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# Seventy years of food-web change in South Bay, Lake Huron

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## ABSTRACT

Though aquatic ecosystems (and the Laurentian Great Lakes in particular) have faced many stressors over the past century, including fisheries collapses and species invasions, rarely are data available to evaluate the long-term impacts of these stressors on food web structure. Stable isotopes of fish scales from the 1940s to the 2010s in South Bay, Lake Huron were used to quantify trophic position and resource utilization for fishes from offshore (alewife, cisco, lake trout, lake whitefish, rainbow smelt) and nearshore (rock bass, smallmouth bass, white sucker, yellow perch) habitats, providing one of the longest continuous characterizations of food webs in the Laurentian Great Lakes. Mean $\delta^{15}$N and $\delta^{13}$C values for each species were compared across twenty-year time periods. Using directional statistics, no significant community-wide changes were detected between time periods from 1947 to 1999. In contrast, a significant change was detected between 1980-1999 and 2000–2017, with all species showing increased reliance on nearshore resources. The increase in nearshore resource reliance for lake whitefish between these time periods was the greatest in magnitude compared with any other species between any two adjacent time periods. Besides lake whitefish, the increased reliance on nearshore resources was more pronounced for nearshore compared to offshore species. The timing of these shifts coincided with the invasion of dreissenid mussels and round goby, and declines in offshore productivity and prey densities. These results show the unprecedented magnitude of recent food-web change in Lake Huron after 50 years of relative stability.

## Introduction

Many of the world's large lakes have experienced numerous stressors, including species invasions, overfishing, and climate change (Jenny et al., 2020). Impacts of these stressors include changes to habitat productivity, shifts in food-webs, and changes in the relative importance of different energy sources and pathways (Collingsworth et al., 2017; Ives et al., 2019). In lakes with long histories of disturbance, the food-web impacts of historical stressors are often unknown, but are important for characterizing base-line conditions prior to more recent stressors, comparing current to past conditions, informing restoration efforts, and assessing potential impacts of stressors to ecosystem services, such as fishery yields (Allan et al., 2013; Collingsworth et al., 2017; Ives et al., 2019).

Among the most significant recent stressors affecting many North American and European freshwater ecosystems is the invasion of dreissenid mussels, namely the zebra *Dreissena polymorpha* and quagga *Dreissena rostriformis bugensis* mussels (Smith et al., 2015). The conceptual nearshore phosphorus shunt model hypothesizes that dreissenid mussels filter feeding in the nearshore benthic zone divert nutrients from the pelagic-profundal energy pathway to the nearshore-benthic pathway (Hecky et al., 2004). With the invasion of quagga mussels and their subsequent colonization of deeper waters than zebra mussels, Vanderploeg et al. (2010) further hypothesized that mid-depth (30–50 m) benthic areas can become nutrient sinks, particularly in areas where suitable substrate for dreissenid colonization is lacking in the shallow nearshore. Consequences of this shift in energy pathways include increased biomass of nearshore benthic algal, macrophyte, bacterial and zoobenthic communities, at the expense of pelagic phyto- and zooplankton biomass and profundal invertebrate densities (Barbiero et al., 2012; Evans et al., 2011; Higgins and Vander Zanden, 2010; Nalepa et al., 2007; Vanderploeg et al., 2010).

Lake Huron is a prime example of a large lake impacted by a long history of stressors. The establishment of non-native rainbow smelt *Osmerus mordax* and alewife *Alosa pseudoharengus* by the 1930–40s and 1950–60s, respectively (Berst and Spangler, 1972)

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were implicated in the declines of several native fish species through predation and competition (Evans and Loftus, 1987; Madenjian et al., 2008; Myers et al., 2009). Before control methods were implemented, invasive sea lamprey *Petromyzon marinus* abundance peaked in 1948 and, in combination with overfishing, were implicated in the collapse of lake trout *Salvelinus namaycush* and declines in cisco *Coregonus artedi* in the 1940–50s (Berst and Spangler, 1972). The alewife population grew and reached nuisance levels (Berst and Spangler, 1972). Stocking of salmonids followed in the 1960s, including non-native Pacific salmonids, lake trout and splake (*Salvelinus fontinalis* × *Salvelinus namaycush*; Dobiesz et al., 2005). Deepwater ciscoes (*Coregonus* spp.) declined in the 1960s due to overfishing, and only one (bloater *Coregonus hoyi*) of the original six deepwater cisco species currently exists in the lake (Dobiesz et al., 2005). More recent invasive species established in Lake Huron include the spiny water flea *Bythotrephes longimanus* in 1984, followed by the zebra mussel in the 1990s and the quagga mussel and round goby *Neogobius melanostomus* in the 2000s (Bur et al., 1986; Dobiesz et al., 2005; Rennie et al., 2009; Schaeffer et al., 2005). Round goby consume dreissenid mussels, and, in turn, are prey for several predatory fishes in their introduced range (Kornis et al., 2012).

The significant transformation of the Lake Huron ecosystem since the early 2000s, has been described by researchers as a regime (Ridgway, 2010; Ridgway and Middel, 2015) or trophic shift (He et al., 2015). In 2003–2004, the non-native alewife population crashed, and low densities of demersal prey fish populations have been observed since (Dunlop et al., 2010; Riley et al., 2008; Riley et al., 2020). By 2002–2005, severe oligotrophication was occurring in offshore Lake Huron, characterized by declines in primary productivity and zooplankton densities and increases in water clarity (Barbiero et al., 2012; Evans et al., 2011; Rudstam et al., 2020).

Stable isotope analysis is an effective method for tracking impacts of stressors, such as invasive species, on resource use and energy flow in food webs (Layman et al., 2012). Trophic levels can be traced with $\delta^{15}$N, which increases with increasing trophic position in aquatic ecosystems, as well as in shallower to deeper benthic regions (Vander Zanden and Rasmussen, 1999). The base of primary production in food webs can be traced using $\delta^{13}$C, which is enriched in benthic algae compared to pelagic phytoplankton due to boundary layer effects during carbon uptake in photosynthetic algae (Hecky and Hesslein 1995). Therefore, $\delta^{13}$C values in consumers reflects their reliance on nearshore benthic (higher $\delta^{13}$C value) vs. pelagic (lower $\delta^{13}$C value) production (Vander Zanden and Rasmussen, 1999). These tracers have been used to reveal changes in food webs; for example, dreissenid mussels have been associated with an increased reliance on nearshore and benthic energy sources (increased $\delta^{13}$C) in lake whitefish *Coregonus clupeaformis* (Fera et al., 2017; Rennie et al., 2009). Similarly, dreissenid mussel and/or round goby establishment were associated with increased nearshore reliance in Lake Ontario prey fish (Paterson et al., 2014) and lake trout (Rush et al., 2012), fish communities in the offshore of Lake Michigan (Turschak et al., 2014), and both nearshore and offshore fish communities in Lake Simcoe (Rennie et al., 2013). By contrast, in Lake Superior, where dreissenid mussels have not become established in high densities, fish community resource use (as indicated by $\delta^{13}$C) has remained relatively stable through the mid to late 20th century (Schmidt et al., 2009), while the trophic position of deepwater ciscoes (bloater and kiyi (*Coregonus reighardi*)) declined from 1922-1923 to 2014 (Blanke et al., 2018).

The goal of this study was to assess the impacts of 70 years of ecosystem change on the feeding ecology of the Lake Huron fish community using $\delta^{13}$C and $\delta^{15}$N, tracing these changes in the embayment of South Bay as an indicator of changes in the larger lake. Multiple nearshore and offshore species were included to provide a degree of replication within habitats, to evaluate consistency in direction and magnitude of food web changes within habitats, and to identify species most sensitive to ecosystem change. Previous published studies examining changes in isotopic ecology of Great Lakes fish populations have focused on a relatively short time span (i.e. comparing one to several years pre- vs. post-dreissenid invasion, with the earliest samples from the 1980s (Paterson et al., 2014; Rennie et al., 2013; Rush et al., 2012; Turschak et al., 2014), on a single species over a long time span (Fera et al., 2017; Rennie et al., 2009), or on a long time span in a lake with a lower prevalence of non-native species establishment (Schmidt et al., 2009; but see Schmidt, 2008).

Specifically, our research has two objectives. The first is to determine whether the shift to an increased reliance on nearshore resources after dreissenid establishment in Lake Huron has occurred in species other than lake whitefish and whether offshore versus nearshore species show a different response. The second objective is to use fish community $\delta^{13}$C and $\delta^{15}$N to determine whether the magnitude of food-web changes observed since the early 2000s in Lake Huron has any historical precedence. Changes occurring since the early 2000s include the benthification and oligotrophication of the lake, declines in offshore productivity and trophic transfer efficiency, declines in zooplankton density, and decreases in offshore prey fish biomass in the lake (Hecky and DePinto, 2020; Riley et al., 2020; Rudstam et al., 2020; Stewart and Hinderer, 2018).

## Methods

### Study site

South Bay is a 26 km long embayment of Lake Huron which extends into Manitoulin Island, connected to the lake's main basin by a narrow channel (King et al., 1997) (Fig. 1). South Bay is split into two basins: the inner basin has a mean depth of 16 m, a maximum depth of 58.5 m, and surface area of 7,320 ha (King et al., 1997), while the outer basin has a mean depth of 7.6 m, a maximum depth of 13 m, and surface area of 1,361 ha (Henderson and Fry, 1987). These differences in bathymetry between the inner and outer basins result in different fish communities between the two during the open water season. The inner basin supports warm, cool, and coldwater species throughout the year, but the outer basin supports only cool and warmwater species throughout the year due to a lack of hypolimnetic habitat during summer (Henderson and Fry, 1987). Historical tagging studies suggested that fish movement between basins is species-specific; lake white-

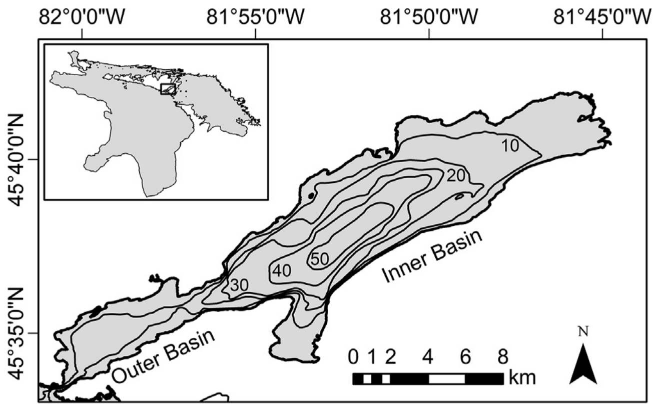


**Fig. 1.** Map of South Bay, with inner and outer basins labelled and bathymetry (in meters). The inset shows the location of South Bay (black rectangle) relative to Lake Huron.

fish populations do not mix between the inner and outer basins (Casselman et al., 1981; Henderson and Fry, 1987), whereas white sucker *Catostomus commersonii* move freely between basins (Henderson, 1986). Abundance of fishes in South Bay has been highly variable over the 20th century, but has closely mirrored trends in the main basin of Lake Huron, including the collapse of lake trout and invasions of rainbow smelt, alewife, and sea lamprey (Henderson and Fry, 1987). While stocking of Pacific salmonids beginning in the 1960s was an important change in the fish community of Lake Huron, these fishes were rarely captured in monitoring nets and are likely in low abundance in South Bay (Ontario Ministry of Natural Resources and Forestry, unpublished data). Various fish monitoring surveys have occurred in South Bay since the 1940s, and fish scales collected from these surveys originally archived for fish aging purposes facilitated isotopic analyses reported here.

### *Stable isotope analysis*

Archived fish scales from South Bay were used to extract $\delta^{13}$C and $\delta^{15}$N values. Scale $\delta^{13}$C and $\delta^{15}$N values are correlated with values derived from muscle tissues (Kelly et al., 2006; Perga and Gerdeaux 2003; Rennie et al., 2009) and have been used in recent studies examining food web change over time (e.g., Fera et al. 2017, Rennie et al. 2013). Species included were the most common nearshore species (rock bass *Ambloplites rupestris*, smallmouth bass *Micropterus dolomieu*, white sucker, and yellow perch *Perca flavescens*) and offshore species (alewife, cisco, lake trout, lake whitefish, rainbow smelt) captured in fisheries independent monitoring surveys in South Bay.

Fish scales were obtained from offshore, late summer gillnetting conducted in the inner basin from 1947 to 2017 by the Ontario Ministry of Natural Resources and Forestry (MNRF). Netting protocols during the 1940s–1990s were described by Henderson and Fry (1987), Morbey et al. (2008) during the 2000s, and Sandstrom et al. (2010) for 2017 netting. In 2017, gillnets were additionally used in October to increase lake trout sample size (n = 3) for that year. Similarly, scales from two white sucker, one cisco, and one rock bass were used from October gillnetting in 1954 to increase sample sizes in that year. Fish scales were stored dry in envelopes.

Scales were processed from five (fewer if unavailable) randomly selected fish per species per year, a sample size with which significant changes in isotopic values were detected for a similar mix of species following dreissenid establishment (Rennie et al., 2013). To reduce the impacts of fish size and ontogenetic diet shifts on stable isotope ratios, only scales from adult-sized fish were used. Fork lengths used to define a minimum adult size (Table 1) were determined from length-at-age and length-at-maturity values derived from South Bay gillnetting data (MNRF unpublished data) and published age- and length-at-maturity values in Scott and Crossman (1973) when relevant South Bay data were not available. We assumed no significant ontogenetic changes in fish diet once adult size was reached, and therefore did not apply a maximum size cutoff.

Scales were prepared for stable isotope analysis following the methodology of Rennie et al. (2013). Scales were soaked overnight in distilled water, cleaned of any soft tissue and dried overnight at 60 °C. The first two scale annuli were removed from species with known ontogenetic diet shifts: lake whitefish, cisco, smallmouth bass (using a 3 mm or 2 mm biopsy punch as appropriate) and lake trout (using a modified 21G syringe). All remaining scale tissues were weighed and placed in a tin cup. Depending on scale size, one or multiple scales were used per fish to ensure enough tissue for stable isotope analysis. Stable isotope analyses for most specimens were conducted at the Water Quality Centre at Trent University, Peterborough, Ontario, Canada. Isotope ratios were determined using an EuroEA3028-HT EuroVector Elemental Analyzer (EuroVector SpA, Milan, Italy) to combust the solid samples to $CO_2$ and $N_2$ gas followed by a Micromass IsoPrime Continuous Flow Isotope Ratio Mass Spectrometer (Micromass, UK). Standards used for calibration included IAEA certified reference materials USGS40 ($\delta^{15}$N = −4.56‰; $\delta^{13}$C = −26.39‰) and USGS41 ($\delta^{15}$N = +47.6‰; $\delta^{13}$C = +37.63‰) and internal working standards Casein (Elemental Microanalysis; $\delta^{15}$N = +5.94‰; $\delta^{13}$C = −26.98 ‰) and Dg(a1) (Sigma $\delta^{15}$N = −2.49‰; $\delta^{13}$C = −14.12‰). The standard deviation of analysis of $\delta^{15}$N was ±0.20‰ and of $\delta^{13}$C is ±0.10‰. We used isotopic values for lake whitefish from 1947 to 2005 that were analyzed and published previously (Rennie et al., 2009), but conducted new stable isotope analysis on lake whitefish scales from 2006 to 2017.

Duplicate samples were processed for 199 randomly selected fish, which included samples from all species, to assess analytical precision of stable isotope analysis. There were no significant differences for either isotope between duplicates (paired *t*-test pooled across all species; $\delta^{13}$C: t = 1.1856, p = 0.2372, mean difference between duplicates = 0.097‰; $\delta^{15}$N: t = 1.1355, p = 0.2575, mean difference between duplicates = 0.038‰). To avoid pseudoreplication, one of these two duplicates was selected randomly to include in analyses described below.

### *Statistical analyses*

The time series was broken into 4 periods of approximately 20 years each coinciding with major ecological changes in South Bay: (a) 1947–1959, which characterized the collapse of the lake trout population and establishment of alewife at high densities (Berst and Spangler, 1972); (b) 1960–1979, which reflects a recovery of lake trout densities due to stocking and sea lamprey control

**Table 1**
Number of fish for which scales were processed, minimum targeted fork length of fish included in the study and range of actual fork lengths of fish (in parentheses) by species and time period. Fish species are categorized as typically offshore or typically nearshore.

| Species | Minimum targeted fork length (mm) | Number of fish and actual fork length range (mm) per time period | | | |
|---|---|---|---|---|---|
| | | 1947–1959 | 1960–1979 | 1980–1999 | 2000–2017 |
| ***Offshore*** | | | | | |
| Alewife | 150 | 19 (152–198) | 75 (152–174) | 59 (151–188) | 0 |
| Cisco | 210 | 50 (216–325) | 20 (215–353) | 5 (270–295) | 14 (247–383) |
| Lake Trout | 410 | 35 (411–543) | 5 (436–497) | 55 (423–667) | 13 (437–662) |
| Lake Whitefish | 300 | 12 (307–469) | 18 (307–416) | 24 (307–421) | 32 (303–469) |
| Rainbow Smelt | 150 | 43 (157–213) | 93 (156–229) | 24 (157–221) | 5 (152–165) |
| ***Nearshore*** | | | | | |
| Rock Bass | 160 | 20 (165–246) | 10 (165–246) | 15 (161–232) | 5 (161–194) |
| Smallmouth Bass | 250 | 0 | 9 (263–357) | 30 (252–342) | 7 (252–460) |
| White Sucker | 300 | 50 (305–485) | 75 (302–431) | 60 (301–428) | 15 (310–506) |
| Yellow Perch | 215 | 42 (216–292) | 73 (218–328) | 64 (216–332) | 10 (222–287) |

(Anderson and Collins, 1995), and was prior to several other species invasions; (c) 1980–1999, which captured the invasion of several species, including *Bythotrephes* in 1984 (Bur et al., 1986) and zebra mussels in 1997 (McNickle et al., 2006); and (d) 2000–2017, characterized by quagga mussel and round goby invasions in South Bay (in 2004 and 2005, respectively) (Rennie et al., 2009; MNRF unpublished data) and the collapse of alewife populations (Riley et al., 2008). Values of $\delta^{13}$C were corrected for changes in atmospheric carbon ratios (Suess effect) using the method of Verburg (2007); corrected values were used in all subsequent analyses (as in Fera et al., 2017). Isotopic values were not corrected to baseline values because samples of primary consumers (such as unionid mussels, Cabana and Rasmussen, 1996) were not available for historical time periods. The fish isotope dataset is available in Electronic Supplementary Material (ESM) Table S1.

The number of fish for which scales were available for a species within a time period (Table 1) reflected changes in netting effort, agency priorities on which species should have ageing structures collected, and changes in the fish community over time (e.g., alewife, due to their collapse, were unavailable in the 2000–2017 time period).

Potential outlier stable isotope values were assessed using one-sided Grubb's tests for each species within a time period at a $p < 0.05$ significance level using the R package *outliers* (Komsta, 2011). Outliers were removed, and the Grubb's test was re-run until no further outliers were identified. In total, 2.7% of fish were removed as outliers. Subsequent analyses were run with and without outliers excluded to assess their impact on our overall conclusions.

Circular statistics were used to assess changes in isotopic values for the fish community between time periods (Schmidt et al., 2007). Change between adjacent time periods for a species was calculated as the difference between two points (the species' means) in a $\delta^{15}$N-$\delta^{13}$C biplot, which gave a vector with an angle and length. A Rayleigh test was used to assess whether the distribution of species' angles varied from uniformity (in circular statistics, uniformity refers to angles that are evenly distributed in all directions; Schmidt et al., 2007) using the R package *CircStats* (Lund and Agostinelli, 2018); this was conducted for all species, for nearshore species only and for offshore species only. The mean vectors between time periods were calculated. A mean vector has a direction (the mean angle) and a length (r). The length (r) is a measure of angle dispersion and ranges from 0 to 1, with 0 indicating a uniform distribution of angles and 1 indicating all angles are in the same direction (Schmidt et al., 2007). Differences in the directionality of mean angles were tested with a Watson-Williams test using the R package *circular* (Lund et al., 2017). This test was conducted only for those distributions of angles which the Rayleigh test showed were significantly different than uniform.

Two-way ANOVAs were performed to test whether $\delta^{13}$C and $\delta^{15}$N values varied significantly between time periods and species. Each ANOVA used time period, species and time period by species interaction as independent variables and $\delta^{13}$C or $\delta^{15}$N as the dependent variable. Interaction plots of isotopic value by time period and species were used to examine any significant effects. Normality and homogeneity of variance of residuals from the ANOVAs were checked using plots of residual distributions to ensure the assumptions of the ANOVAs were met.

## Results

Between 1947-1959 and 1960–1979, the community-wide distribution of angles was not significantly different from uniform (Z = 0.72, p = 0.50, mean angle = 111.2°, angular standard deviation = 88.8°, Table 2, Fig. 2a), indicating community-wide stability in isotopic values. Furthermore, the distribution of angles was not significantly different than uniform when considering only nearshore (Z = 1.00, p = 0.40) or only offshore species (Z = 0.41, p = 0.69). The species-specific isotopic values changed little between these time periods (<1.17‰ change in either $\delta^{15}$N or $\delta^{13}$C for any species).

Between 1960-1979 and 1980–1999, the community-wide distribution of angles was not significantly different from uniform (Z = 0.40, p = 0.68, mean angle = 116.3°, angular standard deviation = 101.2°, Table 2, Fig. 2b), again indicating stability in community-wide isotopic values. Similarly, the distribution of angles was not significantly different than uniform when considering only nearshore (Z = 1.67, p = 0.20) or offshore (Z = 0.72, p = 0.51) species and the isotopic values for each species changed little during this time period (<1.26‰ change in either $\delta^{15}$N or $\delta^{13}$C for any species).

Unlike previous time periods, differences in isotopic positions between 1980-1999 and 2000–2017 were marked, with significant differences in the distribution of angles from uniform when considering all species (Z = 6.83, $p < 0.0001$), nearshore species only (Z = 3.95, $p < 0.01$), or offshore species only (Z = 3.13, p = 0.032, Table 2, Fig. 2c). The mean angle of all species change was 86.3° (angular standard deviation = 22.8°), which is in the direction of increased $\delta^{13}$C values (increased reliance on nearshore resources). All species had higher average $\delta^{13}$C values in 2000–2017 than in any other time period. Lake whitefish showed the greatest magnitude of change, with an increase of 4.59‰ in $\delta^{13}$C, and a decline in $\delta^{15}$N of 1.66‰. Prior to 2000, lake whitefish had among the lowest $\delta^{13}$C values of any species. By 2000–2017, average $\delta^{13}$C values for whitefish were higher than for nearshore species in 1980–1999 (Fig. 3). The remaining offshore species showed smaller increases in $\delta^{13}$C than did lake whitefish and either increases (cisco, lake trout) or a small decrease (rainbow smelt) in $\delta^{15}$N (changes in isotopic values by species: cisco $\delta^{13}$C 1.82‰, $\delta^{15}$N 1.37‰; lake trout $\delta^{13}$C 0.78‰, $\delta^{15}$N 0.84‰; rainbow smelt $\delta^{13}$C 1.14‰, $\delta^{15}$N −0.12‰). To assess whether lake whitefish were the sole drivers of the significant result for offshore species, the Rayleigh test was re-run excluding lake whitefish (i.e. only including lake trout, cisco and rainbow smelt). While the mean angle of 63.8° still indicated a shift towards higher $\delta^{13}$C, this result was not significant (r = 0.92, angular standard deviation = 22.9, Z = 2.56, p = 0.066). The nearshore species all showed increases in $\delta^{13}$C, but none as great as lake whitefish, and either decreases (rock bass, smallmouth bass, yellow perch) or a small increase (white sucker) in $\delta^{15}$N (changes in isotopic values by species: rock bass $\delta^{13}$C 2.98‰, $\delta^{15}$N −0.03‰; smallmouth bass $\delta^{13}$C 3.17‰, $\delta^{15}$N −0.86‰; white sucker $\delta^{13}$C 2.75‰, $\delta^{15}$N 0.046‰; yellow perch $\delta^{13}$C 2.67‰, $\delta^{15}$N −0.43‰).

The significance of the Rayleigh test results did not differ with the inclusion of outliers in any of the above analyses, indicating our results are robust. No Watson-Williams tests were performed because the Rayleigh test was only significant for one set of adjacent time periods (1980–1999 compared to 2000–2017).

The two-way ANOVA with $\delta^{13}$C as the dependent variable showed that species ($F_{8,1023}$ = 279.64, $p < 0.0001$), time period ($F_{3,1023}$ = 509.51, $p < 0.0001$), and their interaction ($F_{22,1023}$ = 19.59, $p < 0.0001$) were all significant predictors. Average $\delta^{13}$C values were clearly higher in 2000–2017 compared to all other time periods, whereas differences between other time periods were smaller in magnitude and inconsistent between species (Fig. 4a). Specifically, nearshore species of fish (rock bass, smallmouth bass, white sucker, yellow perch) demonstrated greater shifts towards more positive $\delta^{13}$C with time, whereas the response in most offshore species (cisco, lake trout, rainbow smelt) was similar in direction but more muted in magnitude. Interestingly, lake whitefish grouped primarily with offshore fishes in the first 3 time periods, but grouped with nearshore fishes in the most recent

**Table 2**
Rayleigh tests of directional change in $\delta^{13}$C - $\delta^{15}$N space between time periods for all species, nearshore species (rock bass, smallmouth bass, white sucker, yellow perch), and offshore species (alewife, cisco, lake trout, lake whitefish, rainbow smelt). r is the length of the mean resultant vector (ranges from 0 to 1). Bold p-values are significant at the $p < 0.05$ level. n is the number of species.

| Time step | | Mean vector | | | Rayleigh's test | |
|---|---|---|---|---|---|---|
| | n | Direction (°) | Length (r) | Circular SD (°) | Z | p |
| ***All species*** | | | | | | |
| 1947–1959 to 1960–1979 | 8 | 111.2 | 0.30 | 88.8 | 0.72 | 0.50 |
| 1960–1979 to 1980–1999 | 9 | 116.3 | 0.21 | 101.2 | 0.40 | 0.68 |
| 1980–1999 to 2000–2017 | 8 | 86.3 | 0.92 | 22.8 | 6.83 | **0.000046** |
| ***Nearshore species*** | | | | | | |
| 1947–1959 to 1960–1979 | 3 | 147.1 | 0.58 | 59.9 | 1.00 | 0.40 |
| 1960–1979 to 1980–1999 | 4 | 163.5 | 0.65 | 53.5 | 1.67 | 0.20 |
| 1980–1999 to 2000–2017 | 4 | 95.9 | 0.99 | 6.5 | 3.95 | **0.0078** |
| ***Offshore species*** | | | | | | |
| 1947–1959 to 1960–1979 | 5 | 65.8 | 0.28 | 90.7 | 0.41 | 0.69 |
| 1960–1979 to 1980–1999 | 5 | 30.3 | 0.38 | 79.6 | 0.72 | 0.51 |
| 1980–1999 to 2000–2017 | 4 | 75.5 | 0.88 | 28.4 | 3.13 | **0.032** |

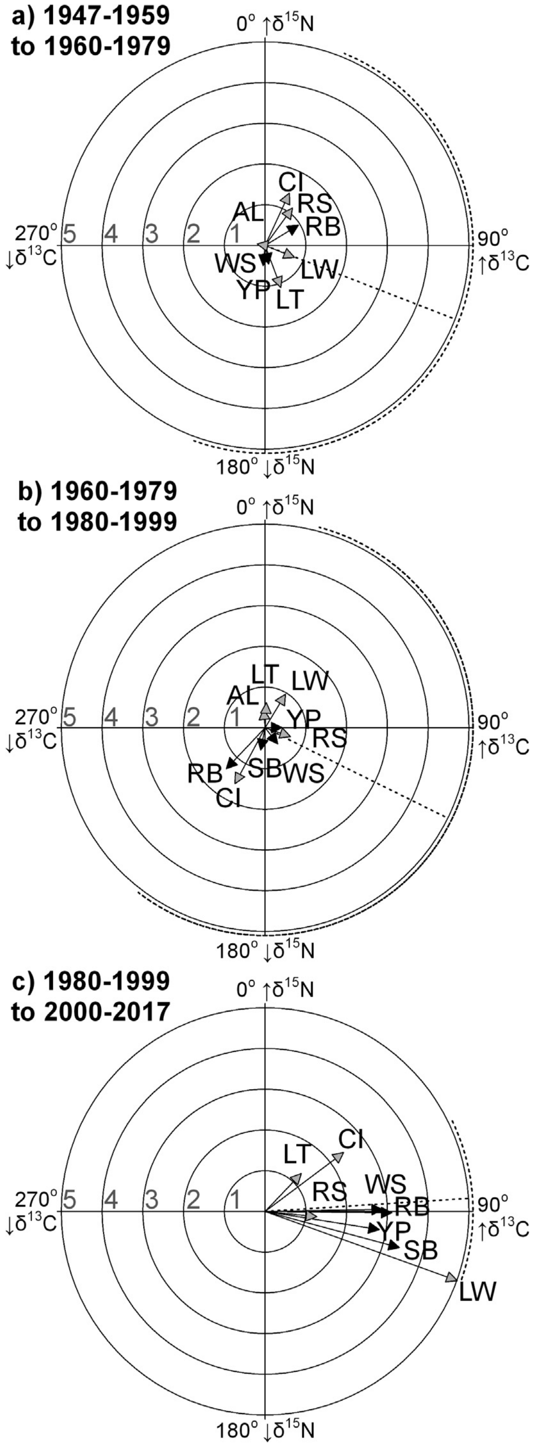
(post-dreissenid) time period. The two-way ANOVA with $\delta^{15}$N as the dependent variable showed that species ($F_{8,1023} = 360.40$, $p < 0.0001$), time period ($F_{3,1023} = 5.04$, $p < 0.01$), and their interaction ($F_{22,1023} = 9.59$, $p < 0.0001$) were all significant predictors. There were no obvious differences between time periods consistent among species in $\delta^{15}$N values (Fig. 4b), although certain species showed changes between specific time periods (e.g. lake whitefish decline in $\delta^{15}$N from 1980-1999 to 2000–2017 versus more stable trends in most other species).

## Discussion

Considering the 70-year time span of this study, the most dramatic change in isotopic values occurred between 1980-1999 and 2000–2017. The change in the later time period was consistent with a shift in reliance to nearshore and/or benthic energy sources, and was significant for all species together, nearshore species only, and offshore species only (although for offshore species the result was driven primarily by the dramatic shift in lake whitefish). Changes in $\delta^{15}$N over the same time period were much more variable among species than the changes in $\delta^{13}$C. Prior to 2000, there were no significant community-wide changes in $\delta^{13}$C and $\delta^{15}$N values, indicating food web stability despite several changes in the ecosystem (e.g. lake trout collapse and recovery, *Bythotrephes* invasion), and also highlighting the magnitude of shifts associated with ecosystem changes occurring in the most recent time period (i.e., dreissenid and round goby establishment).

Lake whitefish exhibited the greatest change in $\delta^{13}$C and $\delta^{15}$N values of all species from 1980-1999 to 2000–2017. Rennie et al. (2009) reported increased lake whitefish $\delta^{13}$C and decreased $\delta^{15}$N values following the invasion of zebra mussels in 1997 in South Bay (Rennie et al., 2009). Quagga mussels and round goby were first detected in South Bay in 2004 and 2005, respectively (Rennie et al., 2009; MNRF unpublished data). Furthermore, quagga mussels replaced zebra mussels in shallower waters following their invasion in Lake Huron, as well as colonized deeper offshore areas not inhabited by zebra mussels (Rudstam et al., 2020). Thus, quagga mussels and round gobies could have affected lake whitefish feeding ecology beyond what was observed in Rennie et al. (2009), motivating the decision to extend our isotopic analysis to more recent years. To determine the impact of these additional species on lake whitefish isotopic values explicitly, we compared the previously reported period (2000–2005) to 2006–2017 using a *t*-test, and found no difference in lake whitefish between time periods for $\delta^{13}$C (2000–2005 mean = −16.57‰, 2006–2017 mean = −16.59‰; $t = 0.0727$, $df = 25.02$, $p = 0.94$) or $\delta^{15}$N (2000–2005 mean = 9.73‰, 2006–2017 mean = 10.11‰; $t = -1.95$, $df = 26.55$, $p = 0.061$). Thus, the most dramatic changes in lake whitefish were primarily associated with the invasion of zebra mussels.

The dramatic changes in lake whitefish isotopic values are likely attributed to the changes in diet and distribution of lake whitefish within South Bay that occurred following the establishment of zebra mussels. The timing of lake whitefish isotopic value shifts (occurring by 2005) coincides with the decline of *Diporeia*, which occurred by 2002–2003, within five years of the first detection of zebra mussels in South Bay (McNickle et al., 2006). While *Diporeia* declines in the Great Lakes are correlated with dreissenid mussel invasion, the mechanism of *Diporeia* declines remains unclear (Rudstam et al., 2020). Following dreissenid mussel establishment and the loss of *Diporeia* (McNickle et al., 2006), lake whitefish in South Bay switched their diet from a high consumption of *Diporeia* and other profundal prey items to one dependent on more nearshore prey (Rennie et al., 2009). The energy density of the lake whitefish diet declined, contributing to declines in growth (McNickle et al., 2006). At the same time, the average depth of capture of lake whitefish in monitoring nets in South Bay became shallower following dreissenid mussel invasion (Rennie et al., 2009; Rennie et al., 2015). The decline in *Diporeia* was most evident in the deepest parts of South Bay (31–57 m) which had previously been the area of highest *Diporeia* density (McNickle et al., 2006). Increases in lake whitefish $\delta^{13}$C occurred broadly across the Great Lakes following dreissenid establishment and declines in *Diporiea*, but did not occur in Lake Superior sites where dreissenids have not become established (Fera et al., 2017). Declines in *Diporeia* occurred throughout Lake Huron, although some low density pockets of *Diporeia* remain in areas with depths greater than 90 m (Rudstam et al., 2020). Interestingly, the increase in lake whitefish $\delta^{13}$C values in South Bay was among the largest and most rapid of 14 Great Lakes sites previously examined (Fera et al., 2017). *Diporeia* may have been depleted quickly in South Bay following dreissenid invasion because it is an enclosed, relatively shallow basin (Fera et al., 2017). Conversely, lake whitefish at other Great Lakes sites adjacent to deep, offshore water initially shifted their distribution deeper following dreissenid invasion (with a subset subsequently moving shallower), possibly to access remaining deepwater populations of *Diporeia* (Rennie et al., 2015). Therefore, while changes to lake whitefish isotopic niche space have occurred elsewhere in the Great Lakes where dreissenids have become established (Fera et al., 2017), the magnitude of the shifts in South Bay may be more pronounced than some other locations due to less access to deepwater habitat for *Diporeia*.



a) 1947-1959 to 1960-1979

b) 1960-1979 to 1980-1999

c) 1980-1999 to 2000-2017

**Fig. 2.** Changes in mean species positions in $\delta^{13}$C - $\delta^{15}$N space between time periods a) 1947–1959 to 1960–1979, b) 1960–1979 to 1980–1999, and c) 1980–1999 to 2000–2017. Length of arrows show the magnitude of change for each species between time periods in $\delta^{13}$C and $\delta^{15}$N values (‰). Species abbreviations are as follows: AL: alewife, CI: cisco, LT: lake trout, LW: lake whitefish, RB: rock bass, RS: rainbow smelt, SB: smallmouth bass, WS: white sucker, YP: yellow perch. The straight dotted lines are the mean community angles and the curved dotted lines show the angular standard deviations. Black arrows indicate nearshore species and grey arrows indicate offshore species. The community angles from 1980- 1999 to 2000–2017 are the only ones that significantly differ from a uniform distribution (Rayleigh test, $p < 0.0001$).

Although all species had higher $\delta^{13}$C values in 2000–2017 than any other time period, there was variation in the magnitude of the changes observed. Other than lake whitefish, the remaining offshore species (cisco, lake trout, rainbow smelt) showed relatively small increases in $\delta^{13}$C (ranging from 17.4 to 39.7% of the increase observed in lake whitefish). All nearshore species (rock bass, smallmouth bass, white sucker, yellow perch) showed large increases in $\delta^{13}$C values in 2000–2017 (ranging from 58.3 to 69.1% of the increase observed in lake whitefish). The finding of larger increases in $\delta^{13}$C in nearshore vs. offshore fishes (with the exception of lake whitefish) mirrors the results of Rennie et al. (2013) for Lake Simcoe. However, this finding differs from that of Turschak et al. (2014) for Lake Michigan, who found a more consistent change in offshore species shifting to higher $\delta^{13}$C than nearshore species. The differences between study findings could be due to differences in lake, species, and timeframe considered. Turschak et al. (2014) compared isotopic values between time periods of low to high dreissenid mussel density (2002–2003 vs. 2010–2012) rather than pre- and post-invasion and the specific nearshore (longnose dace *Rhinichthys cataractae*, round goby, spottail shiner *Notropis hudsonius*, yellow perch) and offshore species (alewife, bloater, deepwater sculpin *Myoxocephalus thompsonii*, lake trout, rainbow smelt, slimy sculpin *Cottus cognatus*) considered were mostly different than in our study. In addition, a long-term (1909–2006) study of Lake Michigan's offshore fish community found no consistent directional change in isotopic values until community-wide $\delta^{13}$C increased following dreissenid mussel invasion (Schmidt, 2008).

Recent changes towards increased dependence on nearshore resources across the fish community coincided with the establishment of zebra and quagga mussels and round goby, as well as declines in offshore productivity and prey species. Dreissenid colonization is associated with increased nearshore and benthic productivity, increased nearshore benthic invertebrate biomass and decreased pelagic plankton density and profundal invertebrate density (Barbiero et al., 2012; Evans et al., 2011; Higgins and Vander Zanden, 2010). Increased use of nearshore resources by fish observed in this study is likely a response to increased nearshore and benthic productivity and decreased offshore and profundal productivity. The specific mechanism of increased reliance on nearshore resources could be an increase in overall benthic productivity in the nearshore resulting in greater importance of benthic energy pathways over time. This was observed in Lake Simcoe, where both benthic invertebrates and fish showed increased $\delta^{13}$C values following dreissenid invasion, whereas offshore fish and invertebrates were relatively stable (Rennie et al., 2013). Alternately, increased reliance on nearshore resources could be due to fish feeding more in the nearshore zone. In several locations across the Great Lakes where dreissenid mussels have become established, lake whitefish shifted to shallower, more nearshore depths following dreissenid establishment (Rennie et al. 2015). In addition, there is evidence of shifting fish diet coincident with recent invasions in the Great Lakes that could explain increased $\delta^{13}$C values from 1980-1999 to 2000–2017. Specifically, round goby is an abundant prey that can provide a trophic link from the increased nearshore productivity to piscivorous fishes (Kornis et al., 2012). For example, lake whitefish in the Great Lakes shifted their diet to include round goby following their invasions (Lehrer-Brey and Kornis, 2014; Pothoven and Madenjian, 2013). Round goby have been documented in the diets of several other species in the Great Lakes basin, including lake trout in Lakes Huron, Michigan and Ontario (Happel et al., 2017; Luo et al., 2019; Mumby et al., 2018; Roseman et al., 2014); yellow perch in Lake Michigan (Truemper et al., 2006) and Saginaw Bay, Lake Huron (Staton et al., 2014); smallmouth bass in Lake Erie (Crane and Einhouse, 2016); cisco in Lake Michigan (Breaker et al., 2020); and rock bass in Lake Simcoe (Finigan et al. 2018). Diet data collected from South Bay during netting in 2017 showed round goby were found in the stomachs of rainbow smelt, yellow perch,

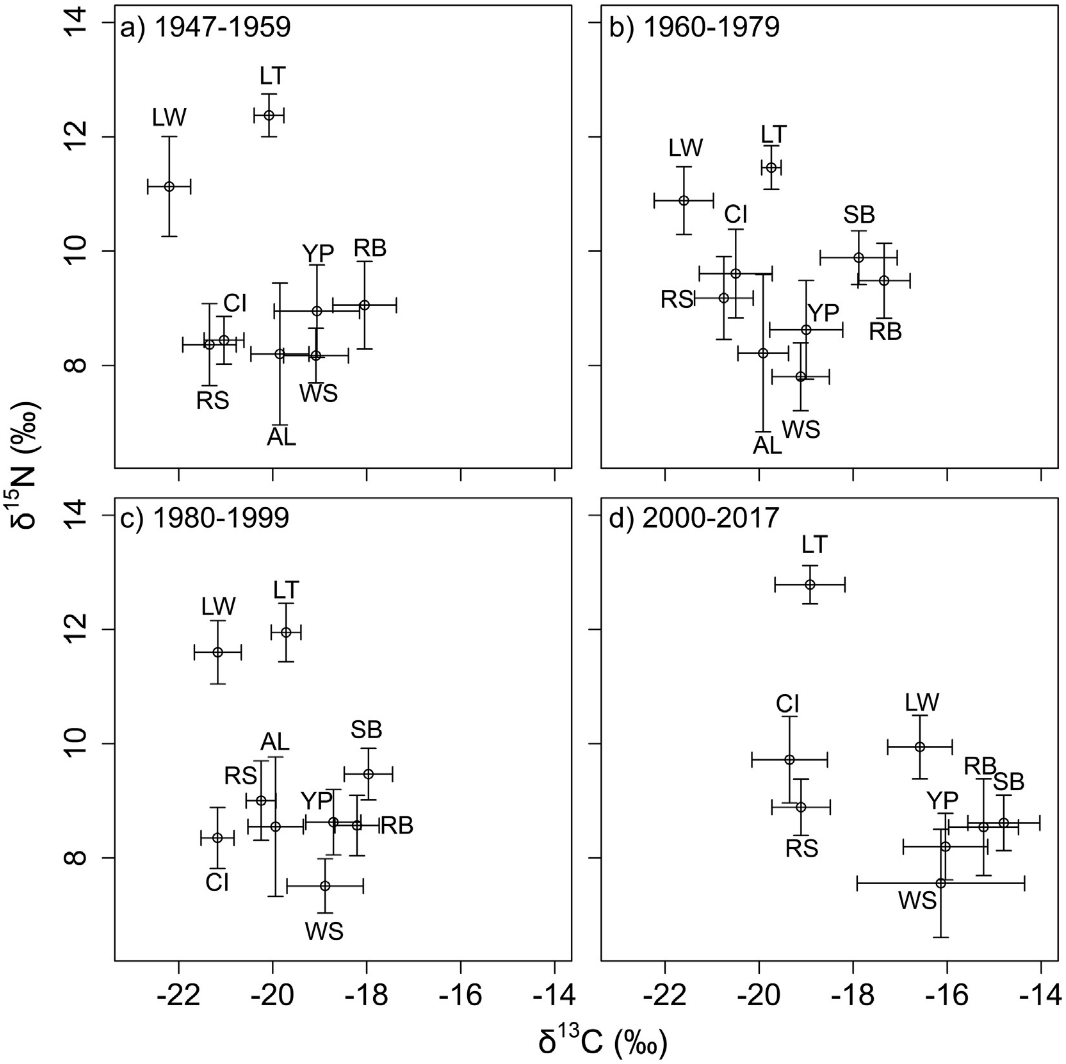


**Fig. 3.** Mean (circles) and standard deviation (bars) of stable isotope values by species for a) 1947–1959, b) 1960–1979, c) 1980–1999, and d) 2000–2017. Species abbreviations are as follows: AL: alewife, CI: cisco, LT: lake trout, LW: lake whitefish, RB: rock bass, RS: rainbow smelt, SB: smallmouth bass, WS: white sucker, YP: yellow perch.

and smallmouth bass (Electronic Supplementary Material (ESM) Table S2).

The hypothesis that fishes' increased dependence on nearshore and benthic energy sources is driven by recent dreissenid and round goby invasions is supported by the consistency of study results across several lakes. Multiple studies have observed an increase in fish $\delta^{13}C$ after dreissenid mussel and/or round goby invasion (Fera et al., 2017; Paterson et al., 2014; Rennie et al., 2009; Rennie et al., 2013; Rush et al., 2012; Schmidt, 2008; Turschak et al., 2014). Furthermore, McEachran et al. (2019) showed higher $\delta^{13}C$ values in warm and cool water fishes in Minnesota lakes with dreissenid mussels compared to those without, further supporting dreissenid mussels as a factor increasing fish dependence on nearshore and benthic energy sources.

Climate may have also played a role in the observed trends in isotopic signatures. The thermocline became shallower and the stratification period lengthened in South Bay from the 1950s to the 2000s (King et al., 1997; Rennie et al., 2009). Nearshore species could be restricted to shallower water for a greater part of the year, partially explaining the increase in $\delta^{13}C$ values in those species over time. However, it seems unlikely that changes in stratification duration alone could explain the large increases in $\delta^{13}C$ values community wide from 1980-1999 to 2000–2017 after relative stability for the previous 50 years given that there was no concurrent sudden shift in water temperature regime observed over this time (Rennie et al., 2009). Furthermore, an increased length of stratification cannot explain the large increase in $\delta^{13}C$ in lake whitefish, which is a hypolimnetic dwelling cold-water species.

A shift in phytoplankton size structure is a possible explanation for increased fish community $\delta^{13}C$ values. Dreissenid mussel filtering causes declines in large phytoplankton concentrations, resulting in a shift towards smaller taxa (Fahnenstiel et al., 2010). Smaller phytoplankton taxa are enriched in $\delta^{13}C$ compared to large taxa (Laws et al., 1995; Rau et al., 1996; Popp et al., 1998). Therefore, increased $\delta^{13}C$ values in higher trophic levels (including fish) could be driven by changes in phytoplankton size structure. Turschak et al. (2014) assessed this possibility in Lake Michigan by comparing $\delta^{13}C$ values of dreissenid mussels in 2002–2003 to 2010–2012, with the assumption that increases in phytoplankton $\delta^{13}C$ will increase the $\delta^{13}C$ values of the filter-feeding mussels. No change in $\delta^{13}C$ values of dreissenid mussels were detected, suggesting this mechanism was not responsible for detected increases in fish $\delta^{13}C$ (Turschak et al., 2014). While we lack the data to assess this possibility for South Bay, Turschak et al.'s (2014) findings may

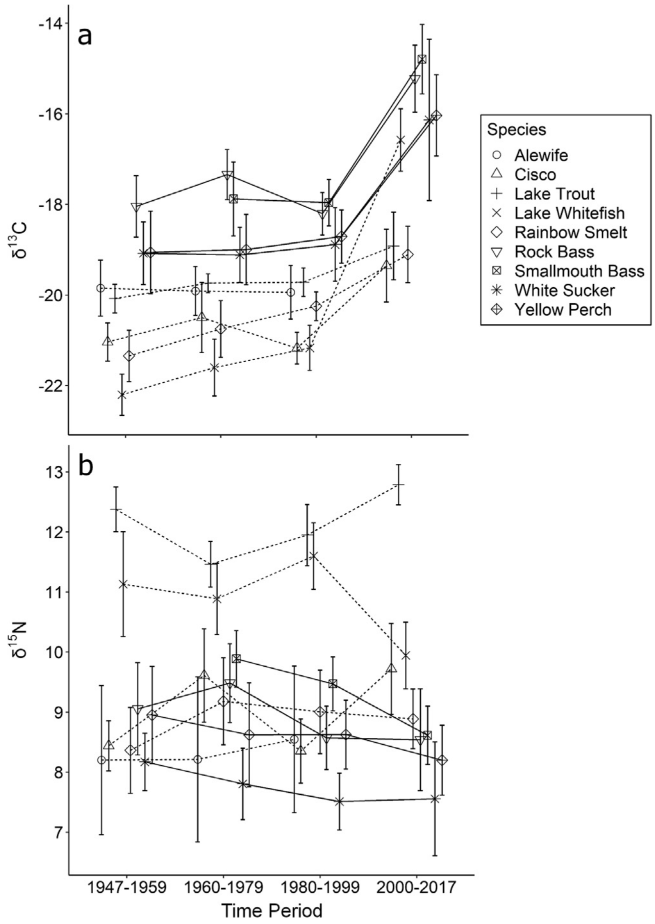


**Fig. 4.** Average $\delta^{13}$C (a) and $\delta^{15}$N (b) values and standard deviations (bars) by species and time period. Dotted lines show offshore species and solid lines show nearshore species. The horizontal position of species averages within each time period are offset from each other to increase legibility.

also hold true for South Bay. Furthermore, we expect that offshore fish species would be more affected by increased phytoplankton $\delta^{13}$C than nearshore fish species, whereas we observed greater increases in nearshore fish $\delta^{13}$C rather than offshore fish (with the exception of lake whitefish).

Variation in stable isotope values over time and space can vary due to shifting background isotope values related to biogeochemistry. For example, concentrations of $^{13}$C and $^{15}$N are affected by nutrient loading (Cabana and Rasmussen, 1996; Gerdeaux and Perga, 2006). In this study of South Bay, fish isotopic values were not corrected to baseline values (as is commonly done for across-site studies, Vander Zanden and Rasmussen, 1999) because samples of primary consumers (such as unionid mussels, Cabana and Rasmussen, 1996) were not available for the time period of study going back to the 1940s. However, by studying changes in isotopes across time in one location, confounding issues with geographical differences in isotopic baseline values can generally be avoided. Furthermore, there is no evidence of changes in nutrient loading in South Bay of the magnitude required to result in the observed changes in isotopic signatures (Fernandez et al., 2009; Rennie et al., 2009). Though spring total phosphorus concentrations have declined in Lake Huron from 1983 to 2017 (Rudstam et al., 2020), the effect of this reduction in nutrients on fish $\delta^{13}$C would be in the opposite direction observed in our study (Gerdeaux and Perga, 2006). Therefore, changes in phosphorus concentrations are an unlikely explanation for the recent increase in $\delta^{13}$C values in fish in South Bay. As well, if increased $\delta^{13}$C was purely due to an increase in baseline $\delta^{13}$C, we would expect to see similar increases in $\delta^{13}$C in all fish species, whereas we observed more pronounced increases in lake whitefish and nearshore species compared to the remaining offshore species. Finally, $\delta^{13}$C values were corrected for known changes in atmospheric C composition (the Suess effect; Verburg, 2007), ruling out this driver as a possible contributing factor to the patterns reported here.

Understanding changes to fish feeding ecology are important given the commercial and recreational fisheries on Lake Huron. Lake whitefish, the most important commercially harvested species in Lakes Huron and Michigan (Brenden et al., 2013), underwent substantial declines in juvenile and adult growth and condition following dreissenid mussel establishment as a result of the near disappearance of *Diporeia* from these lakes (Cottrill et al., 2020; Fera et al., 2015). Lake whitefish stocks have also shifted their spatial distribution (Ebener et al., 2010; Rennie et al., 2015) and undergone substantial declines in abundance, spawning stock biomass, recruitment, and yield (Ebener et al., 2021; Gobin et al., 2015). These changes have been most notable in Lakes Huron and Michigan, but have also occurred broadly across the Great Lakes in most locations except for Lake Superior where dreissenid mussels have not become established (Ebener et al., 2021). Our study highlights that the consequences of dreissenid mussel establishment appear to be more substantive for lake whitefish than for several other species in the food web. Furthermore, the dreissenid-induced changes in growth and recruitment have reduced the biomass of lake whitefish that can be sustainably harvested (Gobin et al., 2016). On the other hand, some species may benefit from increased nearshore production and changes to feeding ecology. Smallmouth bass in Lake Erie, for instance, had increased growth with increased reliance on round goby as prey (Crane and Einhouse, 2016) and healthy populations of smallmouth bass in parts of Lake Huron have been attributed to abundant round goby as a prey (Fielder et al., 2020).

## Conclusions

The South Bay fish community shifted to increased dependence on nearshore and benthic resources between 1980-1999 and 2000–2017, after stability in isotopic values since 1947. All fish species examined showed at least some shift towards increased $\delta^{13}$C values between 1980-1999 and 2000–2017, and, except for lake whitefish, nearshore species showed a greater increase in $\delta^{13}$C values than offshore species. Lake whitefish, an important commercially fished species in Lake Huron, showed the greatest increase in $\delta^{13}$C values of any of the species studied. This time frame of change is coincident with major changes to the Lake Huron ecosystem, notably the invasion of dreissenid mussels and round goby and declines in offshore productivity and prey fish communities. Evidence from the literature showing (i) recent shifts in diet to nearshore prey and (ii) similar responses across multiple lakes suggests a role of recent invasive species in changing the feeding ecology of multiple South Bay fish species. The long time-series of isotope data reveals the profound magnitude of recent changes compared to those of the previous 50 years, a perspective that is not available from studies comparing only pre- and post- invasion time periods.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jglr.2022.06.003.

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