

# Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea

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The Ponto-Caspian round goby (*Neogobius melanostomus*) was introduced to the Gulf of Gdańsk, southern Baltic Sea, in the late 1980s, and it has now become the dominant demersal fish species in shallow water. This study aimed to assess diet preferences and the degree of diet overlap between the round goby and the native flounder (*Platichthys flesus*). Results from time-series of stomach contents and stable isotope analyses of wild-caught fish, together with prey preference experiments carried out in the laboratory, showed that the two species consumed similar species and sizes of prey. The similarities in diet suggest potential for food competition. Catch data showed both reverse depth distributions of round goby and flounder when round gobies were abundant and that the abundances of the two species were negatively correlated. The diet overlap between small flounders and round gobies was greatest when goby abundance was least, suggesting that abundance of round gobies may restrict flounder habitat utilization and, therefore, also food availability to the latter. Therefore, round gobies may have a negative influence on the commercially important flounder.

**Keywords:** diet overlap, diet preference, invasive species, ontogenetic diet shifts, stable isotopes.

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## Introduction

As a consequence of increased global transport, the number of non-indigenous species is rapidly increasing in coastal areas around the world (Carlton, 1996; Ruiz *et al.*, 1997), where they can affect native species and alter ecosystem functioning (Lodge, 1993; Ruiz *et al.*, 1997; Mack *et al.*, 2000). This may result in economic damage to fisheries, tourism, and other industries (Ruiz *et al.*, 1997; Leppäkoski, 2002). Dramatic ecological effects on native fish through direct predation by non-indigenous fish species has been observed in Lake Victoria and Lake Michigan (Wells and McLain, 1972; Witte *et al.*, 1992). Negative ecological effects of competition are more difficult to demonstrate, and this perhaps is the reason why competition is considered to be a less serious consequence of invasions (Lodge, 1993; Williamson, 1996). However, competition is an important factor that structures communities, and resource partitioning is an important mechanism that allows species to coexist (Piet and Guruge, 1997).

In general, habitat and diet are the most important niche dimensions separating coexisting fish species (Schoener, 1974; Ross, 1986); both high and low overlap in these dimensions could be indicative of competition (Ebeling and Hixon, 1991; Hansson, 1995; Begon *et al.*, 1996; Horta *et al.*, 2004; Raborn *et al.*, 2004). When species that have not co-evolved start to interact, the risk of competition increases, and non-indigenous fish species may compete directly with native fauna for resources (Moyle and Light, 1996; Vander Zanden *et al.*, 1999; Balshine *et al.*, 2005). The round goby (*Neogobius melanostomus*) is a demersal benthivore originating in the Ponto-Caspian region.

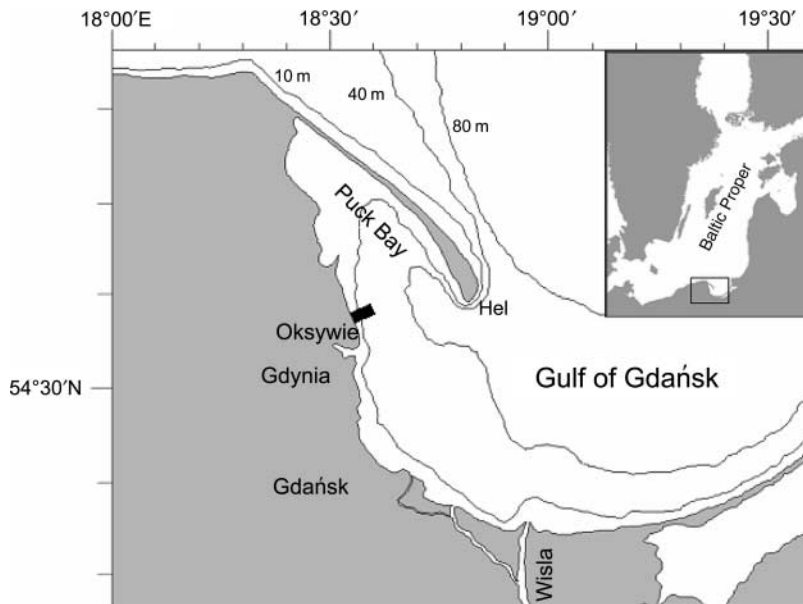
In the late 1980s, it entered the Gulf of Gdańsk, Southern Baltic, the Laurentian Great Lakes, North America, and the Moscow River, Russia, in ballast water (Sokolov *et al.*, 1989; Jude *et al.*, 1992; Skóra and Stolarski, 1993). In the Gulf of Gdańsk, the area round gobies occupy overlaps with that of the native flounder (*Platichthys flesus*), which also feeds on benthic fauna (Mulicki, 1947; Molander, 1964; Aarnio and Bonsdorff, 1997; Ostrowski, 1997; Rzeznik 1997), and concerns have been raised that the round goby may be outcompeting flounder for both food and space (Skóra and Rzeznik, 2001; Wandzel, 2003; Corkum *et al.*, 2004). Notwithstanding, comparable studies of diet and habitat have not been conducted for the two species.

Here we assess the spatio-temporal overlap, and diet preferences and overlap between round goby and native flounder by a combination of gillnet fishing, stomach content analyses, stable isotope analyses, and laboratory experiments conducted during summer 2004 in the Gulf of Gdańsk.

## Material and methods

### Study area and sampling

Fish were sampled off Oksywie (54°33'N 18°33'E), during June (7–10), July (17–20), and September (1–3) 2004 (Figure 1). Fishing grounds off Oksywie are located at the border of Puck Bay, a vast, shallow area with a bottom characterized by a mixture of sand, clay, gravel, and boulders (Mojski *et al.*, 1995). There, round goby, followed by flounder, were the most abundant fish species during July and August 2003 (GA, pers. obs.). The study area started some 200 m from shore (water depth 3 m)



**Figure 1.** Gulf of Gdańsk, showing the sampling site outside Oksywie. Inset shows the Baltic Proper, with the rectangle marking the area of interest.

and extended 2.7 km out to a depth of 13 m. Four fishing stations (at 3, 7, 10, and 13 m) were established using fixed coordinates, and 20, 19, and 16 nets were distributed at the stations in June, July, and September, respectively. In June, both surface and bottom temperature decreased with distance from shore, at the surface from 10.6°C (3 m station) to 9.0°C (13 m) and at the bottom from 10.6°C (3 m) to 5.8°C (13 m). In July and September, the water column was almost homothermic, at 16.1 ± 0.9°C and 17.4 ± 0.3°C (mean ± s.d.), respectively. Salinity was 6.9 for all periods and depths.

Fish were collected using Nordic coastal survey nets (45 m long, 1.8 m deep, divided into nine sections with bar mesh sizes of 10, 12, 15, 19, 24, 30, 38, 47, and 60 mm). The nets were set overnight (for about 10 h) and covered the periods of dusk and dawn, when both species are thought to feed (Pihl, 1982; Janssen and Jude, 2001). Catch per unit effort (cpue) was calculated for each fishing station (3, 7, 10, and 13 m) as the average number of fish caught per net. Total length was recorded to the nearest millimetre and weight to the nearest 0.1 g for all round gobies and flounders. The digestive tracts were immediately dissected out and preserved in 90% ethanol for later analysis. To compare size classes of round gobies and flounders, we established gape size (maximum height of gape, measured with a slide calliper without tension) to body length regressions. Corresponding size classes (small, medium, and large) have similar gape size, although body length differs (Table 1).

### Stomach content analyses and estimates of diet overlap

Guts and stomachs from 323 round gobies and 209 flounders from all depths were analysed (Table 2). All prey in the digestive tract were identified to the lowest possible taxon under a stereo microscope (×10 magnification). The number of food components was determined for each stomach and, taking into consideration the extent of digestion, e.g. broken bivalves could be approximately reconstructed, their maximum lengths were measured with a

slide calliper. Shell-free (not to overestimate the importance of, e.g. bivalves) dry weights of the various food components were estimated using conversion factors from the literature (Ankar and Elmgren, 1976; Evans, 1977; Brey *et al.*, 1988; Furman and Crisp, 1989). Prey other than those shown in Table 2 constituted a negligible part of the stomach contents and were not included in the analyses. Diet overlap was estimated with Morisita's index ( $C$ ) (cf. Horn, 1966; Cortés, 1997):

$$C = \frac{2\sum X_i Y_i}{\sum X_i^2 + \sum Y_i^2},$$

where  $X_i$  and  $Y_i$  are the proportions of the  $i$ th food category (Table 2) in the diet of species  $X$  and  $Y$ , respectively. An index of 0 means total dissimilarity of the diet, and a value of 1 represents identical stomach contents; according to Zaret and Rand (1971), the overlap is ecologically significant if the value is  $\geq 0.6$ .

### Stable isotope analysis

As a complement to stomach analyses, muscle tissue from each size class of each species was analysed for stable nitrogen isotopes. Stable isotopic signatures reflect long-term (weeks–years) diet composition (Hobson, 1999), whereas stomach contents analysis

**Table 1.** Gape size (mm) and corresponding total fish length (mm) per size class.

Size	Gape size	Round goby	Flounder
Small	< 14.5	60–120	100–120
Medium	14.5–17	120–140	200–250
Large	> 17	> 140	> 250

Categorization based on regression analyses: flounder:  $r^2 = 0.955$ ,  $F_{1,29} = 597.21$ ,  $p < 0.0001$ ; round goby:  $r^2 = 0.956$ ,  $F_{1,45} = 945.87$ ,  $p < 0.0001$ .

**Table 2.** Diet composition (shell-free dry weight, %) from stomach analyses.

Species	Size	Month	n	% empty	Dry weight (mg)	% Myt.	% Mac.	% Car.	% Mya	% Bal.	% Hyd.	% Ner.	% Cor.	% Gam.	% Gas.
Rg	S	June	35	40	19.6	30.9	1.7	0	0	0	39.3	28.1	0	0	0
Rg	S	July	42	24.4	22.1	30.9	0.8	0	0	0.3	19.2	48.9	0	0	0
Rg	S	September	70	26.1	8.3	13.9	15.3	22.9	0.8	4.6	31.3	11.1	0	0	0
Rg	M	June	42	23.8	30.0	36.0	5.8	2.8	0	0.1	38.2	16.0	0	1.0	0
Rg	M	July	17	33.3	17.9	49.3	2.2	0	0	8.5	12.6	27.5	0	0	0
Rg	M	September	39	5	22.3	36.6	19.6	9.7	0.1	4.0	22.8	7.3	0	0	0
Rg	L	June	35	48.6	39.8	41.6	9.5	0.4	0	0.6	24.5	21.2	0	2.3	0
Rg	L	July	22	40.9	17.8	34.4	21.9	0	0	0.4	39.3	0	0	4.0	0
Rg	L	September	21	4.8	82.2	75.4	12.7	0.3	0	0.2	6.6	0.1	0	0	4.8
Fl	S	June	16	43.8	317.9	0.1	56.6	0	0	0.2	11.1	32.0	0	0	0
Fl	S	July	19	47.4	8.6	20.0	41.0	0	0	0.0	19.2	19.7	0	0	0
Fl	S	September	37	27	43.9	0	14.5	18.4	0.1	0.3	7.8	35.0	24.0	0	0
Fl	M	June	17	17.6	94.3	9.6	49.3	9.0	0	0.0	10.2	21.8	0	0	0
Fl	M	July	25	20.8	39.2	3.5	63.3	5.0	0	5.1	1.3	17.7	4.0	0	0
Fl	M	September	30	26.7	116.0	4.6	40.9	6.4	1.1	0.1	3.2	16.7	27.1	0	0
Fl	L	June	20	10	576.9	10.2	56.9	0.0	0	6.6	0.0	16.4	0	0	9.8
Fl	L	July	18	50	271.2	14.4	62.2	3.5	0.0	0.1	2.1	6.4	5.1	0	6.3
Fl	L	September	17	23	307.9	10.9	56.7	11.3	0.0	0	0.3	8.9	7.8	0	4.0

From left, species (round goby and flounder), size class (small, medium, and large), month, number of fish analysed, *n*, percentage of fish with empty stomachs, total dry weight of stomach contents, and the food items in terms of percentage: *Myt.*, *Mytilus edulis*; *Mac.*, *Macoma balthica*; *Car.*, *Cardium* sp.; *Mya*, *Mya arenaria*; *Bal.*, *Balanus improvisus*; *Hyd.*, *Hydrobia*; *Ner.*, *Nereis diversicolor*; *Cor.*, *Corophium* sp.; *Gam.*, *Gammarus* sp.; *Gas.*, *Gasterosteus aequalatus*.

indicates intake over the previous few hours. Nitrogen isotopic composition is usually expressed in per mil deviations ( $\delta^{15}\text{N}$ ) between the isotope ratio in a sample and that of atmospheric  $\text{N}_2$ , according to the formula

$$\delta^{15}\text{N} = \left( \frac{{}^{15}\text{N}_{\text{sample}}/{}^{14}\text{N}_{\text{sample}}}{{}^{15}\text{N}_{\text{air}}/{}^{14}\text{N}_{\text{air}}} - 1 \right) \times 10^3.$$

Samples for isotope analyses (a 2–3 cm piece of muscle from just behind the head, above the lateral line) were excised immediately after capture (Hansson *et al.*, 1997), from five random specimens (in July, only three) of each species, size class, and sampling period. The samples were dried at 50°C, homogenized with a mortar and pestle, transferred to foil capsules ( $1 \pm 0.2$  mg), and analysed for  $\delta^{15}\text{N}$  relative abundance by mass spectrometry at the University of California, Davis Stable Isotope Facility.

### Prey preference

Fish and mussels for prey preference experiments were collected at the beginning of July off Hel Marine Station, at the tip of the Hel Peninsula (Figure 1). Fish were acclimatized and starved for a week before the experiment. In all, 60 fish were selected for the experiment ( $n = 10$  per size class and species). They were placed individually in 35 cm high, 40 × 90 cm glass aquaria, filled to 75% with seawater flow-through (at natural temperature and salinity regimes around 17°C and 6.9), a 2 cm sieved (mesh size 1 mm) layer of sand on the bottom, and a stone (the size of a fist) as refuge. For food, the two most abundant (Wiktor, 1985) mussel species in the area, *Macoma balthica* and *Mytilus edulis*, were collected by trawl, measured with a slide calliper, and divided into three size classes: small (3–6 mm), medium (7–12 mm), and large (>12 mm). An hour before addition of the

fish, eight mussels of each species and size class (48 in total) were distributed randomly on the bottom of each aquarium. The outer walls of the aquaria were covered with black plastic film to reduce visual stress. This was important, because flounders are mainly visual feeders (Mattila and Bonsdorff, 1998). Round gobies can forage in total darkness using their complete lateral line system (Fuller *et al.*, 2006), but probably also use their well-developed eyes (Jude, 1993) to search for food. Fish were allowed to forage for 18 h, including both dusk and dawn periods, imitating the natural light regime. At the end of each experiment, the sand was sieved and all mussels retrieved were again measured and assigned to a size class. Non-feeding fish (mainly large flounders) were excluded from the analyses because they were assumed to respond negatively to laboratory conditions.

Food selectivity was calculated using Manly's  $\alpha$  (Manly, 1974; Chesson, 1978, 1983; Swenson and McCray, 1996):

$$\alpha_i = \frac{(d_i/N_i)}{\sum_{j=1}^k (d_j/N_j)},$$

where  $i$  is the prey type (mussel species and size class),  $k$  the number of prey types in the experiment,  $d_i$  the number (or proportion) of prey of type  $i$  in the diet sample, and  $N_i$  is the density (or proportion) of prey type  $i$  in the environment. For the analysis,  $k = 6$ , because six prey types were used (two species of mussel, three size classes). Values of  $\alpha$  range from 0 (complete avoidance) to 1 (complete preference). When  $\alpha_i > 1/k$  there is selection for, and when  $\alpha_i < 1/k$  there is selection against, prey  $i$ . When  $\alpha = 1/k$ , the predator is feeding randomly, and the composition of the diet simply reflects the availability of prey in the environment.

### Data processing and statistics

When possible, we used analysis of variance (ANOVA) to test for differences among species, size classes, and depths. If transformed data failed assumptions of normality or equal variance, non-parametric tests were used (Kruskal–Wallis, Mann–Whitney *U*-test). When estimating the depth distribution of species, data from stations of similar depth were merged to generate sufficient replicates (number of nets per depth), when appropriate. Similarly, when calculating diet overlap, fish from all depths were merged to obtain a sufficiently large data set, because empty stomachs (Table 2) reduced the number of replicates per size class. All statistical tests were made with STATISTICA® software.

## Results

### Depth distributions of round gobies and flounders

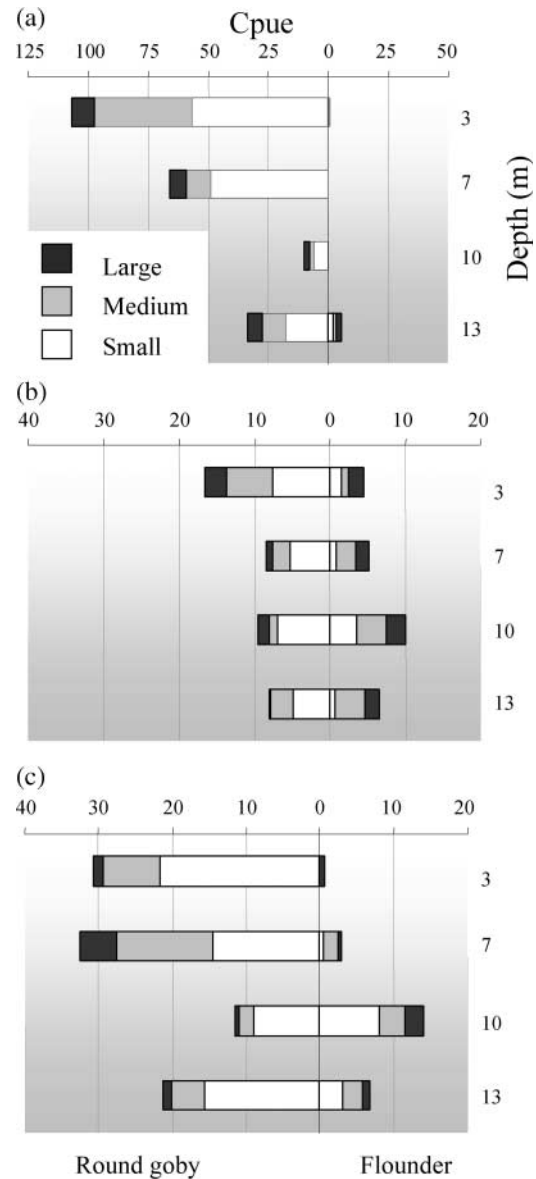
The cpue of round gobies and flounders differed significantly among sampling periods and depths (Figure 2). In June (Figure 2a), flounders were abundant only at 13 m. The cpue of round goby was significantly higher (Mann–Whitney *U*-test,  $n = 19$ ,  $p < 0.05$ ) in shallower water (3 and 7 m merged together) than at 13 m. In July (Figure 2b), the abundance of round gobies at 3 and 7 m had decreased almost 10-fold from June, and flounders were more or less evenly distributed at all depths. In September (Figure 2c), goby densities increased in shallow water when compared with July. The depth distribution of small flounders was nearly opposite to that of round gobies. Flounder cpue peaked at 10 m in September where goby cpue was least, resulting in a significant statistical interaction ( $F_{1,28} = 12.33$ ;  $p < 0.0015$ ) in cpue between species and depth (merging 3–7 and 10–13 m depths, respectively). Overall, merged data of size classes, depths, and periods showed a negative correlation between round goby and flounder cpue (log-transformed data,  $p = 0.044$ ,  $r = -0.59$ ).

### Diet composition and overlap

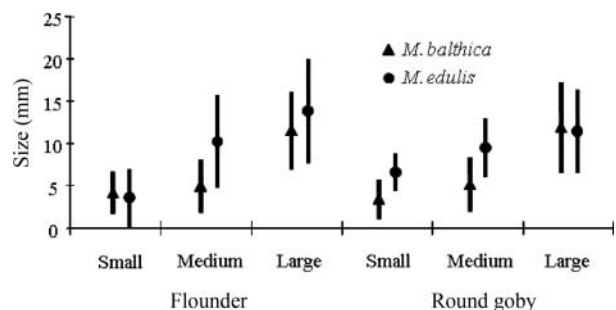
The bivalves *M. balthica* and *M. edulis*, the polychaete *Nereis diversicolor*, and the gastropod *Hydrobia* sp. were important food items for all size classes of both species (Table 2). In general, the most common food item of flounders was *M. balthica*, constituting some 50% of the diet (shell-free dry weight), and *M. edulis* accounted for 30–50% of the round goby diet. Flounders and round gobies of corresponding size classes consumed *M. balthica* of equal mean size (Figure 3). The size of consumed *M. balthica* increased with size class of the fish (ANOVA,  $F_{5,184} = 18.456$ ,  $p < 0.05$ ), except that there was no significant difference in size of consumed mussels between small and medium-sized flounders ( $p = 0.14$ ). The size of *M. edulis* consumed also increased with fish size (Figure 3), but the size differences of mussels consumed were not significant.

In September, the percentage of *M. balthica* (mean size  $< 6$  mm; Figure 3) in the diet of small and medium-sized round gobies increased 10-fold over that in June and July (Table 2). Simultaneously, the consumption of *M. balthica* of the same size (Figure 3) decreased among small flounders (ANOVA,  $F_{2,43} = 5.603$ ,  $p < 0.05$ ), and there was a non-significant decline among medium-sized flounders: ANOVA,  $F_{1,40} = 2.752$ ,  $p = 0.105$ ).

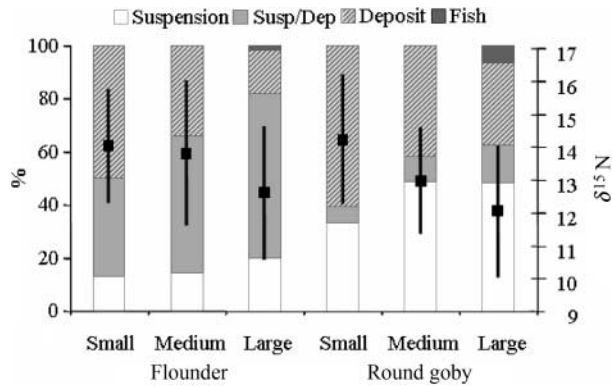
There was a significant diet overlap ( $0.66 \pm 0.10$ ) between small flounders and all size classes of gobies in July (low round goby abundance; Figure 2b). In June and September (high round goby abundance; Figures 2a and 2c), the value of *C* between small



**Figure 2.** Catch rate (cpue) of small, medium-sized, and large flounders and round gobies in (a) June, (b) July, and (c) September at different depths (3, 7, 10, 13 m). Note the different scales on the x-axes.



**Figure 3.** Sizes of consumed *M. balthica* and *M. edulis* for small, medium, and large flounders ( $n_{Macoma} = 114$ ,  $n_{Mytilus} = 24$ ) and round gobies ( $n_{Macoma} = 76$ ,  $n_{Mytilus} = 110$ ). Mean  $\pm$  s.d.



**Figure 4.** Proportion of prey items divided into functional groups of small, medium, and large flounders and round gobies. Also shown are the values of  $\delta^{15}\text{N}$  for flounders and round gobies of different size classes. Periods (June, July, and September) are merged. Mean  $\pm$  s.d.

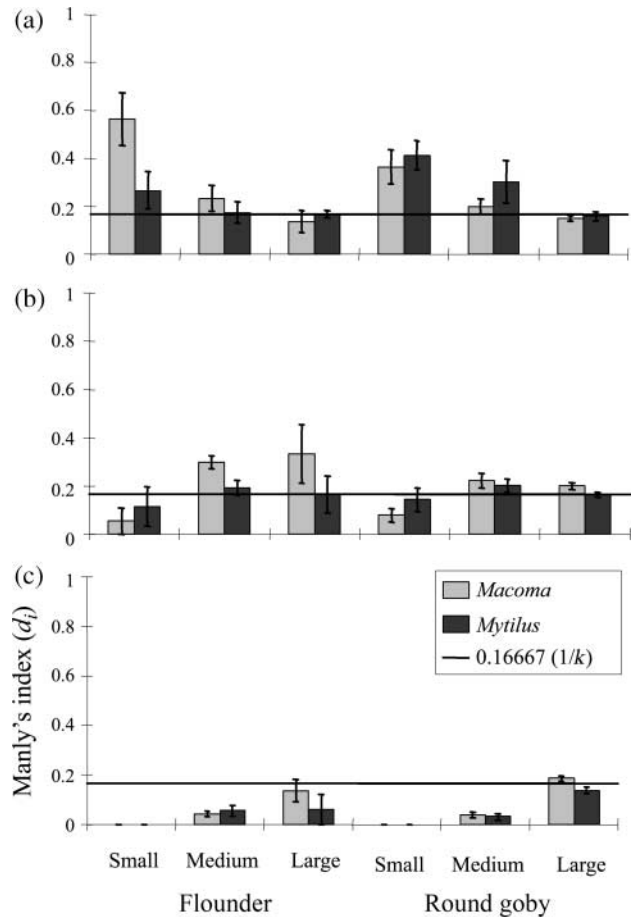
flounders and round gobies was significantly lower, ( $0.36 \pm 0.17$ , ANOVA,  $F_{2,8} = 8.07$ ,  $p < 0.05$ ). Medium-sized and large flounders had values below 0.6 for all periods ( $0.38 \pm 0.12$ ), and there was no significant effect of round goby abundance on diet overlap ( $p = 0.14$  and  $0.64$ , respectively).

#### Stable isotope analysis and size-dependent diet shifts

Round gobies and flounders of corresponding size classes were similarly enriched in  $\delta^{15}\text{N}$ . Although the only significant difference in  $\delta^{15}\text{N}$  enrichment was between large and small gobies (ANOVA,  $F_{2,71} = 6.107$ ,  $p < 0.01$ , Figure 4), small fish of both species tended to be more enriched than large and medium-sized fish. Prey organisms for all sampling periods (June, July, and September) were divided into functional groups according to Wiktor (1985; Figure 4): suspension-feeders (*M. edulis*, *Cardium* sp., and *Balanus improvisus*), facultative suspension/deposit-feeders (*M. balthica*, *Mya arenaria*), deposit-feeders (*N. diversicolor*, *Hydrobia* sp., *Gammarus* sp., and *Corophium* sp.), and fish (*Gasterosteus aculeatus*). The importance of *N. diversicolor* in the diet decreased significantly with increased fish size for round gobies and flounders (Mann–Whitney *U*-test,  $p < 0.05$  for both species, Figure 4). Concurrently, the proportion of suspension-feeders and facultative suspension/deposit-feeders (*M. edulis* and *M. balthica*, respectively) in the diet increased with fish size (Mann–Whitney *U*-test,  $p < 0.05$ ).

#### Prey preference

Flounders of all sizes seemed to prefer *M. balthica* to *M. edulis*, whereas round gobies, irrespective of size class, did not discriminate between prey species (Figure 5). Small ( $n = 8$ ) and medium-sized ( $n = 6$ ) flounders exhibited significantly greater positive selection for small- and medium-sized *M. balthica*, respectively, than for *M. edulis* of similar size (ANOVA:  $F_{1,5} = 6.441$ ,  $p < 0.05$ ;  $F_{1,7} = 4.945$ ,  $p < 0.05$ ). Small round gobies ( $n = 9$ ) selected small mussels, and medium-sized gobies ( $n = 9$ ) selected both small and medium-sized mussels. Large gobies ( $n = 10$ ) ate all mussels available. Just two large flounders consumed mussels during the experimental period.



**Figure 5.** Selection index of (a) small, (b) medium-sized, and (c) large *M. balthica* and *M. edulis* for small, medium, and large flounders and round gobies. Values above the horizontal line indicate selection for species and size of mussel. Mean  $\pm$  s.e.

#### Discussion

The results indicate that round gobies have the potential to impact flounder habitat and food resource utilization in a negative manner. Catch data showed reverse depth distributions of round gobies and flounders when round gobies were abundant, and that total abundance of the two species was negatively correlated. At times of high round goby abundance, flounder depth distribution was constrained to deeper areas (10 and 13 m), but when round goby abundance was low, as in July, flounders were found at all depths. The great abundance of round gobies in shallower water in June possibly reflects a migration from wintering habitats to shallower waters further into Puck Bay (Figure 1). In July, the small catch of round gobies also at the shallow sampling station (3 m) suggests that spawning was taking place in even shallower water ( $< 1.5$  m, not sampled) on rocky and stony substrata close to the shore (Moskal'kova, 1996; Pinchuk *et al.*, 2003). The availability of nesting sites is limited in the Gulf of Gdańsk (Sapota, 2004), and at Oksywie the main rocky habitat is restricted to the artificial stonewall at the shore. Studies from the North American Great Lakes have shown that round gobies are aggressive and territorial (Dubs and Corkum, 1996; Janssen and Jude, 2001; Balshine *et al.*, 2005), and that behavioural interaction between species is likely. Therefore, it is reasonable to suggest that

reduced abundance of gobies at the depths sampled in July made the habitat more available for flounders. Alternative explanations to such habitat partitioning between the species, e.g. differences in migratory patterns, temperature preferences, predation, and/or depth-dependent distribution of preferred food items, are less plausible. Flounders migrate between the coast and offshore to feed and to spawn, respectively. In the Gdańsk deep, they spawn in early spring (February–mid-April), then return to shallower water in May (Cięglewicz, 1947; Molander, 1964; I. Psuty-Lipska, Sea Fisheries Institute Gdynia, pers. comm.). Hence, flounders were likely inhabiting the shallow water well before our sampling in June. Nor can possible differences in temperature preference between species explain the depth partitioning we observed in June, because flounders were evenly distributed over all depths in July, when temperature was considerably higher. As the sampled area was almost devoid of predatory fish such as cod and perch (AMLK and GA, pers. obs.), predation cannot explain the abundance and depth distribution patterns. In terms of food distribution, Wiktor (1985) found that *M. balthica*, which was selected more by flounders than was *M. edulis* in the preference experiment, constituted more of the bottom fauna at 3–5 m than at 8–10 m.

Results from stomach analyses and the prey preference experiment showed that both species fed extensively on bivalves, and that fish with similar gape size selected bivalves of similar size.

The prey preference experiment clearly showed that flounders preferred *M. balthica* whereas round gobies exhibited a wider preference of bivalves. As *M. balthica* constituted some 50% of flounder diet, we infer that flounders depend largely on that species. The results from the stomach content analyses and experimental food preference studies may have been biased by species-dependent differences in the intestines, evacuation rates, and behaviour. Also, the importance of some prey items that were well digested could have been over- or underestimated. Consumption of *N. diversicolor* could have been overestimated because the bristles may remain in the stomach for a long time. In contrast, bivalve consumption could have been underestimated because round gobies at least might swallow only the flesh and not the shells. However, these issues are probably of minor importance, because all bivalves consumed in the prey preference experiment were swallowed whole. For large fish, the selection results are not clear, partly because large flounders seemed to be less easily acclimatized to laboratory conditions than gobies (only 2 of 10 fish foraged). Prey depletion attributable to limited prey offered in relation to foraging time precluded conclusions about food preferences for large gobies.

It could be argued that high goby abundances may result in local depletion of preferred food items for flounders (specifically *M. balthica*), so affecting its habitat distribution. In the Laurentian Great Lakes, Kuhns and Berg (1999) showed that round gobies were able to reduce significantly the densities of benthic invertebrates. For flounders, *M. balthica* is more efficiently digested than other shelled food items, because it does not survive the passage through the gut (Aarnio and Bonsdorff, 1997). However, in September, the percentage of *M. balthica* in the diet of small flounders was considerably less than in June and July, whereas *M. balthica* of the same size (Figure 3) increased 10-fold in the diet of small and medium-sized round gobies (Table 2). The lesser proportion of such high-energy food in the diet of small flounders indicates a competition-induced shift to suboptimal food resources.

The decline of native benthic fish populations in the Great Lakes has been related to round goby predation on early life stages of native fish (French and Jude, 2001). As roe and fish constitute only a minor part of the diet of round gobies, it is likely that goby-induced declines of native species in the Baltic Sea would be more by competition than by predation.

The recently invaded non-indigenous polychaete *Marenzelleria viridis* was not observed in any fish stomach, although the species is reported from the area (Zmudzinski *et al.*, 1997).

The similarities in diet composition between round gobies and flounders were supported by comparable  $\delta^{15}\text{N}$  values, suggesting that fish of both species with similar gape size share the same trophic level. A consumer is enriched in  $^{15}\text{N}$  with 3–4‰ relative to its diet (Owens, 1987), so the  $^{15}\text{N}$  value reflects the importance of prey items with different  $^{15}\text{N}$  values consumed. Hence, the  $^{15}\text{N}$  enrichment in an animal's tissue can be used as a proxy for trophic level. Stable nitrogen isotopes also prove a good indicator of diet change during ontogeny (Gaines *et al.*, 2002; Cocheret de la Moriniere *et al.*, 2003). Interestingly, the  $\delta^{15}\text{N}$  value decreased with size for both species. This is in contrast to commonly reported ontogenetic development, i.e. trophic level of a species increases with size (France *et al.*, 1998; Gaines *et al.*, 2002; Cocheret de la Moriniere *et al.*, 2003), because body size determines the range of prey sizes a predator is able to consume (Cohen *et al.*, 1993). From this analysis, we deduce that small fish consumed more deposit-feeders, especially *N. diversicolor*, than larger fish (Figure 4). Deposit-feeders are generally more enriched in  $^{15}\text{N}$  than suspension-feeding bivalves, which assimilate pelagic phytoplankton (Kang *et al.*, 2003). The  $\delta^{15}\text{N}$  value of *N. diversicolor* is significantly higher than that of the bivalve *M. edulis* in the northern Baltic (R. Neidemann, Stockholm University, pers. comm.). In support of the nitrogen isotope signatures, feeding on bivalves by both species investigated here increased with size of fish, indicating an ontogenetic diet shift in both species, as suggested by Skóra and Rzeznik (2001) and Jennings *et al.* (2001). However, a high  $\delta^{15}\text{N}$  value may also indicate starvation (Haubert *et al.*, 2005) and a competition-induced shift to suboptimal food resources in the diet of small flounders could possibly result in starvation.

The diet similarities suggest a potential for food competition to develop, if resources become limiting. Nevertheless, because of opposite seasonal peaks in consumption of important food items, the diet overlap was low to moderate on all sampling occasions and combinations of size classes. However, significant overlap was noted between small flounders and all size classes of round gobies in July, when the abundance of the latter species was at its lowest and flounders were evenly distributed at all depths. This interaction between diet overlap and round goby abundance is important, because it suggests that high round goby abundance can restrict flounder habitat utilization and thereby also food availability for the latter species. In addition to heavy fishing pressure (Psuty-Lipska, 2001; Draganik and Psuty-Lipska, 2002), limited food resources may have negative local effects on the flounder population. Our results therefore support what many authors have suggested before, that round gobies compete with flounders for resources.

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