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# Niche plasticity in invasive fishes in the Great Lakes

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**Abstract** The geographic range of an invasive species is a key determinant of relative impact in the invaded region. Comparison of invasive species that are widespread or rare in invaded ranges can highlight mechanistic traits that determine the risk of impact from invasion. Round Goby (*Neogobius melanostomus*) is more geographically widespread and abundant than Tubenose Goby (*Proterorhinus semilunaris*) across invaded ranges of the Laurentian Great Lakes. We used stable isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) in liver and muscle to contrast the isotopic niche breadth and niche plasticity of Round Goby and Tubenose Goby near the inflow and outflow of Lake St. Clair and in western Lake Superior. At all sites, Round Goby and Tubenose Goby that matched in size (21–53 mm standard length) had distinct isotopic niches with no overlap, driven by higher  $\delta^{15}\text{N}$  in Round Goby. The variation in isotopic niche, and the mean difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between muscle and liver, was greater for Round Goby, suggesting both greater seasonal shifts in diet and niche plasticity in this more widely established invader. Round Goby that were significantly larger than Tubenose Goby had broader isotopic niches and greater niche plasticity in

the majority of cases and this was associated with isotopic niche overlap with smaller Round Goby and Tubenose Goby. Our findings suggest that a broad and plastic isotopic niche provides scope for wider establishment range in invasive fish species.

**Keywords** Round Goby · Tubenose Goby · Isotopic niche · Niche plasticity · Great Lakes

## Introduction

Invasive species are one of the leading causes of extinction in the world and second only to habitat destruction for North American fishes (Clavero and García-Berthou 2005; Jelks et al. 2008). Habitat destruction often facilitates further successful establishment of invasive species (Marchetti and Moyle 2001; Marvier et al. 2004; Ricciardi 2001; Shea and Chesson 2002) and invasive species themselves are often ecosystem engineers that dramatically alter habitats from their pre-invasion state (Jude and DeBoe 1996; Karlson et al. 2007). Extensive establishment in invasive species is often associated with flexible habitat use facilitated by a broad diet and environmental tolerance (Marvier et al. 2004; Shea and Chesson 2002); thus, higher temperatures from global warming during the last century and increasing fragmentation from habitat destruction could provide a catalyst for further biological invasions (Harka and Bíró 2007).

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Some invasive species are more widely established than others, despite retaining apparent similarities and a certain degree of relatedness. Study of the traits of widespread and rarely established invasive species can provide insights on the drivers of geographic spread and establishment success (Van Kleunen et al. 2010). High genetic and phenotypic diversity are often suggested to be important in the survival of populations following introduction events (Reid and Orlova 2002; Stepien et al. 2005); and variability in phenotype can provide scope for phenotypic plasticity, acclimation or adaptation (Holt 2009). Analysis of ecological niche is regularly used as a method for studying variation in phenotype and resource use (Moyle and Marchetti 2006; Peterson and Vieglais 2001).

A broad ecological niche driven by flexible diet and habitat use is often considered to be important for successful colonization, establishment, and spread of invasive species (Peterson and Vieglais 2001). The use of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes is common in studies of diet history, trophic ecology, and food web dynamics of fishes (Brush et al. 2012; Post et al. 2007; Vander Zanden et al. 1997) and stable isotopes are increasingly used to depict dietary niche and diet-driven habitat niche (e.g. Guzzo et al. 2013; Jackson et al. 2012). This technique proves particularly useful for comparing the breadth of resources assimilated by different populations where they overlap in distribution. Due to the different assimilation rates of tissue, and thus stable isotope, the comparative analysis of multiple tissues can provide an indication of seasonal changes in diet, diet plasticity, and generalist and specialist feeding strategies (Bearhop et al. 2004). Therefore, we investigated for dietary driven differences in ecological niche of two invasive fish species using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ .

The Gobiidae are one of the largest fish families with over 2500 species in over 200 genera and include the widely established Round Goby (*Neogobius melanostomus*) and narrowly established Tubenose Goby (*Proterorhinus semilunaris*) that are both invasive in the Laurentian Great Lakes (Miller 2004). Round Goby and Tubenose Goby were first discovered in the St. Clair River in 1990 and were probably established in Lake St. Clair by this time (Jude et al. 1992). Round Goby has since established in high densities throughout much of the Great Lakes (Kornis et al. 2012), whereas, Tubenose Goby has remained restricted to Lake St. Clair, Lake Erie and western

Lake Superior (Vanderploeg et al. 2002; See USGS 2014 for current detection data). The co-occurrence of these two gobiids provides an excellent opportunity to determine the traits that are most prevalent in species that survive novel environments. Furthermore, comparison of these two species where they overlap in distribution can help us understand the factors that enable two similar species to share the same habitat space.

The aim of this study was to compare the relative diet plasticity and niche of Round Goby and Tubenose Goby using stable isotopes. Liver and muscle of each species and population of gobies were analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  to quantify 'isotopic niche breadth'. The different assimilation rates of isotopes in tissues (liver, muscle) were utilized to represent change in diet over time and thus plasticity in trophic niche (variation in  $\delta^{15}\text{N}$ ) and diet-driven habitat niche (variation in  $\delta^{13}\text{C}$ ). We hypothesized that the more successful (widely established) Round Goby would have a broader isotopic niche and greater niche plasticity than the less successful (narrowly established) Tubenose Goby. Analysis of phenotypic traits is integral to driving better understanding of the factors that drive greater establishment success in invasive species. Study of niche breadth and niche plasticity can help determine which species are more likely to persist as on-going climate change and habitat destruction lead to novel environments and continue to threaten the stability of ecosystems and the maintenance of biodiversity.

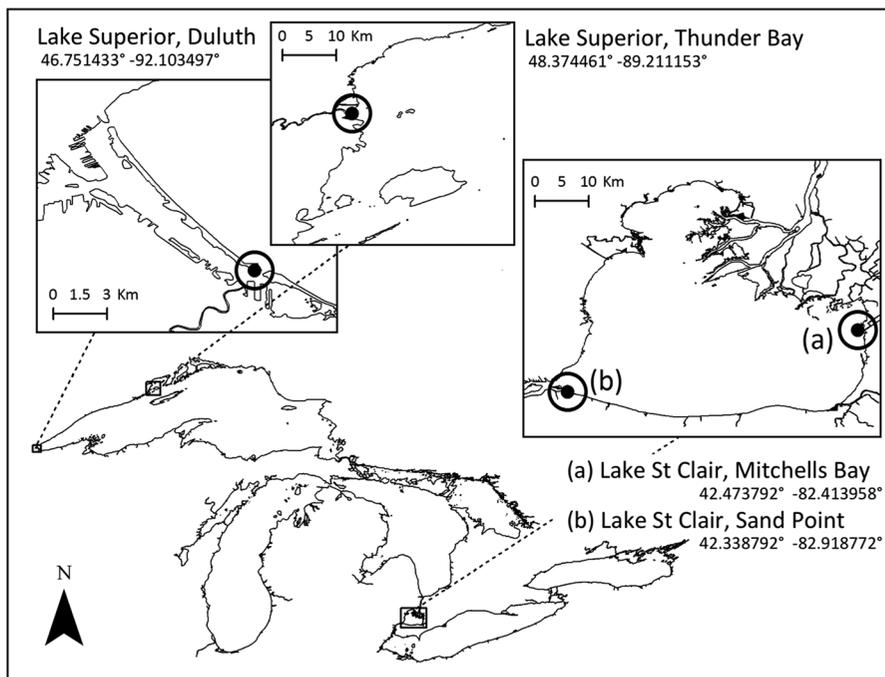
## Methods

### Study sites and sample collections

Samples of Round Goby, Tubenose Goby, and bivalves were collected from the littoral edges of Lake St. Clair and western Lake Superior (W. Lake Superior; Fig. 1). Mitchell's Bay is at the edge of a river delta in Lake St. Clair and Sand Point is at the head of the Detroit River. In Thunder Bay, Tubenose Goby was collected from Mission Marsh near the mouth of the Kaministiquia River, and Round Goby was collected from within the Duluth Harbor basin at the head of the St. Louis River.

Gobies were collected using a bag seine net (Model SEM-03: 15.2 m long, 1.2 m tall with

**Fig. 1** Collection sites for Round Goby and Tubenose Goby in Lake St. Clair  
**a** Mitchell's Bay (September 2011) and  
**b** Sand Point (October 2012) and western Lake Superior (August 2012), Duluth and Thunder Bay



1.2 × 1.2 × 1.2 m cod end and 6.4 mm mesh. Franklin Net and Twine, Wheatley, ON), angling, and minnow traps (42 cm torpedo with 53 cm openings). Fishes were euthanized, bagged individually, placed on ice, and returned to the laboratory where measurements were taken before freezing to  $-40^{\circ}\text{C}$  (wet weight  $\pm 0.1$  g; total length and standard length minimum  $\pm 0.1$  mm using 150 mm calipers). Whole fishes were later thawed, and skinless and boneless dorsal muscle and liver tissue were removed and re-frozen before freeze-drying. Fishes were sexed by external urogenital papilla (Miller 2004). Many individuals were too small to accurately sex and were deemed immature; papilla is generally visible at  $> \sim 15$  mm in Tubenose Goby (Leslie et al. 2002) and  $> \sim 20$  mm in Round Goby (Leslie and Timmins 2004).

Primary consumers are considered to be the most appropriate baseline for spatial and temporal comparison of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  (Guzzo et al. 2013; Post 2002). Bivalves were collected from each site (10–30 per location, Zebra Mussel/*Dreissena polymorpha* from Lake St. Clair and Duluth; unionids from W. Lake Superior, not identified to species level), kept on ice, then frozen to  $-40^{\circ}\text{C}$  in the laboratory. Bivalves were later thawed, weighed (tissue wet weight  $\pm 0.1$  g), measured (shell length and shell width  $\pm 0.1$  mm),

tissue and shell separated, frozen to  $-80^{\circ}\text{C}$ , and freeze-dried. Similar-size individual bivalves were matched for comparison between locations and whole individual tissue samples were run for stable isotope analysis.

#### Stable isotope analysis

All dried tissue samples were ground to homogenous sample using mortar and pestle and scissors. Fish liver and bivalve whole body tissues were lipid extracted (Solvent Distillation Method: 2× agitation of tissue in 2:1 chloroform/methanol solution for 24 h, solvent decanted, sample air dried; modification of method outlined by Bligh and Dyer 1959). Muscle tissues were not lipid extracted due to low lipid content based on C:N ratio  $< 3.5$  in gobies (Post et al. 2007). Samples were weighed into 5 mm × 9 mm tin cups (400–700  $\mu\text{g}$  per sample;  $\pm 1$   $\mu\text{g}$ ). Samples and standards were then run for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , C% and N%, using a Delta V IRMS (Thermo Electron Corporation, Waltham, Massachusetts, USA) equipped with an elemental analyzer (Costech, Santa Clarita, California, USA). The abundances of carbon and nitrogen isotopes in each sample were expressed in delta notation relative to standard materials, using the following equation:

$$\delta R(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R is the ratio  $^{15}\text{N}/^{14}\text{N}$  or  $^{13}\text{C}/^{12}\text{C}$ . Standard reference materials were Pee Dee Belemnite (PDB) carbonate for  $\text{CO}_2$ , and atmospheric nitrogen for  $\text{N}_2$ . NIST standard 8414 and an internal fish muscle standard (Nile Tilapia, *Oreochromis niloticus*) were analyzed every 12<sup>th</sup> sample. To assess repeatability every 10<sup>th</sup> sample was run in triplicate. Precision of analysis based on the standard deviation of the two reference standards ranged from 0.07 to 0.08 ‰ for  $\delta^{13}\text{C}$  and 0.12 to 0.13 ‰ for  $\delta^{15}\text{N}$  (NIST 8414 and Nile Tilapia muscle standards, respectively;  $n = 247$ ). Accuracy based on the difference between our NIST standard data and certified data for NIST standards ranged from 0.03 to 0.14 ‰ for  $\delta^{13}\text{C}$  (NIST 8542, 8573) and 0.05 to 0.31 ‰ for  $\delta^{15}\text{N}$  (NIST 8573, 8548, 8547).

### Statistical analyses

As Round Goby grow to a larger size than Tubenose Goby and a size-related ontogenetic dietary shift is often reported to occur in Round Goby (Kornis et al. 2012), multiple groups were formed for statistical comparison based on size class in relation to the size range of Tubenose Goby. Significantly different groups were determined using box-whisker plots of standard length and wet weight and Student *T* tests. An additional group was formed for a small subset of Tubenose Goby that were within the size range of young-of-year (YOY) Tubenose Goby in the Great Lakes (Leslie et al. 2002) and significantly smaller than all other fishes in this study (Thunder Bay only, Student *T* test,  $p < 0.05$ ). In summary, the following groups were formed: (1) Round Goby matched in size with Tubenose Goby; (2) Tubenose Goby matched in size with Round Goby; (3) Round Goby significantly larger than all other fishes; and, iv. Tubenose Goby significantly smaller than all other fishes. Prior to further analyses, the standard length (or shell length),  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of each size group from each location was found to have a normal distribution (Kolmogorov–Smirnov) and homoscedasticity (Levene's equality of variance). Standard length,  $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and sex of each population in each location were compared independently for liver, muscle tissue and whole bivalve tissue using MANOVA followed by post hoc least significant difference (LSD) pairwise

comparisons for each variable. Cohen's power analysis was used to determine the influence of sample size, which gives a value ranging from 0 (strong effect) to 1 (no effect). For power  $< 0.8$ , samples were bootstrapped ( $n = 2000$ ) and the comparison repeated. Statistical analyses were conducted in SPSS v.22 or R v.3.1.0. Significance threshold of  $p < 0.05$  was used for all statistical analyses.

### Populations metrics and standard ellipse areas

To compare niche breadth of the two goby species at the different locations, ellipses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bi-plots were constructed using a multivariate Bayesian package in R (Stable Isotope Bayesian Ellipses in R-SIBER; Jackson et al. 2011). Measures of variability in mean  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of all samples at each location were used as a proxy for the limits to niche breadth for the goby populations. In the SIBER package, these metrics are based on five community metrics originally developed by Layman et al. (2007) that represent key aspects of trophic structure. Standard Ellipse Area's (*SEA*'s) are used as a measure of mean isotope variability. The *SEA* of bivariate data is calculated from the variability in  $x$  and  $y$  of the stable isotope bi-plot. The *SEA* represents approximately 40 % of the spread of data, thus, with sufficient sample sizes ( $> 30$ ), is expected to represent the core niche and be insensitive to sample size (Cummings et al. 2012; Jackson et al. 2012). Use of the transformed version, *SEA<sub>C</sub>*, accounts for loss of a second degree of freedom when using bivariate data and provides for an unbiased correction of *SEA* for sample sizes  $< 30$ :

$$SEA_C = SEA \times (n - 1)/(n - 2)$$

*SEA<sub>C</sub>* was then used to determine the degree of overlap in isotopic niche breadth between populations. The probability of one population having a smaller isotopic niche than another population was calculated from credible intervals produced from multiple Bayesian iterations of *SEA* ( $10^5$  posterior draws; see Jackson et al. (2011) for details). The Bayesian estimate of *SEA* (*SEA<sub>B</sub>*) is analogous to a bootstrapping procedure, in that it also provides a robust adjustment for differences in sample size. Probability values (hereafter labeled as *P*) of isotopic niche size differences ranged from zero to one; zero meaning no difference. Probability of overlap or niche size difference  $> 0.6$  was considered to be significant, which is the same criteria used in the

Schoener's diet index (Wallace 1981) and also used by Guzzo et al. (2013) in the comparison of native Yellow Perch (*Perca flavescens*) and invasive White Perch (*Morone americana*)  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  SEA's. In the present study, we used the total area of ellipses for bivalves at each location to represent variability in isotopic niche at the base of the food web and a measure of variation in isotopic niche available to the gobies at each location. As primary consumers, the isotope signature of bivalve tissues is more responsive than fishes to source-driven changes in isotope signature through time. Thus, variation in baseline isotope signature (or baseline isotope niche breadth) indicates the degree of temporal and spatial variation in secondary and tertiary consumers that is due to source-driven changes in isotope concentrations, as opposed to shifts in diet.

### Niche plasticity

It is well established that muscle tissue represents a longer integration of stable isotope assimilation than liver tissue (Post et al. 2007). We used the difference in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  from muscle to liver tissue to quantify the degree to which the isotopic niche in an individual changed. We compared the difference in isotopic niche ( $SEA_B$ ) between muscle and liver and the probability of overlap in isotopic niche ( $SEA_C$ ) between muscle and liver as a measure of isotopic niche plasticity in a population. In addition, we compared liver and muscle for  $\delta^{13}\text{C}$  and then for  $\delta^{15}\text{N}$  in each individual using paired Student *T* tests and compared the calculated difference between liver and muscle for each population using independent *T* tests.

## Results

A total of 190 Round Goby and 102 Tubenose Goby were collected where they overlap in distribution from two sites at the littoral edges of Lake St. Clair (Mitchell's Bay, Sep 2011 and Sand Point, Oct 2012) and W. Lake Superior (Thunder Bay and Duluth Aug 2012; Table 1, Fig. 1). The two species were not available from the same location in W. Lake Superior, although they were present in both locations the previous year (Schloesser et al. 2013).

### Baseline bivalves

The baseline bivalves from the two locations in Lake St. Clair had significantly different  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ; with a total difference of 1.4 ‰ lower  $\delta^{13}\text{C}$  and 1 ‰ higher  $\delta^{15}\text{N}$  in bivalves from Sand Point, at the head of Detroit River, than Mitchell's Bay (ANOVA,  $F_{1,55} = 57.3$  and  $79.8$  for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  respectively,  $p < 0.01$ , see Table 1 for sample sizes and stable isotope mean  $\pm$  S.E.). Although the total Standard Ellipse Area ( $SEA_C$ ) was larger in bivalves from Mitchell's Bay (Table 1), the Bayesian inference from multiple iterations of Standard Ellipse Areas ( $SEA_B$ ) were not significantly different (probability (*P*) Sand Point 2012 Bivalve  $SEA_B <$  Mitchell's Bay 2011 Bivalve  $SEA_B = 0.56$ , which is lower than the predefined significance of  $P > 0.6$ ). W. Lake Superior, Duluth Harbor bivalves were much higher in  $\delta^{15}\text{N}$  (10 ‰) and significantly lower in  $\delta^{13}\text{C}$  (2 ‰; ANOVA,  $F_{1,19} = 148.7$ ,  $p < 0.01$ ) than Thunder Bay bivalves. Therefore, niche overlap between Round Goby and Tubenose Goby was not a comparable metric for W. Lake Superior. However,  $SEA_B$  was not significantly different between the two baseline populations ( $P = 0.59$ ), which suggests the isotopic niche breadth available to the fishes was similar and the ellipse sizes of the fish populations could be compared.

### Round Goby and Tubenose Goby

Once separated by size group, tissue and location, our samples of gobies for which ellipses were drawn ranged from 20 to 38 individuals, with exception for one group of 13 (Table 1). Reliability in ellipse estimations reduces considerably with sample sizes  $< 10$  (Jackson et al. 2011), therefore, we suggest caution in the interpretation of ellipses for YOY (young-of-year) Tubenose Goby from Thunder Bay ( $n = 8$ ) despite the inherent sample size correction provided by  $SEA_C$  and  $SEA_B$ . All other comparisons involving W. Lake Superior Round Goby and Tubenose Goby that matched in size and YOY Tubenose Goby were bootstrapped due to the high effect from differences in sample size identified by Cohen's power analysis. All other power values were  $> 0.8$ .

The sex composition for each size class at each site was (Male/female/immature/unsexed: Mitchell's Bay:

**Table 1** Length, weight and stable isotope data (mean ± SE), population metrics, SIBER ellipses and ellipse overlap between Round Goby and Tubenose Goby collected at mouth (Mitchell's Bay) and outflow (Sand Point) of Lake St. Clair and in western Lake Superior (Thunder Bay and Duluth)

<i>n</i> <sup>A</sup>	Wet Wt <sup>B</sup>	<i>L</i> <sub>T</sub> <sup>C</sup>	<i>L</i> <sub>S</sub> <sup>D</sup>	δ <sup>13</sup> C	δ <sup>15</sup> N	CR <sup>E</sup>	NR <sup>F</sup>	SEAC <sup>G</sup>	Overlap (%) <sup>H</sup>
<i>Baseline Bivalves<sup>I</sup></i>									
<i>Mitchell's Bay</i>									
30	70.4 ± 0.4	10.0 ± 0.1	5.1 ± 0.1	-19.1 ± 0.1 <sup>a</sup>	7.2 ± 0.1 <sup>b</sup>	1.5	1.4	0.4 <sup>a</sup>	
27	80.2 ± 0.4	12.5 ± 0.1	6.4 ± 0.1	-20.5 ± 0.2 <sup>a</sup>	8.2 ± 0.1 <sup>c</sup>	1.0	1.2	0.2 <sup>a</sup>	
<i>Thunder Bay</i>									
12	25.6 ± 0.3	8.0 ± 0.1	6.7 ± 0.1	-25.9 ± 0.2 <sup>b</sup>	3.5 ± 0.1 <sup>a</sup>	1.6	0.8	0.3 <sup>a</sup>	
14	21.9 ± 0.3	9.2 ± 0.1	5.2 ± 0.1	-27.9 ± 0.1 <sup>b</sup>	13.5 ± 0.2 <sup>d</sup>	1.0	1.9	0.2 <sup>a</sup>	
<i>Mitchell's Bay Muscle</i>									
32	1.5 ± 0.1	48.0 ± 1.2	40.6 ± 1.2	-18.7 ± 0.1 <sup>b</sup>	12.0 ± 0.1 <sup>b</sup>	2.7	1.9	1.2 <sup>c</sup>	1. (10.0)
34	4.6 ± 0.3	69.0 ± 1.2	58.0 ± 1.1	-19.6 ± 0.1 <sup>a</sup>	12.1 ± 0.1 <sup>b</sup>	2.9	1.4	0.7 <sup>a</sup>	1. (30.0)
<i>Tubenose Goby</i>									
29	1.4 ± 0.1	49.1 ± 1.2	39.5 ± 1.0	-18.7 ± 0.1 <sup>b</sup>	10.5 ± 0.1 <sup>a</sup>	2.7	1.9	1.0 <sup>b</sup>	
<i>Mitchell's Bay Liver</i>									
25	1.6 ± 0.2	49.2 ± 1.1	41.8 ± 1.3	-18.9 ± 0.1 <sup>b</sup>	10.2 ± 0.1 <sup>b</sup>	1.4	2.7	0.8 <sup>a</sup>	2. (73.8), 3. (2.5)
27	4.3 ± 0.3	67.5 ± 1.3	57.0 ± 1.3	-19.3 ± 0.2 <sup>a</sup>	10.3 ± 0.1 <sup>b</sup>	3.2	2.9	1.3 <sup>b</sup>	2. (45.5)
<i>Tubenose Goby</i>									
22	1.4 ± 0.1	49.5 ± 1.4	39.9 ± 1.2	-19.1 ± 0.1 <sup>a</sup>	9.3 ± 0.1 <sup>a</sup>	2.4	1.4	0.8 <sup>a</sup>	3. (2.5)
<i>Sand Point Muscle</i>									
38	0.7 ± 0.1	41.9 ± 1.3	34.3 ± 1.1	-17.2 ± 0.1 <sup>b</sup>	11.5 ± 0.1 <sup>b</sup>	2.2	2.6	0.9 <sup>a</sup>	4. (3.3)
36	8.3 ± 1.0	84.0 ± 2.5	69.7 ± 2.2	-17.8 ± 0.1 <sup>a</sup>	10.7 ± 0.2 <sup>a</sup>	2.4	4.3	1.6 <sup>c</sup>	5. (57.5), 4. (1.9)
<i>Tubenose Goby</i>									
29	0.6 ± 0.1	39.4 ± 1.4	31.8 ± 1.3	-17.8 ± 0.1 <sup>a</sup>	10.6 ± 0.1 <sup>a</sup>	2.5	2.9	1.1 <sup>b</sup>	5. (83.6)
<i>Sand Point Liver</i>									
25	10.1 ± 1.3	90.0 ± 2.6	74.6 ± 2.2	-18.5 ± 0.1 <sup>b</sup>	9.4 ± 0.2 <sup>a</sup>	2.5	3.3	1.7 <sup>b</sup>	6. (8.8)
<i>Tubenose Goby</i>									
22	0.6 ± 0.1	41.0 ± 1.7	33.3 ± 1.5	-19.0 ± 0.1 <sup>a</sup>	10.3 ± 0.1 <sup>b</sup>	2.6	1.2	0.7 <sup>a</sup>	6. (21.4)
<i>West Superior Muscle</i>									
27	0.6 ± 0.0	36.7 ± 0.5	30.5 ± 0.4	-30.5 ± 0.3 <sup>a</sup>	12.3 ± 0.2 <sup>d</sup>	6.0	3.4	3.0 <sup>c</sup>	7. (28.3)
23	2.1 ± 0.2	54.8 ± 1.4	45.3 ± 1.3	-30.4 ± 0.3 <sup>a</sup>	10.6 ± 0.2 <sup>c</sup>	4.7	3.3	1.9 <sup>b</sup>	8. (67.4)
<i>Tubenose Goby</i>									
23	0.4 ± 0.0	35.1 ± 1.1	28.0 ± 0.9	-19.4 ± 0.2 <sup>c</sup>	5.4 ± 0.1 <sup>a</sup>	2.2	2.1	1.1 <sup>a</sup>	9. (14.5)
<i>YOY Tubenose Goby</i>									
21	0.1 ± 0.0	22.4 ± 0.8	17.6 ± 0.6	-21.1 ± 0.2 <sup>b</sup>	5.9 ± 0.2 <sup>b</sup>	3.7	2.6	1.9 <sup>b</sup>	
<i>West Superior Liver</i>									
13	0.6 ± 0.1	37.3 ± 0.1	30.6 ± 0.1	-30.3 ± 0.4 <sup>c</sup>	11.7 ± 0.2 <sup>c</sup>	4.3	1.8	2.5 <sup>c</sup>	10. (10.0), 7. (34)
<i>Larger Round Goby</i>									
20	2.2 ± 0.2	55.1 ± 1.6	45.7 ± 1.5	-30.6 ± 0.3 <sup>c</sup>	10.7 ± 0.2 <sup>b</sup>	4.0	2.6	1.7 <sup>b</sup>	10. (14.7), 8. (75.3)

**Table 1** continued

	$n^A$	Wet Wt <sup>B</sup>	$L_T^C$	$L_S^D$	$\delta^{13}C$	$\delta^{15}N$	CR <sup>E</sup>	NR <sup>F</sup>	SEAC <sup>G</sup>	Overlap (%) <sup>H</sup>
Tubenose Goby	21	0.4 ± 0.0	35.0 ± 1.1	27.9 ± 0.1	-19.6 ± 0.1 <sup>a</sup>	4.7 ± 0.1 <sup>a</sup>	2.3	1.4	0.9 <sup>a</sup>	9. (17.8)
YOY Tubenose Goby	8	0.1 ± 0.0	25.5 ± 0.1	19.8 ± 0.1	-20.9 ± 0.2 <sup>b</sup>	4.9 ± 0.2 <sup>a</sup>	1.8	1.4	1.0 <sup>a</sup>	

<sup>abcd</sup> Different lower case letters denote significantly different groups for each tissue within each location (LSD post hoc to MANOVA,  $p < 0.05$ )

<sup>A</sup>  $n$  denotes total sample numbers obtained for analysis from each location for each species, size group and tissue. Liver tissue sample numbers were less than muscle due to the difficulty in obtaining sufficient sample of liver for stable isotope analysis

<sup>B</sup> Wet weight of whole fish (g) or *Baseline* bivalve tissue (mg)

<sup>C</sup> Total length (mm) of fish or *Baseline* bivalve shell

<sup>D</sup> Standard length (mm) of fish or width of *Baseline* bivalve shell

<sup>E</sup>  $\delta^{15}N$  range

<sup>F</sup>  $\delta^{13}C$  range

<sup>G</sup>  $SEA_C$  is the Standard Ellipse Area calculated from stable isotope population metrics with sample size correction (additional degree of freedom) and incorporates 40 % of the total stable isotope data range

<sup>H</sup> *SIBER overlap* function, which compares the degree of overlap between two ellipses ( $SEA_C$ ). Matching numbers (1–10) denote the overlapping population or tissue ellipses, with % of ellipse that is overlapping in parenthesis. See Fig. 2 to observe ellipse overlap on  $\delta^{15}N$  and  $\delta^{13}C$  bi-plots

<sup>I</sup> Bivalves used as baseline for spatial comparison of stable isotope data were dreissenids (Lake St. Clair and Duluth) and unionids (Thunder Bay)

*Larger* Round Goby were individuals that were significantly larger in  $L_S$  and Wet Wt than other fishes at each location (ANOVA,  $p < 0.05$ )

*YOY* indicates young-of-year Tubenose Goby that were significantly smaller than all other fishes and within the size range of *YOY* Tubenose Goby in the Great Lakes (Leslie et al. 2002)

RG 8/4/0/20, larger RG 4/23/0/7, TG 5/1/0/23. Sand Point: RG 3/2/0/33, larger RG 25/9/0/2, TG 17/9/0/3. W. Lake Superior: RG 9/6/5/7, larger RG 14/6/0/3, TG 21/1/0/1, YOY TG 8/4/8/1). The only comparison for which sex had a significant effect was for  $\delta^{15}\text{N}$  in Mitchell's Bay Round Goby (ANOVA where F tested the effect of sex on  $\delta^{15}\text{N}$  in muscle tissue:  $F_{3,57} = 5.2$ ,  $p = 0.003$ ). In Mitchell's Bay, male Round Goby had higher  $\delta^{15}\text{N}$  ( $12.5 \pm 0.5$  ‰  $p < 0.05$ ) than immature ( $11.8 \pm 0.4$  ‰), unsexed ( $11.9 \pm 0.4$  ‰) and female Round Goby ( $12 \pm 0.4$  ‰). However, note the high proportion of 'unsexed' fishes in Mitchell's Bay and Sand Point.

#### Trophic position and isotopic niche overlap

Across all sites and size classes, Round Goby had a higher trophic position (higher  $\delta^{15}\text{N}$ ) than Tubenose Goby, with exception for the grouping of Round Goby at Sand Point that were significantly larger than all other fishes (*larger* Round Goby, Table 1, lower case letter denotes significance). Round Goby and Tubenose Goby that were within the same size range (*size-matched*) also had significantly different  $\delta^{13}\text{C}$  in all cases except Mitchell's Bay muscle tissue, and *larger* Round Goby had significantly different  $\delta^{13}\text{C}$  than Tubenose Goby in Mitchell's Bay muscle tissue and Sand Point liver (no liver was available for *size-matched* Round Goby from Sand Point; Table 1). The differences in W. Lake Superior seemed to be partially due to spatial differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  between the two sampling locations (See *Baseline Bivalves*, Table 1, Fig. 1), so one should avoid drawing conclusions on the lack of niche overlap between the two species. However, baseline isotopic niche breadth was similar (see *Baseline Bivalves* section), which suggests a similar range in isotopic niche breadth was available to the fishes.

The ellipse, or isotopic niche, of *size-matched* Round Goby and Tubenose Goby at each location were distinct with no significant overlap, which was predominantly due to the higher  $\delta^{15}\text{N}$  in Round Goby (Fig. 2, see Table 1 for % overlap). In Sand Point a high percentage of Tubenose Goby ellipses (83.6 and 21.4 % muscle and liver respectively) were covered by *larger* Round Goby ellipses. There was also significant overlap between the two size groups of Round Goby in Mitchell's Bay and W. Lake Superior but not Sand Point (Fig. 2; Table 1).

#### Isotopic niche breadth

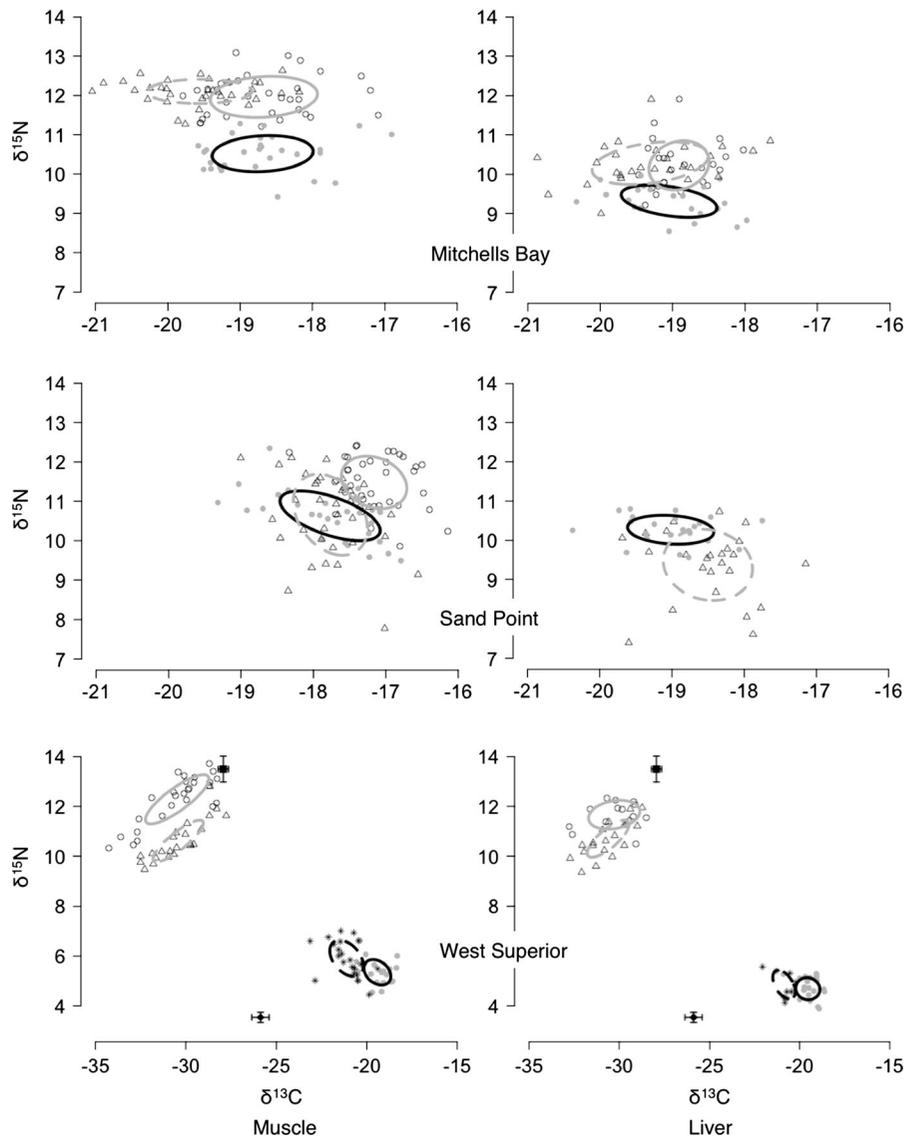
Across all size classes, in 11 of 15 comparisons, we found significantly broader isotopic niche to occur in the widely established Round Goby, compared to the narrowly established Tubenose Goby (Table 1; Fig. 3). Exceptions were *size-matched* Round Goby from Sand Point and *larger* Round Goby from Mitchell's Bay, both of which had significantly smaller isotopic niche than Tubenose Goby when comparing muscle tissue ( $P = 0.79$  and  $0.85$ , respectively). Again, when comparing muscle tissue, *size-matched* Round Goby and Tubenose Goby isotopic niche were also not significantly different in Mitchell's Bay and neither was the isotopic niche of *larger* Round Goby and YOY Tubenose Goby ( $P < 0.6$  in both cases).

Overall, differences in isotopic niche were driven by variation in both  $\delta^{15}\text{N}$  (NR) and  $\delta^{13}\text{C}$  (CR). But in Lake St. Clair, broader isotopic niche in Round Goby was predominantly driven by higher nitrogen range (NR), whereas in W. Lake Superior there was a larger difference in the carbon range (CR) of gobies than NR (Table 1). In W. Lake Superior, *size-matched* Round Goby had a significantly broader isotopic niche than *larger* Round Goby ( $P = 0.90$  and  $0.78$ , muscle and liver, respectively; Fig. 3), as did YOY Tubenose Goby compared to *size-matched* Tubenose Goby ( $P = 0.93$  in muscle, liver sample size too small for reliable comparison). In Mitchell's Bay, *size-matched* Round Goby also had a significantly broader isotopic niche than *larger* Round Goby for muscle tissue ( $P = 0.94$ ), but for all other intra-specific comparisons *larger* Round Goby had a broader isotopic niche (Fig. 3).

#### Isotopic niche plasticity

Across all size groups, the difference between liver and muscle tissue, or niche plasticity, was more pronounced for Round Goby than for Tubenose Goby. See Fig. 3 for significant differences (\*) between muscle and liver  $SEA_B$ . See Fig. 4 for significant differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  between tissues of individuals (\*), and comparison of mean difference between tissues for different species and size groups of gobies (letters denote significantly different groups within each site). There was a higher probability of muscle  $SEA_B$  being broader than liver  $SEA_B$  in 3/5 comparisons between Round Goby and Tubenose

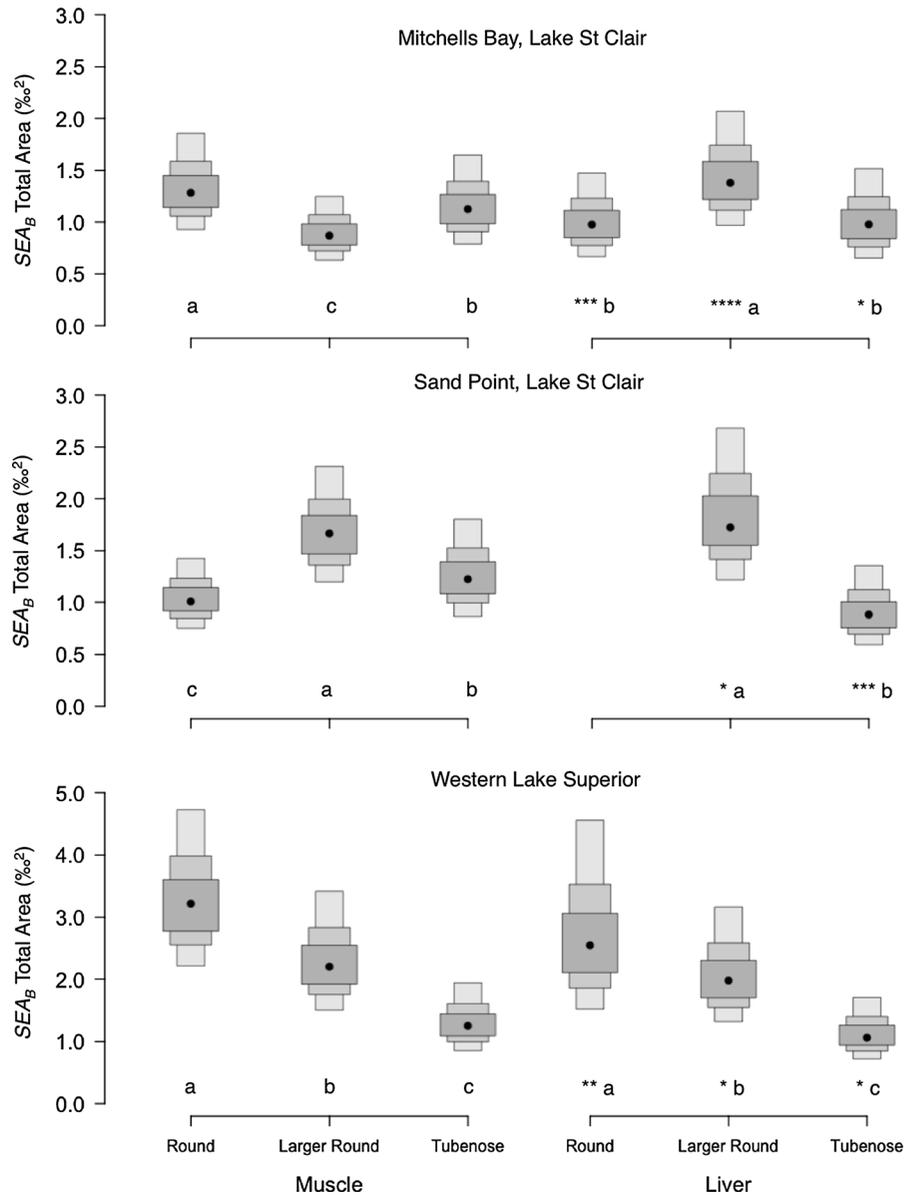
**Fig. 2** Bi-plot of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  with Standard Ellipse Areas ( $SEA_C$ ) of bulk muscle and lipid-extracted liver from Lake St. Clair (Mitchell's Bay and Sand Point) and western Lake Superior Round Goby and Tubenose Goby. For same size Round Goby (Open circles, solid gray ellipses) and Tubenose Goby (Solid gray circles, black ellipses), Round Goby larger than all other fishes (Standard Length,  $p < 0.05$  T test; open triangle, dashed gray ellipses) and Tubenose Goby significantly smaller than all other fishes (Black star and black dashed ellipses). Stable isotope data (Mean  $\pm$  SD) are shown for bivalves from Duluth (black square) and Thunder Bay (black diamond), western Lake Superior. Note different range on the x and y axis for western Lake Superior. See Table 1 for niche metrics, total ellipse areas and ellipse overlap data



Goby (Fig. 3). One exception was *larger* Round Goby in W. Lake Superior that had similar probability of isotopic niche breadth ( $SEA_B$ ) being different between tissues as Tubenose Goby (sample size for YOY Tubenose Goby liver was too low for this comparison). In W. Lake Superior, overlap between muscle and liver isotopic niches was also higher for Round Goby (28.3–75.3 %) than Tubenose Goby (14.5–17.8 %). The second exception was the only case in which Tubenose Goby had a greater probability of difference in  $SEA_B$  between tissues than Round Goby (Lake St. Clair, Fig. 3).

There were three comparisons for which mean difference in  $\delta^{15}\text{N}$ , or niche plasticity, was greater between tissues for Round Goby than for Tubenose Goby (Fig. 4a). In contrast, there was only one comparison in which Tubenose Goby had significantly greater mean difference in  $\delta^{15}\text{N}$  than Round Goby and this was for YOY Tubenose Goby in comparison to *larger* Round Goby in W. Lake Superior (note sample size of YOY Tubenose Goby liver, Table 1, Fig. 4a). Mean difference in  $\delta^{15}\text{N}$  between tissues was also greater for *size-matched* Round Goby than Tubenose Goby from W. Lake Superior ( $0.3 \pm 0.2$  ‰ more

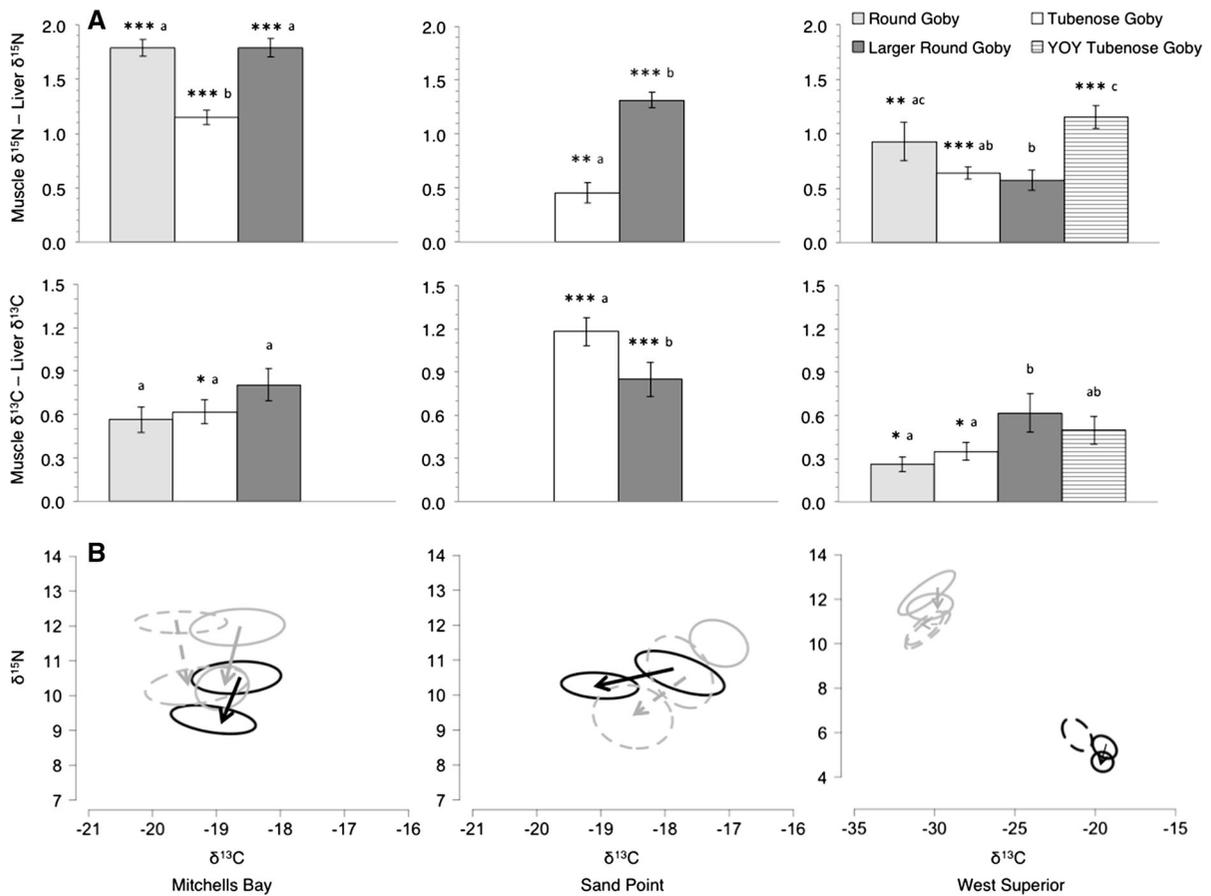
**Fig. 3** Density box-plots of Bayesian estimates of Standard Ellipse Area ( $SEA_B$ ) for bulk muscle and lipid extracted liver tissue for *size-matched* Round Goby and Tubenose Goby and *larger* Round Goby (>6 cm) that were significantly larger than all other fishes ( $T$  test,  $p < 0.05$ ). Note different y-axis maximum for western Lake Superior. *Black circles* are mode total area ( $\% \text{ } ^2$ ) and *grey boxes* represent 50, 75 and 95 % credible intervals produced from  $10^5$  Bayesian iterations of  $SEA_B$ . *Different lower case letters* denote significant difference in  $SEA_B$  between groups within each location for muscle and liver independently. \*Probability of difference between muscle and liver  $SEA_B$  within each population, higher number denotes higher probability \*0.6–0.69, \*\*0.7–0.79, \*\*\*0.8–0.89, \*\*\*\*0.9–1



difference, Fig. 4a, right panel). But comparison of bootstrapped samples did not yield a significant difference (note sample size differences, Table 1).

There was a significant difference in the  $\delta^{15}\text{N}$  between muscle and liver of individuals within every group, with exception for *larger* Round Goby from W. Lake Superior (Fig. 4a). Including *larger* Round Goby from W. Lake Superior,  $\delta^{13}\text{C}$  was significantly different between tissues of individuals for 5/9 groups (3 Tubenose Goby, 2 Round Goby). Sand Point gobies

had particularly variable  $\delta^{13}\text{C}$  between tissues, and this was the only case in which Tubenose Goby had significantly higher variation in  $\delta^{13}\text{C}$  between tissues than Round Goby ( $0.49 \pm 0.2 \text{ } \text{‰}$  greater difference, Fig. 4, Table 1). Variable  $\delta^{13}\text{C}$  (habitat niche) in Sand Point seemed to be the driving force for the only case of greater difference in  $SEA_B$  between tissues of Tubenose Goby than Round Goby (Fig. 4b). Otherwise  $\delta^{15}\text{N}$  (trophic niche) was the dominant metric driving variation in isotopic niche plasticity.



**Fig. 4 a** Mean difference ± SE between bulk muscle and lipid extracted liver δ<sup>13</sup>C and δ<sup>15</sup>N in Round Goby and Tubenose Goby in Mitchell's Bay, Sand Point (both Lake St. Clair) and western Lake Superior. \*Significant difference between muscle and liver δ<sup>13</sup>C or δ<sup>15</sup>N within each population (paired *T* tests) \**p* < 0.05, \*\**p* < 0.01, \*\*\**p* < 0.001. Different lower case

letters denote significantly different calculated mean difference of liver and muscle between each group (*p* < 0.05, ANOVA or independent *T* test). **b** Standard Ellipses Areas (SEA<sub>C</sub>) of bulk muscle and lipid extracted liver (arrows point from muscle to liver) δ<sup>13</sup>C and δ<sup>15</sup>N in Round Goby (gray) and Tubenose Goby (black)

## Discussion

Broad trophic and habitat niche are often considered to be facilitators of successful establishment of aquatic invasive species (Marvier et al. 2004; Shea and Chesson 2002), our findings indicate that this is the case for Round Goby, at least, in comparison to Tubenose Goby. A number of studies have suggested broad diet and habitat use facilitate the establishment and spread of Round Goby in North America (Brush et al. 2012; Diggins et al. 2002; Raby et al. 2010). Our study and a study by Vašek et al. (2014) on gobies in the Danube basin using stomach contents, are the first to demonstrate broader niche and higher plasticity in Round Goby

than Tubenose Goby where they occur in the same habitat. In our study, we used stable isotope analysis of multiple tissues to investigate niche plasticity. Bearhop et al. (2004) warned of the effects of differences in physiology that can result in different fractionation levels when comparing tissue types to infer temporal changes in diet from stable isotope data. Although Round Goby and Tubenose Goby grow to different maximum body sizes, the two species are commonly found within the same size range, are closely related, share similar environments (Miller 2004), and have similar field metabolic rates (O'Neil 2013). Thus, metabolic turnover of nutrients and stable isotopes in tissues is expected to be similar between the two species.

We also found higher trophic niche plasticity in Round Goby than Tubenose Goby based on variation in isotope niche ellipses between populations and  $\delta^{15}\text{N}$  between muscle and liver. This is consistent with other studies that have found Round Goby to have a plastic diet across invaded ranges in North America (Brush et al. 2012) and Europe (Brandner et al. 2013; Polačik et al. 2009), as well as in prey-choice laboratory experiments (Coulter et al. 2011). Kornis et al. (2012) suggested diet plasticity allows this species to exploit locally abundant food sources in invaded locations. Given other studies have suggested plasticity in trophic niche of invasive fish species facilitate rapid growth and invasion success (Hayden et al. 2014) and reduced competition with sympatric native species (Hayden et al. 2013) and other invasive species (Jackson and Britton 2014), niche plasticity is likely a common attribute of successful invasive fish species. Layman and Allgeier (2012) found individuals of the invasive lionfish (*Pterois volitans/miles*) to have a specialist feeding strategy, which suggests that there could be exceptions to this conclusion. This was, however, a marine species and the study did not compare directly to a less successful invasive species.

In the present study, Round Goby was found to have a higher  $\delta^{15}\text{N}$  (higher trophic position) relative to Tubenose Goby that was within the same size range, while the  $\delta^{13}\text{C}$  that was not significantly different between species suggested they consume resources from the same habitat. Higher trophic position implies that Round Goby could be more of a piscivore than similar-size Tubenose Goby and feed on other small fishes, such as Tubenose Goby juveniles. The lower trophic position of Tubenose Goby suggests the reverse is unlikely, although Tubenose Goby has been reported to consume Round Goby eggs in very small quantities relative to other prey available (Vašek et al. 2014). Round Goby has been reported to feed on eggs and fry of several fishes (Kornis et al. 2012) including Tubenose Goby, although also in small quantities (Vašek et al. 2014). It should be noted that the differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  between W. Lake Superior Round Goby and Tubenose Goby seem to be primarily ecosystem driven (i.e. different baseline signatures). Although the two locations in W. Lake Superior share relatively similar fish communities (Schloesser et al. 2012, 2013), prey communities could be different between the two locations, which could also be driving differences in trophic niche between the two goby species.

In Lake St. Clair, the higher  $\delta^{15}\text{N}$  of Round Goby seemed to be a catalyst for a clear distinction in the isotopic niches of similar-sized Round Goby and Tubenose Goby. It is unlikely that separate species will occupy the same niche in one place and time (Elton 1927). Although, since that publication, several studies have demonstrated that niche overlap can occur under certain conditions. For instance, when species invade a novel environment, niche overlap can occur due to a lack of prior co-existence (Davis 2003; Guzzo et al. 2013; Jackson and Britton 2014). The unique isotopic niches of these gobiids could have been facilitated by either their co-existence in the Ponto-Caspian region prior to invasion, or their relatively long co-existence in Lake St. Clair (> 20 years since invasion; Kornis et al. 2012). Round Goby and Tubenose Goby have been reported to have some dietary overlap in Lake St. Clair (French and Jude 2001) and in invaded ranges in Europe (Simonovic et al. 2001; Vašek et al. 2014) based on stomach contents, although Adámek et al. (2007) also reported diet divergence between the two species at an invasion front in the Danube River. These somewhat conflicting findings could relate to time since invasion, but the prevalence of trophic niche plasticity in Round Goby or Tubenose Goby at invasion fronts in the Great Lakes has not been thoroughly investigated.

In the present study, a broader isotopic niche in Round Goby was often associated with higher isotopic niche overlap with Tubenose Goby and/or a different size group of Round Goby. Prolonged niche overlap is thought possible if resources are in abundance and/or if the overlap is short-lived. Otherwise, competition could increase and lead to the diversification of niches, competitive exclusion, or even extirpation (Bolnick 2001; Elton 1927). Jackson and Britton (2014) also suggested trophic ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) niche overlap in sympatric aquatic invasive species is avoided through plasticity in resource use, which leads to the diversification of niches. Round Goby is often found in high abundances (Lynch and Mensinger 2011; Moran and Simon 2013), which is expected to increase intra-specific competition and is, thus, a logical driving force for niche plasticity (Bolnick 2001; Bolnick et al. 2003). Lynch and Mensinger (2011) suggested high abundances in Round Goby and the associated resource competition could ultimately drive individuals to move or change their diet. Interestingly, Tubenose Goby can also be found in high abundances

in native Ukraine (Yuriy Kvash, National Academy of Sciences of Ukraine, personal communication) and invaded North America (Lake St. Clair and western Lake Erie; Nicholas Mandrak, Fisheries and Oceans Canada, pers. comm.; Thunder Bay, Schloesser et al. 2012), but this does not appear to have provided plasticity in trophic niche in North American populations (present study).

We found body size-based ontogenetic shifts in niche breadth and niche plasticity in Round Goby, but the trends were not consistent which suggests it is a plastic trait. Ontogenetic niche shifts relating to morphological divergence are commonly found in invasive fishes (Borcherding et al. 2013; Groen et al. 2012), including the Round Goby (Brandner et al. 2013) and fishes in general. With increased body size, Round Goby increased its capacity for omnivory; to feed at multiple trophic positions and/or multiple species within the same trophic position simultaneously and, thus, inflating niche size and demonstrating plasticity. The narrower niche of larger Round Goby in W. Lake Superior could be due to a shift towards bivalves, as larger individuals of Round Goby (> 70 mm) generally had a higher proportion of dreissenids in their diet in this study (Pettitt-Wade, H. pers. obs.) and in other studies (Brandner et al. 2013; Ray and Corkum 1997). The ability of Round Goby to shift to alternate prey, such as dreissenid mussels, beyond the gape size of potential competitors, such as Tubenose Goby, has previously been suggested as a facilitator of invasion success (French and Jude 2001; Ray and Corkum 1997). Although Tubenose Goby possess pharyngeal teeth, dreissenids have never been reported in its diet, nor in this study, and limited gape size driven by total body size has been suggested to be the cause (Diggins et al. 2002).

We found Tubenose Goby to have plasticity in habitat niche, as determined by variation in  $\delta^{13}\text{C}$  between tissues, which was also suggested by Erős et al. (2005) in comparison to other invasive gobiids. But the lack of trophic niche breadth and niche plasticity (variation in  $\delta^{15}\text{N}$ ) indicates a lack of an ability to avoid competition for specific prey, which suggests Tubenose Goby could be associated with prolonged and sustained competition with native species. Both Tubenose Goby and Round Goby choose dipteran chironomid larvae over other prey (Adámek et al. 2010; Kocovsky et al. 2011) and lower contributions of dipteran chironomid in the diet of Tubenose

Goby have been associated with competition with native Rainbow Darter (*Etheostoma caeruleum*) in Lake St. Clair (French and Jude 2001) and Lake Erie (Kocovsky et al. 2011). Van Kessel et al. (2011) suggested competition for shelter would occur with native *Cottus perifretum* in European rivers invaded by Tubenose Goby. With exception of Rainbow Darter (*Etheostoma caeruleum*), minimal competition for prey has been suggested for Tubenose Goby with the majority of co-occurring native fishes in the Great Lakes (French and Jude 2001; Kocovsky et al. 2011). Conversely, Round Goby has been associated with niche displacement of several native fish species in the Great Lakes (e.g. Balshine et al. 2005; Bergstrom and Mensinger 2009; Groen et al. 2012). In the Dyje River, where Tubenose Goby overlap with Round Goby, Tubenose Goby was suggested to avoid dipterans in place of Ephemeroptera and Trichoptera (Vašek et al. 2014). Further research would be required to determine if niche displacement occurs between these species during novel interactions but, as previously mentioned, distinct trophic niches were found for the two Gobiidae where they share the same habitat niche.

Our findings promote the hypothesis that a broad and flexible niche provides scope for acclimatization to available resources and is associated with the expanding range of invasive species following introduction (Peterson and Vieglais 2001). A broad niche in Round Goby increased opportunity for niche overlap, but high niche plasticity suggests omnivory and that prolonged niche overlap can be avoided. A strong dependence on specific prey species, as indicated in the Tubenose Goby, could be a risk to food web stability following invasion, particularly in unstable food webs such as those that suffer perpetual invasions (Ricciardi 2001). The maintenance of many weak and few strong omnivorous interactions is thought to be critical to ecosystem stability (Gellner and McCann 2012) and a high frequency of niche differences are necessary for the maintenance of species diversity (Levine and HilleRisLambers 2009). Niche separation can be expected to occur as part of a natural progression following long-term establishment of invasive species. Comparison with native Ponto-Caspian populations could help determine if the niches displayed by gobies in North America are part of an adaptive response to a novel environment and the potential for community resistance from further invasion (Shea and Chesson 2002), such as from the other species of Gobiidae invasive in Europe.

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