Freshwater Biology

Freshwater Biology (2014) **59,** 2150–2161 doi:10.1111/fwb.12418

Ecological tracers reveal resource convergence among prey fish species in a large lake ecosystem

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SUMMARY

1. We measured stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) and fatty acid profiles in Lake Ontario alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*), slimy sculpin (*Cottus cognatus*) and round goby (*Neogobius melanostomus*) collected from 1982 to 2008 to investigate how temporal variability in these ecological tracers can relate to ecosystem-level changes associated with the establishment of highly invasive dreissenid mussels.

2. Prey fish $\delta^{15}N$ values remained relatively constant, with only slimy sculpin exhibiting a temporal increase in $\delta^{15}N$. In contrast, $\delta^{13}C$ values for alewife, rainbow smelt and, especially, slimy sculpin became less negative over time and were consistent with the benthification of the Lake Ontario food web associated with dreissenids.

3. Principal components analysis revealed higher contributions of 14:0 and 16:1n-7 fatty acids and increasingly negative $\delta^{13}C$ values in older samples in agreement with the greater historical importance of pelagic production for alewife, rainbow smelt and slimy sculpin.

4. Temporal declines in fatty acid unsaturation indices and Σn-3/Σn-6 ratios, and also increased 24:0/14:0 ratios for alewife, rainbow smelt and slimy sculpin, indicated the increasing importance of nearshore production pathways for more recently collected fish and resulted in values more similar to those for round goby.

5. These results indicate a temporal convergence of the food niche, whereas food partitioning has historically supported the coexistence of prey fish species in Lake Ontario. This convergence is consistent with changes in food-web processes associated with the invasion of dreissenid mussels.

Keywords: *Dreissena* spp., fatty acids, nearshore, offshore, stable isotopes

Introduction

Understanding temporal and spatial patterns in habitat and food resource exploitation by consumers is central in ecology (Schoener, 1974). For individuals feeding at a similar height in aquatic food webs, quantifying the extent of habitat and dietary overlap can provide significant insights into the mechanisms that contribute to species composition and diversity (Hutchinson, 1961). Furthermore, the number of stressors (e.g. invasive species, climate change, contaminants) that can act in concert to affect habitat, nutrient and energy availability in aquatic ecosystems is increasing (MEA, 2005). Therefore, being able to quantify the extent of resource overlap among

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coexisting species allows us to document and assess exactly how specific stressors cause perturbations in aquatic ecosystems.

The introduction and establishment of invasive dreissenid mussels (*Dreissena polymorpha* and *D. bugensis*) has profoundly affected aquatic ecosystem structure and processes (Vanderploeg *et al.*, 2002; Hecky *et al.*, 2004; Higgins & Vander Zanden, 2010). Owing to their capacity to restructure their environment physically, to redirect and alter nutrient availability in introduced habitats and to facilitate secondary invasions, dreissenid mussels have been identified as ecosystem engineers (Vanderploeg *et al.*, 2002; Hecky *et al.*, 2004). The Laurentian Great Lakes are among the mostly heavily affected aquatic ecosystems by dreissenid mussels (Vanderploeg *et al.*, 2002). For example, the establishment of large dreissenid mussel colonies in Lake Ontario has been accompanied by a temporal decline in zooplankton biomass (Munawar & Munawar, 2003) and reduced abundances of native benthic invertebrates, including bivalves and oligochaetes and amphipods in the genus *Diporeia* (Watkins *et al.*, 2007; Barbiero *et al.*, 2011).

Stable isotopes (SI) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) have become increasingly valuable for quantifying the long-term effects of stressors, such as the introduction of non-indigenous species to aquatic ecosystems. For example, SI analysis of archived Lake Ontario lake trout (*Salvelinus namaycush*) demonstrated a temporal transition in resource exploitation for this top predator consistent with the redirection of ecosystem production from offshore pelagic regions to the nearshore areas invaded by *Dreissena* (Rush *et al.*, 2012). In addition, Rennie, Sprules & Johnson (2009) performed SI analysis on archived Lake Huron Lake Whitefish (*Coregonus clupeaformis*) scale samples collected over a *c.* 50-year period. They demonstrated significant changes in habitat and food resource exploitation by Whitefish consistent with increased foraging in shallower water in the period after invasion (Rennie *et al.*, 2009). Similarly, a comparison of SI values for the littoral benthos collected from Lake Simcoe demonstrated a significant increase in the use of carbon derived from the nearshore during the introduction and establishment of *Dreissena* (Ozersky, Evans & Barton, 2012). These studies demonstrate the value of SI analyses, especially when applied to long-term tissue archive samples, for characterising species responses to the ecosystem-wide changes associated with the introduction of invasive species.

Fatty acids (FAs) provide a complementary approach to SI analysis in terms of their ability to quantify specific aspects of food-web dynamics (Iverson, 2009). Dietary FAs are good indices of diet quality, because they are key nutritional components required for normal growth, development and reproduction (Arts & Wainman, 1999; Arts, Ackman & Holub, 2001). They can also be used to reveal changes in food-web structure. For example, changes in consumer FA profiles have been used to document changes in Herring Gull (*Larus argentatus*) foraging (Hebert *et al.*, 2008), the health and nutritional status of the freshwater mysid shrimp (*Mysis diluviana*; Schlechtriem, Arts & Johannsson, 2008), the impacts of non-indigenous species introductions (Nordin *et al.*, 2008) and temporal and spatial changes in nearshore food webs (Czesny *et al.*, 2011). Thus, FAs and SI provide a powerful and complementary way of examining food webs that cannot be gained with either technique alone (Hebert *et al.*, 2009).

We quantified $\delta^{13}C$ and $\delta^{15}N$ values and FA profiles in Lake Ontario alewife (*Alosa pseudoharengus*), rainbow smelt (*Osmerus mordax*; herein referred to as smelt), slimy sculpin (*Cottus cognatus*; herein referred to as sculpin) and round goby (*Neogobius melanostomus*; herein referred to as goby) collected from 1982 to 2008 to examine the usefulness of these ecological tracers for identifying temporal trends in habitat and food resource exploitation among these species. Significant changes have occurred in the Lake Ontario ecosystem during this time, including the establishment of zebra and quagga mussels in 1989 and 1991, respectively, and their expansion throughout the lake by 2008 (Watkins *et al.*, 2007; Pennuto *et al.*, 2012). This proliferation was accompanied by the disappearance of native taxa, such as *Diporeia*, from large areas of the lake and the introduction of the goby in the late 1990s (Dermott, 2001; Mills *et al.*, 2003). Consequently, we hypothesised that: (i) recent fish samples would indicate a higher reliance on benthic nutrients and energy than formerly and (ii) niche partitioning (as indicated by SI and FA profiles) among fish species has been reduced over time.

Methods

Fish collections

Alewife, smelt, sculpin and goby specimens were collected with bottom trawls towed at offshore sites in Lake Ontario near Niagara-on-the-Lake, Cobourg, Port Credit, and within the eastern basin during summer/autumn 2007 and 2008. Upon collection, fish were sorted by species and size, placed in food grade plastic bags (ULINE, Toronto, ON, Canada) and immediately placed on dry ice and stored at −80 °C prior to analysis.

Prey fish specimens have been collected from Lake Ontario since 1977 as part of Environment Canada's Great Lakes Fish Contaminants Monitoring and Surveillance Programme (Kiriluk *et al.*, 1997; McGoldrick *et al.*, 2010). Biological information including fork and total lengths and mass was collected from individual fish, with similarly sized individuals subsequently pooled together and homogenised into whole-body samples for other studies (e.g. pollutant analyses). Approximately 50 g of sample homogenate were archived and stored at −20 or −80 °C in a tissue bank, without chemical preservatives (National Aquatic Biological Specimen Bank – NABSB; McGoldrick *et al.*, 2010). Aliquots (*c.* 5 g) of alewife, smelt and sculpin, collected from Lake Ontario between 1982 and 2003, were obtained from the NABSB archive. Goby samples were provided from the archive for 2003 and 2004 only because there were no specimens available for the 1982–2000 period.

Owing to limited sample availability for some of the collection years, samples of prey fish were separated into two time periods (1982–2000 and 2001–2008). This was carried out to maintain statistical rigour and also because these time periods directly relate to specific changes that have occurred in Lake Ontario. For example, the density of *Diporeia* had declined significantly throughout Lake Ontario by the late 1990s (Barbiero *et al.*, 2011), with limited numbers observed even in deepwater refugia (>90 m) by 2000 (Watkins *et al.*, 2007). Thus, 1982–2000 represents a period of higher *Diporeia* density and availability than 2001–2008, when populations of this prey item collapsed in Lake Ontario.

Tracer analyses

Prior to SI analysis, subsamples of homogenates of prey fish were freeze-dried for 48 h and then cryogenically homogenised in liquid nitrogen using a mortar and pestle. Stable isotope analyses were completed using a Delta Plus isotope ratio mass spectrometer (ThermoFinnigan, San Jose, CA, U.S.A.) coupled with an elemental analyser (Costech, Valencia, CA, U.S.A.). Results for δ^{13}C and δ^{15}N were assessed against three internal laboratory standards and a NIST (number 8414 bovine muscle) standard, run every 12 samples. The analytical precision based on the standard deviation of NIST standard 8414 (72 standards analysed) for δ^{15}N was 0.19% and for δ^{13}C was 0.04%. Analysis of additional NIST standards including sucrose (NIST 8542) and ammonium sulphate (NIST 8547) ($n = 3$ for each) generated values that were within 0.01 and 0.07% of certified values for δ^{15}N and δ^{13}C, respectively. To account for the potential influence of lipids on sample δ^{13}C results, prey fish δ^{13}C values were normalised using sample carbon:nitrogen ratios (Post *et al.*, 2007). Prey fish specimens were processed and analysed for SI at the Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada.

Prey fish FA mass fractions (μg FA mg^{-1} dry mass) were determined following a three-step procedure, as in McMeans *et al.* (2012). Briefly, freeze-dried whole-body homogenates were first lipid extracted three times using a 2:1 chloroform:methanol solution for gravimetric determination of whole-body lipid content (Folch, Lees & Sloane-Stanley, 1957). This was followed by conversion of FA to fatty acid methyl esters (FAME) using sulphuric acid in methanol (1:100 mixture; Morrison & Smith, 1964). FAME were separated using a Supelco (Bellefonte, PA, USA) SP-2560 column mounted in a Hewlett Packard 6890 series gas chromatograph. Individual FAME compounds were identified using a 37-component standard (Supelco number 47885-U) which was also used to generate separate calibration curves for quantification of each FAME. Sample extraction efficiencies were estimated using an internal standard spike of α-cholestane [Sigma (St. Louis, MO, USA) number C-8003] which was added to each sample prior to extraction. Prey fish specimens were processed and analysed for FA at Environment Canada's National Water Research Institute, Burlington, ON, Canada.

Data analysis

All statistical analyses were completed using the R statistical package (R Development Core Team, 2010) with the criterion of significance set at $P < 0.05$. Data were tested for normality using Shapiro–Wilk tests and normal probability plots. Temporal comparisons of tracer data collected for the two time periods (1982–2000 and 2001–2008) for each species were completed using either student's *t*- or Mann–Whitney *U*-tests. All multiple pairwise comparisons were completed using analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) test when ANOVA results were significant. For alewife and smelt 24:14 FA ratios, smelt body mass and sculpin δ^{13}C and Σn-3/Σn-6 FA ratio results that did not conform to normality following transformation, temporal comparison were completed using Mann–Whitney *U*-tests. Prey fish ΣFA mass proportions and unsaturation indices (UI) did not meet the assumptions of normality and were $\log_{10}$ and square-root transformed, respectively. Unless otherwise indicated, results are presented as mean ± 1 SE.

To test for any spatial patterns associated with individual samples collected from specific locations, Grubbs test (Grubbs, 1969) was used to identify outliers within the respective collection period for each species and with reference to collection location. Herein, if an outlier was identified, that value was removed from the data set. The analysis was then repeated on the reduced data set to identify additional outliers contributing to spatial patterns within the data. This analysis was completed on δ^{13}C, Σn-3/Σn-6, 24:0/14:0 and UI values under the hypothesis that these markers were those likely to reflect bottom-up effects of dreissenid mussels as related to the nearshore shunt hypothesis (Hecky *et al.*, 2004).

Principal component analysis (PCA) was used to investigate patterns in prey fish SI and FA profiles. Lake Ontario prey fish FA were expressed as relative proportions (percentage of total assayed FA). Principal components analyses were conducted using individual FA that constituted at least 1% of the total sum of FA quantified in each prey fish species. Sum proportions of saturated FA (ΣSAFA), mono- (ΣMUFA) and poly-unsaturated FA (ΣPUFA) were also included in ordinations. Additionally, Σn-3/Σn-6 and 24:0/14:0 ratios (unit less) were used to provide semi-quantitative indices of aquatic versus terrestrial and allochthonous versus autochthonous FA sources, respectively, in the prey fish species (Kainz, Arts & Mazumder, 2004; Hebert *et al.*, 2008). Unsaturation indices (UI) were also calculated as a metric related to cold water tolerance and thermal habitat selection (Hennessey & Nelson, 1983; Snyder & Hennessey, 2003). The UI was calculated as the sum total of individual PUFA concentrations multiplied by the number of double bonds present in the compound [$\Sigma(\mu\text{g FA mg}^{-1} \times$ number of double bonds)]. To stabilise normality and variance, the appropriate transformation of log (mass fraction) or logit (proportional data; Warton & Hui, 2011) was applied prior to analysis. All FA data were standardised to a mean of zero and unit variance prior to inclusion in the PCA. Fatty acids that had loadings >0.5 were considered influential to that component (McGarigal & Cushman, 2000). Student's *t*-tests were used to compare sample principal components scores for each of alewife, smelt and sculpin collected in 1982–2000 and 2001–2008. These tests were completed to test whether statistically significant differences were present in each species' ordinations between the two collection periods for the combination of SI and FA markers included in the PCA.

Results

A summary of prey fish collection and SI data is provided in Table 1. This study comprised a total of 101 composite samples consisting of 1102 individual fish. There were no significant differences in either total length or body mass between 1982–2000 and 2001–2008 for any of the prey fish species ($P \geq 0.076$). Mean lipid content of fish samples ranged from 10.3 to 32.7% (dry mass) with samples of goby and alewife collected from 1982 to 2000 representing these extremes. No significant differences in lipid content were determined for smelt ($P = 0.101$) or sculpin ($P = 0.644$) samples between the collection periods. For alewife, mean lipid content declined from 32.7 ± 2.1 to 19.8 ± 2.8% from 1982–2000 to 2001–2008 ($P < 0.001$).

For sculpin, alewife and smelt, δ^{13}C values for samples collected in 2001–2008 were consistently less negative than values from 1982 to 2000 (Table 1; Fig. 1). This temporal change in δ^{13}C was significant for sculpin ($P < 0.001$). In comparison, δ^{13}C values for goby averaged 21.3 ± 0.3% for samples collected from 2001 to 2008. Mean values of δ^{15}N for sculpin increased from 14.6 ± 0.2 to 16.4 ± 0.1% between 1982–2000 and 2001–2008 ($P < 0.002$). In contrast, the average δ^{15}N of smelt declined 0.6% between 1982–2000 and 2001–2008 ($P = 0.035$). For alewife, δ^{15}N values differed little between 1982–2000 and 2001–2008 ($P = 0.713$). Goby collected in 2001–2008 had an average δ^{15}N of 12.9 ± 0.2%.

Table 1 Summary sample size, biological, stable isotope and fatty acid information for four Lake Ontario prey fish species. Values are means ± SE

Species	Period	*n**	Mean length (cm)	Mean mass (g)	Mean lipid (% dry mass)	Mean δ^{13}C (%)	Mean δ^{15}N (%)
Slimy sculpin	1982–2000	8 (40)	10.3 ± 0.5	12.6 ± 1.5	28.9 ± 1.4	−27.4 ± 0.2	14.6 ± 0.2
	2001–2008	17 (286)	9.3 ± 0.3	10.4 ± 0.9	27.7 ± 2.2	−24.4 ± 0.1	16.0 ± 0.1
Alewife	1982–2000	10 (55)	15.0 ± 1.2	27.0 ± 1.8	32.7 ± 2.1	−22.7 ± 0.2	12.8 ± 0.1
	2001–2008	15 (43)	16.6 ± 0.4	33.7 ± 2.5	19.8 ± 1.8	−22.5 ± 0.2	12.7 ± 0.2
Rainbow smelt	1982–2000	13 (65)	13.4 ± 1.2	22.3 ± 5.8	26.7 ± 1.1	−24.6 ± 0.4	15.3 ± 0.2
	2001–2008	14 (136)	14.4 ± 1.0	19.1 ± 0.6	18.5 ± 3.1	−24.4 ± 0.1	14.7 ± 0.1
Round goby	1982–2000	–	–	–	–	–	–
	2001–2008	24 (477)	9.7 ± 1.0	23.7 ± 6.3	10.3 ± 1.7	−21.3 ± 0.3	12.9 ± 0.2

*Sample sizes include number of composite samples analysed. Value in parentheses indicates total number of individual fish included in sample composites.

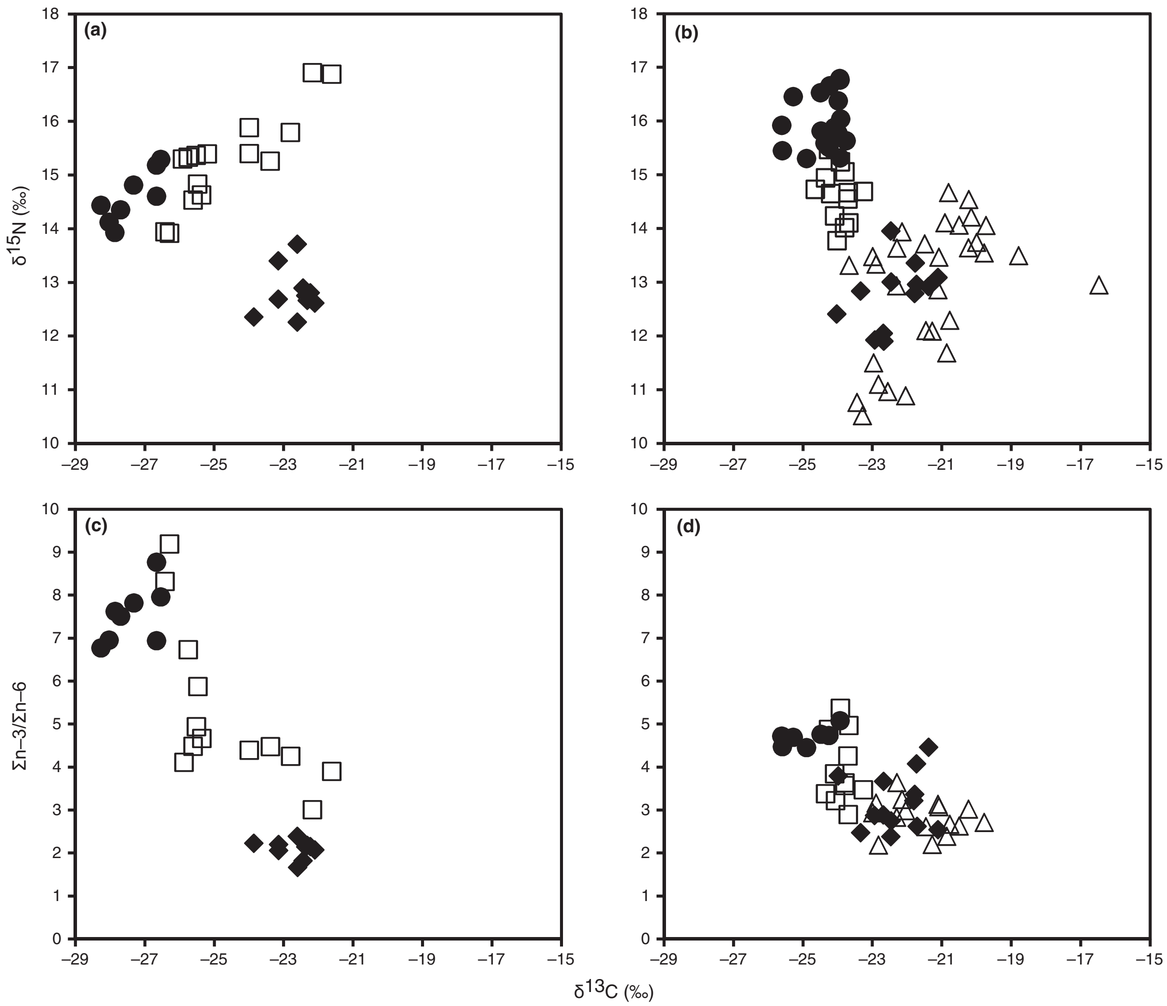

Fig. 1 Biplots of stable nitrogen (δ^{15}N) isotope and Σn-3/Σn-6 fatty acid ratios versus corresponding δ^{13}C values for Lake Ontario alewife (♦), rainbow smelt (□), slimy sculpin (●) and round goby (△) collected between (a, c) 1982–2000 and (b, d) 2001–2008.

Smelt and sculpin Σn-3/Σn-6 ratios declined from means of 5.3 ± 0.5 to 3.9 ± 0.2 and 7.5 ± 0.2 to 4.7 ± 0.1, respectively, from 1982–2000 and 2001–2008 ($P \leq 0.029$; Figs 2 & 3). However, for alewife, Σn-3/Σn-6 ratios increased by approximately 51.4% from a mean of 2.1 ± 0.2 to 3.2 ± 0.1 between 1982–2000 and 2001–2008 ($P < 0.001$). These compare to a mean Σn-3/Σn-6 of 2.8 ± 0.1 for goby collected between 2001 and 2008. For 2001–2008 samples, ANOVA demonstrated that Σn-3/Σn-6 ratios for smelt and sculpin were higher than that for goby ($F_{3,43} = 19.423$; $P \leq 0.011$) for samples collected from 2001 to 2008. However, no significant differences were found between alewife and goby Σn-3/Σn-6 ratios ($P = 0.407$) or between smelt and sculpin Σn-3/Σn-6 ($P = 0.097$).

Other FA tracers changed between 1982–2000 and 2001–2008, as observed for SI (Fig. 2). For example, UI of alewife, smelt and sculpin declined between 1982–2000 and 2001–2008. The average UI of smelt declined from 374 ± 25 to 319 ± 35 from 1982–2000 to 2001–2008 ($P = 0.212$) with sculpin declining from an average UI of 443 ± 42 to 409 ± 36 ($P = 0.607$) during this time. For alewife, mean UI declined from 325 ± 22 to 320 ± 23 ($P = 0.893$). These temporal declines for alewife, smelt and sculpin resulted in UI values that were more similar to the lower magnitude UI values determined for goby (152 ± 20) collected from 2001 to 2008. The fatty acid 24:0 was not detected in any sculpin collected from 1982 to 2000. Mass fractions of 24:0 quantified in alewife did not change significantly between 1982–2000 and 2001–2008 ($P = 0.354$). In contrast, 24:0 mass fractions in smelt increased by approximately 140% ($P < 0.001$) between the two same periods, and mass fractions of 14:0 decreased significantly for alewife, smelt and sculpin ($P \leq 0.025$). Thus, 24:0/14:0 values for alewife, smelt and sculpin also exhibited consistent

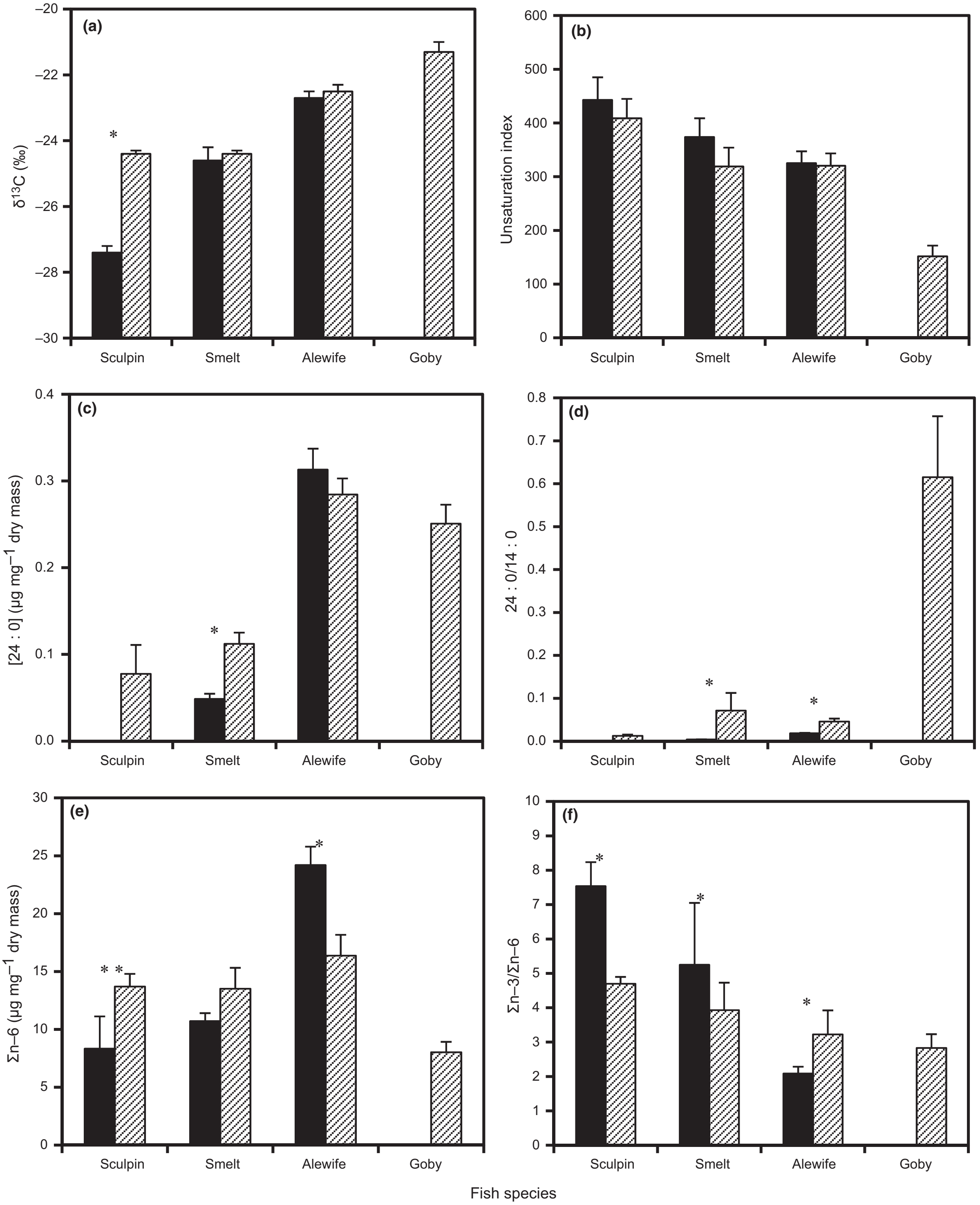

Fig. 2 Mean (± SE) (a) δ^{13}C, (b) UI (c) 24:0 (d) 24:0/14:0 (e) Σn-6 and (f) Σn-3/Σn-6 values for alewife, smelt and slimy sculpin collected from Lake Ontario from 1982 to 2008. Solid and hatched bars indicate specimens collected between 1982–2000 and 2001–2008, respectively. No gobies were collected from 1982 to 2000. Asterisks indicate significant difference (P < 0.05) between collection periods for each species.

temporal trends. For example, alewife 24:0/14:0 increased from a mean of 0.019 ± 0.001 to 0.042 ± 0.008 between 1982–2000 and 2001–2008 (P = 0.005). Similarly, smelt 24:0/14:0 ratios increased from 0.004 ± 0.001 to 0.081 ± 0.054 between the collection periods (P = 0.032). The absence of the 24:0 in sculpins collected in 1982–2000 meant that we could not calculate 24:0/14:0 ratios for that period. However, 24:0 was detected in sculpins

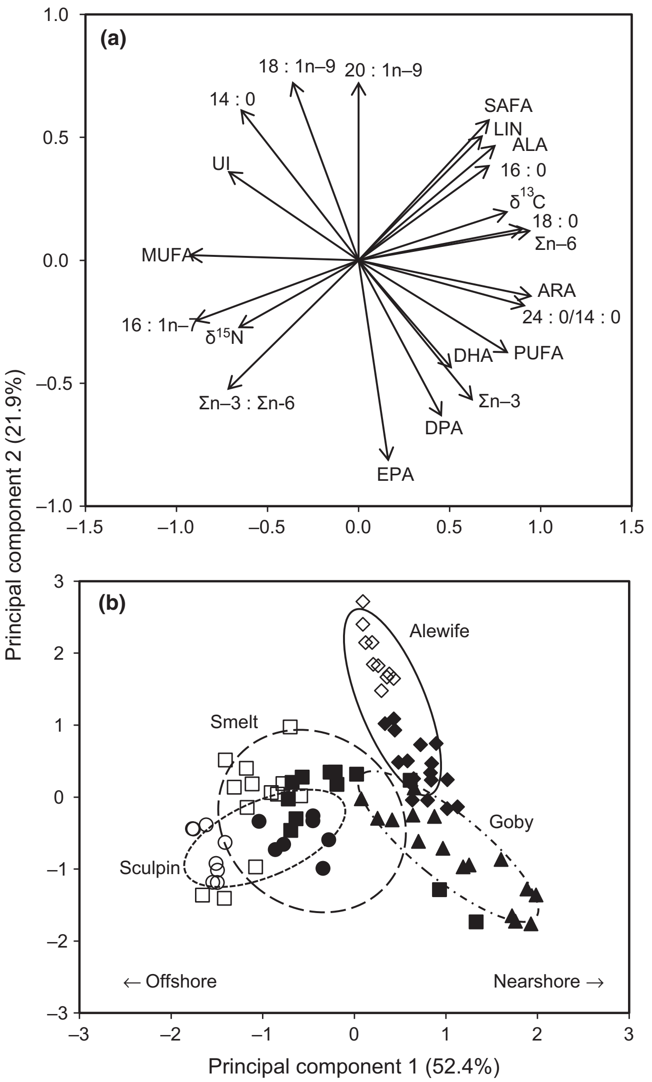

Fig. 3 (a) Principal component loadings and (b) ordination of fatty acid proportions (percentage of total), marker ratios, and stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes quantified in Lake Ontario alewife (◇), rainbow smelt (□), slimy sculpin (○) and round goby (▲). Open and solid symbols for alewife, smelt and sculpin represent specimens collected between 1982–2000 and 2001–2008, respectively. Ellipses represent the 95% confidence regions for the SI and FA profiles for each fish species, and total variance explained by each principal component is included with axis labels.

collected in 2001–2008, resulting in a mean 24:0/14:0 value of 0.013 ± 0.003. Values of 24:0/14:0 in goby averaged 0.493 ± 0.128 for fish collected from 2001 to 2008.

The mean mass fractions of Σn-6 FA increased by 26.3 and 64.5% in smelt and sculpin, respectively, between the two time periods ($P \leq 0.003$; Fig. 2). However, for alewife, the mean mass fraction of Σn-6 FA decreased by approximately 32.3% from 1982–2000 to 2001–2008 ($P = 0.007$). In comparison, Σn-3 FA exhibited minimal change between 1982–2000 and 2001–2008 among each of alewife, smelt and sculpin ($P = 0.605$). The ratio Σn-3/Σn-6 for smelt and sculpin declined by 25.1 and 37.7%, respectively, between the collection periods ($P \leq 0.029$). For alewife, mean Σn-3/Σn-6 ratio increased by 54.6% from 2.1 ± 0.2 to 3.2 ± 0.7 between 1981–2000 and 2001–2008 ($P < 0.001$). For each of alewife, smelt and sculpin, these changes in Σn-3/Σn-6 ratio resulted in values more similar to the average of 2.8 ± 0.4 estimated for gobies collected in 2001–2008.

Outlier analysis indicated no distinct spatial patterns in $\delta^{13}C$, Σn-3/Σn-6, 24:0/14:0 and UI for any of alewife, smelt and sculpin. For example, only two outliers were identified in the $\delta^{13}C$ data including one sample for each of alewife ($T_{crit} = 1.868$; $Z = 1.925$; $P = 0.047$) and smelt ($T_{crit} = 1.830$; $Z = 1.904$; $P = 0.037$). Two smelt Σn-3/Σn-6 values identified as outliers represented fish collected before the dreissenid invasion, from the Port Credit location. However, a total of six samples were included from this location with no other smelt samples from this site identified as outliers. No outliers were evident in UI or 24:0/14:0 values for alewife, smelt or sculpin.

Principal components analysis of prey fish FA proportional data, marker ratios and SI values provided good separation of all four prey fishes in addition to demonstrating temporal changes in these ecological tracer profiles (Fig. 3). SI and FA markers such as $\delta^{13}C$, 24:0/14:0, UI and Σn-3/Σn-6 ratios were strongly (loadings > ± 0.720) correlated with the first principal component (PC1) and used to characterise this PC. For example, both $\delta^{13}C$ (0.823) and 24:0/14:0 (0.919) were strongly positively loaded on PC1 with this direction of the axis considered to represent increasing importance of nearshore-associated SI and FA tracers. In contrast, Σn-3/Σn-6 ratios (−0.720) and UI values (−0.722) were strongly correlated in the negative direction on PC1 with this direction describing higher contributions of increasingly offshore habitat and food resources. Combined, PC1 and PC2 accounted for 74.3% of the total variance.

Smelt and sculpin samples collected in 1982–2000 scored in the negative direction of PC1 with sculpin generally scoring the most negative along this axis (Fig. 3). The 1982–2000 sculpin samples also scored negatively on PC2 in comparison with smelt which scored central to the origin of the PC2 axis. Alewives collected from 1982 to 2000 scored along the PC1 axis origin and also had the highest positive scores along PC2. More recently collected alewife, smelt and sculpin also scored in more positively on PC1 and in the general direction of ordination for the goby samples. These samples also exhibited a greater degree of individual overlap relative to 1982–2000 collected fish which were distinctly separated.

Student's *t*-tests demonstrated PC1 scores for alewife ($t = -6.043$; $P < 0.001$), smelt ($t = -4.716$; $P < 0.001$) and sculpin ($t = -8.608$; $P < 0.001$) collected from 2001 to 2008 were significantly more positive relative to 1982–2000 collected fish. Alewife PC2 scores were significantly different between samples collected in 1982–2000 and 2001–2008 ($t = -9.621$; $P < 0.001$). However, for smelt ($t = -0.192$; $P = 0.850$) and sculpin ($t = 1.378$; $P = 0.191$), student's *t*-tests did not demonstrate any significant differences in sample PC2 scores between the collection periods. Analysis of variance indicated that PC1 scores were significantly different among the four species collected in 2001–2008 ($F_{3,47} = 24.258$; $P < 0.001$). However, Tukey's post hoc test indicated that PC1 scores were not significantly different between alewife and goby ($P = 0.222$) and also between smelt and sculpin ($P = 0.245$) collected in this time. For 1982–2000 collected alewife, smelt and sculpin, pairwise comparison tests indicated that sample PC1 scores were significantly different among these species ($F_{2,28} = 162.6$; $P < 0.001$).

Discussion

Analysis of SI and FA in Lake Ontario prey fish found convergence among samples collected from 1982 to 2008, emphasising the complementary nature of these tracers for examining temporal changes in food webs. Specifically, principal components analysis of the predominant FA compounds and markers and SIs in alewife, smelt and sculpin indicated an increasing degree of similarity in tracer profiles among these species and with those determined for goby. For smelt and sculpins collected more recently, temporal changes in specific FA markers including UI values, Σn-6 and 24:0 were representative of increased reliance on food resources derived from the nearshore. Sculpin also exhibited the greatest temporal change in SI values, with $\delta^{13}C$ becoming significantly less negative and more consistent with the values associated with the shallow benthic habitats typically preferred by goby (Taraborelli *et al.*, 2009; Brush *et al.*, 2012). These observed changes in SI values and FA profiles are consistent with the redirection of pelagic production through nearshore benthic pathways and the ecosystem-scale changes associated with the establishment of dreissenid mussels in the Laurentian Great Lakes (Vanderploeg *et al.*, 2002; Hecky *et al.*, 2004; Higgins & Vander Zanden, 2010). Convergence of SI and FA tracers among these prey fish represents a reduction in the extent of food and habitat resource partitioning that historically facilitated the coexistence of these species in Great Lakes food webs (Urban & Brandt, 1993; Davis, Savino & Ogilvie, 2007).

High proportions of long-chain n-3 FA, such as EPA (20:5n-3) and DHA (22:6n-3), in aquatic consumer FA profiles commonly indicate a pelagic food web supported by diatoms (Napolitano, 1999). The reduced proportions of these FAs in smelt and sculpins collected recently may have implications for their growth and production. Polyunsaturated fatty acids help maintain membrane fluidity and cold water tolerance in fish, including alewife (Snyder & Hennessey, 2003). Given the ubiquity of dreissenids in the Laurentian Great Lakes (Bunnell *et al.*, 2014), the condition of cool–cold water fish may be compromised.

There have evidently been substantial increases in Σn-6 FA in smelt and sculpin in recent years. The primary n-6 FA identified included 18:2n-6 and 20:4n-6. Freshwater mussels, including dreissenids, are high in these FA, especially 20:4n-6 (Newton *et al.*, 2013). These compounds, in addition to 24:0/14:0, were all positively correlated with the first principal component in our sample ordination. Recent samples of alewife, smelt and sculpin scored more positively on this axis than did archived samples. In contrast, the negative direction of PC1 was described by FA such as 14:0 and 16:1n-7, which are most strongly associated with autochthonous resources in general and particularly diatom production, respectively, thereby inferring a greater importance of pelagic production for archived samples (Napolitano, 1999; Goedkoop *et al.*, 2000). Lower proportions of 16:1n-7 in *Diporeia* have been associated with greater reliance on detritus in lakes invaded by quagga mussels, owing to the impact of mussel filtering on phytoplankton biomass in offshore waters (Watkins *et al.*, 2012). For Lake Ontario, however, *Diporeia* populations had collapsed by the late 1990s, indicating different mechanisms for the shift in 16:1n-7 content of alewife, smelt and sculpin.

Diporeia density began to decline in Lake Ontario in the early 1990s, with the few remaining individuals in deep water (>90 m) having largely disappearing by 2000 (Dermott, 2001; Owens & Dittman, 2003; Watkins *et al.*, 2007). Since this collapse, *Mysis* has become an increasingly important prey item for all of alewife, smelt, sculpin and goby. For example, Stewart, Sprules & O'Gorman (2009) contrasted gut content information for alewives collected before (1972–1988) and after (2004–2005) the introduction of dreissenids. Alewife diets formerly consisted primarily of cladocerans and copepods, with only a limited contribution of *Mysis* (Mills *et al.*, 1992; Stewart *et al.*, 2009). Fish collected recently, however, had switched to *Mysis*, with additional contributions from the non-native zooplankton *Bythotrephes longimanus* and *Cercopagis pengoi* (Stewart *et al.*, 2009).

This contrasts with the diets of both smelt and sculpin which were always dominated by *Mysis* and have remained so through the invasion of dreissenids (Lantry & Stewart, 1993; Owens & Weber, 1995; Walsh *et al.*, 2008). Goby diets in Lake Ontario include mainly dreissenids and *Mysis*, the latter dominating the diet of individuals in deep water (>95 m) offshore (Walsh, Dittman & O'Gorman, 2007). In the current study, SI and FA profiles of smelt and sculpin became more similar to those of goby, despite their diets having changed only slightly. These results suggest that ecological changes that have affected the nutrition of *Mysis* have had further consequences for the tracer profiles of fish that consume them.

Zooplankton biomass and density of the benthic amphipod *Diporeia* have declined throughout Lake Ontario over the course of this study, and these species have historically represented substantial components of the diet of *Mysis* in Lake Ontario (Johannsson *et al.*, 2001; Mills *et al.*, 2003; Bunnell *et al.*, 2014). In addition, the increased water clarity associated with dreissenid mussels may have limited vertical migration of *Mysis*, resulting in their increased spatial separation from planktonic food such as diatoms and zooplankton (Boscarino *et al.*, 2010). While little is known of how these changes may have affected *Mysis* diets in Lake Ontario, *Mysis* is also known to ingest sediments in Lake Ontario, with the extent of sediment consumption being positively correlated with depth (Johannsson *et al.*, 2001; Sierszen *et al.*, 2011). Quagga mussels have expanded into deeper waters typically occupied by *Mysis* in Lake Ontario and now dominate the benthic invertebrate biomass (Watkins *et al.*, 2007; Pennuto *et al.*, 2012). Watkins *et al.* (2012) demonstrated significant differences in the FA composition of surficial sediments between lakes with and without quagga mussels. Importantly, differences in FA composition of sedimentary organic matter were reflected in *Diporeia.* Fatty acids, such as 16:1n-7, were significantly lower in *Diporeia* from the lakes invaded by quagga mussel (Watkins *et al.*, 2012). In our study, contributions of 16:1n-7 were significantly lower in alewife, smelt and sculpin collected recently than in older samples. Given the persistence of *Mysis* as a substantial component of the diets of smelt and sculpin, the decline in 16:1n-7 in these fish cannot be associated with a significant shift in taxonomic composition of prey. For alewives, the more recent shift to include *Mysis,* combined with a concurrent decline in 16:1n-7, provides further support for the importance of *Mysis* in the changed FA profiles quantified in these fish.

Additional evidences for bottom-up effects on tracer profiles induced by *Mysis* are supported by changes in δ^{13}C values reported for Lake Ontario *Mysis* between 1992 and 2008. For example, Kiriluk *et al.* (1995) reported δ^{13}C values of −30.8 and −32.5% for animals collected in 1992, before the lake-wide establishment of dreissenids. This contrasts with a mean of −29.0% reported by Rush *et al.* (2012) for *Mysis* collected in 2008. Such a temporal change in δ^{13}C is greater than the *c.* 1% generally attributed to the extent of δ^{13}C fractionation associated with trophic transfer (Vander Zanden & Rasmussen, 2001) and is also consistent with the less negative δ^{13}C values associated with benthic and nearshore production pathways (Hecky & Hesslein, 1995).

The FA marker 24:0 also increased between 1982–2000 and 2001–2008 for alewife, smelt and sculpin in Lake Ontario. When the lake is thermally stratified, gobies occupy nearshore benthic habitats, where physical processes such as wave action and terrestrial run-off may help to indirectly introduce more 24:0 to the FA pool relative to pelagic habitats (Smith *et al.*, 2007; Kornis, Mercado-Silva & Vander Zanden, 2012). Benthic detritivores, including chironomids, have been identified in the gut contents of Lake Ontario alewives (Stewart *et al.*, 2009). Chironomids are higher in 24:0 than other benthic invertebrates such as amphipods and oligochaetes (Sushchik *et al.*, 2007). High concentrations of 24:0 have also been reported for benthic omnivores, such as pumpkinseed sunfish (*Lepomis gibbosus*), that consume many chironomids (Maazouzi *et al.*, 2011). High mass fractions of 24:0 observed in alewife, smelt and sculpin collected from 2001 to 2008 suggest that chironomid prey may represent an important source of this terrestrial marker to prey fish in Ontario (Maazouzi *et al.*, 2011). For example, in the absence of *Diporeia*, chironomids now represent the second most common prey item (after *Mysis*) identified in the gut contents of sculpins (Walsh *et al.*, 2008). Also, 24:0 was not detected in sculpins collected during 1982–2000, suggesting a greater reliance on pelagic production when *Diporeia* were more abundant in Lake Ontario. The gradient in 24:0 mass fractions from alewife > smelt > sculpin is also consistent with the thermal preferences of these species and depth selection as indicated by δ^{13}C. Alewife prefers warmer epilimnetic waters relative to the increasingly cooler meta-hypolimnetic and offshore benthic habitats preferred by smelt and sculpin, respectively (Brandt, Magnuson & Crowder, 1980). A trend reflected in the increasingly negative δ^{13}C values for alewife, smelt and sculpin as associated with such habitats in aquatic ecosystems (Vander Zanden & Rasmussen, 1999). These results may reflect the expanding quagga mussel population in the offshore waters of Lake Ontario. Specifically, the ecological tracer profiles commonly associated with the littoral zone are being extended offshore, consistent with other studies that have documented the increased 'benthification' of food webs in ecosystems invaded by dreissenids (Vanderploeg *et al.*, 2002; Hecky *et al.*, 2004; Higgins & Vander Zanden, 2010).

Seasonal changes in depth distribution have occurred for both alewife and smelt following the establishment of dreissenids in Lake Ontario (O'Gorman *et al.*, 2000). Values of δ^{13}C for smelt determined here were consistently more negative than alewife, agreeing with the negative relationship observed between δ^{13}C and habitat depth in freshwater lakes (Vander Zanden & Rasmussen, 1999). The difference in δ^{13}C values between alewife and smelt is also consistent with historical observations of temperature selection for these two species. For example, the consistently more negative δ^{13}C determined for smelt is consistent with the deeper, cooler, waters preferred by this species, whereas the relatively less negative δ^{13}C values for alewife may reflect its occupation of shallower, warmer water (Brandt *et al.*, 1980; Vander Zanden & Rasmussen, 1999). Further, Brush *et al.* (2012) reported a mean δ^{13}C of −19.1% for Lake Ontario chironomids, indicating that such benthic prey may contribute more to the assimilate of the alewife than indicated by gut contents alone (Stewart *et al.*, 2009).

The temporal changes described here indicate an increasing overlap of SI and FA tracer profiles among Lake Ontario prey fish that has occurred since dreissenid establishment. Specifically, the extent of niche or resource partitioning among these prey fishes has been diminished over time, and such convergence has important consequences in the context of trophic ecology, interspecific competition and the extent of predation pressure exerted on a common forage base (Schoener, 1974). Aquatic food webs are highly complex, and quantifying the capacity of species to adapt to such ecosystem changes induced by stressors remains challenging (Vanderploeg *et al.*, 2002).

Acknowledgments

We thank Anna Hussey and Jerry Chao for their assistance with the SI and FA analyses, respectively, and the crews of the OMNR Steelcraft, R/V Kaho and DFO Kelso research vessels for assistance with fish collection. This research was funded by the Fishery Research Programme of the Great Lakes Fishery Commission. Additional funding was received from the Canada Research Chair programme and the Department of Wildlife, Fisheries & Aquaculture at Mississippi State University. Any use of trade, product or firm names is for descriptive purposes only and does not imply endorsement by the governments of Canada, the United States, the Province of Ontario, or New York State. This article is contribution number 1860 of the United States Geological Survey Great Lakes Science Center.

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(Manuscript accepted 28 June 2014)