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Evaluation of Lake Ontario salmonid niche space overlap using stable isotopes

Michael J. Yuille [a,*], Aaron T. Fisk [b], Tom Stewart [a], Timothy B. Johnson [a]

[a] Glenora Fisheries Station, Ontario Ministry of Natural Resources, Picton, Ontario K0K 2T0, Canada
[b] Great Lakes Institute for Environmental Research, University of Windsor, 401 Sunset Ave., Windsor, Ontario N9B 3P4, Canada

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ABSTRACT

The Lake Ontario ecosystem has undergone substantial ecological change over the past five decades. In this time, an economically important sport fishery developed around non-native salmon and trout species (i.e., Chinook and coho salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*)). While trying to maintain this economically important recreational fishery, fishery managers are also trying to restore native species to the ecosystem (i.e., lake trout (*Salvelinus namaycush*) and Atlantic salmon (*Salmo salar*)). We describe the trophic niche space of five ecologically and socioeconomically important Lake Ontario salmonid species (Chinook and coho salmon and rainbow, brown (*Salmo trutta*) and lake trout) using stable isotopes of carbon and nitrogen (^{13}C and ^{15}N, respectively). Using a modified standard ellipse analysis, we found a high degree of stable isotope niche space overlap in Lake Ontario salmonid species. Lake trout had the largest trophic niche space and the smallest proportion of overlap relative to the other four salmonid species (14%–28%), whereas coho salmon had the smallest stable isotope niche space and exhibited the highest degree of overlap with the other species (66%–99%). This study identifies and quantifies dietary resource sharing between Lake Ontario salmonids and highlights the importance of other prey fish species to the restoration and sustainability of Lake Ontario salmonid fish stocks.

Introduction

The Lake Ontario ecosystem has undergone substantial ecological change over the past five decades. Numerous stressors, such as invasive species, fishery exploitation and eutrophication have contributed to the degradation of the Lake Ontario fish community (Mills et al., 2003). Since 1970 and the establishment of the Great Lakes Water Quality agreement in 1972, the negative effects of fish exploitation, sea lamprey (*Petromyzon marinus*), eutrophication and increasing alewife (*Alosa pseudoharengus*) abundances have been subdued, paving the way for the recovery and restoration of the Lake Ontario ecosystem. In this time, an economically important recreational sport fishery evolved around several non-native salmon and trout species (i.e., Chinook and coho salmon (*Oncorhynchus tshawytscha* and *Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*)) in Lake Ontario (Pearce et al., 1980). These predators were effective in controlling alewife populations, which through top-down effect, started to restore balance and stability in the lower trophic levels and ultimately the Lake Ontario food web (Mills et al., 2003).

Sea lamprey predation resulted in the extirpation of Lake Ontario lake trout (*Salvelinus namaycush*) in the 1950s and hindered the success of early salmonid stocking programs (Elrod et al., 1995; Schneider et al., 1983). In 1971, sea lamprey control began (Elrod et al., 1995) and in 1973 lake trout stocking was renewed in hopes of re-establishing a self-sustaining population (Schneider et al., 1983). In addition to lake trout, brown trout (*Salmo trutta*), rainbow trout, Atlantic salmon (*Salmo salar*), Chinook salmon and coho salmon were also stocked in an attempt to find the most suitable mixture of fish species for the lake. Chinook salmon were an attractive stocking species to both fishery managers and recreational anglers as they are a large, fast-growing salmon, that could consume large numbers of alewife, and have lower hatchery production costs (Mills et al., 2003). With the establishment of an annual $7 billion dollar recreational Great Lakes salmonid fishery (Dettmers et al., 2012), fishery managers find themselves trying to maintain the balance of supporting a diversity of salmon and trout dominated by trophy-sized Chinook salmon, and protection and restoration of native species (i.e., lake trout and Atlantic salmon) (Stewart et al., 2013).

Increasing the number of top predators in the offshore has led to an increasing need to understand how all of Lake Ontario's salmon and trout species (both native and non-native) are able to co-exist. Understanding the trophic ecology and interactions of the salmonid fishes in Lake Ontario will help resource managers identify potential for sustaining a large and diverse salmonid fishery without jeopardizing native species restoration or upsetting the predator–prey balance (Brenden et al., 2012; Murry et al., 2010; Stewart et al., 2013; Tsehaye et al., 2014). A food web characterizes dominant taxa and trophic interactions

* Corresponding author. Tel.: +1 613 476 2746.
E-mail address: michael.yuille@ontario.ca (M.J. Yuille).

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among prey and predators in an ecosystem. Food webs, including the relative importance of different linkages can change in response to ecological changes (e.g., prey die offs or environmental effects), making them dynamic by nature. Food webs can also be used to describe the trophic "niche" of a species (Jackson et al., 2011; Layman et al., 2007; Post et al., 2007). A species "niche" has been defined as the sum of all the interactions that link it to other species in an ecosystem. As such, a species niche is strongly connected to its position in the food web, and describing the niche accurately can be vital in identifying resource availability and subsequently, potential competition among species.

Traditionally, food webs were constructed using gut content data. The presence and relative dominance of prey found in the species stomach helped quantify the predator–prey interaction, and collectively these species associations defined the food web (Brandt, 1986; Hyslop, 1980). The benefit of this approach is the high resolution of prey identification that can occur, however, the stomach contents represent a small temporal "snapshot" of the predator's diet. Extensive diet analyses, spanning spatial and temporal scales reflective of the species behavior are needed to accurately characterize the species interactions. Stable isotopes can be used complementary to diet analyses, to provide a time integrated depiction of assimilated food, albeit at a lower level of taxonomic resolution. Stable isotopes of nitrogen ($\delta^{15}N$; ratio of ^{15}N to ^{14}N) and carbon ($\delta^{13}C$; ratio of ^{13}C to ^{12}C) are commonly used in food web ecology and are derived from all trophic pathways culminating in that individual; therefore, they can be used to depict trophic linkages in a food web as well as trophic niche (Jackson et al., 2011; Layman et al., 2007; Peterson and Fry, 1987; Post, 2002).

Layman et al. (2007) proposed six different metrics describing "community-wide" measures of trophic structure using stable isotope ratios. Four of the metrics ($\delta^{15}N$ range, $\delta^{13}C$ range, total convex hull area and mean distance to centroid) measure the total extent of spacing within isotope biplot space and the other two metrics reflect relative position of species to each other within trophic niche space and can be used to estimate the extent of trophic redundancy. The third metric proposed by Layman et al. (2007), total convex hull area (TA), represents the total area encompassed by all individuals of a species in $\delta^{13}C$–$\delta^{15}N$ biplot space. It represents a measure of the total amount of trophic niche space occupied, allowing inferences to be made surrounding the total extent of trophic diversity within a food web. The metrics proposed by Layman et al. (2007) moved the analysis and interpretation of stable isotope food webs from qualitative to quantitative. Most of the attention has revolved around the use of TA to describe the trophic niche width of an organism or community (Layman et al., 2007; Quevedo et al., 2009); however there are some disadvantages to using this metric.

One disadvantage to using the TA metric proposed by Layman et al. (2007) is that the metric is sensitive to sample size (Hoeinghaus and Zeug, 2008; Jackson et al., 2011). This is less than ideal where sample sizes differ among samples within studies, or when comparisons across multiple studies are conducted. Jackson et al. (2011) proposed the use of standard ellipses (Batschelet, 1981) to describe and make inference on isotopic niche space, instead of using convex hulls and other extreme value metrics. The advantage of this method is that the effect of small sample sizes on the standard ellipses is reduced (Batschelet, 1981); furthermore, Jackson et al. (2011) have provided an alternative sample size correction for the standard ellipses, allowing for robust meta-analyses between studies that contain different sample sizes. Both papers by Layman et al. (2007) and Jackson et al. (2011) provide ecologists with tools to help discern and describe key factors driving community structure.

This study is the first to describe the isotopic trophic niche space of the Lake Ontario salmonid community. With growing public concern surrounding potential competition among salmonid species (i.e., lake trout and Chinook salmon), including efforts to rehabilitate native salmonids (Atlantic salmon and lake trout), we use the standard ellipse (Batschelet, 1981) approach proposed by Jackson et al. (2011) to evaluate the extent of isotopic trophic niche overlap (hereafter referred to as niche overlap) within the Lake Ontario salmonid community.

Methods

Sample collection

Eight hundred twenty salmonids were sampled from multiple sites throughout Lake Ontario using either bottom-set, graded-mesh gillnets (50-m panels of 38- to 151-mm monofilament mesh in 12.7-mm increments) or from tissues taken from angler caught fish using a biopsy punch. At each sampling location (Table 1), three or four nets were set parallel to depth contours beginning at the 10 °C isotherm, rarely shallower than 25 m, and proceeding in 10 m depth increments to a maximum of 50 m (Rush et al., 2012). The angler caught fish were sampled during routine Ontario Ministry of Natural Resources (OMNR) Lake Ontario creel surveys during which interviewed anglers were asked to volunteer their catch for tissue sampling. Using a Unicore 3.5 mm biopsy punch (Ted Pella Inc., Redding, CA), skinless boneless dorsal muscle tissue was extracted from each fish and placed in a storage vial. Between sampling each fish, the biopsy needle was sterilized in bleach and rinsed in distilled water to prevent cross contamination of tissue samples. The use of the biopsy needle to sample angler fish proved to be quite successful and provided 92 tissue samples from five salmonid species that are not easily accessible through traditional netting techniques (Ontario Ministry of Natural Resources, 2013). Initially vials were held in coolers on ice until they could be moved to −20 °C freezer for storage. All tissue samples were freeze-dried in cryotubes for 48 h and homogenized with a glass rod prior to stable isotope analyses.

Stable isotope analysis

For tissues collected from 2008 to 2012 Rush et al. (2012) give details of stable isotope tissue preparation. Briefly, stable isotope analyses were completed using lipid-extracted (LE) sample preparations (chloroform–methanol extraction, Bligh and Dyer, 1959). Tissue samples collected between 2009 and 2011 were not lipid extracted prior to stable isotope analysis. To facilitate comparisons, results for these samples were adjusted using sample carbon/nitrogen ratios (Boecklen et al., 2011; Post et al., 2007). Stable isotope analyses were completed using a Delta Plus isotope-ratio mass spectrometer (Thermo Finnigan, San Jose, CA, U.S.A.) coupled with an elemental analyzer (Costech, Valencia, CA, U.S.A.). Values of $\delta^{13}C$ and $\delta^{15}N$ were quantified in relation to three internal laboratory standards and an NIST standard (#8414 bovine muscle), which was run every 12 samples. Atmospheric nitrogen and Vienna Pee Dee Belemnite carbonate were the standard reference materials for ^{15}N and ^{13}C respectively. The analytical precision based on the standard deviation of reference standards, which were $\pm 0.05‰$ for $\delta^{13}C$ and $\pm 0.12‰$ for $\delta^{15}N$ for NIST standard 8414 ($n = 207$), and $\pm 0.12‰$ for $\delta^{13}C$ and $\pm 0.17‰$ for $\delta^{15}N$ for an internal fish muscle standard ($n = 214$). Standard deviations of replicate samples were $\pm 0.24‰$ for $\delta^{13}C$ and $\pm 0.18‰$ for $\delta^{15}N$ ($n = 179$). All stable isotope analyses on 2008 to 2012 tissues were completed by the Chemical Tracers Laboratory at the University of Windsor's Great Lakes Institute for Environmental Research.

Statistical analyses

Due to the small sample size of small fish (22 of 886 < 300 mm fork length), only large fish were considered in our analyses. This effectively removed strong ontogenetic effects, known to occur with these salmonid species. As our data came from multiple years, we used an ANOVA to test whether stable isotope values for each species changed through time. If year was not a significant effect, the data were pooled.

To examine stable isotope niche overlap, we followed the methods outlined in Jackson et al. (2011) using standard ellipses (Batschelet,

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