug					0.3 (0.3)	0.0 (0.0)		
DS	28 Apr					2.9 (2.9)			
	2-4 May		1.3 (0.9)	2.1 (0.9)		2.7 (1.5)	2.2 (2.2)	0.8 (0.4)	
	14-16 May		0.8 (0.8)	1.1 (1.1)		3.9 (1.4)	1.4 (1.0)		
	1 June					1.0 (0.7)	0.0 (0.0)		
	15 June					0.0 (0.0)	0.7 (0.7)		
	6-9 July		0.0 (0.0)	0.7 (0.7)		0.0 (0.0)	0.0 (0.0)	0.5 (0.5)	0.3 (0.3)
	27-28 July				0.0 (–)	0.0 (0.0)	0.0 (0.0)		
	10-11 Aug				0.0 (0.0)	0.0 (0.0)	0.5 (0.5)		
	21 Aug					0.0 (0.0)	0.0 (0.0)		
	26-29 Aug		0.0 (0.0)	0.0 (0.0)				0.6 (0.4)	2.1 (2.1)
SS	15 June				0.0 (–)	13.8 (5.9)	0.0 (0.0)		
	23-25 June				1.2 (1.2)				
	6-9 July		0.9 (0.9)	2.6 (0.0)		5.1 (3.4)	2.5 (0.1)		1.1 (1.1)

Table 1–7. Mean (SE) length (mm) of larval fishes captured in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula. These estimates include the entire seasonal period of occurrence for each species. -- indicate tows were taken, but no larvae were captured. Also note that the standard error could not be estimated for cases in which only one larva was captured.

Species	Cruise	Ontonagon			Houghton			Eagle Harbor	
		Riverine	Inshore	Offshore	Riverine	Inshore	Offshore	Inshore	Offshore
LH	15 Apr					11.4 (0.5)			
	28 Apr					12.9 (0.1)			
	2-4 May		12.6 (0.2)	10.3 (0.2)		13.0 (0.1)	12.0 (--)	12.0 (0.2)	11.9 (0.3)
	14-16 May		13.5 (0.4)	10.3 (--)		13.0 (0.4)	11.4 (0.6)		
	1 June					12.2 (0.3)	12.7 (0.4)		
	15 June				--	16.8 (0.8)	10.9 (0.8)		
	23-25 June	--	--			13.4 (0.9)	16.2 (1.4)		
	6-9 July		21.8 (--)	--		--	16.9 (--)	--	--
RS	2-4 May		6.0 (0.3)	--		--	--	--	--
	14-16 May		6.2 (0.1)	--		--	--		
	1 June					7.4 (0.2)	7.8 (0.7)		
	15 June				11.5 (0.7)	11.3 (0.5)	--		
	23-25 June				5.9 (0.1)				
	6-9 July		22.3 (1.8)	--		--	24.4 (2.7)	13.9 (--)	21.2 (--)
BR	15 Apr				--	4.1 (--)			
	28 Apr					4.1 (0.1)			
	2-4 May		4.1 (--)	--		4.1 (0.1)	--	--	--
	14-16 May		4.5 (0.1)	--		--	--		
	1 June					4.6 (0.2)	3.9 (0.1)		
	15 June				--	5.3 (0.3)	3.7 (0.1)		
	23-25 June				--				
	6-9 July		10.1 (0.4)	11.5 (--)		--	--	5.8 (1.2)	12.0 (--)
	27-28 July				--	12.4 (--)	17.3 (--)		
	10-11 Aug				--	14.6 (--)	--		
DS	21 Aug					8.5 (--)	--		
	28 Apr					13.9 (0.9)			
	2-4 May		13.3 (0.5)	14.5 (1.0)		14.8 (0.9)	13.1(0.4)	17.0 (2.8)	
	14-16 May		15.5 (--)	13.5 (--)		13.8 (1.2)	13.3 (1.2)		
	1 June					16.4 (1.5)	--		
	15 June					--	15.2 (1.3)		
	6-9 July		--	17.0 (1.3)		--	--	17.7 (--)	17.9 (--)
	27-28 July				--	--	--		
	10-11 Aug				--	--	10.4 (--)		
	21 Aug					--	--		
SS	26-29 Aug		--	--				10.8 (0.7)	10.7 (0.2)
	15 June				--	7.0 (0.1)	--		
	23-25 June				8.7 (0.4)				
	6-9 July		7.5 (--)	10.6 (1.3)		10.2 (0.4)	10.0 (0.3)		8.3 (--)

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CHAPTER 2

Zooplankton Inshore-Offshore Distribution in Lake Superior off the Western Coast of the Keweenaw Peninsula, Michigan

ABSTRACT

Zooplankton by-catch associated with larval fish sampling from Lake Superior in 1998 and 1999 was used to study the distribution of larger and less abundant zooplankton taxa. Calanoids constituted over 70% of the total catch in both years, dominating the majority of the collecting season (spring and summer) in both inshore (1 km from shore) and offshore (5 or 9 km from shore) locations. Seasonal warming appeared to be the major factor that limited planktonic catches of the primarily benthic *Mysis* and *Diporeia* while simultaneously stimulated growth and reproduction of the cladocerans *Daphnia*, *Holopedium*, and *Bythotrephes*. *Mysis* and *Diporeia* occurred in surface waters at night, primarily offshore before thermal stratification (late April and May) when surface waters were 4.8°C inshore and 5.5°C offshore. But after thermal stratification (mid July to end of Aug), when surface waters were 18.5°C inshore and 17.7°C offshore, *Mysis* were caught only in tows below the thermocline mainly offshore at night, and *Diporeia* was completely absent from the planktonic catches. The cladocerans increased in numbers with inshore warming (June and early July), when surface waters were 15.1°C inshore and 10.9°C offshore, and were especially abundant in offshore waters following thermal stratification. The greatest abundances were generally encountered offshore, even for the cladocerans, which apparently expanded from inshore to offshore locations with seasonal warming.

INTRODUCTION

In aquatic communities, zooplankton consume phytoplankton or other zooplankton, and in turn, many fishes consume zooplankton (Wetzel 2001). Accordingly, the ecological role of zooplankton linking the primary production of phytoplankton to fish populations underscores the importance of studying zooplankton distribution and abundance as part of fisheries management (Royce 1996, Brander et al. 2003). Likewise, in the Great Lakes, zooplankton distribution has been studied in relation to environmental changes and introduced species, both of which may ultimately affect fish populations. Earlier studies have documented zooplankton distributions in relation to cultural eutrophication (Patalas 1969, 1972). More recently, zooplankton community changes have been related to reductions in phosphorus emissions (Carrick et al. 2001, Hall et al. 2003), and to the unintentionally-introduced zebra mussels *Dreissena* spp. (Johannsson 2000), spiny waterflea *Bythotrephes cederstroemi* (Lehman 1991), and alewife *Alosa pseudoharengus* (Strus and Hurley 1992).

In addition to adult zooplankton being consumed as food for juvenile and adult fishes, the young, or otherwise small, zooplankton are consumed by developing larval fishes (Helfman et al. 1997). This ecological interaction between young zooplankton and larval fishes additionally proposes the use of zooplankton distribution as an indicator of food production for larval fishes. The availability of food, in part, has been implicated in controlling recruitment in fish populations (Houde 1987, Cowan and Shaw 2002), including those of yellow perch *Perca flavescens* (Dettmers 2003), bloater *Coregonus hoyi* (Brown and Eck 1992), lake whitefish *Coregonus clupeaformis* (Freeberg et al. 1990), and lake herring *Coregonus artedii* (Kowalchyk 1996) in the Great Lakes. Zooplankton

studies may further complement larval fish studies because hydrodynamic features such as currents, fronts, and upwellings may have parallel effects on adult zooplankton and larval fishes of similar size. Hydrodynamic features potentially affect organisms by transporting them into habitats that could be either favorable or unfavorable for survival.

Sampling for larval fishes in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan, in 1998 and 1999 yielded an abundant by-catch of zooplankton. This zooplankton by-catch can accordingly be used to complement the study of larval fishes as well as reveal general patterns of zooplankton distribution in Lake Superior. Zooplankton has been studied in Lake Superior in relation to lake-wide distribution patterns (Patalas 1972, Watson and Wilson 1978), vertical migrations (Swain et al. 1970), and life histories (Selgeby 1975). In addition, change in the zooplankton community over the past two decades has been related to increased predation pressure by the recovering lake herring, *Coregonus artedii* (Link et al. 2004), and predation by the introduced spiny waterflea, *Bythotrephes cederstroemi* (Brown and Branstrator 2004).

There are inherent limitations, however, in interpreting the zooplankton by-catch distribution data, primarily because the employed sampling protocol was designed to capture larval fishes. First of all, the employed net mesh size of 500 μm was much larger than the 60 – 70 μm mesh typically used to capture most adult crustacean zooplankton (Kalff 2002) or the 100 – 200 μm mesh used to capture middle-sized zooplankton (Horne and Goldman 1994, Omori and Ikeda 1984, Wetzel and Likens 1990). Thus, many of the smaller species and individuals would have been extruded through the larger mesh of the employed net (Omori and Ikeda 1984, Horne and Goldman 1994). Second, the net was towed horizontally through the water, whereas many zooplankton distribution and

abundance studies perform vertical net hauls to capture zooplankton (Kalff 2002). Zooplankton typically migrate between surface and deeper waters daily (Wetzel 2001). This diel vertical migration would have caused zooplankton densities within particular strata to fluctuate during the duration of sampling cruises in this study, which sometimes lasted several days in order to complete a certain spatial coverage. In addition, slight changes in light availability due to cloud cover, turbidity, or moonlight influences the depth distribution of zooplankton (Dodson 1990, Wetzel 2001). Therefore, change in density within a discrete stratum, as measured with horizontal tows, could result from a true change in population density or a change in the depth distribution of zooplankton. Vertical net hauls are not prone to such ambiguity because they sample all zooplankton under a given surface area regardless of zooplankton depth. Finally, because of the large number of samples collected, it was not feasible to identify all captured zooplankton to species. Interpretations of the spatial and temporal patterns of pooled taxa may be obscured by dissimilar distributions of the component species and their relative abundances.

Despite these limitations, there are also advantages to the sampling protocol and thus value in presenting the zooplankton data. The large net diameter coupled with a long towing duration filtered a much greater volume of water than is typical of zooplankton studies. Because of this, rare species were more likely to be encountered, and density estimates should not have been subjected to small-scale horizontal patchiness that may bias vertical net hauls (Malone and McQueen 1983). Likewise, large and fast swimming species, such as mysids, do not effectively evade capture from a larger net

(Covich and Thorp 2001). Therefore, the zooplankton by-catch data should adequately represent the distribution of the larger and less abundant species.

Here I examine the zooplankton distribution data for spatial patterns with the same approach used for the distribution of larval fishes (see Chapter 1). In particular, I examine the data for inshore-offshore differences as they may relate to the spring thermal bar, terrestrial inputs, or the Keweenaw Current.

METHODS

Field Sampling

From April to August in 1998 and 1999, large zooplankton were collected from Lake Superior while sampling for larval fishes (see Chapter 1 for further details). Samples were collected from an “inshore” location and an “offshore” location on three transects (Ontonagon, Houghton, and Eagle Harbor) that ran perpendicular to the western coast of the Keweenaw Peninsula, Michigan. In 1998, the distances from shore of the inshore and offshore locations sometimes varied between cruises. Inshore distances were 1.0 km for Ontonagon, 0.2, 0.5, 1.0, or 3.0 km for Houghton, and 0.5 or 1.0 km for Eagle Harbor. Offshore distances were 9.0 km for Ontonagon, 5.0 or 7.0 km for Houghton, and 5.0 km for Eagle Harbor. In 1999, the inshore location was limited to 1.0 km from shore on all transects, and the offshore location was limited to 9.0 km from shore for Ontonagon and 5.0 km from shore for Houghton and Eagle Harbor.

At each location, surface and deep samples were collected during two day periods, daytime and nighttime, by towing a 1-m diameter, 500- μ m mesh, conical (3:1 length to diameter ratio) plankton net horizontally through the water and parallel with shore typically for 10 min at a speed of 0.77 – 1.03 m/s (1.5 – 2.0 knots), starting from

the transect line. Surface tows were taken from immediately below the water surface. Deep tows were taken from immediately below the metalimnion when present, and close to bottom when absent. A center-mounted (General Oceanics Inc.; Model 2030) flow meter recorded the flow of water through the net which was used to calculate the volume of water filtered for each tow. A Sea-Bird Electronics CTD (SBE-25) or a Hydrolab® MiniSonde® was used to measure the water temperature profile before each tow and during additional non-sampling cruises.

In 1998, whenever possible, two samples were collected from each location for both depths and both day periods. In 1999, three samples were collected from the inshore location and two samples were collected from the offshore location for both depths and both day periods. Replicate surface tows were alternately taken with deep tows at a particular location. Samples were preserved in the field by adding a small amount of 10% formalin. In total, 80 samples were collected in 1998 (16 from Ontonagon, 41 from Houghton, and 23 from Eagle Harbor) and 291 samples were collected in 1999 (84 from Ontonagon, 164 from Houghton, and 43 from Eagle Harbor), where, on average \pm SE, a sample filtered $430 \pm 165 \text{ m}^3$ of water.

Laboratory Measurements

Most samples needed to be subsampled before zooplankton could be identified and enumerated because samples usually contained numerous zooplankton individuals. A sample was split into halves, 1 to 11 times, with a Folsom plankton splitter until only approximately one hundred individuals remained in each half. The zooplankton of these final halves were identified following Balcer et al. (1984) and enumerated under a dissecting microscope. The average of the two halves was then used to back multiply

abundance in the entire sample. Zooplankton taxa that were present in the original sample but absent or rare in the final halves were also identified and enumerated in a split with double the volume of each final half. This “back-split” provided a greater opportunity to observe less-abundant zooplankton by examining a greater volume of the original sample. For these less-abundant species, the counts from the two final halves were first added together. This sum was then averaged with the counts of the back-split (each representing equal volumes), and the average was used to back multiply abundance in the entire sample. Sample abundance was then converted to density (number/m³) by dividing the number of individuals of each zooplankton species by the estimated volume of water sampled.

Data Analysis

Given that this sampling protocol primarily targeted larval fishes, smaller zooplankton would have been extruded through the 500 µm mesh. Thus, I focused my attention only on the mature individuals of the larger zooplankton taxa: calanoids, *Daphnia* spp., *Holopedium gibberum*, *Bythotrephes cederstroemi*, *Mysis relicta*, and *Diporeia* spp. Analyses used to examine the distribution of zooplankton mirrored the procedures previously used to examine larval fish distributions (see Chapter 1 for further details).

I started by identifying the seasonal periods of occurrence for each species. Next, I tested the validity of pooling the limited number of twilight tows (a total of 12 tows from 7 cruises) collected in 1999 with corresponding nighttime tows of a particular location, cruise, and depth. I compared corresponding daytime, twilight, and nighttime tows with a two-factor ANOVA on square-root ($\sqrt{X + 0.5}$) transformed data (Zar 1999)

for factors, depth and day period, followed by the Tukey multiple comparison test (Zar 1999). For further analyses, twilight tows were pooled with nighttime tows when results were not statistically different, and were omitted when results were significant, so to avoid biasing nighttime estimates.

Next, I tested for differences between depths and day periods. I employed data that formed a balanced set of surface vs. depth tows and daytime vs. nighttime tows from a particular location during a particular cruise when catches were abundant. I analyzed for differences with a two-factor ANOVA on $\log(X + 1)$ transformed data (Zar 1999), pooled across years, for factors, depth and day period, followed by the Tukey multiple comparison test (Zar 1999).

Finally, I employed data from the depth and day period for which particular zooplankton were most abundantly caught to analyze for differences in densities between inshore and offshore locations. In order to have sufficient sample sizes for the Mann-Whitney test (Zar 1999), I pooled Ontonagon/Houghton data for May/June/July in 1998, and May/June and July/Aug in 1999. All statistical analyses were performed with SYSTAT 10 (SPSS Inc.).

RESULTS AND DISCUSSION

Seasonal Occurrence

Catches of zooplankton consisted of 12 taxa with calanoids being the overwhelming dominant (Table 2–1). The overall abundances of calanoids were partly amplified, though, by being a taxon consisting of several species that together extended their abundance throughout the collection season. The dominance of calanoids during spring and summer in Lake Superior was also observed by Watson and Wilson (1978)

with lake-wide sampling, and more recently by Link et al. (2004) for the Apostle Islands and Keweenaw regions and by Brown and Branstrator (2004) for the western region.

The other abundant taxa similarly occurred throughout the majority of the collection season, but with more confined peaks in abundance (Figure 2-1). *Diporeia* and *Mysis* were most abundant earlier in the season, while the cladocerans *Daphnia*, *Holopedium*, and *Bythotrephes* were most abundant later in the season (Figure 2-1). The seasonal abundance of *Holopedium* supports a substantial population increase observed since the 1970s in Lake Superior (Link et al. 2004, Brown and Branstrator 2004). Many studies have documented the spread and biology of *Bythotrephes* in the Great Lakes since its accidental introduction (e.g., Makarewicz and Jones 1990, Lehman 1991, Branstrator 1995, Yurista 1997, Pothoven et al. 2003). *Bythotrephes* was first recorded in Lake Superior in 1987 (Cullis and Johnson 1988), and appears to have increased in abundance in the Keweenaw region since the early 1990s, when Link (1995) recorded densities rarely exceeding 2 individuals/m³.

Dates on which half of the cumulative seasonal catches were collected occurred approximately one month later in 1999 than in 1998 for the calanoids, *Daphnia*, *Diporeia*, and *Holopedium*, and almost two months later for *Mysis* (Figure 2-1). In contrast, these dates for *Bythotrephes* were nearly the same between years. In 1999, the later occurrences for most taxa likely followed the slightly later spring warm up (Figure 2-1). For example, at Ontonagon on 19 May, the inshore location was 1 °C colder and the offshore location was 3 °C colder in 1999 compared to 1998. After June, however, surface water temperatures were similar between years.

Others have noted that the seasonal increase in water temperature is the primary factor that drives the growth and reproduction of zooplankton, especially the cladocerans (Watson and Wilson 1978, Brown and Branstrator 2004). Accordingly, cladocerans have been observed to be rare in spring and most abundant in mid to late summer when waters are well stratified (Selgeby 1975, Evans et al. 1980, Brown and Branstrator 2004). In contrast, *Mysis* and *Diporeia* primarily occupy the bottom waters (Balcer et al. 1984) where temperatures remained low in Lake Superior during stratification. They have limited tolerances for warmer waters (Smith 1972, Rudstam et al. 1999) and usually avoid shallow areas and surface waters in summer (Wells 1960, Beeton and Bower 1982, Johnson 1988, Shea and Makarewicz 1989, Auer and Kahn 2004). Thus, it was expected that *Mysis* and *Diporeia* would be rarely caught in surface plankton tows after stratification.

Seasonal warming appeared to be the major factor that limited planktonic catches of *Mysis* and *Diporeia* while simultaneously stimulated cladoceran growth and reproduction. Accordingly, spring and summer can be divided into three thermal periods with contrasting zooplankton catches. First, in spring (late April and May), surface water temperatures were comparatively cold between inshore (mean of 5.5 °C) and offshore (mean of 4.8 °C) locations (mean difference of 0.74 °C; paired *t*-test; *n* = 18, *P* = 0.09). During this period, calanoids dominated the seasonally low zooplankton catches (Figure 2-2) and *Mysis* and *Diporeia* readily occurred in the surface waters at night. Second, in early summer (June and early July), seasonal warming resulted in the greatest difference between inshore (mean of 15.1 °C) and offshore (mean of 10.9 °C) water temperatures, at least in 1999 (maximum difference of 5.2 °C for Ontonagon, 4.8 °C for Houghton, and

10.5 °C for Eagle Harbor) (mean difference of 4.2 °C; paired t -test, $n = 8$, $P = 0.006$).

During this period, cladocerans started to increase in numbers especially inshore, *Mysis* rarely occurred in the surface waters, and *Diporeia* were still present in the offshore surface waters at night. Finally, in late summer (mid July to end of Aug), the entire study region was well-stratified resulting in comparably warm, although statistically different, surface water temperatures between the inshore (mean of 18.5 °C) and offshore (17.7 °C) locations (mean difference of 0.85 °C; paired t -test; $n = 27$, $P = 0.0002$). During this period, the cladocerans, *Holopedium* and *Bythotrephes*, achieved their peak abundances, *Mysis* were only caught in deep tows mainly offshore, and *Diporeia* were completely absent in the planktonic catches.

Diel Vertical Migration

I analyzed for differences in densities for the few twilight samples taken in 1999 to justify pooling with post-twilight nighttime samples, as twilight samples are known to sometimes yield higher densities of zooplankton (e.g., McNaught and Hasler 1964).

Bythotrephes densities were statistically greater during twilight compared to daylight and post-twilight nighttime samples taken at the surface (Table 2–2, Table 2–3; Tukey test; least significance difference, $P < 0.025$). Accordingly, I omitted surface twilight tows for *Bythotrephes* from subsequent analyses so not to inflate the nighttime estimates, and pooled twilight tows with nighttime tows for the other species.

Zooplankton are generally known to migrate daily, ascending toward surface waters at sunset to feed, and descending toward deep waters before daylight, most likely to avoid predators (Lampert 1989). This vertical migration pattern was also observed among the Lake Superior zooplankton. Their densities were greater at the surface at

night than during daylight (Table 2–4), which resulted in a significant day period by depth interaction for all taxa except *Bythotrephes* (Table 2–5). Swain et al. (1970) observed that zooplankton in Lake Superior vertically migrated mainly within the epilimnion and metalimnion (top 20 m of water), while lower densities of zooplankton in deeper waters (20 – 30 m) exhibited little movement.

The diel shift for *Bythotrephes*, as indicated by the twilight analysis (Table 2–2, Table 2–3), overall was not as prominent as that of the other taxa (Table 2–4). Even with the one surface twilight tow that was omitted for this analysis, *Bythotrephes* still did not show a significant day period by depth interaction ($P < 0.08$). *Bythotrephes* may exhibit a more complex diel pattern, in which sinking occurs at night after a twilight ascent, like that observed in species of *Daphnia* (e.g., McNaught and Hasler 1964, Young and Watt 1993). Alternatively, *Bythotrephes* may not be as dependent on diel vertical migration for predator avoidance because of protection conferred by its extraordinarily long tail spine (3 – 4 times body length). *Bythotrephes* is readily consumed by several fish species in the Great Lakes (Branstrator and Lehman 1996, Baker et al. 1992, Hartman et al. 1992, Schneeberger 1991, Keilty 1990, Cullis and Johnson 1988), however, small-size fishes avoid consumption of *Bythotrephes* (Barnhisel 1991a, Barnhisel 1991b, Barnhisel and Harvey 1995) with the tail spine possibly causing internal injuries when consumed (Compton and Kerfoot 2004).

The surface samples during daylight were completely absent by *Mysis* and *Diporeia*, as might be expected given these species are known to be primarily bottom-dwelling or benthic (Balcer et al. 1984). *Mysis* is well known for their nightly vertical feeding migrations that are cued by light intensity (Balcer et al. 1984, Covich and Thorp

2001). In Lake Superior, Swain et al. (1970) did not capture *Mysis* during daylight with planktonic samples from the top 40 m of water. In this study, *Mysis* exhibited a partial upward migration at night, with deep water densities exhibiting a greater increase at night compared to the increase at the surface (Table 2–4). This pattern likely resulted from *Mysis* halting their nightly ascent at the thermocline (Beeton and Bower 1982) to avoid warmer surface waters that can impair feeding rate over 14°C (Rudstam et al. 1999).

Diporeia is known to be a sediment-burrowing species (Balcer et al. 1984), and their presence in plankton tows in May and June may signify spawning migrations (Marzolf 1965) or open-water feeding (Donner et al. 1987). The seasonally-limited pelagic occurrence suggests spawning rather than feeding. A possible vertical migration later in the season for feeding could have been inhibited by the thermocline (Wells 1960), however, the observed densities for deep samples did not show such an aggregation of *Diporeia* below the thermocline. Alternatively, spawning for *Diporeia* in deep waters may occur in different periods of the year including summer (Green 1968, Winnell and White 1984, Auer and Kahn 2004). In addition, the planktonic catches of *Diporeia* consisted only of larger individuals, similar to that observed by Marzolf (1965).

Inshore-Offshore Distribution

Zooplankton abundances were expected to be greater inshore where warmer waters can foster zooplankton growth and reproduction, and, coupled with nutrient inputs from terrestrial runoff, warmer waters can foster phytoplankton production for grazing. However, in general, densities were greater offshore than inshore, except for *Bythotrephes*, which had a statistically greater density inshore in 1999 (Table 2–6, Table 2–7, Table 2–8). Calanoids seem to show a seasonal shift in abundance from inshore, in

May and June, to offshore, in July and August, although the inshore-offshore difference sometimes fluctuated between cruises. *Holopedium* densities were also periodically high in both inshore and offshore locations. Upwelling events, common to this region (Niebauer et al. 1977), may have caused some of this fluctuation by temporarily displacing nearshore waters, along with zooplankton, into offshore areas (Haffner et al. 1984). *Daphnia* catches were low until late in the collection season, at which time densities were higher offshore at least at Ontonagon and Houghton. However, early catches of *Daphnia* hint at an inshore to offshore seasonal expansion, as documented by Watson and Wilson (1978) for cladocerans, cyclopoids, and small calanoids. As for the benthic species, *Mysis* occurred rarely in inshore waters, and *Diporeia* was completely absent from inshore samples.

Similar inshore-offshore differences have been observed by others. In Lake Michigan, Gannon (1975) found calanoids prevailing offshore (>18 km from shore) and cladocerans prevailing inshore (<18 km from shore) during summer (but not in fall, winter, or spring). Evans et al. (1980) also observed the dominance of calanoids offshore (20 – 50 m depth) and cladocerans inshore (5 – 20 m depth) in Lake Michigan during fall. Watson and Wilson (1978) observed a similar pattern with lake-wide sampling in Lake Superior. In Lake Ontario, Shea and Makarewicz (1989) consistently caught more *Mysis* at a 100 m deep station than at a 35 m deep station, especially after higher temperatures in shallower waters forced *Mysis* into deeper waters. Likewise, in Lake Michigan, Pothoven et al. (2004) encountered a greater density of *Mysis* offshore (75 – 110 m depth) than inshore (45 m depth). Within this study area of Lake Superior, Auer and Kahn (2004), with ponar sampling, observed peaks in *Diporeia* abundance on the slope,

located offshore 6 – 10 km at Ontonagon, 3 – 5 km at Houghton, and 1 – 2 km at Eagle Harbor. Also in this region, Osterberg (2003), with an optical plankton counter, found a summer zooplankton concentration encompassing the metalimnion and extending offshore from the slope region. For *Bythotrephes*, a greater abundance in shallower waters (5 m vs. 10, 15, and 18 m depth contour) was observed with limited sampling in Lake Michigan by Baker et al. (1992). In contrast, Pothoven et al. (2003) observed a greater *Bythotrephes* abundance offshore (80 – 150 m depth) than inshore (45 m depth) in Lake Michigan, although densities were at times highly variable. *Bythotrephes* has been observed to spread from nearshore to offshore regions in Lake Ontario several years after establishment (Makarewicz and Jones 1990).

Lake Superior may not show the expected inshore-offshore pattern in zooplankton abundance because of its large size and ultra-oligotrophic condition. The water budget of Lake Superior is dominated by precipitation and evaporation over stream input and discharge (Matheson and Munawar 1978). Accordingly, nutrient concentrations are low in summer without notable vertical or horizontal gradients (Weiler 1978). Chlorophyll *a*, instead of being concentrated in shallow, inshore waters, peaks below the thermocline, approximately 23 – 35 m deep, in offshore waters (Auer and Bub 2004, Barbiero and Tuchman 2004). In addition, surface water temperatures were similar between inshore and offshore locations from mid July. Therefore, even if some taxa expanded from inshore to offshore locations with seasonal warming, we generally observed the greatest abundances offshore.

Although too small to be captured in this study, copepod nauplii, a major dietary item for larval fishes, have been documented to co-occur with adult copepods in spring

and summer (Brown and Branstrator 2004), and even occupy shallow waters (5 – 10 m depth) where adults are scarce (Evans et al. 1980). Thus, food for larval fishes may not be concentrated only in offshore regions. The majority of adult zooplankton, like that of most larval fishes, occurred later in the season after the spring thermal bar progressed offshore. Thus, nauplii that first occur inshore appear to expand their range to offshore regions as they develop and the nearshore waters continue to warm. Larval fishes, after a brief encounter in spring and early summer, become quite rare thereafter. They either become large enough to avoid capture, become too scarce to be encountered regularly, and/or migrate to deeper, offshore waters where zooplankton food sources apparently become concentrated.

Table 2–1. Types and estimated numbers of zooplankton caught in 1998 and 1999 with plankton net tows (80 tows in 1998; 291 tows in 1999) from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

Taxa	1998			1999		
	inshore (n = 48)	offshore (n = 32)	%	inshore (n = 180)	offshore (n = 111)	%
Calanoids	1,057,594	1,401,757	79.0	3,153,824	6,523,008	71.0
<i>Holopedium gibberum</i>	84,131	373,571	14.7	1,682,251	1,180,531	21.0
<i>Bythotrephes cederstroemi</i>	22,645	75,168	3.1	462,387	132,463	4.4
<i>Daphnia</i> spp.	15,874	34,050	1.6	132,683	283,338	3.1
<i>Mysis relicta</i>	4,268	13,661	0.6	7,820	40,680	0.4
<i>Diporeia</i> spp.	680	25,536	0.8	432	17,105	0.1
<i>Bosmina</i> spp.	68	320	< 0.1	8,000	0	0.1
Ostracoda	128	0	< 0.1	826	2,034	< 0.1
<i>Diaphanosoma</i> spp.	0	0	< 0.1	1,280	0	< 0.1
<i>Polyphemus pediculus</i>	22	40	< 0.1	628	63	< 0.1
<i>Leptodora kindti</i>	224	260	< 0.1	0	0	< 0.1
<i>Cyclops</i> spp.	20	32	< 0.1	4	16	< 0.1
other	1,922	2,351	< 0.1	2,416	536	< 0.1

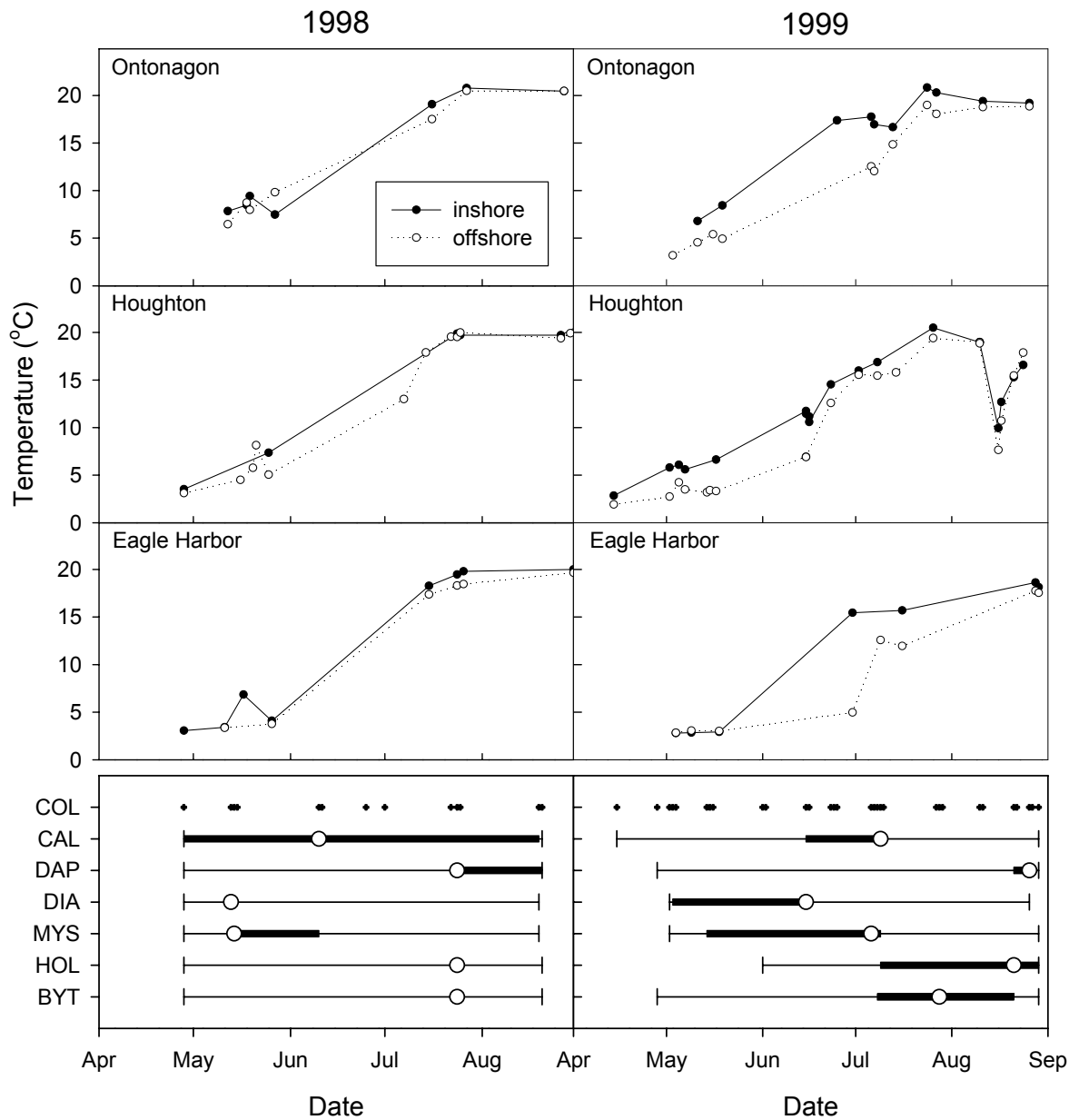


Figure 2-1. Surface water temperatures, sampling dates, and seasonal occurrences of large zooplankton species caught in 1998 and 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. COL = sampling date; CAL = calanoids, DAP = *Daphnia*, DIA = *Diporeia* spp.; MYS = *Mysis relicta*; HOL = *Holopedium gibberum*; BYT = *Bythotrephes cederstroemi*. For seasonal occurrences, T-bars extend from first to last day of capture, dark bars extend from dates when 25 – 75% of individuals were caught, and open dots represent dates when 50% of individuals were caught.

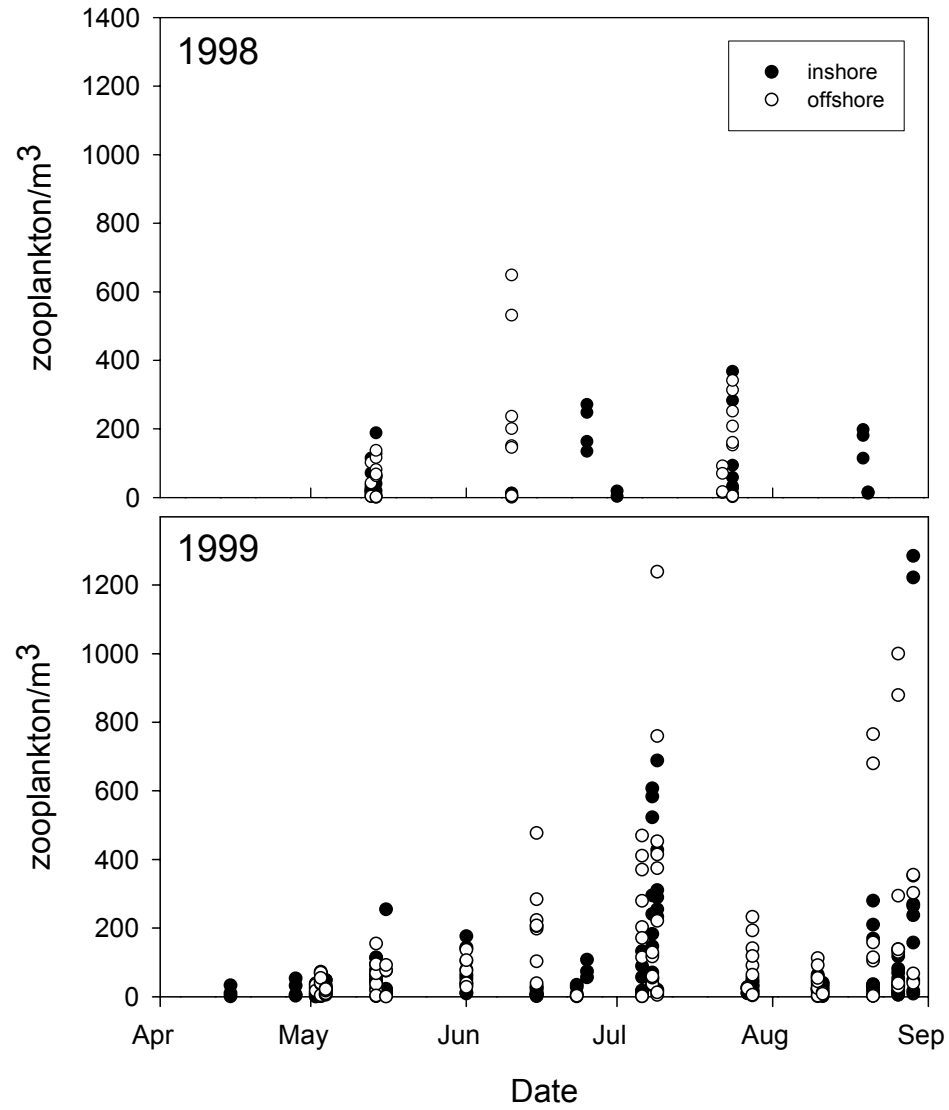


Figure 2-2. Catch of total zooplankton throughout the collection season for all three transects in Lake Superior off the western coast of the Keweenaw Peninsula.

Table 2–2. Mean (SE) density (individuals/m³) of large zooplankton captured within daytime, twilight, and nighttime tows, separated by depth, in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Date = most abundant seasonal period from which these estimates were calculated, D = daytime, T = twilight, N = nighttime.

Species	Date	Surface			Deep		
		D	T	N	D	T	N
calanoids	5/2 – 8/10	17.7 (7.1)	21.9 (4.7)	108.2 (46.0)	66.0 (17.1)	87.8 (28.0)	97.0 (31.7)
<i>Daphnia</i>	7/28, 8/10	0.0 (0.0)	0.5 (–)	4.1 (2.5)	0.6 (0.3)	0.9 (0.5)	0.8 (0.0)
<i>Diporeia</i>	6/1, 6/15	0.0 (0.0)	0.2 (0.0)	1.5 (0.6)	3.9 (3.9)	0.0 (–)	0.0 (–)
<i>Mysis</i>	6/1, 6/15	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.1 (2.1)	0.2 (–)	2.7 (1.2)
<i>Holopedium</i>	7/28, 8/10	1.8 (0.4)	3.7 (–)	29.7 (11.3)	14.4 (6.9)	13.7 (8.1)	5.7 (3.2)
<i>Bythotrephes</i>	7/28, 8/10	0.4 (0.1)	25.4 (–)	4.8 (3.1)	0.3 (0.2)	2.3 (1.8)	0.6 (0.2)

Table 2–3. Results (*P*-values) of two-factor ANOVA for comparing daytime, twilight, and nighttime samples, separated by depth, of zooplankton captured in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. *n* = total number of samples (tows) for each analysis.

Species	<i>n</i>	Depth	Day Period	Interaction
calanoids	60	0.01	0.03	0.36
<i>Daphnia</i>	16	0.62	0.09	0.14
<i>Diporeia</i>	14	0.93	0.80	0.33
<i>Mysis</i>	14	0.11	0.58	0.61
<i>Holopedium</i>	16	0.76	0.35	0.04
<i>Bythotrephes</i>	16	0.001	0.0007	0.007

Table 2–4. Mean density (individuals/m³) \pm SE of zooplankton captured with daytime vs. nighttime and surface vs. deep tows in 1998 and 1999 from Lake Superior off the western coast of the Keweenaw Peninsula. Date = most abundant seasonal period from which these estimates were calculated, *n* = number of tows in each combination, and * indicate the depth and diel combinations of each species used for subsequent transect and offshore location analyses (shown on 1999 estimates).

Taxa	Date	<i>n</i>	Daytime		Nighttime	
			Surface	Deep	Surface	Deep
1998						
Calanoids	5/13 – 7/24	12	2.7 ± 0.6	55.3 ± 19.9	141.4 ± 62.3	79.8 ± 20.8
<i>Daphnia</i>	5/14 – 7/24	6	0.7 ± 0.5	1.6 ± 0.7	9.3 ± 7.3	4.1 ± 2.1
<i>Diporeia</i>	5/14 – 6/10	4	0.0 ± 0.0	0.0 ± 0.0	2.7 ± 0.6	0.4 ± 0.1
<i>Mysis</i>	5/13 – 6/10	6	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 0.5	2.9 ± 0.6
<i>Holopedium</i>	5/14 – 7/24	4	5.1 ± 2.9	10.5 ± 6.3	92.1 ± 61.4	18.9 ± 9.5
<i>Bythotrephes</i>	6/10 – 7/24	4	1.3 ± 1.1	19.3 ± 11.1	10.9 ± 8.0	12.0 ± 7.7
1999						
Calanoids	5/2 – 8/29	50	8.3 ± 2.7	77.0 ± 16.5	85.3 ± 26.2*	61.2 ± 10.4
<i>Daphnia</i>	7/8 – 8/29	26	0.5 ± 0.2	4.7 ± 1.6	25.3 ± 10.5*	3.0 ± 1.1
<i>Diporeia</i>	5/3 – 6/15	5	0.0 ± 0.0	2.4 ± 2.4	2.3 ± 1.1*	0.3 ± 0.2
<i>Mysis</i>	5/3 – 7/6	11	0.0 ± 0.0	0.6 ± 0.6	0.5 ± 0.4	1.8 ± 0.5*
<i>Holopedium</i>	7/6 – 8/29	30	26.5 ± 18.3	36.4 ± 8.7	175.7 ± 57.8*	30.8 ± 8.3
<i>Bythotrephes</i>	6/15 – 8/29	34	8.9 ± 4.4	5.5 ± 1.2	13.1 ± 2.5 *	9.2 ± 2.0

Table 2–5. Results (*P*-values) of two-factor ANOVA for depth and diel differences in zooplankton densities.

Taxa	Day Period	Depth	Interaction
Calanoids	< 0.0001	< 0.0001	< 0.0001
<i>Daphnia</i>	0.0003	0.80	0.0003
<i>Diporeia</i>	< 0.0001	0.0007	0.0007
<i>Mysis</i>	< 0.0001	0.003	0.004
<i>Holopedium</i>	0.0004	0.99	0.0001
<i>Bythotrephes</i>	0.001	0.71	0.10

Table 2–6. Mean (SE) densities (individuals/m³) of zooplankton captured in 1998 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

Species	Date	Ontonagon		Houghton		Eagle Harbor
		Inshore	Offshore	Inshore	Offshore	Inshore
Calanoids	13-15 May	117.9 (60.1)	100.2 (24.2)			12.9 (1.0)
	10-11 June			11.9 (0.0)	585.9 (60.8)	
	22-25 July			16.0 (6.0)	19.6 (2.6)	
<i>Daphnia</i>	13-15 May	2.8 (1.2)	0.0 (0.0)			0.0 (0.0)
	10-11 June			0.0 (0.0)	0.4 (0.1)	
	22-25 July			0.4 (0.4)	24.9 (20.9)	
<i>Diporeia</i>	13-15 May	0.0 (0.0)	3.6 (0.8)			0.1 (0.1)
	10-11 June			0.0 (0.0)	1.8 (0.5)	
<i>Mysis</i>	13-15 May	0.1 (0.1)	1.9 (0.9)			2.6 (0.4)
	10-11 June			0.0 (0.0)	4.1 (1.2)	
	22-25 July			0.1 (0.1)	2.8 (0.3)	
<i>Holopedium</i>	13-15 May	3.5 (1.4)	0.0 (0.0)			0.0 (0.0)
	10-11 June			0.0 (0.0)	0.0 (0.0)	
	22-25 July			16.2 (4.2)	180.7 (83.0)	
<i>Bythotrephes</i>	13-15 May	0.3 (0.0)	0.2 (0.2)			0.0 (0.0)
	10-11 June			0.3 (0.1)	0.0 (0.0)	
	22-25 July			13.0 (2.4)	21.6 (12.5)	

Table 2–7. Mean (SE) densities (individuals/m³) of zooplankton captured in 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. CAL = calanoids, DAP = *Daphnia*, DIA = *Diporeia* spp.; MYS = *Mysis relicta*; HOL = *Holopedium gibberum*; BYT = *Bythotrephes cederstroemi*.

Species	Date	Ontonagon		Houghton		Eagle Harbor	
		Inshore	Offshore	Inshore	Offshore	Inshore	Offshore
CAL	2-4 May	54.0 (14.3)	41.5 (6.5)	7.0 (1.0)	31.5 (1.7)	44.0 (--)	21.0 (1.7)
	14-16 May			95.5 (9.8)	20.9 (3.7)		
	1 June			124.7 (34.9)	33.5 (5.4)		
	15 June			14.4 (4.4)	379.2 (95.9)		
	6-9 July	3.8 (1.5)	302.3 (63.4)	32.4 (12.7)	14.3 (1.5)		857.1 (262.9)
	27-28 July			7.6 (2.4)	113.4 (99.4)		
	10-11 Aug			4.3 (1.1)	11.7 (3.3)		
	21 Aug			8.5 (2.2)	167.1 (98.1)		
	26-29 Aug	4.2 (1.8)	108.5 (24.1)			23.6 (6.2)	
DAP	2-4 May	1.7 (0.7)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (--)	0.0 (0.0)
	14-16 May			0.0 (0.0)	0.0 (0.0)		
	1 June			0.0 (0.0)	0.0 (0.0)		
	15 June			0.0 (0.0)	0.0 (0.0)		
	6-9 July	0.3 (0.2)	1.0 (1.0)	12.0 (5.5)	2.1 (0.4)		9.5 (1.7)
	27-28 July			0.5 (0.3)	5.4 (3.8)		
	10-11 Aug			0.2 (0.2)	1.0 (0.5)		
	21 Aug			3.5 (2.6)	124.0 (11.3)		
	26-29 Aug	3.0 (1.1)	183.6 (19.7)			98.5 (7.0)	
DIA	2-4 May	0.0 (0.0)	4.9 (0.9)	0.0 (0.0)	0.4 (0.2)	0.0 (--)	0.0 (0.0)
	14-16 May			0.0 (0.0)	0.5 (0.3)		
	1 June			0.0 (0.0)	0.2 (0.0)		
	15 June			0.0 (0.0)	1.5 (0.6)		
MYS	2-4 May	0.0 (0.0)	1.9 (0.1)	0.0 (0.0)	1.3 (0.6)	1.9 (0.1)	
	14-16 May			0.1 (0.1)	3.0 (0.6)		
	1 June			0.1 (0.1)			
	15 June			0.1 (0.1)	1.9 (1.1)		
	6-9 July	0.0 (0.0)	3.5 (0.7)	0.3 (0.3)	3.2 (0.5)		2.4 (0.5)
	27-28 July			0.0 (0.0)	1.2 (0.6)		
	10-11 Aug			0.0 (0.0)	1.8 (1.8)		
	21 Aug			0.0 (0.0)	2.9 (--)		
	26-29 Aug	0.0 (0.0)	4.6 (1.0)			1.6 (0.2)	
HOL	6-9 July	3.0 (1.7)	19.9 (18.6)	390.9 (91.2)	25.1 (8.2)		101.8 (8.6)
	27-28 July			7.6 (4.1)	23.5 (16.3)		
	10-11 Aug			10.3 (2.7)	22.9 (19.2)		
	21 Aug			82.7 (64.9)	423.5 (127.3)		
	26-29 Aug	41.2 (9.7)	632.3 (60.0)			1113.4 (10.5)	
BYT	1 June			0.2 (0.1)	0.0 (0.0)		
	15 June			1.8 (0.6)	0.0 (0.0)		
	6-9 July	2.9 (1.3)	1.5 (0.2)	31.2 (4.3)	4.5 (0.0)		30.7 (16.3)
	27-28 July			10.5 (4.1)	5.8 (5.1)		
	10-11 Aug			22.0 (12.9)	2.7 (--)		
	21 Aug			21.4 (12.8)	7.6 (2.0)		
	26-29 Aug	11.0 (2.8)	14.9 (5.1)			17.5 (7.7)	

Table 2–8. Results of Mann-Whitney test comparing inshore and offshore densities of zooplankton captured in 1998 and 1999 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Results are for Ontonagon and Houghton samples pooled. *P*-values are exact for 1998 and approximate for 1999.

	month	sample sizes (inshore, offshore)	<i>P</i> -value	inshore mean	offshore mean
<i>1998</i>					
Calanoids	May/June/July	6, 6	0.10	48.613	235.211
<i>Daphnia</i>	May/June/July	6, 6	>0.20	1.065	8.416
<i>Diporeia</i>	May/June/July	6, 6	0.20	0.007	1.794
<i>Mysis</i>	May/June/July	6, 6	0.005	0.039	2.915
<i>Holopedium</i>	May/June/July	6, 6	> 0.20	6.557	60.248
<i>Bythotrephes</i>	May/June/July	6, 6	> 0.20	4.530	7.253
<i>1999</i>					
Calanoids	May/June	15, 10	0.66	59.130	101.329
	July/Aug	18, 12	0.0002	10.130	119.551
<i>Daphnia</i>	July/Aug	18, 12	0.03	3.267	52.855
<i>Diporeia</i>	May/June	15, 10	< 0.0001	0.002	1.490
<i>Mysis</i>	May/June	14, 9	< 0.0001	0.059	1.982
	July/Aug	16, 12	< 0.0001	0.036	2.913
<i>Holopedium</i>	July/Aug	18, 12	0.19	89.285	191.194
<i>Bythotrephes</i>	July/Aug	18, 11	0.03	16.490	6.472

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CHAPTER 3

Factors Influencing Otolith Microstructure in Larval Lake Herring (*Coregonus artedii*)

ABSTRACT

Lake herring (*Coregonus artedii*) larvae were reared in the laboratory from eggs collected from Lake Superior in order to validate the use of otolith microstructure for aging and back-calculating growth. Throughout a 75-day rearing period, water temperatures in two laboratory streams were progressively increased (from 5.6 to 7.0 °C and from 6.1 to 12.3 °C), mimicking the range larvae would likely experience in Lake Superior. Otolith increments were deposited at a rate that was not statistically different from one per day starting from yolk-sac absorption, which occurred approximately 29 days after hatching. Feeding frequency (twice-daily, once-daily, alternate-day, and starvation) did not affect the prominence of subdaily marks (i.e., bands occurring within daily increments), but a 5-day period of starvation reduced increment contrast in some larvae. The reduced rations, especially when coupled with a lower water temperature, partly explained lower growth rates among larvae, and larvae with lower growth rates could not be aged as accurately by otolith analysis. An accessory check mark was induced by a sudden decrease in temperature, but not by a reciprocal increase in temperature (between 7.1 °C and 12.3 °C). In addition, increment widths were correspondingly narrowed by the colder temperature and widened by the warmer temperature. For larvae up to 75 days of age, the otolith diameter to larval total length relationship was logarithmic and dependent on temperature, which differed by 2.0 °C overall between laboratory streams. These results indicate the potential of using otolith analysis for aging larval lake herring, while heeding its limits at reduced growth rates.

INTRODUCTION

Lake herring (*Coregonus artedii*) historically was the most commercially productive species in the Great Lakes, until overexploitation led to its decline beginning in the early 1900s (Smith 1968, 1972, Fleischer 1992). Presently, substantial stocks of lake herring persist only in Lake Superior, the St. Marys River, and northern Lake Huron including Georgian Bay (Fleischer 1992). In Lake Superior, recovery to pre-exploitation levels has been inhibited by highly variable recruitment (Bronte et al. 2003), emphasizing the need for a better understanding of early life ecology. Daily aging, made possible by otolith microstructural analysis (Pannella 1971), has potential to greatly benefit studies of early life growth and survival of lake herring, and thus further the understanding of lake herring recruitment dynamics.

The examination of otolith microstructure has already improved estimates of larval fish age and growth in many species (Jones 1986). Estimated age and growth can then be further utilized to study recruitment dynamics, mortality, and the timing of life history transitions (Brothers 1981, Campana and Neilson 1985), as well as to locate spawning and nursery locations and migratory routes (Brothers 1981, Jones 2002). Despite the increased use of otoliths for aging and back-calculating growth of larval fishes (Jones 1992), otolith analysis still requires validation because of interspecific variation and interpretation error (Beamish and McFarlane 1983). Such validation has yet to be performed for lake herring.

Otoliths, the inner ear bones used in hearing and balance, probably originate as calcified primordia excreted by inner ear cells (Campana and Neilson 1985). Otoliths

then grow by differential deposition of calcium carbonate (aragonite structure), which forms the broad and translucent incremental zones, and the protein otolin, which forms the narrow and opaque discontinuous zones (Campana and Neilson 1985, Jones 2002). The daily deposition of both zones as a growth increment has been hypothesized to be driven by an endogenous circadian rhythm entrained by photoperiod (Campana and Neilson 1985). However, short-term temperature fluctuations (Brothers 1981) or feeding periodicity (Neilson and Geen 1982) may mask this regular pattern with subdaily increments. Otoliths may also be characterized by distinctly prominent bands, called check marks, which likely signify periods of stress (Campana and Neilson 1985), such as from hatching, yolk-sac absorption, or metamorphosis (Jones 2002). In addition, the commencement of daily increment deposition varies among species, commonly occurring before hatching, at hatching, or shortly after hatching, particularly at yolk-sac absorption or first feeding (Jones 1986). This interspecific variation underscores the importance of validation despite the seemingly universal phenomenon of daily increments.

Such variation in increment deposition also exists among congeners of lake herring. Rice et al. (1985) found that daily increments for bloater (*C. hoyi*) from Lake Michigan began at first feeding, while Eckmann and Rey (1987) found that the whitefishes *C. lavaretus* and *C. fera* from Lake Constance (Germany) exhibited daily deposition from hatching. In contrast, Huuskonen and Karjalainen (1995) could not confirm that deposition was daily for vendace (*C. albula*) and the whitefish *C. lavaretus* from Lake Pyhäselkä (Finland), possibly because of low calcium concentrations in Finnish lakes (Huuskonen et al. 1998). A low growth rate induced by limited food

rations (Rice et al. 1985) or low water temperatures (Klink and Eckmann 1992) can also obscure daily deposition in coregonids.

In this study, I examined the otoliths of lab-reared lake herring larvae to validate the use of otolith microstructure in daily aging and growth back-calculations. In particular, I determined 1) if increments are formed daily, 2) if daily increments commence with a check mark at hatching, first feeding, or at yolk-sac absorption, and 3) if temperature, feeding periodicity, or sudden temperature shifts affect incremental deposition or induce the formation of check marks.

METHODS

Egg Collection and Rearing Protocol

Larval lake herring were reared in the laboratory from eggs. Spawning lake herring were caught with a gill net off the eastern coast of the Keweenaw Peninsula in December 2001 and eggs were squeezed from three ripe females and fertilized with the milt of two males following the dry method (Wood and Dunn 1948). Fertilized eggs were refrigerated overnight until they could be placed into a “living stream” in the laboratory. A “living stream” consisted of a rectangular tank (204 x 52 x 56 cm) with a water chiller and pump which circulated water passed the eggs, through a charcoal filter, and then returned the water via a channel under the floor of the tank. The tank had a water velocity of 1 – 3 cm/s after being filled to 40 cm with tap water that was aged for several days.

Eggs were incubated at a mean temperature of 3.9 °C (range: 2.2 – 5.4 °C) (Figure 3-1) under a 12 hr (florescent) light:12 hr dark daily cycle, with dead (opaque) eggs removed daily. When eggs developed visibly pigmented eyes (approximately 35 days

after fertilization) they were transferred from the floor of the tank to three mesh nursery baskets (16 x 12 x 13 cm) floated with foam collars. Another living stream was set up in a similar manner but with a water temperature that was initially 1.5 °C higher (Figure 3-1). Hatching occurred between 62 to 102 days after fertilization, with 50% hatch achieved at 96 days after fertilization (Figure 3-1). Despite a protracted hatching period of 41 days, 74% of 1,421 larvae hatched during a 6-day span near the end of the hatching period, following a temperature increase of 1.7 °C over 8 days. Each day, newly hatched larvae were transferred to an empty nursery basket located in either of the two streams so that the day of hatching was known for all larvae. Larvae were fed fresh brine shrimp (*Artemia salina*) nauplii once-a-day from 44 days after first hatch, then twice-a-day from 67 days after first hatch. Earlier attempts to feed early hatched larvae were unsuccessful. Approximately 6% of the tank water was exchanged weekly starting from the eyed-egg stage. From the latter half of the hatching period, the temperature of both tanks was increased incrementally, to mimic seasonal warming, the second tank more so than the first.

Validation and Experimental Treatments

To assess if a check mark was deposited at hatching, several embryos were preserved during the hatching period along with larvae prior to first feeding. To assess if a check mark was deposited at first feeding, the day of first feeding was known for each larva by separating larvae that did not feed from those that did, when food was offered for the first time. These larvae were then preserved incrementally throughout the rearing period to further assess if increments were deposited daily.

The different temperatures of the two tanks caused larvae to grow at different rates (see Results). Larvae from both tanks were preserved to assess the effects of growth rate on otolith deposition rate and on the fish length to otolith diameter relationship.

To assess the effects of feeding regime on otolith deposition, larvae were subjected to one of four treatments: twice-a-day feeding (control), once-a-day feeding, alternate-day feeding, or no feeding (starvation). These feeding treatments lasted for 13 – 19 days except for the starvation treatment, which lasted for only 5 days. This experiment was used to assess if the rate of increment deposition can be influenced by feeding frequency, and to determine at what point reduced larval growth rates affect normal increment deposition.

The effects of sudden temperature changes on otolith deposition were assessed by transferring larvae from one stream to the other without an acclimation period. In addition, to separate the effect of the temperature change from the effect of being in a new temperature, larvae were floated for ~30 min in their own stream within a plastic container containing water from the other stream. This allowed larvae to experience the sudden temperature change before being quickly acclimated back to its original temperature. For controls, larvae were transferred in a similar manner to a different basket within the same stream.

Otolith Mounting and Measurements

Total length, yolk length, and yolk depth were measured on live larvae immediately before preservation in 95% ethanol. Measurements were taken from digital images (640 x 480 pixels) of larvae using SigmaScan Pro 5 (SPSS Inc.). Images were captured with a personal computer from a camera equipped on a dissecting microscope.

Yolk volume was calculated as a prolate spheroid, with length being the longer axis and depth and girth being the shorter and equal axes.

This study utilized only the majority of the hatch (86%), which occurred during a 12-day span near the end of the hatching period. Earlier larvae may have hatched prematurely, as they were smaller with larger yolks at hatching and neglected to swim until a later date on which newly hatched larvae readily swam (see Appendix B). For the majority of the hatch, left and right sagittae were removed with dissecting needles under a dissecting microscope equipped with a polarizing filter, which increased the reflectance of the otoliths. The otoliths were then mounted concave side down on a microscope slide with CrystalBond™ (SPI Supplies), a thermoplastic mounting medium.

Once mounted, individual otoliths were read blind, in random order, each side separately, with a compound microscope using up to 1000 times magnification. The most consistent of three or more increment counts from each sagitta of a pair was used to calculate a mean count for the larva. The maximum diameter of each sagitta and the maximum diameter of the check region were measured from a digitally captured image with a computer image analysis program (SigmaScan Pro 5; SPSS Inc.). Mean diameters of the left and right sagittae were calculated to represent each larva. For the temperature shock experiment, the width of an increment was calculated by measuring a span of five increments in the posterior region then dividing this length by five.

Growth Estimation and Analysis

Larvae from both the validation and experimental aspects of this study were used to determine the effect of growth rate on otolith deposition. Among these larvae, a reduced growth rate could have been caused by lower water temperatures, reduced

rations, or other factors, such as density, social dominance, or genetics. First of all, total length at hatching was estimated with the following linear regression because total length at hatching (*TL*) increased with hatch date (*DATE*): $TL = 2.24 + 0.08 * DATE$ ($n = 33$, $r^2 = 0.76$, $P < 0.0001$). The average daily growth rate for an individual larva could then be calculated as the increase in length from hatching to preservation divided by age in days. Age of each larva was predicted from otolith increment number using the linear regression generated from the validation aspect of this study (see Results). This predicted age could then be compared to the actual age with the following percent error equation:

$$\text{percent error in age estimation} = \frac{\text{predicted age} - \text{actual age}}{\text{actual age}} * 100\%$$

Negative deviations signify cases with fewer observed increments than what was expected based on the actual age. Larvae that were less than 40 days old were excluded for two reasons. First, actual growth (see Results) was not linear as assumed in the individual growth calculation, and young larvae would have had exceptionally low growth rates compared to older larvae. Second, the potential for the predicted age to deviate from the actual age would be less for younger larvae because of the fewer increments they could possibly obtain even with optimal growth. For larvae 40 – 75 days old, neither daily growth rate (linear regression, $n = 61$, $r^2 = 0.08$, $P = 0.02$) nor percent error in age estimation (linear regression, $n = 61$, $r^2 = 0.04$, $P = 0.10$) showed a strong relationship with actual age, even if the growth rate to age relationship was significant. Finally, percent error in age estimation was compared to average daily growth rates. Statistical analyses were performed with SYSTAT 10 (SPSS Inc.), except for logarithmic regression, which was performed with SigmaPlot 8 (SPSS Inc.).

RESULTS

At hatching, otoliths had a mean (\pm SD) diameter of $64.7 (\pm 5.5) \mu\text{m}$ and a mean (\pm SD) of $5.4 (\pm 1.2)$ increments. The nuclei of sagittae usually contained 4 – 8 primordia. When a check mark was formed, it had a mean (\pm SD) diameter of $64.6 (\pm 6.1) \mu\text{m}$, and this diameter did not differ between streams (two-sample t -test, $n_1 = 29$, $n_2 = 26$, $P = 0.30$). In addition, the check diameter did not differ with larval age (linear regression, $n = 55$, $r^2 = 0.002$, $P = 0.73$), indicating that the check mark could be consistently identified regardless of otolith size. The check region contained 3 – 11 increments (mean \pm SD of 5.8 ± 1.8), and increment number also did not differ between streams (two-sample t -test, $n_1 = 31$, $n_2 = 26$, $P = 0.16$) nor with larval age (linear regression, $n = 57$, $r^2 = 0.009$, $P = 0.48$). Increments within the check mark were usually broad and faint compared to increments formed after the check mark. Because otoliths at hatching and at check formation did not differ in increment number (two-sample t -test, $n_{\text{hatch}} = 4$, $n_{\text{check}} = 57$, $P = 0.76$) or maximum diameter (two-sample t -test, $n_{\text{hatch}} = 4$, $n_{\text{check}} = 55$, $P = 0.93$), there was no indication of significant otolith deposition occurring between hatching and check formation.

The larval age (*AGE*) to post-check increment number (*RINGS*) relationship (Figure 3-2) did not differ statistically between the two rearing streams in terms of their slopes ($P = 0.92$) or intercepts ($P = 0.12$) (GLM, $n = 34$, $r^2 = 0.95$). Therefore, a pooled linear regression equation was estimated, where $AGE = 28.09 + 1.04 * RINGS$ ($n = 34$, $r^2 = 0.94$, $P < 0.0001$). Increment deposition after check formation did not differ statistically from a daily frequency, as indicated by a slope that was not statistically different from one ($P = 0.88$). However, check formation did not commence at hatching,

but rather commenced approximately 28 days after hatching, as indicated by the intercept ($P < 0.0001$). A linear regression using age after first feeding (FF) instead of age after hatching also estimated an intercept that was statistically greater than zero ($FF = 14.98 + 1.05 * RINGS$; $n = 32$, $r^2 = 0.92$, $P < 0.0001$ for $H_0: \beta_0 = 0$), indicating that check formation commenced after first feeding as well. Complete yolk absorption is the next early life event on which the check mark may have been formed. Using yolk presence/absence data, there was a 50% likelihood of a larva exhausting its yolk by 29.04 days of age (with 95% Fieller CI of [23.73, 32.71]), independent of rearing stream (logistic regression, $n = 54$, $P = 0.21$). Because this age corresponded closely to the intercept age of 28.09 days, daily deposition from check formation commenced near the time of yolk depletion. In addition, there was a close correspondence in total length when there was a 50% likelihood of a larva exhausting its yolk (13.18 mm with 95% Fieller CI of [12.50, 14.55]) and when achieving a check mark (13.52 mm with 95% Fieller CI of [12.79, 14.84]).

Despite having a common age-to-increment number relationship between streams, larval growth did differ between streams. In both streams, the growth rate of larvae closely followed increases in water temperature. In stream 1, larvae grew at a steadily increasing rate (Figure 3-3), matching the steady increases in temperature (Figure 3-1). Larval growth rates in stream 2 largely surpassed that of stream 1 between intervals of 20 – 40 and 60 – 80 days of age (Figure 3-3), matching two sharp increases in temperature (Figure 3-1). Stream 2 was 2.2 °C higher than stream 1 after the first increase in temperature and 5.3 °C higher after the second. From a mean (\pm SD) hatch length of 10.67 (\pm 0.40) mm, larvae achieved mean (\pm SD) lengths of 20.44 (\pm 0.65) mm in stream

1 and 25.41 (± 1.05) mm in stream 2 after 75 days. In contrast, yolk depletion followed similar patterns of exponential decay in both streams (Figure 3-4). From a mean (\pm SD) hatch volume of 3.63 (1.18) mm³, larvae exhausted their yolks within 22 – 38 days of age.

Although the age-to-increment number relationship did not differ between streams, the otolith diameter-to-fish length relationship did (Figure 3-5). Otoliths in both streams displayed no growth during the first 2 – 3 mm of larval growth, further supporting that little, if any, otolith deposition occurred between hatching and check formation. When larvae were 14 – 20 mm in length, otoliths in both streams grew at an increasing rate with fish length, but otoliths from stream 1 were smaller than that of stream 2. For larvae up to 75 days old, the overall otolith diameter (*OD*) to fish total length (*TL*) relationship was closely logarithmic in stream 2 ($TL = -23.82 + 8.76 \ln OD$, $r^2 = 0.95$, $P < 0.0001$), but the early period of no otolith growth greatly obscured a close logarithmic fit for stream 1 ($TL = -34.84 + 11.33 \ln OD$, $r^2 = 0.65$, $P < 0.0001$).

The number of post-check increments for 43 – 63 day old larvae did not differ among the four feeding treatments ($P = 0.36$) but did differ between streams ($P = 0.001$) without an interaction effect ($P = 0.61$) (ANCOVA with age as covariate; $n = 30$, $r^2 = 0.59$). However, some otoliths displayed a band of faint increments that corresponded to the 5-day period of starvation. Differences in feeding frequency did not affect the prominence of subdaily marks, which were faint and only present between wider increments during faster growth. During this feeding frequency experiment (141 – 161 days after fertilization), water temperatures were on average 6.6 °C (range: 5.9 – 7.0 °C) in stream 1 and 9.0 °C (range: 8.1 – 9.4 °C) in stream 2.

Physically moving larvae from 12.3 °C water in stream 2 to 7.1 °C water in stream 1 (cold shock) induced an accessory check mark followed by low contrast increments. When larvae were subjected to a cold shock without remaining in the colder water thereafter, a slightly darker increment was formed, but it was not easily distinguished from the natural variation in increment contrast. Moving larvae from stream 1 to stream 2 (heat shock) did not induce a check mark, nor was a check mark induced in the controls. Exposure to the new water temperature for 5 – 8 days affected otolith increment width of these larvae, which were 73 – 75 days old when the experiment concluded. Mean increment width decreased from 3.86 to 2.83 μm (paired *t*-test; $n = 4$, $P = 0.02$) with a decrease in temperature, and increased from 1.29 to 3.64 μm (paired *t*-test; $n = 4$, $P = 0.002$) with an increase in temperature. In contrast, the control larvae exhibited only marginal increases in increment width, from 1.18 to 1.70 μm in stream 1 (paired *t*-test; $n = 4$, $P = 0.02$) and from 4.07 to 5.40 μm in stream 2 (paired *t*-test; $n = 4$, $P = 0.05$).

Estimated individual growth rates varied from 0.06 to 0.25 mm/day for 41 – 75 day old larvae. This variation in growth rate can be partly attributed to the different temperatures in the two streams and the reduced ration treatments. When experimental and non-experimental larvae that were fed twice-a-day were pooled together, a two-factor ANOVA ($n = 61$) revealed a significant effect for treatment ($P < 0.0001$) and stream ($P = 0.05$) but not for their interaction ($P = 0.17$). The average growth rate for the starved treatment was statistically lower than that of the other treatments (Tukey test, least significant comparison, $P = 0.01$), while the other treatments were not statistically different from each other (most significant comparison, $P = 0.69$), even though there was a tendency for growth rate to be higher with increased feeding frequency. The ANOVA

model, however, explained only 53% of the variation in individual growth rate. In turn, individual growth rate explained 47% of the variation in percent error associated with estimating larval age (Figure 3-6) (linear regression, $n = 61$, $P < 0.0001$). Specifically, larvae with lower growth rates could not be aged as accurately as larvae with higher growth rates.

DISCUSSION

Otolith increment deposition did not differ statistically from a daily rate once yolk was completely absorbed at approximately 28 days after hatching. Complete yolk absorption for each individual, however, could have occurred anytime within approximately a 15-day span. The time of yolk absorption could not have been determined individually without stressing larvae by repeatedly removing them from water for microscopic examinations. Such stress might have caused artificial patterns in their otolith microstructure. Accordingly, variation in time to yolk absorption among individuals likely contributed to some of the variation in the increment count to age relationship. It appeared though that the rate of yolk utilization was unaffected by the temperature difference between rearing streams, nor was it affected by experimentally delaying exogenous feeding (see Appendix B). In addition, Kowalchyk (1997) found that lake herring from Keweenaw Bay in Lake Superior depleted their yolks at a similar size to what was observed in the laboratory. In contrast, the greatest variation in time to yolk absorption occurred among larvae of different hatch dates. The earliest of the hatch was estimated to require approximately twice the time to utilize their yolk reserves (Appendix B). However, if natural populations have a similar hatching pattern, early hatched larvae would constitute only a small fraction of the annual cohort. Therefore, the slight

variation in time to yolk absorption should have only a limited influence on aging accuracy.

Increased feeding frequency has been known to increase increment counts slightly (Neilson and Geen 1982), probably by increasing the occurrence of subdaily marks which may confound daily counts (Campana 1983, Campana and Neilson 1985). In this study, treatments of twice-daily, once-daily, and alternate-day feeding did not affect increment counts, nor did they affect the prominence of subdaily marks. Faint subdaily marks in lake herring were only visible between wider increments during faster growth. Eckmann and Rey (1987) found that subdaily marks in *Coregonus lavaretus* and *C. fera* were also easily distinguishable from daily increments. In contrast, subdaily marks during faster growth confounded daily deposition in *C. albula* (Huuskonen and Karjalainen 1995), but probably because of a lower calcium concentration in the water (Huuskonen et al. 1998).

The rate of increment deposition did not differ between rearing streams of different temperatures. However, limited rations due to reduced feeding frequencies, especially when coupled with a lower temperature, reduced individual growth rates, and low growth rates appeared to inhibit the accuracy in age estimation. For example, larvae that grew less than 0.10 mm/day exhibited greater than 20% error in estimated age. These factors may have delayed the onset of daily deposition, or if daily deposition already commenced, may have suppressed the deposition rate of subsequent increments. Klink and Eckmann (1992) found that reduced temperatures delayed the onset of daily deposition in *C. lavaretus* by 9 – 18 days at 6 °C and 17 – 30 days at 4 °C (compared to 8 °C), and more so were coupled with limited feeding (once daily compared to every two hours). In comparison, Marshall and Parker (1982) found that daily increment deposition

in sockeye salmon (*Oncorhynchus nerka*) ceased because of reduced temperatures ($< 5^{\circ}\text{C}$ compared to $\sim 12^{\circ}\text{C}$), and after normal conditions resumed, recovery to a daily rate was further impeded when a 3-week period of starvation was coupled with the reduced temperatures. The narrowing of increments with a 5-day period of starvation indicated that daily deposition in lake herring can be obscured by a poor feeding condition. In addition, there was a tendency, although not significant, for daily deposition to commence approximately 3 days later in stream 1 than in stream 2, but thereafter, the deposition rate was nearly identical between streams. Therefore, fewer increments may have been produced under reduced growth rates because of both a slight delay in the onset of daily deposition and an interruption of daily deposition with adverse feeding conditions.

A sudden temperature transition from warm (12.3°C) to cold (7.1°C), but not the reverse, induced a check mark in lake herring with subsequent increments being narrower and of lower contrast. Likewise, Eckmann and Rey (1987) found that a cold shock from 12.5 to 4.5°C induced a check mark in 60% of *C. lavaretus* and *C. fera*, followed by narrower increments. Additional accessory check marks were also observed in lake herring, but only in a small percentage (16%) of otoliths examined. They did not appear to follow any particular event, and even if they did, only a small percentage of larvae would have responded to such an event by depositing an accessory check mark. Until it is better understood what causes accessory check marks to form in lake herring, accessory check marks will provide limited use as markers of environmental conditions. Drastic changes in increment width, though, may prove useful as markers of temperature transitions, as possibly created by currents, upwellings, or migrations.

The larval total length to otolith diameter relationship was logarithmic for lake herring up to 75 days of age. Linear relationships are sometimes observed for other species (e.g., Marsall and Parker 1982, Neilson and Geen 1982, Klink and Eckmann 1992), but, especially for older larvae and juveniles, this relationship tends to be curvilinear (e.g., Rice et al. 1985, Moksness and Wespestad 1989, Jenkins and Davis 1990, Huuskonen and Karjalainen 1995). This relationship was also affected by differences in growth between rearing streams. The dependence of this relationship on growth rate has been observed for many taxa, including *Coregonus* spp. (Klink and Eckmann 1992, Huuskonen and Karjalainen 1995). Because of the typical effect of growth rate on this relationship, simple linear regression should not be used to back-calculate length using otolith size (Campana and Jones 1992). Alternative methods involving a biological intercept (Campana 1990), quadratic regression (Secor and Dean 1992), or time-varying growth (Sirois et al. 1998) should improve back-calculations for lake herring as well, especially since it is not clear from this study at what point growth rate begins to have a significant influence on the otolith length to fish length relationship.

The onset of daily deposition in lake herring was later than most other *Coregonus* spp. (Rice et al. 1985, Eckmann and Rey 1987, Klink and Eckmann 1992, Huuskonen et al. 1998). Klink and Eckmann (1992) have shown that the onset of daily deposition in *C. lavaretus* can be delayed by low temperatures. Rearing temperatures for lake herring were initially ~1 °C lower than that of Rice et al. (1985) for Lake Michigan bloater, but they were still slightly greater than Lake Superior spring temperatures (~3 – 6 °C) in which lake herring were initially caught (Oyadomari and Auer, 2004). It might have been possible to induce an earlier onset of daily deposition by subjecting lake herring

larvae to higher temperatures than what they experienced in this study or what they would experience in Lake Superior. For example, by acclimating *C. lavaretus* larvae to 12 °C upon hatching, Eckmann and Rey (1987) found that daily deposition started with a check mark at hatching. However, wild-caught *C. lavaretus* larvae did not exhibit daily deposition until a few weeks after hatching when growth rate accelerated with increasing temperatures (Eckmann and Pusch 1989, Rey and Eckmann 1989). Rey and Eckmann (1989) also noted that in the laboratory *C. lavaretus* did not exhibit daily increments when reared at 4 or 6 °C (compared to 8 °C or above), but hatching in nature occurs in 4°C or less water. Because this study strived to mimic conditions that lake herring larvae typically experience in nature, these results more likely represent the otolith microstructure of wild-caught larvae than if laboratory conditions were set to optimize larval growth at higher, but unnatural, temperatures.

It was also possible that feeding influenced the onset of daily deposition. The lake herring I used for otolith analysis began feeding 14 – 19 days after hatching. This first feeding age is typical for lake herring in nature (Pritchard 1930, Savino and Hudson 1995), although feeding may begin as early as at hatching (John and Hasler 1956, Selgeby et al. 1994). The lab-reared lake herring were given enough food, with some remaining in the rearing stream, so that their guts always contained food between feedings. Growth rates within the lab were also comparable to what Rice et al. (1985) observed for their lab-reared bloater. Therefore, it is unlikely that lake herring exhibited a delayed onset of daily deposition in the laboratory because of unnatural or substandard feeding conditions.

In conclusion, otolith analysis can be used to age larval lake herring from approximately the time they absorb their yolks. The accuracy of aging, however, is dependent on larval growth rates. Further studies using electron microscopy will be needed to determine if daily deposition ceases at reduced growth rates (e.g., Klink and Eckmann 1992), or if daily increments continue to be deposited but are too narrow to be discernable with light microscopy (Campana and Neilson 1985). If daily increments are still deposited, electron microscopy could greatly improve estimates of larval age. The otolith size to fish size relationship for lake herring varied with growth rate, and thus back-calculating growth will require a model that accounts for the growth rate effect. Otolith increment patterns may also prove useful in tracking environmental changes larvae experience (e.g., Rice et al. 1987, Eckmann and Pusch 1989). For lake herring in particular, shifts in increment width and contrast may signify shifts in temperature or feeding success, and the formation of accessory check marks may signify sudden decreases in temperature. However, further studies will be needed to determine the extent of a temperature decrease necessary to induce a check mark and to determine what other factors can induce similar check marks. In general, otolith analysis has potential to improve our understanding of the dynamics of early life survival and recruitment in lake herring by providing a method that can be used to track larval movements with age distributions and increment patterns, as well as determine the favorability of different habitats with estimated larval growth rates.

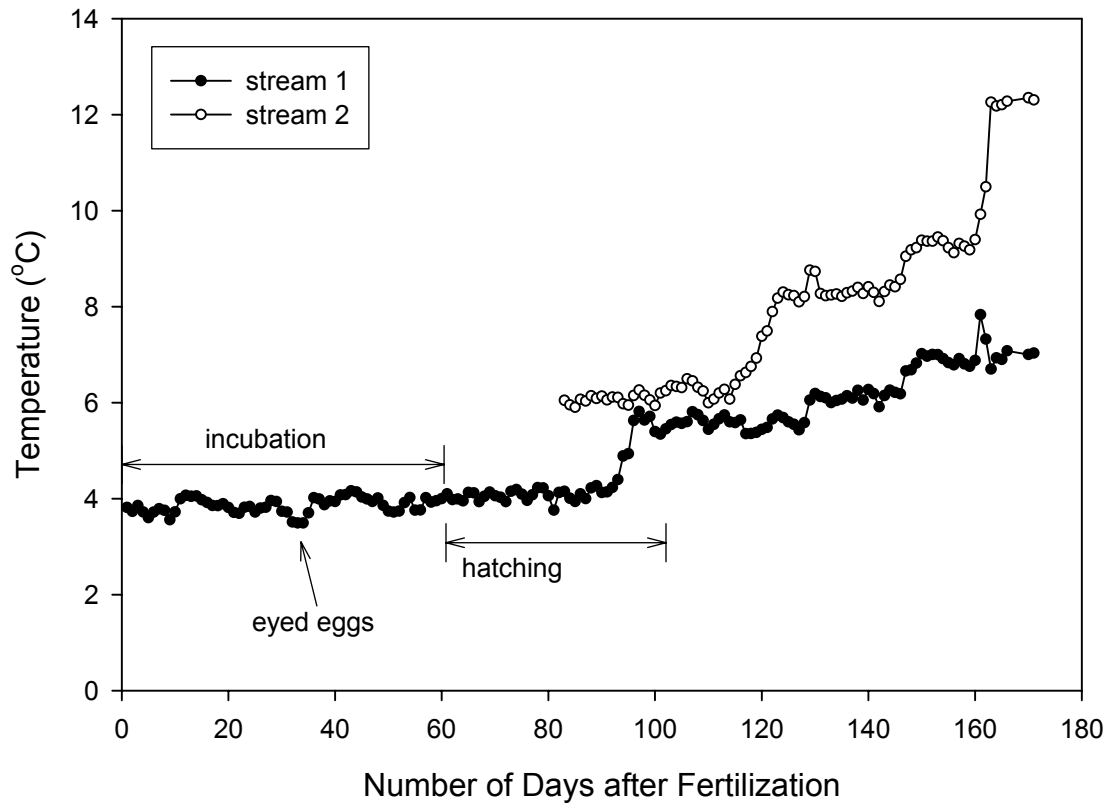


Figure 3-1. Water temperatures in the two laboratory streams in which lake herring were reared from eggs. Eggs were incubated in stream 1 and larvae were transferred to a separate nursery basket in either stream upon hatching. Water temperatures were increased periodically from the end of the hatching period.

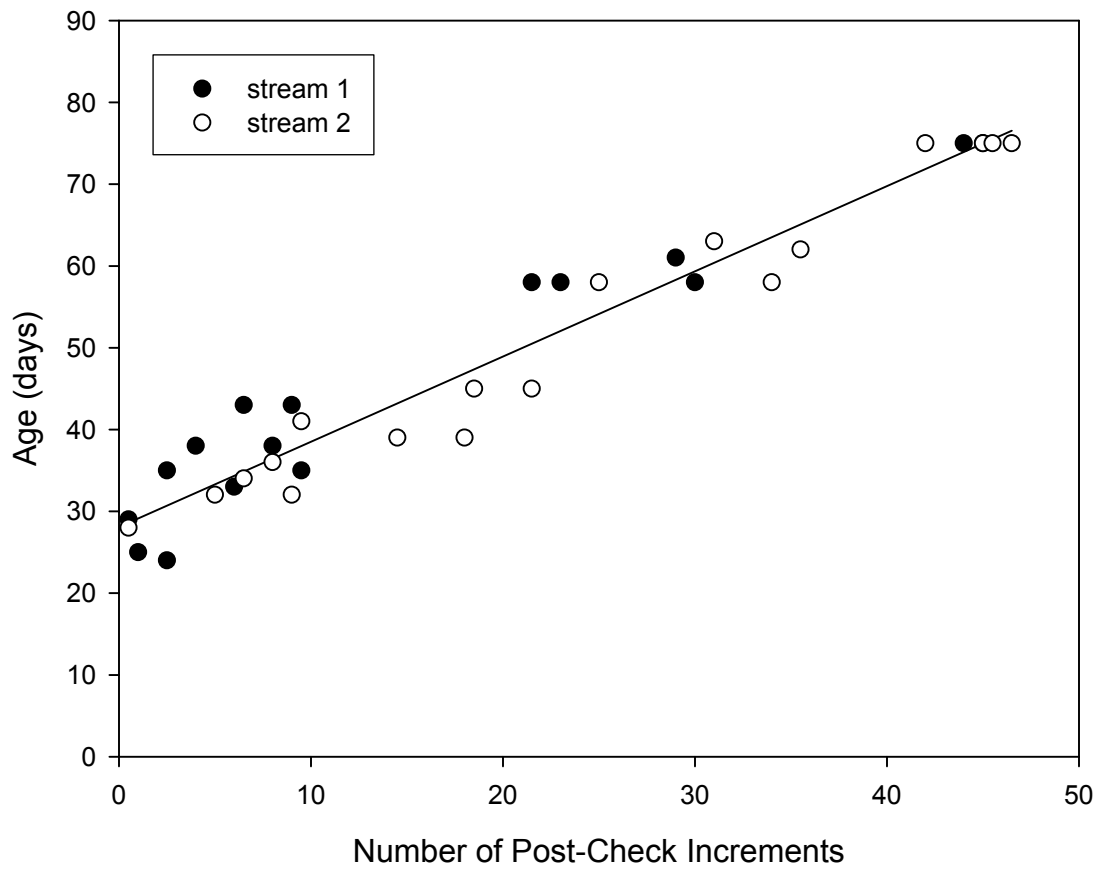


Figure 3-2. Relationship between age and number of otolith increments exterior to a check mark for larval lake herring reared in two laboratory streams that differed in water temperature.

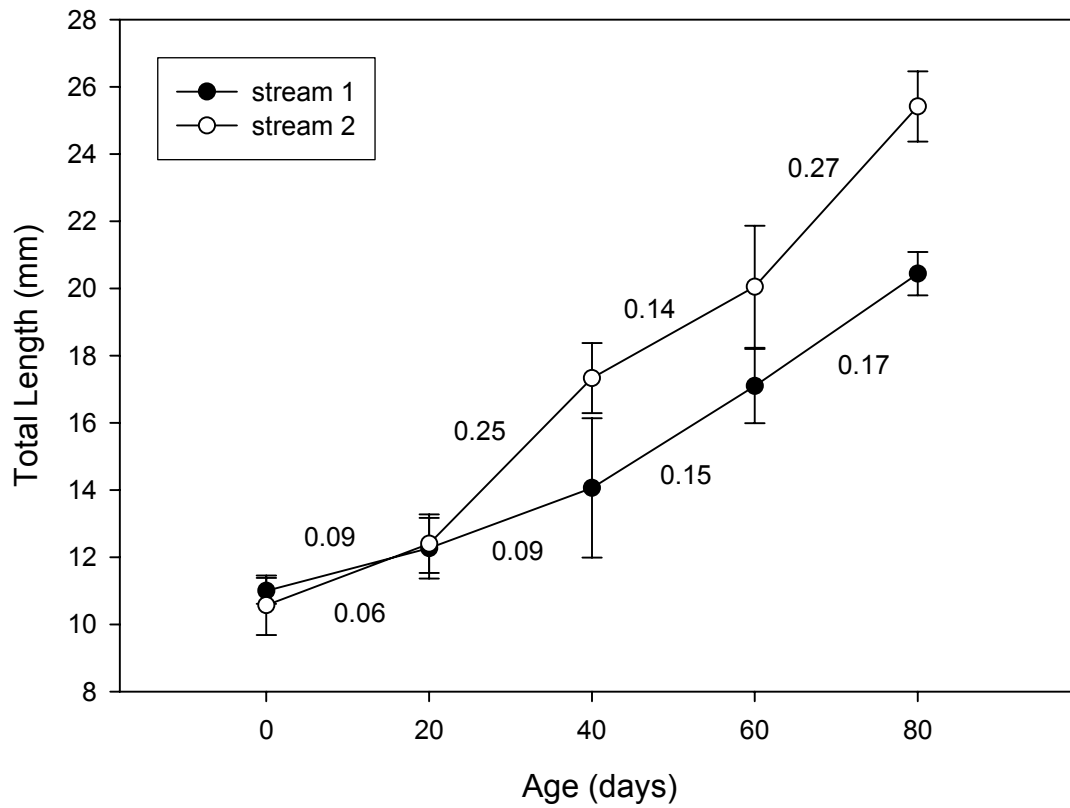


Figure 3-3. Growth of larval lake herring reared in two laboratory streams that differed in water temperature. Plots are of means \pm SD, where each mean represents data within \pm 5 days of the labeled age. Numbers between adjacent means are average daily growth rates (mm/day). Sample sizes for each mean ranged from 3 to 68 larvae. These data include larvae additional to those examined for otolith validation.

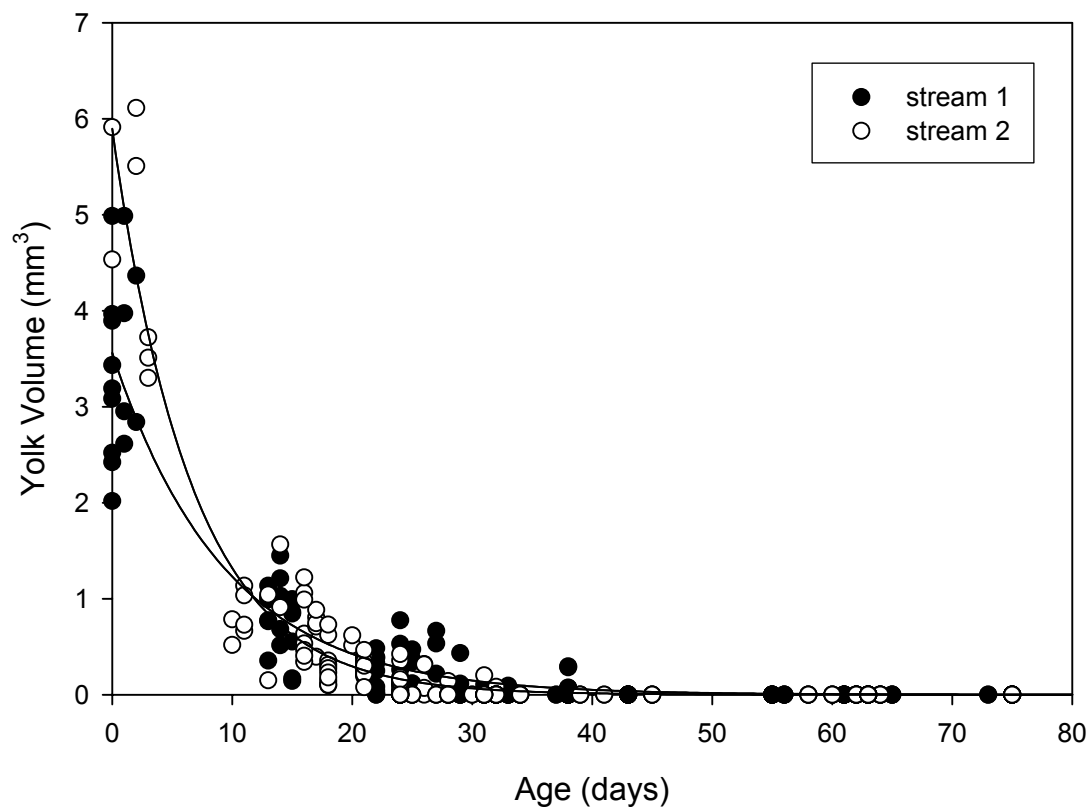


Figure 3-4. Yolk depletion of larval lake herring reared in two laboratory streams that differed in water temperature. These data include larvae additional to those examined for otolith validation.

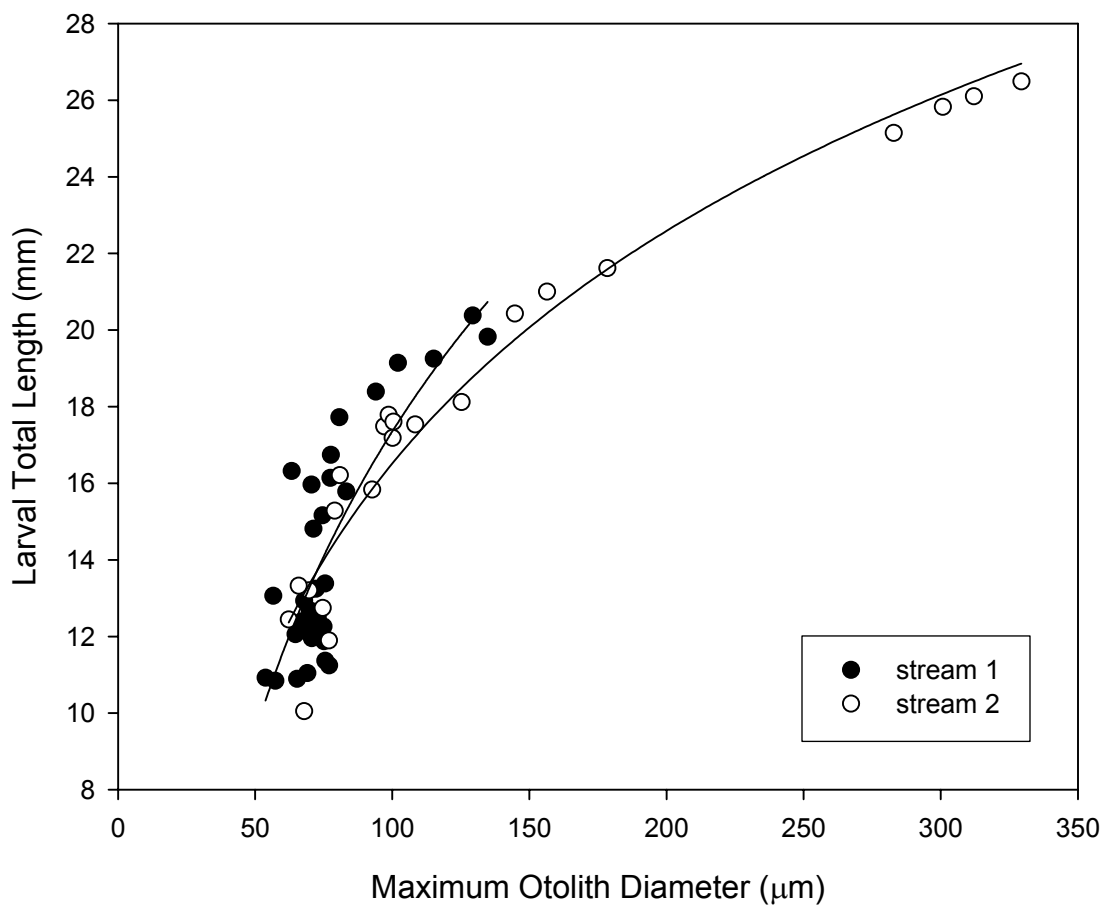
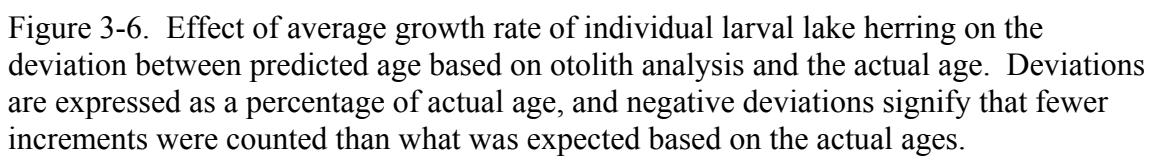


Figure 3-5. Relationship between larval total length and maximum otolith diameter for lake herring reared in two laboratory streams that differed in water temperature.



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CHAPTER 4

Transport and Growth of Larval Lake Herring (*Coregonus artedii*) in the Keweenaw Current Region of Lake Superior

ABSTRACT

Larval lake herring were sampled from Lake Superior off the western coast of the Keweenaw Peninsula to determine if the Keweenaw Current influences their distribution and growth. Larval net tows were collected from transects at Ontonagon and Houghton, from 0.1 – 17 km from shore, during April – June 2000. Otolith analysis was used to estimate ages, from which hatch dates and growth rates were calculated. Lake herring tended to be slightly more abundant, larger, and older at inshore locations, but there was also a dense peak (up to 884 larvae/1000 m³) of younger larvae (mean age of 30 days) far offshore (7 – 13 km) at Ontonagon on 21 May. Later hatched larvae first appeared offshore at Ontonagon, before subsequently being encountered at inshore locations at both Ontonagon and Houghton. During this time, earlier hatched larvae disappeared from the previously-occupied inshore locations. This progressive pattern followed what would be expected if larvae were being transported by prevailing currents from the more productive spawning regions in western Lake Superior. Estimated growth rates were higher for later hatched larvae (0.22 compared to 0.12 mm/day), and were suppressed at offshore locations at Houghton compared to elsewhere (0.13 compared to 0.17 mm/day). Differences in surface water temperatures partly explained why growth decreased with distance from shore at Houghton, but not at Ontonagon, with temperatures at Ontonagon apparently being mostly above a threshold (8 °C) beyond which temperature did not limit growth. These results indicate that lake herring larvae may be transported great distances

from spawning concentrations by longshore currents, and the temperature regime of the location they settle into may largely control their growth.

INTRODUCTION

In Lake Superior, commercial yields were historically dominated by lake herring (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), and lake trout (*Salvelinus namaycush*), with lake herring contributing nearly 75% of the total yield by weight during its peak harvest year of 1941 (Lawrie and Rahrer 1973). In the 1950s, lake trout and lake whitefish yields declined precipitously shortly after the predatory sea lamprey (*Petromyzon marinus*) invaded Lake Superior (Smith 1968, Lawrie 1978). Lake herring followed with a precipitous decline in the 1960s, most likely resulting from sequential overfishing of discrete stocks (Lawrie and Rahrer 1973, Selgeby 1982). With harvest regulations, a sea lamprey control program, and extensive stocking from the 1950s, lake trout stocks have been recovering and are now approaching historic levels (Hansen et al. 1995, Bronte et al. 2003). Lake whitefish stocks have also been recovering (Bronte et al. 2003), but the recovery of lake herring in Lake Superior has been slow and largely inhibited by highly variable recruitment (Bronte et al. 2003, Hoff 2004), even after fishing pressures have been substantially relaxed since the early 1970s (Lawrie 1978, MacCallum and Selgeby 1987). Lake herring historically dominated commercial harvests within the other Great Lakes as well (Smith 1968), but currently, only Lake Superior, the St. Mary's River, and northern Lake Huron contain stocks substantial enough to support commercial or sport fisheries (Fleischer 1992).

Recruitment failures of lake herring in Lake Superior underscore the importance of understanding the dynamics of early life survival in fishes. In general, starvation and

predation are the two major causes of mortality among larval fishes (Houde 1987, Cowan and Shaw 2002). For lake herring in particular (John and Hasler 1956), as well as for other coregonids (Rice et al. 1987, Dabrowski 1989), starvation is thought to be inconsequential as a direct cause of mortality, because their larvae can survive protracted periods without food. Alternatively, the accidentally-introduced rainbow smelt (*Osmerus mordax*) was implicated in the widespread lake herring declines in the upper Great Lakes because of inverse correlations in their abundances (Smith 1972, Christie 1974).

However, for Lake Superior, Selgeby et al. (1978) concluded that rainbow smelt predation on larval lake herring was not significant enough to be suppressing lake herring stocks in Black Bay (Ontario) and in the Apostle Islands region (Wisconsin). There was also no evidence of food competition between larval lake herring and rainbow smelt in these regions because of either diet or spatial separation (Selgeby et al. 1994).

Furthermore, lake herring recruitment failures continue to occur even after rainbow smelt numbers declined and remained low since the early 1980s (Bronte et al. 2003). However, rainbow smelt may still be influential—Cox and Kitchell (2004), using an ecosystem model based on nearly a century's worth of harvest and survey data, concluded that rainbow smelt was more important in limiting lake herring recruitment than lake trout, the primary native predator of lake herring.

Lake herring recruitment appears to be controlled by a combination of biotic and abiotic factors. Within U.S. waters of Lake Superior, Kinnunen (1997) found that the spatial abundance of yearlings was positively correlated with surface water temperatures during their first two months of life; however, temperature did not explain annual fluctuations in yearling abundance. Annual fluctuations were greater than spatial

variations (Kinnunen 1997), as evident by recruitment success tending to be synchronized among different stocks across the lake independent of stock size (Bronte et al. 2003). In Wisconsin waters of Lake Superior, Hoff (2004) concluded that recruitment from the mid 1980s to late 1990s was negatively controlled by slimy sculpin (*Cottus cognatus*) predation on eggs, lake trout predation on young-of-the-year, and adult lake herring predation on their young, which was reduced by higher wind speeds during the month of hatching.

Hoff's (2004) results imply that wind-driven currents may be important for reducing predation by dispersing larvae away from spawning concentrations. The extent to which lake herring disperse from spawning locations is not clearly known, but it is believed that lake herring are not strong dispersers (VanOosten 1929, Smith 1956), and stocks can be distinguished by otolith microchemistry (Bronte et al. 1996), growth rate (Coffin et al. 2003), parasite community (Hoff et al. 1997), and whole-body morphometrics (Hoff 2004). However, lake herring stocks could not be differentiated genetically (Todd 1981, Synder et al. 1992). Stocks could develop phenotypic differences without genetic differences if genes are mixed among adjacent stocks by dispersing larvae before juveniles and adults develop phenotypic differences by limiting their schooling range to a particular geographic area. Dispersal, especially by currents, would force larvae to encounter varying conditions that could either favorably or adversely influence growth and survival. Lake herring larvae may also have the ability to select a nursery habitat among different locations encountered while dispersing, and correlations between abundance and habitat conditions may result from habitat selection rather than differential mortality. However, it is not known in what ways lake herring

can actively face the challenges of early survival, nor is it known to what extent they can select particular habitats despite the flow of currents.

The general circulation pattern of Lake Superior is counterclockwise, with the Keweenaw Current being a particularly strong current that flows northeasterly along the western coast of the Keweenaw Peninsula, Michigan (Lam 1978, Beletsky et al. 1999). Velocities of this current can exceed 75 cm/s in July, 0.7 km from shore near Eagle Harbor, and 8 m beneath the surface (Niebauer et al. 1977). Water currents in Lake Superior have potential to transport larvae far from their hatching location and expose them to varying abiotic conditions and biotic interactions. The objective of this study was to determine how transport within the Keweenaw Current region of Lake Superior affects larval lake herring distribution and growth, as it may relate to recruitment dynamics.

METHODS

Field Sampling

Larval lake herring were sampled from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan during six cruises from April to June 2000. A dual 70-cm diameter, 500- μ m mesh bongo-type net was employed, providing two replicate samples per tow. A side-mounted flow meter recorded the volume of water filtered for each tow. Four transects (Ontonagon North and South, and Houghton North and South) that ran perpendicular to the western coast of the Keweenaw Peninsula, Michigan were sampled at 4 – 9 distances from shore ranging from 0.1 – 17 km (Figure 4-1). One surface tow (from the top 1 m of water) was collected from each distance, virtually all during daylight (21 May Houghton was the exception). The net was towed parallel with

shore (except for the first sampling cruise during which it was towed perpendicular to shore), and horizontally through the water at a speed of 0.77 – 1.03 m/s (1.5 – 2.0 knots) for 15 min, thus filtering on average (\pm SD) 217.3 (\pm 76.3) m³ of water.

A total of 79 tows (158 samples) were collected—28 tows from the Ontonagon transects and 51 tows from the Houghton transects. For preservation, a turkey baster with its opening covered with 500 μ m mesh was used to remove most of the water from the samples before adding 95% ethanol. Ethanol was used so otoliths would be preserved for otolith analysis. A Sea-Bird Electronics CTD (SBE-25) or a Hydrolab® MiniSoude® was used to measure water temperatures at the start of each tow, and sometimes from additional distances from shore.

Laboratory Measurements and Otolith Analysis

To determine spatial patterns in growth and development, several morphological characteristics of larval lake herring were measured. In the laboratory, lake herring were first separated from the samples and stored in 70% ethanol. Total length of all larvae was measured to the nearest 0.05 mm with a dial caliper. For a subsample of five randomly selected larvae per sample, or the entire sample when five or less larvae were captured, caudal fin rays were counted, and yolk depth and length were measured to the nearest 0.01 mm at 0.9 – 2.0 times magnification using a dissecting microscope equipped with an ocular micrometer. As an indicator of energy reserves, yolk measurements were used to calculate yolk-sac volume, assuming a prolate spheroid with length as the longer axis and depth and girth as the shorter and equal axes (Luczynski et al. 1986). The number of caudal fin rays was used as an indicator of developmental stage, knowing that larvae hatch with no fin rays and progressively develop up to 28 fin rays when juveniles

(Hinrichs and Brooke 1975). Total length (TL) and yolk volume (YV) were corrected for preservation-induced shrinkage (for preservation in 70% ethanol) with linear regressions developed from laboratory-reared and preserved lake herring: $live\ TL = 1.20 + 0.91 * preserved\ TL$ and $live\ YV = 0.50 + 0.96 * preserved\ YV$ (see Appendix A).

Ages in days of the five randomly selected lake herring per sample were estimated by otolith analysis following the procedures of a joint otolith validation study (see Chapter 3). Left and right sagittae were removed with needles under a dissecting microscope equipped with a polarizing filter. Dissected otoliths were then transferred to a microscope slide and mounted concave side down with CrystalBond™ (SPI Supplies), a thermoplastic mounting medium. The number of otolith increments after check formation was counted under a compound microscope using up to 1000 times magnification, and counts from left and right sagittae were averaged for each larva. Age in days was then calculated from the number of otolith increments (RINGS) with a linear regression developed from laboratory-reared lake herring: $AGE = 28.09 + 1.04 * RINGS$ (see Chapter 3). Age was further used to calculate hatch dates by subtracting age from the date of capture.

In order to estimate the growth rate for the last five days before capture using the biological intercept procedure (Campana 1990, Campana and Jones 1992), first, a linear relationship between fish length and otolith size had to be established, and fish length and otolith size at the biological intercept had to be determined. Otolith radius was measured as a metric of otolith size. Because lake herring otoliths form from multiple primordia (see Chapter 3 and Appendix C), and having multiple primordia increases the variability in otolith nuclear dimension (Neilson et al. 1985), the radius was measured from the

posterior edge to the check mark, and thus the nuclear region was excluded. Otoliths were measured from digitally-captured images with a computer image-analysis program (SigmaScan Pro 5; SPSS Inc.), and measurements from left and right sagittae were averaged. The total length (TL) to otolith radius (RA) relationship was curvilinear, so otolith radius was square-root transformed (sqrt RA) to produce a linear relationship: $TL = 8.8 + 1.31 * \sqrt{RA}$ ($n = 111$, $r^2 = 0.80$, $P < 0.0001$). In this case, the biological intercept represented the point of check formation, during which the otolith radius would be zero. Larval total length when there was a 50% likelihood that a larva contained a check mark was estimated to be 11.04 mm (with 95% Fieller bounds of [10.64, 11.32]) with probit analysis ($n = 232$, $P < 0.0001$) (Tabachnick and Fidell 1996). Fish length at previous age a could now be estimated with the following equation: $L_a = L_c + (O_a - O_c)(L_c - L_o)(O_c - O_o)^{-1}$, where L_a is fish length at previous age a , O_a is otolith size at previous age a , L_c is fish length at capture, O_c is otolith size at capture, L_o is fish length at the biological intercept, and O_o is otolith size at the biological intercept (Campana 1990). Using this equation, larval length at five days before capture was predicted with square-root transformed radial length that excluded the last five increments. Finally, increase in total length during the last five days was expressed as a daily growth rate. For comparison, the average lifetime growth rate was also calculated for groups of larvae with length-to-age linear regressions, wherein the slope represents the daily growth rate. These two measures of growth not only differ in temporal coverage (lifetime vs. last five days), but also in the pool of larvae that could be employed. For recent growth, larvae had to have at least five increments, while for length-to-age growth, larvae only had to have a check mark.

Data Analysis

Of the six sampling cruises, four (15 – 17 May, 21 May, 30 May, and 19 – 20 June) captured sufficient numbers of larval lake herring for statistical analyses. Preliminary analyses did not show statistical differences between the north and south transects of either Ontonagon or Houghton. Accordingly, data from the two transects were pooled into a “region” for Ontonagon and a “region” for Houghton for all subsequent analyses. For some analyses, it was necessary to pool adjacent distances from shore into three transect divisions (0.1 – 2 km, 3 – 5 km, and 7 – 17 km) to increase sample sizes. These divisions spanned different ranges so that there would be greater spatial resolution nearer to shore.

Offshore trends in density were modeled separately for each region and cruise with linear or nonlinear regressions. Spatial differences in larval characteristics were assessed separately for each cruise with multiple linear regressions for cruises with both regions sampled, and simple linear regressions for cruises with only one region sampled.

For 26% of the larvae for which otoliths were examined, age could not be estimated with otolith analysis because they had yet to produce a check mark. For these larvae, age was estimated with age-to-length linear regressions generated with data from the same cruise, region, and transect division. Although these estimated ages were probably not as accurate as ages estimated directly by otolith analysis, it was important to incorporate the younger larvae into calculations of mean age so that these means would not be biased toward the older larvae.

Hatch dates were not compared among distances from shore for each region and cruise, as described previously for the other metrics, because hatch dates are linearly

dependent upon capture date (cruise) and age. Such an analysis would only show transposed results from that of age. Instead, hatch dates were compared among cruises, separately by region, with single-factor ANOVA, wherein all distances from shore were pooled. However, because not all larvae of large samples were aged with otolith analysis, larger samples would be under-represented in pooled means if subsample means are weighted by their subsample sizes. Accordingly, subsample sizes were adjusted so that they were the same proportions of their total subsample size as capture numbers (from which subsamples were drawn) were to their total sample size, while still maintaining the same total subsample size. In this manner, pooled means should reflect pooled populations and will not be biased by subsample sizes being unequally proportional to capture numbers. Hatch dates were also grouped into three hatch periods (early: 3/22 – 4/8, bulk: 4/9 – 4/26, and late: 4/27 – 5/17) for some analyses. These categories comprised an estimated 9, 81, and 10%, respectively, of all captured larvae.

For each cruise, the movement or transport of larvae was assessed by graphically displaying the percentages of larvae from each hatch period for each region, transect division, and sampling cruise. This allowed for the assessment of where recently hatched larvae first appeared and where earlier hatched larvae last appeared, as well as the spatial and temporal progression of recently hatched larvae replacing earlier hatched larvae.

Growth rates estimated by length-to-age relationships were analyzed for spatial and hatch date differences with general linear models (GLM) (Neter et al. 1996). Spatial differences were assessed by determining if the length-to-age slope varied with region and distance from shore, and hatch date differences were assessed by determining if the slope varied with hatch period. Spatial differences were also assessed for back-calculated

recent growth by determining if the growth rate varied with region or distance from shore (Neter et al. 1996). Age needed to be included as an independent variable in this model as well, because growth rates are typically dependent on age, and mean ages can vary spatially. Larvae for which age was estimated with total length because they were too young to age with otolith analysis were excluded from the growth rate analyses.

To determine if spatial differences in growth rates were correlated with spatial differences in temperature, growth rates were regressed on temperature for each region. Furthermore, a temperature threshold, below which temperature was proposed to inhibit growth, was estimated by dividing the dataset repeatedly by different temperatures, in 0.5 °C increments from 7 – 9 °C, instead of by region, then observing at what temperature the greatest inhibitory effect existed below it. Statistical analyses were performed with SYSTAT 10 (SPSS Inc.), except for nonlinear regression, which was performed with SigmaPlot 8 (SPSS Inc.).

RESULTS

Seasonal Occurrence of Lake Herring

The sampling season commenced before the bulk of the hatch and extended to the time when larvae became rare. During the first cruise (27 – 29 April), surface water temperatures averaged 3.1 °C (range: 2.5 – 4.5 °C) (Figure 4-2), and only two larval lake herring were captured with 20 samples (overall mean density of 2.5 larvae/1000 m³). The highest densities (overall mean density of 77.0 larvae/1000 m³) of lake herring were obtained during the second half of May, when temperatures averaged 6.0 °C (range 3.1 – 8.5 °C). Catches greatly diminished by June (overall mean density of 3.4 larvae/1000

m³), when temperatures averaged 8.2 °C (range 4.6 – 11.4 °C), although there were great spatial differences in abundance during this period.

Spatial Distribution in Temperature, Density, and Larval Size

As expected, surface water temperatures decreased with distance from shore for all cruises, and the shallower waters at Ontonagon fostered higher temperatures than at Houghton from 21 May onward (Figure 4-3). Surface waters of less than 4 °C were still observed at Houghton on 21 May from 5 km outward and on 30 May from 7 km outward, but not at Ontonagon up to 13 km from shore on 21 May.

By the second cruise, 15 – 17 May, lake herring catches were sufficient for statistical analyses. Lake herring densities during this cruise decreased linearly with distance from shore at Ontonagon (linear regression, $n = 8$, $r^2 = 0.79$, $P = 0.003$), but at Houghton, offshore densities most closely followed a log normal trend (log normal regression, $n = 28$, $r^2 = 0.45$, $P = 0.001$) because of zero catches at 0.25 km from shore (Figure 4-3). Total lengths of larvae (GLM, $n = 187$, $r^2 = 0.07$), however, did not differ with region, ($P = 0.06$), distance from shore ($P = 0.20$), or their interaction ($P = 0.90$) (Figure 4-3).

During the next cruise, 21 May, we sampled to a much farther offshore extent at both Ontonagon and Houghton than previously. At Ontonagon, there were greater densities inshore than offshore up to 5 km from shore, but beyond that, we encountered a high density patch of lake herring extending to at least 13 km from shore (Figure 4-3). Therefore, the offshore trend in density closely followed a quadratic equation (quadratic regression, $n = 24$, $r^2 = 0.97$, $P < 0.0001$). At Houghton, the trend was similarly quadratic (quadratic regression, $n = 16$, $r^2 = 0.52$, $P = 0.009$), although densities were

substantially lower, which may have resulted, in part, from these samples being collected at night. In contrast to the previous cruise, total lengths of larvae (GLM, $n = 1035$, $r^2 = 0.21$) now decreased with distance from shore ($P < 0.0001$), but did not differ between regions ($P = 0.66$) or for their interaction ($P = 0.81$) (Figure 4-3).

On 30 May, only Houghton was sampled, and sampling extended to the same offshore extent (7 km) as for the 15 – 17 May cruise. By this time, densities have greatly diminished, yet interestingly, they exhibited a similar log normal trend as previously (log normal regression, $n = 18$, $r^2 = 0.54$, $P = 0.003$), with no larvae captured at 0.5 km from shore. Total length also did not differ with offshore distance (linear regression, $n = 21$, $r^2 = 0.003$, $P = 0.81$) (Figure 4-3).

On 5 – 7 June, sampling was conducted only at Houghton, but only seven lake herring were captured in 26 samples, so these data are not presented. On the last cruise, 19 – 20 June, larvae were captured only at Ontonagon. The distribution of these larvae, were scattered, with peaks at 0.5 – 1.0 km and at 9 km from shore (Figure 4-3). For total length, a decreasing trend with distance from shore was still evident (linear regression, $n = 25$, $r^2 = 0.16$, $P = 0.04$) (Figure 4-3).

Spatial Distribution in Age, Yolk Volume, and Number of Caudal Fin Rays

Estimated ages decreased with distance from shore on 21 May (GLM, $n = 116$, $r^2 = 0.24$, $P < 0.0001$ for distance from shore, $P = 0.71$ for region, $P = 0.22$ for distance from shore by region interaction) and 19 – 20 June (multiple regression, $n = 22$, $r^2 = 0.20$, $P = 0.04$) (Figure 4-4), the two cruises for which total length decreased with distance from shore. For the two cruises during which total length did not differ with distance from shore, age also did not differ with distance from shore (15 – 17 May: GLM, $n = 89$,

$r^2 = 0.04$, $P = 0.81$ for distance from shore, $P = 0.23$ for region, $P = 0.91$ for distance from shore by region interaction) (30 May: linear regression, $n = 20$, $r^2 = 0.02$, $P = 0.51$) (Figure 4-4).

The offshore distribution for yolk volume and number of caudal fin rays support the trends observed for age. When age decreased with distance from shore on 21 May, there was a tendency for offshore larvae to have greater yolk volumes (GLM, $n = 129$, $r^2 = 0.13$, $P = 0.001$ for distance from shore, $P = 0.41$ for region, $P = 0.16$ for distance from shore by region interaction) and fewer caudal fin rays (GLM, $n = 129$, $r^2 = 0.12$, $P = 0.0004$ for distance from shore, $P = 0.96$ for region, $P = 0.32$ for distance from shore by region interaction) (Figure 4-4). The same was also true for the other cruise with an offshore age trend, 19 -20 June, for number of caudal fin rays (linear regression, $n = 21$, $r^2 = 0.19$, $P = 0.05$), but not for yolk volume (linear regression, $n = 22$, $r^2 = 0.04$, $P = 0.36$), although very few larvae still had yolks at this point in the season. Conversely, cruises that did not show an offshore trend for age, also did not show an offshore trend for yolk volume (15 – 17 May: GLM, $n = 99$, $r^2 = 0.04$, $P = 0.23$ for distance from shore, $P = 0.10$ for region, $P = 0.09$ for distance from shore by region interaction) (30 May: linear regression, $n = 20$, $r^2 = 0.04$, $P = 0.41$) or number of caudal fin rays (15 – 17 May: GLM, $n = 98$, $r^2 = 0.06$, $P = 0.46$ for distance from shore, $P = 0.26$ for region, $P = 0.95$ for distance from shore by region interaction) (30 May: linear regression, $n = 20$, $r^2 = 0.01$, $P = 0.62$) (Figure 4-4).

Hatching Period of Lake Herring

Captured lake herring were estimated to have hatched from 22 March to 17 May, with the bulk of the hatch occurring from mid-April to early May. Mean hatch dates

increased with cruise for both Ontonagon (single-factor ANOVA, $n = 149$, $r^2 = 0.43$, $P < 0.0001$) and Houghton (single-factor ANOVA, $n = 98$, $r^2 = 0.36$, $P < 0.0001$), whereby, for both regions, each cruise was statistically different from each other (Tukey test, least significant comparison, $P < 0.001$ for Ontonagon, $P < 0.05$ for Houghton) (Figure 4-5). Correspondingly, the ranges of hatch dates tended to be shifted toward more recent dates with subsequent cruises (Figure 4-5), meaning that earlier hatched larvae did not exist in later catches, and later hatched larvae did not exist in earlier catches, even when most of later hatched larvae hatched prior to the earlier sampling dates.

Larval Transport

Both the high concentration of younger larvae far offshore at Ontonagon and the increase in hatch dates with subsequent sampling cruises could have resulted from larvae being transported through the study region by prevailing currents. Further evidence for larval transport was investigated with plots of the percentages of larvae from different hatch periods (early, bulk, and late hatch) for each transect division (0.1 – 2 km, 3 – 5 km, and 7 – 17 km from shore), region (Ontonagon and Houghton), and sampling cruise (Figure 4-6). Here we see that during 15 – 17 May, early hatch larvae comprised a small percentage of the inshore catch and late hatch larvae were not present. During the next cruise, 21 May, early hatch larvae were still concentrated inshore, and now few late hatch larvae were encountered offshore, but only at Ontonagon. Late hatch larvae were encountered at Houghton on 30 May, and by 19 – 20 June, late hatch larvae comprised approximately half of the catch at Ontonagon, with early hatch larvae being completely absent in the samples. These patterns show that larvae did not arrive and depart the study region from random locations, but rather followed the flow of the Keweenaw Current.

Spatial and Hatch Date Differences in Growth Rates

A length-to-age linear regression for all captured larvae, showed an average (\pm SE) growth rate of 0.18 (\pm 0.008) mm per day (Figure 4-7). First, this overall growth rate was separated by larvae of different hatch periods to determine if later hatched larvae grew faster because they hatched into, and spend more of their lives in, warmer waters. A statistical model for total length as the dependent variable, with age, hatch period, and their interaction as independent variables, showed that the length-to-age relationship was statistically affected by hatch period (GLM, $n = 168$, $r^2 = 0.77$, $P = 0.03$ for hatch period by age interaction). By estimating a separate linear regression for each hatch period, we see that the slope (growth rate) does in fact increase with subsequent hatch periods, as expected (Figure 4-8), but only slopes for the early and late hatch periods were statistically different from each other (Tukey test, $P < 0.01$).

Second, the overall grow rate was separated by larvae of different spatial locations (regions and distances from shore) to determine if warmer waters inshore, especially at Ontonagon, fostered faster growth. A statistical model (GLM, $n = 168$, $r^2 = 0.78$) for total length as the dependent variable, with age, region, distance from shore, and all interactions as independent variables, showed that the length-to-age relationship was statistically affected by distance from shore ($P = 0.02$ for distance from shore by age interaction) but not by region ($P = 0.19$ for region by age interaction), however, the effect with distance from shore differed by region ($P = 0.01$ for region by distance from shore by age interaction). Growth rates were calculated directly from the data as slopes of separate linear regressions for regions, with adjacent distances from shore pooled to achieve sufficient sample sizes (Figure 4-9). Estimated slopes (growth rates) decreased with distance from shore at Houghton, but not at Ontonagon (Figure 4-9). Furthermore,

when estimating models separately by region, an effect for distance from shore occurred at Houghton (multiple regression, $n = 84$, $r^2 = 0.67$, $b = -0.036$ and $P = 0.006$ for distance from shore by age interaction), but not at Ontonagon (multiple regression, $n = 84$, $r^2 = 0.79$, $b = 0.00024$ and $P = 0.93$ for distance from shore by age interaction).

Spatial differences in growth can similarly be assessed using estimated growth rates for the last 5 days before capture. This measure of growth more likely represents the habitat a larva was captured from, considering that lake herring have the potential to travel great distances during their early lives. A similar statistical model (GLM, $n = 88$, $r^2 = 0.18$), including age as a covariate, showed an effect for distance from shore ($P = 0.04$) and not for region ($P = 0.11$), however, region interacted with distance from shore ($P = 0.04$), as would be expected based on the previous growth results. A similar trend was observed graphically with plotted mean growth rates (Figure 4-9), in which rates of recent growth decreased with distance from shore at Houghton, but not at Ontonagon. Separate analyses by region confirm that the recent growth rate was statistically affected by distance from shore at Houghton (multiple regression, $n = 37$, $r^2 = 0.24$, $b = -0.024$ and $P = 0.03$ for distance from shore), but not at Ontonagon (multiple regression, $n = 51$, $r^2 = 0.13$, $b = -0.00002$ and $P = 0.99$ for distance from shore).

Relationship between Growth Rates and Water Temperatures

The spatial trend in growth rates at Houghton intuitively followed patterns of water temperatures, but further investigation was required to explain why such a trend was not seen at Ontonagon, where water temperatures also decreased with distance from shore. By regressing the length-to-age relationship on surface water temperature instead of distance from shore, it was observed that the growth rate decreased with decreasing

temperatures more strongly at Houghton (multiple regression, $n = 84$, $r^2 = 0.65$, $b = 0.025$ and $P = 0.09$ for temperature by age interaction) than at Ontonagon (multiple regression, $n = 84$, $r^2 = 0.81$, $b = 0.017$ and $P = 0.01$ for temperature by age interaction), although strangely, the effect was more significant at Ontonagon. The same trend was observed for recent growth rates, but with less statistical significance, in which Houghton (multiple regression, $n = 37$, $r^2 = 0.15$, $b = 0.008$ and $P = 0.28$ for temperature) showed a stronger effect over Ontonagon (multiple regression, $n = 51$, $r^2 = 0.13$, $b = 0.00036$ and $P = 0.96$ for temperature). These trends can be visualized by plotting the residuals of length vs. age and recent growth rate vs. age against water temperatures, so that the data are standardized for differences in age (Figure 4-10). From this figure it can be seen that, first of all, Houghton and Ontonagon contained different ranges of temperature, and secondly, growth rate tended to decrease with temperature at the colder temperatures observed at Houghton, and was unaffected by temperature at the generally warmer temperatures observed at Ontonagon.

Finally, the dataset was divided, not by region as done previously, but by proposed threshold temperatures, below which temperature was expected to inhibit growth relative to growth above the proposed threshold. The greatest effect of temperature was below a proposed threshold of 8.5°C with the length-to-age approach to estimating growth rate (multiple regression; $n = 128$, $r^2 = 0.65$, $b = 0.027$ and $P = 0.02$ for age by temperature interaction), and below 8 °C with the back-calculated approach (multiple regression; $n = 45$, $r^2 = 0.08$, $b = 0.013$ and $P = 0.11$ for temperature) (Figure 4-11). But overall there was still great variation in growth rates at given temperatures, even after the data were standardized for differences in age.

DISCUSSION

The distribution patterns of lake herring followed what would be expected if larvae were being transported by currents from the more productive spawning regions in western Lake Superior, where spawning regions are indicated in Goodyear et al. (1982). It is also possible that some larvae originated from historic spawning grounds from within the study area, at either Ontonagon or at Houghton. It was expected that larvae would be more abundant nearer to spawning grounds and less abundant as they disperse away from them. In fact, the greatest densities were observed far offshore at Ontonagon, and Ontonagon generally had higher densities than Houghton. The high density patch encountered at 7 – 13 km from shore at Ontonagon consisted of larvae that were younger than those captured nearer to shore. However, these offshore larvae did not hatch recently, but instead averaged slightly less than 30 days of age. Therefore, even if the offshore larvae were encountered at a high concentration akin to a hatching location, these larvae also had sufficient time to travel from some distant location.

The progression of hatch dates with subsequent cruises also supports the conclusion that lake herring were transported eastward, following the general flow of currents. The lack of earlier hatched larvae in samples from later cruises can be explained by larvae migrating or being transported out of the study area, or by the following alternative mechanisms. First, because earlier hatched larvae would have to survive for a longer duration to still exist at later dates compared to recently hatched larvae, a greater cumulative mortality for earlier hatched larvae could account for their absence at later dates (Campana and Jones 1992). Second, earlier hatched larvae may have grown beyond the size range for which they are susceptible to capture with larval plankton nets (Karjalainen and Viljanen 1992). In contrast, the lack of later hatched

larvae in samples from earlier cruises can not be explained by these alternative mechanisms. The later hatched larvae would have been more susceptible to capture by plankton nets and would have undergone less cumulative mortality on earlier dates than on later dates. Therefore, the presence of later hatched larvae only on the later sampling dates, in conjunction with an increase in mean hatch date with subsequent cruises, further supports the conclusion that larvae were transported from adjacent regions. In addition, a cruise on 27 – 29 April captured only two larvae with 2715.2 m³ of water sampled even though this cruise occurred during the peak of the hatch.

The spatial patterns of larvae of different hatch periods point to offshore Ontonagon as the location where later hatched larvae first arrived into the study region. From there, they appeared to have dispersed inshore and up the Keweenaw coast to Houghton. In addition, earlier hatched larvae were concentrated inshore during earlier cruises and were rare or absent on later cruises. Therefore, it appeared that lake herring moved progressively through the study region, and by the time the later hatched larvae arrived to inshore areas, earlier hatched larvae were virtually gone.

Water currents in oceanic systems are known to be important in transporting pelagic larvae of some fishes from spawning grounds to nursery grounds (Norcross and Shaw 1984). Fishes may even be adapted to spawn at particular locations and times so to better ensure that their eggs or larvae will be successfully transported to nursery grounds (Parrish et al. 1981). Water movements on difference scales can also adversely affect larvae by transporting them to areas with low food resources or dense predators (Simpson 1987). In most freshwater lakes, however, transport of larval fishes by currents may be less important for recruitment success because small lakes usually lack strong and

predictable currents (Werner 2002, Moyle and Cech 2004). In contrast, very large lakes tend to have regular currents in the form of a gyre (Hutchinson 1957). In this respect, Lake Superior, with its large size, may behave more like an ocean than a lake, and current-driven transport of pelagic larvae may play an important role in fish recruitment. For lake herring in particular, the results of Hoff (2004) indicate that wind-driven dispersal of larvae away from spawning grounds can be important for reducing predation by adult lake herring. Their survival will then depend on the conditions they encounter while being transported and the habitat they finally settle into.

Once in the study region, lake herring tended to congregate at Ontonagon and at inshore areas at both Ontonagon and Houghton. The larvae persisted at Ontonagon later in the season than at Houghton, but if they were only drifting passively through the study region, Houghton should have contained the last of the larvae. Likewise, inshore areas contained a concentration of older larvae which unlikely would have formed and persisted if larvae were only passive drifters. They seemed to be able to remain in the study region for a longer duration when at inshore locations or at Ontonagon, where they likely avoided most of the influence of the Keweenaw Current, compared to larvae at farther distances from shore or further along the Keweenaw coast where waters deepen and the current intensifies (Niebauer et al. 1977, Green and Terrell 1978). In fact, larvae at Houghton on 5 – 7 June were rarely encountered, despite extensive sampling from both north and south transects from distances of 0.5 – 7.0 km from shore, and during the last cruise, Houghton samples was completely devoid of lake herring. Therefore, after a period of current-driven transport, lake herring settled into nearshore areas where they

probably had more control of which habitat to occupy, and more larvae remained near Ontonagon.

Larval growth rates were estimated and compared in order to determine if larvae received some benefit that would have attracted them to inshore locations rather than remain at offshore locations, and to maintain a position at Ontonagon rather than continue drifting along the coast to Houghton or beyond. It was expected that growth would be higher in the warmer inshore waters, especially at Ontonagon. The morphological characteristics alone indicated that inshore captured larvae were larger than larvae caught at farther distances from shore, and sampling in this study region during previous years revealed a similar trend (Oyadomari and Auer 2004). But age then explained much of this difference, with inshore larvae being correspondingly older. When analyzing for differences in growth rates, while accounting for the variation in age, only the Houghton catches displayed an offshore trend, in which growth was slower at farther distances from shore. The growth rates of the offshore larvae at Houghton appeared to have been suppressed from what was achieved at Ontonagon. The difference between regions in the offshore relationship with growth rate could be explained by temperature differences, whereby water temperatures at Ontonagon were usually high enough not to limit growth. At these higher temperatures, another factor, most likely food resources, apparently limited growth; however, there was still great variation in the trends. This variation probably resulted from the fact that larvae were moving, and the temperature at which they were captured likely did not represent the temperature they experienced for most of their lives. Temperature could also explain the increase in growth rate with later hatch

dates. Because of seasonal warming, larvae that hatched later would have spent less time in colder waters.

Otolith analysis provided estimates of hatch dates and growth rates directly from age, which was not previously feasible for lake herring without a validation study (Chapter 3). The estimated hatch dates, primarily from mid-April – early May, corresponded to what was observed previously with distribution data from western Lake Superior (Hatch and Underhill 1988) and from the St. Marys River (Jude et al. 1998). Estimated mean growth rates of 0.12 – 0.22 mm/day were comparable to a mean estimate of 0.27 mm/day for the St. Marys River (Jude et al. 1998), but were lower than an estimate of 0.69 mm/day for western Lake Superior by Hatch and Underhill (1988), although they believed this was an overestimate.

Water temperature has been shown to be important for growth in other *Coregonus* spp. as well. Early growth of the whitefish *C. lavaretus* from Lake Constance (Germany) closely tracked spring warming and not zooplankton abundance (Rey and Eckmann 1989, Eckmann and Pusch 1989), and subsequent year-class strength was associated with early thermal stratification (Eckmann et al. 1988). Earlier hatched bloater (*C. hoyi*) larvae from Lake Michigan grew slower, and consequently, suffered greater mortality, probably due to increased predation (Rice et al. 1987).

Temperature appears to be important for growth in lake herring, as well as for other *Coregonus* spp. In the laboratory, lake herring growth was observed to increase with temperature in the range 3 – 18 °C, however, mortality started to increase substantially from approximately 13 °C (McCormick et al. 1971). The final preferendum, preferred temperatures given an infinite temperature range and an unlimited acclimation

duration, for lake herring is 9 – 14 °C (Wismer and Christie 1987), thus, it was reasonable to find that temperature inhibited growth below 8 °C. Higher temperatures may not have continued to foster faster growth in the field because of an increased metabolic demand. Larvae at higher temperatures would have to consume more food to match the same growth rate at a lower temperature (Houde 1989). Therefore, a higher growth rate at higher temperatures can only be obtained with an adequate food supply. In addition, continued seasonal warming is what probably drives larvae away from nearshore areas later in the season, in late June to early July (Clady 1976, Hatch and Underhill 1988, Oyadomari and Auer 2004).

With faster growth within a suitable habitat, lake herring larvae would have a greater probability of survival. In general, larvae that obtain larger sizes have greater swimming abilities, are more successful at feeding, are more resistant to starvation, and are less susceptible to predators (Miller et al. 1988, Jones 2002). Larger-sized lake herring in particular have been shown to better survive a simulated winter (Pangle et al. 2004). Because of the lack of a sufficient number of older larvae, size-selective mortality could not be evaluated with otolith analysis for lake herring, but mortality in many species has commonly been shown, with otolith analysis, to be size-dependent, whereby smaller larvae or juveniles suffer greater mortality (e.g., Post and Prankevicius 1987, West and Larkin 1987, Gleason and Bengtson 1996, Folkvord et al. 1997, Meekan et al. 1998, Gronkjaer et al. 2004).

A strong year-class for lake herring requires successful reproduction, followed by high survival of eggs, larvae, and juveniles. It is only after hatching that offspring have some control over their survival. Larvae can increase their probability of survival by

inhabiting areas that foster faster growth and contain fewer predators. Reaching such areas, however, may be impossible for larvae with limited swimming abilities without the aid of longshore currents. These wind-driven currents in Lake Superior have potential to disperse larvae away from spawning concentrations and into adjacent areas. If larvae are not dispersed, they may suffer greater mortality by attracting predators, or by competing for limited food resources. Because of the large size of Lake Superior and the pelagic nature of lake herring larvae, recruitment success may be tied to meteorological and hydrodynamic features akin to many oceanic fisheries. There is still more to be learned about the factors that influence the survival of individual lake herring, as well as the factors that can be used to predict large-scale recruitment success.

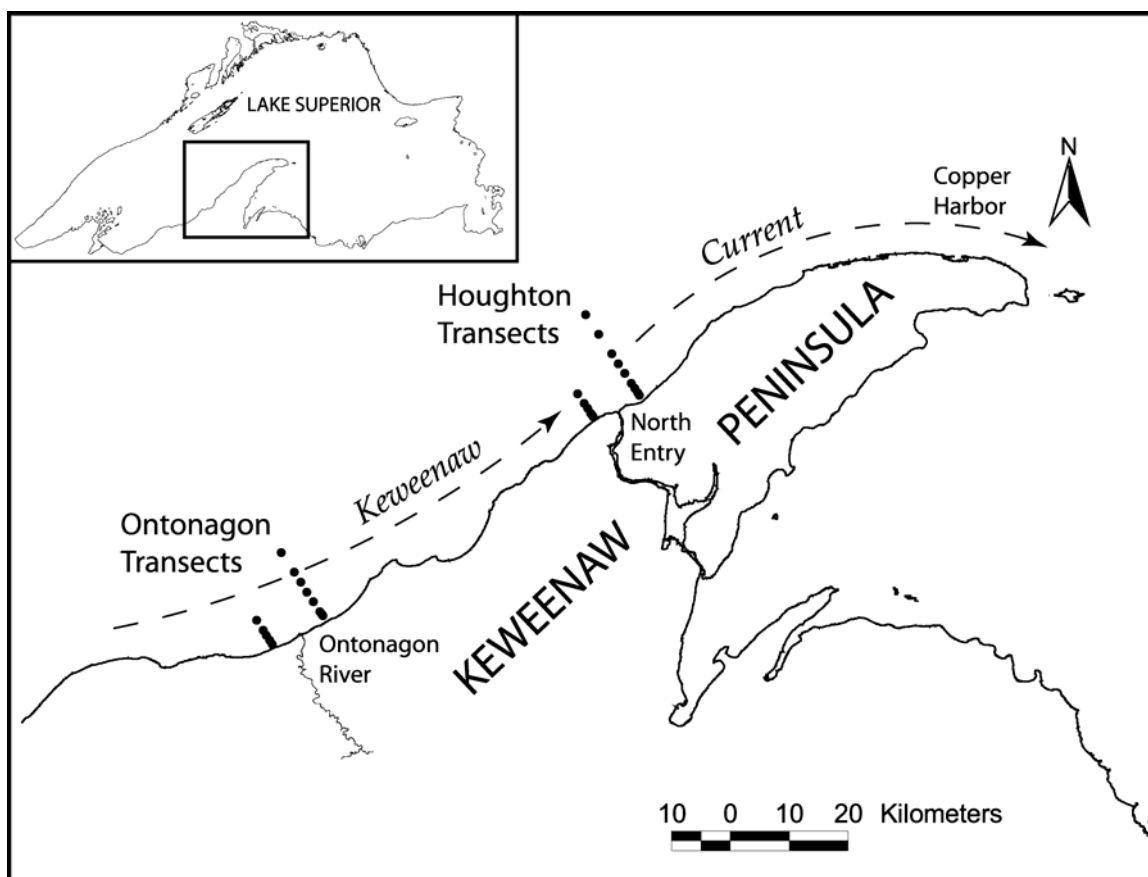


Figure 4-1. Study area in Lake Superior showing the four sampling transects off the western coast of the Keweenaw Peninsula, Michigan.

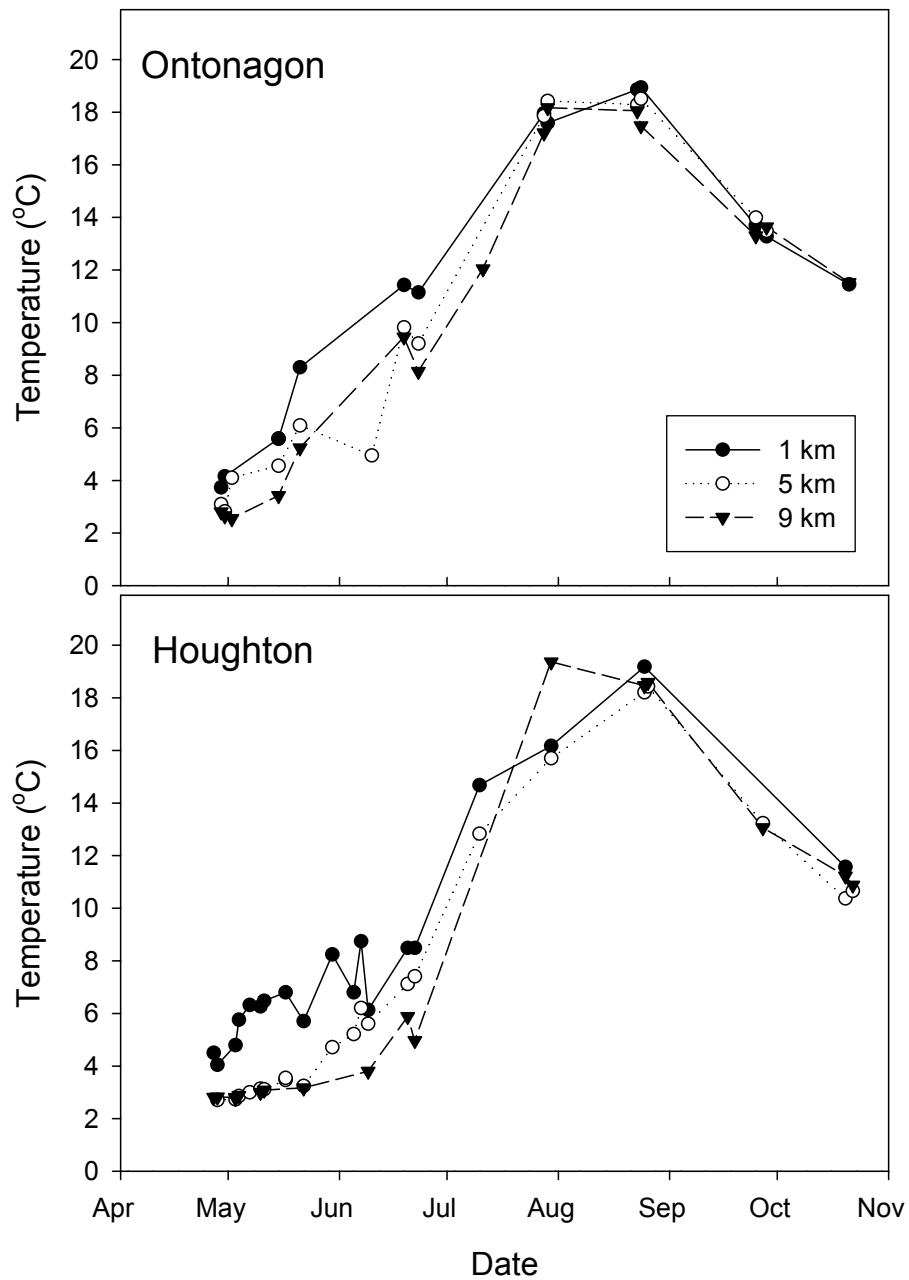


Figure 4-2. Seasonal changes in surface water temperature in 2000 at three offshore locations on the north Ontonagon and Houghton transects in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

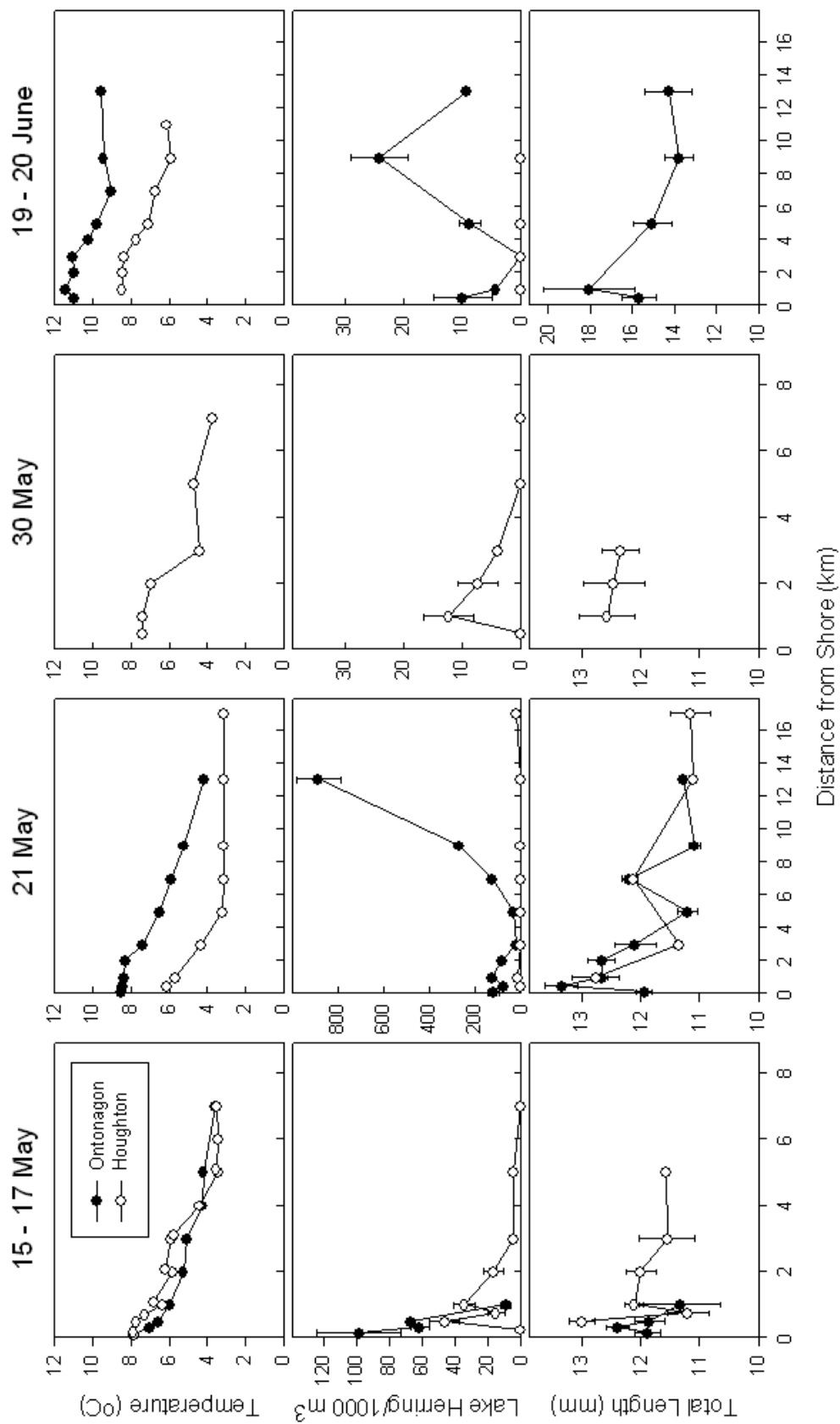


Figure 4-3. Offshore trends in surface water temperature, and mean (\pm SE) density and total length of larval lake herring collected during four sampling cruises in 2000 from two regions in Lake Superior, off the western coast of the Keweenaw Peninsula, Michigan.

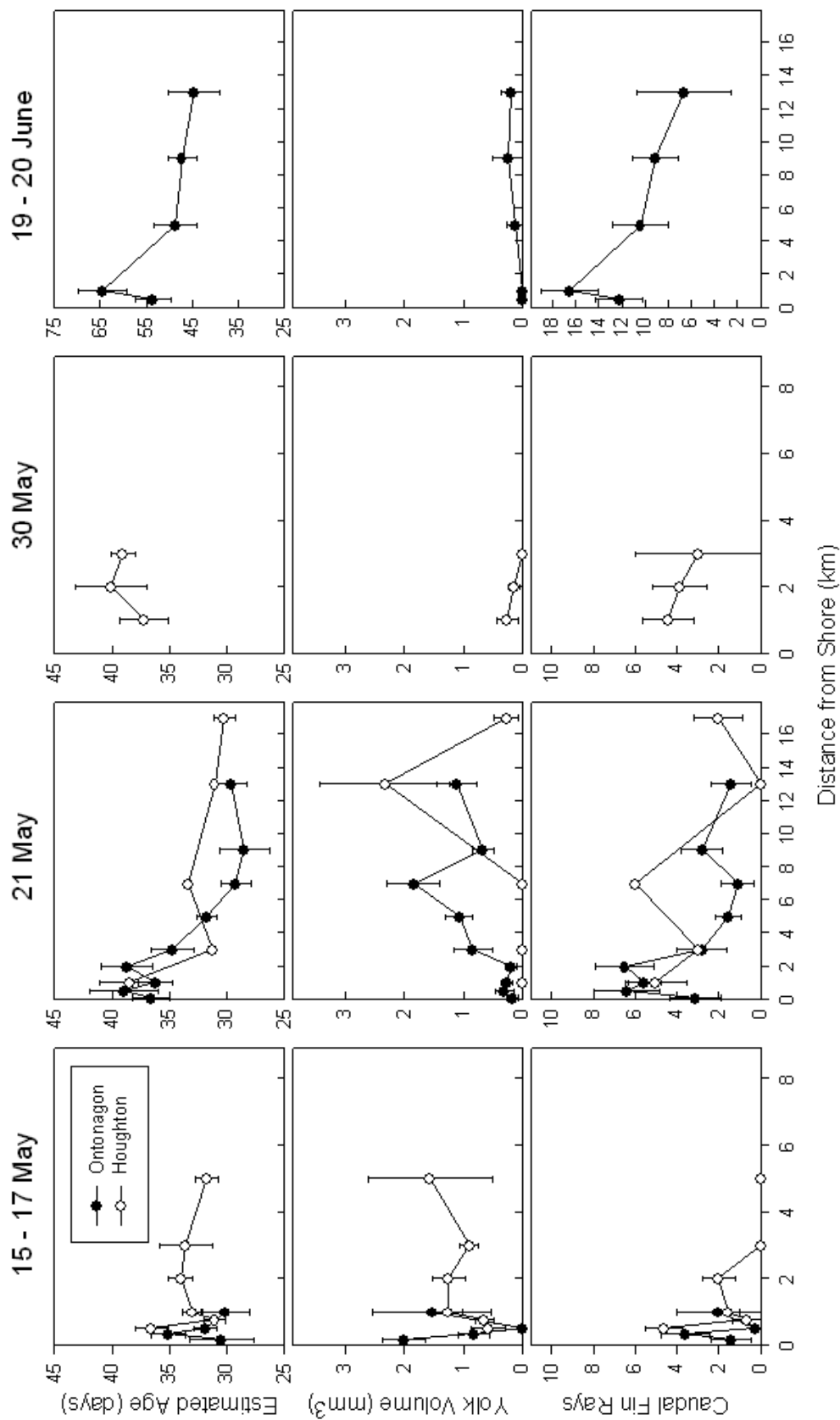


Figure 4-4. Offshore trends in mean (\pm SE) age, yolk volume, and number of caudal fin rays of larval lake herring collected during four sampling cruises in 2000 from two regions in Lake Superior, off the western coast of the Keweenaw Peninsula, Michigan.

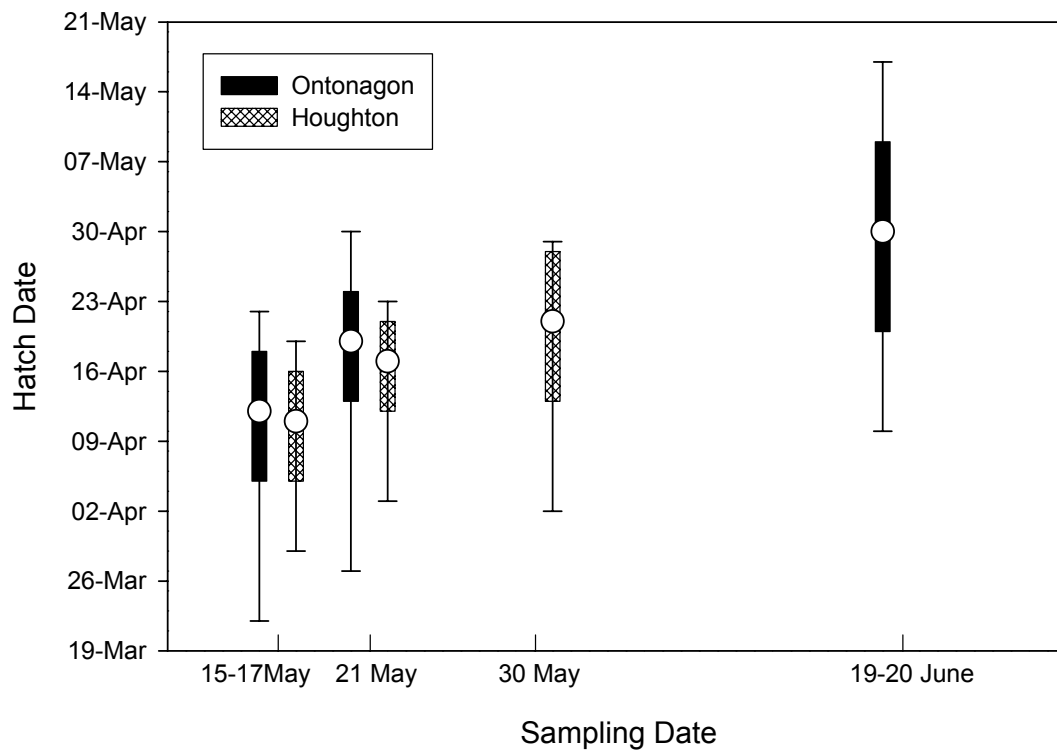


Figure 4-5. Hatch date of larval lake herring collected during four sampling cruises in 2000 from two regions in Lake Superior, off the western coast of the Keweenaw Peninsula, Michigan. Open dots represent the mean, wide bars represent the standard deviation, and T-bars represent the range in hatch dates.

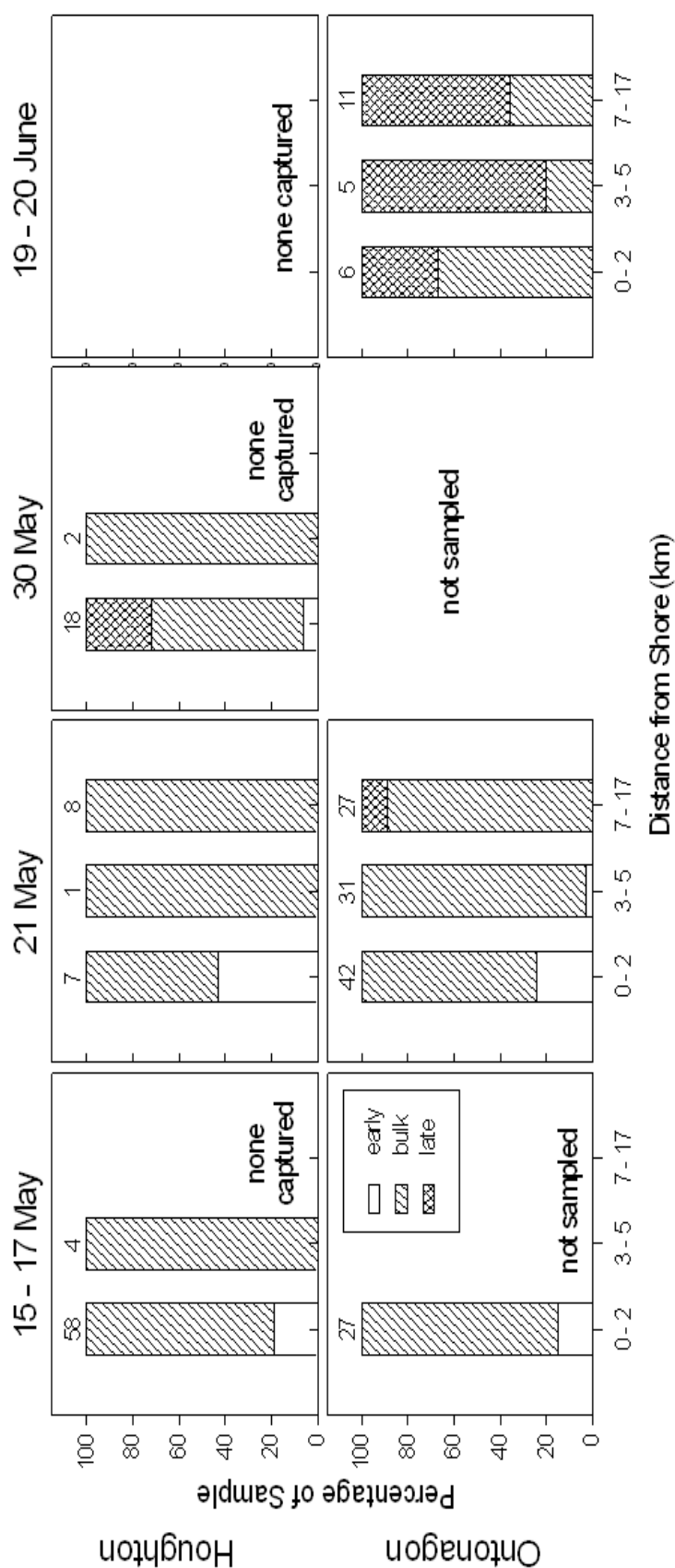


Figure 4-6. Percentage of larval lake herring from each hatch period for each sampling cruise in 2000, transect division, and region in Lake Superior, off the western coast of the Keweenaw Peninsula, Michigan. Hatch periods were 22 March – 8 April for early hatch, 9 April – 27 April for bulk hatch, and 27 April – 17 May for late hatch. Sample sizes are noted above each bar.

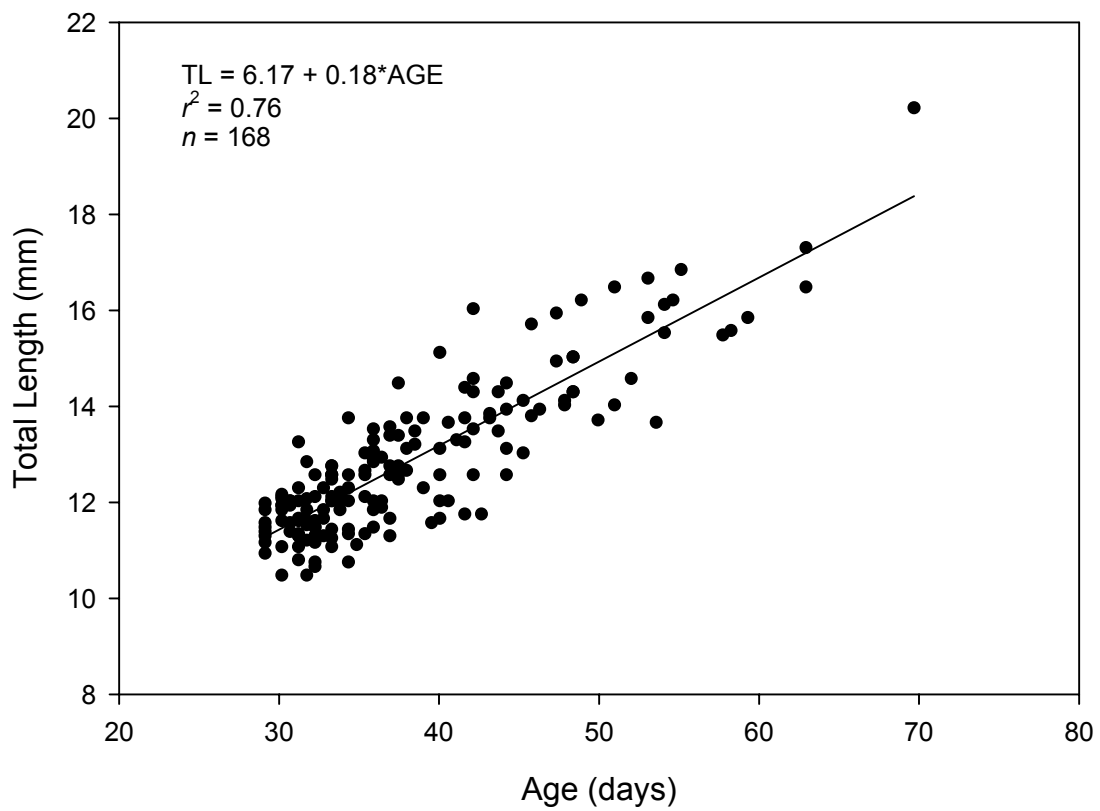


Figure 4-7. Total length (TL) to age relationship of larval lake herring collected in 2000 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. The slope of the linear regression indicates the overall daily growth rate.

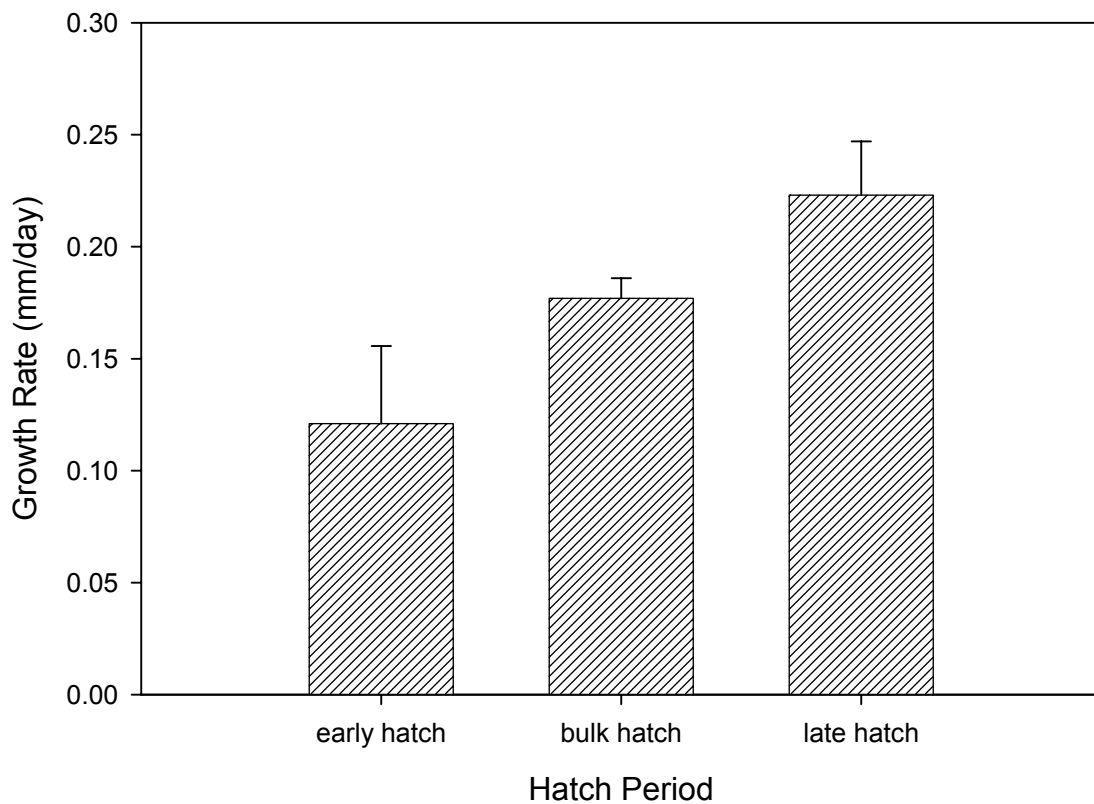


Figure 4-8. Growth rates (+ SE) of larval lake herring that hatched during the different hatch periods (early hatch = 22 March – 8 April, bulk hatch = 9 April – 27 April, and late hatch = 27 April – 17 May). Growth rates were estimated as the slope of length-to-age linear regressions for larval lake herring collected in 2000 from Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

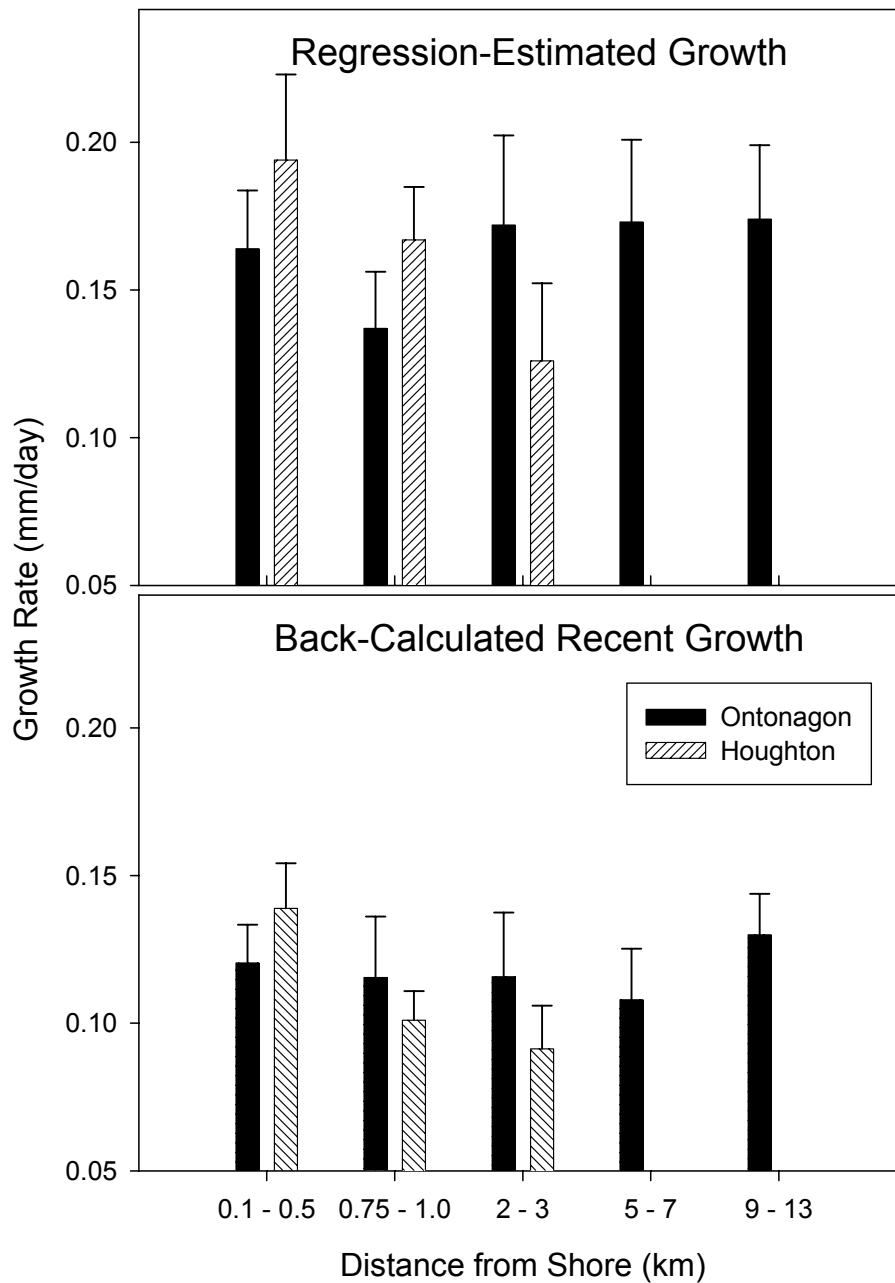


Figure 4-9. Spatial differences in growth rates of larval lake herring, where growth rates were calculated by length-to-age linear regressions (slope + SE) and by back-calculating growth for the last 5 days before capture (mean + SE). Lake herring were collected in 2000 from different distances from shore at two regions in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan.

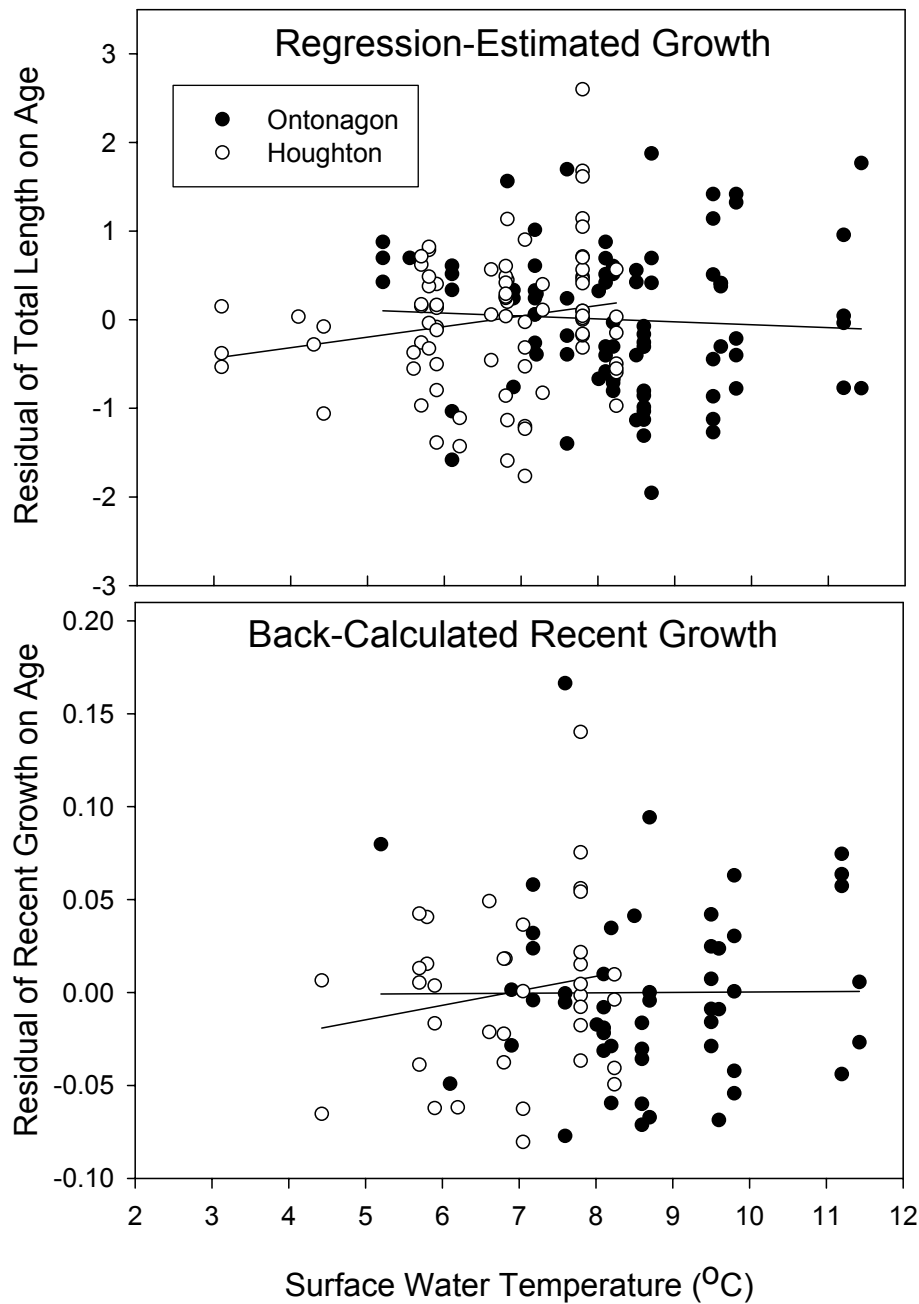


Figure 4-10. Relationship between growth rate of larval lake herring and surface water temperature. Lake herring were collected in 2000 from different distances from shore at two regions in Lake Superior off the western coast of the Keweenaw Peninsula, Michigan. Growth rates were estimated by length-to-age linear regressions and by back-calculating growth for the last 5 days before capture for each region. The effect of age was standardized by presenting the residuals of each model. Residuals were calculated separately for each region.

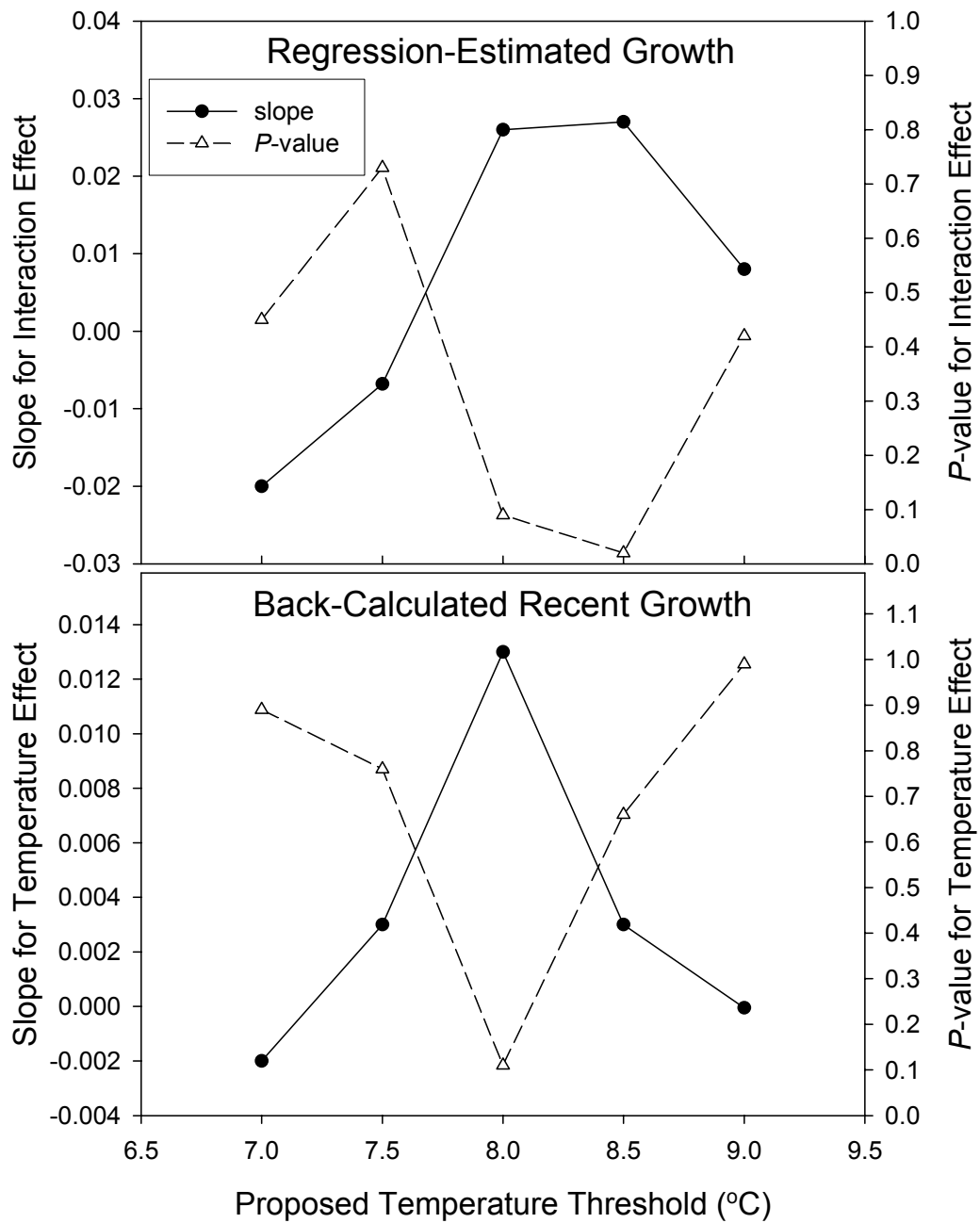


Figure 4-11. Regression coefficients (slopes) and *P*-values for linear regression models below proposed threshold temperatures. For regression-estimated growth, slopes and *P*-values are for the age by temperature interaction, and for back-calculated recent growth, slopes and *P*-values are for the temperature main effect. Age was also included in the back-calculated model as a covariate.

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APPENDIX A

Conversion Factors for Preservation-Induced Shrinkage and Different Length Measurements for Larval Lake Herring (*Coregonus artedii*)

INTRODUCTION

Estimating larval growth with or without otolith analysis requires accurate measurements of fish length. However, preservation in the field can decrease larval length to a certain degree, based on the type of preservative used, before measurements are taken in the laboratory. Preservation-induced shrinkage is especially a concern with larval fishes because of their small sizes. In addition, researchers may present their measurements as either total length or standard length, making it difficult to compare results across studies. Accordingly, I developed regression equations that can convert preserved measurements to live measurements and can convert between standard length and total length for lake herring.

Total length, standard length, yolk length, and yolk depth of the lab-reared larvae used for otolith validation were measured before and 10 – 14 months after preservation in 95% EtOH, 70% EtOH, or 4% formalin. Measurements were taken from digital images (640 x 480 pixels) of larvae using SigmaScan Pro 5 (SPSS Inc.). Images were captured with a personal computer from a camera equipped on a dissecting microscope. Yolk volume was calculated as a prolate spheroid, with length being the longer axis and depth and girth being shorter and equal axes. Statistical analyses were performed with SYSTAT 10 (SPSS Inc.).

EFFECTS OF PRESERVATION

Preservation-induced shrinkage in total length was greater for smaller larvae, as evident by regression y-intercepts that were significantly greater than zero and slopes that were significantly less than one (Table A-1). The extent of shrinkage in total length also differed slightly among the different preservatives. For 8 – 12 mm larvae, the average decrease was greatest for 4% formalin (6% decrease), followed by 95% EtOH (4% decrease), then by 70% EtOH (2% decrease). However, for 12 – 20 mm larvae, percent decrease was identical for 4% formalin and 95% EtOH (3% decrease), and only marginally less for 70% EtOH (2% decrease). Therefore, with increase in larval size, the extent of shrinkage lessened and became more equal among the different preservatives.

Preservation effects were greater but more variable for yolk volume. The slope for 95% EtOH was significantly greater than 1, indicating greater shrinkage with larger yolks (Table A-1). However, the slopes for the other two preservatives were not significantly different from one and all y-intercepts were not significantly different from zero (Table A-1). Accordingly, 8 – 12 mm larvae showed a 51% decrease in 95% EtOH, while changes in 70% EtOH (17% decrease) and 4% formalin (10% increase) were suitably nonsignificant given their effects were sometimes negative and sometimes positive among individual larva. The variability in preservation effects to yolk volume was probably exacerbated from a larger contribution of measurement error associated with taking smaller measurements, especially when preservation-induced opaqueness made it difficult to observe the yolk and when calculating volume compounds small errors in linear measurements.

CONVERSION BETWEEN STANDARD LENGTH AND TOTAL LENGTH

Regression estimates for converting total length (TL) to standard length (SL) and vice versa were similar for live larvae and larvae preserved with 4% formalin, 70% EtOH, and 95% EtOH ($P > 0.25$ for both slope and intercept). Accordingly, pooled equations were calculated: $TL = -1.20 + 1.15SL$ and $SL = 1.09 + 0.86TL$ ($n = 246$, $r^2 = 0.99$, $P < 0.0001$ for $H_0: \beta_0 = 0$, $P < 0.001$ for $H_0: \beta_0 = 1$) for larvae of 8.42 – 26.49 mm TL . Standard length became a decreasing percentage of total length with larval size, going from 96% for 8 – 15 mm larvae, to 93% for 15 – 20 mm larvae, and then to 90% for 20 – 25 mm larvae.

Table A–1. Linear regression equations for converting preserved to live measurements (total length and yolk volume) of larval lake herring when preserved in 4% formalin, 70% EtOH, or 95% EtOH. Preservation duration was 10 – 14 months. Size ranges indicate the range of preserved total lengths (mm) and yolk volumes (mm^3) used to estimate these equations. n = sample size, r^2 = coefficient of determination, TL = live total length, PL = preserved total length, YV = live yolk volume, PY = preserved yolk volume.

	size range	n	r^2	equation	P -value $H_0: \beta_0 = 0$	P -value $H_0: \beta_1 = 1$
Total Length						
4% formalin	8.42 – 22.26	45	0.99	$TL = 1.01 + 0.96PL$	< 0.0001	< 0.01
70% EtOH	9.64 – 22.42	41	0.98	$TL = 1.20 + 0.91PL$	0.0001	< 0.001
95% EtOH	9.13 – 27.73	38	0.98	$TL = 1.18 + 0.93PL$	< 0.0001	< 0.001
Yolk Volume						
4% formalin	0.28 – 14.88	25	0.91	$YV = 0.11 + 0.99PY$	0.76	> 0.50
70% EtOH	0.22 – 8.06	24	0.84	$YV = 0.50 + 0.96PY$	0.14	> 0.50
95% EtOH	0.04 – 7.16	21	0.86	$YV = 0.25 + 1.51PY$	0.40	< 0.002

APPENDIX B

Characteristics of Lab-Reared Larval Lake Herring (*Coregonus artedii*)

INTRODUCTION

Lake herring were reared in the laboratory from eggs for otolith validation (Ch 3). As a component of the validation experiments, standard length, total length, yolk length, and yolk depth of live larvae were measured. Measurements were taken from digital images (640 x 480 pixels) of larvae using SigmaScan Pro 5 (SPSS Inc.). Images were captured with a personal computer from a camera equipped on a dissecting microscope. Yolk volume was calculated as a prolate spheroid, with length being the longer axis and depth and girth being shorter and equal axes. Statistical analyses were performed with SYSTAT 10 (SPSS Inc.). Patterns in these measurements are presented here as they may enhance the understanding of the development of the lab-reared larvae on which otolith validation was based. These patterns may also facilitate the understanding of natural patterns observed by larval fish surveys.

HATCHING

Hatching started from 62 days after fertilization and lasted for 41 days (Figure B-1). The bulk of the larvae (74% of 1,421 larvae) hatched during 6 consecutive days near the end of the hatching period, following a temperature increase of 1.7 °C over 8 days. This hatching pattern is consistent with the common observation that spring warming is the major trigger for hatching.

I examined if the developmental state at hatching varied with hatch date, by measuring several larvae at hatching throughout the hatching period. I found that live total length increased linearly and yolk volume decreased exponentially with hatch date

(Figure B-2). Thus, embryos continued to grow and utilize yolk as they awaited hatching in a manner similar to free-swimming larvae (Figure B-6). Because hatching appeared to be largely dependent on an environmental trigger, larvae hatched at different developmental states. However, larvae that hatched during the first 21 days of the hatching period were likely prematurely released. These larvae did not swim up until a later date on which newly hatched larvae were able to immediately swim up.

ONSET OF FEEDING

I examined if the commencement of exogenous feeding is triggered by larval size, age, or yolk volume. Feeding could start immediately after hatching to maximize growth, or it may be necessary for larvae to develop to a certain state before exogenous feeding is possible or desired.

Total length and yolk volume of larvae, separated among 6 nursery baskets in stream 1, were measured after an initial feeding attempt. Each basket contained 6 – 10 larvae of the same age that hatched between the 14 – 24th day of the hatching period. Larvae were given brine shrimp nauplii between 14 and 32 days of age.

Each basket contained both feeders and non-feeders, regardless of the constant age of larvae within each basket. Overall, larvae that fed ($n = 19$) were of similar size to larvae that did not feed ($n = 22$) (Figure B-3; two-sample t -test, $P = 0.28$). However, feeders had 64% less yolk than non-feeders (Figure B-3; two-sample t -test, $P = 0.002$). Because this pattern pervaded baskets of variously aged larvae from different hatch dates, reduced yolk volume appeared to be more important in initiating exogenous feeding than age or size. Considering that yolk volume and size at hatching were dependent on hatch date, it was expected that earlier hatched larvae did not initiate exogenous feeding until a

much later age, apparently because of the larger yolks at hatching. For example, larvae that hatched on the 5th day of the hatching period still did not feed at 40 days of age, while larvae that hatched on the 32nd day of the hatching period fed at 13 days of age.

EFFECTS OF FEEDING ON DEVELOPMENT

I examined how exogenous feeding affects growth and yolk absorption of yolk-sac larvae. It was expected that feeding would naturally increase growth, but feeding could affect the rate of yolk absorption in different ways. Feeding might increase yolk absorption if yolk no longer has to be rationed for survival, or feeding might decrease yolk absorption if yolk could be further rationed for future uncertainties.

In stream 2, 16-day old and 18-day old larvae were each separated into two baskets. The 16-day old baskets contained about 30 larvae each, while the 18-day old baskets contained 12 larvae each. One of each pair of baskets was given food while the other was not. Larvae were removed and measured throughout this fed vs. starved treatment that lasting for 14 – 15 days.

Growth of fed larvae were statistically greater than the marginal growth of the starved larvae (Figure B-4; multiple regression, $n = 41$, $P = 0.0002$). However, yolk volume followed nearly identical rates of utilization in both treatments (Figure B-4; multiple regression on $\log(Y + 1)$ data, $n = 41$, $P = 0.43$). Therefore, exogenous feeding did not affect the rate of yolk utilization, but was necessary for growth even when yolk was still present.

EFFECTS OF TEMPERATURE ON DEVELOPMENT

I examined the influence of temperature on growth and yolk utilization by comparing larvae raised in the different streams. It was expected that larvae would

naturally grow faster in warmer water, but it was not clear if increased temperatures would affect the rate of yolk absorption. Increased metabolism from higher temperatures may increase yolk absorption, or an increased metabolism may instead compromise the amount of energy and resources for growth.

Larvae of the bulk hatch (33 – 38th day of the hatching period) were used in this comparison. After this hatch, mean monthly temperatures increased, over 3 months, from 5.7 to 7.3 °C in stream 1 and from 7.1 to 12.3 °C in stream 2.

Growth up to 102 days of age followed an exponential curve, with growth in stream 2 being greater than that of stream 1 (Figure B-5; multiple regression on log (Y +1) data, $n = 231$, $R^2 = 0.88$, $P < 0.0001$). In contrast, the depletion of yolk was nearly identical in both streams (Figure B-5; multiple regression on log (Y +1) data and age limited to 25 days, $n = 80$, $R^2 = 0.89$, $P = 0.26$). By 25 – 30 days of age, virtually all larvae lacked yolk. In comparison, complete yolk absorption of early hatched (3 – 25th day of the hatching period) larvae in stream 1 was predicted to occur much later, at 40 – 60 days of age (Figure B-6).

CONCLUSIONS

Because lake herring embryos continued to grow and utilize yolk as they awaited hatching, later hatched larvae had decreased yolk volumes and increased total lengths over the 41 day hatching period. Larvae with larger yolks that hatched earlier took a longer time to start exogenous feeding, and to completely absorb their yolk reserves. Yolk absorption was not affected by exogenous feeding or temperature differences. However, exogenous feeding was necessary for growth even when yolk was still present, and growth was greater at a higher temperature.

Because most of the larvae hatched in bulk over 6 days near the end of the hatching period, the time to yolk absorption for the majority of larvae could be confined to occur at 25 – 30 days of age. Predicting a critical life history event like yolk absorption is important as it may be reflected in the microstructure of otoliths. It is also simplifying to know that the rate of yolk absorption did not vary because of temperature or exogenous feeding. The greatest variance in the time to yolk absorption was attributed to variation in hatching date. Through initial yolk volume and the timing of exogenous feeding, hatching date indirectly affected growth rate, which may also be reflected in otolith microstructure. Because lake herring larvae may hatch at different developmental states, otolith analysis may be less precise in estimating daily age, if incremental deposition does not initiate at hatching but instead a later developmental event like first feeding or yolk absorption.

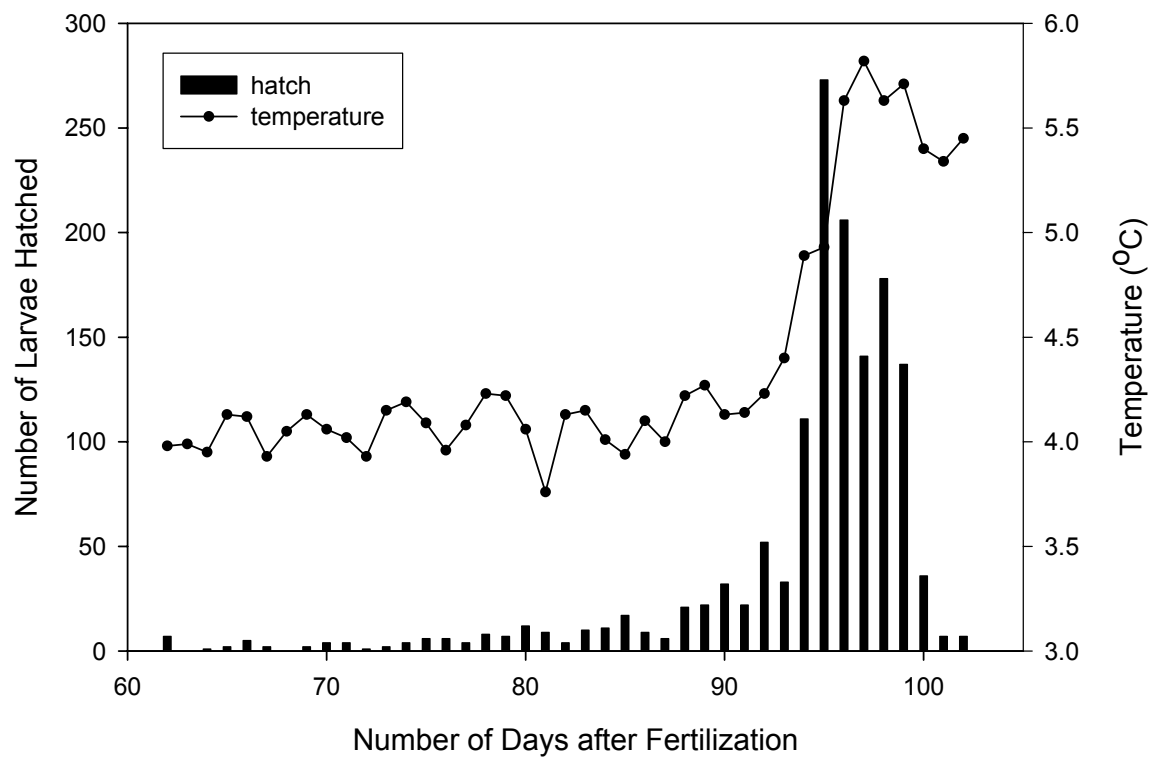


Figure B-1. The daily hatching frequency of lab-reared lake herring and mean water temperatures during the 41-day hatching period.

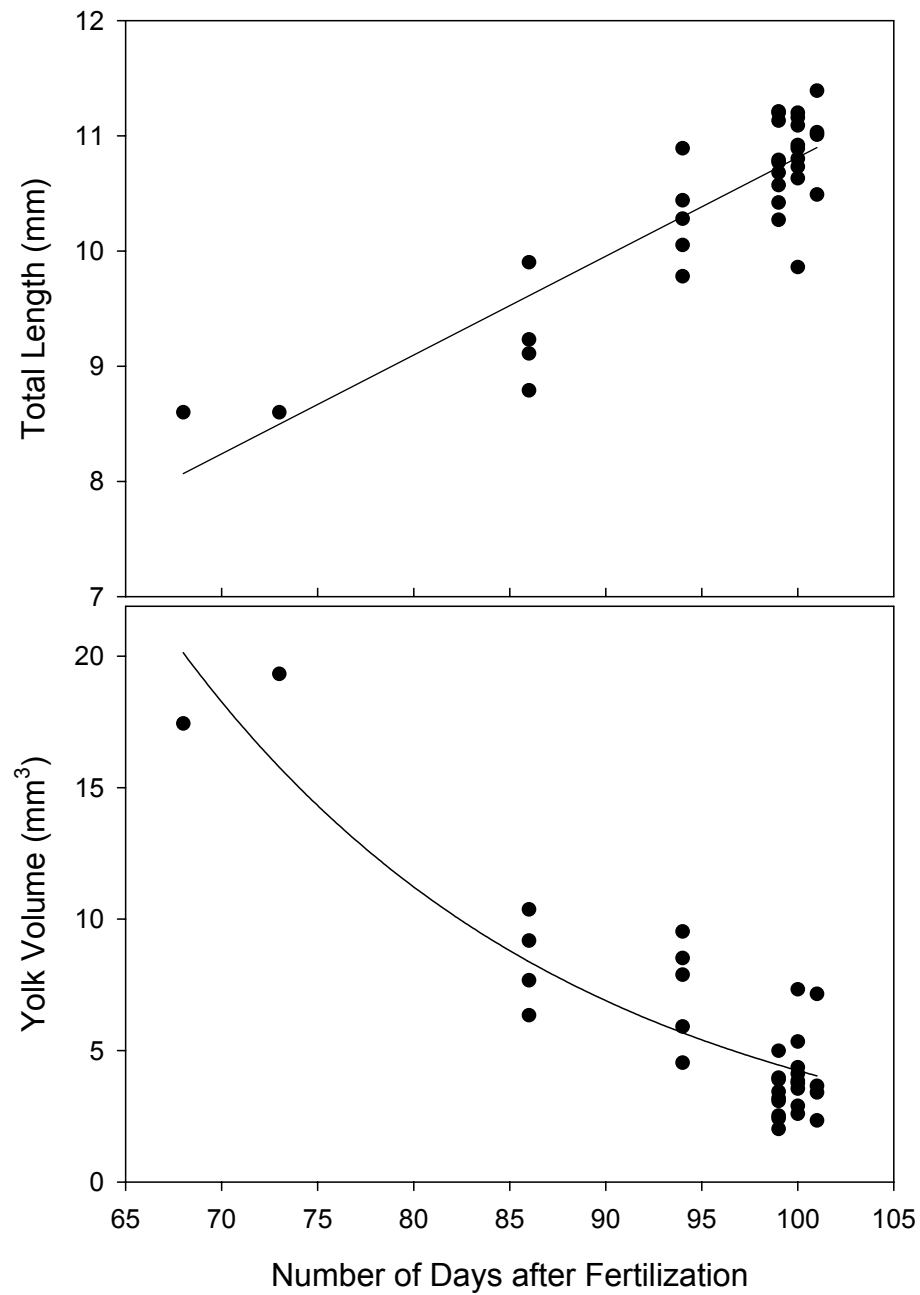


Figure B-2. Changes in total length (TL) and yolk volume (YV) at hatching with increased hatch date ($DATE$) of lab-reared lake herring. The regression for total length is $TL = 2.24 + 0.08DATE$ ($n = 33$, $R^2 = 0.76$, $P < 0.0001$) and the regression for yolk volume is $YV = 550.66e^{-0.048DATE}$ ($n = 33$, $R^2 = 0.79$, $P < 0.0001$).

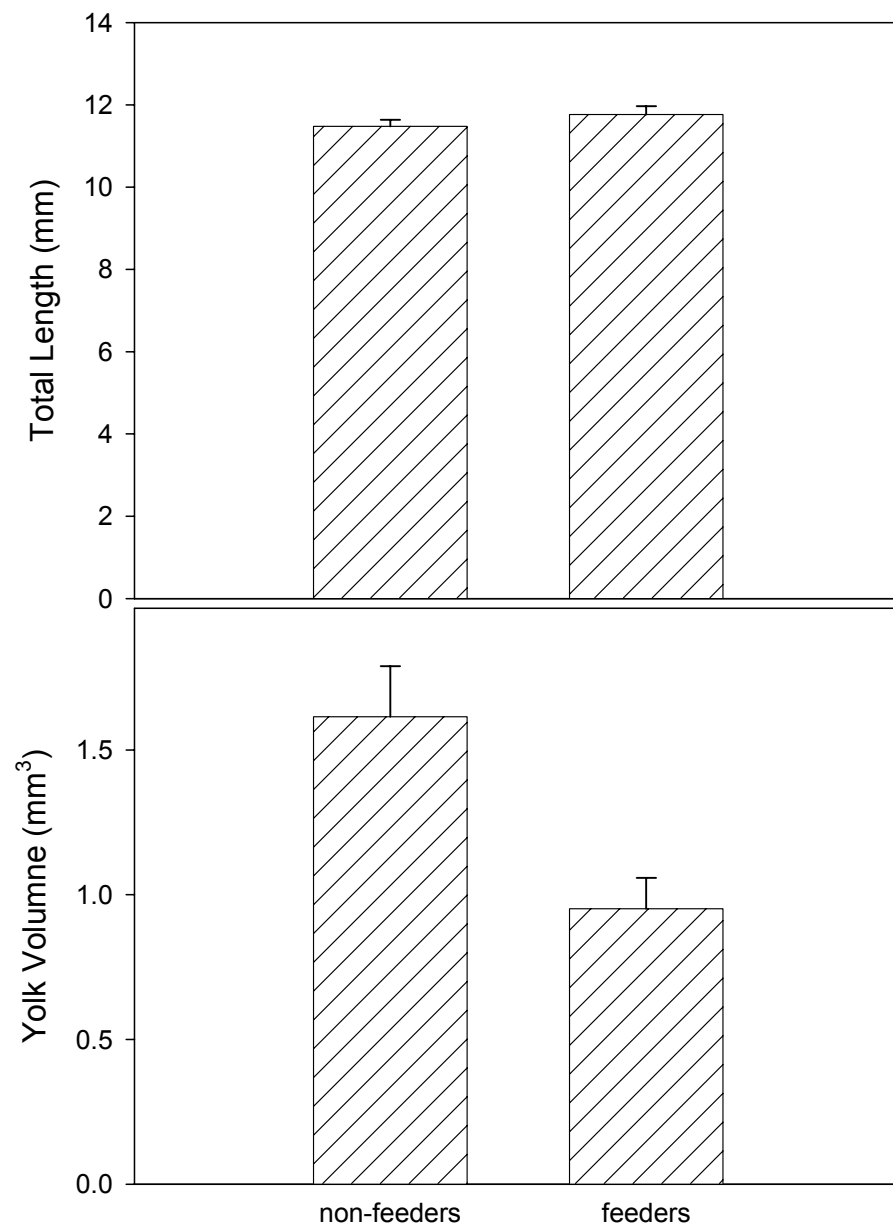


Figure B-3. Total length and yolk volume of larvae that fed or did not feed when given food for the first time.

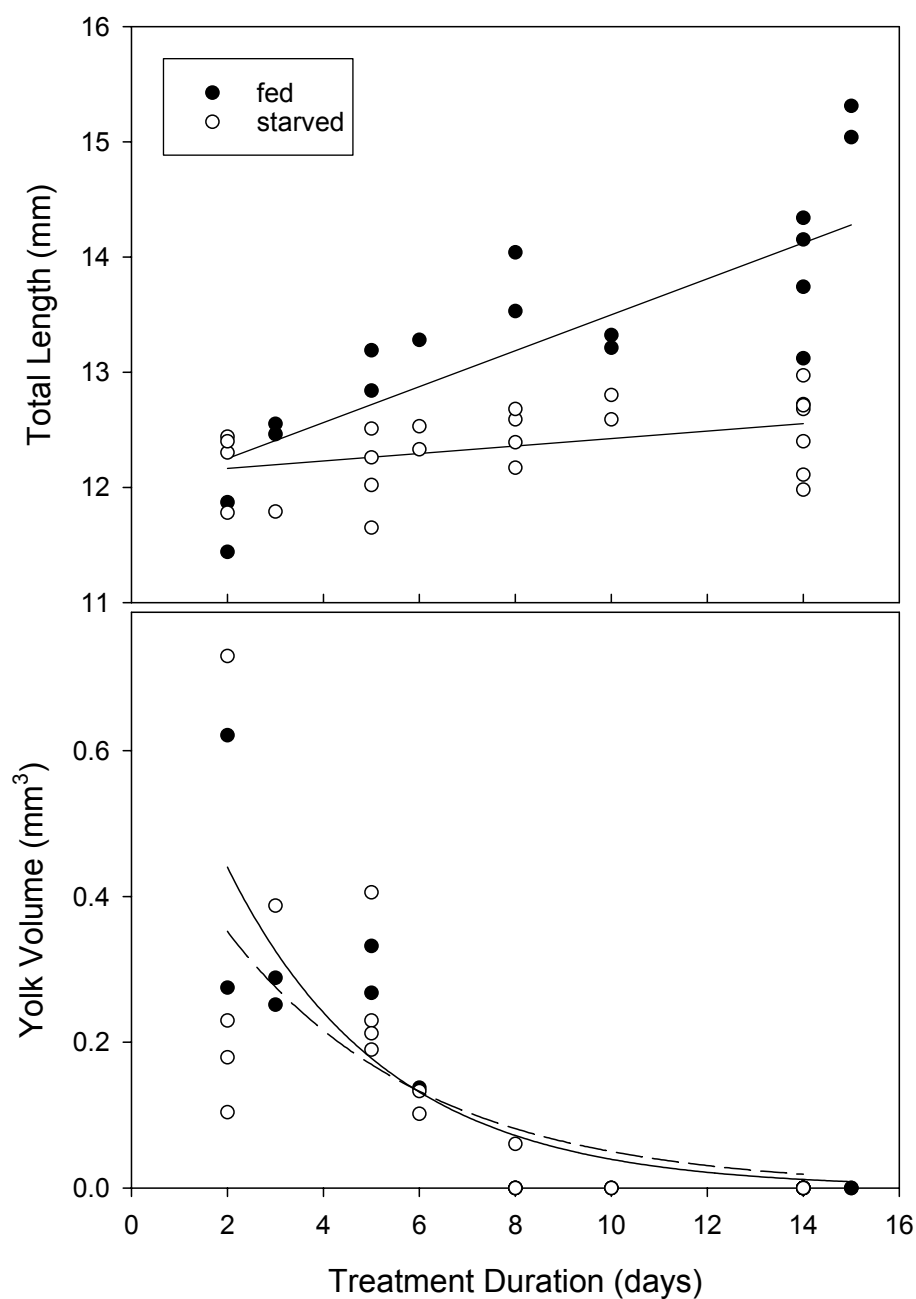


Figure B-4. Growth and yolk utilization of lake herring that were either fed or starved. Regressions for the fed treatment were $TL = 11.94 + 0.156DAYS$ ($n = 18$, $R^2 = 0.77$, $P = 0.0002$) and $YV = 0.80e^{-0.30DAYS}$ ($n = 18$, $R^2 = 0.79$, $P < 0.0001$). Regressions for starved treatment are $TL = 12.10 + 0.032DAYS$ ($n = 23$, $R^2 = 0.18$, $P = 0.05$) and $YV = 0.57e^{-0.24DAYS}$ ($n = 23$, $R^2 = 0.52$, $P = 0.0001$).

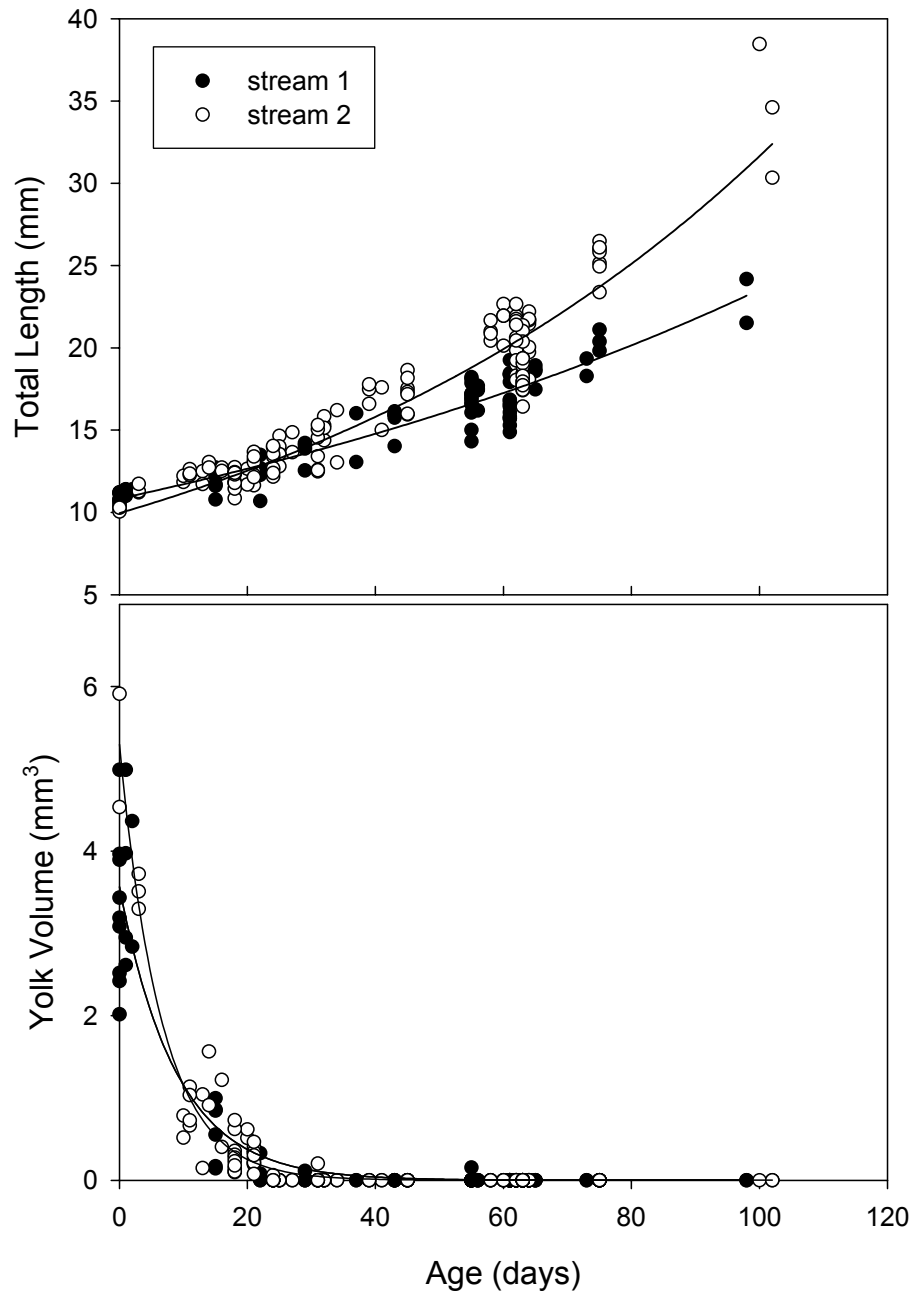


Figure B-5. Growth and yolk utilization of lake herring reared in two living streams of different temperatures that hatched in bulk near the end of the hatching period.

Regressions for growth were $TL = 10.84e^{0.0078DAYS}$ ($n = 84$, $R^2 = 0.90$, $P < 0.0001$) for stream 1 and $TL = 9.95e^{0.012DAYS}$ ($n = 145$, $R^2 = 0.89$, $P < 0.0001$) for stream 2.

Regressions for yolk depletion were $YV = 3.57e^{-0.11DAYS}$ ($n = 84$, $R^2 = 0.90$, $P < 0.0001$) for stream 1 and $YV = 5.30e^{-0.15DAYS}$ ($n = 145$, $R^2 = 0.95$, $P < 0.0001$) for stream 2.

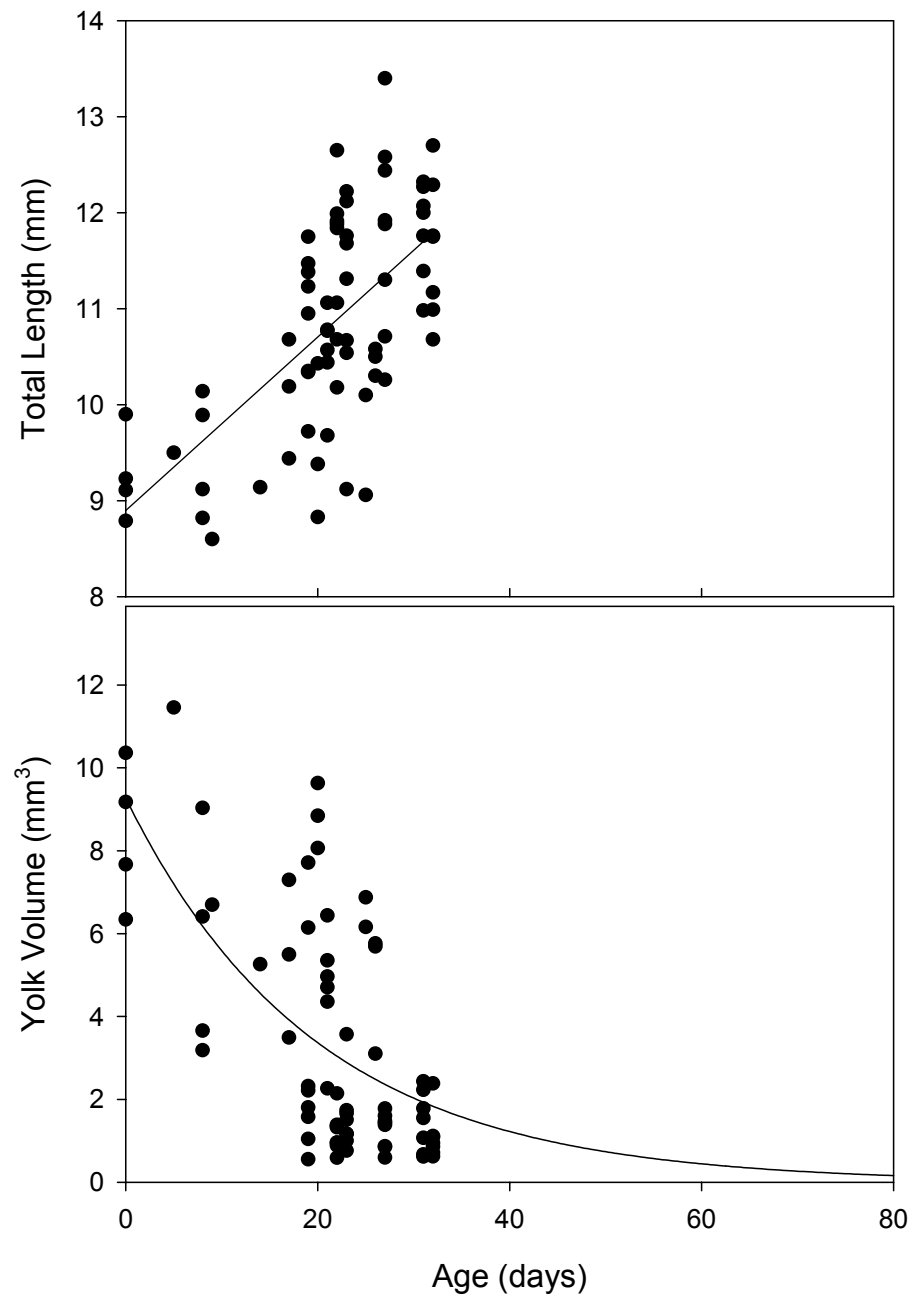


Figure B-6. Growth and yolk utilization of lake herring reared in stream 1 that hatched early in the hatching period. Regression for growth was $TL = 8.90 + 0.09DAYS$ ($n = 74$, $R^2 = 0.43$, $P < 0.0001$) and regression for yolk depletion was $YV = 9.27e^{-0.051DAYS}$ ($n = 74$, $R^2 = 0.42$, $P < 0.0001$).

APPENDIX C

Images of Larval Lake Herring (*Coregonus artedii*) Otoliths

This appendix contains select images of larval lake herring otoliths (sagittae) from the laboratory validation study.

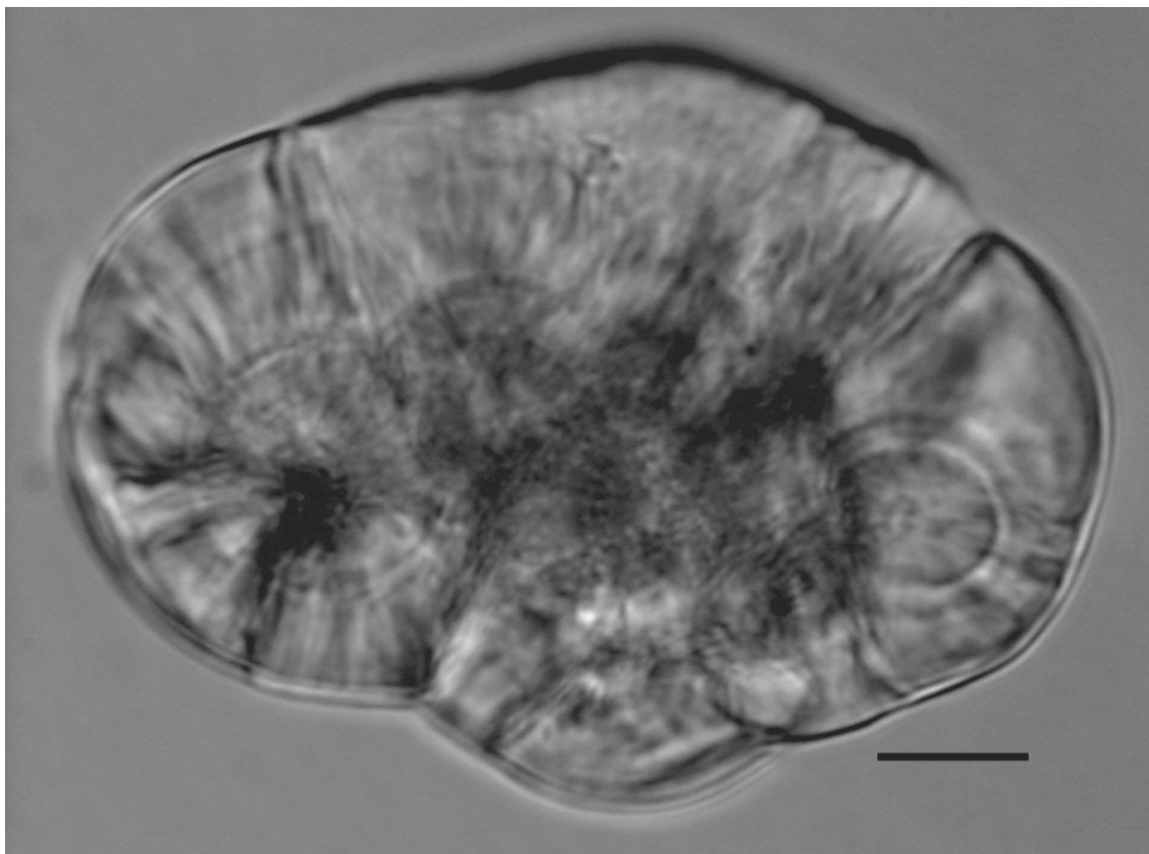


Image C-1. Right sagitta from a larva at hatching. The larva had a total length of 10.89 mm and a yolk volume of 4.12 mm³. This otolith had a maximum diameter of 71.78 µm and a nucleus that contained at least 7 primordia. Several faint increments are visible in the top left region. Scale bar = 10 µm.

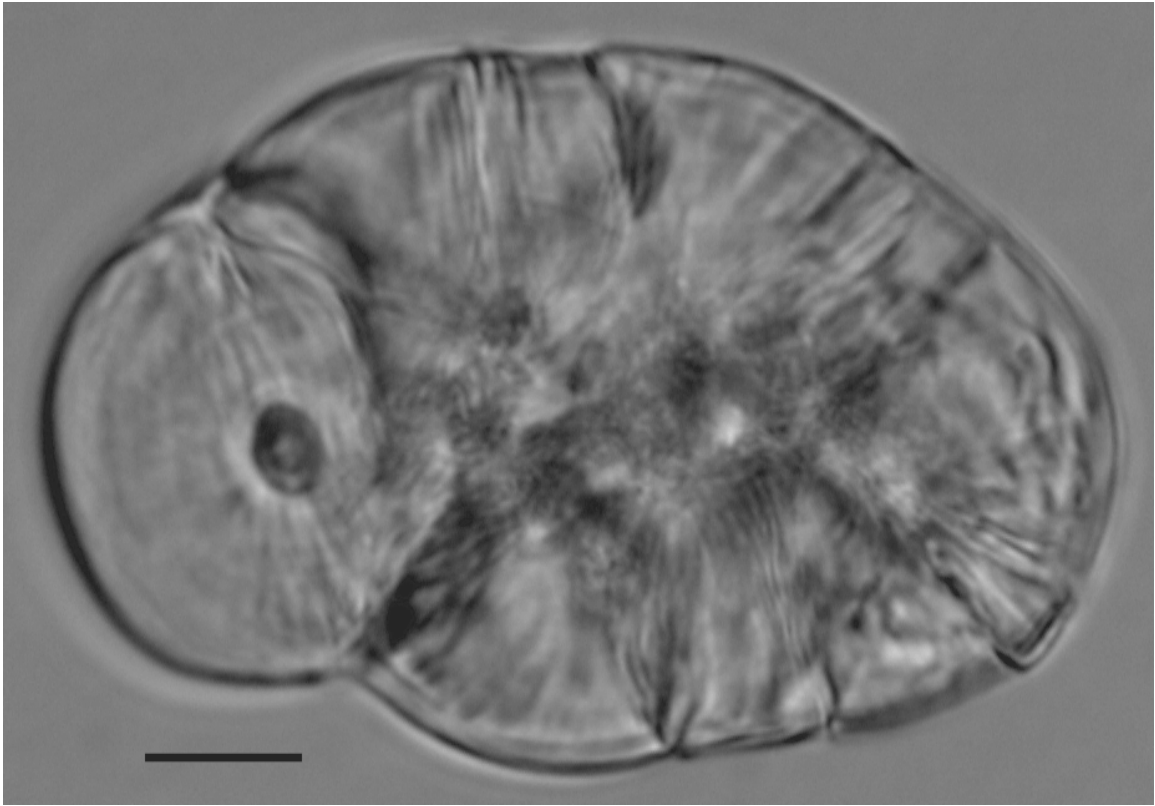


Image C-2. Right sagitta from a 24 day old larva reared in stream 1. The larva had a total length of 12.49 mm and a yolk volume of 0.77 mm³. This otolith had a maximum diameter of 70.31 µm. A check has yet to form but several faint increments encircle the nucleus, most of which were probably deposited before hatching. Scale bar = 10 µm.

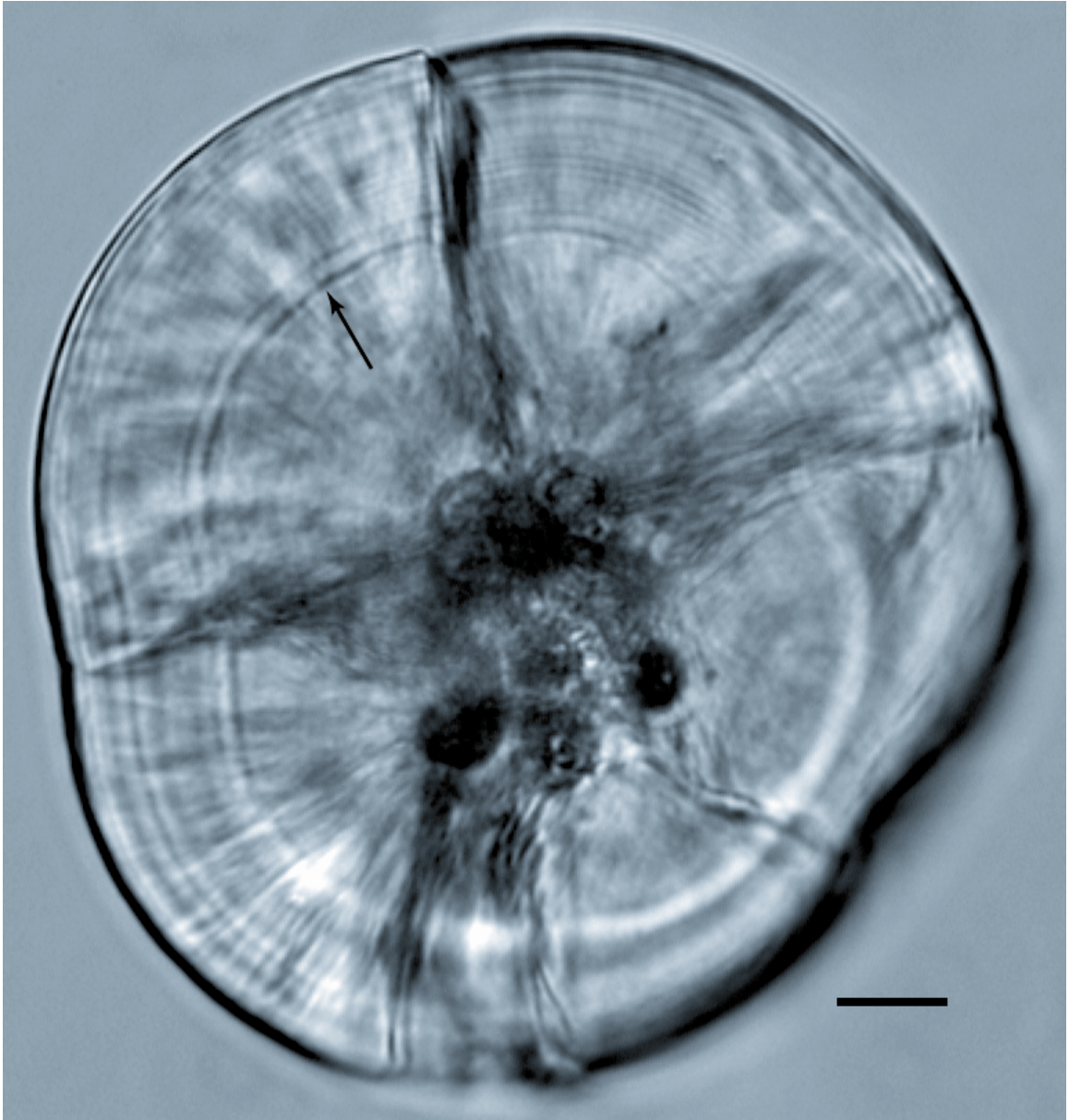


Image C-3. Left sagitta from a 45 day old larva reared in stream 2. The larva had a total length of 17.31 mm and no yolk. This otolith had a maximum diameter of 101.41 μm and a check diameter of 65.92 μm . The arrow points to the check mark, after which about 17 increments were deposited, as visible in the top region. These increments, when improperly focused, appear as 7 broad increments, as visible in the bottom region. Scale bar = 10 μm .



Image C-4. Right sagitta from a 75 day old larva reared in stream 2. The larva had a total length of 25.14 mm. This otolith had a maximum diameter of 279.93 μm and a check diameter of 69.58 μm . The arrow points to the check mark, after which about 44 increments were deposited, although not all increments in the interior section are visible in this view. Scale bar = 20 μm .

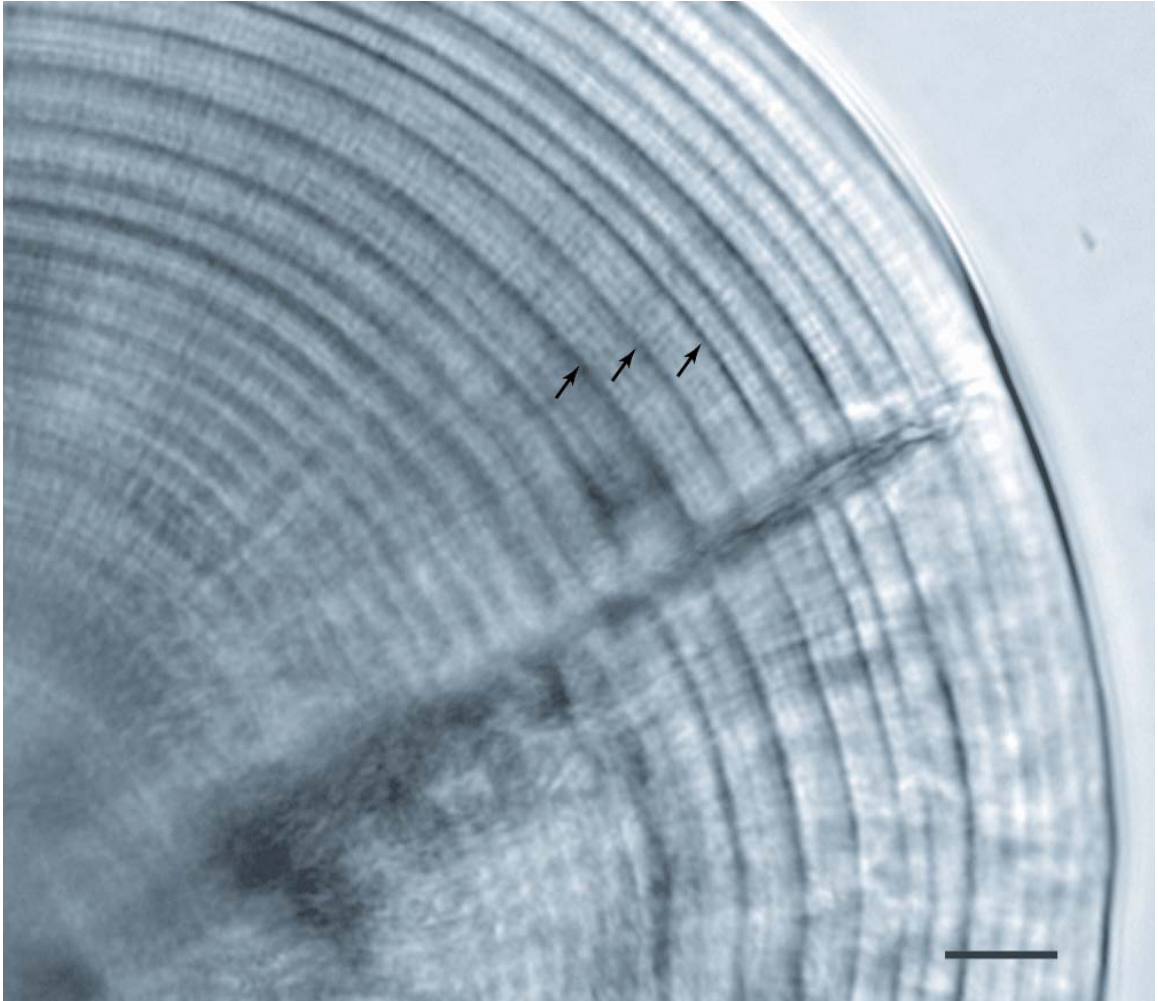


Image C-5. Left sagitta from a 75 day old larva reared in stream 1. The larva had a total length of 28.62 mm. This otolith had a maximum diameter of 281.55 μm and a check diameter (not shown) of 71.95 μm . The arrows indicate increments that were part of the daily series. Between the daily increments 1 – 4 subdaily increments are visible. These subdaily increments diminished from view when readjusting the focus. Scale bar = 10 μm .

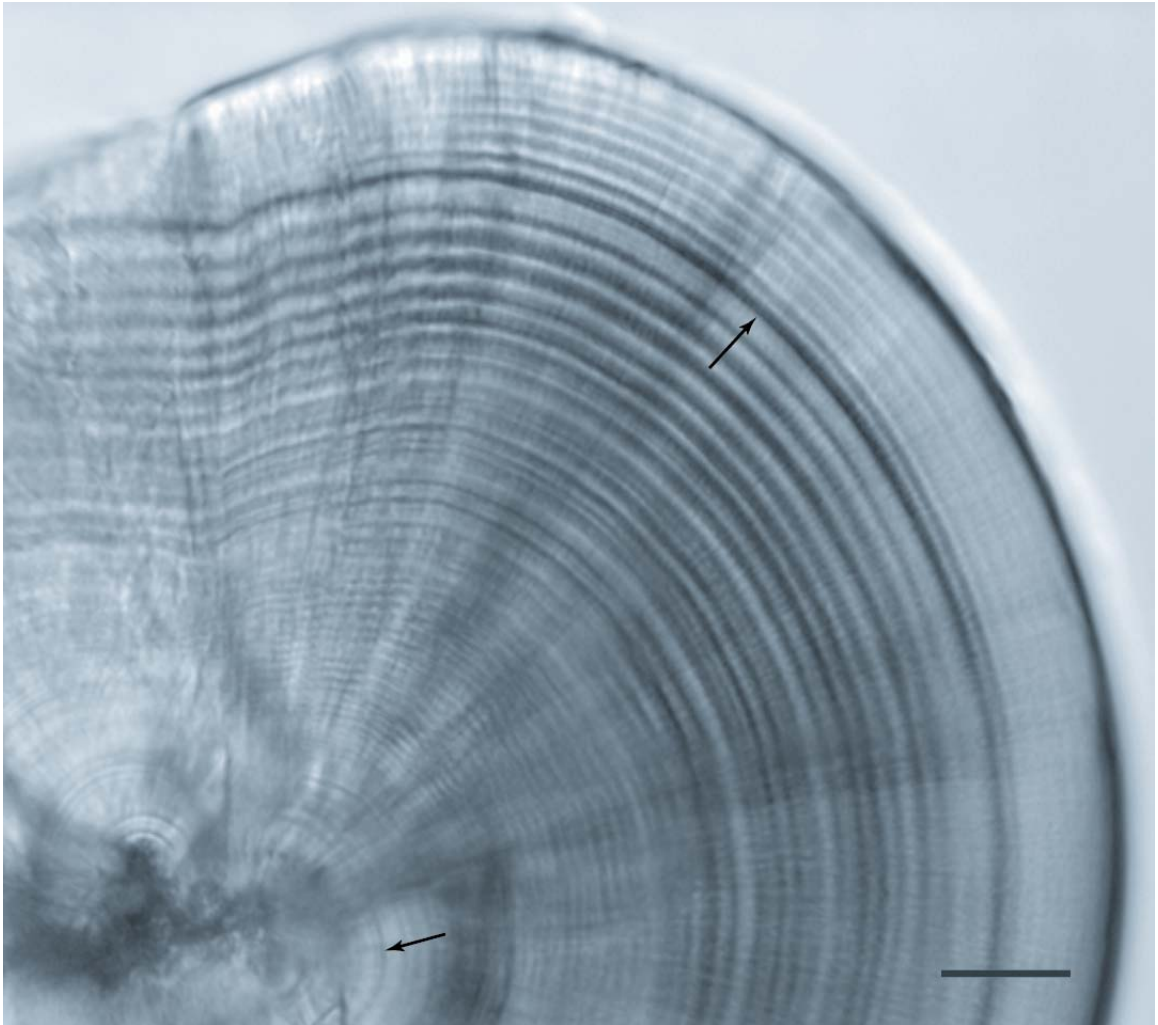


Image C-6. Left sagitta from a 75 day old larva reared in stream 2 then transferred to stream 1 eight days before preservation. The larva had a total length of 25.54 mm. This otolith had a maximum diameter of 297.73 μm and a check diameter of 73.12 μm . The inner arrow points to the check mark and the outer arrow points to a prominent increment formed from the cold temperature shock, after which increments were more faint and narrow. Scale bar = 20 μm .

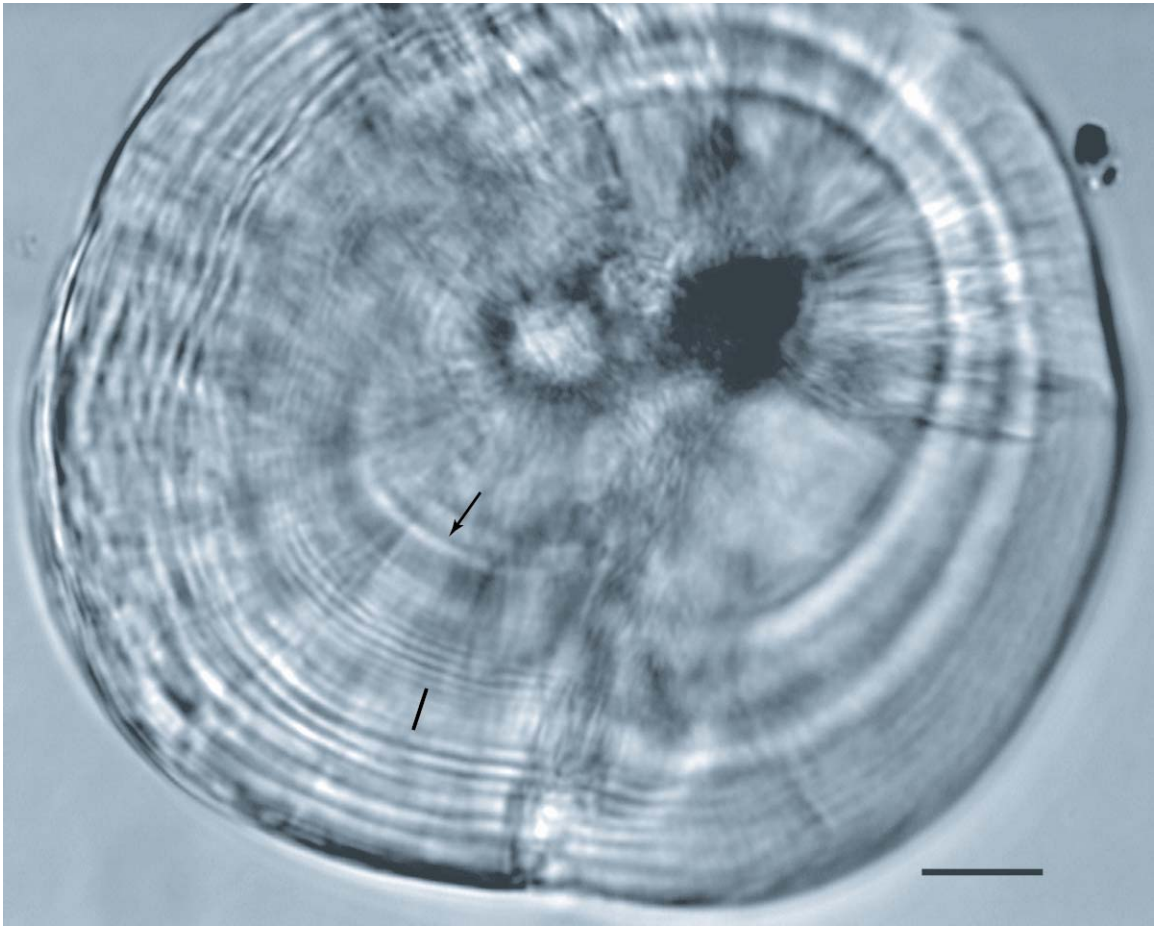


Image C-7. Left sagitta from a 63 day old larva that was starved for 5 days, then refed for 14 days before preservation. The larva had a total length of 14.46 mm. This otolith had a maximum diameter of 95.54 μm and a check diameter of 50.78 μm . The arrow points to the check mark and the bar on the image indicates the period of starvation, during which increments became progressively more faint and narrow. Only 8 increments represent the 14 days after the 5 days of starvation. Scale bar = 10 μm .

APPENDIX D

Distribution of Larval Lake Herring (*Coregonus artedii*) in Lake Superior near the North Entry of the Keweenaw Waterway

INTRODUCTION

In 2000, larval net samples were collected from immediately off the North Entry of the Keweenaw Waterway, in addition to the samples collected offshore in Lake Superior (see Ch. 4). These samples were collected to access if a riverine discharge can influence the distribution of larval fishes. Similar samples were collected during 1998 and 1999 (see Ch. 1), but they were mostly collected later in the season when lake herring numbers were already largely diminished.

Riverine samples in 2000 were collected during 15 – 17 May, 30 May, and 5 – 7 June, but only during the first two of these cruises were catches of lake herring great enough to analyze. The 5 – 7 June cruise captured only 4 larvae with 18 samples, which filtered a total of 1718 m³ of water. During the 15 – 17 May cruise there was a visible murky water plume, and samples were collected from immediately within (0.3 km from shore) and immediately out of the plume front (0.5 km from shore). During the 30 May cruise, no plume was visible, so samples were collected from 0.5 and 1.0 km from shore, along with additional samples from within the break wall. All samples were taken from surface waters during the day. Tow durations were either 3 or 6 minutes during the 15 – 17 May cruise and varied from 5 to 15 minutes during the 30 May cruise, depending on the spatial extent of what was being sampled. Yolk volume was calculated as a prolate spheroid, and total length and yolk volume were corrected for preservation-induced shrinkage, as done for the offshore samples (see Chapter 4). The daily growth rate was

estimated by regressing total length on age, but excluded larvae for which age needed to be estimated with total length because they had yet to produce a check.

Here the data for these riverine samples are presented so that they can be used to supplement the offshore sampling results for 2000, as contained in Chapter 4. First, the density and physical characteristics of larvae within the North Entry region was assessed for spatial differences. Second, the riverine samples were compared to samples at similar distances from shore on the Houghton transects (north and south transects were pooled). In this manner, the riverine influence was assessed on two spatial scales. All statistical analyses were performed with SYSTAT 10 (SPSS Inc.).

LARVAL LAKE HERRING DISTRIBUTION NEAR NORTH ENTRY

During 15 – 17 May, surface water temperatures were less than a degree different within and out of the plume, despite visible differences in turbidity. Larval lake herring were 3.0 times more abundant immediately out of the plume front than within it (two-sample *t*-test, $n_{\text{in plume}} = 4$, $n_{\text{out of plume}} = 2$, $P = 0.02$) (Figure D-1). Larval characteristics were similar within and out of the plume in terms of total length (two-sample *t*-test, $n_{\text{in plume}} = 20$, $n_{\text{out of plume}} = 35$, $P = 0.05$), age (two-sample *t*-test, $n_{\text{in plume}} = 10$, $n_{\text{out of plume}} = 5$, $P = 0.24$), yolk volume (two-sample *t*-test, $n_{\text{in plume}} = 10$, $n_{\text{out of plume}} = 5$, $P = 0.70$), and number of caudal fin rays (two-sample *t*-test, $n_{\text{in plume}} = 10$, $n_{\text{out of plume}} = 5$, $P = 0.50$) (Figure D-1).

By 30 May, densities of lake herring were greatly reduced but they still differed spatially (single-factor ANOVA, $N = 16$, $P = 0.02$), with density at 1.0 km being 5.0 times greater than at 0.5 km (Tukey test, $P = 0.04$) and 18.7 times greater than within the canal (Tukey test, $P = 0.03$) (Figure D-1). However, the canal and the 0.5 km densities

did not differ statistically (Tukey test, $P = 0.90$). Only one larva was captured within the canal, so lake herring apparently did not readily enter the approximately 3 °C warmer water within the canal. Because of the low catch within the canal, only the 0.5 and 1.0 km locations were analyzed for differences in larval characteristics. Larvae at the 0.5 km location were on average 1.6 mm longer (two-sample t -test, $n_{0.5 \text{ km}} = 8$, $n_{1.0 \text{ km}} = 58$, $P = 0.003$), 7 days older (two-sample t -test, $n_{0.5 \text{ km}} = 8$, $n_{1.0 \text{ km}} = 20$, $P = 0.009$), and had approximately 4 more caudal fin rays (two-sample t -test, $n_{0.5 \text{ km}} = 8$, $n_{1.0 \text{ km}} = 20$, $P = 0.02$) than larvae at the 1.0 km location (Figure D-1), despite the 1.0 km location having greater densities. In contrast, yolk volume did not differ statistically between locations (two-sample t -test, $n_{0.5 \text{ km}} = 8$, $n_{1.0 \text{ km}} = 20$, $P = 0.26$).

COMPARISON OF LARVAL LAKE HERRING DISTRIBUTIONS BETWEEN THE NORTH ENTRY AND THE HOUGHTON TRANSECTS

At a larger spatial scale, during 15 – 17 May, density of lake herring about the North Entry plume (with within plume and out of plume locations pooled) was 4.7 times greater than at the Houghton transects within 0.5 km from shore (two-sample t -test, $n_{\text{North Entry}} = 6$, $n_{\text{Houghton}} = 8$, $P = 0.01$) (Figure D-2). Larvae from the Houghton transects were on average 0.72 mm longer than larvae from North Entry (two-sample t -test, $n_{\text{North Entry}} = 55$, $n_{\text{Houghton}} = 51$, $P = 0.02$) (Figure D-2). However, larvae from these locations did not differ statistically in terms of age (two-sample t -test, $n_{\text{North Entry}} = 15$, $n_{\text{Houghton}} = 20$, $P = 0.73$), yolk volume (two-sample t -test, $n_{\text{North Entry}} = 15$, $n_{\text{Houghton}} = 21$, $P = 0.89$), or number of caudal fin rays (two-sample t -test, $n_{\text{North Entry}} = 15$, $n_{\text{Houghton}} = 21$, $P = 0.68$).

Densities at both North Entry and the Houghton transects within 1.0 km from shore were greatly reduced by 30 May, but the North Entry density was still greater, by 4.8 times, although not statistically greater (two-sample t -test, $n_{\text{North Entry}} = 12$, $n_{\text{Houghton}} =$

8, $P = 0.07$) (Figure D-2). However, larvae between locations did not differ statistically in terms of total length (two-sample t -test, $n_{\text{North Entry}} = 66$, $n_{\text{Houghton}} = 11$, $P = 0.93$), age (two-sample t -test, $n_{\text{North Entry}} = 28$, $n_{\text{Houghton}} = 10$, $P = 0.62$), yolk volume (two-sample t -test, $n_{\text{North Entry}} = 28$, $n_{\text{Houghton}} = 10$, $P = 0.53$), or fin rays (two-sample t -test, $n_{\text{North Entry}} = 28$, $n_{\text{Houghton}} = 10$, $P = 0.41$) (Figure D-2).

Surface water temperatures differed by less than a half degree Celsius between North Entry and the Houghton transects for both cruises (Figure D-2). However, daily growth rates, as estimated by regressing total length on age, were greater on the Houghton transects than at North Entry during both cruise (Figure D-3), but only statistically greater for the first cruise (15 – 17 May cruise: multiple regression, $n = 31$, $R^2 = 0.81$, $P = 0.04$ for age X location interaction; 30 May cruise: multiple regression, $n = 33$, $R^2 = 0.82$, $P = 0.33$ for age X location interaction).

CONCLUSIONS

These results show that a riverine discharge can influence the distribution of larval lake herring. Lake herring congregated off North Entry at higher densities than what was observed for similar distances from shore on nearby transects. Yet, there was no evidence that lake herring benefited, in terms of growth rate, from the slightly warmer discharge, nor was there evidence, in terms of age, that larvae maintained a position near North Entry longer than they do at nearby locations in the lake. However, for the 30 May cruise, larvae at the nearer to shore location were larger, older, and more developed, following a trend that was evident on a much larger scale within Lake Superior (see Chapter 4). The front of the riverine plume, or the area of potential riverine influence when a plume was not visible, seemed to have been attractive to larvae, despite water

temperatures differing only slightly within the riverine area, and from the riverine area to nearby locations in the lake. Larvae most likely had to actively choose to be in the riverine location for higher densities to persist there. Yet, it still remains a mystery what benefit larvae experience by choosing to congregate around a riverine discharge, and for how long larvae are willing to remain, or are capable of remaining, in such an area.

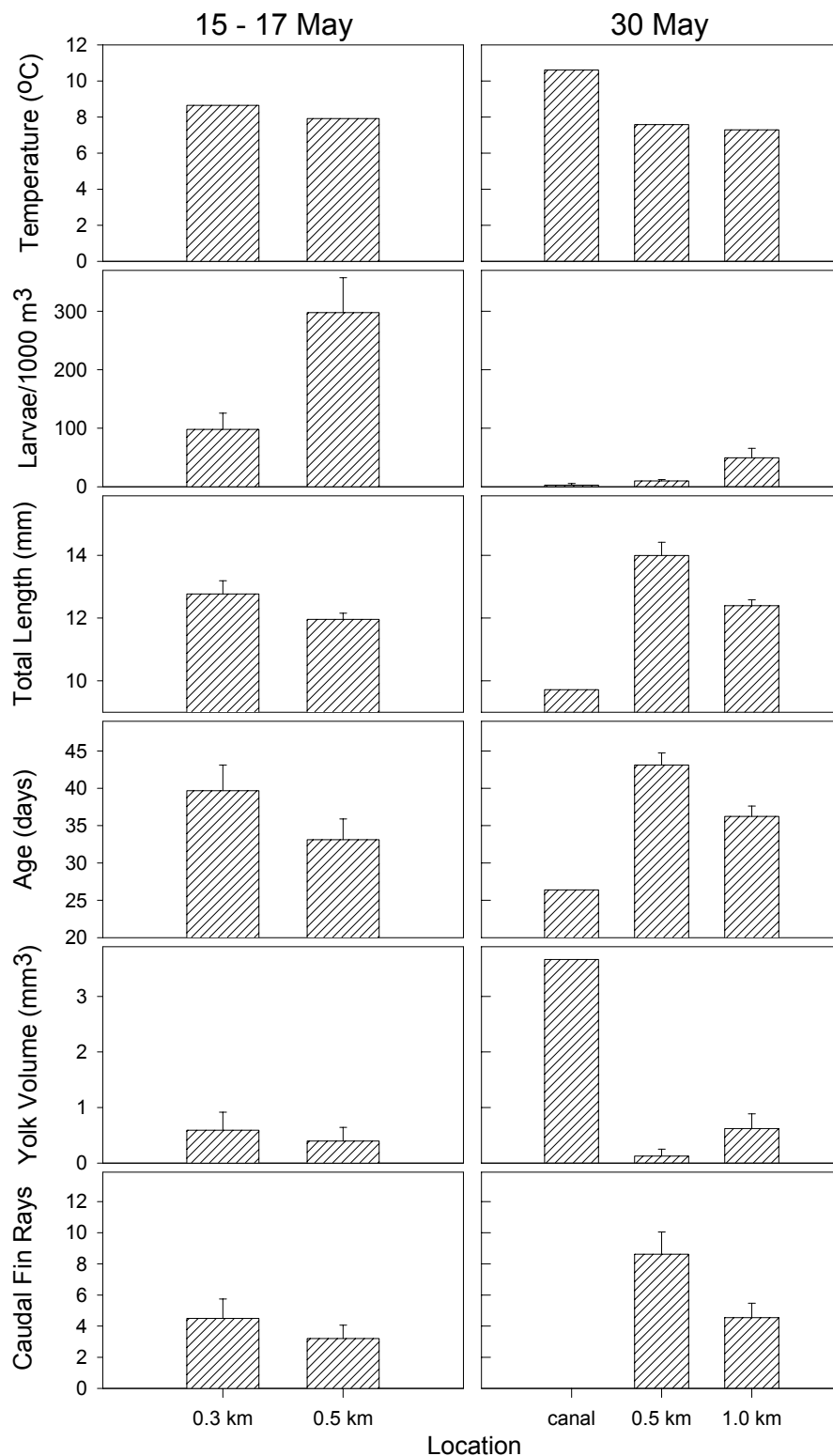


Figure D-1. Densities and characteristics of larval lake herring captured in Lake Superior in 2000 from near the North Entry of the Keweenaw Waterway, Michigan, and surface water temperatures at these locations.

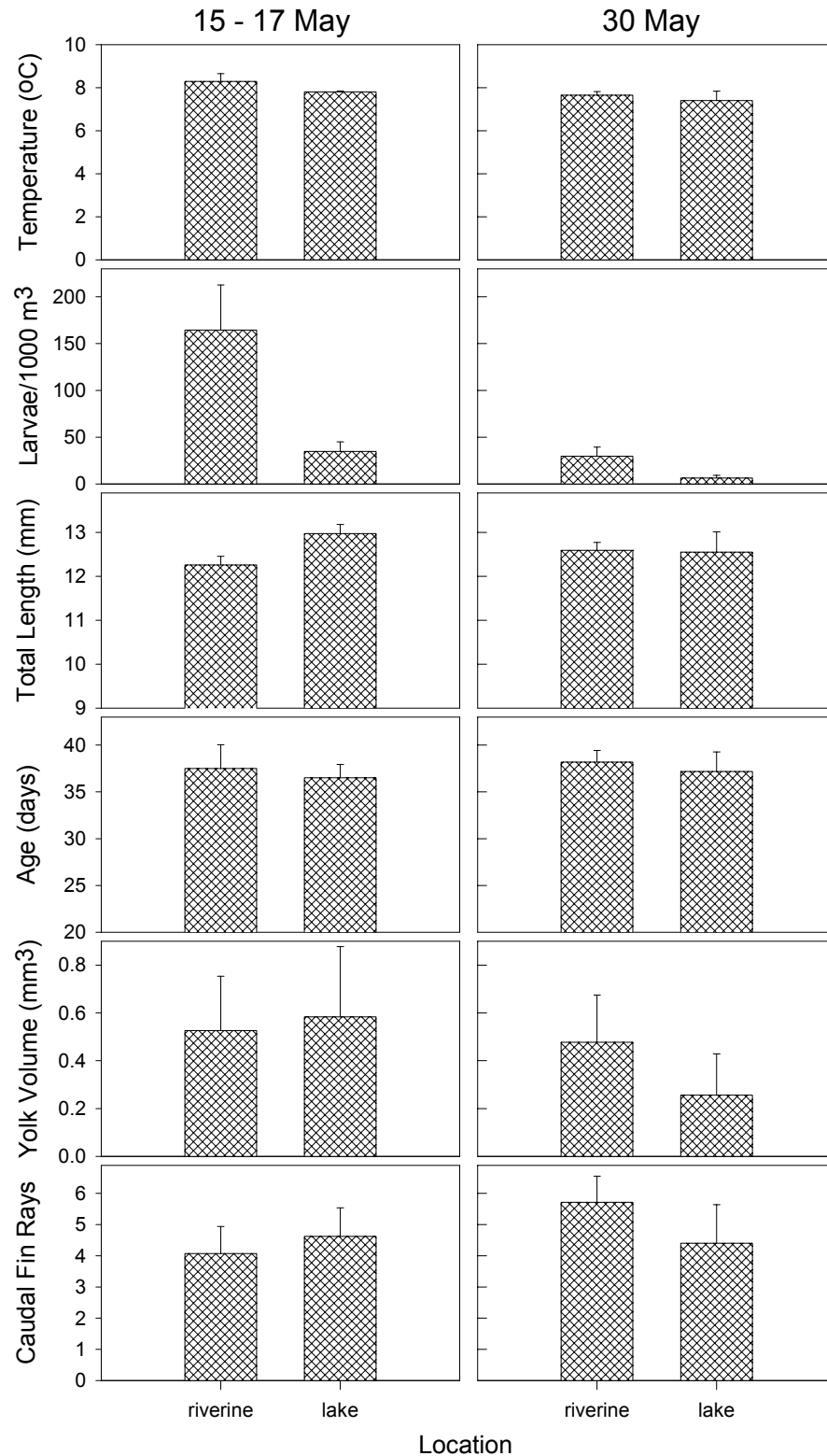


Figure D-2. Comparison of larval lake herring captured in Lake Superior in 2000 from near the North Entry of the Keweenaw Waterway, Michigan, and from transects in Lake Superior at similar distances from shore.

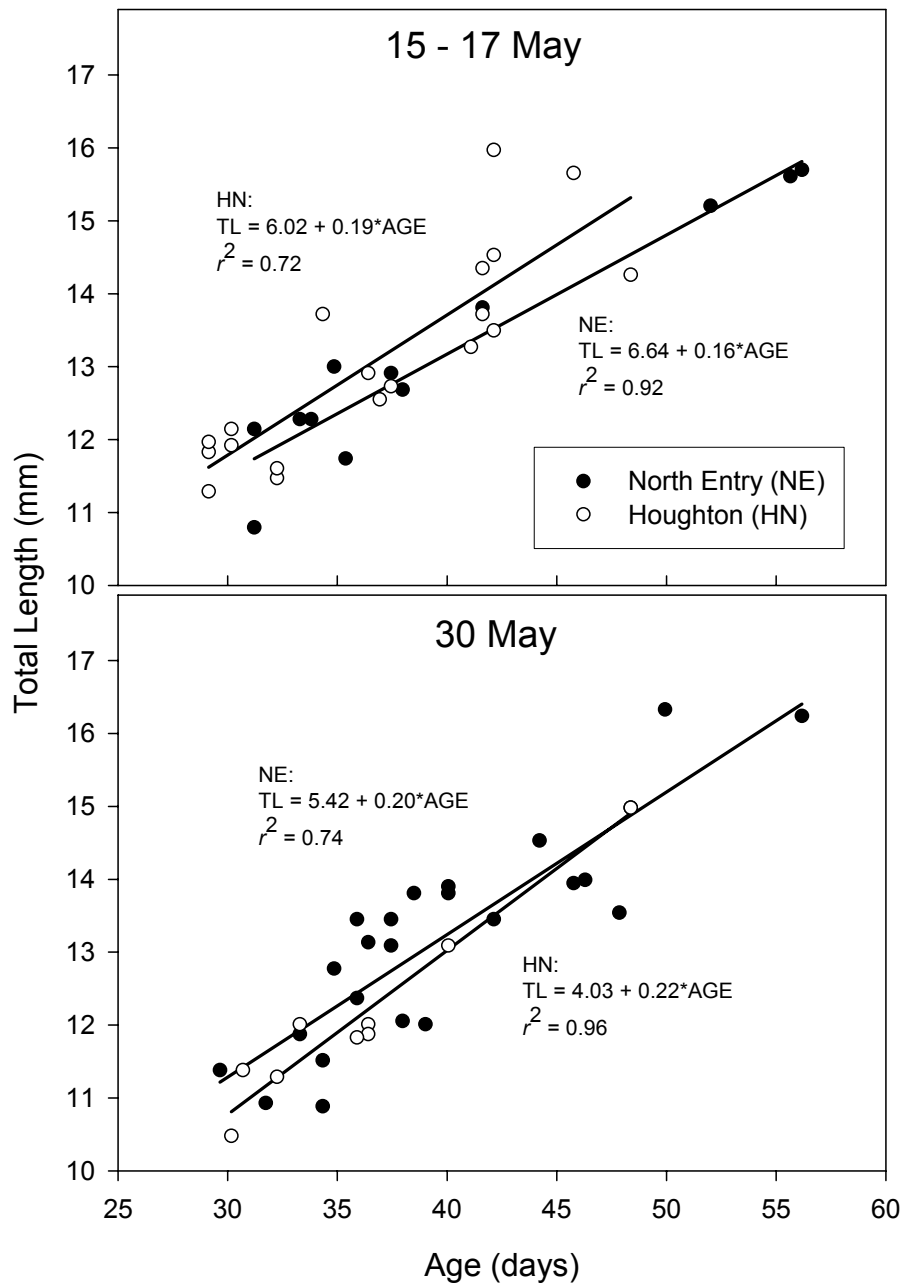


Figure D-3. Total length (TL) vs. age regressions for larval lake herring captured in Lake Superior in 2000 from near the North Entry of the Keweenaw Waterway, Michigan, and from transects in Lake Superior at similar distances from shore. The slopes of the regressions indicate the difference in daily growth rate between the two locations for the two sampling cruises.