Energy Content of Rainbow Smelt (*Osmerus mordax*) in Lake Huron, and a Comparison between Lake Huron and Erie

By

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Abstract

Rainbow smelt (*Osmerus mordax*) is major planktivorous fish species in Lake Huron, providing important energy and nutrient pathways for piscivores. The main objective of this study was to identify current status of energy content of rainbow smelt under declining lake productivity in Lake Huron. Rainbow smelt were sampled by bottom and mid-water trawls on research vessels in Lake Huron and Lake Erie from April to September in 2017. A total of 1603 rainbow smelt were later processed and measured in the laboratory. Overall, before spawning in April, female rainbow smelt from Lake Huron had 9.2% higher energy density than males, and also had increasingly higher total energy content at larger TL. Energy density of rainbow smelt decreased 10% from April to June after spawning, then increased 3.6% from June to July and 9.9% from July to September. Energy density in September was 3.5% higher than that in April. Energy density of rainbow smelt from Lake Erie was up to 60.3% higher for small rainbow smelt (< 90 mm) and up to 36.5% higher for large fish (≥ 90) than that from Lake Huron. Within Lake Huron, energy density of rainbow smelt from North Channel was slightly higher than that from other regions. Rainbow smelt from Georgian Bay generally had the lowest energy density. Across 6 sites in both lakes, chlorophyll *a* concentration had a strong positive correlation with energy density for both small ($r = 0.99$) and large ($r = 0.99$) rainbow smelt. Rainbow smelt started to become mature at 80 mm in total length and all fish became mature when longer than 120 mm in total length. Results in this study showed that energy density of rainbow smelt in Lake Huron was 4-31% lower than historical data from studies before 2004.

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Introduction

The Laurentian Great Lakes have experienced substantial changes in nutrient inputs, productivity, fish composition, and biomass (Bunnell et al., 2014; O'Brien et al., 2016). To maintain and enhance their ecosystem services after substantial anthropogenic changes, the lakes have been subject to many management strategies in the last few decades, such as stocking of salmonid piscivores (Dobiesz et al., 2005) and reducing nutrient input to control the extent of eutrophication (Paterson et al., 2014). At the same time, other unintended influences by human activities, such as invasions of spiny waterflea (*Bythotrephes longimanus*) (Colautti et al., 2005), nonindigenous zebra and quagga mussels (*Dreissena* spp.) (Nicholls et al., 1999), and round goby (*Neogobius melanostomus*) (Charlebois et al., 2001) also have reconstructed aquatic ecosystems. These changes in Lake Huron have resulted in a reduction in the concentration of chlorophyll *a* (Bunnell et al., 2014). Crustacean zooplankton biomass, particularly cyclopoid copepod and herbivorous cladocerans, has declined dramatically (Barbiero et al., 2009; Bunnell et al., 2014). Amphipods like *Diporeia,* which are benthic invertebrates, also showed a continuous decrease with the increase of nonindigenous dreissenid mussels (Bunnell et al., 2014). The results of declines in primary production, as well as secondary production and biomass in the lower food web, could limit production of planktivorous fish in the upper food web.

Planktivorous fish in Lake Huron, such as rainbow smelt (*Osmerus mordax*), alewife (*Alosa pseudoharengus*), and bloater (*Coregonus hoyi*), which mainly feed upon zooplankton, benthic macroinvertebrates and early life stages of many fish species (Feiner et al., 2015), are primary food sources for commercially and recreationally important piscivores. As a result, they play an important role in transfer of nutrients and energy from lower trophic levels to piscivores, and could face both bottom-up and top-down regulation (Paterson et al., 2014). Acoustic surveys conducted by US Geological Survey in Lake Huron showed that biomass of alewife, rainbow smelt, and bloater were all considerably lower in 2015 compared to 1997 (O'Brien et al., 2016). Specifically, the alewife population collapsed in 2003 (Dunlop and Riley, 2013), which further damaged the Chinook salmon (*Oncorhynchus tshawytscha*) (Madenjian et al., 2004) fishery and resulted in cessation of salmon stocking in southern Lake Huron. Thus, it is essential to investigate current growth of planktivorous fish species. From an ecosystem perspective, the decrease of lake productivity due to dreissenid mussels and reduced annual total phosphorus inputs (TP) (Bunnell et al., 2014) could reduce the biomass of planktivorous fish species (Gorman and Weidel, 2012; Bunnell et al., 2013). The declining biomass of planktivorous fish could also increase predation pressure from piscivores.

Among all planktivorous fish species in Lake Huron, rainbow smelt is important due to its dominant biomass (O'Brien et al., 2016). Rainbow smelt, a nonnative prey fish species, was abundant across all the Laurentian Great Lakes since the 1940s (Norman et al., 2006). It is an important food source for many piscivores, including lake trout (*Salvelinus namaycush*), walleye (*Sander vitreu*s), Chinook salmon, coho salmon (*Oncorhynchus kisutch*), and steelhead (*Oncorhynchus mykiss*) (Brandt, 1986; Diana, 1990; Lantry, 2001, Jacobs et al, 2010; Sheppard et al., 2015). In addition, rainbow smelt can influence other planktivorous fish species by competing with bloater, alewife, and cisco (*Coregonus artedi*) for declining densities of plankton and benthic invertebrates that are not dreissenids. They can also directly consume young life stages of these fish species (Anderson and Smith, 1971a, 1971b; Myers et al., 2009). Recently, the biomass of rainbow smelt in the main basin of Lake Huron decreased to less than 15% of peak biomass in the 1980s (O'Brien et al., unpublished data from USGS). Also, rainbow smelt collected in the 2010s had a truncated age structure and reduced growth rate compared to the 1970s (Feiner et al., 2015). Nonetheless, rainbow smelt was still the most abundant planktivorous fish species in Georgian Bay and the North Channel in Lake Huron in 2017, where they comprised 58% and 75% of planktivorous fish biomass, respectively. Rainbow smelt also comprised about 25% of planktivorous fish biomass in the main basin (O'Brien et al., unpublished data from USGS Great Lakes Science Center). Significant changes of both planktivorous fish biomass and species composition may not only influence the diet of piscivores, but also change predation pressure on lower trophic levels from planktivorous fish species. Because rainbow smelt play an important role as the food source for piscivores in Lake Huron (Roseman et al., 2014), potential changes of its energy content due to decreasing biomass and production in its invertebrate prey are likely to dramatically influence piscivores, and potentially affect other planktivorous fish species indirectly by changing the food selection of piscivores.

Considering declines in lake productivity and rainbow smelt biomass, I sought to test whether reduced productivity could influence energy content of rainbow smelt. Here, energy density is a useful metric (Rand et al., 1994) since it is related to food quality and quantity (Madenjian et al., 2000) and it provides fish information on growth, reproduction, and overwintering ability (Pothoven et al., 2006). As a result, energy density can be used to analyze how changes of productivity in lower trophic levels can affect planktivorous fish production. For example, Madenjian et al. (2006) showed that since the invasion of nonindigenous dreissenid mussels in Lake Michigan during the 1990s, the energy density of adult alewife had declined 23%, which was attributed to the decline of *Diporeia* in adult alewife diet. Energy density of planktivorous fish may also affect their rate of consumption by piscivores, as Madenjian et al. (2006) showed a decline of energy density of alewife caused Chinook salmon to consume more individual prey to maintain similar level of growth. This would exert more predation pressure on planktivorous fish. Paterson et al. (2014) measured the trend of energy density for 100-150 mm rainbow smelt in the main basin of Lake Huron from 1989-2011 and concluded that energy density declined 12%, concomitant with 50% reductions of phytoplankton and zooplankton biomass from 1999 to 2006, and reduced abundance of native benthic invertebrates after invasion by dreissenid mussels (Barbiero et al., 2011a; Barbiero et al., 2012). Paterson et al. (2014) also mentioned the growth of piscivores seemed to be limited because of reduced production capacity in lower trophic levels. In addition to temporal changes in energy density of rainbow smelt, energy density is also likely to vary spatially due to differences in production of its food in different regions, and seasonally due to different energy use during spawning and overwintering.

In this project, I evaluated growth conditions of rainbow smelt through changes in energy content and explored limiting factors for its energy content. My first objective was to evaluate seasonal, sex-specific, and age-specific trends in energy density and total energy content of rainbow smelt. My second objective was to make comparisons of energy density for rainbow smelt across different regions in Lake Huron, including the Main Basin, Georgian Bay, North Channel, and Saginaw Bay, as there may be different productivity in these regions. Considering the significantly higher primary productivity in western Lake Erie, I also compared energy density of rainbow smelt from western Lake Erie to Lake Huron. My third objective was to determine whether chlorophyll *a* concentration, as an index of lower trophic level productivity, can explain differences in energy density among collection locations. For my first objective, I expected to find differences of energy density and total energy content between sexes due to different amount of investment in reproduction by males and females. I also expected to find seasonal differences of energy density with a decline after the spawning season. For my second objective, I expected to find much higher energy density in rainbow smelt from western Lake Erie because of higher primary production. I also expected that rainbow smelt energy density in Lake Huron would vary along with primary production in different sites. For my third objective, I expected to find a strong positive relationship between chlorophyll *a* concentration and rainbow smelt energy density.

Materials and Methods

Field sampling

Rainbow smelt were sampled by bottom and mid-water trawls in different ports, except Saginaw Bay, in Lake Huron by the USGS Great Lakes Science Center, as a part of Coordinated Science and Monitoring Initiative from April to September in 2017. Field sampling was conducted on R/V Arcticus and R/V Sturgeon at night. Fish were sampled with a 10 min tow of a bottom trawl (12 m headrope with 13 mm mesh in the cod end) dragged on a depth contour, or by a mid-water trawl (16 m headrope with 6.4 mm mesh in the cod end liner) dragged in the water column at night. Sampling depths ranged from 46 to 82 m for bottom trawl, and 18 to 46 m for mid-water trawl. The complete sampling mission included transects at nine ports: Thessalon River and Spanish River in North Channel (NC); French River, Parry Sound and Nottawasaga River in Georgian Bay (GB); Saugeen River and Hammond Bay in Northern Main Basin (NMB), and Harbor Beach and Maitland River in Southern Main Basin (SMB) (Fig. 1). In April, sampling occurred in all nine ports. In June, sampling only occurred in Thessalon River and Spanish River in North Channel and Hammond Bay in Northern Main Basin. In July, sampling occurred in all nine ports. In September, sampling occurred in Thessalon River and Spanish River in North Channel, and French River and Parry Sound in Georgian Bay. At each port and depth, the goal was to collect up to 20 large (≥ 90 mm total length (TL)) and 40 small (< 90 mm TL) rainbow smelt. Once captured, all rainbow smelt were separated by size category, bagged with water, and immediately frozen at -80°C on the research vessel. After each sampling mission, rainbow smelt were transported to a freezer in the laboratory at the USGS Great Lakes Science Center in Ann Arbor, Michigan. Smelt in Saginaw Bay (SB) were collected by Steve Pothoven at NOAA in May and September, 2017 using 10-15 minute tows of a bottom trawl (7.6 m headrope with 32 mm stretched-mesh liner). All other methods were similar to those described above. Rainbow smelt were also sampled in western Lake Erie (LE) during daylight hours by 10 min tows of a bottom trawl (11.2 m headrope with 14 mm stretched-mesh liner) in June and September, 2017, by the USGS Lake Erie Biological Station. Sampling depths ranged from 24.6 to 48.3 m. All other protocols were similar to those listed above.

Laboratory analysis

To prepare the rainbow smelt to be dried, fish were thawed in the USGS laboratory. For each group, up to 20 large and 40 small rainbow smelt were processed. Individual TL was measured to the nearest mm. To estimate the ages of rainbow smelt with TL $\geq$ 50 mm, both pectoral fins were cut as near to the base as possible to avoid obscuring the inner annuli, and then stored in envelopes based on the protocol in Walsh et al. (2008a). The stomach of each individual was removed to prevent diet items from biasing the energy density estimate. Sex and maturity condition were visually determined for each fish based on the development of gonads. Each rainbow smelt was placed on a pre-weighed aluminum tin and weighed to the nearest 0.0001 g to estimate wet weight. Fish were dried in an oven at 65°C to constant weight (nearest 0.0001 g). For rainbow smelt TL < 50 mm, neither pectoral fins nor the stomach was removed before weighing and drying, and up to 7 individuals for a given length class (5-mm intervals, e.g. 40-44, 45-49 mm) were combined on an aluminum tin to estimate dry weight for the group.

To prepare dried tissue for bomb calorimetry, up to 15 large rainbow smelt per port (pooled across depths) were selected for each month to be representative of the length distribution of the sample. They were individually ground using a coffee grinder and stored in glass jars. Small rainbow smelt (< 90 mm) were combined into composite samples to be ground so that the total dry weight was at least 0.4 g. Individual small fish whose dried weight exceeded 0.4 g were ground individually. Up to 15 samples (composites or individuals) per port per month were ground for small rainbow smelt and stored in glass jars. The ground sample in each jar was combusted in a Parr 1261 isoperibol bomb calorimeter standardized with benzoic acid to obtain energy density per dry weight (kJ/g dry weight) for each individual or composite. Then, energy density (kJ/g wet weight) for each bombed individual or composite was calculated based on dry weight : wet weight (DW: WW), and total energy content was obtained for these fish by multiplying energy density (kJ/g wet weight) and wet weight (g).

Estimation of chlorophyll a concentration

Chlorophyll sampling was done along with fish sampling at each site. Water samples were collected in top, middle and bottom layers. In Lake Huron in unstratified water, 1L of water was sampled by a Niskin bottle at 5 m below surface, at 2 m above the bottom, and halfway between the near-top and near-bottom collection depths. In stratified water, the near-top and near-bottom collection depths were the same as in unstratified waters, but the middle depth (termed “Fmax”) was either the depth where chlorophyll *a* maximum was > 2 times the baseline based on fluorescence estimated from a Seabird bathythermograph or midway down the metalimnion if no Fmax was observed. The water sample was filtered immediately using a 47 mm Whatman GF/F filter, and then placed in a foil covered vial in a freezer, and later processed by the EPA Mid-Continent Laboratory in Duluth, Minnesota, using the modified fluorometric technique (Arar and Collins, 1997). Chlorophyll *a* concentration (ug/L) at each sampling site was averaged based on the three water layers sampled in each month. Chlorophyll *a* data in Lake Huron was available in spring (April + May), June, July and August, 2017. When I compared chlorophyll *a* concentration in Lake Huron sites, I averaged it across all months for each site. Chlorophyll *a* data in Lake Erie were obtained from Great Lakes Environmental Database (GLENDA), EPA, which included April and August data for western Lake Erie in 2017. All sampling methods were the same as done for chlorophyll *a* in Lake Huron, except sampling at 2 m below surface for the top layer. When I conducted across-lake analyses, I averaged chlorophyll *a* data from months that were available for both lakes.

Aging

Rainbow smelt collected in April that were ≥ 90 mm were used for aging. Collections from North Channel, Georgian Bay, and Main Basin all had enough large rainbow smelt to give reasonable results. In the laboratory, up to 10 individuals from each TL class (e.g. 90-99 mm, 100-109 mm) were chosen from each port. The method used for aging was based on Walsh et al. (2008a). A pectoral fin ray was imbedded on a cardboard tag in 30 min epoxy resin, which was mixed with charcoal powder to ensure contrast. After 24 hours, a thin section (0.2 – 0.4 mm) of each pectoral fin ray was cut near the base to avoid obscuring inner annuli. All cutting work was done with 102 × 0.3 mm diamond wafering blades on a low-speed precision saw (Buehler, Lake Bluff, Illinois). Thin sections were mounted on glass microscope slides using Shandon-mount, and covered by cover slips. The reading process included three steps by two readers. First, the two readers aged all 174 fin rays at 100× magnification (Fig. 2) and compared results. Second, all fin rays with different estimates were aged again, independently by the two readers. Third, if disagreements remained, the two readers tried to achieve a consensus age. Otherwise, they discarded that fin ray. Finally, 19 of 174 fin rays were determined unreadable and were discarded.

Data analysis

Because I did not measure energy density for all individuals, I tested whether DW : WW could be used to predict energy density for all remaining dried individuals and composites. I plotted energy density against DW : WW to verify their relationship and also explored whether this relationship varied with fish size, lake, or season. If not, I used a universal model to estimate energy density based on DW : WW for remaining fish without direct measurements. Otherwise, I separated rainbow smelt and used different models to reduce bias.

I explored whether variation in energy density was best explained by rainbow smelt WW or TL, so that I could use it as the covariate for correction in later analysis of covariance (ANCOVA). I did not find a highly consistent relationship between WW and energy density in the two lakes, while TL showed a continuous positive linear relationship with energy density. TL was used as a covariate in the statistical tests.

To evaluate whether energy density and total energy content of rainbow smelt varied between males and females from North Channel (where most large fish were collected), I first studied the maturity of males and females in each age stage and size class in April. I used ANCOVA where TL was a covariate and sex was a fixed factor, and the interaction was evaluated. If the interaction was not significant, Least Squares Means (LS Means) of energy density and total energy content were calculated to compare males and females. Otherwise, energy density and total energy content were compared at different TL.

To evaluate whether energy density of rainbow smelt changed seasonally, I focused on North Channel because there were rainbow smelt available from all four time periods. I pooled fish from both sites (e.g., Thessalon River and Spanish River) and to facilitate comparison with previous studies I used rainbow smelt ≥ 100 mm (Rand et al., 1994; Vondracek et al., 1996). I used ANCOVA where TL was a covariate and month was a fixed factor, and the interaction was evaluated. If the interaction was not significant. LS Means of energy density in different time periods were compared with Bonferroni correction. Otherwise, energy density was compared at different TL.

To evaluate whether rainbow smelt energy density differed among regions (i.e., Main Basin, Georgian Bay, North Channel, Saginaw Bay, and western Lake Erie), I separated large and small rainbow smelt. I first tested whether there was significant interaction between TL and region. If the interaction term was not significant, energy density was compared across regions in each month using an ANCOVA and LS Means were also compared with a Bonferroni correction. If the interaction term was significant, energy density was compared at different TL based on values from linear regressions with energy density as the independent variable, and region and TL as dependent variables. Because I aged large rainbow smelt in April, I was also able to explore energy density and total energy content of individuals from different age classes. I used ANOVA to make regional comparisons of age-based energy density and total energy content.

I evaluated the linkage between chlorophyll *a* concentration and energy content using Pearson's correlation. I calculated the arithmetic mean energy density for rainbow smelt < 90 mm and ≥ 90mm in the North Channel and Georgian Bay in July, the month with the largest sample size. Because previous studies (Rand et al., 1994; Vondracek et al., 1996) indicated that energy density of rainbow smelt was lower in June than that in July, energy density of rainbow smelt in June in Lake Erie should be a conservative estimate for that in July. Thus, it is reasonable to combine rainbow smelt in Lake Erie in June and rainbow smelt in Lake Huron in July into Pearson's correlation model. Besides exploring Pearson's correlation, I also compared chlorophyll *a* concentration between each site in Lake Huron and between two lakes using ANOVA.

All tests were done using RStudio (Version 1.1.383, R Core Team, 2017), with significance level = 0.05.

Results

Based on 436 and 39 bombed individuals and composites in Lakes Huron and Erie, respectively, the energy density of rainbow smelt was strongly correlated to DW : WW. This relationship from bombed fish varied between the two lakes ($F_{1, 513} = 16.6$, $P < 0.001$) (Fig. 3), with energy density at a given DW : WW ratio higher in Lake Erie than in Lake Huron, especially when DW : WW became larger. To be conservative, separate models were used to estimate energy density for remaining unmeasured 831 and 44 dried individuals and composites in Lakes Huron and Erie, respectively. The regression for Lake Huron was: energy density (kJ/g wet) = - 0.219 + 23.112 $\times$ DW : WW, $r^2 = 0.938$. The regression for Lake Erie was: energy density (kJ/g wet) = - 1.404 + 29.080 $\times$ DW : WW, $r^2 = 0.908$. In total, energy density and total energy content of 881 small (Table 1) and 722 large (Table 2) rainbow smelt were directly measured or estimated by DW : WW.

In both lakes, energy density of rainbow smelt increased with TL and WW, but patterns were different. Energy density increased linearly with TL in both lakes (Fig. 4a), with $r^2 = 0.72$ for Lake Huron and 0.65 for Lake Erie. However, the relationship between WW and energy density did not show a consistent pattern between lakes (i.e., linear in Erie and non-linear in Huron, Fig. 4b). Because TL varied linearly with energy density in both lakes, I used TL as the covariate in all analyses below.

For large rainbow smelt in North Channel in April, 2017, females had higher energy density than males, and also had increasingly higher total energy content at larger

TL. The relationship between energy density and TL did not vary between sexes for large fish in April ($F_{1, 54} = 0.90$, $P = 0.346$). There was a significant difference in energy density between male and female fish ($F_{1, 55} = 15.44$, $P < 0.001$) (Fig. 5a). Females had 9.2% higher energy density than males based on LS Means (Female: 4.54 kJ/g; Male: 4.16 kJ/g). The relationship between total energy content and TL did vary between sexes for large fish ($F_{1, 54} = 7.17$, $P = 0.010$), and TL of rainbow smelt was important in determining total energy content. At 90 mm, females had almost the same total energy content as males, then the difference increased with TL until females had 28.1% higher total energy content than males at 130 mm (Fig. 5b).

Energy density of rainbow smelt in North Channel decreased significantly after spawning, then gradually increased in summer and autumn. The relationship between energy density and TL did not vary by month ($F_{3, 280} = 1.02$, $P = 0.384$). Energy density of rainbow smelt decreased 10% from April (LS mean = 4.29 kJ/g) to June (LS mean = 3.90 kJ/g) ($F_{1, 118} = 40.56$, $P < 0.001$), then increased 3.6% from June to July (LS mean = 4.04 kJ/g) ($F_{1, 164} = 6.61$, $P = 0.011$) and 9.9% July to September (LS mean = 4.44 kJ/g) ($F_{1, 164} = 59.19$, $P < 0.001$) (Fig. 6). Energy density in September was 3.5% higher than that in April ($F_{1, 118} = 6.98$, $P = 0.009$).

Energy density of rainbow smelt from Lake Erie was always much higher than that from Lake Huron (Fig. 7). In June, for small rainbow smelt, the relationship between energy density and TL did not differ across regions in the two lakes ($F_{2, 122} = 0.32$, P =

0.727). A comparison of LS Means revealed small fish from western Lake Erie were 35% more energy dense than those from Northern Main Basin and North Channel (Fig. 7a). The relationship between energy density and TL differed across regions for large rainbow smelt in June ($F_{2, 144} = 9.66$, $P < 0.001$), and those from western Lake Erie still had higher energy density than fish from Northern Main Basin and North Channel (Fig. 7b). The difference in energy density increased with TL. For example, for a 90-mm rainbow smelt, energy density in western Lake Erie was 21.1% and 17.7% higher than in North Channel and northern Main Basin, respectively. For a 110-mm rainbow smelt, differences became 36.5% and 29.4%, respectively. In September, for small rainbow smelt, the relationship between TL and energy density also varied across regions ($F_{3, 210} = 3.49$, $P = 0.017$, Fig. 7c). I limited the comparisons to where TL overlapped among the sites. At 50 mm, rainbow smelt in western Lake Erie had 58.5% and 60.3% higher energy density than in North Channel and Saginaw Bay, respectively (Fig. 7c). Although TL of rainbow smelt in western Lake Erie and Georgian Bay did not overlap (LE: 42-55 mm; GB: 75-89 mm), the arithmetic mean energy density of small fish in western Lake Erie was 16.7% higher despite having a smaller mean TL (LE: 3.95 kJ/g vs GB: 3.38 kJ/g). In September, for large rainbow smelt, the relationship between TL and energy density did not vary across lakes ($F_{3, 127} = 2.19$, $P = 0.093$). Large rainbow smelt in western Lake Erie had significantly higher energy density than in all sampled regions of Lake Huron (Fig. 7d). LS Means of energy density in LE was 12.6%, 18.9%, and 27.4% higher than in NC, GB, and SB, respectively.

In spatial comparisons within Lake Huron, energy density of rainbow smelt from North Channel generally was slightly higher than from other regions (Fig. 8). In spring, the relationship between TL and energy density did not differ across regions for large ($F_{3, 218} = 1.94$, $P = 0.125$, Fig. 8a) or small ($F_{2, 302} = 2.10$, $P = 0.124$, Fig. 8b) fish. Large ($F_{1, 171} = 14.78$, $P < 0.001$) and small rainbow smelt ($F_{1, 301} = 32.44$, $P < 0.001$) in North Channel had higher energy density than in Georgian Bay (Fig. 8a and 8b), with LS Means 6.3% and 6.7 % higher, respectively. In spring, small rainbow smelt in North Channel also had 12.7 % higher energy density than in Northern Main Basin ($F_{1, 100} = 5.40$, $P = 0.022$). In July, the relationship between TL and energy density did not vary across regions for large fish ($F_{2, 206} = 0.85$, $P = 0.431$, Fig. 8c). Large rainbow smelt in North Channel still showed higher energy density than in Georgian Bay ($F_{1, 205} = 9.38$, $P = 0.002$), but the difference was only 3.1%. Small rainbow smelt did not have this pattern (Fig. 8d). In September, the relationship between TL and energy density did not vary across regions for large rainbow smelt ($F_{3, 127} = 2.19$, $P = 0.093$, Fig. 8e). Large rainbow smelt in North Channel showed 5.6% and 13.1% higher energy density than in Georgian Bay and Saginaw Bay (NC-GB: $F_{1, 122} = 13.22$, $P < 0.001$; NC-SB: $F_{1, 87} = 8.10$, $P = 0.006$). Small rainbow smelt did not have this pattern (Fig. 8f).

After separating rainbow smelt into different age classes that had enough samples (age 2 and 3), rainbow smelt in Southern Main Basin had the largest TL and highest total energy content, while rainbow smelt in Georgian Bay were the opposite. Age 2 fish from Southern Main Basin had almost 2 times higher total energy content than from North Channel and Georgian Bay (SMB vs GB: $F_{1, 52} = 69.39$, $P < 0.001$; SMB vs NC: $F_{1, 37} = 17.23$, $P < 0.001$) (Fig. 9). Fish from North Channel had 25.8% higher total energy content than from Georgian Bay ($F_{1, 77} = 7.52$, $P = 0.008$). Age 3 fish from Southern Main Basin had 46.6% higher total energy content than from Georgian Bay ($F_{1, 26} = 6.51$, $P = 0.017$) (Fig. 9). The rank of TL in these three regions was similar to total energy content, with 127 ± 8 (± sd), 110 ± 13, and 132 ± 10 mm for age 2 fish in SMB, NC, and GB, respectively, and 132 ± 10, 122 ± 14, 117 ± 19 mm for age 3 fish in SMB, NC, and GB, respectively.

Over half of rainbow smelt became mature at age 1, and about 80% of the fish were mature by age 2. From age 1 to 4, proportions of maturity were 58.4%, 79.1%, 95.5%, and 90.9%, respectively. Considering the limited number of rainbow smelt in age 1 and 4, I only separated males and females in age classes 2 and 3. The maturity of age 2 fish was 80.4% for males and 93.9% for females after excluding unidentifiable individuals. The maturity of age 3 fish was 96.7% for males and 100% for females after excluding unidentifiable individuals. Rainbow smelt started to become mature at 80 mm TL, then maturity increased with TL. Eventually, all fish longer than 120 mm were mature (Fig.10). For spawning condition, results showed 96.8% of rainbow smelt collected in April had not spawned yet.

Chlorophyll *a* concentration had a highly positive correlation with energy density for both small ($t = 10.01$, $df = 3$, $P = 0.002$, $r = 0.99$) and large fish ($t = 14.22$, $df = 4$, $P < 0.001$, $r = 0.99$) when including both lakes. Average chlorophyll *a* concentration in western Lake Erie (5.15 ± 1.67 ug/L) was significantly higher ($F_{1, 8} = 22.92$, $P = 0.001$) than in North Channel (1.06 ± 0.11 ug/L), which was the region with highest chlorophyll *a* concentration in Lake Huron excluding Saginaw Bay. For Pearson's correlation among 5 ports in Lake Huron, energy density of small or large fish was not significantly related to chlorophyll *a* concentration. However, chlorophyll *a* concentration in North Channel (1.14 ± 0.12 ug/L) was significant higher ($F_{1, 11} = 147.9$, $P < 0.001$) than in Georgian Bay (0.59 ± 0.05 ug/L).

Discussion

I was able to detect a large difference (typically > 20%) in energy density between lakes Huron and Erie for both large and small rainbow smelt. Also, rainbow smelt in North Channel consistently showed higher energy density compared to most other regions of Lake Huron, especially Georgian Bay. These patterns in regional differences generally agreed with expectations for my second objective that western Lake Erie would have much higher energy density. Mean energy density from a given site had a strong positive correlation with chlorophyll *a* concentration, which agreed with expectations for my third objective that there would be a close relationship between primary production and energy density of rainbow smelt. Besides regional differences of rainbow smelt energy density, I also found a difference in energy density between males and females. Energy density of rainbow smelt varied during the year and there was a significant reduction that occurred during the spawning season. Sex and seasonal results generally agreed with my expectations for the first objective that there would be sex differences of energy density and total energy content, and seasonal changes of energy density during spawning season.

The strong positive correlation between chlorophyll *a* concentration in lakes Huron and Erie and energy density of rainbow smelt in two lakes implies food limitation influenced the growth of rainbow smelt in Lake Huron. Chlorophyll *a* concentration could be heavily influenced by biomass of cyanobacteria in summer, especially in western Lake Erie, so that the concentration of chlorophyll *a* in summer may not totally reflect the availability of food for rainbow smelt since many organisms cannot use cyanobacteria efficiently as a food source (Ger et al., 2014). Barbiero et al. (2011b) showed a strong correlation between chlorophyll *a* concentration and major zooplankton biomass in Lake Huron, including cladocerans, cyclopoid and calanoid copepods. Nicholls (1999) stated zooplanktivore abundance strongly controlled phytoplankton density in Lake Erie. Since rainbow smelt consumes mostly small zooplankton, such as copepods and cladocerans, and even algae at young ages, then larger prey, like *Mysis* and other benthos as it grows (Evans and Loftus, 1987; Dauvin and Dodson, 1990; Mills et al., 1995; Johnson et al., 2004; Stetter et al., 2005; Walsh et al., 2008b). Thus, the abundance of prey for rainbow smelt could be closely linked to primary production. As a result, chlorophyll *a* concentration should be an effective indicator of food availability for rainbow smelt. In 2017, chlorophyll *a* concentration in Lake Huron (exclude Saginaw Bay) was only about 11 to 21% of what it was in western Lake Erie. Energy density of rainbow smelt in Lake Huron was also dramatically lower than in Lake Erie, up to about a 50% difference for small fish. Such a big difference in energy density between two lakes implies food limitation in Lake Huron, especially for small rainbow smelt. Without enough nutrient and energy intake, survival, gonad development and reproduction of fish could be affected (Anderson and Sabado, 1995; Platt et al., 2003; Donelson et al., 2010) in Lake Huron. However, such comparison between two lakes could not fully explain the reason for the energy density difference. Bottom food webs vary between the two lakes. For example, *Mysis,* which is important prey for many planktivorous fish species in Lake Huron (Mohr and Ebener, 2005; Pothoven and Madenjian, 2008), does not exist in western Lake Erie because of warmer climate. Also, in Lake Erie, the *Hexagenia* mayfly recruitment recovered and increased in western Lake Erie (Krieger et al., 1996; Bridgeman et al., 2006), providing an alternative high quality food for rainbow smelt (Gordon, 1961). Different food webs potentially caused different prey availability for rainbow smelt.

Both energy content of rainbow smelt and chlorophyll *a* concentrations have regional differences in Lake Huron, but there was not a significant correlation between these two variables. I know of no previous studies of regional energy density of rainbow smelt in Lake Huron that would help explain these differences. For age-based comparisons of total energy content in April, rainbow smelt from the Southern Main Basin showed fastest growth and similar energy density compared to other regions. Notably, all fish (41 individuals) in Southern Main Basin were collected in Maitland, and only one of them was < 100 mm. However, chlorophyll *a* concentration in Maitland was one of the lowest among ports in Lake Huron. This implies that rainbow smelt collected in Maitland may grow in other regions with higher food availability and quality, and then migrate to Maitland River for spawning. Besides Southern Main Basin, energy density of rainbow smelt in North Channel was higher than in Georgian Bay for small and large fish, together with about 2 times higher chlorophyll *a* concentration in North Channel than in Georgian Bay. This implies better growth conditions for rainbow smelt in North Channel than in Georgian Bay, especially for juveniles.

To further investigate reasons for different energy densities between North Channel and Georgian Bay, I compared fish biomass in two regions because Madenjian et al. (2000) showed fish density could affect feeding rates, and thus energy content of fish. O'Brien et al. (2014) also found evidence for density-dependent mortality of rainbow smelt from intraspecific competition in the Main Basin of Lake Huron. Based on acoustic surveys in 2017 (O'Brien et al., unpublished data from USGS), biomass of rainbow smelt in North Channel was nearly 4 times higher than in Georgian Bay; the same difference holds for planktivorous fish biomass in total. As a result, North Channel supported much higher biomass of rainbow smelt, together with higher energy density and faster growth at young ages. Higher biomass of rainbow smelt did not appear to result in significant interspecific or intraspecific competition in North Channel, most likely because the smelt density was still below the threshold for competitive effects to occur.

Female rainbow smelt generally had a higher energy density and faster growth rate than males before spawning. Compared to previous studies, Vondracek et al. (1996) did not find such a significant difference between sexes in Lake Superior, although the limited number of fish collected in each month (109 individuals in 10 months) could affect this discrepancy. For rainbow smelt from Lake Michigan, in April before spawning, energy density in testes and ovaries were 7.5% and 13.7% higher than somatic tissues, and ovaries were heavier than testes (Foltz and Norden, 1977). In April, gonads in mature rainbow smelt I collected were already fully developed. As a result, the difference between sexes in energy density could be largely attributed to the difference in gonads, where ovaries had more energy than testes. Besides energy density, longer females in my study had increasingly higher total energy content than males. This supports the hypothesis that females had higher growth rate than males, especially at older ages, thus implies higher energy and nutrient requirement for old females than males.

Seasonal energy density of rainbow smelt in North Channel decreased to the lowest level after spawning in June, then increased to the highest level in fall. The lowest energy density also occurred in June for rainbow smelt in Lake Superior (Vondracek et al., 1996) and Lake Michigan (Foltz and Norden, 1977). This confirms the spawning season of rainbow smelt in May and great energy input for annual reproduction during this period. Dobiesz (2003) found an increase of energy density from April to June, then a decrease from June to August, which is contradictory to normal reproduction schedule of rainbow smelt (O'Brien, 2010), perhaps due to limited sample sizes in each month. The highest energy density in fall was also supported by all previous studies in the Great Lakes (Foltz and Norden, 1977; Rand et al., 1994; Vondracek et al., 1996; Dobiesz, 2003). This implies rainbow smelt stored a large amount of energy for overwintering. Also, I found both sexes of rainbow smelt in September had considerably developed gonads, which also required much energy.

Rainbow smelt collected in all months showed lower energy density compared to many previous studies in the Great Lakes (Foltz and Norden, 1977; Rand et al., 1994; Vondracek et al., 1996; Dobiesz, 2003) (Fig. 12), except the most recent studies by Paterson et al. (2014), which I will discuss below. In April 2017, energy density was only 75-78% of what rainbow smelt was for studies prior to 2004. In June and July, it was 69-84%. In September, it was 74-96%. The Paterson et al. (2014) study enabled me to explore recent annual trends of energy density of rainbow smelt. To compare it to my study, I followed their standard and included only rainbow smelt sampled from the Main Basin in June to September with TL between 100-150 mm. Rainbow smelt from my study had a mean energy density of 4.1 ± 0.2 (± sd) kJ/g, which was 11% higher than mean energy density reported for 2011 (3.7 ± 0.3 kJ/g), but similar to what was reported for 2010 (about 4.0 ± 0.4 kJ/g). This comparison reveals large interannual variation in energy density, probably due to temperature variation, which influenced primary production, or simply sampling differences. Overall, it seems energy density of rainbow smelt in Lake Huron in 2017 was much lower than fish sampled before 2004 but did not change much since 2010 based on data from Paterson et al. (2014). Such lower energy density in Lake Huron in 2017 demonstrates current growth condition of rainbow smelt is much worse, which could result from the decrease of primary production in recent decades (Bunnell et al., 2014).

Besides energy condition of rainbow smelt, I confirmed that using a cutoff at 90 mm to separate adult and juvenile rainbow smelt was reasonable since half of rainbow smelt at 90-99 mm were mature, and few individuals became mature at sizes smaller than 90 mm. This is a reduction from historical data, with mature rainbow smelt typically longer than 130 mm before 2000 (Vondracek et al., 1996) and longer than 115 mm before 2010 (Feiner et al., 2015).

There were some limitations of my study. First, although I was able to obtain over 2000 individuals in total, most were collected in North Channel and Georgian Bay, which could limit the comparison between my results and the Paterson et al. (2014) study in the Main Basin. Limited individuals collected in the Main Basin and Saginaw Bay made me unable to find consistent results in those sites compared to North Channel and Georgian Bay. More comprehensive regional information could be obtained if more sampling work could be conducted in all regions. Second, I was not able to analyze age for rainbow smelt < 90 mm due to limited time. This influenced the estimation of TL and total energy content for age 1 rainbow smelt. If I had aged fish from a broader range of TL, more accurate and detailed growth and maturation information could have been obtained, including von Bertalanffy growth curves. Third, it was difficult to visually determine sex other than in April, so I could not determine annual trends and differences among sexes of fish. Lastly, I tried to include other environmental variables (biomass of planktivorous fish, rainbow smelt, and *Mysis*) into analyses, to find whether they influenced energy density of rainbow smelt. However, different sampling methods and techniques in the two lakes, together with limited samples, made me unable to complete these analyses accurately.

Overall, I was able to estimate growth, maturity, and energy density of rainbow smelt in lakes Huron and Erie, and compare them to previous studies. In 2017, rainbow smelt in Lake Huron became mature at shorter TL compared to fish in the Great Lakes decades ago (Vondracek et al., 1996; Gorman, 2007; Feiner et al., 2015). Also, rainbow smelt in Lake Huron contained much lower energy density compared to previous studies in the Great Lakes before 2004 (Foltz and Norden, 1977; Rand et al., 1994; Vondracek et al., 1996; Dobiesz, 2003), but energy density did not seem to change a lot in Lake Huron after 2010 (Paterson et al., 2014). Regional comparisons showed positive correlation between primary production and energy density of rainbow smelt. As a whole, despite other mechanisms potentially influencing the growth of rainbow smelt, such as top-down control from piscivore predation, reduced primary productivity is an important factor. From the perspective of fishery management, poor energy density and growth of rainbow smelt due to limited primary production in Lake Huron could affect the health and biomass of recreationally important piscivores. Higher nutrient levels to stimulate primary production could also cause environmental issues. How to achieve a balance, is a tough but important topic for scientists. Overall, studies of the factors driving population dynamics of planktivorous fish species, which are important nutrient and energy pathways for piscivores in the Great Lakes, are important to make optimal management strategies.

Tables:

Date	n	TL (mm)	WW (g)	DW : WW (%)	Energy density (kJ/g wet weight)	Total energy content (kJ)
North Channel (Lake Huron)						
April	99	71.7±7.8	1.59±0.59	0.16±0.02	3.37±0.41	5.48±0.25
June	103	70.7±7.5	1.53±0.65	0.15±0.01	3.17±0.36	5.03±2.68
July	109	74.2±9.8	2.01±0.85	0.15±0.02	3.27±0.42	6.83±3.37
September	67	61.7±10.6	1.10±0.63	0.13±0.01	2.81±0.32	3.25±2.23
Georgian Bay (Lake Huron)						
April	205	62.2±9.5	1.04±0.57	0.14±0.01	2.93±0.31	3.18±2.10
July	57	76.7±8.0	2.31±0.69	0.15±0.01	3.29±0.19	7.64±2.44
September	20	82.4±4.2	2.46±0.37	0.16±0.01	3.38±0.21	8.34±1.36
Northern Main Basin (Lake Huron)						
April	4	77.3±5.9	1.86±0.41	0.15±0.01	3.14±0.13	5.89±1.57
June	10	78.1±8.1	2.23±0.79	0.16±0.01	3.43±0.42	7.83±3.53
July	34	30.4±3.2	0.12±0.09	0.11±0.01	1.25±0.19	0.31±0.24
Southern Main Basin (Lake Huron)						
July	26	32.7±6.4	0.16±0.11	0.11±0.01	2.48±0.28	0.41±0.32
Saginaw Bay (Lake Huron)						
May	1	73.0±0	2.19±0	0.15±0	3.37±0.00	7.37±0.00
September	116	54.3±10.5	0.96±0.58	0.12±0.02	2.67±0.47	2.76±2.04
Western Lake Erie (Lake Erie)						
June	15	76.7±8.9	2.30±0.91	0.21±0.01	4.50±0.32	10.58±4.77
September	15	47.9±4.1	0.48±0.13	0.18±0.02	3.95±0.34	1.93±0.63

Table 1. Number of small (< 90 mm) rainbow smelt (n = 881, total), monthly mean (± sd) total length (TL), wet weight (WW), dry weight : wet weight (DW:WW), energy density (kJ/g wet weight), and total energy content (kJ) sampled in different regions of Lake Huron and in western Lake Erie in 2017.

Date	n	TL (mm)	WW (g)	DW : WW (%)	Energy density (kJ/g wet weight)	Total energy content (kJ)
North Channel (Lake Huron)						
April	61	113.9±14.9	7.94±3.62	0.19±0.02	4.29±0.45	34.36±17.39
June	92	109.4±12.6	6.29±2.26	0.18±0.01	3.86±0.31	24.45±9.44
July	118	109.6±11.4	6.75±2.26	0.18±0.02	3.99±0.39	27.18±10.17
September	85	118.9±16.5	9.15±4.30	0.20±0.02	4.35±0.42	40.75±20.94
Georgian Bay (Lake Huron)						
April	113	103.6±10.8	5.99±2.38	0.18±0.02	3.93±0.42	23.88±10.44
July	90	109.1±12.1	6.65±2.74	0.18±0.01	3.83±0.31	25.61±10.91
September	40	116.2±13.7	7.86±3.20	0.18±0.01	4.08±0.40	32.95±15.27
Northern Main Basin (Lake Huron)						
June	5	112±14.3	7.24±2.44	0.19±0.01	4.09±0.29	29.82±10.44
Southern Main Basin (Lake Huron)						
April	41	128.4±10.1	11.76±3.01	0.19±0.02	4.25±0.49	50.58±15.48
July	4	139.0±3.4	14.13±0.61	0.19±0.01	4.12±0.11	58.16±2.46
Saginaw Bay (Lake Huron)						
May	10	119.0±16.9	10.33±5.08	0.19±0.02	4.28±0.51	46.10±27.04
September	5	142.2±7.5	16.64±2.77	0.18±0.01	4.23±0.44	70.94±17.19
Western Lake Erie (Lake Erie)						
June	53	103.5±7.3	6.17±1.43	0.22±0.01	5.07±0.42	31.62±9.00
September	5	105.4±8.3	5.40±1.72	0.22±0.02	4.69±0.67	26.08±11.59

Table 2. Number of large (≥ 90 mm) rainbow smelt (n = 722, total), monthly mean (± sd) total length (TL), wet weight (WW), dry weight : wet weight (DW:WW), energy density (kJ/g wet weight), and total energy content (kJ) of individual large rainbow smelt sampled in different regions of Lake Huron and in western Lake Erie in 2017.

Figures:

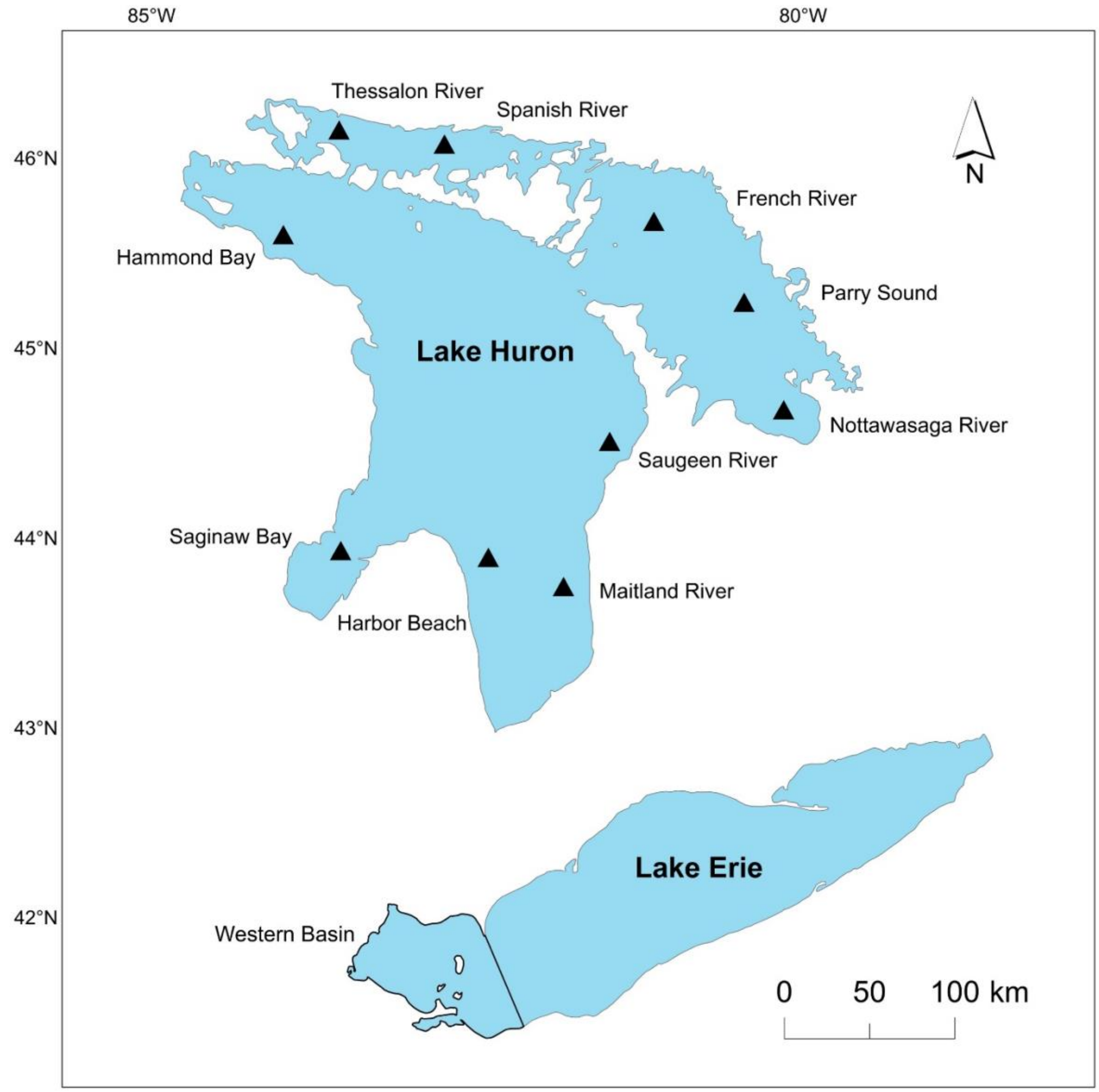

Fig. 1. Map of sampling sites in Lake Huron and Erie, 2017.

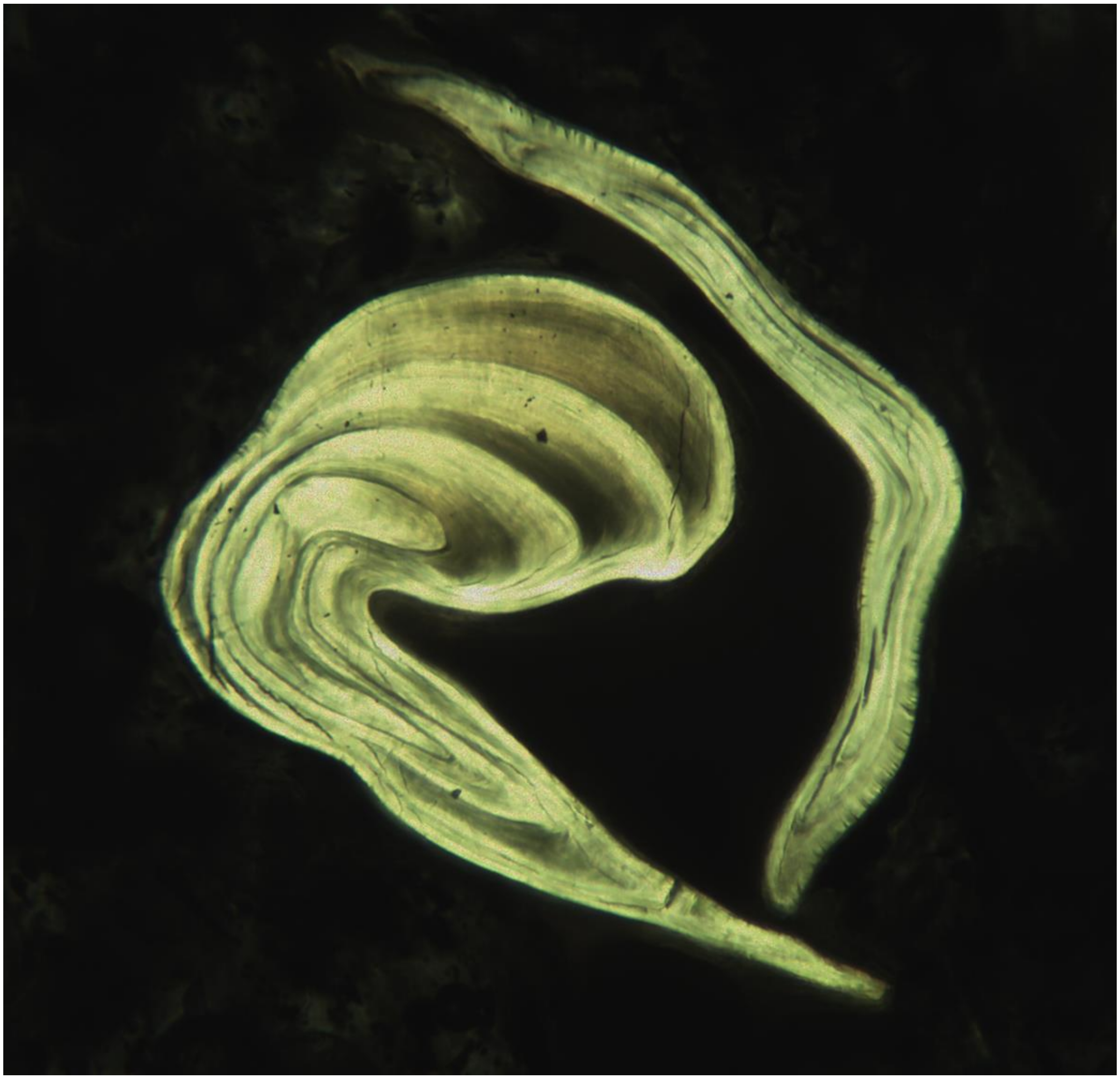

Fig. 2. A cross-section of a rainbow smelt pectoral fin ray. This individual was estimated to be age 4.

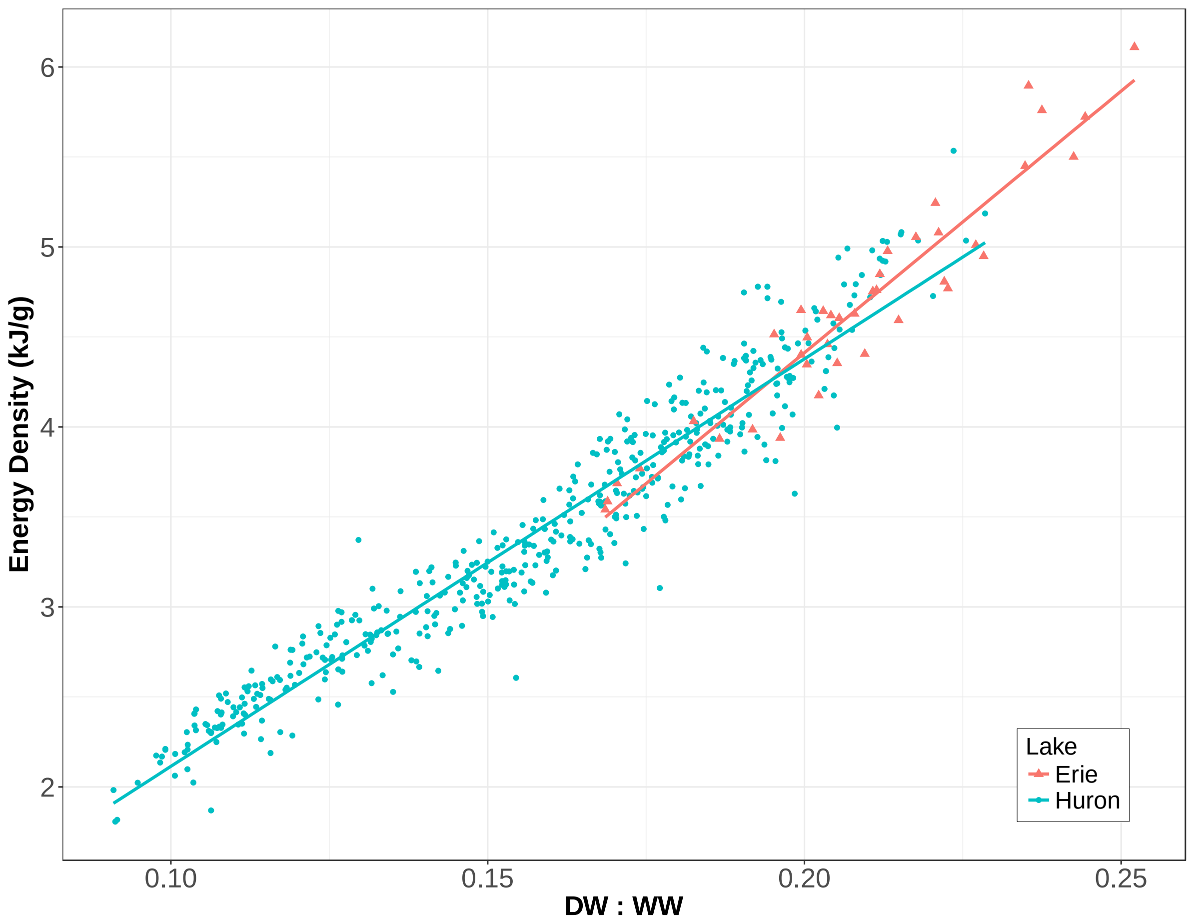

Fig. 3. Energy density (kJ/g wet weight) as a function of dry weight : wet weight (DW : WW) for rainbow smelt sampled from Lakes Huron and Erie in 2017.

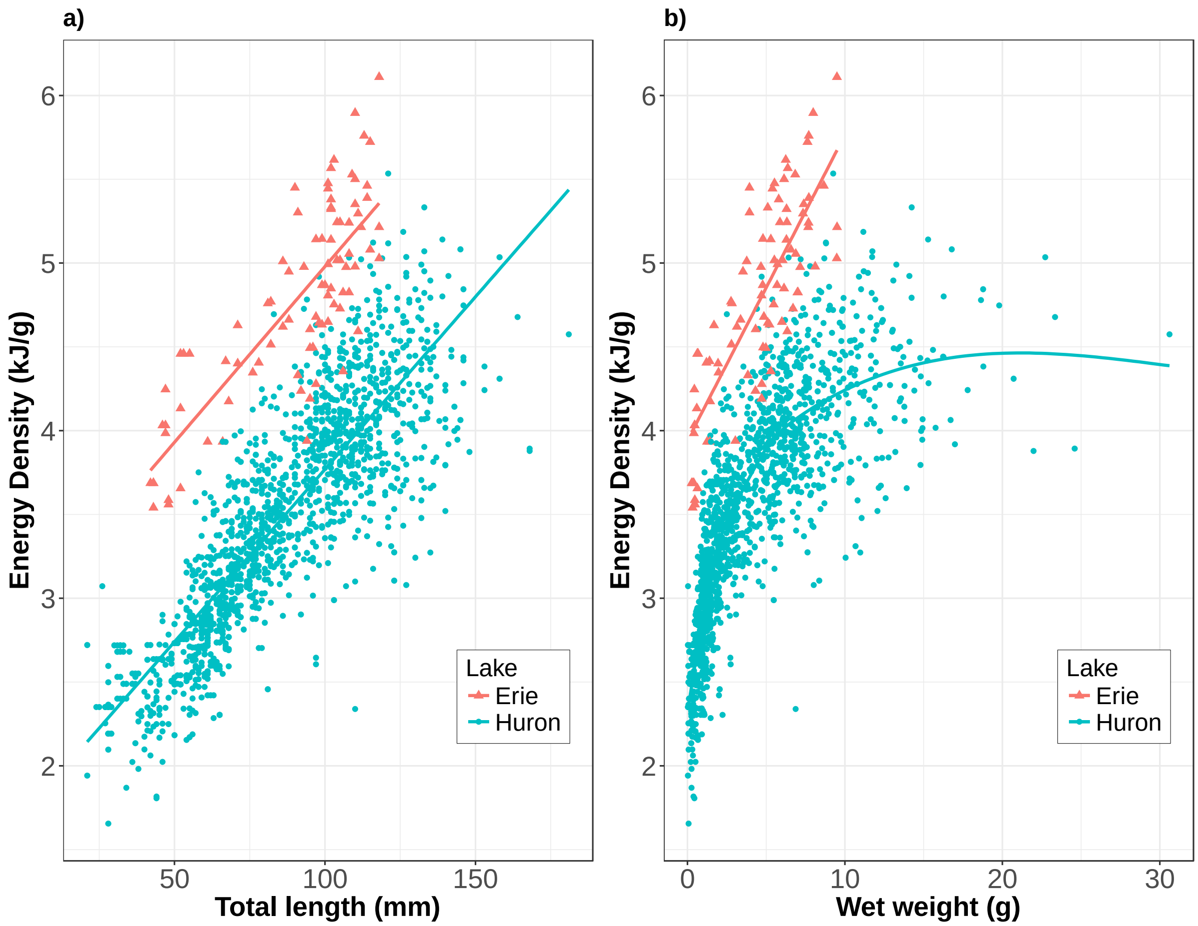

Fig. 4. Energy density (kJ/g wet weight) as a function of total length (mm) (a) and wet weight (g) (b) in all sampled rainbow smelt from Lakes Huron and Erie in 2017. Small smelt in one composite were described by united energy density value.

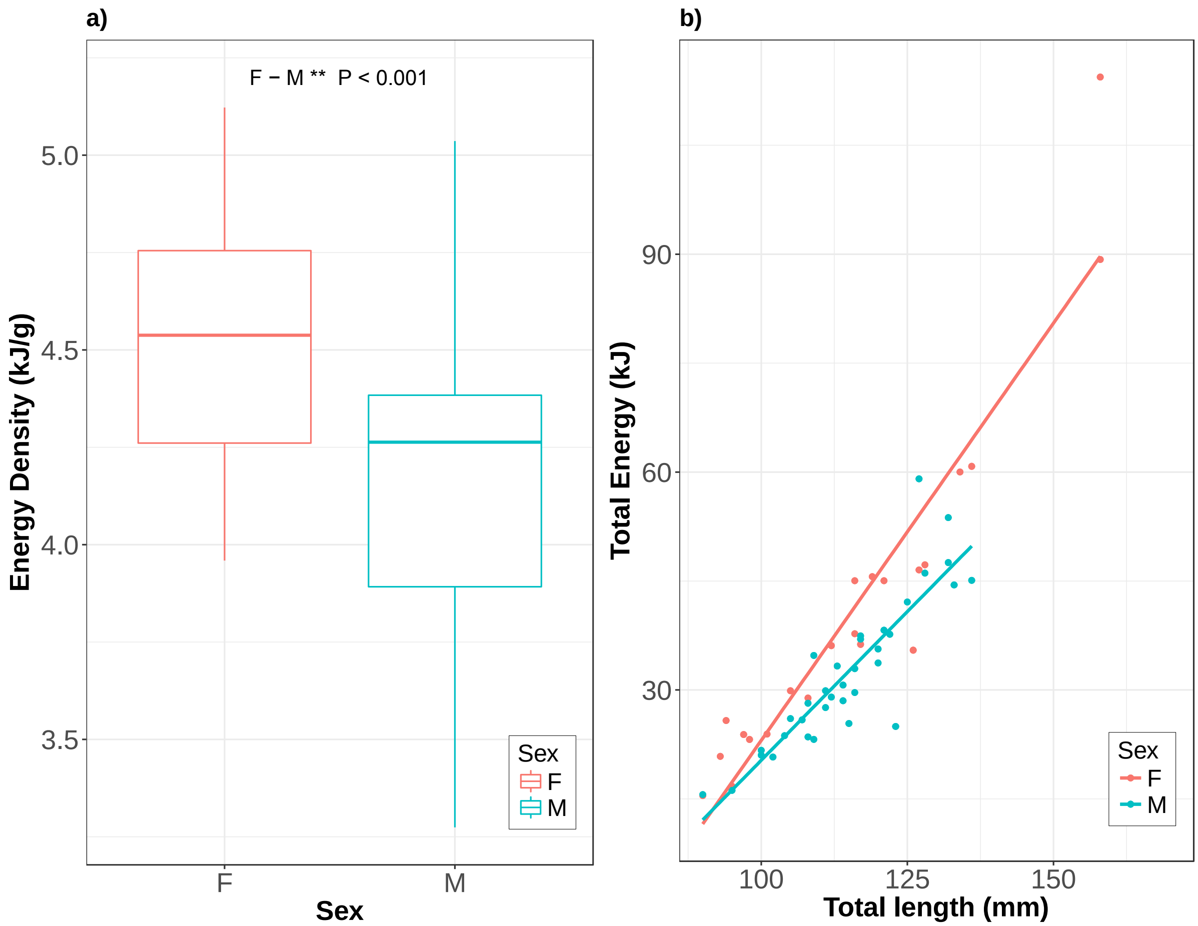

Fig. 5. Panel a) depicts a box plot of energy density (kJ/g, panel a) of male and female rainbow smelt showing differences between sexes ($F_{1, 55} = 15.44$, $P < 0.001$). Panel b) depicts total energy content (kJ) as a function of total length for female and male rainbow smelt. For both panels, analyses were limited to fishes with lengths ≥ 90 mm and collected from North Channel, Lake Huron in April, 2017. In a), horizontal line = median value; box = first quartile to third quartile; vertical line = 1.5 × interquartile range (IQR)..

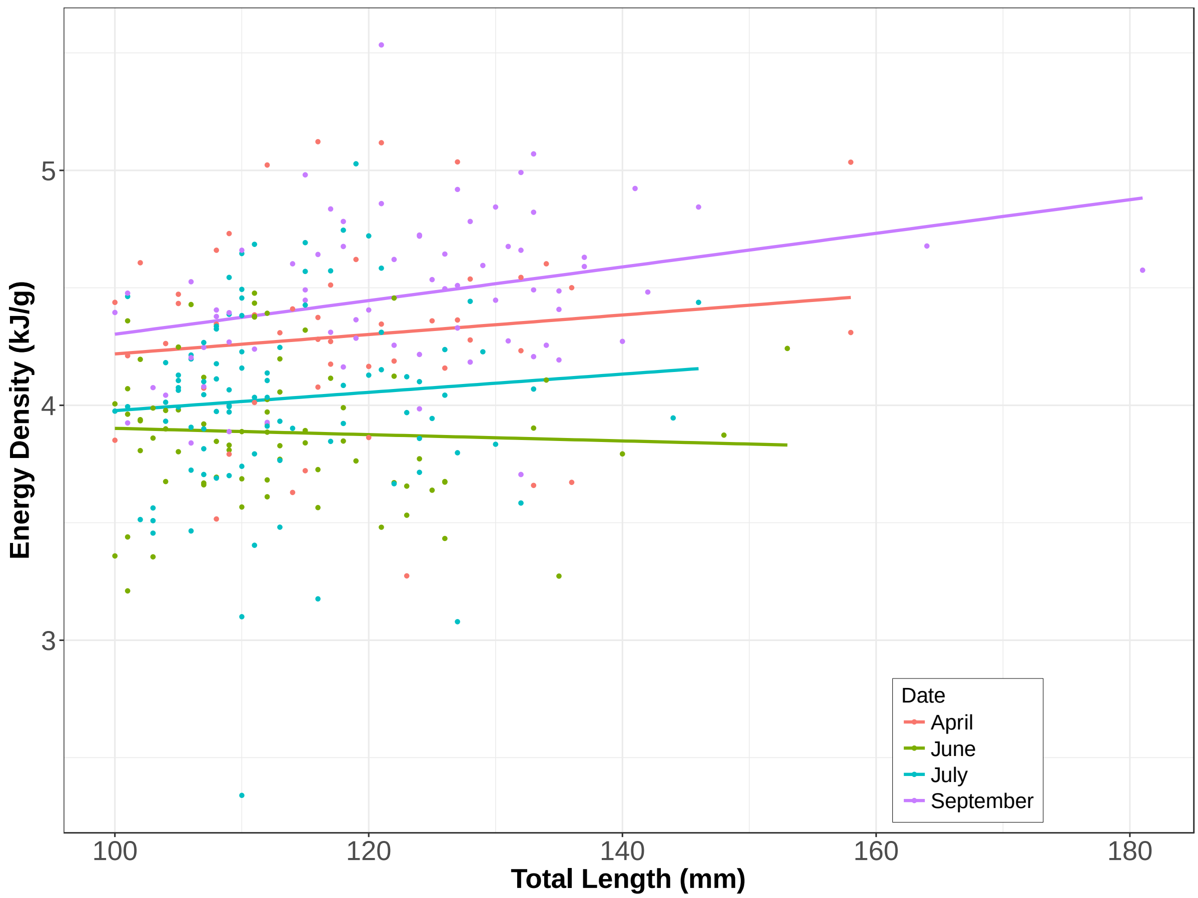

Fig. 6. Energy density (kJ/g) as a function of total length (mm) of rainbow smelt for sampled in different months in North Channel, Lake Huron in 2017.

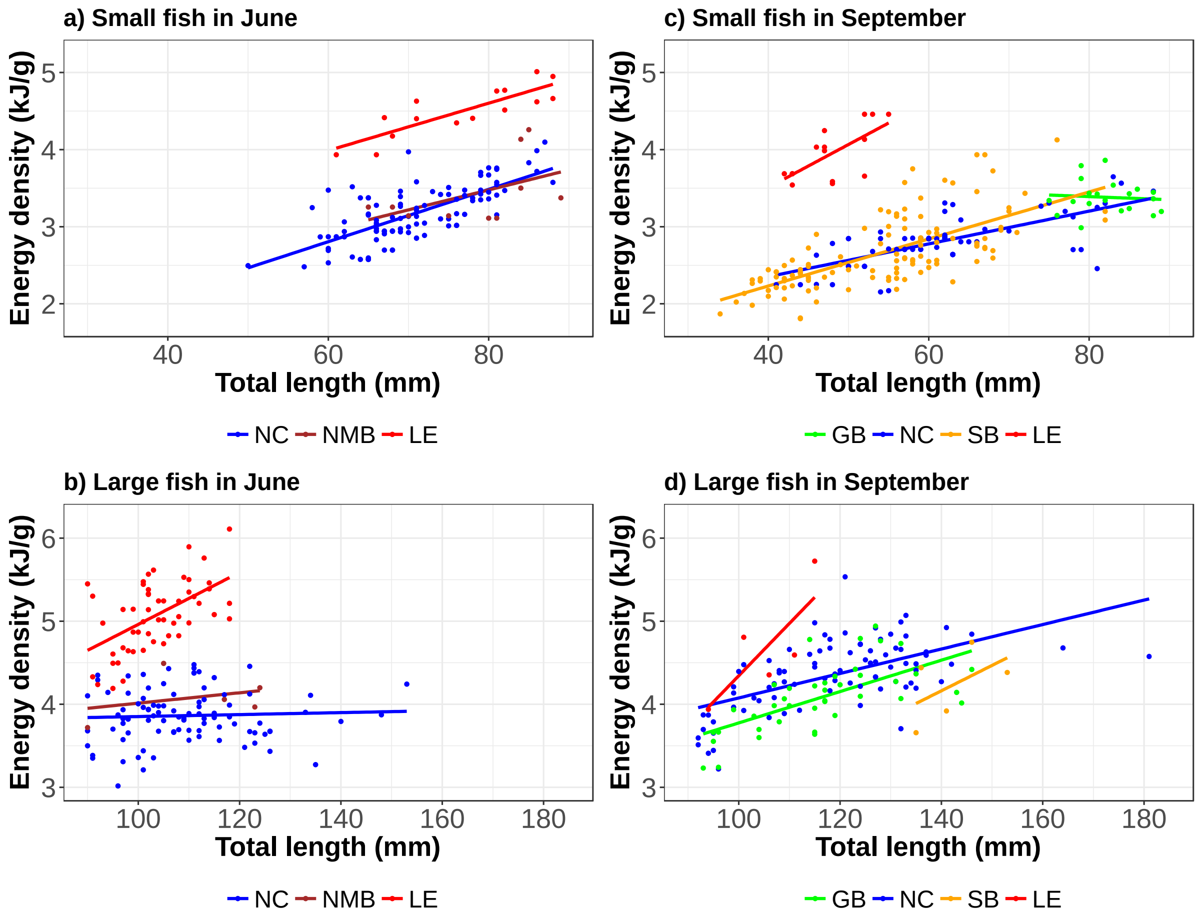

Fig. 7. Regional plots of energy density as a function of total length for large (≥ 90 mm) and small (< 90 mm) rainbow smelt in western Lake Erie, and different regions in Lake Huron in June and September, 2017. NC = North Channel, GB = Georgian Bay, NMB = Northern Main Basin, SB = Saginaw Bay, LE = western Lake Erie.

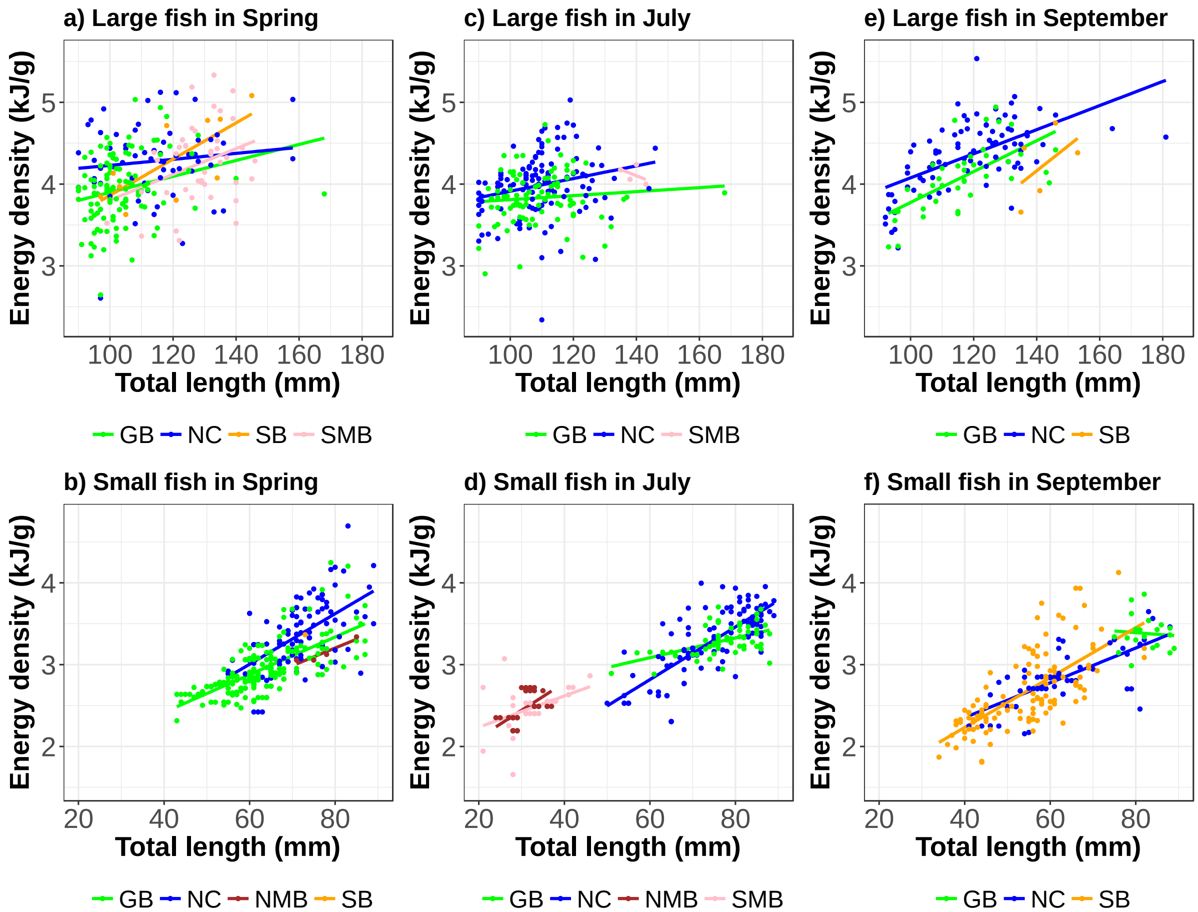

Fig. 8. Regional distributions of energy density for large (≥ 90 mm) and small (< 90 mm) rainbow smelt in Lake Huron in Spring (April + May), July and September, 2017. NC = North Channel, GB = Georgian Bay, NMB = Northern Main Basin, SMB = Southern Main Basin, SB = Saginaw Bay.

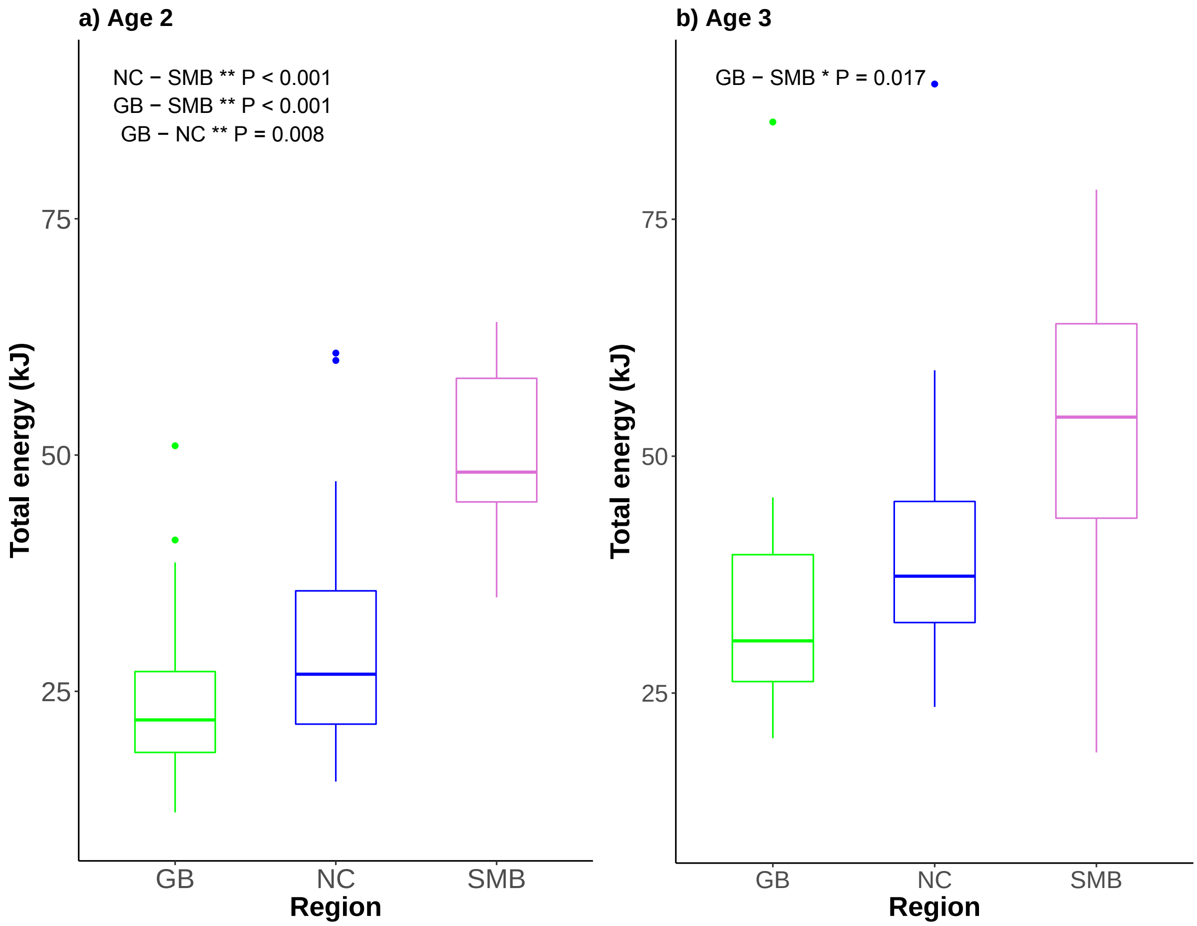

Fig. 9. Box plots of total energy content of age 2 (a) and age 3 (b) rainbow smelt in Georgian Bay (GB), North Channel (NC), and Southern Main Basin (SMB) in Lake Huron in April, 2017. Points = outliers; horizontal line = median value; box = first quartile to third quartile; vertical line = 1.5 × interquartile range (IQR).

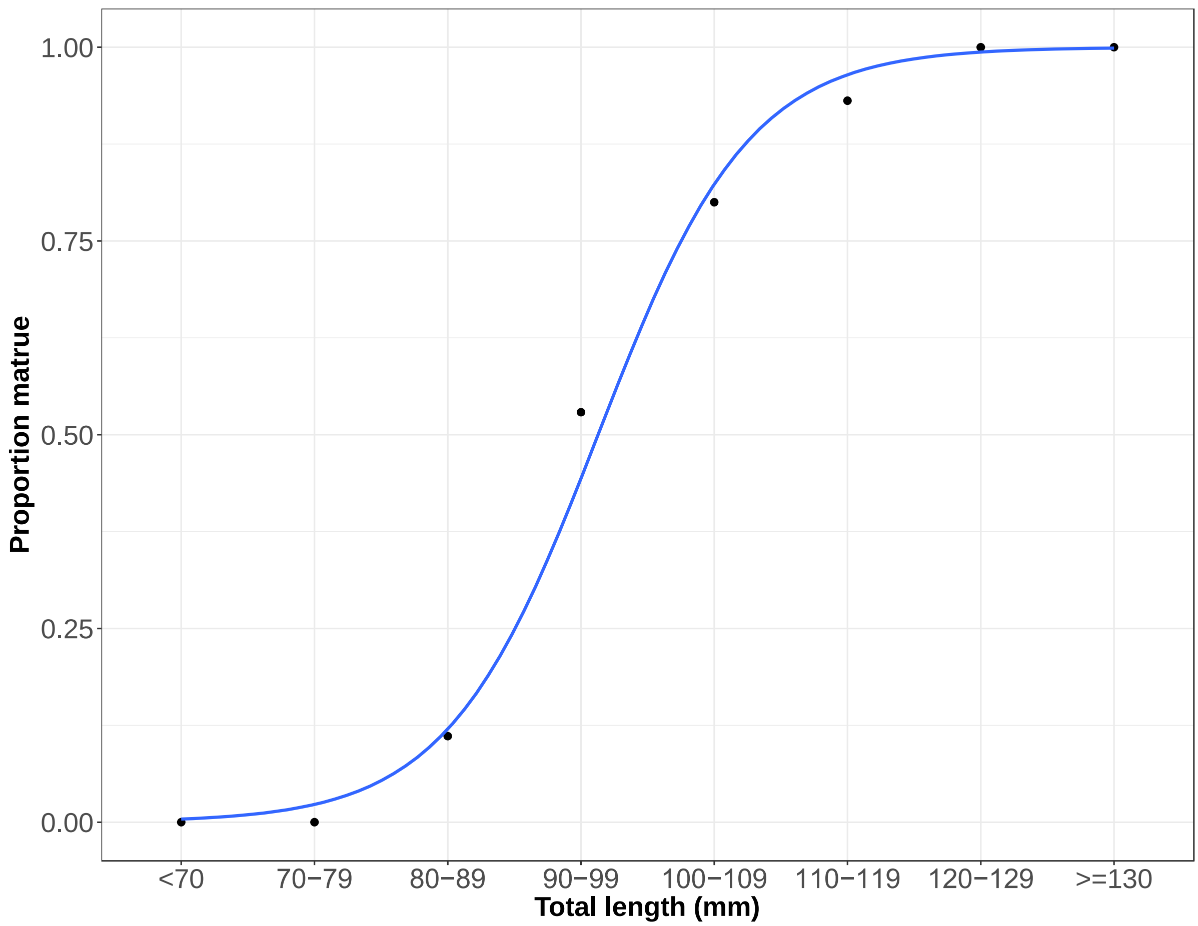

Fig. 10. Proportion mature of rainbow smelt in different length classes in North Channel, Lake Huron in April, 2017. The line represented predicted proportion mature from logistic model based on rainbow smelt collected.

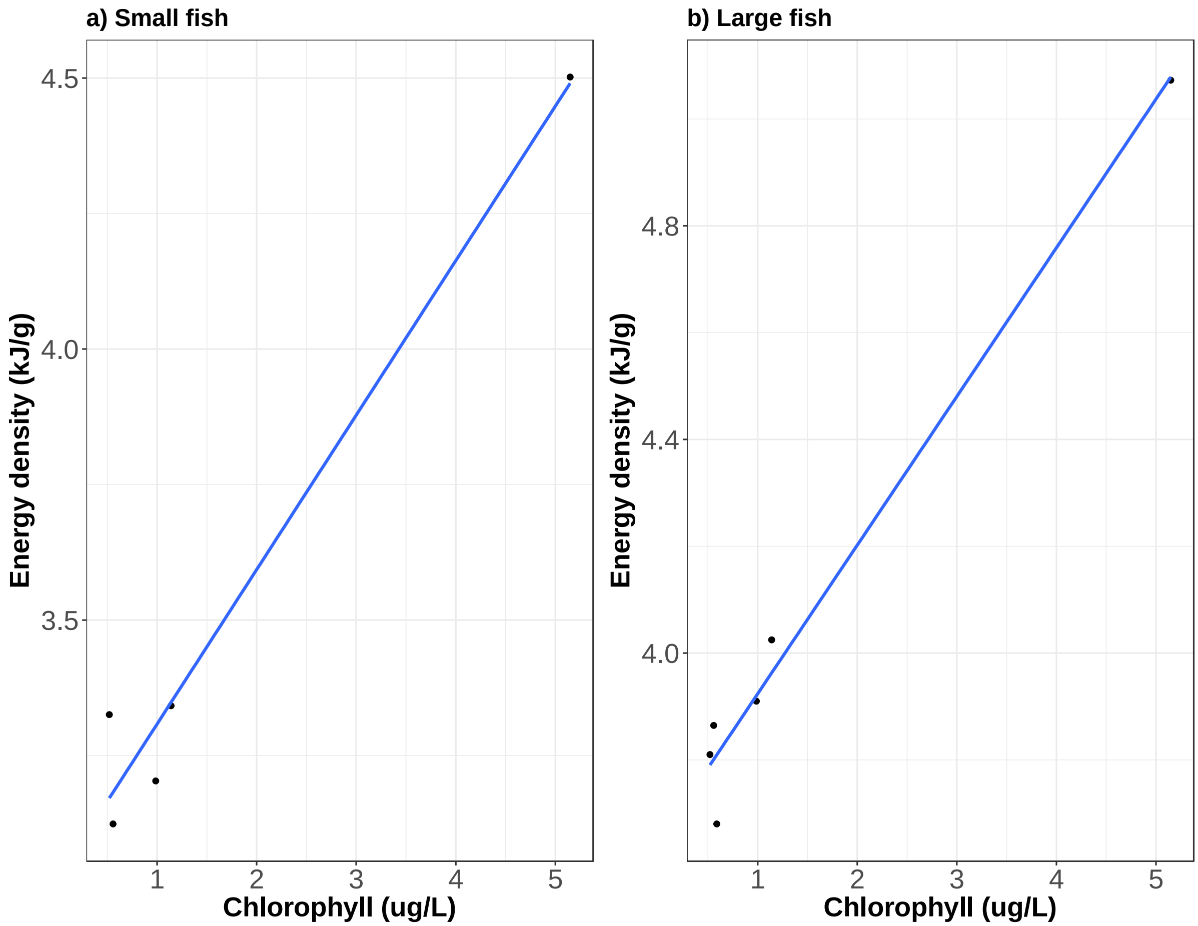

Fig. 11. Correlation between chlorophyll *a* concentration and energy density of small (a) (< 90 mm) and large (b) (≥ 90 mm) rainbow smelt. Small rainbow smelt: $t = 10.01$, $df = 3$, $P = 0.002$. Large rainbow smelt: $t = 14.22$, $df = 4$, $P < 0.001$. The Pearson's correlation coefficients were both 0.99.

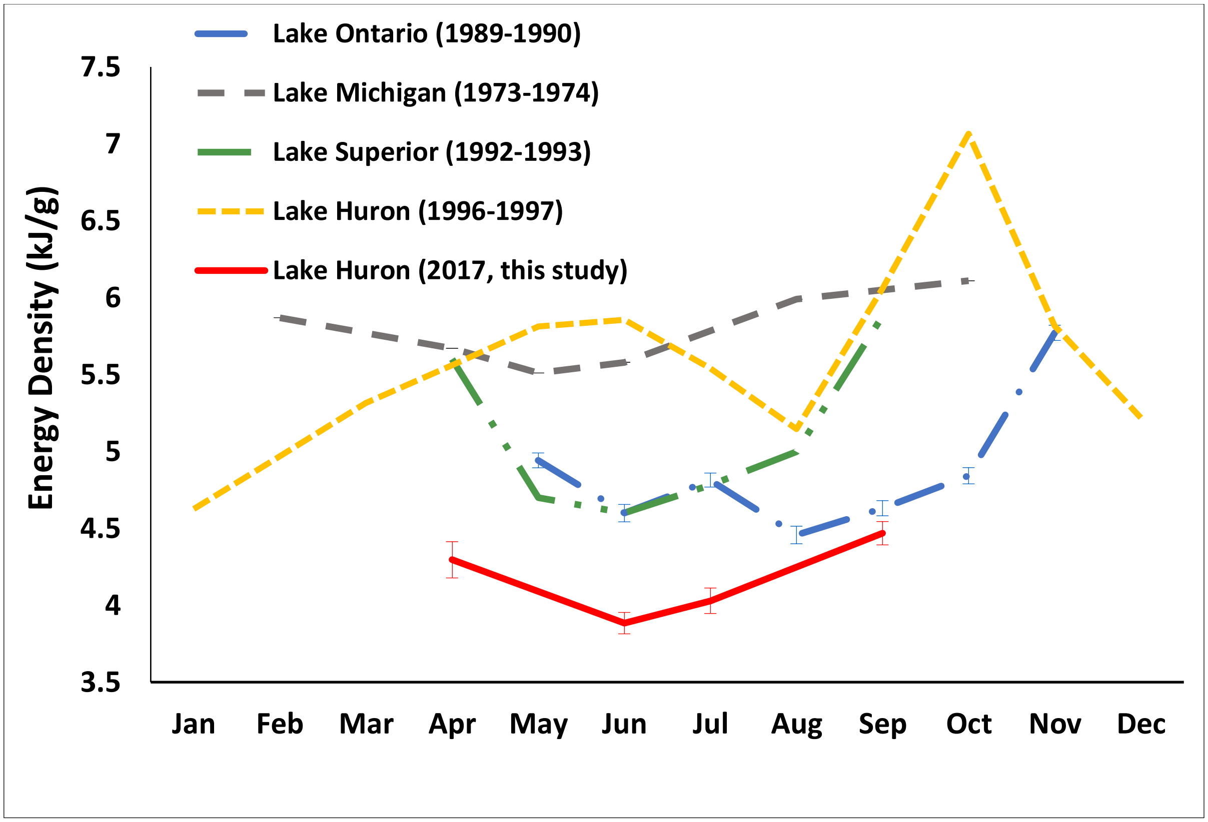

Fig. 12. Monthly mean energy density (± 2 se) of rainbow smelt in North Channel, Lake Huron in 2017 (average; vertical line = 1.5 × interquartile range (IQR). ; vertical line = 1.5 × interquartile range (IQR).d across all sites in North Channel for a given month, for sizes > 100 mm), combined with other four historical studies of rainbow smelt in the Great Lakes. TL ranges for all five studies were: Lake Huron 100-181 mm (2017, this study), Lake Superior 100-206 mm (Vondracek et al., 1996), Lake Michigan unknown (Foltz and Norden, 1977), Lake Ontario 100-169 mm (Rand et al., 1994), Lake Huron unknown (Dobiesz, 2003).

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