Effects of Round Gobies (*Neogobius melanostomus*) on Dreissenid Mussels and Other Invertebrates in Eastern Lake Erie, 2002–2004

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ABSTRACT. *From 2001 through 2004, the densities of* Dreissena bugensis *and Amphipoda (*Gammarus fasciatus *and* Echinogammarus ischnus*) decreased by 94% and 85%, respectively, in the rocky northern nearshore (2–10 m depth) zone of eastern Lake Erie. Densities of Chironomidae and Oligochaeta did not change. The decline in* D. bugensis *was most evident for individuals with shell lengths in the 3 to 14 mm range. The mean (±SD, n) abundance of round gobies* (Neogobius melanostomus) *at 10-m depth increased from 6.5 (± 1.9, 12)/m² in 2001 to 14(±1.0, 15/m² in 2002. Analyses of stomach contents in 2001 and 2003, and stable isotopes of carbon in prey and muscle tissue in 2002, indicated that the diet of round gobies in 2001 was predominately dreissenids, but that chironomids and amphipods became more important as the abundance of appropriately sized mussels declined. Round gobies collected in 2003 contained more individual prey, but less total mass of prey than did gobies collected in 2001. Our observations suggest that round gobies probably became food-limited in eastern Lake Erie by 2002.*

INDEX WORDS: *Round goby, diet, Lake Erie, Amphipoda, Chironomidae,* Dreissena.

INTRODUCTION

The round goby (*Neogobius melanostomus*) was first collected in the St. Clair River in 1990 (Crossman 1991) and has since spread throughout the Great Lakes and many tributaries. Round gobies have the potential to compete with native fishes for food and habitat (Vanderploeg *et al.* 2002). The diet of small round gobies includes the same invertebrates preferred by several native fishes including yellow perch (*Perca flavescens*), slimy sculpin (*Cottus bairdi*) and logperch (*Percina caprodes*) (Pothoven *et al.* 2000, French and Jude 2001). Dreissenid mussels are thought to be the most important food of larger gobies (Vanderploeg *et al.* 2002). Round gobies also prey on juvenile fish (French and Jude 2001) and fish eggs (Chotkowski and Marsden 1999). Dubs and Corkum (1996) re-ported that round gobies aggressively attacked and displaced mottled sculpin (*Cottus bairdi*) under laboratory conditions, and suggested that this may be responsible for the recent decline and displacement to deeper water of sculpins in the St. Clair River.

The densities of round gobies increased dramatically in eastern Lake Erie during 1999–2002 (P. Ryan, Ontario Ministry of Natural Resources, personal communication), and they are now the most abundant fish in the shallow nearshore zone. From 2001 through 2004, we conducted surveys of benthic macroinvertebrates in the eastern basin of Lake Erie as part of a study of the effects of dreissenid mussels on nutrient dynamics. This presented an (unanticipated) opportunity to observe the initial impacts of an exotic species, the round goby.

Our objective here is to document the changes in the benthic fauna of the northern nearshore zone of eastern Lake Erie that occurred during the early stages of the establishment of the round goby. We suggest that similar effects can be expected elsewhere in the Great Lakes, and beyond, as round gobies expand their range in North America.

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MATERIALS AND METHODS

Benthic invertebrates and round gobies were sampled along the northwestern shore in the eastern basin of Lake Erie at Peacock Point (42° 47′ N, 79° 59′ W), and invertebrates were also sampled at Evans Pont (42° 50′ N, 79° 45′ W) and near Port Ryerse (42° 45′ N, 80° 15′ W) (Fig. 1). The substratum at Peacock and Evans Points is shelving limestone bedrock extending offshore to a depth of > 10 m. The bedrock is overlain by flat boulders, with gravel and shell filling the interstitial spaces. At Port Ryerse the substratum is boulders and cobbles in shallow water, and fine, silty gravel and coarse sand at depths > 6 m. *Cladophora glomerata* grows luxuriantly on all hard surfaces to a depth of about 6 m from early May through late September, except in early August when much of the alga sloughs off.

Benthic invertebrates were sampled in late May and late August 2001 and 2002, and late May 2004, by SCUBA divers. A circular quadrat (0.032 m²) was dropped to the bottom and all enclosed animals were removed using an airlift fitted with a 250-μm aperture mesh collecting bag (Barton and Hynes 1978). Dreissenid mussels were dislodged using a paint scraper, and any loose rocks were cleaned and removed by hand. Three replicate samples were collected from quadrats dropped randomly, but at least 2 m from one another, at depths of 2, 5, and 10 m on each visit to each sampling site. The substratum at the 10-m depth at Port Ryerse was muddy sand, so samples were collected with a petite Ponar grab (0.024 m²). The contents of each grab were washed in a 250-μm aperture mesh net to remove fine sediments. All samples were preserved immediately in buffered 10% formaldehyde. Upon return to the laboratory, each sample was rinsed thoroughly in water and all invertebrates were removed to 70% ethanol with the aid of a dissecting microscope. Animals were identified to the lowest practical taxonomic level, but only the most abundant broader taxa are reported here. All *Dreissena* were measured to the nearest mm.

The abundance of round gobies was estimated by divers at a depth of 10 m at Peacock Point on 8 and 16 July 2001. A weighted rope quadrat (1 × 10 m) was laid out on the lake bottom, then left undisturbed for at least 5 min. A diver then counted round gobies within the quadrat from a distance of at least 1 m while swimming slowly along the quadrat three times. The quadrat was moved at least 5 m between the four repetitions of the procedure.
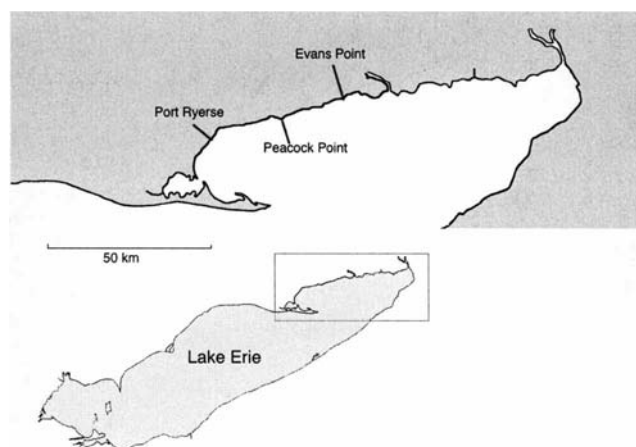

FIG. 1. Locations of sites where benthic invertebrates and round gobies were collected in eastern Lake Erie during 2001–2004.

The estimated density of round gobies was the average of the 12 counts.

A modification of this technique was used at depths of 2, 5, and 10 m at Peacock Point on each of 2 days during the third and fourth weeks of August 2002. A weighted rope quadrat (three 1 m × 1 m cells) was laid out on the lake bottom by SCUBA-equipped divers who then moved away to collect other samples. After 5–10 min, the two divers slowly approached to within 1 m of the quadrat and each diver counted the number of gobies in each of the three cells. This procedure was repeated at each depth after moving the quadrat at least 3 m in a haphazardly chosen direction. A third set of counts was obtained on the first sampling day. The estimated density of round gobies was the average of all counts by both divers at each depth.

Additional information about the relative abundances of round gobies in the western portion of the eastern basin of Lake Erie was obtained from the Ontario Ministry of Natural Resources during the Long Point Bay Index Gillnetting Survey, 2000–2004. Four 380-m gangnets consisting of panels of 2.5 cm to 15 cm gillnet were set overnight during each of 10 weeks each year (11 weeks in 2000) (D. Greenway, Lake Erie Management Unit, Ontario Ministry of Natural Resources, Port Dover).

Round gobies for analysis of diets were captured by angling at depths ranging from 2 to 10 m at Peacock Point from 12 to 14 August 2001. All fish were stored on ice until they could be frozen at the Ontario Ministry of Natural Resources station at

Port Dover, Ontario, later on the day of capture. Fish were sexed using the genital papillae, weighed (wet mass ±0.01 g), and measured for total length (± 0.1 cm). The entire digestive tract (esophagus to anus) was removed and opened under a dissecting microscope. Prey items were identified and counted. Because of fragmentation of the shells, we counted pairs of umbos and estimated the size of mussels consumed as the midpoint between the largest and smallest intact shells. Shell-free dry mass of mussels consumed by each fish was then estimated using length/mass relationships developed by M. Patterson (Patterson *et al.* 2005). Total dry mass of amphipods and chironomids in each fish was calculated using the mean values for the date and depth of capture in Szabo (2004).

Round gobies were also collected in August 2002 at depths of 2 m and 10 m for stable isotope analysis, and in August 2003 from 2 m for stomach content analysis. Standard cylindrical minnow traps baited with crushed quagga mussels were deployed for a minimum of 20 min to catch smaller fish. Larger gobies were caught by angling. Fish were placed on ice, which killed them within 2–5 min. Additional gobies for stable isotope and stomach content analyses were obtained from catches made by the Ontario Ministry of Natural Resources in gill nets (3.8 and 4.4 cm stretched mesh) set at a depth of 2–3 m during August and September 2002, and in bottom trawls at depths of 10–15 m on 13 August 2003, near Peacock Point.

The total length of each fish was measured to the nearest mm and stomachs of fish collected in 2003 were immediately removed and preserved in either 10% formalin or 70% ethanol. Individual prey items were identified and enumerated to the lowest taxonomic level possible under a dissecting microscope. Stomach contents were expressed as the mean percentages of individual prey items after grouping fish into 1-cm size intervals.

Dorsal muscle tissue of larger fish (> 7 cm) or the whole body minus head and viscera for smaller fish (< 7 cm) were retained for stable isotope analysis. Stable isotope ratios were also determined for amphipods, chironomids and soft tissue from quagga mussels from Peacock Point (Szabo 2004). All tissues were dried for 48 h at 60°C and ground to a fine powder (Retch MM 2000 ball mill) for isotope analysis. Subsamples of approximately 1 mg of each powdered tissue were analyzed for C and N isotopes simultaneously, using a Micromass VG Isochrom continuous-flow isotope ratio mass spectrometer connected to a Carlo Erba elemental ana-

lyzer (Environmental Isotope Laboratory, University of Waterloo). The ratio of stable isotopes is expressed as delta values (δ) and measured as parts per thousand (‰) (or per mil) difference between the isotope ratio of the sample and the international standard following the formula:

$$\delta^{13}C \text{ or } \delta^{15}N = [(R_{sample} - R_{standard})/R_{standard}] \times 1,000$$

where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$ (Fry 1991). Samples are more depleted in the heavier isotope of ${}^{13}C$ or ${}^{15}N$ when the $\delta^{13}C$ or ${}^{15}N$ is more negative (Rounick and Winterbourn 1986). The standard used to measure $\delta^{13}C$ is Peedee Belemnite carbonate (DeNiro and Epstein 1978), while standard atmospheric N_2 was used to measure $\delta^{15}N$ (DeNiro and Epstein 1981). All international standards are set at a value of 0‰.

Differences in the abundances of benthic invertebrates were assessed using ANOVA after $\log_{10}$-transformation of the sample counts. Numbers of items in stomach from the two years were compared using t-tests (independent samples without assuming equal variances (SPSS 11.0.2 for Macintosh).

RESULTS

The most abundant benthic invertebrates at depths < 10 m were quagga mussels (*Dreissena bugensis*), oligochaetes, chironomids, and amphipods (*Gammarus fasciatus* and *Echinogammarus ischnus*). Most of the other animals were Hydroptilidae (Trichoptera), Isopoda, Hydracarina, Gastropoda, Turbellaria, and Ephemeroptera, but together these accounted for less than 5% of the individuals collected.

The mean density of quagga mussels declined from 2.33×10^4/m² in 2001, to 8.6×10^3/m² in 2002, and 1.58×10^3/m² in 2004 (Fig. 2). The difference between June 2001 and June 2002 was not statistically significant because of variability among replicates and stations, but densities in June 2004 were significantly lower than in previous years (ANOVA, F = 25.686, df = 2,94, p < 0.001). No *Dreissena polymorpha* were found in any sample. The frequency distributions of shell length from each collecting period were bimodal and the abundance of mussels < 3 mm in length varied relatively little over the course of the study (Fig. 3). However, the abundance of individuals in the 3–15 mm size range decreased, and the average size of mussels > 15 mm in length increased over time.
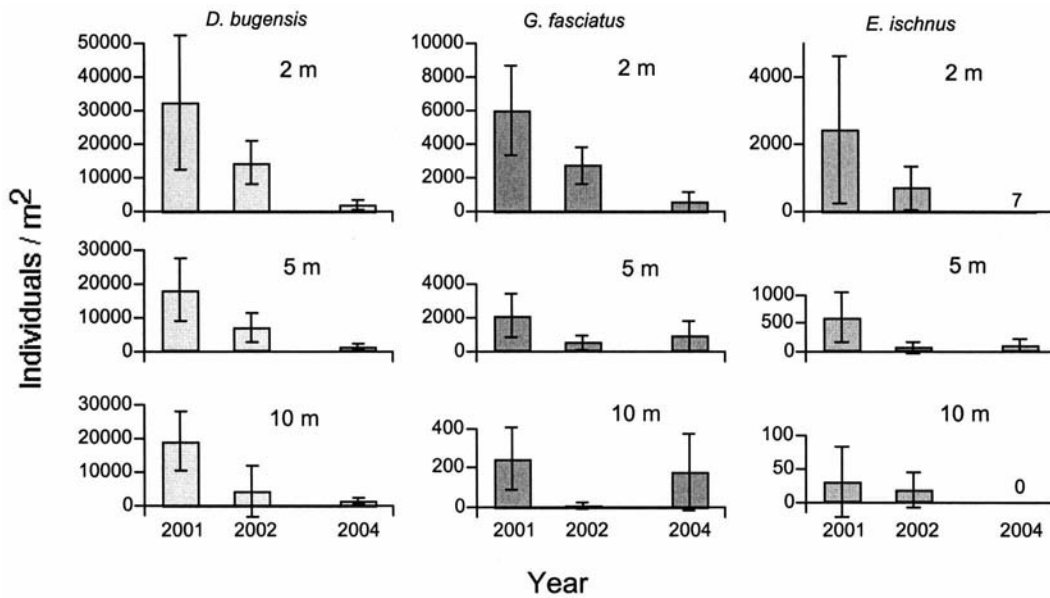
FIG. 2.   Mean (± S.E.) densities of quagga mussels* (Dreissena bugensis) *and amphipods (*Gammarus fasciatus *and* Echinogammarus ischnus*) in airlift samples collected from depths of 2, 5, and 10 m at Evans Point, Peacock Point, and Port Ryerse during late May or early June 2001, 2002, and 2004.

The densities of amphipods declined significantly each year (F = 20.330, df = 2,94, p ≤ 0.001), from ca. 3,800/m^2 in 2001, to 1,350/m^2 in 2002, and 600/m^2 in 2004 (Fig. 2). The proportion of *E. ischnus* in the samples declined from 26.7% of all amphipods in 2001, to 6.8% in 2004.

In contrast, the overall density of chironomids (F = 4.316, df = 2,94, p = 0.016) was greatest in 2002, and greater in 2004 than in 2001 (Fig. 4). The range of variation in mean density of Oligochaeta among years was less than for any other major group, and differences among years were not significant (F = 2.472, df = 2,94, p = 0.090) (Fig. 4).

Round gobies were the most abundant fish (benthic or pelagic) observed at Peacock Point; the only other fish occasionally seen by divers were smallmouth bass and yellow perch. Based on divers' counts, the mean density of round gobies at 10 m in July 2001 was 6.5/m^2. The mean density at 10 m in July 2002 (14 /m^2) was significantly greater than at 2 or 5 m (9 /m^2) (F$_{2, 87}$ = 4.897, P = 0.01). Total catches of round gobies (corrected for effort) in the OMNR index gillnetting survey were 40 in 2000, 359 in 2001, 1,270 in 2002, 204 in 2003, and 202 in 2004.

The stomach contents of round gobies varied with size of the fish, depth of capture and year (Tables 1 to 4). The most important prey were quagga mussels,

chironomids and amphipods. Cladocerans (especially *Bythotrephes*) were commonly eaten but contributed very little to the mass of stomach contents. Other prey included small numbers of gastropods,
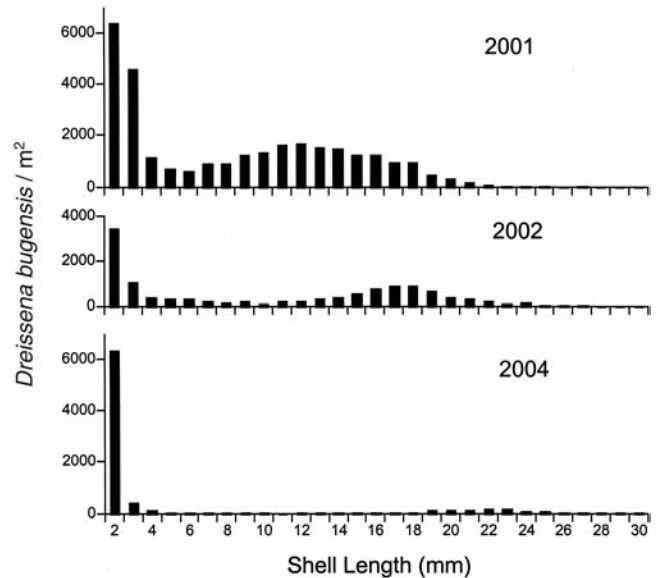

FIG. 3.   Mean densities of* D. bugensis *in 1 mm size classes in airlift samples collected from depths of 2, 5, and 10 m at Evans Point, Peacock Point, and Port Ryerse during late May or early June 2001, 2002, and 2004.

FIG. 4.   Mean densities (± S.E.) of Chironomidae and Oligochaeta in airlift samples collected from depths of 2, 5, and 10 m at Evans Point, Peacock Point, and Port Ryerse during late May or early June 2001, 2002, and 2004.
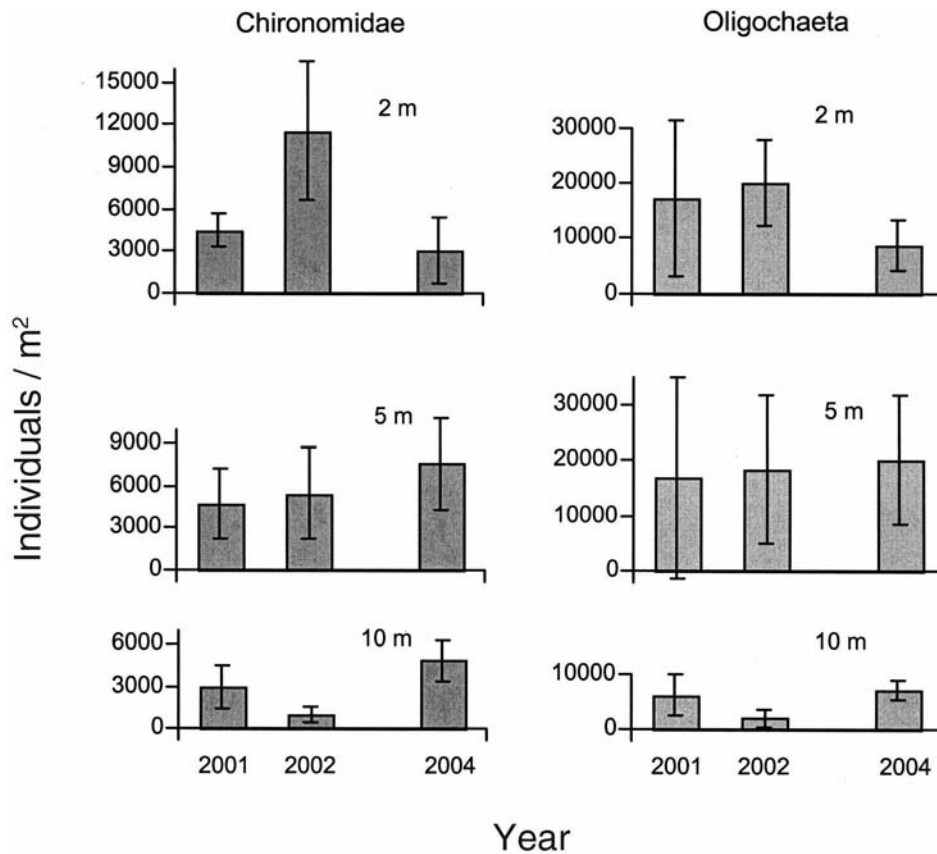
ostracods, water mites and hydroptilid caddisflies. In general, the importance of quagga mussels increased, and that of chironomids and amphipods decreased, with increasing total length of fish. Fish captured in deeper water contained more mussels and *Bythotrephes*, and fewer amphipods, than those from depths < 5 m. Round gobies contained significantly more individual prey items (Tables 1 and 3) in 2003 (mean = 13.5) than in 2001 (mean = 8.8) (t = 2.24, df = 47, p = 0.03), but the estimated mass of the stomach contents (Tables 2 and 4) was significantly greater in 2001 than in 2003 (10.3 vs. 7.3 mg dry weight, t = 2.95, df = 100, p = 0.04). Relative to 2001, fish collected in 2003 had eaten more individual Chironomidae (5.9 vs 2.4, t = 2.74, df = 41, p = 0.04) and Amphipoda (2.1 vs 0.3, t = 2.56, df = 36, p = 0.02) but fewer *Dreissena* (3.7 vs 4.9, t = 1.95, df = 63, p = 0.06).

The isotopic signatures of round gobies also differed with depth of capture and size of fish. Of the gobies from depths ≤ 5 m, those 7 to 10 cm in length were slightly more ^{15}N-enriched than smaller or larger individuals (Fig. 5). The δ^{15}N signatures of deepwater gobies did not vary with size. The ^{15}N signatures of all invertebrate groups were similar and were generally within the range of values expected for the prey of round gobies. Chironomidae exhibited seasonal variability with more enriched values in May.

Round gobies collected at depths of 8–10 m were significantly more ^{13}C-depleted ($F_{3, 109}$ = 8.682, P < 0.001) than those from depths ≤ 5 m (Fig. 6). δ^{13}C signatures became increasingly depleted with increasing size of fish from both depth intervals. Regression analysis indicated the slopes were different between depths (–0.302 ± 0.080 and –0.173 ± 0.106 for ≤ 5 m and ≥ 8 m, respectively). Both Amphipoda and *D. bugensis* collected at 10 m were more ^{13}C-depleted than those from 2 m (Fig. 6). The carbon signatures of chironomids exhibited the same general

TABLE 1. Mean (±S.E.) numbers of individual prey in stomachs of round gobies of different total lengths collected in 2001 and 2003.

Year	Total Length (cm)	n	*Dreissena*	Chironomidae	Amphipoda	*Bythotrephes*
2001	< 10	21	2.0 ± 0.5	6.6 ± 1.3	1.3 ± 0.5	1.0 ± 0.4
	10–15	47	5.1 ± 0.4	1.6 ± 0.8	< 0.1	1.9 ± 1.2
	> 15	28	6.8 ± 0.6	0.4 ± 0.2	< 0.1	0.1 ± 0.1
	< 10	16	2.1 ± 0.3	8.0 ± 2.4	4.6 ± 1.2	1,9 ± 1.2
	10–15	10	2.6 ± 0.5	7.5 ± 3.8	0	2.9 ± 1.6
	> 15	9	7.8 ± 1.0	0.6 ± 0.2	0	0.1 ± 0.1

TABLE 2. Estimated mean (± S.E.) dry mass (mg) of prey in stomachs of round gobies of different total lengths collected in 2001 and 2003.

Year	Total Length (cm)	n	*Dreissena* (shell-free)	Chironomidae	Amphipoda
2001	<10	21	1.74 ± 0.44	0.97 ± 0.24	0.22 ± 0.09
	10–15	47	10.12 ± 0.84	0.33 ± 0.17	0.01 ± 0.01
	>15	28	15.20 ± 1.38	0.10 ± 0.05	0.01 ± 0.01
2003	<10	16	2.24 ± 0.35	1.62 ± 0.56	0.78 ± 0.21
	10–15	10	4.71 ± 0.98	1.66 ± 0.86	0
	>15	9	12.93 ± 1.32	0.12 ± 0.05	0

TABLE 3. Mean (± S.E.) numbers of individual prey in stomachs of round gobies collected at depths of 2–5 m and 8–10 m in 2001 and 2003.

Year	Depth (m)	n	*Dreissena*	Chironomidae	Amphipoda	*Bythotrephes*
2001	2–5	58	4.2 ± 0.4	2.2 ± 0.6	0.5 ± 0.2	0.2 ± 0.1
	8–10	38	6.0 ± 0.6	2.6 ± 1.0	< 0.1	2.6 ± 1.5
2003	2–5	16	3.2 ± 0.7	1.2 ± 0.4	4.6 ± 1.2	0
	8–10	19	4.1 ± 0.8	9.9 ± 2.6	0	3.2 ± 1.2

TABLE 4. Estimated mean (± S.E.) dry mass (mg) of prey in stomachs of round gobies collected at depths of 2–5 m and 8–10 m in 2001 and 2003.

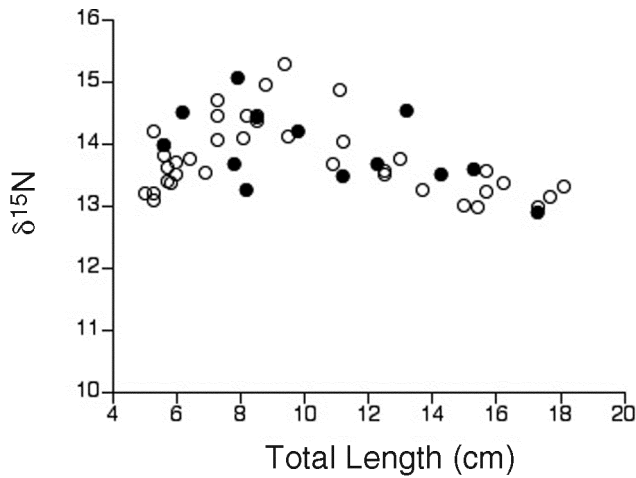| Year	Depth (m)	n	*Dreissena* (shell-free)	Chironomidae	Amphipoda
2001	2–5	58	7.91 ± 0.78	0.28 ± 0.08	0.09 ± 0.03
	8–10	38	12.63 ± 1.40	0.59 ± 0.23	0.01 ± 0.01
2003	2–5	16	5.04 ± 1.28	0.10 ± 0.04	0.78 ± 0.21
	8-10	19	6.24 ± 1.22	2.21 ± 0.59	0

FIG. 5. *The relationship between total length and nitrogen isotopic signature (δ15N) for round gobies collected at depths of 2–5 m (open) and 8–10 m (solid) off Peacock Point in August 2002 and 2003.*

FIG. 6. *The relationship between total length and carbon isotopic signature (δ13C) for round gobies collected at depths of 2–5 m (top) and 10–15 m (bottom) off Peacock Point in August 2002 and 2003. Bars on the right side of the graph show the ranges of δ13C values of potential prey collected from the two depth intervals. The equation of the linear regression for shallow-water gobies was y = –1.731x – 22.1(1 R² = 0.61) and for deep-water gobies was y = –1.403x – 17.7 (R² = 0.24).*

pattern, and overlapped those of amphipods at both depths. The carbon signatures of the larger gobies collected at 2 m confirmed the importance of mussels in the diet indicated by the stomach contents. Similarly, the carbon signatures of gobies from depths of ≥ 10 m suggested increasing consumption of mussels with increasing fish size, but few fish were ^{13}C-depleted enough to have derived all of their carbon from quagga mussels. Again, this is in agreement with the results of the examination of stomach contents.

DISCUSSION

The densities of dreissenid mussels and amphipods along the Ontario shore of eastern Lake Erie decreased significantly from 2001 through 2004. The relatively stable densities of Chironomidae and Oligochaeta during the three surveys suggest that these declines were real, not a result of differences in sampling efficiency among the field crews. Both visual estimates and standardized gill-netting showed that the density of round gobies in this part of Lake Erie increased dramatically from the year 2000 through 2002. Analyses of stomach contents and stable isotopes, together with the changes in the size distribution of *D. bugensis* in the nearshore zone, suggest that the declines in the abundances of both mussels and amphipods are the result of predation by round gobies, and that the
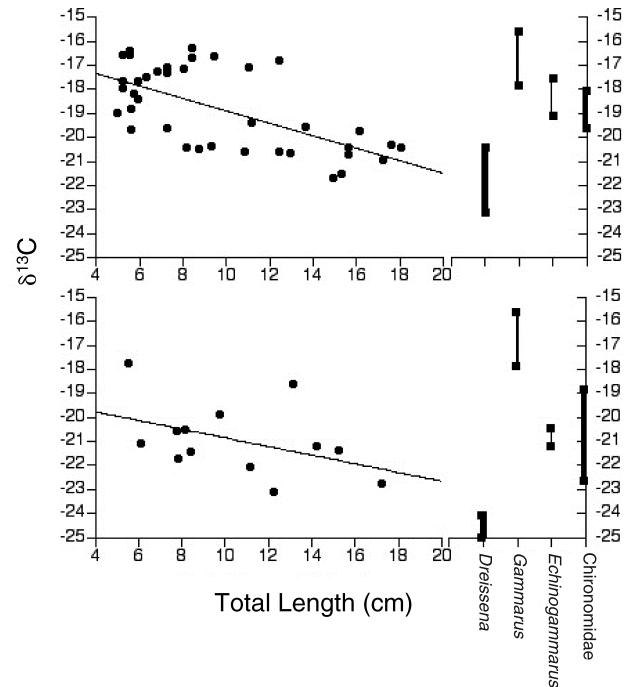
diets of round gobies have shifted somewhat in response to the decline in abundance of mussels.

The initial establishment of an alien species in new habitat often includes an exponential increase in abundance, but the size of the population over the long-term is less predictable (MacNeil *et al.* 2003). Predation could result in a sharp decline from an early maximum consistent with the decrease in the density of quagga mussels and *E. ischnus* that we observed between 2001 and 2004. The abrupt decline in abundance of mussels did not involve the entire population: recruitment appeared to be fairly consistent over time, the numbers of individuals in the 3–14 mm size class decreased each year and the average size of larger mussels increased as their numbers slowly declined. Such change seems most consistent with size selective predation by round gobies (Ray and Corkum 1997).

The same kind of predation pressure seems to have been exerted on amphipods, not only the exotic *E. ischnus* but also the native *G. fasciatus* whose density in the nearshore of eastern Lake Erie ranged from 2500 to 4500/m^2 prior to the introduction of *Dreissena* spp. (Barton and Hynes 1978), averaged 2,800/m^2 in 2001, and only 560/m^2 in 2004.

Our visual estimates of 6.5 round gobies/m^2 in 2001, and 9 to 14 round gobies/m^2 in 2002 at Peacock Point are almost certainly conservative even though they are larger than estimates based on underwater video observations made in the west basin in the same year by Johnson *et al.* (2005). Ray and Corkum (2001) counted 0.3–3 gobies/m^2 while swimming transects in the Detroit River, but found 19/m^2 by turning over rocks within a quadrat at the same site. The size of the boulders in our study area did not make this possible, so it is likely that we missed fish sheltering in crevices. Dense filaments of *Cladophora* at depths < 6 m also hampered inspection of crevices and made it difficult to see smaller gobies. The higher estimated density of fish at the 10 m depth may simply reflect the absence of *Cladophora*. Both of these problems were partially offset by the curiosity that round gobies seem to have about stationary divers; however, we took care to stay far enough away to avoid obviously attracting gobies into the quadrat.

Examination of stomach contents suggested that the diet of gobies from Peacock Point in 2001 was much as has been described elsewhere in the Great Lakes area (Ray and Corkum 1997, Janssen and Jude 2001, French and Jude 2001) and in Europe (Skora and Rzeznik 2001). The diet of round gobies deduced from stomach contents tends to shift from soft invertebrates to mussels at body lengths ranging from 7.5 to 10 cm (French and Jude 2001, Skora and Rzeznik 2001). *Dreissena* are preferred over other molluscs in the laboratory (Ghedotti *et al.* 1995), and larger gobies can remove larger mussels from the substratum (Djuricich and Janssen 2001). However, prey choice seems to depend on what is available. Gobies selected amphipods over mussels on physically simple substrata in the laboratory, and total consumption increased when amphipods were offered (Diggins *et al.* 2002). Preferential selection of prey other than mussels is also evident from the work of Kuhns and Berg (1999) who reported a 50% reduction in the density of invertebrates other than mussels and chironomids on artificial substrates exposed to high densities of round gobies (15/m^2).

Stomach contents reflect recent consumption but may be affected by variations in the retention times of different prey organisms (Fange and Grove 1979). Shells and shell fragments may be regurgitated by round gobies (Ray and Corkum 1997) leading to an underestimation of the importance of mussels in the diet. Conversely, if shells and shell fragments (Ghedotti *et al.* 1995) pass through the stomach more slowly than soft-bodied invertebrates, inspection of stomach contents would inflate the importance of dreissenids to the diet of round gobies. Our stable isotope data suggest that this may be the case. While shell remains indicated that *D. bugensis* accounted for most of the mass of the stomach contents of round gobies, the carbon signatures of even the largest gobies were more enriched than would be expected if dreissenids are the source of that much of the carbon assimilated, especially in deeper water. There was better agreement between stomach contents and stable isotopes for fish from depths ≤ 5 m where individual fish appeared to select either mussels or other invertebrates and this was reflected in their ^{13}C-signatures.

This difference in diet with depth is consistent with differences in the physical characteristics of the habitat and availability of prey. Rocks and boulders in shallow water (≤ 5 m) are densely covered with *Cladophora* from May through September and this algal carpet likely reduces the visibility and accessibility of mobile invertebrates. Round gobies are primarily visual predators, as demonstrated by the reduced consumption of amphipods in turbid water and on complex substrata (Diggins *et al.* 2002). Filamentous algae would not only hide invertebrates from visual predators, but also, and more importantly, may interfere with feeding strikes. This physical inhibition of feeding should increase with increasing size of fish, as larger fish would have more difficulty maneuvering among the algal filaments. Sessile mussels would be much easier to capture, and even small gobies in shallow water ate relatively more mussels than did those from deep water. *Cladophora* coverage is very sparse at 10 m, so, though the densities of chironomids and amphipods are lower than in shallower water, these animals would be much more vulnerable to gobies.

The small round gobies we collected in 2001 contained Chironomidae, Amphipoda, and *D. bugensis*, and larger fish contained mostly *D. bugensis*. Fish collected in 2003 contained more individual prey items than in 2001, but fewer mussels and therefore less total mass of prey. This is consistent with the sharp decline in the abundance of

quagga mussels shown by our benthic sampling. Amphipods were also declining in abundance at the same time, so their increased importance in the diet in 2003 suggests strongly selective predation. The numbers of planktonic Cladocera, especially *Bythotrephes*, in the stomachs of round gobies from deeper water indicate that these fish were actively searching for moving prey, not only on the bottom but also in the water column.

The density of round gobies in the nearshore environment of the east basin of Lake Erie in 2002 was at least as great as that of rock-dwelling cichlids in Lake Malawi (Abdullah and Barton 2003). Abdullah and Barton (2003) attributed the very low densities of benthic invertebrates in the rocky littoral of Lake Malawi to predation by these fish, many of which are similar in size to round gobies. Estimates of the maximum daily consumption of mussels by small (8–10 cm long) round gobies range from about 1 to 1.75 g fresh weight, or 36–47 mussels, per day (Ghedotti *et al.* 1995, Ray and Corkum 1997, Lee and Johnson 2005). If round gobies at Peacock Point ate mussels at that rate, they would have consumed the entire population of *D. bugensis* (as of 2001) each month. Lee and Johnson (2005) reported that consumption rates observed in western Lake Erie averaged 26.4% of the predicted maximum, and this is more in line with the rate of decline of quagga mussel abundance we observed in the east basin.

The results of the OMNR index gillnet program indicate that the densities of round gobies probably peaked in 2002. This can at least partially be attributed to predation by a wide variety of native and introduced fish species (T. Johnson, OMNR, pers. comm.). Our data suggest that round gobies have had a strong effect on the benthic biota of the nearshore zone in eastern Lake Erie, so food limitation has probably also been important. The 94% reduction in the density of quagga mussels between 2001 and 2004 suggests that the round goby is a very effective predator on dreissenids, so the accidental introduction of this fish to the Great Lakes could be viewed as fortuitous. However, any prediction of the long-term relationship among the three species presently accounting for most of the biomass in the nearshore zone (*Cladophora glomerata*, *D. bugensis,* and *N. melanostomus*), not to mention the rest of the flora and fauna, would be premature given the rapid pace of biological changes in the nearshore of Lake Erie in recent years. We do expect that the kinds of changes observed in our study area will occur throughout the Great Lakes during the initial expansion of the range of round gobies.

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