*Ann. Zool. Fennici* 48: 129–141 ISSN 0003-455X (print), ISSN 1797-2450 (online)
Helsinki 30 June 2011

# Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem

Leili Järv*, Jonne Kotta, Ilmar Kotta & Tiit Raid

*Estonian Marine Institute, University of Tartu, Mäealuse 14, EE-12618 Tallinn, Estonia (*corresponding author's e-mail: leili.jarv@gmail.com)*

*Received 14 Dec. 2010, revised version received 16 Feb. 2011, accepted 15 Feb. 2011*

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

To date the studies that link community structure of benthic invertebrates with fish feeding are rare as well as factors that are behind this feeding selectivity are poorly known. In this study, we related invertebrate species composition, their dominance structure and fish biological characteristics to the feeding selectivity and overlap of the native flounder, perch and the invasive round goby in Muuga Bay, the Baltic Sea. Species composition and proportion of benthic invertebrates in the diet of fishes differed from what was available in the field. Except for the round goby, the studied fishes preferred small and mobile invertebrates over large bivalves. However, diet of the studied species, namely the round goby and flounder overlapped. Besides, perch preyed on young stages of the round goby indicating that the introduction of round goby may negatively affect flounder but positively perch.

## Introduction

The feeding ecology of fish stands on the two key concepts: Lindeman trophodynamic views (Lindeman 1942) and optimal foraging theory (MacArthur & Pianka 1966). Lindeman's trophodynamic model of ecosystem productivity and energy transfer is the predominant conceptual framework that is used to predict the selectivity and transfer efficiencies of lower trophic levels to fuel the production of consumers. According to the model, the spatial and temporal variability of availability of prey species determines the fluxes of energy/carbon in food webs. Optimal foraging theory, in turn, states that organisms forage in such a way as to maximize their energy intake per unit time. In other words, organisms are expected to consume food containing the most calories while expending the least amount of time possible in doing so. Thus, prey species are central to both of these models and therefore the generic understanding of fish roles in the ecosystem should be based on statistical relationships between availability of prey species and fish feeding.

The coastal environment of the northern Baltic Sea is characterised by diverse benthic habitats that host many fishes of marine, brackish and fresh water origin. Bottom-feeding fishes prevail in the area. Although benthic invertebrates communities have small number of species (Kotta *et al.* 2008b, 2008c), biomass of invertebrates is high (Kotta *et al*. 2007, Kotta *et al*. 2008a) and therefore they provide important source of nutrients to coastal fishes (Ojaveer *et al*. 1999, Kotta *et al*. 2009).

Little is known about how fish feeding relates to benthic invertebrate communities in the Baltic Sea ecosystem. Earlier studies demonstrated that food supply is known to affect the species composition and distribution of fishes (Lappalainen *et al*. 2000), and availability of benthic invertebrates is expected to determine fish diet (Lappalainen *et al*. 2004). The gut contents analyses showed that the most important and common food of fishes in the northern Baltic Sea were different bivalve, gastropod and amphipod species but also insect larvae (Thorman & Wiederholm 1983, Złoch *et al*. 2005, Kotta *et al*. 2008b). Fish feeding is known to vary spatially and temporally and is dependent on their growth in length and age (Karås 1987, Licandeo *et al*. 2006), seasonal changes in temperature (Palomares & Pauly 1998), oxygen (Pihl *et al*. 1992), light (Dabrowski 1982), and fish morphology (Karlson *et al*. 2007). We are not aware of experimental studies that connect fish feeding to their sex and/or maturity stage. There is some circumstantial evidence, though, that sex and reproductive status may largely influence feeding behaviour of fish (Lall & Tibbetts 2009). During their ontogenesis fish species often undergo niche shifts involving habitat use and diet (Bergman & Greenberg 1994). Such distribution patterns and behavioural shifts may be gender-specific (Helfman 1983, Gillanders 1995). In addition, fishes invest energy towards reproduction but this investment likely varies among sexes. Hence, it becomes important to collect dietary information across a range of maturity stages and between sexes. Moreover, earlier studies did not quantifiy in a single framework the links between benthic invertebrate communities and fish diet as well as how fish biological characteristics (including fish maturity and sex) modulate these relationships.

Recently, a new fish species, the round goby (*Neogobius melanostomus*) has been recorded in the northern Baltic Sea. The round goby was first sighted in the region in the Gulf of Riga in 2002 (Ojaveer 2006). Since then the species has dispersed into the Gulf of Finland where it has formed a self-reproducing population, increased its abundance and colonised new areas. Earlier studies indicated strong competition for space and food among coastal fish communities and invasive species (Kostrzewa & Grabowski 2003, Copp *et al*. 2005). The round goby is known to have a broad dietary range and therefore it may potentially compete with many native species including flounder and perch. There have been some reports of bioinvasions into the northern Baltic Sea involving direct aggression on benthic organisms and/or competition for food and space (Kotta *et al*. 2001, Kotta & Ólafsson 2003, Kotta *et al*. 2006, Orav-Kotta *et al*. 2009). However, we are aware of only one study, where the selectivity of the two most important food items, *Macoma balthica* and *Mytilus trossulus,* of round goby and flounder from the experimental/laboratory data were compared (Karlson *et al*. 2007) but there are no reports on selectivity of those species in field conditions.

In this study, we described the relationships between the biomass dominance structure of benthic invertebrate communities, fish biological characteristics, the feeding selectivity and dietary overlap of bottom dwelling fishes — flounder, perch and round goby — in Muuga Bay (Gulf of Finland). Our hypotheses were as follows: (1) Biomass structure of benthic invertebrates largely determines the variability of fish diet but fish species and size modulate the invertebrate–diet relationship. (2) Due to different habitat use and/or varying energy requirements fish diet also varies among different sexes and maturity classes.

## Material and methods

### Study area

Muuga Bay is located in the central part of the southern coast of the Gulf of Finland, northern Baltic Sea (Fig. 1). Muuga Bay has low water salinity (7–8 PSU) and good water exchange with the open Gulf of Finland. The bottom deposits of the bay include mostly gravel sand and silty sand. The benthic vegetation of Muuga Bay is poorly developed and mainly characterised by ephemeral algae. Perennial macroalgae

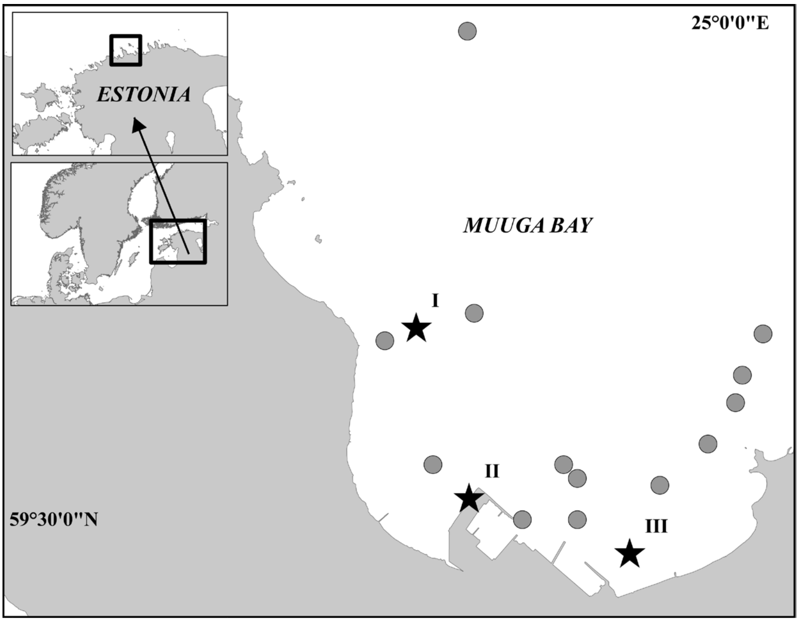

**Fig. 1.** Sampling stations of benthic invertebrate communities (filled circles) and fishes (stars) in Muuga Bay.

and higher plants can be occasionally found in the western parts of the bay. Benthic invertebrate communities have low diversity but the biomasses are often high (Kotta *et al*. 2008a).

## Test organisms

Flounder (*Platichtys flesus*) and perch (*Perca fluviatilis*) are the dominant fish species in Muuga Bay. Besides the native species, the round goby (*Neogobius melanostomus*) is a recent ballast water immigrant and exponentially expands its distribution in the area. Flounder is a widely distributed marine species forming a large number of subspecies. The Baltic Sea is populated by *P. f. trachurus* which has a number of geographical and biological groups. Flounder inhabits mainly sandy or clayey bottoms, younger individuals at smaller depths than older ones. During ontogenesis the food composition of flounder changes considerably. Larvae feed mostly on phytoplankton and different stages of copepods. At the length of 2–3 cm flounder starts consuming benthos and their food markedly differs among areas (Weatherley 1989). Juveniles gradually transfer to the food of adult fish i.e. polychaetes, bivalves, gastropods and even small fish (Vinagre *et al*. 2008).

Perch is widely distributed in fresh- and brackish coastal waters preferring shallow, sheltered and heterogeneous habitats rich in macrophytes. Perch is a voracious feeder. Young perch feeds mainly on plankton but also on mysids, gammarids, bivalves, gastropods and small fishes (Pihu *et al*. 2003). At certain length perch switches on feeding mainly on fishes but they still continue to feed on plankton and benthic invertebrates. Perch also preys on the eggs of other fishes (Roots *et al*. 2004).

Round goby originates from the Ponto-Caspian region and is one of the well-known invasive species in the Baltic Sea (Ruiz *et al*. 1997). The species prefers shallow sandy, gravelly or rocky bottoms with moderate aquatic vegetations. The round goby was observed for the first time in the Estonian waters in 2002. Since 2004 the species is a common inhabitant in Muuga Bay where it has formed a healthy and further expanding population. The round goby has an aggressive feeding behaviour and feeds mainly on molluscs, smaller fish and fish eggs (Ojaveer 2006).

## Sampling and laboratory analyses

Benthic invertebrates were sampled at 13 sampling stations in Muuga Bay in July, August and

September 2008 (Fig. 1). Sampling was done with an Ekman type bottom grab (0.02 $m^2$) and one sample was collected from each station. The samples were sieved in the field through 0.25 mm mesh screens. The residuals were stored in a deep freezer at –20 °C and subsequent sorting, counting and determination of invertebrate species were performed in the laboratory using a stereomicroscope. All species were determined to the species level except for oligochaetes, insect larvae and juveniles of gammarid amphipods. The dry weight of species was obtained after drying the individuals at 60 °C during 48 hours. For the bivalves shell and shell free weights were determined.

Fish sampling was carried out at three stations in July, August and in October 2008 (Fig. 1). At each station, the monitoring gill nets (1.8 × 28.7 m) with mesh sizes of 32, 44, 60, 72, 80, 92, 100 and 120 mm were used. The following parameters were measured: species composition of catches, total length (mm), gape size (maximum height of gape), weight (g), age, sex and maturity stage of all specimens of all species caught by net with given mesh size. Maturity stage was determined according to a routine six-point macroscopic maturity scale: immature (I), maturing (II–IV), running (V) and spent (VI). This classification is based on the degree of clasper calcification, and development of testes and reproductive ducts for males and on the condition of uteri, oviducal glands and ovarian follicles for females (Anon. 2007: 9–10). In addition food composition of flounder, perch and round goby were assessed. In order to determine the food composition of fishes their stomach content was fixed immediately after catching in 70% alcohol. The quantitative composition of stomach contents was determined in the laboratory using a similar procedure as above.

## Data analyses

Multivariate data analyses were performed with the statistical program "PRIMER" ver. 6.1.5 (Clarke & Gorley 2006). Prior to analyses, all distribution data were standardized by dividing biomass values of each invertebrate species by total invertebrate biomasses of the respective station. Similarly, the gut content data were standardized by dividing the biomass values of invertebrate species eaten by the total biomass of the gut content. Similarities between each pair of samples were calculated using a zero-adjusted Bray Curtis coefficient. The coefficient is known to outperform most other similarity measures and enables samples containing no organisms at all to be included (Clarke *et al*. 2006). A non-metric multidimensional scaling analysis (MDS) on macrobenthic biomasses was used to visualize the dissimilarities in the community composition of benthic invertebrates within gut of different fish species. Statistical differences in benthic invertebrate communities and fish diet were assessed by the ANOSIM permutation test (Clarke 1993). A BEST analysis (BIOENV procedure) was used to relate the fish characteristics such as species, length, weight, sex, maturity and age to the gut content of fish. The variables of fish characteristics were normalized prior to analyses. The analysis shows which fish characteristic (or combination of different characteristics) best predicts the observed feeding pattern. A Spearman rank correlation ($\rho$) was computed between the similarity matrices of fish characteristics and gut content. A global BEST match permutation test was run to examine the statistical significance of observed relationships.

In order to standardize fish feeding among species, regressions between body length and the gape size (maximum height of gape) of fishes were found (Karlson *et al*. 2007). The fit of the linear regression models was generally good (round goby: $r^2 = 0.955$, $F_{1,29} = 597.21$, $p < 0.0001$; flounder: $r^2 = 0.955$, $F_{1,29} = 597.21$, $p < 0.0001$; perch: $r^2 = 0.954$, $F_{1,27} = 589.87$, $p < 0.0001$). The relationships between body length and gape size classes is presented in Table 1.

The Manly-Chesson index $\alpha$ (Manly 1974, Chesson 1978, 1983) was calculated to evaluate prey selection. The index formula is as follows:

$$\alpha_i = \frac{r_i / p_i}{\sum_{i=1}^{m} r_i / p_i}$$

with $r_i$ = the proportion of food item i in the diet and $p_i$ = the proportion of food item $i$ in the environment, $m$ = the number of food items in the environment. The values of $\alpha$ range from 0 (complete avoidance) to 1 (complete preference). If $\alpha = 1/m$, the predator is feeding randomly and the preys are consumed in proportion to abundance in environment, whereas $\alpha > 1/m$ indicates preference and $\alpha < 1/m$ indicates avoidance. The shell-free biomass was used to calculate fish feeding selectivity and the contribution of different benthic invertebrates to fish diet.

The diet overlap between the studied species was estimated using Morisita's index ($C$) (Horn 1966, Cortés 1997):

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

where $X_i$ and $Y_i$ are the proportions of the $i$th food category in the diet of species $X$ and $Y$, respectively. The values close to zero suggest large dissimilarities in the diet, and the values close to 1 represent similar stomach contents. According to Zaret and Rand (1971), the overlap $\geq 0.6$ results in strong competitive interactions among species.

**Table 1.** Gape size classes (mm) and corresponding total lengths (mm) of round goby, flounder and perch. The defined gape size classes are as follows: small gape size ≤ 14.5 mm, medium 14.6–17.0, large > 17.0. The sample sizes are given in parentheses.

| Fish species | Gape size class | | |
|---|---|---|---|
| | Small | Medium | Large |
| Round goby | 60–120 (29) | 120.1–140 (116) | > 140 (96) |
| Flounder | 100–120 (63) | 200.1–250 (116) | > 250 (15) |
| Perch | 80–150 (81) | 150.1–200 (160) | > 200 (58) |

## Results

Altogether 26 taxa of infaunal and epifaunal invertebrates were collected from Muuga Bay (Table 2). The available benthic food resource in the area was clearly dominated by bivalves, particularly *Macoma balthica* and *Mytilus trossulus* and these species constituted 65% and 24% of

**Table 2.** Biomass of benthic invertebrate taxa (g dw. m$^{-2}$) in Muuga Bay in 2008.

| Taxa | Minimum | Average | Maximum | SD |
|---|---|---|---|---|
| *Balanus improvisus* | 0 | 1.605 | 10.098 | 0.994 |
| *Bathyporeia pilosa* | 0 | 0 | 0.002 | 0 |
| *Cerastoderma glaucum* | 0 | 1.896 | 8.641 | 0.873 |
| Chironomidae | 0 | 0.005 | 0.020 | 0.002 |
| *Corophium volutator* | 0 | 0.058 | 0.452 | 0.044 |
| *Gammarus* juv. | 0 | 0.024 | 0.177 | 0.017 |
| *Gammarus oceanicus* | 0 | 0.015 | 0.069 | 0.009 |
| *Gammarus salinus* | 0 | 0.016 | 0.094 | 0.010 |
| *Halicryptus spinulosus* | 0 | 0.066 | 0.635 | 0.063 |
| *Hediste diversicolor* | 0 | 0.047 | 0.172 | 0.019 |
| *Hydrobia ulvae* | 0.026 | 0.496 | 1.319 | 0.148 |
| *Hydrobia ventrosa* | 0 | 0.023 | 0.111 | 0.011 |
| *Idotea balthica* | 0 | 0.009 | 0.044 | 0.005 |
| *Idotea chelipes* | 0 | 0 | 0.002 | 0 |
| *Macoma balthica* | 4.611 | 72.706 | 169.372 | 18.015 |
| *Marenzelleria neglecta* | 0 | 0.001 | 0.007 | 0.001 |
| *Monoporeia affinis* | 0 | 0.029 | 0.213 | 0.021 |
| *Mya arenaria* | 0 | 1.438 | 10.291 | 0.999 |
| *Mytilus trossulus* | 0 | 26.948 | 141.294 | 14.322 |
| *Neomysis integer* | 0 | 0.059 | 0.188 | 0.013 |
| *Oligochaeta* | 0 | 0.035 | 0.336 | 0.034 |
| *Palaemon adspersus* | 0 | 5.864 | 20.003 | 4.781 |
| *Piscicola geometra* | 0 | 0 | 0.002 | 0 |
| *Potamopyrgus antipodarum* | 0 | 0.141 | 0.783 | 0.074 |
| *Prostoma obscurum* | 0 | 0.003 | 0.016 | 0.002 |
| *Saduria entomon* | 0 | 0.128 | 1.283 | 0.128 |
| *Theodoxus fluviatilis* | 0 | 0.073 | 0.515 | 0.052 |

**Table 3.** Composition of fish diet by gape size classes (% of invertebrate taxa in the total stomach content, bivalves' shell dry weight excluded). The diet composition was calculated taking into account only stomachs that contained food. The defined gape size classes are as follows: small gape size ≤ 14.5 mm, medium 14.6–17.0, large > 17.0.

| | Flounder | | | Round goby | | | Perch | | |
|---|---|---|---|---|---|---|---|---|---|
| | Small | Medium | Large | Small | Medium | Large | Small | Medium | Large |
| *n* | 63 | 116 | 15 | 29 | 116 | 96 | 81 | 160 | 58 |
| Percentage of non fed | 52.4 | 43.1 | 33.3 | 13.8 | 13.9 | 63 | 14.8 | 15.1 | 32.8 |
| *Mytilus trossulus* | 92.3 | 92.4 | 65.7 | 88.12 | 78.74 | 79.51 | 12 | 5.78 | 2.46 |
| *Macoma balthica* | 7.4 | 7.4 | 31.4 | 19.81 | 17.97 | 15.49 | 18.15 | 5.38 | 0.21 |
| *Hydrobia* spp. | 0.17 | 0.17 | 0.08 | 0.07 | 0.81 | 1.9 | 0.046 | 0.041 | 0.00015 |
| *Hediste diversicolor* | 0.13 | 0 | 0 | 0 | 0 | 0.75 | 0.104 | 0.18 | 0.00025 |
| *Neomysis integer* | 0 | 0 | 0 | 0 | 0 | 0 | 0.042 | 0.0014 | 0.000015 |
| *Gammarus* spp. | 0 | 0 | 0 | 0 | 0 | 0 | 0.016 | 0.0006 | 0.000006 |
| *Corophium volutator* | 0 | 0 | 0 | 0 | 0 | 0 | 0.043 | 0.16 | 0.000032 |
| *Palaemon adspersus* | 0 | 0 | 0 | 0 | 0 | 0 | 1.8 | 0 | 1.5 |
| Fish excl. Round goby | 0 | 0 | 2.8 | 0 | 0 | 0 | 55.96 | 68 | 72.99 |
| Round goby | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9.65 | 17.8 |
| Fish egg | 0 | 0 | 0 | 0 | 2.45 | 2.3 | 4.99 | 0 | 2.11 |
| Macerated food | 0 | 0 | 0 | 0 | 0 | 0 | 6.85 | 7.11 | 2.89 |
| Other | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3.7 | 0 |

total dry biomass, respectively. When excluding shell weight, the bivalve species contributed 45% and 15% and the crustacean *Palaemon adspersus* 25% of total biomass, respectively. The cirriped *Balanus improvisus* and the bivalves *Mya arenaria* and *Cerastoderma glaucum* had elevated biomasses only at some stations. The biomass of other taxa did not exceed 1% of the total biomass.

The gut content analyses indicated that flounder and perch mainly fed on benthic invertebrates and to a lesser extent on other food items (Table 3). Altogether 8 benthic invertebrate taxa were found in the stomach samples, including some of the most dominant species. The food spectra of benthic invertebrate species did not match the availability of prey. ANOSIM showed large differences between the species composition of benthic invertebrate communities and those consumed by fishes. Except for the differences in the gut content between perch and flounder, the composition of gut content significantly varied among fish species (Table 4).

**Table 4.** Differences in the species composition of benthic invertebrates between the field and the guts of different fish species as well as between the guts of different fish species as evidenced by ANOSIM. Permutation/randomisation methods on the resemblance matrix (the actual number of permutation 999) were used.

| Pairwise tests | $\rho$ | $p$ |
|---|---|---|
| Round goby *vs*. Flounder | 0.072 | < 0.001 |
| Round goby *vs*. Perch | 0.123 | < 0.001 |
| Round goby *vs*. Availability of prey | 0.932 | < 0.001 |
| Flounder *vs*. Perch | 0.050 | 0.057 |
| Flounder *vs*. Availability of prey | 0.954 | < 0.001 |
| Perch *vs*. Availability of prey | 0.967 | < 0.001 |

Similarly, the proportion of benthic invertebrates in the diet of fishes differed from what was available in the field and the proportions of different food items in diet differed statistically among fish species (Table 5). Flounder preyed less on *M. trossulus* and *M. balthica* and more on *Hydrobia* spp. and *Hediste diversicolor* than was expected from their proportions in the field. Similarly, perch consumed less *M. trossulus*, *M. balthica* but also *P. adspersus* and more *Hydrobia* spp., *Neomysis integer*, *H. diversicolor* and *Gammarus* spp. than was expected from their proportions in the field. The round goby preferred *M. trossulus*, *Hydrobia* spp. and *H. diversicolor* over *M. balthica*.

However, as indicated by low distances among groups (i.e. within group variability was not much smaller that between group variability; *see* the $\rho$ values in Table 4), the diet of the studied

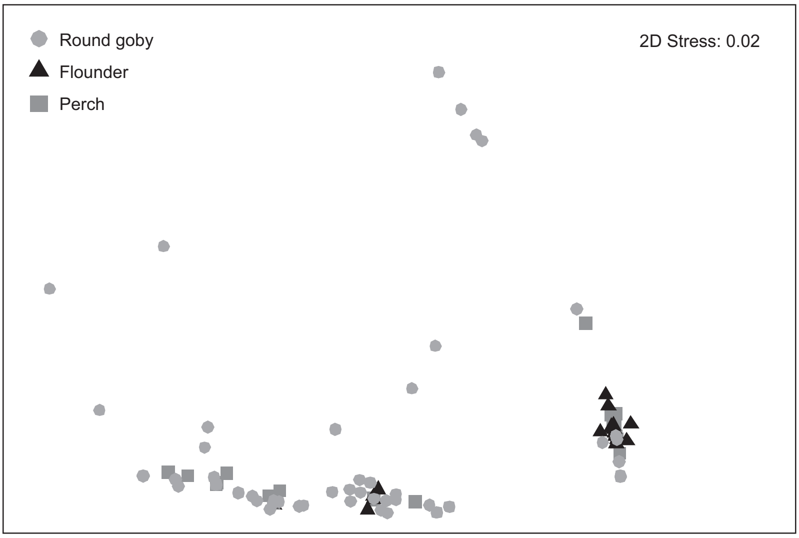

**Fig. 2.** MDS ordination of biomasses of benthic invertebrate species in the stomach of fishes.

species largely overlapped. This is also shown by the MDS ordination of fish stomach contents (Fig. 2). Round goby had the largest variability in the stomach content whereas variability in the stomach content of flounder was the smallest.

The BEST permutation analysis demonstrated that besides the biomass structure of benthic invertebrate communities, the stomach content of fish was explained by the separate effect of fish weight and age and to a lesser extent by fish length, maturity and sex. However, when both fish weight and age were included into models, fish length, maturity and sex did not explain additional variability of the models of fish feeding (Table 6).

**Table 5.** Differences in the biomass dominance of benthic invertebrate species between the field and the guts of different fish species as well as between the guts of different fish species as evidenced by ANOSIM. Permutation/randomisation methods on the resemblance matrix (the actual number of permutation 999) were used.

| Pairwise tests | $\rho$ | $p$ |
|---|---|---|
| Round goby *vs*. Flounder | 0.079 | < 0.001 |
| Round goby *vs*. Perch | 0.130 | < 0.001 |
| Round goby *vs*. Availability of prey | 0.210 | 0.021 |
| Flounder *vs*. Perch | 0.057 | 0.039 |
| Flounder *vs*. Availability of prey | 0.355 | < 0.002 |
| Perch *vs*. Availability of prey | 0.491 | < 0.001 |

Similar to the multivariate ANOSIM analysis, the Manly-Chesson index gave analogous preferences of benthic invertebrates in the diet of fishes with strong interspecific and size effects (Fig. 3). Likewise, the multivariate MDS analysis, the univariate comparison of feeding spectra showed a considerable overlapping between all size groups of the round goby and young (100–120 mm) flounder ($I_M = 0.64 \pm 0.1$). The overlapping between feeding spectra of round goby and > 250 mm flounder was considerably lower ($I_M = 0.32 \pm 0.12$). The dietary overlap between

**Table 6.** Relationship between the fish characteristics and the gut content of fish (BEST analysis, BIOENV procedure, $p < 0.01$ i.e. the number of permuted statistics greater than or equal to $\rho$ was 0). $\rho$ denotes a Spearman rank correlation between the similarity matrices of fish characteristics and gut content.

| Variables | $\rho$ |
|---|---|
| **Separate contribution** | |
| Species | 0.168 |
| Length | 0.120 |
| Gape size | 0.026 |
| Weight | 0.142 |
| Age | 0.130 |
| Sex | 0.012 |
| Maturity | 0.018 |
| **Best results** | |
| Species × Weight × Age | 0.346 |
| Species × Weight | 0.178 |

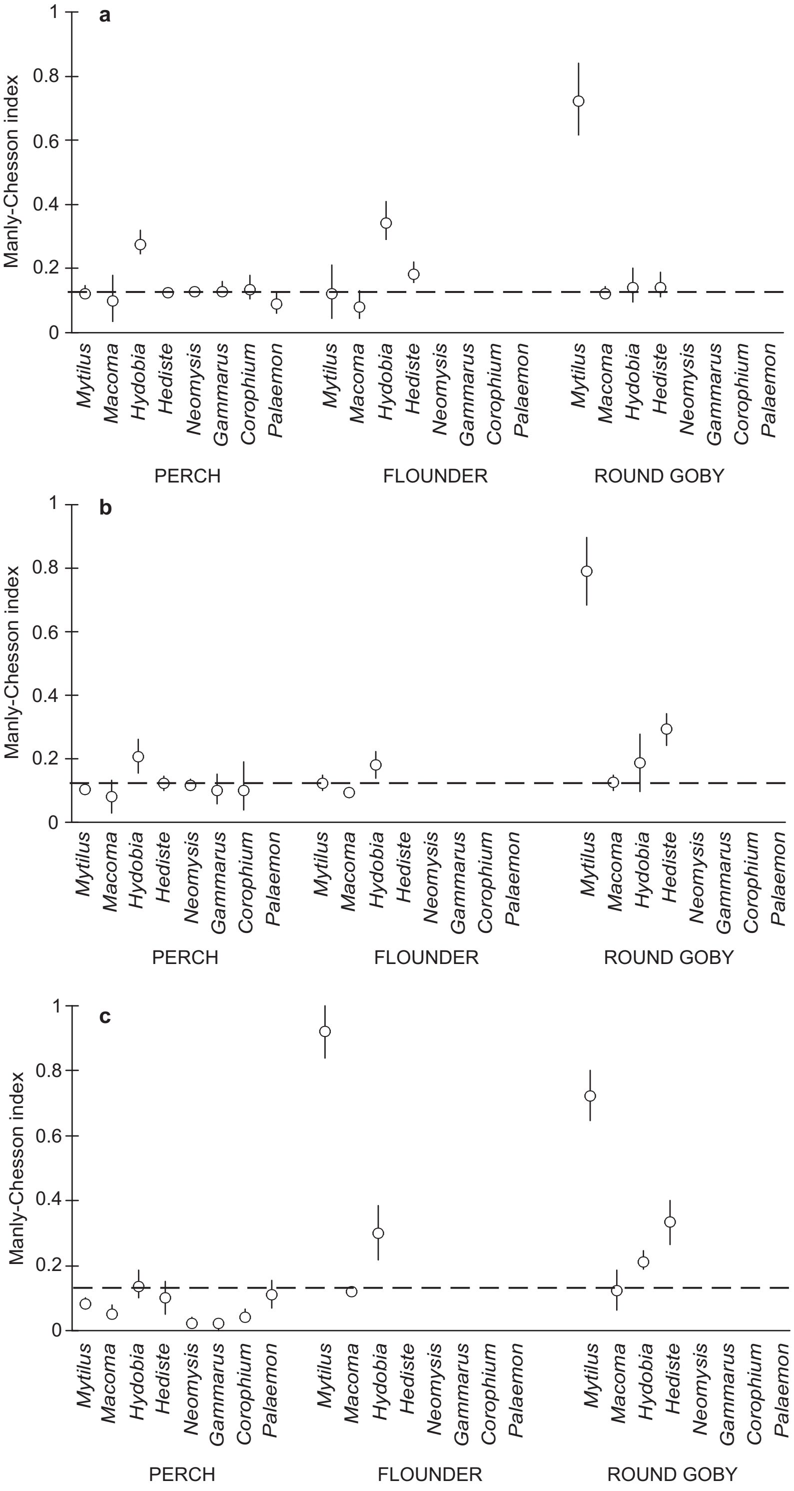

**Fig. 3.** Manly-Chesson selection index (minimum, mean, maximum) of main food items for (**a**) small perch, flounder and round goby (gape size ≤ 14.5 mm), (**b**) medium perch, flounder and round goby (gape size 14.6–17.0 mm), and (**c**) large perch, flounder and round goby (gape size > 17.0 mm). Values above the dashed line indicate preference, values on the line refer to proportional intake and values below the line show avoidance of prey.

80–150 mm perch and 120–140 mm round goby was also low ($I_M$ = 0.31 ± 0.16) (Table 7). Only flounder and perch preyed to a large extent on different food items.

## Discussion

We predicted that biomass structure of benthic invertebrates largely determines the variability of fish diet (first part of hypothesis 1). Our study did not conform the hypothesis as fish diet was only weakly associated with the availability of prey in the field. Therefore, our study gives further evidence that the studied fish species are highly selective (Ghedotti *et al*. 1995, Aarnio & Bondorff 1997, Adamek *et al*. 2004, Truemper & Lauer 2004, Andersen *et al*. 2005).

The results also indicate that food availability is likely not a limiting factor in the growth of founder and perch but may limit the growth of round goby. The bivalves *Mytilus trossulus* and *Macoma balthica* were the two of main food items for the studied fishes and only round goby preyed on *M. trossulus* more than was expected from their proportions in the field, i.e. had a potential to reduce the relative biomass of the prey species.

We also predicted that the selectivity of fish varied among species (second part of hypothesis 1). Our data supported the hypothesis except for significant overlap of diet between round goby and small flounder. Although some authors reported broad dietary overlap among estuarine fishes (Ley *et al*. 1994), our findings suggest that food partitioning is the main coexistence mechanism in the study area regardless of high invertebrate biomasses. Fishes that avoid dietary overlapping avoid competition.

We also predicted that fish diet varied with size as it is expected that the gape size of fish is related to its length (second part of hypothesis 1). Our analyses showed that fish weight and age largely modified the feeding of fishes, especially that of flounder and perch. The diet composition of flounder clearly reflected the physical capabilities of fish to swallow the prey, supporting the conclusion of Karlson *et al*. (2007) that the size of the food items depends on the width of mouth.

Finally, we predicted that fish diet varied with sex and maturity class (hypothesis 2). Our data did not support the hypothesis. Instead, the analyses showed that the dependence of fish diet on sex and maturity was largely modulated by fish length and weight. This agrees with the findings of earlier studies performed outside the Baltic Sea area with no relationship between fish sex, maturity stage and diet composition (e.g. Barbini *et al*. 2010, Powter *et al*. 2010). The significant effects of sex on fish feeding are only expected when the analyses are performed separately for different size classes. Such finding is also supported by previous feeding studies of many fish species including white bream, bream, perch and others (Wielgosz & Tadajewska 1988, Wziątek *et al*. 2004).

The gut content analyses showed that flounder had both low individual feeding variability (difference in gut content among individuals) and low overall feeding diversity (number of species preyed). This indicates that flounder is a specialist feeder with a small niche width. Round goby in turn was characterised by both high feeding variability and diversity, i.e. generalist feeding strategy. Perch had the broadest feeding spectra (high feeding diversity) but moderate feeding variability and therefore is an opportunistic feeder that feeds on all exposed items (Fishelson 1977, Mavuti *et al*. 2004). However, as perch switches from invertebrate food to other prey already at very young stages (Leach

**Table 7.** Average Morisita index (± SE) of dietary overlap ($I_M$) by fish species and their gape size classes. The defined gape size classes are as follows: small gape size ≤ 14.5 mm, medium 14.6–17.0, large > 17.0.

| | Small round goby | Medium round goby | Large round goby |
|---|---|---|---|
| Small perch | 0.23 ± 0.16 | 0.31 ± 0.12 | 0.11 ± 0.18 |
| Medium perch | 0.21 ± 0.16 | 0.28 ± 0.16 | 0.18 ± 0.16 |
| Large perch | 0.19 ± 0.16 | 0.2 ± 0.16 | 0.19 ± 0.16 |
| Small flounder | 0.64 ± 0.10 | 0.64 ± 0.10 | 0.64 ± 0.10 |
| Medium flounder | 0.38 ± 0.12 | 0.38 ± 0.12 | 0.38 ± 0.12 |
| Large flounder | 0.1 ± 0.18 | 0.32 ± 0.12 | 0.32 ± 0.12 |

*et al*. 1997) the species is not so much dependent on the availability of benthic invertebrates as compared with flounder and round goby. Our results clearly demonstrated that perch can prey on young stages of fishes including the round goby. Flexibility in the feeding behaviour of perch and round goby enables them to efficiently utilize the available food and give them a competitive advantage over specialized feeder in the dynamic ecosystems of the Baltic Sea (Mavuti *et al*. 2004, Balshine *et al*. 2005).

The coexistence of species in the communities is primarily regulated by the competition for food and space (Schoener 1974, Ross 1986). Introduction of a new species potentially intensifies competitive interactions and may destabilize native communities. Stronger effects are expected in young ecosystems such as the Baltic Sea (Balshine *et al*. 2005). The round goby, invading with ballast waters, has shown itself a successful competitor in a number of waterbodies such as the US Great Lakes (Jude *et al*. 1992), Gdansk Bay (Leppäkoski *et al*. 2002), and Curonian Bay (Rakauskas *et al*. 2008) just to name a few. The evidence from Great Lakes shows that round goby successfully outcompetes yellow perch (*Perca flavescens*), close relative of European perch, both for space and food (John 2001). Similarly it has been shown that the abundant population of the round goby depleted benthic fauna in Gdansk Bay (Skóra & Rzeźnik 2001). It is interesting to note that although Karlson *et al*. (2007) carried out their study in the laboratory and our study is based on the field observations, the patterns found in both studies were exactly the same, namely diets of small flounder and round goby overlap significantly. Thus, based on earlier evidence and the results of our study, round goby is expected to compete with young flounder in the coastal zone of the northern Baltic Sea including Muuga Bay (Karlson *et al*. 2007). On the other hand, our results also show that perch can prey on young stages of round goby. Thus, abundant European perch population can potentially control the population growth of round goby in the study area since the share of the invasive species in the diet of perch is expected to increase with further expansion of round goby. This indicates that the introduction of round goby may negatively affect flounder but positively perch (Almqvist *et al*. 2010).

In addition to interspecific interactions, the invasion of round goby may have a positive implication from a food-web efficiency point of view. Namely, round goby was the only studied fish species that consumed proportionally more deposit and suspension feeding bivalves than was expected from their proportions in the field. Being itself eaten by perch, round goby increases trophic transfer of bivalves up the food chain (Almqvist *et al*. 2010). The northern Baltic Sea is characterised by high benthic secondary production but low benthivorous fish biomass and therefore these trophic groups are largely not consumed by predators but rather channelled into the detritus food chain (Tomczak *et al*. 2009).

## Conclusions

1. The food spectra of benthic invertebrate species did not match the availability of prey but was influenced by fish species and size.
2. Except for round goby, the studied fish species preferred small and mobile invertebrates over large bivalves.
3. Despite of many significant differences, diet of the studied species somewhat overlapped with round goby having the largest and flounder having the smallest variability in its stomach content.
4. The study suggests that food availability is likely not a limiting factor in the growth of founder and perch but may be important for round goby.
5. Introduction of round goby may negatively affect flounder but positively affect perch and therefore perch may potential control the population growth of the round goby in the study area. The validity of such hypotheses, however, should be tested in future experimental studies.

### Acknowledgements

Funding for this research was provided by target financed project SF0180013s08 of the Estonian Ministry of Education and Research, by the Estonian Science Foundation grants 7813, 8254, the EU FP7 project VECTORS (grant agreement 266445) and by the Port of Tallinn.

## References

Aarnio, K. & Bonsdorff, E. 1997: Passing the gut of juvenile flounder, *Platichthys flesus*: different survival of zoobenthic prey species. — *Marine Biology* 129: 11–14.

Adamek, Z., Musil, J. & Sukop, I. 2004: Diet composition and selectivity in 0+ perch (*Perca fluviatilis* L.) and its competition with adult fish and carp (*Cyprinus carpio* L.) stock in pond culture. — *Agriculturae Conspectus Scientificus (ACS)* 69: 21–27.

Almqvist, G., Strandmark, A. K. & Appelberg, M. 2010: Has the invasive round goby caused new links in Baltic food webs? — *Environmental Biology of Fishes* 89: 79–93.

Andersen, B. S., Carl, J. D., Grønkjer, P. & Støttrup, J. G. 2005: Feeding ecology and growth of age 0 year *Platichtys flesus* (L.) in a vegetated and bare sand habitat in a nutrient rich fjord. — *Journal of Fish Biology* 66: 531–552.

Anon. 2007: *Manual for the Baltic trawl surveys*. — International Council for the Exploration of the Sea, Rostock.

Balshine, S., Verma, A., Chant, V. & Theysmayer, T. 2005: Competitive interactions between round gobies and logperch. — *Journal of Great Lakes Research* 31: 68–77.

Barbini, S. A., Scenna, L. B., Figueroa, D. E., Cousseau, M. B. & Díaz de Astarloa, J. M. 2010: Feeding habits of the Magellan skate: effects of sex, maturity stage, and body size on diet. — *Hydrobiologia* 641: 275-286.

Bergman, E. & Greenberg, L. A. 1994: Competition between a planktivore, a benthivore, and a species with ontogenetic diet shifts. — *Ecology* 75: 1233–1245.

Chesson, J. 1978: Measuring preference in the selective predation. — *Ecology* 59: 211–215.

Chesson, J. 1983: The estimation and analysis of preference and its relationship to foraging models. — *Ecology* 64: 1297–1304.

Clarke, K. R. 1993: Non-parametric multivariate analysis of changes in community structure. — *Australian Journal of Ecology* 18: 117–143.

Clarke, K. R. & Gorley, R. N. 2006: PRIMER v6. user manual/tutorial. — *PRIMER-E, Plymouth*.

Clarke, K. R., Somerfield, P. J. & Chapman, M. G. 2006: On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. — *Journal of Experimental Marine Biology and Ecology* 330: 55–80.

Copp, G. H., Bianco, P. G., Bogutskaya, N. G., Erős, T., Falka, I., Ferreira, M. T., Fox, M. G., Freyhof, J., Gozlan, R. E., Grabowska, J., Kováč, V., Moreno-Amich, R., Naseka, A. M., Peňáz, M., Povž, M., Przybylski, M., Robillard, M., Russell, I. C., Stakėnas, S., Šumer, S., Vila-Gispert, A. & Wiesner, C. 2005: To be, or not do be, a non-native freshwater fish? — *Journal of Applied Ichthyology* 21: 242–262.

Cortés, E. 1997: A critical review of methods of studying fish feeding based on analyses of stomach contents: application to elasmobranch fishes. — *Canadian Journal of Fisheries and Aquatic Sciences*. 54: 726–738.

Dąbrowski, K. R. 1982: The influence of light intensity on feeding of fish larvae and fry. — *Zoologische Jahrbuch. Allgemeine Zoologie. Physiologie* 86: 353–360.

Fishelson, L. 1977: Sociobiology of feeding behaviour of coral fish along the coral reef of the Gulf of Elat (Gulf of Aqaba), Red Sea. — *Israel Journal of Zoology*. 26: 114–134.

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

Gillanders, B. M. 1995: Feeding ecology of the temperate marine fish *Achoerodus viridis* (Labridae): size, seasonal and site-specific differences. — *Marine and Freshwater Research* 46: 1009–1020.

Helfman, G. S. 1978: Patterns of community structure in fishes: summary and overview. — *Environmental Biology of Fishes* 3: 129–148.

Horn, H. S. 1966: Measurement of "overlap" in comparative ecological studies. — *The American Naturalist* 100: 419–424.

John, R. P. & French, D. J. 2001: Diets of nonindigenous Gobies and small benthic native fish coinhabiting the St. Clair River, Michigan. — *Journal of Great Lakes Research* 27: 300–311.

Jude, D., Reider, R. & Smith, G. 1992: Establishment of Gobiidae in the Great Lakes Basin. — *Canadian Journal of Fisheries and Aquatic Sciences* 49: 416–421.

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

Karås, P. 1987: Food consumption, growth and recruitment in perch (Perca fluviatilis L.). — *Acta Universitatis Upsaliensis* 108: 2–19.

Kostrzewa, J. & Grabowski, M. 2003: Opportunistic feeding strategy as a factor promoting the expansion of racer goby (*Neogobius gymnotrachelus* Kessler, 1857) in the Vistula basin. — *Lauterbornia* 48: 91–100.

Kotta, J., Orav, H. & Sandberg-Kilpi, E. 2001: Ecological consequence of the introduction of the polychaete *Marenzelleria viridis* into a shallow water biotope of the northern Baltic Sea. — *Journal of Sea Research* 46: 273–280.

Kotta, J. & Ólafsson, E. 2003: Competition for food between the introduced exotic polychaete *Marenzelleria viridis* and the resident native amphipod *Monoporeia affinis* in the Baltic Sea. — *Journal of Sea Research* 342: 27–35.

Kotta, J., Kotta, I., Simm, M., Lankov, A., Lauringson, V., Põllumäe, A. & Ojaveer, H. 2006: Ecological consequences of biological invasions: three invertebrate case studies in the north-eastern Baltic Sea. — *Helgoland Marine Research* 60: 106–112.

Kotta, J., Lauringson, V. & Kotta, I. 2007: Response of zoobenthic communities to changing eutrophication in the northern Baltic Sea. — *Hydrobiologia* 580: 97–108.

Kotta, J., Herkül, K., Kotta, I., Orav-Kotta, H. & Aps, R. 2008a: Effects of harbour dredging on soft bottom invertebrate communities: does environmental variability affect the community responses? — In: *US/EU-Baltic International Symposium, 2008 IEEE/OES: US/EU-Baltic International Symposium, Tallinn, Estonia, 27–29 May 2008*, IEEE Conference Proceedings, 10.1109/BALTIC.2008.4625534.

Kotta, J., Jaanus, A. & Kotta, I. 2008b: Haapsalu and Matsalu Bay. — In: Schiewer, U. (ed.), *Ecology of Baltic coastal waters*: 245–258. Ecological Studies 197, Springer, Berlin–Heidelberg.

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K. & Ojaveer, H. 2008c: Gulf of Riga and Pärnu Bay. — In: Schiewer, U. (ed.), *Ecology of Baltic coastal waters*: 217–243. Ecological Studies 197, Springer, Berlin–Heidelberg.

Kotta J., Kotta, I., Simm, M. & Põllupüü, M. 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.

Lall, S. & Tibbetts, S. 2009: Nutrition, feeding, and behavior of fish. — *Veterinary Clinics of North America: Exotic Animal Practice* 12: 361–372.

Lappalainen, A., Shurukhin, A., Alekseev, G. & Rinne, J. 2000: Coastal fish communities along the northern coast of the Gulf of Finland, Baltic Sea: responses to salinity and eutrophication. — *International Review of Hydrobiology* 85: 687–696.

Lappalainen, A., Westerbom, M. & Vesala, S. 2004: Blue mussels (*Mytilus edulis*) in the diet of roach (*Rutilus rutilus*) in outer archipelago areas of the western Gulf of Finland, Baltic Sea. — *Hydrobiologia* 514: 87–92.

Leach, J. H., Johnson, M. G., Kelso, J. R. M., Hartmann, J., Nümann, W. & Entz, B. 1977: Responses of percid fishes and their habitats to eutrophication. — *Journal of the Fisheries Research Board of Canada* 34: 1964–1971.

Leppäkoski, E., Gollasch, S. & Olenin, S. 2002: *Invasive aquatic species of Europe. Distribution, impacts and management*. — Kluver Academic Publishers, Dordrecht, Boston, London.

Ley, J. A., Montague, C. L. & McIvor, C. C. 1994: Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. — *Bulletin of Marine Science* 54: 881–899.

Licandeo, R., Barrientos, C. A. & González, M. T. 2006: Age, growth rates, sex change and feeding habits of notothenioid fish *Eleginops maclovinus* from the central-southern Chilean coast. — *Environmental Biology of Fishes* 77: 51–61.

Lindeman, R. L. 1942: The trophodynamic aspects of ecology. — *Ecology* 23: 399–418.

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

Manly, B. F. J. 1974: A model for certain types of selection experiments. — *Biometrics* 30: 281–294.

Mavuti, K. M., Nyunja, J. A. & Wakwabi, E. O. 2004: Trophic ecology of some common juvenile fish species in Mtwapa Creek, Kenya. — *Western Indian Ocean Journal of Marine Sci*ence 3: 179–187.

Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I. & Lumberg, A. 1999: Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. — *ICES Journal of Marine Science* 56: 33–40.

Ojaveer, H. 2006: The round goby *Neogobius melanostomus* is colonising the NE Baltic Sea. — *Aquatic Invasions* 1: 44–45.

Orav-Kotta, H., Kotta, J., Herkül, K., Kotta, I. & Paalme, T. 2009: Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* in the northern Baltic Sea. — *Biological Invasions* 11: 597–608.

Palomares, M. L. & Pauly, D. 1998: Predicting food consumption of fish populations as functions of mortality, food type, morphometrics, temperature and salinity. — *Marine and Fisheries Research* 49: 447–453.

Pihl, L., Baden, S. P. & Schaffner, L. C. 1992: Hypoxia-induced structural changes in the diet of bottom feeding fish and Crustacea. — *Marine Biology* 112: 349–361.

Pihu, E., Järv, L., Vetemaa, M. & Turovski, A. 2003: Perch, *Perca fluviatilis* L. — In: Ojaveer, E., Pihu, E. & Saat, T. (eds.), *Fishes of Estonia*: 289–296. Estonian Academy Publishers, Tallinn.

Powter, D. M., Gladstone, W. & Platell, M. 2010: The influence of sex and maturity on the diet, mouth morphology and dentition of the Port Jackson shark, *Heterodontus portusjacksoni*. — *Marine and Freshwater Research* 61: 74–85.

Rakauskas, V., Bacevičus, E., Pūtys, Ž., Ložis, L. & Arbačiauskas, K. 2008: Expansion, feeding and parasites of the round goby, *Neogobius melastomus* (Pallas, 1811). — *Acta Zoologica Lituanica* 18: 180–190.

Roots, O., Järv, L. & Simm, M. 2004: DDT and PCB concentrations dependency on the biology and domicile of fish: an example of perch (*Perca fluviatilis* L.) in Estonian coastal sea. — *Fresenius Environmental Bulletin* 13: 620–625.

Ross, S. T. 1986: Resource partitioning in fish assemblages — a review of field studies. — *Copeia* 2: 352–358

Ruiz, G., Carlton, J., Grosholz, E. & Hines, A. 1997: Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent and consequences. — *American Zoologist* 37: 621–632.

Schoener, T. W. 1974: Resource partitioning in ecological communities. — *Science* 185: 27–39.

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

Thorman, S. & Wiederholm, A.-M. 1983: Seasonal occurrence and food resource use of an assemblage of near-shore fish species in the Bothnian Sea, Sweden. — *Marine Ecology Progress Series* 10: 223–229.

Tomczak, M. T., Järv, L., Kotta, J., Martin, G., Minde, A., Müller-Karulis, B., Põllumäe, A., Razinkovas, A. & Strake, S. 2009: Trophic networks and carbon flows in south-eastern Baltic costal ecosystems. — *Progress in Oceanography* 81: 111–131.

Truemper, H. A. & Lauer, T. E. 2004: Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. — *Journal of Fish Biology* 66: 135–149.

Vinagre, C., Cabral, H. & Costa, M. J. 2008: Prey selection by flounder, *Platichthys flesus*, in the Douro estuary, Portugal. — *Journal of Applied Ichthyology* 24: 238–243.

Weatherley, N. S. 1989: The diet and growth of O-group flounder, *Platichthys flesus* (L.), in the River Dee, North Wales. — *Hydrobiologia* 178: 193–198.

Wielgosz, S. & Tadajewska, M. 1988: Factors determining diet composition and food availability for bream *Abramis brama* L. and white bream *Blicca bjorkna* (L.) in Włocławek Dam reservoir. — *Acta Ichthyologica Et Piscatoria* 18: 79–100.

Wziątek, B., Poczyczyński, P., Kozłowski, J. & Wojnar, K. 2004: The feeding of sexually mature European perch (*Perca fluviatilis* L.) in lake Kortowskie in the autumn–winter period. — *Archives of Polish Fisheries* 12: 197–201.

Zaret, T. & Rand, S. 1971: Competition in tropical stream fishes: support for the competitive exclusion principle. — *Ecology* 52: 336–342.

Złoch, I., Sapota, M. & Fijałowska, M. 2005: Diel food composition and changes in the diel and seasonal feeding activity of common goby, sand goby and young flounder inhabiting the inshore waters of the Gulf of Gdansk, Poland. — *Oceanological and Hydrobiological Studies* 34: 69–84.