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TROPHIC ECOLOGY AND MERCURY BIOACCUMULATION AMONG LAKE SUPERIOR LAKE TROUT ECOTYPES

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Abstract

The Lake Superior lake trout population consists of siscowet, lean, humper and redfin ecological morphotypes or ‘ecotypes’. In addition to morphological differences, these ecotypes occupy different habitats in Lake Superior and partition various invertebrate and fish prey resources. In this study, I measured the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and mercury concentrations among these ecotypes collected from Lake Superior waters surrounding Isle Royale. Average mercury concentrations were highest for redfins (1389 ng/g dry wt) followed by siscowets (823 ng/g), humpers (799 ng/g) and leans (519 ng/g) and differed significantly among the ecotypes ($p < 0.05$). This pattern in Hg contamination among the ecotypes was consistent even when data were corrected for differences in fish ages among the ecotypes. Diet predictions indicated that the predominance of diet energy (kJ/g) for redfins (52.2 %) and humpers (64.8 %) was gained from invertebrate prey for the size ranges of these ecotypes included here. In contrast, fish prey were predicted to be the primary source of dietary energy for the sizes of siscowets (63.0 %) and leans (72.6 %) sampled. Relationships between Hg concentrations and fish lengths also differed significantly ($p < 0.05$) among ecotypes and were concluded to reflect the extent to which insect or fish prey dominate ecotype diets. This difference was concluded to represent the increased time and energy required by redfin and humper ecotypes to forage on small bodied and low energy invertebrate prey. Stable isotope niche modeling demonstrated that siscowets occupy the largest niche in Isle Royale waters with humpers occupying the smallest. However, the $\delta^{13}C$ and nitrogen $\delta^{15}N$ results also demonstrated a high degree of overlap suggesting that none of these ecotypes occupy a unique niche in the waters surrounding Isle Royale. This study emphasizes the role of ecology in regulating mercury bioaccumulation among these sympatric lake trout.

1 Introduction

Lake Superior lake trout (*Salvelinus namaycush*) are unique relative to other Great Lakes populations in that they are self-sustaining in the absence of any major hatchery stocking efforts, and that there are four distinct forms or ecological morphotypes (‘ecotypes’) identified within the population (Muir et al. 2012; 2014). These include the lean, humper, redfin and siscowet ecotypes, each of which are recognized by differences in their morphological appearance, their physiological composition, and the habitats that they occupy within Lake Superior (Muir et al. 2014, Marsden et al. 2021). Within Lake Superior, all four ecotypes co-occur across a range of habitats including, but not limited to, the waters surrounding Isle Royale and submerged outcroppings including Superior Shoal and Stannard Rock (Hansen et al. 2021). Also, these ecotypes demonstrate differences in diet which may be important for their exposure to anthropogenic pollutants such as mercury (Hg; Cabana et al. 1994; Sitar et al. 2020, Vinson et al. 2020). For example, lake trout are commonly the top predator in the food webs they occupy and thus susceptible to the processes of food-web bioaccumulation and biomagnification (Cabana et al. 1994). Therefore, differences in ecology and biology among these ecotypes may affect the extent to which they bioaccumulate environmental pollutants such as Hg.

In general, lake trout use water temperatures that are < 15 ºC and high in dissolved oxygen (> 4 mg/L^{-1}; Marsden et al. 2021). The most commonly recognized ecotype is the lean form, which also characterizes the predominant form of lake trout present throughout the Great Lakes basin (Muir et al. 2012). This ecotype is considered a ‘nearshore’ variant as they are typically found in shallower (≤ 70 m) waters and also generally have the lowest whole-body lipid contents among the four ecotypes (Marsden et al. 2021). This contrasts the siscowet which frequently inhabits waters > 100 m deep and is also the ecotype with the highest lipid contents with whole body values exceeding 60 % (dry wt.; Bronte et al. 2003; Sitar et al. 2008, 2020). The humper ecotype is commonly found on shoals and offshore banks (ie ‘humps’) that are usually surrounded by waters exceeding 100 m deep and have lipid levels intermediate between lean and siscowet ecotypes (Sitar et al. 2020; Marsden et al. 2021). The redfin is the most recently identified ecotype in Lake Superior (Muir et al. 2014). Available information suggests that this ecotype inhabits waters ranging from 50 – 100 m deep and tend to have lipid contents similar to those measured in lean individuals (Sitar et al. 2020, 2022; Marsden et al. 2021). In addition to differences in lipid levels that associate with these selected depths of habitat selection (Sitar et al. 2020), morphological differences are also present among the ecotypes that generally associate with these habitat differences.

Lean lake trout are the most commonly recognized ecotype in Lake Superior likely as associated with their value in commercial, recreational and indigenous fisheries (Muir et al. 2012). This ecotype is generally characterized by a relatively large head with small eyes and a long snout (Muir et al. 2014). Additionally, leans also tend to have a long and narrow caudal peduncle and short pectoral and pelvic fins (Muir et al. 2014). Siscowet lake trout are perhaps among the more recognizable of the other three ecotypes as it is widely distributed across Lake Superior and also represents the predominant lake trout biomass in this ecosystem (Kitchell et al. 2000; Bronte et al. 2003; Sitar et al. 2008). Siscowets are also characterized by a relatively large head but a short snout and larger eyes that are positioned more dorsally relative to lean and redfin ecotypes (Muir et al. 2014). This ecotype also has a shorter and deeper caudal peduncle but with longer pectoral and pelvic fins (Muir et al. 2014). The humper is characterized by a small head but with a short snout and upper jaw and with large eyes positioned higher on the head similar to the siscowet but a short and narrow caudal peduncle (Muir et al. 2014). Redfins tend to have the deepest body with a large head, red coloration to their fins (Chaverie et al. 2021), and are also characterized by having the longest pectoral and pelvic fins of the four ecotypes (Muir et al. 2014). These morphological differences are also likely contributing factors toward the diversity of diets demonstrated by these ecotypes.

Lake trout demonstrate highly plastic feeding habits with diets that can vary substantially among individuals and populations (Martin 1966; Pazzia et al. 2002). For example, Martin (1966) demonstrated that lake trout will quickly transition to feeding on fish prey such as cisco (*Coregonus artedi*) when present but will feed almost exclusively on invertebrates in the absence of such prey fish. For the Lake Superior ecotypes, the diversity of available habitats is likely a factor contributing to their sympatry in this ecosystem and is also a likely contributor to what is known for the diets among them (Magnan et al. 2002). For example, humpers tend to feed on zooplankton, insect larvae and small fishes (Sitar et al. 2020; Vinson et al. 2020; Marsden et al. 2021). This compares to lean and siscowet which tend to consume fish prey but with leans commonly feeding on shallower prey fish species such as rainbow smelt (*Osmerus mordax*) in comparison to deepwater cisco (*C. johannae*) frequently identified in siscowet stomachs (Vinson et al. 2020, 2021). For the recently identified redfin, less is known regarding their diets but available information suggests benthic prey including invertebrates such as the mysid shrimp (*Mysis diluviana*) and fishes such as burbot (*Lota lota)* and sculpin species (*Cottus spp; Myoxocephalus thompsoni*) are common prey items (Sitar et al.

2020; Vinson et al. 2020). This range of diet items among ecotypes spans a diversity of invertebrate and vertebrate prey and also encompasses benthic, pelagic, and offshore profundal depths and could be an important factor regulating pollutant exposure across ecotypes.

The primary anthropogenic sources of Hg pollution include fossil fuel combustion and artisanal gold mining practices but natural processes including the weathering of bedrock also contribute to global Hg inputs (Streets et al. 2011; Driscoll et al. 2013). Subsequently, Hg is a pollutant of global concern and the exposure of humans and wildlife most commonly occurs through the consumption of contaminated food and prey resources, respectively (Driscoll et al. 2013). For top predators such as lake trout, Hg levels tend to be higher relative to prey items due to processes including food web bioaccumulation and biomagnification (Cabana et al. 1994; Driscoll et al. 2013). For example, lake trout feeding on primarily invertebrates tend to accumulate lower concentrations of Hg relative to lake trout that feed more exclusively on fish prey such as cisco (*C. artedi*), alewife (*Alosa pseudoharengus*) or smelt (Cabana et al. 1994). This suggests for the differing diets indicated for Lake Superior lake trout ecotypes that Hg bioaccumulation may differ owing to dietary exposures. Total Hg concentrations for Lake Superior zooplankton and mysid shrimp have been recently reported to range from 3.2 - 18.3 ng/g (wet wt), respectively (Omara et al. 2015). In comparison, Hg concentrations for Lake Superior fish prey such as deepwater sculpin, coregonid species, and rainbow smelt have been reported to range from 28.1 - 130 ng/g (Omara et al. 2015). This trend in potential prey Hg concentrations will be an important contributor to Hg bioaccumulation among Lake Superior lake trout ecotypes. However, additional characteristics such as fish age and growth are also factors that can contribute to pollutant bioaccumulation and biomagnification among fishes (Moriarty 1975; Biddinger and Gloss 1984; Cabana et al. 1994)

Growth dilution of pollutants such as Hg represents the condition in which the rate of increase in body mass exceeds that for the rate of pollutant assimilation by a consumer (Connolly and Pedersen 1987). Fish growth is also highly variable as demonstrated by the wide ranges in size at age that can be exhibited within and among populations (Pauly 1980). For lean lake trout, growth rates have been demonstrated to vary substantially between piscivorous and insectivorous populations with populations that feed primarily on fish prey exhibiting much faster growth (Pazzia et al. 2002). Growth rates among Lake Superior lake trout ecotypes have been demonstrated to vary substantially with the leans and humpers demonstrating faster growth relative to siscowets and redfins with the latter being the slowest growing of the four ecotypes (Hansen et al. 2016). How these differences in growth, in addition to the subtle differences in diet, affect Hg bioaccumulation among Lake Superior lake trout ecotypes, however, remains unknown.

1.1 Goals and Objectives

The primary goal of this study was to examine Hg concentrations among lean, humper, siscowet and redfin lake trout ecotypes collected from the waters surrounding Isle Royale, Lake Superior. Specific objectives were to compare: 1) the trophic ecology of Lake Superior lake trout ecotypes using the stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) to determine potential differences in these ecological markers among ecotypes; 2) to examine otoliths to evaluate ecotype related patterns in growth and; 3) use available diet data to assess the role of ecotype foraging ecology on Hg bioaccumulation. I predicted that there would be significant differences in $\delta^{13}C$ and $\delta^{15}N$ values and growth rates among ecotypes and that Hg concentrations would increase from lean > siscowet > redfins ≥ humpers as associated with the differing habitats and diets across these lake trout ecotypes

2 Methods

2.1 Data Collection

Lake trout ecotypes were collected from waters surrounding Isle Royale in May 2019 by the staff and crew of the Michigan Department of Natural Resources (MIDNR) Lake Char vessel. Fish were collected using multifilament gill nets with stretched mesh sizes of 5.1, 6.4, 7.6, 6.4, 10.2, 11.4, 12.7, 14.0, and 15.2 cm and were set in depths ranging from 85 – 485 m. Ecotype assignment was conducted in the field by MIDNR staff using fish morphometric measurements that included: shape and size of head, size of fins, length of maxilla, depth of caudal peduncle, position of the eye, and the diameter of the eye with depth of collection also included in ecotype assignment. Fish total lengths (± 1 mm), mass (± 5 g) and sex were also determined at the time of collection. Lipid contents of each fish were measured in the field using a handheld battery powered microwave oscillator (Distell Model 693 Fish Fatmeter, Distell Inc). Fish were then placed on dry ice for transport to Michigan Technological University where they were stored at -20 °C until further processing. During processing at MTU, fish were dissected to confirm sex and stomachs were removed and any prey items documented. Calcified structures including sagittal otoliths and pectoral fin clips were collected from each fish for aging purposes.

2.2 Fish Processing

Following dissection, fish were refrozen and then sectioned into approximately 2.5 cm cubes using a saw and cleaver and then homogenized whole through a stainless-steel commercial meat grinder. Fish were processed individually through the grinder a minimum of 3 times to ensure complete mixing of tissues. Approximately 35 g of the whole-body homogenate was then stored in a clean stainless-steel container at -20° C until ready for stable isotope and Hg analysis. All sample processing equipment were thoroughly cleaned and rinsed with soap, tap water and deionized water between processing each fish.

2.3 Stable Isotope Analysis

Samples for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope and Hg analyses were prepared from 1 g subsamples of each whole-body homogenate that were dried at 60 °C for 48 hrs. Dried samples were then ground to a powder using a glass mortar and pestle with the ground tissue transferred into a pre-cleaned 20 mL glass vial. For stable isotope analysis, between 0.9 – 1.0 mg of dried homogenate was added to a 5 x 9 tin capsule that was subsequently folded closed and then placed into a 96-well collection plate. Isotope analyses were completed at the Cornell University Stable Isotope Laboratory (COIL) using a Delta Plus Isotope Ratio Mass spectrometer (Thermo Scientific, Waltham, MA) coupled to an Elemental Analyzer (Costech, Valencia, Ca). Quality assurance and control measures included analysis of externally certified in-house plant (Corn), animal (Deer), and an amino acid (methionine) standards with every 10 samples. Overall standard deviation for the animal standard was ± 0.04 ‰ for $\delta^{13}C$ and ± 0.03 ‰ for $\delta^{15}N$ from the certified mean values. Linearity of instrument response across the range of sample values for the methionine standard was ± 0.39 ‰ for $\delta^{13}C$ and ± 0.27 ‰ for $\delta^{15}N$. At least one individual from each ecotype was also analyzed in triplicate as an additional measure of analytical precision and sample homogeneity.

To account for the potential role of lipid content on sample $\delta^{13}C$ values, lake trout $\delta^{13}C$ results were corrected using equation (1) below derived by Hoffman et al. (2015) for Lake Superior fishes:

$$\delta^{13}C_{lipid\ free} = \delta^{13}C_{bulk} - f_{lipid} \times \delta^{13}C_{lipid} \qquad (1)$$

where $\delta^{13}C_{\text{lipid free}}$ represents the lipid corrected $\delta^{13}C$ isotope value, $\delta^{13}C_{\text{bulk}}$ is the raw uncorrected carbon stable isotope value, f_{lipid} is the sample lipid content estimated from field Fatmeter results, and $\Delta\delta^{13}C$ is an average discrimination factor ($\delta^{13}C_{\text{lipid free}}$ - $\delta^{13}C_{\text{bulk}}$) estimated from Lake Superior fishes by Hoffman et al. (2015). Lipid correction was not necessary for fish with a C:N value ≤ 4 ($n = 2$; Hoffman et al. 2015).

2.4 Isotope Modeling

To evaluate the trophic ecology and pattern of resource partitioning among the lake trout ecotypes, two-dimensional niche ellipses and overlaps ($\delta^{13}C$ and $\delta^{15}N$) encompassing 95% of the data were estimated using the R package ‘nicheROVER’ (Swanson et al., 2015).

2.5 Mercury Analysis

Mercury analyses were completed using a Milestone DMA-80 direct Hg analyzer instrument housed at Michigan Technological University’s Great Lakes Research Center. For Hg analysis, between 20 – 35 mg of dried homogenate was added to a tared nickel weigh boat and then transferred into the instrument carousel with each ecotype being analyzed as a single instrument run. An in-house yellow perch standard was analyzed twice with each ecotype sample run and a certified reference material (DORM-4;

National Research Council of Canada, Ottawa, ON) also analyzed with each sample run. Analysis of the yellow perch standard met Environmental Protection Agency guidelines for repeated analysis of reference standard materials (mean ± 2 standard deviations; EPA) and results of the DORM-4 analysis averaging 96.6 % of the certified concentration (412 ug/kg). As per $\delta^{13}C$ and nitrogen $\delta^{15}N$ analyses, one individual from each ecotype was also analyzed in triplicate for Hg as an additional measure of analytical precision and sample homogeneity. Nickel boats were pre-cleaned by thoroughly washing in soap and water followed by triple rinsing with deionized water. Boats were allowed to dry and then combusted at 650 °C for 30 minutes prior to use. Background Hg values generated from boat blanks averaged 0.2 % of sample Hg detection and sample concentrations were not blank corrected.

2.6 Data Analysis

Ecotype growth rates were estimated using the von Bertalanffy growth curve described in equation (2):

$$L_t = L_\infty \times (1-e^{-k \times t}) \tag{2}$$

where L_t is the predicted length (cm) at time 't' in years, L_∞ is the asymptotic length (cm), and k is the von Bertalanffy growth coefficient (yr^{-1}).

Proportions of invertebrate and fish prey included in the diet for individual fish were predicted using the ecotype prey selections described by Sitar et al. (2020) for varying length classes of these ecotypes collected from waters surrounding Isle Royale. Specifically, Sitar et al. (2020) evaluated diets among the four ecotypes and determined proportional contributions of the various invertebrate and fish prey resources consumed by lake trout across 100 mm length increments for the lake trout sampled in their study. Using these results, diets were predicted for the lake trout collected for this study using fish total lengths and the specific proportions reported by Sitar et al. (2020) for the length categories for each ecotype. Similarly, the proportional [%] contributions of invertebrate and fish prey to dietary energy densities (kJ/g) were predicted for each fish using the relative energy contributions described by Sitar et al. (2020) for these two dietary groups across ecotype diets and length classes.

Prior to completing any statistical comparisons including analysis of variance (ANOVA) and covariance (ANCOVA), all data were tested for normality using normal probability plots and Shapiro-Wilk tests. Fish total length, mass and Hg results required $\log_{10}$ transformation to meet the assumptions of normality with z-score correction required for $\delta^{15}N$ values. No transformation was required for fish age or $\delta^{13}C$ results to meet normality requirements. All pairwise comparisons included total length, mass or age covariates when significant interactions were determined.

To account for the potential influence of fish age on Hg accumulation among ecotypes, age correction of lake trout Hg results followed that described Scudder-Eikenberry et al. (2015) in equation (3):

$$Hg_{corr} = \left(\frac{Hg_i}{Age_i}\right) x \ Age_{\bar{x}} \tag{3}$$

where Hg_{corr} is the age corrected Hg concentration, Hg_i is the uncorrected Hg concentration determined an individual fish, Age_i is the age estimate for that individual fish, and $Age_{\bar{x}}$ is the average age of all fishes for the individual's respective ecotype.

For regressions describing the relationships between ecotype Hg concentrations and $\delta^{15}N$, body mass or total length, ANCOVAs were used to determine the similarity of regression slopes within predicted diets (i.e. insectivorous vs. piscivorous) and suitability for pooling of ecotype data. A second ANCOVA was then completed to compare regression slopes describing the relationships between Hg concentrations and $\delta^{15}N$, body mass or total length between the two predominant diets (i.e. insectivorous vs. piscivorous). All statistics were completed using Microsoft Excel^{TM} and SYSTAT for Windows version 11 (SYSTAT 2004) with a significance criterion of $p < 0.05$.

3 Results

Summary biological data for the fish collected for this study are provided in Table 1. A total of 41 individual lake trout were collected from the waters surrounding Isle Royale including 10 siscowet, 12 humper, 10 lean and 9 redfin ecotypes. On average, redfins were the heaviest fish (2102 ± 1538 g) with humpers having the lowest average body mass (815 ± 218 g). Individual fish weights ranged from 475 g for a humper ecotype to 5995 g for a redfin. Analysis of variance (ANOVA) demonstrated significant differences in body mass ($p < 0.001$) and total length ($p < 0.001$) among the ecotypes. Fatmeter results for individual fish ranged from 9.6 % for a redfin to 67.2 % for a siscowet and differed significantly among the ecotypes ($p < 0.001$) with the latter ecotype also having the highest average lipid content (49.7 ± 5.2 %). Fish ages ranged from 10 – 36 years old with an average age of 20 years determined across the ecotypes.

Predicted diets for lake trout ecotypes indicated a predominance of invertebrates for humper (69 ± 3.1 %) and redfin (62.9 ± 24.2 %) ecotypes (Fig. 3A). For the size range of siscowets sampled for this study, diet predictions indicated a slightly higher consumption of fish prey (50.4 ± 26.1 %) relative to invertebrates (48.6 ± 25.9 %). Similarly, fish prey were predicted to be the dominant prey type for leans (58.8 ± 4.2 %) relative to invertebrates (39.6 ± 3.7 %). The energetic (kJ/g) contributions of fish prey to ecotype diets was predicted to be highest for the lean ecotype with fish predicted to contribute almost 73% of the caloric intake (Fig. 3B). The highest proportion of dietary energy derived from invertebrates (64.8 ± 1.8%) was predicted for humpers. For redfins, invertebrates were also predicted to represent the predominant dietary energy source (52.2 ± 22.1 %) in comparison to the predicted contribution of fish prey (47.8 ±

22.1%). Fish prey were predicted to represent the primary source of dietary energy (63.0 ± 21.4 %) for siscowets relative to invertebrate prey (37.0 ± 21.4 %).

Von Bertalanffy (VBL) growth model efforts demonstrated differences among ecotype growth rates (Fig. 4; Table 2). The VBL model demonstrated good fit to the siscowet, lean, and humper data ($r^2 \geq 0.232$) but was weakest for the redfin ecotype growth data ($r^2 \geq 0.020$). Siscowets were defined by the largest asymptotic size (L_∞ = 732 mm) with humpers the smallest (L_∞ = 481 mm). Predicted times to reach 99% of L_∞ ranged from 23.6 years for redfins to 58.3 years for siscowets with these two ecotypes representing the fastest and slowest growing, respectively, among the study ecotypes.

A summary of ecotype $\delta^{13}C$ and $\delta^{15}N$ stable isotope results and a biplot of these data are provided in Table 3 and Figure 5, respectively. Individual $\delta^{13}C$ results ranged from -24.3 to -26.9 ‰ and did not differ significantly different among ecotypes (p = 0.197). Nitrogen stable isotope results ranged from 9.3 – 13.0 ‰ with the extremes of this range represented by two siscowet individuals. On average, $\delta^{15}N$ values were lowest for lean lake trout (9.6 ± 0.4 ‰) with siscowets having the highest average $\delta^{15}N$ (11.4 ± 1.2 ‰). Nitrogen stable isotope values were significantly different among ecotypes ($p < 0.001$) with Tukey's pairwise comparison indicating $\delta^{15}N$ values for siscowets to be significantly different from those for the other three ecotypes. Trophic niche space modeling demonstrated siscowets to occupy the greatest isotopic niche space followed by redfins, leans and humpers (Fig. 5). The greatest extent of niche overlap was indicated between lean lake trout into humper niche space (83.2 %; Table 4). Humper ecotypes were estimated have substantial overlap into siscowet (74.3 %) and redfin (75.3 %)

isotopic niche space. In contrast, the smallest extent of overlap (16.7 %) was predicted for the overlap of siscowets into lean lake trout isotopic space.

Individual fish Hg concentrations ranged from 285 – 2773 ng/g dry wt. with the lowest concentration reported for a 11-year-old lean ecotype (658 mm, 2075 g) and the highest represented by a 29-year-old redfin (620 mm, 2565 g; Table 3; Fig. 6). Among ecotypes, redfins had the highest average raw (1389 ± 720.4 ng/g dry wt.) and age corrected Hg (1420 ± 648 ng/g dry wt.) concentrations. Uncorrected Hg concentrations differed significantly among ecotypes with redfins having significantly higher Hg concentrations relative to humper and lean lake trout ($p \leq 0.028$) but not in comparison to siscowets ($p = 0.061$). Lean lake trout had the lowest average uncorrected Hg concentration which was significantly lower than those for the other three ecotypes ($p \leq 0.028$). For the age corrected Hg data, pairwise comparison demonstrated redfins to have significantly higher concentrations relative to humpers ($p = 0.031$) and leans ($p < 0.001$) but not in comparison to siscowets ($p = 0.082$). Age corrected Hg concentrations for siscowets were significantly higher relative to leans ($p = 0.031$) but not in comparison to humpers ($p = 0.050$).

Plots describing the relationships between uncorrected Hg concentrations with ecotype $\delta^{15}N$, body mass, or total length are provided in figures 7 – 9, respectively. For humpers and leans, the regressions describing the relationship between Hg concentrations and $\delta^{15}N$ values were significant ($p \leq 0.032$) but this relationship was not significant for siscowets ($p = 0.387$) or redfins ($p = 0.064$; Fig. 7; Table 5). Positive relationships were also observed between Hg concentrations and body mass for redfins ($p = 0.035$) and humpers (*p* = 0.002). However, for leans (*p* = 0.778) and siscowets (*p* = 0.366), these relationships were non-significant (Fig. 8). A similar trend was evident among the ecotypes for the regressions describing the relationships between Hg concentrations and total length (Fig. 9). Analysis of covariance (ANCOVA) indicated that the regression slopes describing the relationships between Hg concentrations and total length for insectivorous (redfin, humper) vs piscivorous (lean, siscowet) ecotypes differed significantly (*p* = 0.018). However, for the relationships between Hg concentrations and δ^{15}N values, no significant difference was determined between the insectivorous vs piscivorous ecotypes (*p* = 0.162). Lastly, ANCOVA demonstrated that the differences in the regression slopes between Hg concentrations body mass for insectivorous vs. piscivorous ecotypes was approaching significance (*p* = 0.056).

4 Discussion

The hypothesis of this research was that Hg bioaccumulation would differ among Lake Superior lake trout ecotypes with siscowets and leans predicted to exhibit greater Hg bioaccumulation relative to the humpers and redfins. This prediction was made owing to diet information collected for these ecotypes inhabiting the waters surrounding Isle Royale which predicted that siscowets and leans tend to consume more fish prey in comparison to humpers and redfins for which invertebrates represent a greater proportion of their diets (Sitar et al. 2020). However, the results of this study demonstrated the highest Hg concentrations for redfins with the Hg concentrations being of similar magnitude among the other three ecotypes which contradicts the primary hypothesis. Also, the relationships between Hg concentrations and fish total lengths differed significantly among the ecotypes with the predominantly insectivorous humpers and redfins exhibiting much greater Hg bioaccumulation with length relative to the relationships observed between these variables for the more piscivorous siscowets and leans. This contrast in Hg bioaccumulation among the ecotypes suggests that not only is the extent of Hg contamination of their prey a likely contributor to these patterns, but also that their specific ecologies may be an additional factor in these observed differences.

Mercury exhibits the phenomenon of food web bioaccumulation such that concentrations of this pollutant in aquatic organisms tend to increase with their food web trophic position (Cabana et al. 1994). For example, Omara et al. (2015) measured Hg concentrations in Lake Superior prey fish species including cisco (*Coregonus artedi*), bloater (*C. hoyi*) kiyi (*C. kiyi*), shortjaw cisco (*C. zenithicus*), lake whitefish (*C. clupeaformis*), rainbow smelt (*Osmerus mordax*) and deepwater sculpin (*Myoxocephalus* *thompsonii*) that averaged from 28.1 – 182.2 ng/g (wet wt.). This compares to Hg concentrations measured in prey items for these fish species in Lake Superior such as bulk (> 150 µm) zooplankton species (3.2 – 4.5 ng/g), the amphipod *Diporeia* (10.4 – 18.3 ng/g), and the freshwater mysid shrimp (*Mysis diluviana*; 13.8 – 18.3 ng/g; Omara et al. 2015). For the four lake trout ecotypes, coregonid species including cisco, kiyi, bloater, shortjaw cisco and lake whitefish are among the primary prey fish species identified in stomach contents with this taxonomic group (Sitar et al. 2020; Vinson et al. 2020). For example, Sitar et al. (2020) reported proportions of coregonid prey ranging up to 37.4 % and 47.3 % (% of wet biomass) of the stomach contents for Isle Royale lean and siscowets, respectively. This compares to the highest proportions of coregonids reported for Isle Royale humper (6.2%) and redfin (30.4%) stomach contents (Sitar et al. 2020). The freshwater mysid shrimp is the most common aquatic invertebrate identified in the stomach contents of ecotypes collected from multiple locations in Lake Superior with adult stages of terrestrial invertebrates such as Dipteran, Ephemeropteran, Plecopteran and Odonate species representing additional invertebrates consumed by the ecotypes (Vinson et al. 2020; Sitar et al. 2020). For the size ranges of ecotypes included in this study, fish prey were predicted to be the predominant source of dietary energy for both siscowets and leans, with invertebrates representing the predominant energy source for humpers and redfins. However, that humpers and redfins demonstrated much different patterns of Hg bioaccumulation in relationship to fish size while consuming less contaminated invertebrate prey suggests that differences in the foraging strategies among the ecotypes as associated with the extent of insectivory and piscivory helps regulate Hg bioaccumulation.

The ecology of foraging among fishes can be subdivided into five main components including: 1) the search for prey, 2) the pursuit of prey, 3) capturing prey, 4) handling prey and 5) consumption of prey (Pazzia et al. 2002). Lake trout are typically much larger than their prey and tend to capture prey items individually (Pazzia et al. 2002). This suggest that the time and energy invested in the search for prey is likely much greater than that for the other four components associated with foraging (Pazzia et al. 2002). For insectivorous lake trout for which the predator to prey size ratio is likely larger relative to piscivorous lake trout, these fish will require more time and energy searching for small bodied prey. Pazzia et al. (2002) predicted that lake that feed primarily on invertebrates have growth efficiencies that are 50 % lower relative to lake trout that feed primarily on fish prey. This can be attributed to the increased amount of time and metabolic costs incurred by a larger bodied predator foraging on smaller bodied prey such as invertebrates (Kerr 1971a, b). Specifically, more feeding attempts must be made to acquire a given quantity of food mass or energy when fish are feeding on smaller prey.

Pazzia et al. (2002) estimated that a 100 g insectivorous lake trout would need to consume 225 - 10 mg dipteran larvae in one day to gain the same dietary energy as a 100 g piscivorous lake trout consuming a single prey fish weighing 1 g. Using the energy densities provided by Sitar et al. (2020) for mysid shrimp and rainbow smelt, a similar comparison estimates that the lake trout ecotypes at Isle Royale would need to consume approximately 143 - 10 mg mysids to gain the same amount of food energy from consuming a 1 g rainbow smelt. For the size ranges of humpers and redfins included in this study, it was predicted that approximately 65 % and 52 % of their dietary energy comes from invertebrate prey, respectively. This compares to the 27 % and 37 % of dietary energy from invertebrates predicted for leans and siscowets. These differences suggest that humpers and redfins spend on average approximately 1.5 – 2.5-fold more time and energy foraging on invertebrates relative to siscowets and leans. Such extended time and effort on foraging on smaller and lower energy content invertebrate prey also results in lower growth efficiencies for insectivorous lake trout (Pazzia et al. 2022). This is due to the fact that more consumed energy is allocated to foraging costs rather than being available for somatic growth (Kerr 1971a, b; Pazzia et al. 2002). Most importantly, such foraging ecology requires the consumption of a greater number of invertebrate prey to meet daily energy demands relative to the foraging costs associated with feeding on larger more energy dense prey fish species (Kerr 1971a, b). Much of this is associated with the fact that invertebrates tend to be higher in indigestible material such as chitin relative to fish prey and consumption rates must increase appropriately to meet daily energy demands (Stewart et al. 1983; Pazzia et al. 2002). Thus, for humpers and redfins that derive a greater proportion of their diet energy from invertebrates relative to siscowets and leans, these ecotypes are likely consuming a greater number of Hg contaminated invertebrate prey which contributes to the relationships between Hg concentrations and ecotype total lengths observed in this research.

Fish growth is an important factor that can regulate the bioaccumulation of pollutants such as Hg. Specifically, in faster growing fish, the rate of new tissue growth can exceed that of the rate at which pollutants such as Hg are assimilated from the diet resulting in a phenomenon known as growth dilution (Sijm et al. 1992). In contrast, slow growing fishes demonstrate little increase in body mass over time but continue to assimilate Hg from their diet. In this study, von Bertalanffy growth models demonstrated humpers to have the fastest growth rate followed by redfins, leans and siscowets. This agrees well with the magnitudes of growth rate values and general differences in growth determined for these Isle Royale ecotypes reported by Hansen et al. (2016). However, in their study, Hansen et al. (2016) demonstrated that redfins had the slowest growth rate. The von Bertalanffy model applied to redfin samples collected in this study had a poor fit ($r^2 = 0.020$) to the data which is likely a consequence of the smaller sample size and the older ages of fish included here relative to those sampled by Hansen et al. (2016). The redfins included in the current study were also the largest on average and it was predicted that this ecotype derives over half its dietary energy from invertebrates. For such large fish, their foraging costs are predicted to increase more quickly with body size when feeding on smaller prey relative to costs incurred while feeding on larger fish prey (Kerr 1971a, b; Pazzia et al. 2002). So for larger redfins and humpers, the proportion of foraging time and effort required for insectivorous feeding reduces overall growth efficiency relative to the proportion of time spent searching, tracking and capturing larger fish prey. In contrast, for leans and siscowets that derive greater proportions of their dietary energy from larger fish prey, these ecotypes likely demonstrate higher growth efficiencies relative to similarly sized humpers and redfins (Kerr 1971a, b).

The stable isotope results here demonstrated siscowets to occupy the largest ecological niche space among the ecotypes with humpers having the smallest. For siscowets, the larger niche was likely associated with the greater range of δ^{15}N values measured in these samples relative to the other three ecotypes. Siscowet δ^{15}N values were also higher relative to the other three ecotypes but this may not necessarily reflect a higher $\delta^{15}N$ associated food-web trophic position for siscowets relative to the other ecotypes. Jasonowicz et al. (2022) recently used acoustic telemetry tagging to demonstrate the range of water depths and temperatures selected by siscowets, leans and redfins in the waters surrounding Isle Royale. Leans and redfins were demonstrated to remain predominantly in the upper 50 m of the water column throughout the year but siscowets frequently descended into water depths exceeding 200 m over an annual temperature cycle (Jasonowicz et al. 2022). Much of nitrogen cycling including denitrification and ammonification in stratified lakes tends to occur in the profundal depths of these ecosystems (Vander Zanden and Rasmussen 1999). Subsequently, a high degree of microbial isotope fractionation tends to occur that generates a higher $\delta^{15}N$ baseline in such deep habitats relative to shallower and nearshore waters (Wada and Hattori 1978; Macko and Estep 1985; Owens 1987; Vander Zanden and Rasmussen 1999). It has also been proposed that organisms such as *Diporeia* and sculpins inhabiting these deepwater regions also feed on dead and decaying matter than can also become enriched in the heavier ^{15}N isotope due to microbial metabolism (Vander Zanden and Rasmussen 1999). Consequently, high $\delta^{15}N$ values for siscowets likely do not represent an elevated trophic position for this ecotype relative to the others, but demonstrate the diversity of habitat use that is commonly associated with the high degree of vertical habitat integration associated with siscowet ecology (Marsden et al. 2021; Vinson et al. 2021).

Hoffman (2017) determined niche sizes for these lake trout ecotypes at Superior Shoal and Stannard Rock locations in Lake Superior and found that humpers had the largest niches in contrast to the results of the current study. For example, Sitar et al.

(2020) demonstrated that mysid shrimp constitute between 23.5 – 39.8 % of humper diets for fish collected from the waters surrounding Isle Royale. In comparison, for humpers collected from Superior Shoal and Stannard Rock, mysids represent between 47.1 – 69.2 % of the stomach contents biomass (Vinson et al. 2020). Also, deepwater sculpin appear to be a greater component of the humper diets at Superior Shoal and Stannard Rock relative to humpers foraging near Isle Royale (Sitar et al. 2020; Vinson et al. 2020). Both mysids and deepwater sculpin inhabit profundal depths in Lake Superior where the microbial enrichment of ^{15}N can occur (Bowers 1988; Selgeby 1988). The greater proportions of these prey in humper diets for fishes captured near Superior Shoal and Stannard Rock may reflect their greater use of deepwater habitats relative to humper individuals captured from Isle Royale waters. Average δ^{15}N values measured in humpers from Superior Shoal (10.8 ‰) and Stannard Rock (10.4 ‰) were higher on average relative to that determined for Isle Royale humpers collected here (9.8 ‰) suggesting potentially greater reliance on profundal prey resources for the Superior Shoal and Stannard Rock humpers that could influence ^{15}N enrichment as noted above (Hoffman 2017). The niche overlap results for Isle Royale collected fish in this study also demonstrated a high degree of overlap which is consistent with that observed for the ecotypes from Superior Shoal and Stannard Rock. This agrees with previous conclusions that none of these ecotypes occupy a completely unique niche across three of the locations where they can be found in Lake Superior (Hoffman 2017).

4.1 Conclusions

The primary objectives of this thesis were to compare Hg bioaccumulation among lake trout ecotypes inhabiting the Isle Royale waters of Lake Superior and to use the stable isotopes of carbon and nitrogen to contrast their trophic ecologies. Hg concentrations were highest for redfins and similar among the other ecotypes even when considerations for differences in age among ecotypes were completed. Most importantly, the relationships between Hg concentrations and fish total length, mass or δ^{15}N values were different among the ecotypes but appeared dependent on the predominance of either fish or invertebrate prey in ecotype diets. This agrees with previous conclusions by Pazzia et al. (2002) regarding the differing foraging ecologies and dietary energy requirements for lake trout when feeding on either invertebrate or fish prey. That is, foraging for and consuming high dietary proportions of small low energy density invertebrates is less energetically efficient for lake trout relative to the consumption of larger-sized more energy dense fish prey as more energy must be directed to foraging costs while feeding in invertebrates rather than converted into new tissue growth (Pazzia et al. 2002). Subsequently, insectivorous lake trout must consume high numbers of Hg contaminated prey to achieve the same extent of growth as achieved by a piscivorous lake trout that needs to consume much fewer Hg contaminated prey to realize that same extent of growth (Pazzia et al. 2002). This is likely the bioenergetic considerations that results in the differing relationships between the insectivorous and piscivorous ecotypes in this study.

Sample sizes for this study were limited to approximately 10 individuals for each ecotype and it would be valuable to gain more samples. Especially from the consideration of comparing average Hg concentrations across a more broad range of fish sizes and ages among the ecotypes. Such additional samples would also be beneficial for further comparing the relationships between Hg concentrations and total length, δ^{15}N and body mass. Given the generally distinct differences between these relationships depending on whether or not insectivory (humpers and redfins) or piscivory (siscowets and leans) predominates dietary selections and caloric intake, I predict that additional samples would only help to strengthen these relationships. Especially if smaller, younger individuals of each ecotype could be collected as these individuals tend to be those that pass through an ontogenetic niche when the transition from insectivory to piscivory frequently occurs among lake trout ecotypes (Marsden et al. 2021).

Recently, researchers have been applying additional ecological tracer tools to contrast species ecologies and to better understand differences among sympatric and similar species (Hoffman 2017; Besnard et al. 2021; Saavedra et al. *in press*). For example, Hoffman (2017) quantified fatty acid profiles among ecotypes from Superior Shoal and Stannard Rock and was able to provide a greater degree of resolution among ecotypes. Fatty acid analyses can provide over 20 marker compounds that when used in combination with $\delta^{13}C$ and $\delta^{15}N$ may provide greater degree of insight into the habitat and food resource partitioning and potentially resource complementarity that occurs among these ecotypes. For example, mysids are demonstrated to be an important prey for each of the ecotypes but this prey species also exhibits diel vertical migration (Bowers 1988; Sitar et al. 2020; Vinson et al. 2020). During the daytime, mysids tend to reside in deeper profundal waters where they feed on organic detritus and sediment carbon (Bowers 1988). This compares to the night when mysids migrate into the epilimnion to feed on preferred zooplankton prey (Bowers 1988). For siscowets that exhibit substantial daily vertical migrations, excursions to deeper profundal waters could permit feeding on mysids during the day. In contrast, redfins are demonstrated to inhabit 50 - 100 m depths throughout the day and year (Jasonowicz et al. 2022) which may only permit consumption of mysids during their night-time vertical migrations. Given that sediment materials and pelagic zooplankton tend to have much different fatty acid profiles (Arts and Wainman 1999), measuring environmental markers such as fatty acids in Lake Superior lake trout ecotypes may help demonstrate not only such possible complementarity of prey resources, but also the multi-dimensional nature of habitat and food resource partitioning that helps permit the coexistence of these sympatric ecotypes in Lake Superior and other lake ecosystems where they are present (Riley et al. 2021).

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6 Figures

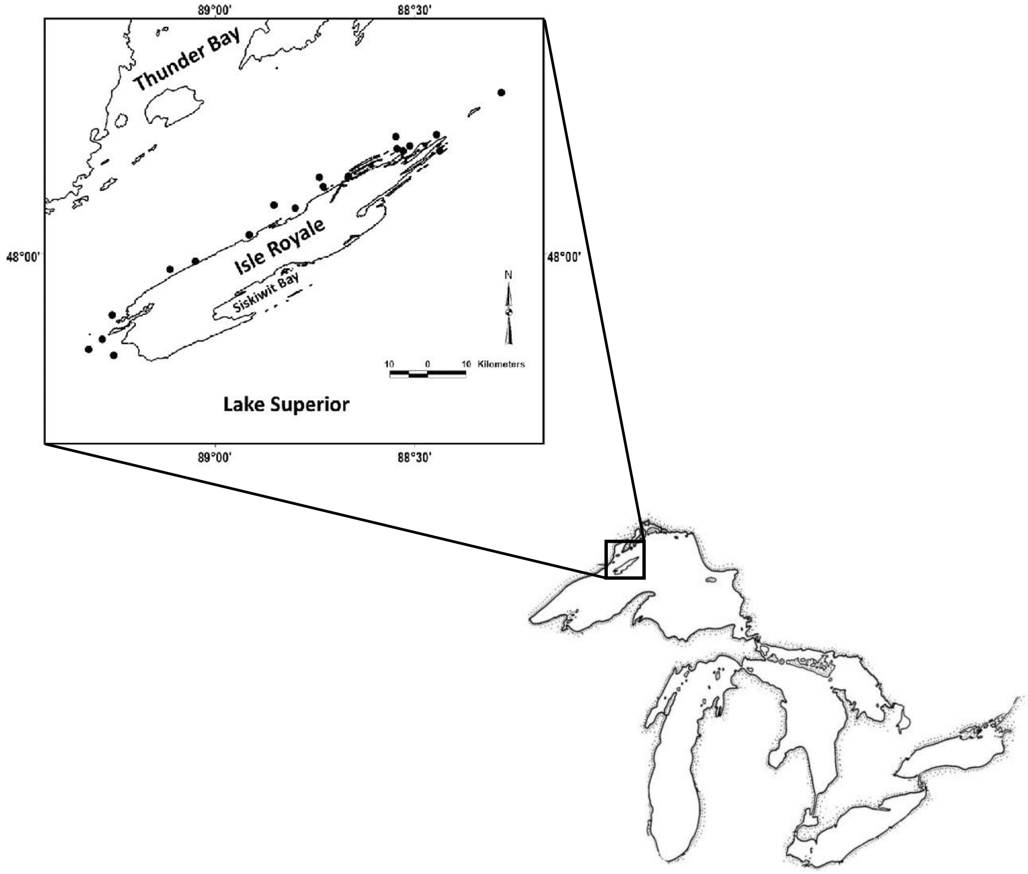

Figure 1: Sampling locations for lake trout ecotypes around Isle Royale (Isle Royale inset from Sitar et al. 2020).

Figure 2: Lake trout sagittal otolith cross section from a humper with an estimated age of 33 years old. Scale bar added for reference (Image D. Norris).

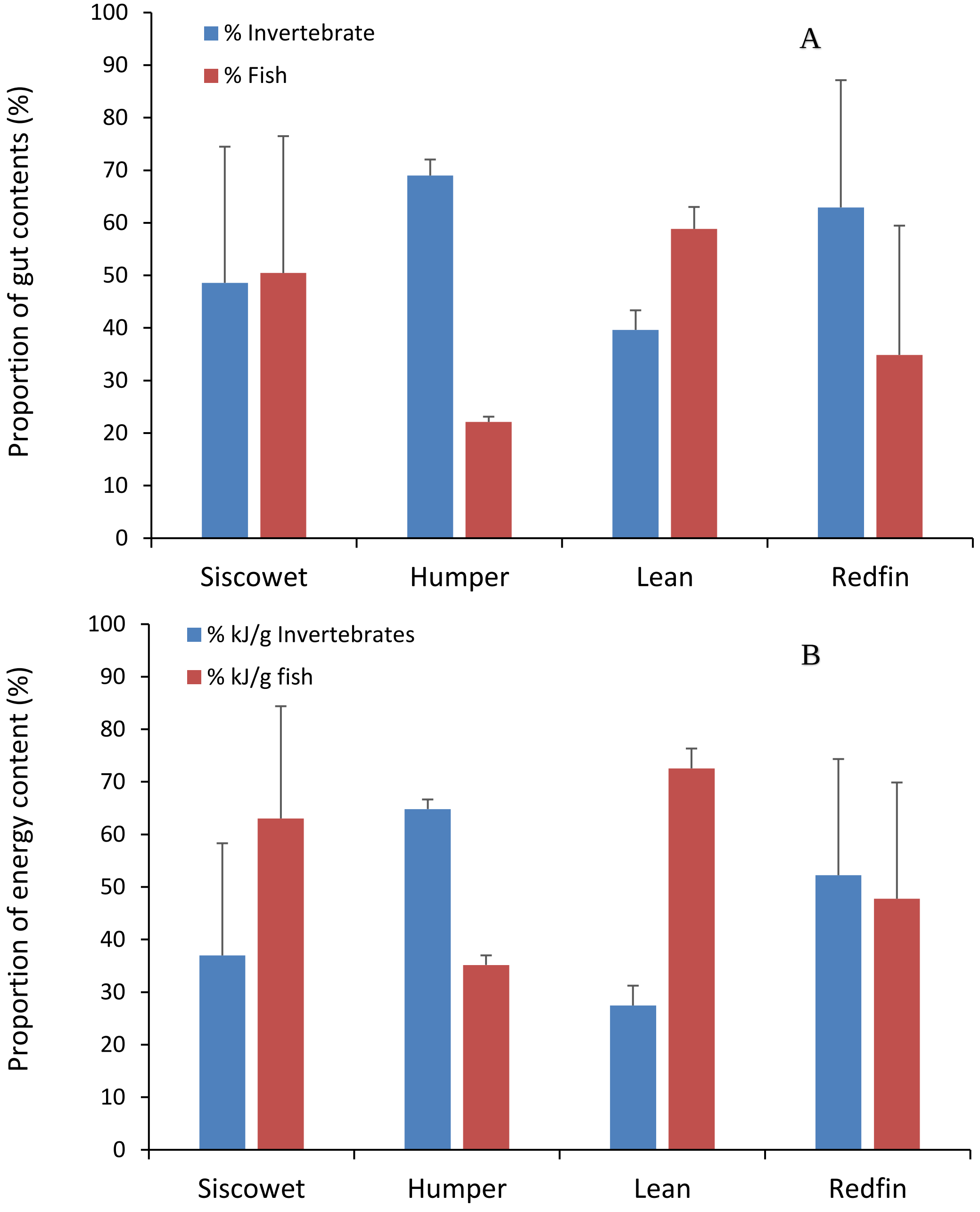

Figure 3: Average predicted proportions of (A) invertebrate and fish prey consumed by Lake Superior lake trout ecotypes and (B) predicted contributions of invertebrate and fish prey to ecotype dietary energy densities. Error bars in both panels indicate ± 1 standard deviation.

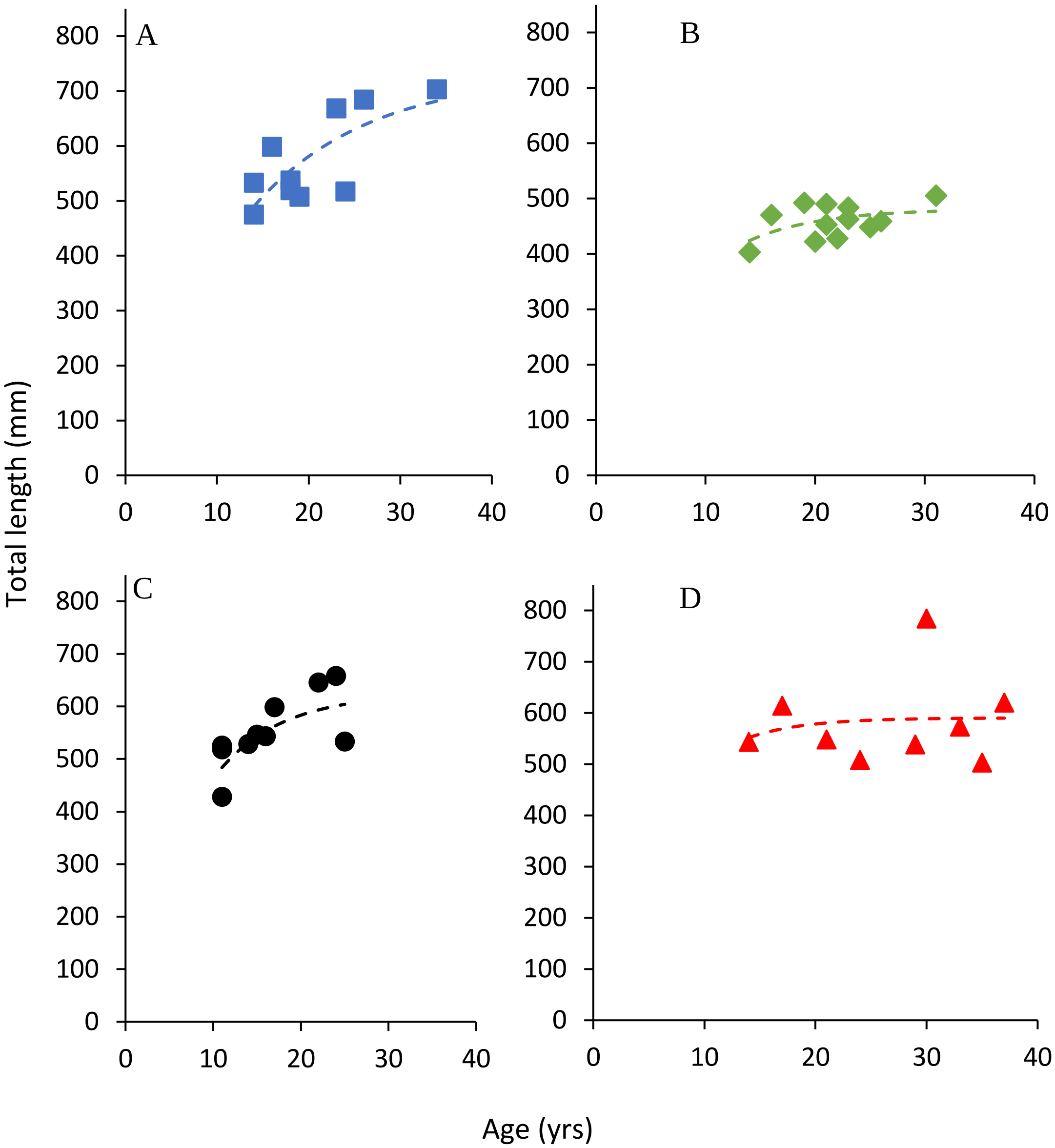

Figure 4: Von Bertalanffy growth curves for Lake Superior (A) siscowet, (B) humper, (C) lean and (D) redfin lake trout ecotypes. Von Bertalanffy growth model parameter values and summary regression statistics are provided in Table 2.

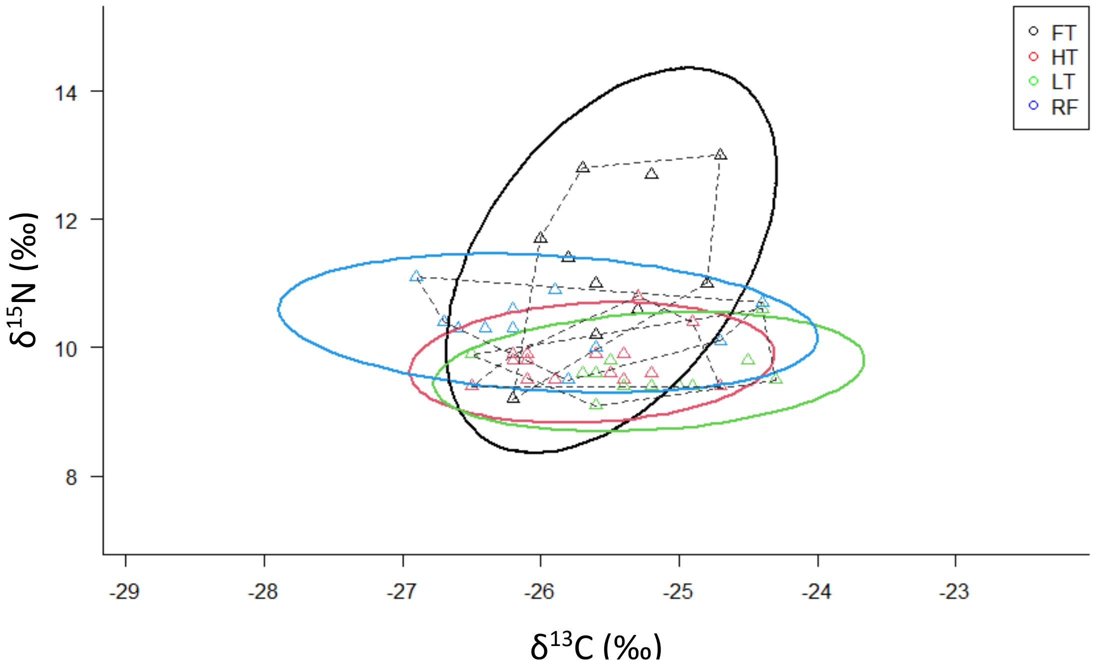

Figure 5: Stable isotope biplot for Lake Superior siscowet (FT), humper (HT), lean (LT) and redfin (RF) lake trout ecotypes. Isotopic niche sizes for each ecotype are provided using both 95% standard ellipse areas (solid lines) and convex hull areas (dashed lines) based on sample $\delta^{13}C$ and $\delta^{15}N$ values (‰). Summarized stable isotope results are provided in Table 3.

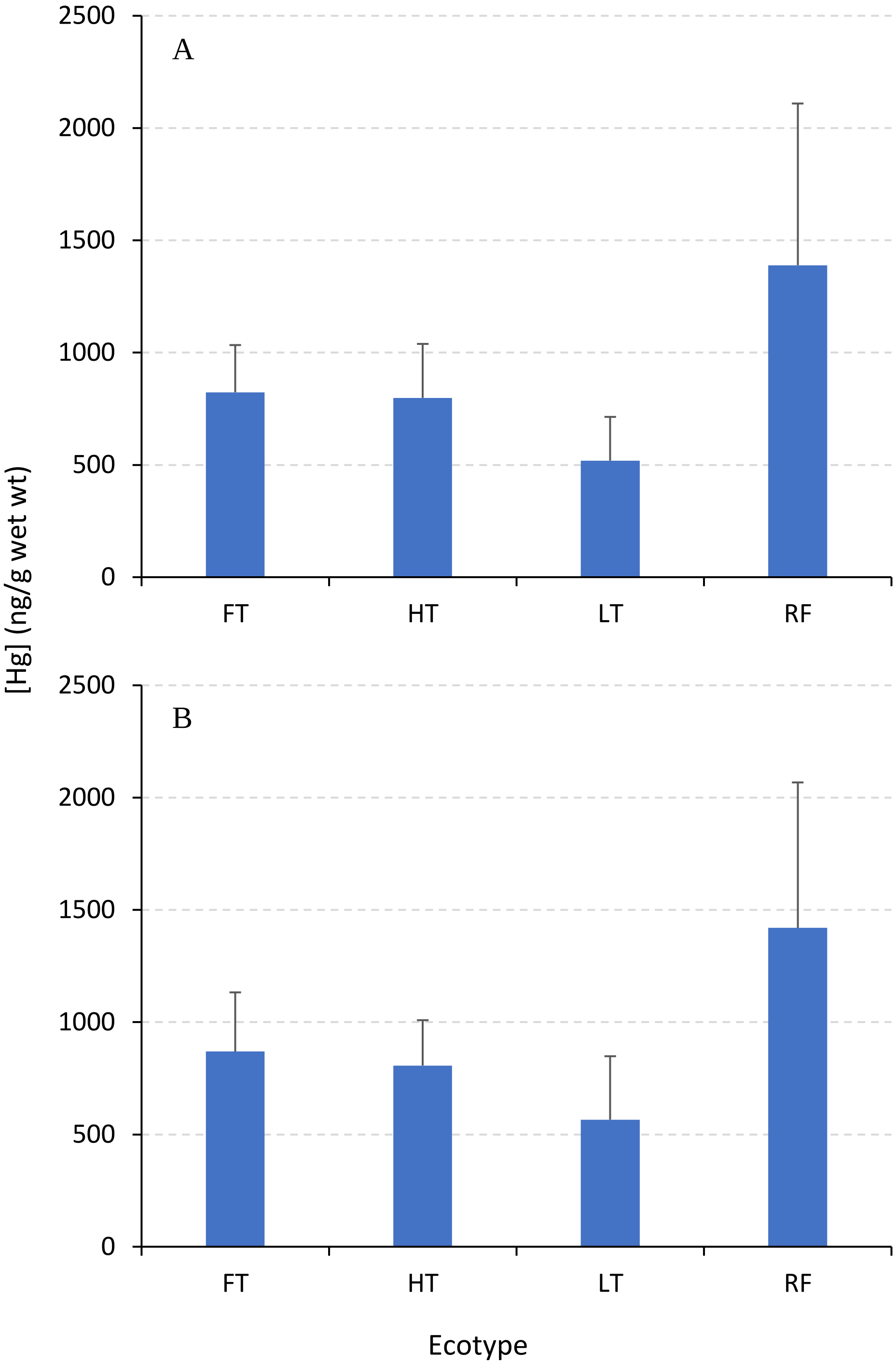

Figure 6: Average (A) uncorrected and (B) age-corrected mercury concentrations for Lake Superior siscowet (FT), humper (HT), lean (LT) and redfin (RF) lake trout ecotypes. Error bars in both panels indicate ± 1 standard deviation.

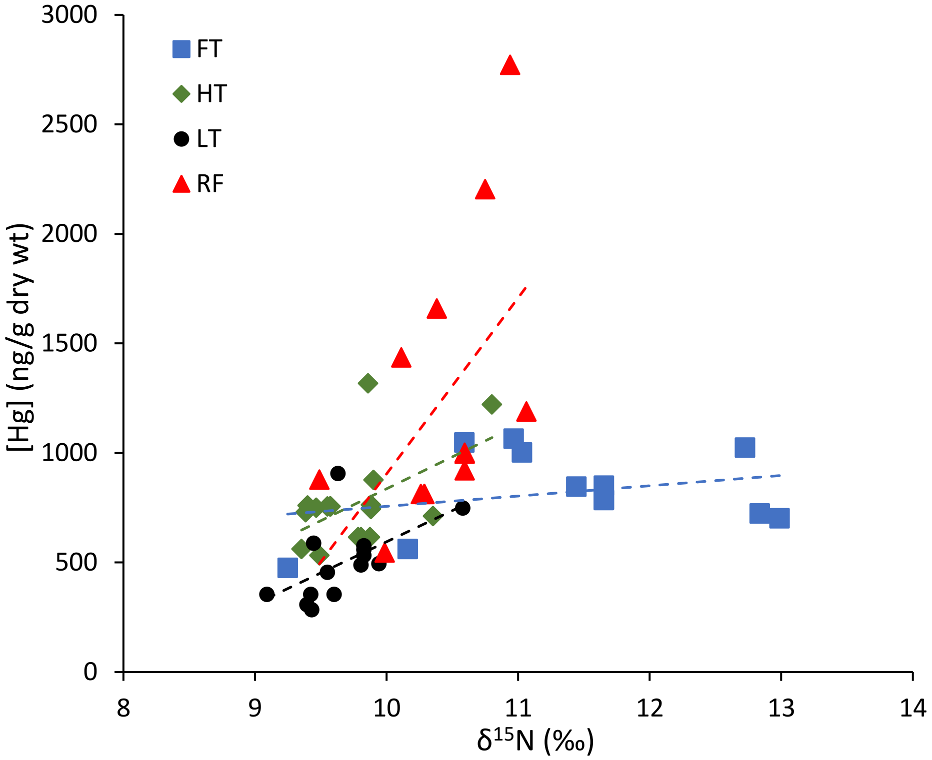

Figure 7: Relationships between uncorrected total mercury concentration (ng/g wet wt) and δ^{15}N (‰) among Lake Superior siscowet (FT), humper (HT), lean (LT) and redfin (RF) lake trout ecotypes. Dotted lines represent the least squares linear regression lines for each ecotype. Summarized regression statistics are provided in Table 5.

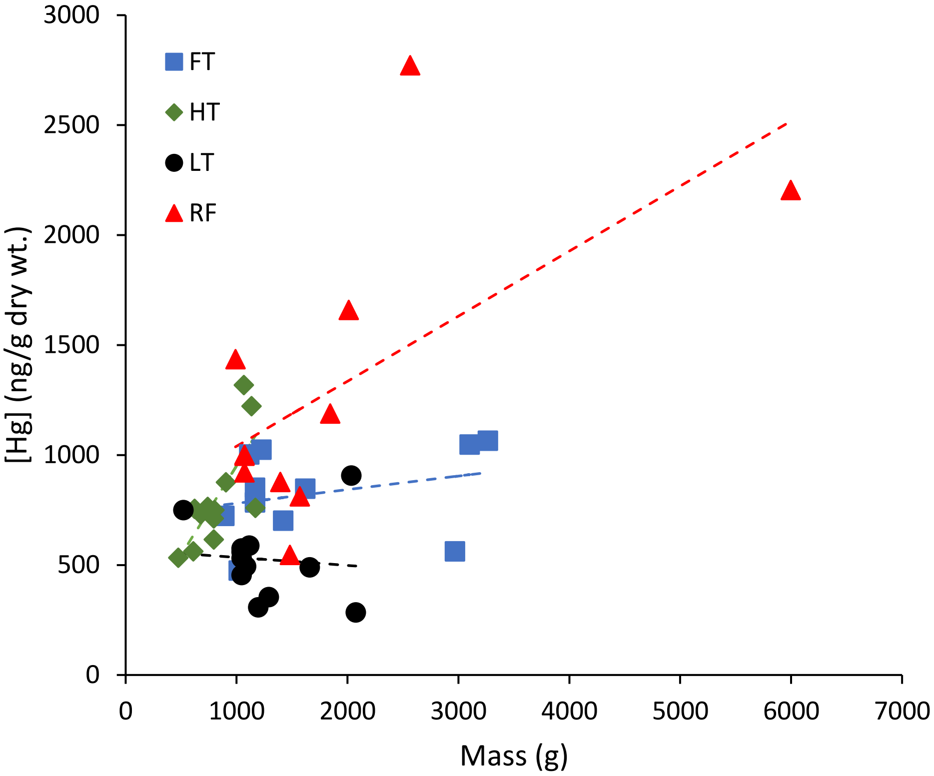

Figure 8: Relationships between uncorrected total mercury concentration (ng/g wet wt) and body mass (g) among Lake Superior siscowet (FT), humper (HT), lean (LT) and redfin (RF) lake trout ecotypes. Dotted lines represent the least squares linear regression lines for each ecotype. Summarized regression statistics are provided in Table 5. Summarized regression statistics are provided in Table 5.

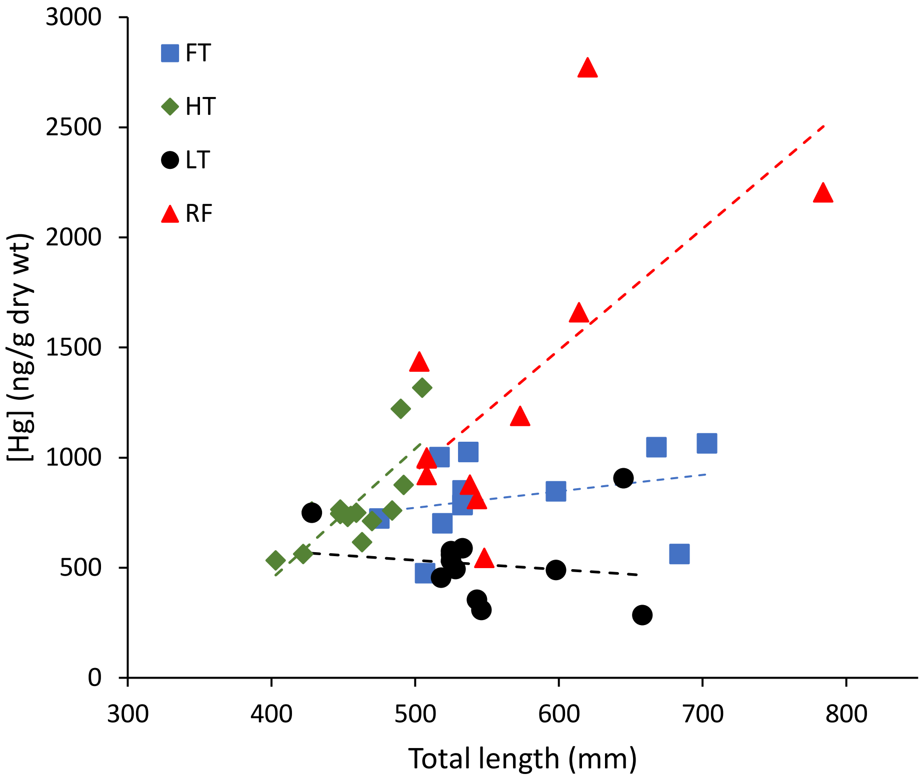

Figure 9: Relationships between uncorrected total mercury concentration (ng/g wet wt) and total length (mm) among Lake Superior siscowet (FT), humper (HT), lean (LT) and redfin (RF) lake trout ecotypes. Dotted lines represent the least squares linear regression lines for each ecotype. Summarized regression statistics are provided in Table 5. Summarized regression statistics are provided in Table 5.

7 Tables

Table 1: Summarized biological data for Lake Superior lake trout ecotypes collected in 2019 surrounding Isle Royale. Values for total length, mass and lipid contents indicate average ± 1 standard deviation.

Ecotype	n	Total length (mm)	Mass (g)	Lipid (% wet wt)	Age range (yrs)	Net depths (m)
Siscowet (FT)	10	574 ± 83	1779 ± 944	49.7 ± 15.2	14 – 35	41 – 148
Humper (HT)	12	460 ± 31	815 ± 218	24.4 ± 3.1	14 – 31	34 – 65
Lean (LT)	10	552 ± 67	1307 ± 483	24.2 ± 8.3	10 – 25	26 – 66
Redfin (RF)	9	581 ± 86	2102 ±1538	18.5 ± 6.4	14 – 36	26 – 106

Table 2: von Bertalanffy growth model parameters for Lake Superior lake trout ecotypes including maximum asymptotic length (L_∞), the von Bertalanffy growth coefficient (k), and times required to reach 50% (t_{50}) and 99% (t_{99}) of the maximum asymptotic length.

Ecotype	r^2	L_∞ (mm)	k (yr^{-1})	t_{50} (yrs)	t_{99} (yrs)
Siscowet (FT)	0.525	732	0.079	8.8	58.3
Humper (HT)	0.232	481	0.152	4.6	30.3
Lean (LT)	0.649	625	0.135	5.1	34.1
Redfin (RF)	0.020	590	0.195	3.6	23.6

Table 3: Stable isotope and mercury concentration data for Lake Superior lake trout ecotypes collected from Isle Royale in 2019. Values indicate average ± 1 standard deviation. Mercury concentrations are provided in both raw ('Uncorrected') and age-corrected formats.

	$\delta^{13}C$	$\delta^{15}N$	Total Hg (ng/g dry wt)	
Ecotype	(‰)	(‰)	Uncorrected	Age-corrected
Siscowet (FT)	-25.5 ± 0.5	11.4 ± 1.2	823.4 ± 210.2	869.0 ± 263.6
Humper (HT)	-25.6 ± 0.5	9.8 ± 0.4	798.5 ± 240.3	806.9 ± 201.9
Lean (LT)	-25.2 ± 0.6	9.6 ± 0.4	519.0 ± 194.8	565.8 ± 282.5
Redfin (RF)	-25.9 ± 0.8	10.4 ± 0.4	1388.9 ± 720.4	1419.7 ± 647.9

Table 4: Total trophic niche overlap (%) estimates between Lake Superior lake trout ecotypes ($\alpha = 0.95$) including siscowets (FT), humpers (HT), leans (LT) and redfins (RF). Two different overlap estimates are presented for each species comparison based on whether the total trophic niche of species A is being compared to species B, or vice versa.

		Species B			
		FT	HT	LT	RF
Species A	FT	-	22.6	16.7	39.7
	HT	74.3	-	83.2	75.3
	LT	51.2	77.9	-	58.7
	RF	66.8	51.1	35.9	-

Table 5: Linear regression parameters describing the relationships between Lake Superior lake trout ecotype nitrogen stable isotope value (δ^{15}N), body mass, total length with whole body total mercury concentrations. Mercury concentrations represent raw values uncorrected for differences in age among ecotypes. Statistically significant regressions ($p < 0.05$) are indicated by *.

	Regression parameters - δ^{15}N (‰) vs Total Hg (ng/g wet wt)			
Ecotype	β (Slope)	α (constant)	r^2	p
Siscowet (FT)	47.0	286.5	0.076	0.387
Humper (HT)	291.6	-2079.9	0.274	0.026*
Lean (LT)	284.7	-2252.6	0.328	0.032*
Redfin (RF)	803.9	-7134.9	0.277	0.064
	Regression parameters - Mass (g) vs Total Hg (ng/g wet wt)			
	β (Slope)	α (constant)	r^2	p
Siscowet (FT)	0.061	719.2	0.082	0.366
Humper (HT)	0.812	138.8	0.548	0.002*
Lean (LT)	-0.036	570.3	0.008	0.778
Redfin (RF)	0.296	744.5	0.405	0.035*
	Regression parameters - Total length (mm) vs Total Hg (ng/g wet wt)			
	β (Slope)	α (constant)	r^2	p
Siscowet (FT)	0.744	400.4	0.089	0.345
Humper (HT)	5.913	-1916.5	0.590	0.001*
Lean (LT)	-0.413	751.1	0.021	0.656
Redfin (RF)	5.521	-1825.0	0.468	0.020*