

Research Article

Effects of introduced round goby (*Neogobius melanostomus*) on diet composition and growth of zander (*Sander lucioperca*), a main predator in European brackish waters

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Abstract

We inspected diet and growth of zander *Sander lucioperca*, a main predator in North European brackish waters, from the Kiel Canal, northern Germany, to analyse effects of the introduced round goby *Neogobius melanostomus* as possible prey. Round goby represented the most important fish prey taxon in the zander diet in 2011–2013 with 21.8% of relative importance index (*RI*) over all inspected specimens. In particular zander of total length ≥ 200 mm fed heavily on round goby, at least in the warmer quarters (2nd and 3rd) of the years under study. *RI* for these quarters was ranging from 10.4% to 52.1% for predator specimens of 200–399 mm and from 45.6% to 79.7% of *RI* for specimens of ≥ 400 mm. In the colder quarters of the inspected years (1st and 4th), zander ≥ 400 mm showed a high amount of cannibalism, with *RI* of young-of-the-year zander as prey ranging from 23.9% to 38.9%. The asymptotic total length (L_{∞}) of the zander, calculated by the von Bertalanffy growth equation, was 937 mm. In comparison with data from 1995/1996, before the round goby invasion in 2006, zander from our study showed considerable differences in diet composition. *RI* of the prey organisms herring and *Pomatoschistus* spp. decreased from 26% to 13.4% and 14.2% to 4.4%, respectively. *RI* of young-of-the-year zander as prey for larger zander increased from 1.2% to 7.7% and round goby occurred as newly established prey taxon. Zander also showed faster growth and a better condition factor. We assume that this development has the potential to enhance the situation of the local fisheries that are strongly related to the catch of zander. In addition, abundance control of round goby seems to result from the high predator abundance.

Key words: Gobiidae, invasive species, diet shift, predator-prey relationships, Kiel Canal

Introduction

The zander *Sander lucioperca* (Linnaeus, 1758) is an important top predator (in terms of ecosystems and fisheries) of many brackish water ecosystems in northern Europe (Lehtonen et al. 1996; Gröger et al. 2007). Total catch from European inland fisheries reported to FAO was 17,892 t in 1999 (FAO 2014). The non-indigenous round goby *Neogobius melanostomus* (Pallas, 1814) has been introduced into many ecosystems in the northern hemisphere and continues to spread (Kornis et al. 2012; Kalchhauser et al. 2013). It is assumed that round goby became established in the eastern parts of the Kiel Canal in 2006 (Neukamm 2009a). It has been abundant in the studied middle region of the Canal since 2009 (see result section).

The establishment of the non-indigenous goby is described as having strong negative impacts

on the invaded ecosystems and its inhabitants. Kornis et al. (2012) summarize that round goby competes with native species by resource competition, spawning interference and displacement to sub-optimal habitats. In addition, the round goby seems to have a strong predation impact on invertebrate communities (e.g. Kuhns and Berg 1999; Lederer et al. 2008).

In contrast to the above mentioned impacts on native fish species of similar trophic level and invertebrates, non-indigenous round goby provide an important food resource for predatory fishes (e.g. Steinhart et al. 2004a; Almqvist et al. 2010; Reyjol et al. 2010; Taraborelli et al. 2010; Pothoven and Madenjian 2013; Rakauskas et al. 2013). The newly available food can enhance growth and have positive effects e.g. on survival and reproduction. The effect of incorporating *N. melanostomus* in diets seems to differ strongly

between species and locations (see Crane et al. 2015). Predator species in North America from the same genus as the studied zander are found to consume high proportions of round goby (Reyjol et al. 2010; Crane et al. 2015). There are also descriptions of important changes in prey composition following round goby invasion for fish eating birds and snakes (e.g. Jakubas 2004; King et al. 2008).

Round goby is not only a potential prey for predatory fish species but can also act as a predator on fish eggs and larvae (e.g. Steinhart et al. 2004b). Kornis et al. (2012) gave multiple examples for species suffering from egg depredation and concluded that benthic eggs of any species were probably vulnerable to predation by round gobies.

Although many predators of round goby have been identified, no study has examined the effects of round goby on zander diet and growth. To fill this gap in knowledge, we investigated these aspects in the framework of a case study in the brackish Kiel Canal. Supported by reports of local fishermen, we hypothesized that the zander in the Kiel Canal showed faster growth due to predation on round goby than before the round goby invasion. To test this hypothesis, we compared the results of our current research from the years 2011–2013 with data from 1995/1996 (Kafemann and Thiel 1998; Kafemann 2000). These analyses were complemented by the inspection of the development of biomasses of zander, round goby and other dominant fish species in the study area in the years 2008–2013.

Materials and methods

Study site

The Kiel Canal in northern Germany is the most commonly used artificial waterway worldwide (Heitmann et al. 2013). In 2012, about 35,000 vessels transporting 104 million tonnes of cargo passed the Kiel Canal (WSD Nord 2013). It was built in the late 19th century and connects the North Sea with the western Baltic Sea over a length of about 100 km. Maximum depth of the Kiel Canal is 11 m and width varies between 162 m and 240 m (Kafemann et al. 2000). The shoreline of the Kiel Canal is mostly lined with stone packaging to avoid damage due to shipping traffic. The stone packaging represents a common way to ensure stability of shorelines, not only in artificial waters but also in large streams and lakes. The canal shows a salinity gradient, caused

by water exchange with the River Elbe at the western end and with the Baltic Sea at the eastern end. Throughout the investigated period (2011–2013), mean salinity near the western end of the canal was 2.7 and 10.4 near the eastern end. The study site (54°19'19" N; 9°42'49" E) was situated close to the city of Rendsburg (Figure 1), where mean salinity was ~7. The fish fauna of the Kiel Canal comprises numerous limnic, euryhaline and marine taxa. In 1995/1996, 46 fish species were recorded in the Kiel Canal by Kafemann (2000), whereby abundance of some fish species in the canal was highly correlated with the seasons.

Sampling

Sampling was performed in collaboration with a resident commercial fishery. The net (opening width 14 m, 10 mm mesh size in the cod end) was trawled along the bottom with a speed of ~2.5 knots, mostly in areas with depth >10 m (verified by echo sounding). Bottom material in this depth was characterised mostly by sand and mud (verified by bottom grab sampling). In 2011 and 2012, monthly sampling from June to October took place with 10 km trawling distance in total (5 hauls, each 1–3 km in length) in the framework of a monitoring program on European eel *Anguilla anguilla* (Linnaeus, 1758). That program has taken place annually since 2007 (compare Neukamm 2009b). Biomass data from the years 2008–2010, later presented in the results section, have been assessed within the above mentioned monitoring program as well. Zander specimens for the months November to March of the years 2011–2013 were provided by fishermen for the same area. The specimens were caught using the same fishing technique and the same net. Thus, an influence of different sampling techniques on the food composition in the digestive tract can be ruled out. Fish were frozen and kept at -20°C until analysis. In large specimens with total length (TL) >350 mm, the digestive tracts and complete heads were frozen after determining weight (0.1 g precision) and TL (to the nearest mm) of the whole individuals.

Biomass calculation

Biomass (B) of zander, round goby and other important fish species in the region under study was calculated as kg ha⁻¹ according to the equation: $B = (B_T / A_T) \times 10,000$, where B_T was the determined biomass of a particular species in

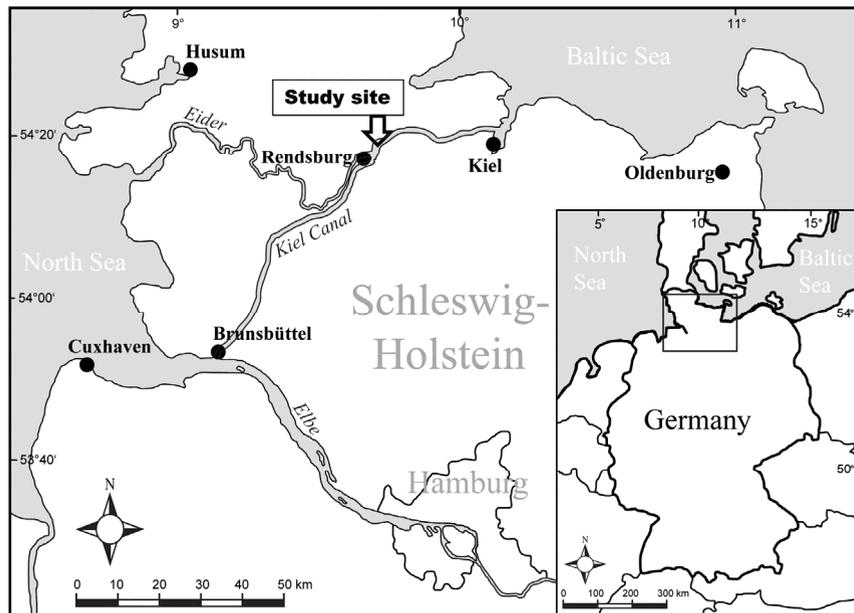


Figure 1. Location of the study site.

the trawled area in kg and A_T was the size of the trawled area in m^2 . For biomass calculations, only results from the trawling procedures from June to October of the years 2011 and 2012 were considered. That was because exact biomass was measured only in the monitoring program described above and not during conventional fisheries.

Diet analysis

Digestive tracts of 504 zander were examined for prey consumed. Investigated fish were grouped into three length classes (TL: juveniles <200 mm ($Z_{<200}$), sub-adults 200–399 mm ($Z_{200-399}$) and adults ≥ 400 mm ($Z_{\geq 400}$) and into quarters of the years (1 = January–March; 2 = April–June; 3 = July–September; 4 = October–December). Used length classes were chosen due to an assumed diet shift with dominance of a piscivorous feeding behaviour from the second year of life (see Lehtonen et al. 1996). In our study a TL of about 200 mm was reached by the zander at the beginning of their second year (see results section). To determine if adult zander possibly preyed on different taxa than juveniles and sub-adults, we included the third length class.

Digestive tracts were defrosted and prey items (from oesophagus and stomach) were determined to the lowest taxon possible (generally to species level, except for few prey items with high rate of digestion). Prey items in different stages of

digestion were counted and their relevant structures (bones or body parts; e.g. otoliths, dentary bones, vertebrae, maxillary bones) were measured for subsequent back calculation of ingested biomass.

Back calculation of biomass was performed using published regression equations between length of structures and total fresh weight of the species (e.g. Härkönen 1986; Debus and Winkler 1996; Dietrich et al. 2006; Tarkan et al. 2007; Verreycken et al. 2011). In cases where no published data were available, we calculated regression equations of prey items based on fresh material from our own trawl net catches. In this regard, we used: $W_i = 0.000005 \times TL^{3.2127}$ (specimens from trawling at the study site 2011: $N = 2170$, range 41–172 mm (TL), $r^2 = 0.9766$, $p < 0.001$) to calculate round goby total weight (W_i) in g from TL in mm (measured directly in intact prey or calculated from the length of round goby bones). To calculate TL of young-of-the-year zander in mm from the maximal length of its dentary bone (LD) in mm we used: $TL = 9.6284 \times LD + 7.3369$ (specimens from trawling at the study site 2012: $N = 13$, range 117–174 mm (TL), $r^2 = 0.9696$, $p < 0.001$).

The relative importance index (RI) of prey taxa was calculated following George and Hadley (1979): $RI_i (\%) = (N_i + B_i + F_i / \sum (N_i B_i F_i)) \times 100$, where $N_i (\%)$ is the number, $B_i (\%)$ is the biomass and $F_i (\%)$ is the frequency of occurrence of the prey component i in the sample.

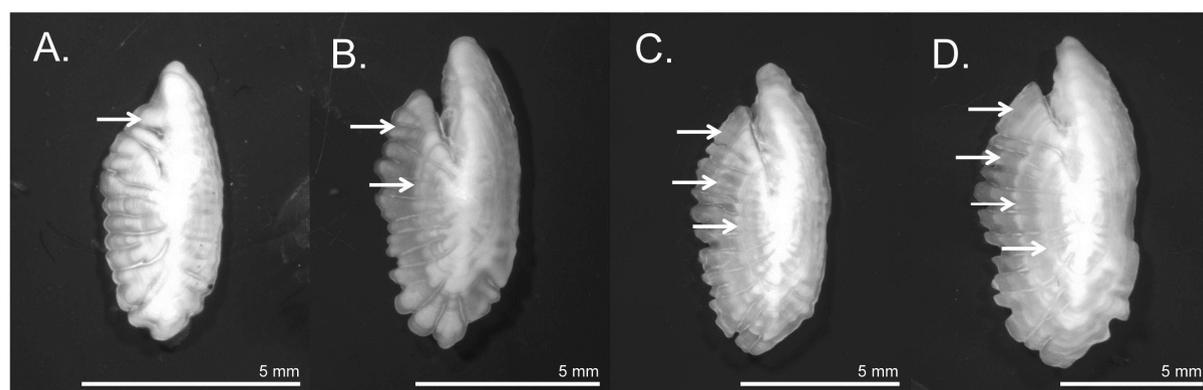


Figure 2. Otoliths of zander: A. age 1+, B. age 2+, C. age 3+ and D. age 4+. Arrows show the location of annuli. Photomicrograph by M. Hempel.

Table 1. Number of age determinations for zander from the Kiel Canal per length classes (TL).

Length class (mm)	Number
0–100	43
>100–200	494
>200–300	156
>300–400	113
>400–500	103
>500–600	45
>600–700	4
>700–800	2
>800–900	1
All sizes	961

One-way ANOVA was performed, using SPSS version 20 (SPSS Inc., Chicago, Illinois) software, to analyse differences in round goby *RI* between the three zander size classes, as well as between the four yearly quarters. Fishers LSD post-hoc tests were conducted to assess pairwise differences, where needed. Cluster analysis was performed using PRIMER version 6 (Primer-E Ltd., Plymouth, UK) to compare the dietary composition of zander from our study with that of zander from 1995/1996 inspected by Kafemann (2000). Therefore the *RI* of different food taxa was used for each year. Prior to analyses, the raw data were fourth root transformed in order to minimize any effect due to oversized replicates. A dendrogram was used to visualize the percentage of Bray-Curtis similarity between samples, calculated by PRIMER 6. This takes into account both the number of shared taxa between years and their *RI* to calculate the percent similarity between pairs of samples.

Growth estimation

Age determination of 961 zander (TL 65–820 mm) was performed using both sagittae otoliths and opercular bones for all specimens. Scales were inspected as well, but annuli were often difficult to read. Otoliths and opercular bones were removed from the defrosted fish or fish heads and cleaned of adherent tissue with water. The material was stored dry until age determination took place, where it was handled under magnification with reflected light in a black dish filled with alcohol (Figure 2) following the procedure of Bostanci (2008).

As the initial annulus was difficult to detect in some older individuals (see Buckmeier et al. 2002), we compared otoliths and opercular bones from young-of-the-year zander from the time of first annulus formation. Fish that showed unclear annuli or different age estimates in otoliths and opercular bones (14 specimens) were excluded from the analysis. Table 1 shows the number of specimens used for age determination per length class. To define an exact age (days since hatching), we used 1st of May as a hypothetical date of birth for the zander (compare Kafemann and Thiel 1998). This is a common time of hatching for zander in the inspected geographical region. To ensure comparability of this study with the data from previous investigations before round goby occurred in the Kiel Canal, we excluded two fish older than eight years from growth analysis as done by Kafemann and Thiel (1998).

The relationship between W_t and TL was characterized by the length-weight equation: $W_t = a \times TL^b$, where the parameter a is a coefficient

for the weight at length and b is a shape parameter for the body form. Growth in length was calculated by the von Bertalanffy growth equation using FISAT II version 1.2.2 (FAO, Rome, Italy): $L_t = L_\infty \times (1 - e^{-k(t-t_0)})$, where L_t is the length at time t (TL, mm), L_∞ is the asymptotic length (TL, mm), k is a growth coefficient and t_0 is the prenatal age (years). The 95% confidence interval for L_∞ was calculated from the standard error given by the FISAT II output, in order to compare growth of zander from the Kiel Canal 1995/1996 and the tidal Elbe River 1992/1993 (Kafemann and Thiel 1998) with those of zander in our study. Additionally, the mean total length for zander at an age of 1–6 years (1995/1996 and 2011–2013 Kiel Canal), calculated by the von Bertalanffy growth equation, was compared using the Wilcoxon signed-rank test in SPSS. Furthermore, the index of growth performance (P), after Pauly (1979), was calculated: $P = \log k \times W_\infty$, where k is a growth coefficient (von Bertalanffy growth equation) and W_∞ is the asymptotic weight in g calculated by the length-weight equation and the asymptotic length (L_∞). To compare condition factor (K), we calculated it for zander of $TL \geq 200$ mm as done by Kafemann and Thiel (1998): $K = (W_t/TL^3) \times 100$, where TL was used in cm.

Results

Trends in biomass

From 2008 to 2012, we found similar trends in the biomasses of round goby and zander in catches from trawling at the study site (Figure 3). After the first appearance of round goby in 2008, its biomass increased rapidly to a maximum of $1.7 \pm 1.8 \text{ kg ha}^{-1}$ (mean \pm SD) in 2011. In 2012, round goby catches decreased to $0.6 \pm 0.4 \text{ kg ha}^{-1}$. Biomass of zander increased to a maximum of $8.1 \pm 8.7 \text{ kg ha}^{-1}$ in the year 2011 and decreased to $5.8 \pm 3.8 \text{ kg ha}^{-1}$ in 2012. Biomass of other fish species in the trawl net catches developed at least slightly differently. The high biomass of bream *Abramis brama* (Linnaeus, 1758) in trawl net catches from the inspected area, seems to follow the same trend but showed an increase in 2012 contrasting with the decrease of zander and round goby. Biomass development of flounder *Platichthys flesus* (Linnaeus, 1758) was relatively similar to that of round goby but showed two maxima with $\sim 2 \text{ kg ha}^{-1}$ in 2009 and 2011. Biomass of European eel was high in 2009 ($\sim 2 \text{ kg ha}^{-1}$), lowest in 2011 and increased again in

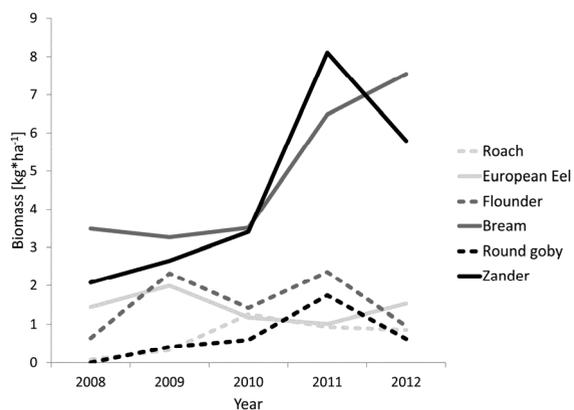


Figure 3. Average biomass of zander, round goby and of all other fish species, reaching a biomass of $>1 \text{ kg ha}^{-1}$ in at least one year, in trawl net catches at the sampling site (years 2008–2012, June–October).

2012. Roach *Rutilus rutilus* (Linnaeus, 1758) occurred with relatively constant biomass of $\sim 1 \text{ kg ha}^{-1}$ since 2010. Thus, the similar trends in biomasses of round goby and zander were not followed by all fish species inspected and possibly did not represent a general productivity pattern.

Diet composition

Differences in zander diet were detected between length classes and seasons (Figure 4). For juvenile zander ($Z_{<200}$), mysid shrimp *Neomysis integer* (Leach, 1814) had the highest relative importance (RI) throughout the studied period ($62.7 \pm 31.2\%$ (mean \pm SD); range 13.6–100%). In the warmer 2nd and 3rd quarters of 2011 and 2012, when young-of-the-year herring *Clupea harengus* Linnaeus, 1758 was abundant at the study site (especially 2nd quarter of 2011), this species comprised considerable percentages of RI ($15.5 \pm 22.6\%$; 0–64%). Other frequent prey taxa of $Z_{<200}$ were decapod shrimp ($5.6 \pm 8.2\%$; 0–22.4%), gobies of the genus *Pomatoschistus* ($5.3 \pm 8.4\%$; 0–22.8%) and young-of-the-year round goby ($4.6 \pm 6.6\%$; 0–16.4%). RI of round goby in the diet of $Z_{<200}$ did not vary significantly between the quarters of the inspected years (ANOVA, $F_{3,7} = 1.879$, $p = 0.274$).

For sub-adult zander ($Z_{200-399}$), the RI of mysid shrimp was lower than for $Z_{<200}$ ($31.1 \pm 13.6\%$; 8.4–50.4%). In contrast, the RI of round goby as prey was considerably higher ($27.8 \pm 17.6\%$; 9–52.1%), reaching values of about 50% in the 2nd and 3rd quarters of 2011. RI of young-of-the-year

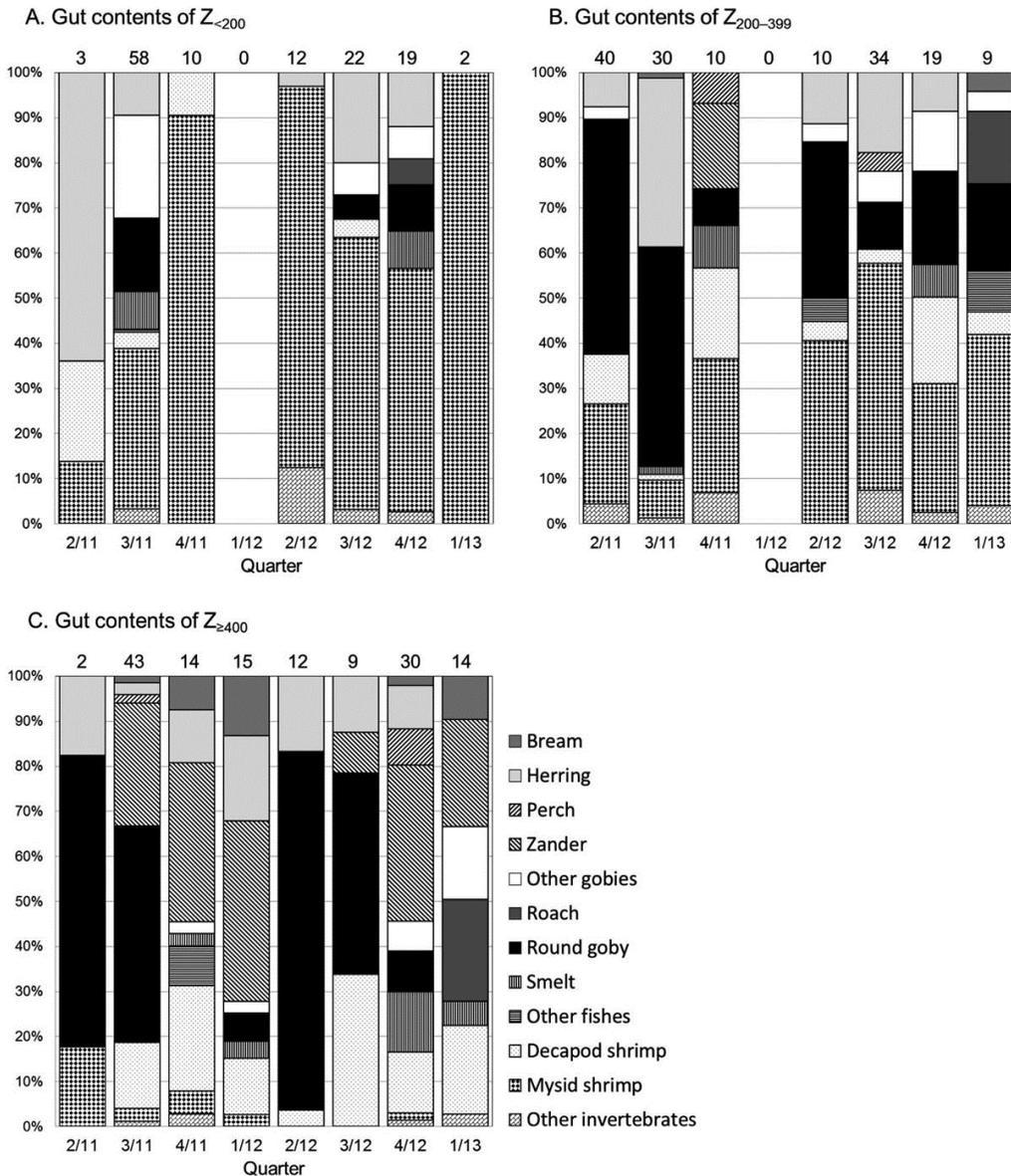


Figure 4. Relative importance index (*RI*) of prey taxa (2nd quarter 2011 to 1st quarter 2013) classified into three length classes (TL) of zander: **A.** <200 mm ($Z_{<200}$), **B.** 200–399 mm ($Z_{200-399}$) and **C.** ≥ 400 mm ($Z_{\geq 400}$). The category “other gobies” includes sand goby *Pomatoschistus minutus* (Pallas, 1770) and common goby *Pomatoschistus microps* (Krøyer, 1838). Fish of TL <400 mm were not available in the 1st quarter of the year 2012. Numbers of non-empty guts examined are given above bars.

herring as prey reached values comparable with $Z_{<200}$ ($11.8 \pm 12.9\%$; 0–37.4%). As for $Z_{<200}$, *RI* of round goby in the diet of $Z_{200-399}$ did not vary significantly between the quarters of the inspected years (ANOVA, $F_{3,7} = 1.633$, $p = 0.316$).

For adult zander ($Z_{\geq 400}$), mysid shrimp did not represent an important prey item ($3.7 \pm 5.9\%$; 0–17.5%). Major prey taxa of this size group were

round goby ($31.9 \pm 31.7\%$; 0–79.7%) and young-of-the-year zander ($20.5 \pm 15.7\%$; 0–38.9%). Other frequent prey taxa of $Z_{\geq 400}$ were decapod shrimp ($15.2 \pm 10.8\%$; 0–33.8%) and herring ($11.4 \pm 7.1\%$; 0–19.8%). Diet of $Z_{\geq 400}$ strongly depended on the season, with high importance of round goby only in the 2nd and the 3rd quarters of 2011 and 2012. Accordingly, we found a significant difference

Table 2. Parameters calculated by the von Bertalanffy growth equation (t_0 , k , L_∞ and 95% confidence interval, W_∞) and index of growth performance (P) for zander from the Kiel Canal 2011–2013 (this study), the Kiel Canal 1995/1996 (Kafemann and Thiel 1998) and other brackish water habitats in northern Germany (Kafemann and Thiel 1998); n.i. = parameter not indicated.

Parameter	t_0 (years)	k	L_∞ (mm)	L_∞ (95% CI)	W_∞ (g)	$1/k + t_0$	P
Kiel Canal 2011–2013	-0.40	0.19	937	845–1029	7085	4.86	3.13
Kiel Canal 1995/1996	-0.36	0.22	685	615–754	2550	4.19	2.75
Tidal Elbe River 1992/1993	-0.88	0.17	987	690–1285	8942	4.99	3.18
Greifswalder Bodden	0.21	0.27	831	n.i.	4011	3.90	2.93
Schlei	0.08	0.22	792	n.i.	4351	4.63	2.98

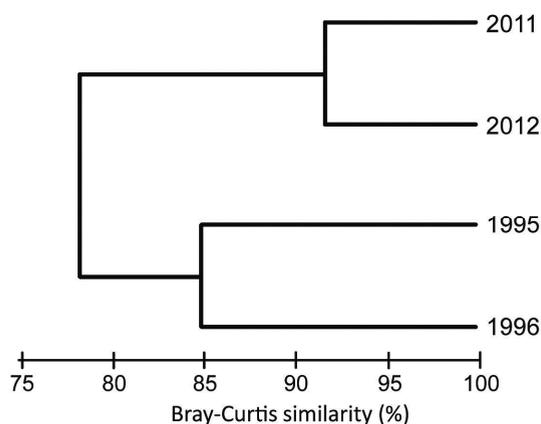


Figure 5. Dendrogram showing the similarity in prey composition (% of relative importance index) between years before round goby invasion (1995/1996) and years of our study (exact sample period 2011: 2/2011–1/2012 and 2012: 2/2012–1/2013), when round goby occurred in the system. Fourth-root transformed data.

in RI of round goby as prey among the inspected quarters (ANOVA, $F_{3,7} = 49.901$, $p = 0.001$). In the 2nd and the 3rd quarter, RI of round goby in the diet was significantly higher than in the 1st and the 4th quarter (Fishers LSD post-hoc test, $p = 0.001$ and $p = 0.003$, respectively). Additionally, it was significantly higher in the 2nd quarter than in the 3rd quarter ($p = 0.022$). No difference was detected between the 1st and the 4th quarter ($p = 0.831$). Cannibalism (predation on young-of-the-year individuals of zander) was most crucial in the 1st and 4th quarters of the studied years.

The RI of round goby in the prey was different between the three size classes (ANOVA, $F_{2,23} = 3.552$, $p = 0.001$). It was significantly higher for $Z_{\geq 400}$ than for $Z_{<200}$ (Fishers LSD post-hoc test, $p = 0.018$). No significant difference was found between $Z_{200-399}$ and $Z_{<200}$ ($p = 0.075$) and $Z_{200-399}$ and $Z_{\geq 400}$ ($p = 0.489$). Regarding the number N (%), biomass B (%) and frequency of occurrence

F (%) of prey taxa (supplementary Table S1), it is most notable that round goby comprised high percentages of ingested biomass for $Z_{200-399}$ ($52.8 \pm 28.5\%$; 19.3–90.1%) and $Z_{\geq 400}$ ($42.4 \pm 44.2\%$; 0–99.2%). In the warmer 2nd and 3rd quarters of both years, it composed 24.6–90.1% and 52.3–99.2% of ingested biomass of $Z_{200-399}$ and $Z_{\geq 400}$, respectively. In the colder 1st and 4th quarters, percentages of round goby biomass in the diet was much lower (16.2–42.9% for $Z_{200-399}$ and 0–8.8% for $Z_{\geq 400}$).

Cluster analysis was carried out to show similarities in prey composition of zander between the years 1995/1996 and the two years of our study (2/2011–1/2012 and 2/2012–1/2013). The related dendrogram (Figure 5) shows relatively high similarities in the prey composition of all considered years. However, the years 1995 and 1996 on the one side and the 1st and 2nd years of our study on the other side formed two clearly differentiable clusters separating at 78.1% of Bray-Curtis similarity.

Growth patterns

Calculated by the von Bertalanffy growth equation, zander reached an asymptotic length (TL) of 937 mm (Appendix 1). In the first autumn, some of the investigated young-of-the-year zander reached more than 200 mm TL. After four years of growth, the mean calculated TL was 531 mm. Zander from the Kiel Canal showed an isometric growth characteristic (Appendix 2). Length and weight proportions remained the same during their lifetime. Mean condition factor (K) for zander of TL ≥ 200 mm was 0.81 ± 0.07 . The index of growth performance (P) for all investigated fish was 3.13.

In comparison with zander from other typical brackish water bodies in northern Germany (Kafemann and Thiel 1998), where the asymptotic length (L_∞) ranged from 792–987 mm (Table 2), specimens of our study showed a high value.

Table 3. Mean total length at age (mm) calculated for the age of 1–6 years by the von Bertalanffy growth equation. Data of 1995/1996 by Kafemann and Thiel (1998).

Age (years)	Mean total length (mm)	
	Kiel Canal 1995/1996	Kiel Canal 2011–2013
1	141	219
2	266	343
3	353	446
4	424	531
5	474	601
6	524	659

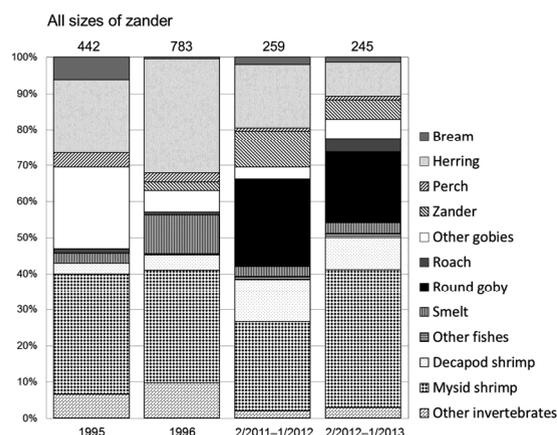


Figure 6. Relative importance index (*RI*) of prey taxa for zander in 1995/1996 and in the 1st (2/2011–1/2012) and 2nd (2/2012–1/2013) years of our study. The category “other gobies” includes sand goby and common goby. Numbers of examined specimens are given above bars.

There is also an obvious difference between the L_{∞} calculated for the Kiel Canal for the years 1995 and 1996 ($L_{\infty} = 685$ mm, 95% confidence interval = 615–754 mm; Kafemann and Thiel 1998) and the higher L_{∞} of our study ($L_{\infty} = 937$ mm, 845–1029 mm; 2011–2013).

Additionally, the mean total length at the age of 1–6 years (Table 3) was significantly higher in our study than in 1995/1996 (Wilcoxon signed-rank test, $Z = 21.000$, $p = 0.028$). The estimated asymptotic length for zander from the Kiel Canal from 2011–2013 is also higher than the calculated values for the Greifswalder Bodden and the Schlei, which both represent large brackish waters adjacent to the Baltic Sea with relatively low depths. Growth parameters for zander in our study are close to the parameters calculated for zander from the highly productive tidal Elbe River in 1992/1993 (Kafemann and Thiel 1998). In our study, zander realized two

thirds of their growth capacity ($1/k + t_0$) after 4.86 years (Table 2). This growth capacity (see Hohendorf 1966) is again comparable to the value for the tidal Elbe River in 1992/1993 (4.99 years). The index of growth performance (P) after Pauly (1979) has the same characteristic with 3.13 (Kiel Canal) and 3.18 (Elbe River). A higher Fulton’s condition factor of the specimens in our study (0.81 ± 0.07) indicates a better constitution than in 1995/1996 (0.75 ± 0.11), with nearly as high value as for the tidal Elbe River in 1992/1993 (0.84 ± 0.12).

Discussion

Trends and interrelations in biomasses of fish species

Due to the similar trends in the development of the biomass of zander and round goby, we hypothesize that the increase in zander biomass 2008–2011 could be related to the high availability of round goby. While the biomasses of both species were highest in 2011, they declined in 2012. The biomass of round goby dropped to about one third within one year whereas the biomass of zander slightly decreased (Figure 3). We hypothesize the decrease in round goby biomass to be caused by the high zander abundance.

Additionally, in 2013 and 2014 low round goby catches were common in the deeper parts of the Kiel Canal, whereas zander catches remained on a high level (own observations and personal communication fishermen). High abundance of round goby was still present in the shallow, rocky areas near to the shore (own observations and information by anglers).

According to Kornis et al. (2012), there is some evidence that high predation by piscivorous fish can lead to a control of round goby abundance. As an example, a population of round goby in Lake Erie, USA, declined during 2004–2008 after burbot *Lota lota* (Linnaeus, 1758) had started to use it as a major prey organism in 2003 (Madenjian et al. 2011). We hypothesize this effect of population control to take place in the Kiel Canal as well. Predation of round goby by zander may contribute to long term stabilization of the round goby population in the Kiel Canal at relatively low abundance. Long-term monitoring will show if a permanent relationship really exists between the biomasses of round goby and zander as its predator.

However, our data from trawling can only reflect trends in biomass in the deeper water area away from the shore. In the shorelines of the

Kiel Canal, covered by stone packaging, the biomass of round goby is supposed to be higher than in the sandy/muddy deeper areas (compare Ray and Corkum 2001). In addition, we suppose that the trawl net used may have caused different catchabilities for zander and round goby, e.g. due to differences in escape behaviour of both species. Overall, we hypothesize that the real biomass of round goby was much higher than determined.

Diet composition and shift

The importance of round goby as prey, identified in our study, is the highest reported for the species zander. In the Curonian Lagoon, a large, shallow freshwater basin connected to the south-eastern Baltic Sea, Rakauskas et al. (2013) calculated by stable isotope analyses that round goby made up 17% (by biomass) of zander diet (August–September 2010, specimens of TL 283 ±54 mm). In contrast, during the same season (3rd quarters of 2011 and 2012), the zander diet from individuals of a comparable length ($Z_{200-399}$) consisted of 82.8 and 24.6% round goby (by biomass) in our study (supplementary Table S1).

Before round goby established in the Kiel Canal, Kafemann (2000) analysed the diet of small to large zander in the years 1995/1996. In that study, mysid shrimp had the highest relative importance (RI ; 32.2 ±1.4%) comparable to that in our study (31.4 ±9.6%) (Figure 6). Herring had the second highest RI in 1995/1996 with 26 ±8%, while in our study it was only half that value (13.4 ±5.8%). Small gobies (*Pomatoschistus* spp.) had a RI of 14.2 ±11.6% in 1995/1996, which was considerable higher than in our study (4.4 ±1.6%). RI of European smelt *Osmerus eperlanus* (Linnaeus, 1758) decreased from 6.7 ±5.6% in 1995/1996 to 2.9 ±0.1% in 2011–2013. Important prey items in our study were young-of-the-year zander with 7.7 ±3.3% of RI in comparison to 1.2 ±1.7% in 1995/1996.

As in our study, the consumption of prey species in 1995/1996 was strongly related to their seasonal availability. Kafemann (2000) described that zander suffered from the absence of adequate prey during summer when it fed mainly on small native gobies (*Pomatoschistus* spp.). These small gobiid species reach a maximum TL of only 95 mm (Miller 1986), while round goby reaches a maximum TL of about 250 mm (Sapota 2006). In our study, mean fresh weight calculated for round goby found in the stomachs of inspected zander specimens (6.36 ±7.92 g)

was about ten times higher than for *Pomatoschistus* spp. (0.57 ±0.46 g). Round goby, which was not existent in the prey composition in 1995/1996, accomplished 21.8 ±3.2% of RI throughout all length classes of zander and all seasons within our study.

The comparison of the diet of zander analysed in 1995/1996 with that of our study is limited due to different sizes of the study sites. Zander was taken along the entire Kiel Canal (~100 km) in 1995/1996, while our fish were taken from a smaller section (~6.5 km). Additionally, adult zander ($Z_{\geq 400}$) represented a smaller percentage of examined specimens in 1995/1996 (N ($Z_{<200}$) = 508, N ($Z_{200-399}$) = 512, N ($Z_{\geq 400}$) = 205) than in 2011–2013 ($Z_{<200}$ = 150, $Z_{200-399}$ = 193, $Z_{\geq 400}$ = 161). Nevertheless, the establishment of round goby clearly resulted in a change of zander prey composition.

Similar to the results of our study on the zander in the Kiel Canal, round goby invasion resulted in important diet shifts in numerous other predatory species in invaded ecosystems. For instance in the Baltic Sea area, important predators include the fish species cod *Gadus morhua* Linnaeus, 1758 and perch *Perca fluviatilis* Linnaeus, 1758 and the bird species great cormorant *Phalacrocorax carbo* (Linnaeus, 1758) and grey heron *Ardea cinerea* Linnaeus, 1758 (Jakubas 2004; Almqvist et al. 2010; Rakauskas et al. 2013). In Lake St. Pierre, St. Lawrence River, North America, Reyjol et al. (2010) found round goby as a prey item in 64.5% of non-empty stomachs of sauger *Sander canadensis* (Griffith and Smith, 1834), a species closely related to the zander.

The high seasonal variability in the prey composition of zander in the Kiel Canal might be a result of different habitat occupancy of zander and round goby. It seems that in the Kiel Canal, in contrast to that described for the Baltic Sea and the Laurentian Great Lakes (see Corkum et al. 2004), round goby occupies the stone packaging throughout the year, with part of the population migrating into the deeper, muddy and sandy areas for the summer.

The water temperature is almost stable throughout the entire water column due to ship introduced turbulences. A higher energy requirement in summer may force a part of the population away from the stone packaging to feed. The described migration pattern was supported by data from trawling (commercial and monitoring program), showing an increase in round goby abundance at the bottom in deeper parts of the channel in spring

which seems to be related to the increasing water temperature. In contrast to round goby, zander concentrate in the deeper areas throughout the year (personal communication fishermen). Therefore, while there is low potential for zander encountering round goby in winter, the round goby summer bottom-migration exposes them to the predator.

Another reason could be a high availability of other prey species in winter. Spring migration of herring, into the Kiel Canal, normally results in higher percentages of this species in the diet and additionally young-of-the-year zander are probably easy to capture when using the same areas as adult zander for wintering. In terms of energy density, with all likelihood, round goby do not generally provide a preferable food item. Ruetz et al. (2009) report the average energy content of round goby in the Muskegon Lake region, North America, to be 4.326 J/g of wet mass. This is comparable to that of *Pomatoschistus* spp. and herring from the German Wadden Sea (4.62 J/g and 4.54 J/g, respectively) and smelt from the river Elbe, Germany (4.16 J/g) found by Temming and Herrmann (2003). However, Jakubas (2004) reports that the calorific value of round goby in the Gulf of Gdańsk can reach 6.3 J/g of wet mass during its spawning period. This can make the round goby a preferable food in this time of the year. Our observations indicated that the spawning period of round goby almost coincided with the warmer quarters in which zander consumed high amounts of this prey.

Due to the importance of round goby in the diet of zander, the predatory pressure on other previously more intensively used prey species may decline. In the Kiel Canal, this possibly especially affects native gobiids (*Pomatoschistus* spp.) which represented a major prey item in zander diet before the round goby invasion. We hypothesize that this can partially compensate for negative effects, such as competition for nesting sites and food. Otherwise, the assumed increased biomass of zander can reduce or even eliminate the effect of reduced predatory pressure.

Growth patterns

We suppose that better growth and condition factor of zander was caused by the occurrence of high round goby biomass in the Kiel Canal. The high availability of this prey, at least during summer, seemed to be an important stimulator for growth of zander. This is clearly supported by the fact that, before the round goby invasion, zander suffered from the absence of adequate

prey in summer while feeding mainly on small native gobies (*Pomatoschistus* spp.) (Kafemann 2000).

Fish growth in general is correlated with the availability of adequate food resources (compare Boisclair and Leggett 1989). For zander, a limitation of growth by food availability was described by Thiel (1989) for young-of-the-year and by Winkler (1991) for older individuals. As round goby often appears in high abundance, it can represent a profitable food source.

The low asymptotic length (L_{∞}) of zander in the Kiel Canal before round goby invasion (Table 2) indicates the low productivity (for zander) of this ecosystem at that time (1995/1996). Therefore, the high profit from the establishment of round goby (L_{∞} almost one third higher in 2011–2013) is possible. Zander populations in other low-productive ecosystems such as the Greifswalder Bodden and the Schlei are more likely to profit from round goby establishment than those in high productive systems such as the tidal Elbe River.

Conclusions

As hypothesized, zander in the Kiel Canal profit from the appearance of round goby by showing better growth patterns. From our data, we can safely conclude that round goby represents a major food taxon for zander in the canal and that growth has improved since 1995/1996 when no round goby were available as food.

We assume that negative effects on the zander in the Kiel Canal caused by the round goby invasion are marginal. A strong competition for food of young-of-the-year zander and round goby in the Kiel Canal seems unlikely. This is supported by the fact that in diet analyses of specimens caught at the study site, we found only a small overlap in the diets of round goby and young-of-the-year zander (unpublished data). In the inspected region, mysid shrimps, that are a main food for young-of-the-year zander, only occurred in low percentages in the stomachs of *N. melanostomus* (<5% of relative importance). Predation of round goby on zander eggs is likely infrequent due to nest guarding behaviour of zander. In contrast to the closely related walleye *Sander vitreus* (Mitchill, 1818) in North America, which is affected by egg predation from round goby (Roseman et al. 2006) and does not exhibit parental care or nest guarding (Nate et al. 2001), zander defends its nest against predators (Wundsched 1963).

Overall, the establishment of round goby may lead to higher yields of the commercially important zander for fisheries at the Kiel Canal. Nevertheless, round goby populations, biomass/growth of zander and trawl catch results should be monitored in the long term. The assumed biological control effect on round goby by zander may result in low abundance of the invader, and with a reduced availability of round goby, zander growth could decrease in the future again. Improvements for zander (and other predators) from round goby invasion are likely a phenomenon of water bodies that were limited by some kind of resource availability before the invasion.

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The following supplementary material is available for this article:

Appendix 1. Length-growth curve estimated for zander from the Kiel Canal (N = 945; years 2011–2013).

Appendix 2. Length-weight relationship of the studied zander from the Kiel Canal (N = 961; years 2011–2013).

Table S1. Number, biomass and frequency of occurrence of prey taxa consumed by zander in the Kiel Canal.

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