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PRIMARY RESEARCH PAPER

# A successful non-native predator, round goby, in the Baltic Sea: generalist feeding strategy, diverse diet and high prey consumption

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**Abstract** The round goby *Neogobius melanostomus* has successfully invaded much of the Baltic Sea. However, very little is known about the feeding habits of the species in this newly invaded environment. Our laboratory experiment showed that the round goby is able to effectively consume a diverse variety of prey when given the choice between dominant benthic invertebrates: bivalves (*Macoma balthica*, *Mytilus trossulus*, *Cerastoderma glaucum*) and amphipods (*Gammarus* spp.). In contrast consumption of the gastropod (*Theodoxus fluviatilis*) was very low in all provided combinations. Nevertheless, the round goby had no statistically significant preference towards any of the prey taxa. The round goby exhibited size-specific consumption of *M. trossulus*, with smaller individuals being consumed at least 25% more than larger size classes. In addition elevated prey density resulted in higher consumption of prey by the fish. The broad diet suggests that shifting densities of benthic invertebrate prey has little influence on the further dispersal of the round goby in the Baltic Sea as the species is potentially able to switch between several native invertebrate taxa. This opportunistic feeding behaviour has likely favoured this invasion and ensured success of the species in the invaded ecosystem.

**Keywords** Baltic Sea · Benthic invertebrate prey · Consumption rates · Generalist · Prey preference

## Introduction

In recent decades, growing numbers of non-indigenous species have significantly influenced biodiversity and dominance structure of benthic communities in coastal habitats (Olenin & Leppäkoski, 1999; Leppäkoski & Olenin, 2000; Bax et al., 2003; Strayer et al., 2006). Non-indigenous species may alter food web dynamics and functioning in the local ecosystem through intensified predation pressure on native species, or by targeting different prey items than native predators (Zavaleta et al., 2001; Laxson et al., 2003). The success and impact of non-native species are partly determined by their feeding strategy and selectivity. A generalist feeding strategy is less affected by shifting prey availability while a specialist feeding strategy could result in fluctuating population abundance of the predator when preferred prey abundance varies (Volterra, 1928). In conditions where prey biomass is not a limiting factor and top predators are absent, a generalist predator could have a more severe effect on communities that they prey upon (Schreiber, 1997).

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In the brackish waters of the north-eastern Baltic Sea, predatory pressure on benthic communities is rather weak (Kautsky, 1981), represented by a few molluscivorous benthic fishes such as flounder *Platichthysflesus* (Linnaeus, 1758) and viviparous eelpout.

*Zoarces viviparous* (Linnaeus, 1758) (Ojaveer et al., 2010). The invasion of the round goby *Neogobius melanostomus* (Pallas 1811) in the early 2000s changed the situation dramatically through notable intensification of top-down control of benthic invertebrates (Järv et al., 2011). High feeding rates and increasing abundance potentially allows the round goby to substantially change the richness and dominance structure of benthic communities (Lederer et al., 2008; Raby et al., 2010; Kornis et al., 2012; Rakauskas et al., 2013).

In order to be a successful invader, a species must be able to adapt to novel environmental conditions that include the available prey. Based on diet studies, the round goby feeds excessively on bivalves, when present, but can also consume other types of food, with a great flexibility in terms of prey species (Corkum et al., 2004; Barton et al., 2005; Kornis et al., 2012). In its native range, in the Ponto-Caspian region, the round goby mainly preys on bivalves (*Cerastoderma* spp., *Mya* spp., *Mytilus* spp.), but gastropods (*Hydrobia* spp.), worms, Gammaridae, fish (sprat *Sprattus sprattus* (Linnaeus, 1758)) and detritus also play an important role in their diet throughout the year (Skazhkina & Kostyuchenko, 1968). In invaded North American rivers, the goby feeds extensively on non-native dreissenid mussels (*Dreissena polymorpha* (Pallas, 1771) and *Dreissena bugensis* (Andrusov, 1897)) when these mussels are present (Raby et al., 2010). Dreissenids are absent from many North American rivers invaded by goby (Carman et al., 2006; Kornis & Vander Zanden, 2010), and in such systems gobies feed primarily on a variety of insect larvae species, but not on native bivalves (Ghedotti et al., 1995; Carman et al., 2006; Kornis et al., 2012). In some Baltic Sea areas, the round goby feeds primarily on *Mytilus trossulus* Gould, 1850 (Skora & Rzeznik, 2001), while in others decapods dominate in the diet (Azour, 2011). In the northern Baltic Sea bivalves serve as the main food source of the round goby and are the dominant benthic invertebrate taxa in the coastal sea (Norling & Kautsky, 2008; Järv et al., 2011).

Obtaining information on species dietary preference is important because selectivity toward some prey species may cause an uneven predatory pressure within a benthic community, and could ultimately modify both community size structure and species composition (Post & Cucin, 1984). The round goby has already shown in other invaded areas that it can significantly lower abundances of dominant prey species (Lederer et al., 2008; Raby et al., 2010). Knowing the consumption rates and preferences of different prey species is key in assessing the impact of the round goby on the size and distribution range of prey species populations. In addition, feeding experiments provide understanding on the round goby's plasticity in terms of prey consumption and therefore assist in evaluating its likely impacts on invaded habitats. Most of the knowledge about the diet of round goby has been obtained from gut analyses (Ray & Corkum, 1997; Skora & Rzeznik, 2001), which may reflect more on prey availability than preference towards particular prey species (Underwood et al., 2004). Estimating prey preference from stomach content analysis is only possible when fine-scale prey availability and predator abundance in the area is known. In the north-eastern Baltic Sea only estimates on average prey density are available for very heterogeneous areas and there are no published values of round goby density. Thus, feeding experiments can offer the opportunity to determine prey preference under controlled conditions. In North America, several studies on the size selection of dreissenid mussels by the round goby showed that the consumption of different-sized mussels is related to the size of the round goby with larger gobies preferring larger mussels (Ghedotti et al., 1995; Andraso et al., 2011). Similar studies have not been conducted in the north-eastern Baltic Sea.

The primary aim of the current study was to experimentally demonstrate whether the round goby has a selective feeding preference among several taxa of locally dominating benthic invertebrates in the north-eastern Baltic Sea. In determining the dietary preference of the species, the following secondary research questions were addressed: (1) are some prey types and sizes consumed more than others, and (2) are prey taxa consumed at a higher rate when provided at higher densities? In addition the used densities reflect naturally low and naturally high prey density and therefore show if the round goby is able to impact benthic invertebrate communities even at seasonal abundance peaks.

## Materials and methods

### Study area

The indoor laboratory experiment was conducted in August 2014 at Kõiguste field station, located in the north-eastern Baltic Sea, in Estonia, on the northern shore of Gulf of Riga (58°22′23.5″N; 22°58′56.3″E). In the laboratory experiment, we created environmental conditions and prey density similar to those in this region of the Baltic Sea. Generally the area is quite shallow with prevailing depths between 1 and 4 metres and a low salinity of 4.0–6.5 psu. The prevailing substrate type is a thin layer of slightly silted sand mixed with pebbles, gravel and boulders. The area has high nutrient levels and habitat diversity, providing abundant algal and invertebrate communities (Kotta et al., 2008). In order to create similar conditions in all aquaria, the complexity of habitat was reduced. Artificial plants provided shelter for amphipods and gastropods, a hollow artificial structure provided shelter for round goby and was an attachment substrate for mussels, and sand provided natural habitat for clams.

### Test organisms

All prey animals were collected adjacent to the field station by a landing net or by a scuba diver, and let to acclimate for 12 h in the aquaria before the experiment. Five key invertebrate taxa typical for the north-eastern Baltic Sea (Lauringson & Kotta, 2006) were used as prey: the bivalves *Mytilus trossulus*, *Macoma balthica* (Linnaeus, 1758) and *Cerastoderma glaucum* (Bruguière, 1789); the gastropod *Theodoxus fluviatilis* (Linnaeus, 1758); and gammarid amphipods (mainly *Gammarus tigrinus* Sexton, 1939, *Gammarus salinus* Spooner, 1947, *Gammarus zaddachi* Sexton, 1912, *Gammarus oceanicus* Segerstråle, 1947). Because of their significant size variation in space and time, *M. balthica* and *M. trossulus* were divided into different size classes. Invertebrate densities (Table 1) reflected their natural densities in the area. Two density levels were used in various treatments to replicate summer (high) and spring (low) density conditions (Kotta et al., 2008; Veber et al., 2009; Martin et al., 2013).

Round goby (33 individuals) were collected live from a local fishermen's basket trap (5 m depth) on 2nd of August 2014, adjacent to the field station, and were kept in separate gently aerated aquaria with no food for 24 h before both runs (see sections below) of the experiment. The goby varied in size (mean total length 131 mm, range 104–177 mm) and sex (67% male). The selected fish represented a similar size frequency distribution to adult round goby in the field, except that juveniles were not used, as the round goby undertakes an ontogenetic shift in its diet (Ray & Corkum, 1997, 2001). Spawning behaviour likely did not affect food consumption of goby during the experiment as only males stop feeding when guarding nests (Corkum et al., 1998), and nests were not present in the aquaria.

### Experimental setup

The experiment was conducted in thirty-three 50 l aquaria (bottom surface area 0.11 $m^2$) in a temperature-controlled room (21°C). The bottom of each aquarium was covered with a 30 mm layer of sand and filled with 40 l of seawater. An empty medium-sized flower pot ($r_{\mathrm{bottom}} = 50$ mm, $r_{\mathrm{top}} = 35$ mm, $h = 100$ mm) and a plastic plant (external surface area 0.06 $m^2$), together with an aerator tube were placed in each aquarium. Sand and seawater were collected adjacent to the experimental site. In order to remove excessive animal and plant material, sand was sundried for 3 days and then sieved through a 1 mm mesh net prior to the experiment. Light intensity (17:7 h L:D) and photoperiod were similar to the local ambient environment in August.

The design of the experiment follows the suggestions of Underwood & Clarke (2005) and subsequent amendments by others (Manly, 2006; Underwood & Clarke, 2006, 2007; Taplin, 2007). As our aim was to determine the feeding rates of the round goby under conditions resembling the field values, the studied prey taxa had different initial densities (Table 1). The design included two stages for prey preference calculations (Table 1): each prey taxon separately at high density conditions (hereafter no choice high density) and all prey taxa together at low density conditions (hereafter choice). Prey preference is indicated when the relative consumption of prey taxon is significantly

**Table 1** Counts of prey taxa used in different experimental treatments in a 40 l aquarium: 1–5 no choice high density (stage 1), 6 choice (stage 2), and 7–11 no choice low density (stage 3)

| Stage | 1 | 1 | 1 | 1 | 1 | 2 | 3 | 3 | 3 | 3 | 3 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Treatment no | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
| Taxon* | | | | | | | | | | | |
| *M. trossulus* total | **124** | | | | | **40** | **40** | | | | |
| Small ($3 \leq \cdots \leq 12$) | 79 | | | | | 24 | 24 | | | | |
| Medium ($12 \leq \cdots \leq 20$) | 39 | | | | | 12 | 12 | | | | |
| Large ($20 \leq \cdots \leq 30$) | 6 | | | | | 4 | 4 | | | | |
| *M. balthica* total | | **110** | | | | **24** | | **24** | | | |
| Small ($3 \leq \cdots \leq 7$) | | 39 | | | | 15 | | 15 | | | |
| Medium ($7 \leq \cdots \leq 12$) | | 65 | | | | 7 | | 7 | | | |
| Large ($12 \leq \cdots \leq 16$) | | 6 | | | | 2 | | 2 | | | |
| *C. glaucum* ($7 \leq \cdots \leq 12$) | | | **90** | | | **5** | | | **5** | | |
| *T. fluviatilis* ($5 \leq \cdots \leq 7$) | | | | **90** | | **25** | | | | **25** | |
| *Gammarus* spp. ($5 \leq \cdots \leq 8$) | | | | | **90** | **30** | | | | | **30** |
| No of replicates | 4 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 |

Each treatment used different 40 l aquaria. Numbers in brackets represent the total length (TL) of individuals in mm. Half of the replicates for all treatments were conducted during the first run and half during the second run

* Bivalves *Mytilus trossulus*, *Macoma balthica*, *Cerastoderma glaucum*, gastropod *Theodoxus fluviatilis* and amphipods *Gammarus* spp

** Numbers in bold represent total counts per taxon

higher in choice conditions compared to no choice high density conditions. We also included a third stage with all prey taxa provided separately and at low density (hereafter no choice low density). When combined with no choice high density (Stage 1), Stage 3 allowed us to assess if the predation of round goby depends on the density of its prey.

A combination of 5 taxa and 3 stages resulted in 11 different treatments (Table 1): no choice high density (altogether 5 treatments, one for each taxon), choice (1 treatment including all taxa), and no choice low density (altogether 5 treatments, one for each taxon). All treatments were replicated 6 times. As an exception, the *M. trossulus* treatment under no choice high density had only 4 replicates. A separate one-way permutational ANOVA analysis showed that the size of the fish did not significantly differ among experimental treatments ($F_{10,53} = 1.658$; $P = 0.1158$).

Most aquaria were used twice. Half of the replicate aquaria of each treatment (see also section above and Table 1) were used in the first run (3 replicates × 11 treatments = 33) and the other half were used in the second run (31). One round goby was used per aquarium. Before the second run, fish specimens were randomly reassigned to aquaria and no goby was used for the same treatment twice. The two runs were conducted 24 h apart. Before the second run the aquaria were set up with new seawater, sediment, plastic plant, flower pot and prey species.

The experiment was run for 16 h from 10 pm until 2 pm, allowing the fish to forage during total darkness and at dawn, a period when round goby typically feed (Karlson et al., 2007 and references therein). In addition, five control aquaria without the round goby were established; in all five aquaria all the prey animals were retrieved alive after the experiment.

## Post experimental invertebrate and fish handling

After the experiment, the round goby's total length was measured to the nearest 0.01 mm and sex was determined through the shape of the urogenital papilla (Charlebois et al., 1997). Sediment with invertebrates was kept in a freezer at −20°C and the remaining prey animals were separated under a binocular microscope from the sediment in the laboratory. Invertebrates were determined to a species level, counted, and their dry weight (dw) was measured to the nearest 0.0001 g after 48 h in a 60°C drying oven. All prey individuals were measured before and after the experiment with an electronic calliper to the nearest 0.01 mm. An additional 20 prey individuals for each taxon and size class served as control to obtain the taxon-specific length-weight relationships and these regression equations were used to calculate the dry weights of consumed prey individuals.

## Data analyses

### *Statistical model*

Permutational tests for factorial ANOVA/ANCOVA design were used in order to compare absolute prey consumption, to assess prey preferences and to investigate size-specific predation of bivalves among the studied factors and treatment levels as well as to assess if predation by the round goby is density dependent (see below sections). Permutational ANOVA/ANCOVA does not assume the data to have any specific distributions. In order to investigate differences between treatment levels, pair-wise comparisons among all pairs of levels of a given factors of interest were obtained by using pseudo-t statistic, a multivariate analogue of the univariate-t statistic. Package Vegan (Oksanen et al., 2015) in the R environment was used for the analyses and all analyses were based on Euclidean distances of the original raw data.

We initially assumed that fish size had significant effects on various metrics of prey consumption and therefore our initial statistical design involved permutational ANCOVA analyses (covariate: fish total length). However, as the effect of the covariate was not statistically significant in any of the statistical tests (all $P > 0.20$), permutational ANOVA analyses without covariate were run and thereby only these results are reported below.

### *Prey taxa preference*

Permutational ANOVA/ANCOVA analyses were used to investigate prey preferences by the round goby. Dependent variables were the relative consumptions of prey in count and in biomass, with prey taxa (*M. trossulus*, *M. balthica*, *C. glaucum*, *T. fluviatilis* and *Gammarus* spp.) and choice (no choice high density, choice) as factors. Relative consumptions were calculated according to Taplin (2007):

$$p_i = a_i \div \sum_{i=1}^{k} a \quad \text{and} \quad q_i = b_i \div \sum_{i=1}^{k} b,$$

where $p_i$ is the ratio of consumptions of each prey taxon ($i = 1, \ldots, 5$) in no choice high density stage ($a_i$) to total prey consumption in no choice high density stage; and $q_i$ is the ratio of consumptions of each prey taxon ($i = 1, \ldots, 5$) in the choice stage ($b_i$) to total prey consumption in choice stage. In choice conditions, a taxon's relative consumption was calculated on the basis of one aquarium (replicated 6 times).Since in no choice high density conditions all species were offered separately, relative consumption was calculated on a basis of randomly assigned groups of all 5 taxa (replicated 6 times).

### *Size-specific consumption*

Permutational ANOVA/ANCOVA analyses were used to investigate size-specific predation of bivalves by the round goby with prey availability (no choice low density, no choice high density and choice) and size (small, medium, large) as factors. The dependent variables included consumed relative count and relative biomass of each of the common bivalves (*M. trossulus* or *M. balthica*). The relative consumption refers to the proportions of consumed prey size to the availability of prey in the same size. Calculations were done for each prey taxon size in no choice low density, no choice high density and choice stage.

### *Density-dependent predation*

Permutational ANOVA/ANCOVA analyses were used to assess if predation by the round goby depends on prey density. In this analysis factors included prey density (no choice low density, no choice high density) and taxa (*M. balthica*, *M. trossulus*, *C. glaucum*, *Gammarus* spp., *T. fluviatilis*). The dependent variables were absolute and relative consumption of either count or biomass of prey. The relative consumption refers to the proportions of consumed prey taxon to the availability of the same prey taxon. Calculations were done for each prey taxon in no choice low density and no choice high density stage.

## Results

The round goby consumed all bivalve species (*M. trossulus*, *M. balthica*, *C. glaucum*) and *Gammarus* spp. The gastropod *T. fluviatilis* was generally avoided with their relative consumption by count remaining below 3%. During the 16 h experimental period, each round goby consumed on average 0.99 ± 0.22 g dw when mixed diet was available and 2.28 ± 0.81 g dw when a single taxon at high density was available.

### Prey taxa preference

The round goby showed no preference towards any of the studied taxa, since relative consumptions of each prey taxon did not differ between no choice ($p_i$) and choice ($q_i$) conditions (Table 2). Although the round goby showed no prey preference towards prey taxa, there were differences in consumption between taxa, with some taxa being consumed more than others (Fig. 1; Table 2). The differences between taxa were different under no choice conditions compared to choice conditions, as reflected by the significant interaction effect (Table 2).

### Size-specific predation of bivalves

The size of bivalves affected the predation rate of round goby and the responses were species specific. There was no statistical evidence of size selection in the relative consumption of *M. balthica* in count between no choice high density, no choice low density or choice stages or within stages (Table 2). In contrast, round goby consumed more small-sized *M. trossulus* over medium-

**Table 2** Statistics from Permutational ANOVA analyses for prey consumption by the round goby

| Analysis | Dependent variable | Factors | df | *F* | *P* |
|---|---|---|---|---|---|
| Prey taxa preference | | | | | |
| | Relative count | Choice | 1, 50 | 0.01 | 0.91 |
| | | Taxon | 4, 50 | 18.85 | **0.001** |
| | | Choice × taxon | 4, 50 | 6.82 | **0.001** |
| | Relative biomass | Choice | 1, 50 | 0.001 | 0.99 |
| | | Taxon | 4, 50 | 30.71 | **0.001** |
| | | Choice × taxon | 4, 50 | 9.52 | **0.001** |
| Size-specific predation of bivalves | | | | | |
| | Relative count of *M. balthica* | Prey availability | 2, 45 | 0.70 | 0.47 |
| | | Prey size | 2, 45 | 1.53 | 0.23 |
| | | Prey availability × density | 4, 45 | 0.50 | 0.77 |
| | Relative count of *M. trossulus* | Prey availability | 2, 39 | 0.75 | 0.51 |
| | | Prey size | 2, 39 | 19.12 | **0.001** |
| | | Prey availability × density | 4, 39 | 1.13 | 0.37 |
| Density-dependent predation | | | | | |
| | Absolute count | Prey density | 1, 48 | 39.40 | **0.001** |
| | | Prey taxon | 4, 48 | 10.16 | **0.001** |
| | | Density × taxon | 4, 48 | 3.89 | **0.01** |
| | Absolute biomass | Prey density | 1, 48 | 68.15 | **0.001** |
| | | Prey taxon | 4, 48 | 22.27 | **0.001** |
| | | Density × taxon | 4, 48 | 16.63 | **0.001** |
| | Relative count | Prey density | 1, 48 | 0.11 | 0.76 |
| | | Prey taxon | 4, 48 | 12.16 | **0.001** |
| | | Density × taxon | 4, 48 | 0.69 | 0.63 |
| | Relative biomass | Prey density | 1, 48 | 0.29 | 0.62 |
| | | Prey taxon | 4, 48 | 17.49 | **0.001** |
| | | Density × taxon | 4, 48 | 2.03 | 0.10 |

* Numbers in bold represent statistically significant *p*-values

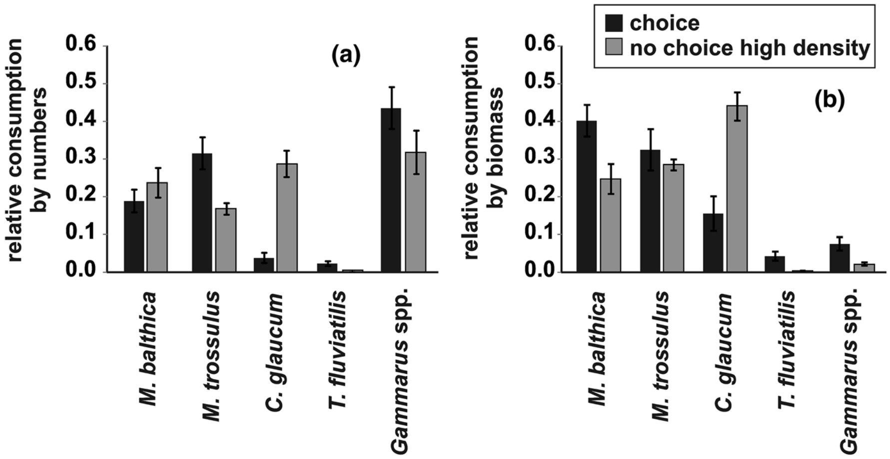

**Fig. 1** The relative consumption of five prey taxa by the round goby in terms of prey numbers (**a**) and biomass (**b**) (g during 16 h) (mean ± SE). Relative consumption refers the ratio of consumption of each prey taxon in no choice high density stage (or choice stage) to total prey consumption in no choice high density stage (or choice stage) (Taplin, 2007). In general, each treatment was replicated 6 times

sized *M. trossulus* in relative count under choice conditions ($P = 0.006$) and more than large-sized *M. trossulus* under no choice low density conditions ($P = 0.007$) and choice conditions ($P = 0.006$) (Table 2).

## Density-dependent predation

The round goby exhibited density-dependent consumption on the investigated prey taxa. In general, the absolute consumption of each prey group increased with increased prey density (Fig. 2). The absolute consumption in both count and biomass depended on prey density, prey taxon and the interaction between prey taxon and density (Table 2). Doubling of prey density led to an average twofold increase in the feeding rate for the three bivalve species and an average 1.5 times increase for *Gammarus* spp. No such patterns were observed for the relative consumption (Fig. 1). The relative consumption both in count and in biomass depended only on prey taxon (Table 2).

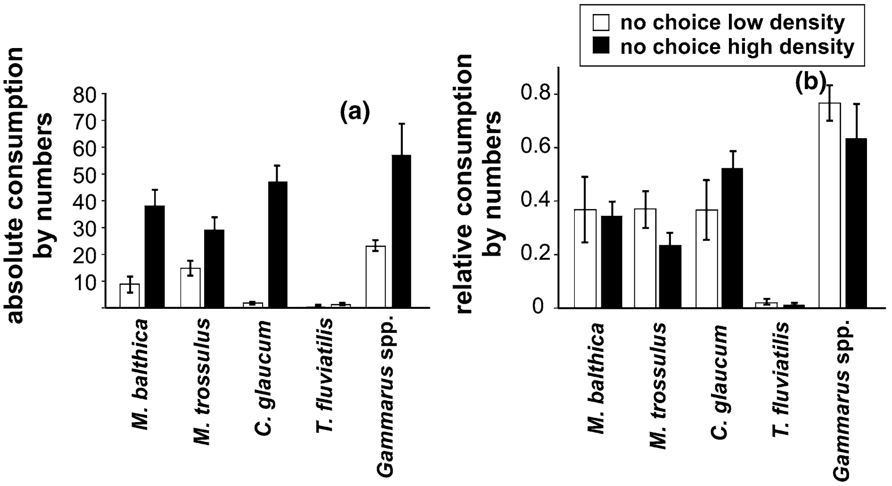

**Fig. 2** Absolute (**a**) or relative (**b**) consumption of five prey taxa by the round goby (mean ± SE) in terms of count (ind per 16 h) of prey. The relative consumption refers to the proportions of consumed prey taxon to the availability of the same prey taxon in the same aquarium (compared to Fig. 1a, where relative consumption is calculated according to Taplin, 2007). Calculations were done for each prey taxon in no choice low density and no choice high density stage. In general, each treatment was replicated 6 times

## Discussion

The key finding of the study is that the round goby does not select for any of the studied key invertebrate taxa in the north-eastern Baltic Sea. This result indicates that this invasive non-indigenous species is a generalist in its diet, as has been shown also in a previous study (Karlson et al., 2007). The round goby consumed most of the available native taxa, similar to results observed in previous studies from North America (Brandner et al., 2013). Together, these results suggest round goby is a feeding generalist, a trait that should favour successful invasion (Ribeiro et al., 2007; Brandner et al., 2013). Earlier investigations indicated the round goby preying more on some prey species than others (Barton et al., 2005). Nevertheless, in the light of the current study, this result cannot be attributed to preference, as such, but rather to the consumption of the dominant species in the benthic realm. This finding has important ecological implications, as with the removal of dominant benthic invertebrate species the round goby may switch to subdominant taxa. Such prey switching may ultimately affect a broad range of benthic communities (including their functions), unless the production of invertebrates exceeds consumption by this invasive fish species, as has been seen in some areas (Kornis et al., 2013).

Some benthic invertebrates such as the gastropod *T. fluviatilis*, that was practically not consumed, could benefit from the presence of round goby. Such protected species may increase their abundance due to declined competition for food resources and habitat. Thus, the consequence of the invasion of the round goby could be strictly context dependent, as evidenced for other non-native species in other invaded ecosystems (e.g. de Moura Queirós et al., 2011; Barrios O'Neill et al., 2014).

The Baltic Sea provides suitable abiotic and biotic conditions for the round goby (Sapota, 2004; Sokołowska & Fey, 2011; Kornis et al., 2012). Our results confirm that the round goby is a generalist feeder capable of consuming a wide spectrum of invertebrate prey, which increases its invasion potential to yet uncolonised areas in the Baltic Sea. The intraspecific aggression previously observed in round goby (Groen et al., 2012) may prevent total depletion of prey as the larger territorial goby force smaller individuals and juveniles to migrate out of good feeding/sheltering grounds (Charlebois et al., 2001).

This experimental study showed the round goby to be a very effective predator and appeared to consume diverse prey at high rates (up to 0.99 g dw per 16 h for a mixed species diet). Since consumption rates of the round goby have not previously been experimentally investigated in the Baltic Sea (Ojaveer & Kotta, 2015), comparisons can only be made with experiments from other areas. Thus, all comparisons must be interpreted with the assumption that the fish were provided with different prey amounts and species and water temperature and round goby size could be substantially different. In general the consumption rates in this study were higher than other areas. In the Laurentian Great Lakes, the bivalve *D. polymorpha* was consumed at a rate of 1 g (max 6.5) wet weight (ww) daily (Ray & Corkum, 1997) and *D. polymorpha* with amphipods up to 0.022 g shell-free dw $h^{-1}$ (corresponding to 0.62 g dw daily, according to Diggins et al., 2002; Jurkiewicz-Karnkowska, 2005). Moreover, laboratory experiments showed that the round goby consumes native clams of the Great Lakes even at lower rates (an average of 4 times less than zebra mussels) (Ghedotti et al., 1995). Taking into account smaller size of the fish in North American populations compared to the Baltic Sea (Sokołowska & Fey, 2011; Kornis et al., 2012), these published values are still considered several times lower than observed in the current experiment.

Round goby is a territorial fish with estimated home range of 5 $m^2$ (Ray & Corkum, 2001). While densities of this species are yet to be determined in the Baltic Sea, the values range from 0.3 to 9 individuals $m^{-2}$ in the Great Lakes (Ray & Corkum, 2001). If the round goby achieves similar densities in the coastal area of the Baltic Sea and prey consumption rates are similar to those observed in our experiment, then providing an average benthic biomass of 50 g dw $m^{-2}$ (Kotta et al., 2009), the round goby could deplete local benthic invertebrate communities in a very short time (within 10 days). Since benthic biomass and fish densities are patchy (Kotta et al. 2015, 2016), such depletions may be localised. In a laboratory experiment the feeding rates are expected to be significantly higher than in nature due to easier foraging for prey, reduced availability of refuges for prey, and reduced overall habitat complexity. Furthermore, in the field during breeding seasons feeding rates of round goby are likely lower due to aggression among males and nest guarding behaviour (Helfman, 1986; Ray & Corkum, 2001; Belanger & Corkum, 2003). In addition, the presence of other predatory fish may further reduce feeding activity of the round goby (Marentette & Balshine, 2012). Nevertheless, the consumed amounts are still high enough to demonstrate that the estimated predation rates of the round goby are much higher than secondary productivity by benthic invertebrates (e.g. Westerbom et al., 2002). Thus, the round goby has the potential to affect benthic communities drastically. However, such severe impacts have not yet been documented in the Baltic Sea, partly because of a lack of such impact studies (e.g. Ojaveer & Kotta, 2015) and round goby may have much lower densities with patchy distributions.

The current study indicated that the relative consumption by the round goby did not vary among the size classes of *M. balthica*; however, the relative consumption of small *M. trossulus* individuals (average 46%) was higher than medium (average 17%) or large (average 3%) individuals. In order to show true size-specific preference, additional experiments with consumption measured separately for each shell size class, are needed (Underwood & Clarke, 2005; Taplin, 2007).

The round goby also exhibited density-dependent feeding behaviour with elevated consumption rates at no choice high prey densities. Such behaviour is also common in other epibenthic species (Mansour & Lipcius, 1991). The density-dependent functional response could be a result of longer foraging time at low prey densities (MacArthur & Pianka, 1966) in which less prey are handled per unit time compared to high prey densities. Alternatively, low abundance allowed mobile prey species to find shelter, as availability of shelter in boulders or gravel has shown to decrease the consumption rates of amphipods by predators even with low availability of shelter (Diehl, 1992; Diggins et al., 2002). Although the absolute consumptions of prey taxa were higher at high prey density, the relative consumptions were similar between low and high prey density levels. Higher absolute consumption shows that the more there is, the more is eaten. The relative consumption rates, however, suggest similar impacts of the round goby to community structure. In field foraging animals are expected to distribute themselves among patches of prey of varying density in a way that the average foraging success for predators is equal in all patches (Kacelnik et al., 1992).

In conclusion, our study suggests that the round goby is capable of severely impacting native benthic invertebrate populations and thereby causing multiple impacts in the coastal ecosystems of the Baltic Sea. A generalist feeding strategy, coupled with exceptionally high consumption rates may result in the increase of the round goby population until significant reductions in the abundance of prey populations take place. Intraspecific competition for food and habitat, multiple physical disturbances and predation by native fish may potentially stabilise the abundance of the round goby in future. In North America, in the Lake Erie burbot *Lotalota* (Linnaeus, 1758) likely controls the abundance of the round goby (Madenjian et al., 2011). To date, however, in the Estonian coastal range (and potentially elsewhere in the Baltic Sea) local predatory fish (perch *Perca fluviatilis* Linnaeus, 1758, zander *Sander lucioperca* (Linnaeus, 1758), northern pike *Esoxlucius* Linnaeus, 1758) have not yet been shown to significantly reduce the round goby population (database of the Estonian Marine Institute).

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## Compliance with Ethical Standards

**Animal rights** Estonian Ethics Commission granted approval (Permission Nr 35/2014) for the use of animals in the research.

## References

Andraso, G. M., M. T. Ganger & J. Adamczyk, 2011. Size-selective predation by round gobies (*Neogobius melanostomus*) on dreissenid mussels in the field. Journal of Great Lakes Research 37: 298–304.

Azour, F., 2011. Fødebiologi hos den sortmundede kutling *Neogobius melanostomus* i danske farvande. http://fiskeatlas.ku.dk/billeder/Sortmundet_kutlings_f_debiologi_i_DK.pdf.

Barrios O'Neill, D., J. T. A. Dick, A. Ricciardi, H. J. MacIsaac & M. C. Emmerson, 2014. Deep impact: in situ functional responses reveal context-dependent interactions between vertically migrating invasive and native mesopredators and shared prey. Freshwater Biology 59: 2194–2203.

Barton, D. R., R. A. Johnson, L. Campbell, J. Petruniak & M. Patterson, 2005. Effects of round gobies (*Neogobius* *melanostomus*) on dreissenid mussels and other invertebrates in Eastern Lake Erie, 2002–2004. Journal of Great Lakes Research 31: 252–261.

Bax, N., A. Williamson, M. Aguero, E. Gonzalez & W. Geeves, 2003. Marine invasive alien species: a threat to global biodiversity. Marine Policy 27: 313–323.

Belanger, R. M. & L. D. Corkum, 2003. Susceptibility of tethered round gobies (*Neogobius melanostomus*) to predation in habitats with and without shelters. Journal of Great Lakes Research 29: 588–593.

Brandner, J., J. Pander, M. Mueller, A. F. Cerwenka & J. Geist, 2013. Effects of sampling techniques on population assessment of invasive round goby *Neogobius melanostomus*. Journal of Fish Biology 82: 2063–2079.

Carman, S. M., J. Janssen, D. J. Jude & M. B. Berg, 2006. Diel interactions between prey behaviour and feeding in an invasive fish, the round goby, in a North American river. Freshwater Biology 51: 742–755.

Charlebois, P. M., J. E. Marsden, R. G. Goettel, R. K. Wolfe, D. J. Jude & S. Rudnika, 1997. The Round Goby, *Neogobius melanostomus* (Pallas), A Review of European and North American Literature. Illinois-Indiana Sea Grant Program and Illinois Natural History Survey, Zion.

Charlebois, P. M., L. D. Corkum, D. J. Jude & C. Knight, 2001. The round goby (*Neogobius melanostomus*) invasion: current research and future needs. Journal of Great Lakes Research 27: 263–266.

Corkum, L. D., A. J. Macinnis & R. G. Wickett, 1998. Reproductive habits of round gobies. Great Lakes Research Review 3: 13–20.

Corkum, L. D., M. R. Sapota & K. E. Skora, 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. Biological Invasions 6: 173–181.

De Moura Queirós, A., J. G. Hiddink, G. Johnson, H. N. Cabral & M. J. Kaiser, 2011. Context dependence of marine ecosystem engineer invasion impacts on benthic ecosystem functioning. Biological Invasions 13: 1059–1075.

Diehl, S., 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. Ecology 73: 1646–1661.

Diggins, T. P., J. Kaur, R. K. Chakraborti & J. V. DePinto, 2002. Diet choice by the exotic round goby (*Neogobius melanostomus*) as influenced by prey motility and environmental complexity. Journal of Great Lakes Research 28: 411–420.

Ghedotti, M. J., J. C. Smihula & G. R. Smith, 1995. Zebra mussel predation by round gobies in the laboratory. Journal of Great Lakes Research 21: 665–669.

Groen, M., N. M. Sopinka, J. R. Marentette, A. R. Reddon, J. W. Brownscombe, M. G. Fox, S. E. Marsh-Rollo & S. Balshine, 2012. Is there a role for aggression in round goby invasion fronts? Behaviour 149: 685–703.

Helfman, G. S., 1986. Fish behaviour by day, night and twilight. In Pitcher, T. J. (ed.), The Behaviour of Teleost Fishes. Springer, US: 366–387.

Jurkiewicz-Karnkowska, E., 2005. Some aspects of nitrogen, carbon and calcium accumulation in molluscs from the Zegrzynski reservoir ecosystem. Polish Journal of Environmental Studies 14: 173–177.

Järv, L., J. Kotta, I. Kotta & T. Raid, 2011. Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem. Annales Zoologici Fennici 48: 129–141.

Kacelnik, A., J. R. Krebs & C. Bernstein, 1992. The ideal free distribution and predator-prey populations. Trends in Ecology & Evolution 7: 50–55.

Karlson, A. M. L., G. Almqvist, K. E. Skóra & M. Appelberg, 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. ICES Journal of Marine Science 64: 479–486.

Kautsky, N., 1981. On the trophic role of the blue mussel (*Mytilus edulis* L.) in the Baltic coastal ecosystem and the fate of the organic matter produced by the mussels. Kieler Meeresforsch 5: 454–461.

Kornis, M. S. & M. J. Vander Zanden, 2010. Forecasting the distribution of the invasive round goby (*Neogobius melanostomus*) in Wisconsin tributaries to Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 67: 553–562.

Kornis, M. S., N. Mercado-Silva & M. J. Vander Zanden, 2012. Twenty years of invasion: A review of round goby *Neogobius melanostomus* biology, spread and ecological implications. Journal of Fish Biology 80: 235–285.

Kornis, M. S., S. Sharma & M. J. Vander Zanden, 2013. Invasion success and impact of an invasive fish, round goby, in Great Lakes tributaries. Diversity and Distributions 19: 184–198.

Kotta, J., V. Lauringson, G. Martin, M. Simm, I. Kotta, K. Herkül & H. Ojaveer, 2008. Gulf of Riga and Pärnu Bay. In Schiewer, U. (ed.), Ecology of Baltic Coastal Waters. Springer, Belin: 217–243.

Kotta, J., I. Kotta, M. Simm & M. Põllupüü, 2009. Separate and interactive effects of eutrophication and climate variables on the ecosystem elements of the Gulf of Riga. Estuarine, Coastal and Shelf Science 84: 509–518.

Kotta, J., K. Oganjan, V. Lauringson, M. Pärnoja, A. Kaasik, L. Rohtla, I. Kotta & H. Orav-Kotta, 2015. Establishing functional relationships between abiotic environment, macrophyte coverage, resource gradients and the distribution of *Mytilus trossulus* in a brackish non-tidal environment. PLoS ONE 10: e0136949.

Kotta, J., K. Nurkse, R. Puntila & H. Ojaveer, 2016. Shipping and natural environmental conditions determine the distribution of the invasive non-indigenous round goby *Neogobius melanostomus* in a regional sea. Estuarine Coastal and Shelf Science 169: 15–24.

Lauringson, V. & J. Kotta, 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. Hydrobiologia 554: 97–105.

Laxson, C. L., K. N. McPhedran, J. C. Makarewicz, I. Telesh & H. J. Macisaac, 2003. Effects of the non-indigenous cladoceran Cercopagis pengoi on the lower food web of Lake Ontario. Freshwater Biology 48: 2094–2106.

Lederer, A. M., J. Janssen, T. Reed & A. Wolf, 2008. Impacts of the introduced round goby (*Apollonia melanostoma*) on Dreissenids (*Dreissena polymorpha and bugensis*) and on macroinvertebrate community between 2003 and 2006 in the littoral zone of Green Bay, Lake Michigan. Journal of Great Lakes Research 34: 690–697.

Leppäkoski, E. & S. Olenin, 2000. Non-native species and rates of spread: lessons from the brackish Baltic Sea. Biological Invasions 2: 151–163.

MacArthur, R. H. & E. R. Pianka, 1966. On optimal use of a patchy environment. American Naturalist 100: 603–609.

Manly, B. F. J., 2006. On a proposed method for analysing experiments on food choice. Journal of Experimental Marine Biology and Ecology 335: 154–155.

Madenjian, C. P., M. A. Stapanian, L. D. Witzel, D. W. Einhouse, S. A. Pothoven & H. L. Whitford, 2011. Evidence for predatory control of the invasive round goby. Biological Invasions 13: 987–1002.

Mansour, R. A. & R. N. Lipcius, 1991. Density-dependent foraging and mutual interference in blue crabs preying upon infaunal clams. Marine Ecology Progress Series 72: 239–246.

Marentette, J. R. & S. Balshine, 2012. Altered prey responses in round goby from contaminated sites. Ethology 118: 1–9.

Martin, G., J. Kotta, T. Möller & K. Herkül, 2013. Spatial distribution of marine benthic habitats in the Estonian coastal sea, northeastern Baltic Sea. Estonian Journal of Ecology 62: 165–191.

Norling, P. & N. Kautsky, 2008. Patches of the mussel *Mytilus* sp. are islands of high biodiversity in subtidal sediment habitats in the Baltic Sea. Aquatic Biology 4: 75–87.

Ojaveer, H., A. Jaanus, B. R. Mackenzie, G. Martin, S. Olenin, T. Radziejewska, I. Telesh, M. L. Zettler & A. Zaiko, 2010. Status of biodiversity in the Baltic Sea. PLoS One 5: e12467.

Ojaveer, H. & J. Kotta, 2015. Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. Hydrobiologia 750: 171–185.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, H. Wagner, 2015. Package 'vegan'. Community ecology package, version 2-2.

Olenin, S. & E. Leppäkoski, 1999. Non-native animals in the Baltic Sea: alteration of benthic habitats in coastal inlets and lagoons. Hydrobiologia 393: 233–243.

Post, J. R. & D. Cucin, 1984. Changes in the benthic community of a small precambrian lake following the introduction of yellow perch (*Perca flavescens*). Canadian Journal of Fisheries and Aquatic Sciences 41: 1496–1501.

Raby, G. D., L. F. G. Gutowsky & M. G. Fox, 2010. Diet composition and consumption rate in round goby (*Neogobius melanostomus*) in its expansion phase in the Trent River, Ontario. Environmental Biology of Fishes 89: 143–150.

Rakauskas, V., Ž. Pūtys, J. Dainys, J. Lesutienė, L. Ložpys & K. Arbačiauskas, 2013. Increasing population of the invader round goby, *Neogobius melanostomus* (Actinopterygii: Perciformes: Gobiidae), and its trophic role in the Curonian Lagoon, SE Baltic Sea. Acta Ichthyologica Et Piscatoria 43: 95–108.

Ray, W. J. & L. D. Corkum, 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. Environmental Biology of Fishes 50: 267–273.

Ray, W. J. & L. D. Corkum, 2001. Habitat and site affinity of the round goby. Journal of Great Lakes Research 27: 329–334.

Ribeiro, F., R. L. Orjuela, M. F. Magalhães & M. J. Collares-Pereira, 2007. Variability in feeding ecology of a South American cichlid: a reason for successful invasion in mediterranean-type rivers? Ecology of Freshwater Fish 16: 559–569.

Sapota, M. R., 2004. The round goby (*Neogobius melanostomus*) in the Gulf of Gdansk – a species introduction into the Baltic Sea. Hydrobiologia 514: 219–224.

Schreiber, S. J., 1997. Generalist and specialist predators that mediate permanence in ecological communities. Journal of Mathematical Biology 36: 133–148.

Skazhkina, E. P. & V. A. Kostyuchenko, 1968. Food of *N. melanostomus* in the Azov Sea. Voprosy Ikhtiologiy 8: 303–311. (in Russian).

Skora, K. E. & J. Rzeznik, 2001. Observations on diet composition of *Neogobius melanostomus* Pallas 1811 (Gobiidae, Pisces) in the Gulf of Gdansk (Baltic Sea). Journal of Great Lakes Research 27: 290–299.

Sokołowska, E. & D. P. Fey, 2011. Age and growth of the round goby *Neogobius melanostomus* in the Gulf of Gdańsk several years after invasion. Is the Baltic Sea a new promised land? Journal of Fish Biology 78: 1993–2009.

Strayer, D. L., V. T. Eviner, J. M. Jeschke & M. L. Pace, 2006. Understanding the long-term effects of species invasions. Trends in Ecology and Evolution 21: 645–651.

Taplin, R. H., 2007. Experimental design and analysis to investigate predator preferences for prey. Journal of Experimental Marine Biology and Ecology 344: 116–122.

Underwood, A. J. & K. R. Clarke, 2005. Solving some statistical problems in analyses of experiments on choices of food and on associations with habitat. Journal of Experimental Marine Biology and Ecology 318: 227–237.

Underwood, A. J. & K. R. Clarke, 2006. Response on a proposed method for analysing experiments on food choice. Journal of Experimental Marine Biology and Ecology 335: 151–153.

Underwood, A. J. & K. R. Clarke, 2007. More response on a proposed method for analysing experiments on food choice. Journal of Experimental Marine Biology and Ecology 344: 113–115.

Underwood, A. J., M. G. Chapman & T. P. Crowe, 2004. Identifying and understanding ecological preferences for habitat or prey. Journal of Experimental Marine Biology and Ecology 300: 161–187.

Veber, T., J. Kotta, V. Lauringson & I. Kotta, 2009. Influence of the local abiotic environment, weather and regional nutrient loading on macrobenthic invertebrate feeding groups in a shallow brackish water ecosystem. Oceanologia 51: 541–559.

Volterra, V., 1928. Variations and fluctuations of the number of individuals in animal species living together. Journal du Conseil International pour l'Exploration de la Mer 3: 3–51.

Westerbom, M., M. Kilpi & O. Mustonen, 2002. Blue mussels, *Mytilus edulis*, at the edge of the range: population structure, growth and biomass along a salinity gradient in the north-eastern Baltic Sea. Marine Biology 140: 991–999.

Zavaleta, E. S., R. J. Hobbs & H. A. Mooney, 2001. Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology and Evolution 16: 454–459.