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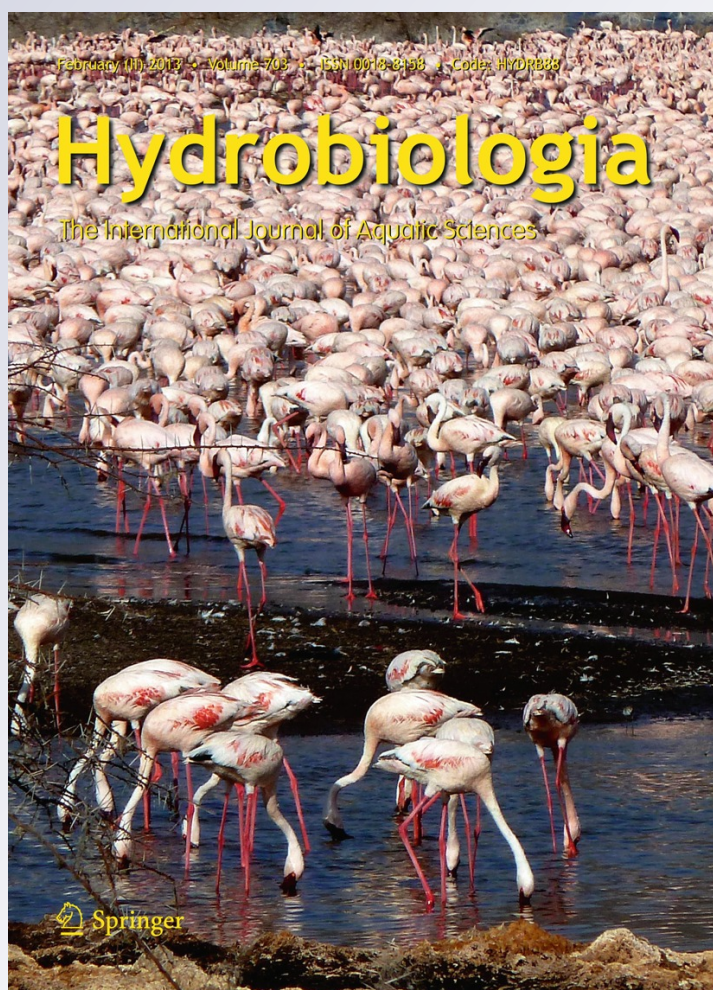
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Comparative feeding ecology of invasive Ponto-Caspian gobies

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Abstract Invasions of Ponto-Caspian gobiid fishes are suspected to cause regime shifts in freshwater ecosystems. This study compared the trophic niche differentiations of *Neogobius melanostomus* and *Ponticola kessleri* in the upper Danube River using stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), gut content analyses and morphometric analyses of the digestive tract. Both species were identified as predacious omnivores with high dietary overlap and a generalistic feeding strategy. Amphipods (especially invasive *Dikerogammarus* spp.) contributed 2/3 to the index of food importance. $\delta^{15}\text{N}$ -signatures of *N. melanostomus* revealed an ontogenetic diet shift and significantly exceeded those in *P. kessleri* by $\sim 1.5\text{‰}$, indicating a niche separation of half a trophic level. *P. kessleri* had

shorter uncoiled intestinal tracts than *N. melanostomus*, indicating a narrower niche and adaptation to animal food. Trophic niches in both species expanded during the growth period with increasing intraguild predation and cannibalism in *P. kessleri* and increasing molluscivory in *N. melanostomus*. *P. kessleri* showed a higher degree of specialization and more stable feeding patterns across seasons, whereas *N. melanostomus* adapted its diet according to the natural prey availability. The feeding patterns of both species observed in the upper Danube River strongly differ from those in their native ranges, underlining their great plasticity. Both goby species consumed mainly other non-native species ($\sim 92\%$ of gut contents) and seemed to benefit from previous invasions of prey species like *Dikerogammarus villosus*. The invasive success of gobies and their prey mirror fundamental ecological changes in large European freshwater ecosystems.

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Introduction

Invasive species are considered one of the major threats to global freshwater biodiversity (Dudgeon et al., 2006; Geist, 2011). Successful invasions of alien species often result in a homogenisation of flora and

fauna, leading to a global ‘biomonotony’ (Mooney & Cleland, 2001; Beisel & Devin, 2007; Moyle & Mount, 2007).

Several invasive Ponto-Caspian gobiid fish species (Teleostei: Gobiidae) have colonized both freshwater and marine ecosystems worldwide with a great potential to cause ecological regime shifts. Goby invasions strongly affect the Laurentian Great Lakes area in North America (Jude et al., 1992; Charlebois et al., 1997; Ricciardi & MacIsaac, 2000; Gutowsky & Fox, 2011; Lynch & Mensinger, 2011) as well as European waterbodies (Corkum et al., 2004; Sapota & Skóra, 2005; Kakareko et al., 2009), including the River Rhine (Borcherding et al., 2011) and the Danube River (Ahnelt et al., 1998; Simonović et al., 1998; Stráňai & Andreji 2004; Jurajda et al., 2005; Harka & Bíró, 2007). The Danube River is the second largest river in Europe, with a total length over 2,800 km. In 1992, the Rhine–Main–Danube junction (RMD canal) connected the formerly separated major drainage systems of the Rhine–Main to the Danube and became one of the most important European shipping routes. Consequently, the Danube River became a part of the so-called Southern Invasive Corridor (Black Sea–Danube–RMD canal–Main–Rhine–North Sea), one of the most important European long-distance dispersal routes for many aquatic invasive species (Bij de Vaate et al., 2002; Karatayev et al., 2008; Leuven et al., 2009; Panov et al., 2009).

In the German section of the Danube River, the bighead goby, *Ponticola kessleri* (Günther, 1861), was first recorded in 1999 (Seifert & Hartmann, 2000), followed by an invasion of the round goby, *Neogobius melanostomus* (Pallas, 1814), which arrived in 2004 (Paintner & Seifert, 2006). According to our own observations, especially the invasive round goby could be found in densities of up to 20 individuals per square metre using electroshocking, and range expansion is still ongoing.

Both fish species have been suspected to cause serious and lasting changes of ecosystems by affecting native communities (Lodge, 1993; Ricciardi, 2001; Minchin, 2007; Van Riel et al., 2007). Especially the rapid expansion of *N. melanostomus* has been linked to the decline of native fish diversity and abundance (Crossman et al., 1992; Jude et al., 1992; Freyhof, 2003; Jurajda et al., 2005; Karlson et al., 2007) and to negative population trends in prey species (Vanderploeg et al., 2002; Barton et al., 2005; Lederer

et al., 2006; Pennuto et al., 2010). Recently, *N. melanostomus* also started invading headwater habitats in the Great Lakes watershed of North America (Kornis & Vander Zanden, 2010; Bronnenhuber et al., 2011), highlighting potential threats to areas with high endemic aquatic biodiversity (Poos et al., 2010). For understanding both the invasive potential and the ecosystem impact of gobies on recently invaded headwater habitats, a better understanding of their ecological and trophic niche differentiation is crucial. While feeding strategies, food resource utilization and food preferences of *N. melanostomus* and *P. kessleri* are documented for specific distribution areas such as the middle and lower Danube River (Simonović et al., 2001; Borza et al., 2009; Poláček et al., 2009), in the Laurentian Great Lakes and their tributaries (Johnson et al., 2005; Kornis et al., 2012), or the Gulf of Gdansk (Skóra & Rzeznik, 2001; Karlson et al., 2007), the trophic interactions between sympatric invasive gobies and benthic communities remain largely unknown. Stable isotope analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have been shown to be powerful markers for middle-to-long-term feeding patterns and trophic niche assessments (Vander Zanden et al., 1997; Post, 2002; Perga & Gerdeaux, 2005), and can complement gut content analyses which provide information on short-term feeding patterns. To date, few studies have combined stable isotope analyses with gut content analyses of invasive gobies in freshwater habitats. Seasonal differences between the feeding habits of both gobies (Borza et al., 2009) suggest an ontogenetic diet shift in *N. melanostomus* nutrition (Campbell et al., 2009) and underline the importance of better understanding the trophic niche separation of gobies and their impacts on aquatic food webs and endemic aquatic biodiversity.

To date, studies on the feeding ecology of gobies, particularly of *P. kessleri*, are limited by only few examined specimens and single sampling timepoints. They thus do not provide a reliable picture (Borza et al., 2009). As most recent studies were focused on specific lotic or marine habitats, there is also limited knowledge on the recently invaded (headwater) habitats, i.e. sampled before invasion-induced changes like food resource limitation or potential dietary adaptations occur.

The objectives of this study were to (i) compare the trophic niche differentiation between *N. melanostomus* and *P. kessleri* using a combination of stable isotope

analyses ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$), gut content analyses and morphometric analyses of the digestive tract; (ii) determine food preferences using a comparison of the natural occurrence of benthic invertebrates as prey with gut contents; and to (iii) assess the role of invasive vs. native prey species in the invasive success of both goby species, considering seasonal patterns. We hypothesize that the invasive success of both species can be largely explained by generalist feeding patterns.

Materials and methods

Field sampling

Fishes and benthic invertebrates were sampled in early summer (29th March–18th June) and late summer (16th August–18th October) 2010 at ten representatively distributed river stretches along the recently invaded headwater reaches of the Danube River, Germany (Fig. 1; Table 1). Sampling covered a total river length of about 200 km within the early and late phases of one growth period. In order to avoid the introduction of a systematic sampling bias (e.g. due to trends in water temperatures), even and uneven river stretches (first even and then uneven numbers) of the numbered river stretches (Fig. 1) were sampled consecutively. A total number of 235 specimens of *P. kessleri* and 283 *N. melanostomus* were collected from shorelines (in ~60 cm water depth) by point abundance electrofishing (ELT62-IIID; Grassl GmbH, Berchtesgaden, Germany).

Several recent studies on neogobiids did not consider the effects of fish size on feeding habits (e.g. Adámek et al., 2007; Borza et al., 2009; Polačik et al., 2009), whereas many other studies described ontogenetic diet shifts in *N. melanostomus* (French & Jude, 2001; Phillips et al., 2003; Barton et al., 2005; Johnson et al., 2005; Karlson et al., 2007; Campbell et al., 2009). The known size effects in at least one of the species analysed were accounted for in two ways: (i) specimens were size-class selected (8–12 cm) with mean total lengths (L_T) of 10.0 cm (SD = 1.9 cm) for *P. kessleri* and 9.6 cm (SD = 1.3 cm) for *N. melanostomus* (see, Table 2). (ii) To test for this effect in *N. melanostomus* nutrition, an additional sample of 16 specimens (L_T of 2–14 cm) was collected at river stretch no. 08_Regensburg (49°01'01.95"N; 12°09'21.09"E) on October 15, 2010 (Fig. 1; Table 1).

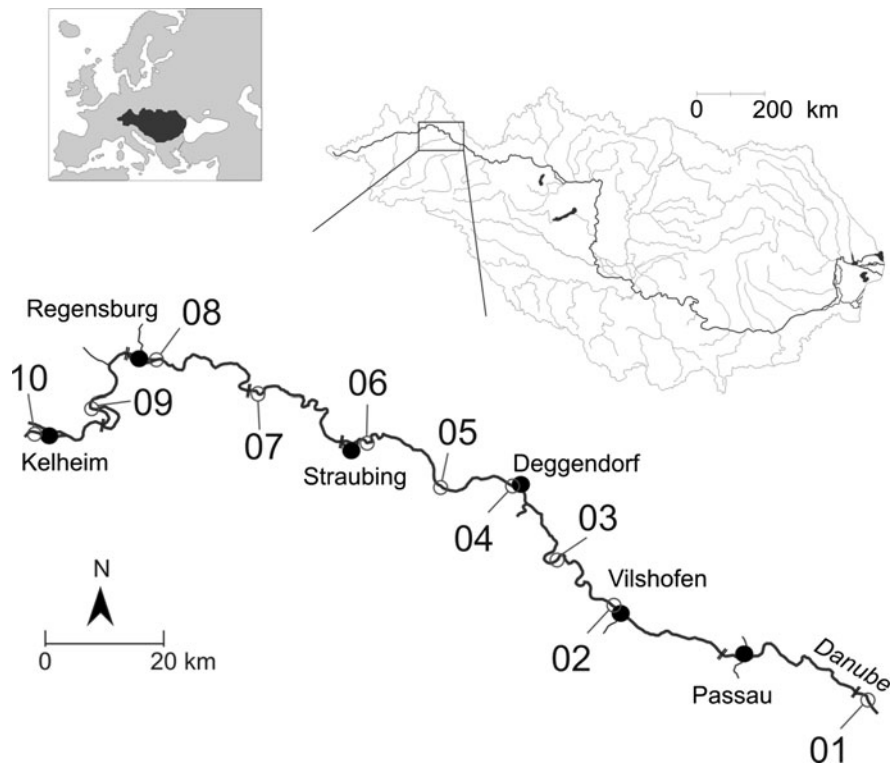
L_T was measured to the nearest mm, wet mass was weighed to the nearest 0.2 g and sex was determined by the morphology of the urogenital papilla (Miller, 1984; Marentette et al., 2009). The gobies were killed using a lethal dose of anaesthetic and immediately frozen on dry ice to avoid degradation of gut contents and muscle tissue.

To obtain quantitative benthos samples, a suction sampling device was designed, modified from Brooks (1994) and Brown et al. (1989). This flow-through system, driven by a water pump (18 l/min, 1.0 bar; Barwig, Germany) inside a duct, integrated a 1000 × 500 µm-mesh for filtering benthic organisms. A flexible tube (Ø = 16 mm with a brush frontend) was used to scrub and collect benthic invertebrates from surfaces and interstices. Efficiency was evaluated in laboratory tests, where mean catch rates of 40.2% (SD = 6.6%, $n = 5$, duration = 120 s; substratum Ø = 5–8 mm) and 26.4% (SD = 8.8%, $n = 5$, duration = 120 s, substratum Ø = 8–16 mm) of the amphipod *Gammarus pulex* (L., 1758) were observed. This suction sampling device allowed for standardized sampling including the collection of gastropods and bivalves. Suction samples were collected from the same sites where gobies were sampled (~60 cm water depth, duration = 120 s). Altogether 190 samples (early summer: $n = 105$, late summer: $n = 85$) of benthic invertebrates were preserved in 70% ethanol immediately after capture. Benthic invertebrates were identified to the lowest possible taxon considering manageable taxonomical levels (e.g. Chironomidae, Oligochaeta). Owing to immaturity and thus poorly developed identification characters, amphipods often could not be determined to species level and thus were counted as 'Amphipoda'. Organisms belonging to the same taxon or cumulative category were counted and expressed as catch per unit effort [CPUE (min^{-1})]. The percent volumetric proportion of each taxon within the sample was visually estimated using a stereo microscope. The values were expressed as 'visually estimated proportion of volume' (%).

Stable isotope analysis

To obtain markers for middle-to-long-term feeding pattern and trophic niche assessment, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analyses of goby specimens and of the most abundant prey items were conducted. $\delta^{13}\text{C}$ and

Fig. 1 Study area with ten sampling stretches covering the goby invasion front along the headwater reaches of the Danube River. European context and location within the drainage area of the Danube River are highlighted. *Filled circles* denote important cities



$\delta^{15}\text{N}$ are relative isotope ratios calculated as $(R_{\text{sample}}/R_{\text{standard}}) - 1$, where R is the ratio of the heavy and the light isotopes and standard is Vienna-PeeDee Belemnite (V-PDB) in the case of carbon and atmospheric N_2 in the case of nitrogen. Pieces of fish flank muscle tissue (about $0.5\text{--}1.0\text{ cm}^3$) were sampled and defatted with a chloroform–methanol (2:1) solution. Benthic invertebrates were held in tap water for 24 h to empty their guts. Subsequently, samples were snap-frozen using liquid nitrogen and stored at -18°C until further analysis. The additional set of samples with greater length variation was analysed to test for (i) correlations between L_T and $\delta^{15}\text{N}$ signatures, and (ii) a diet shift between muscle tissue and gut contents. The $\delta^{15}\text{N}$ values of the gut contents were calculated as averages weighted by their ‘index of food importance’ from mean $\delta^{15}\text{N}$ signatures of benthic invertebrates collected from the upper Danube River (Table 2). This approach was preferred over the direct determination of the isotopic composition of the gut content because a much larger number of replicated measurements for the different food items could be used, better reflecting the average of each food component than the snapshot found in the gut. Furthermore, assumptions on whether

the gut content did still reflect food resources despite digestion or addition of mucus, which may have already changed the isotopic composition of the gut content, can be avoided by this approach. After ultrasonic cleaning, all samples were oven-dried (40°C for 48 h) and ground to homogenous powder, using a mixer mill. Samples of $0.3\text{--}0.4\text{ mg}$ were weighed into tin cups and combusted in an isotope ratio mass spectrometer (Delta plus, Finnigan MAT, MasCom GmbH, Bremen, Germany) interfaced (via ConFlo II, Finnigan MAT, MasCom GmbH, Bremen, Germany) with an elemental analyser (EA 1108, Carlo Erba, Thermo Fisher SCIENTIFIC, Milan, Italy) and a pyrolysis unit (HT Sauerstoffanalysator, HEKAtech GmbH, Wegberg, Germany). Repeated analyses of a solid internal laboratory standard (bovine horn, run after each ten samples) showed maximum standard deviations of 0.15‰ for $\delta^{15}\text{N}$ and 0.15‰ for $\delta^{13}\text{C}$ values.

Fish gut analyses

The digestive tract was removed by cutting off the caudal end of the oesophagus (posterior pharyngeal

Table 1 Ten representatively distributed sampling stretches along the upper Danube River with first recordings of *P. kessleri* (Pk) and *N. melanostomus* (Nm), sorted in upstream to downstream order

Sampling stretch		First recording	Lower boundary		Upper boundary	
No.	River stretch	Pk/Nm	rkm	GPS	rkm	GPS
10	Kelheim	2010 ^a /2010 ^a	2,409	E 11°56'27" N 48°54'29"	2,418	E 11°50'12" N 48°54'01"
09	Bad Abbach	2008 ^a /2009 ^a	2,393	E 12°00'13" N 48°57'57"	2,400	E 12°02'05" N 48°56'03"
08	Regensburg	u/u	2,373	E 12°10'41" N 49°00'34"	2,377	E 12°08'29" N 49°01'22"
07	Geisling	u/u	2,350	E 12°23'37" N 48°58'51"	2,354	E 12°21'02" N 48°58'36"
06	Straubing	1999 ^b /2004 ^c	2,309	E 12°42'26" N 48°53'34"	2,317	E 12°36'56" N 48°53'49"
05	Mariaposching	u/u	2,292	E 12°52'12" N 48°50'28"	2,298	E 12°47'46" N 48°49'33"
04	Deggendorf	u/u	2,280	E 12°59'50" N 48°47'31"	2,289	E 12°54'26" N 48°50'40"
03	Aichet	u/u	2,267	E 13°03'08" N 48°43'37"	2,273	E 13°02'15" N 48°44'32"
02	Vilshofen	u/2004 ^c	2,250	E 13°10'44" N 48°38'24"	2,259	E 13°05'41" N 48°41'02"
01	Engelhartszell	2002 ^d /2003 ^d	2,196	E 13°46'29" N 48°28'32"	2,202	E 13°43'21" N 48°30'48"

Upper and lower boundaries of sampling stretches were delineated by river kilometres (rkm) and GPS-coordinates. ^a Own observations, ^b Seifert & Hartmann (2000), ^c Paintner & Seifert (2006), ^d Zauner (pers. com.), *u* uncertain first recordings

teeth) and the anal aperture. Oesophagus, oesogaster, and intestine were separated from other organs and the length of the uncoiled dissected intestinal tract was measured to the nearest mm. Gut contents from the posterior intestine were not analysed because of progressed digestion process. Therefore, the posterior intestine was cut off at the intestinal-rectal sphincter level following morphological findings of Jaroszewska et al. (2008).

The gut from the oesophagus to the middle intestine termination was weighed to the nearest 0.001 g before and after emptying to obtain the wet weight of gut contents. All food items from digestive tract samples were fixed in ethanol, identified and counted. As several relevant prey taxa in this study occurred in amounts too small for reliable weighing or volumetric measuring by water-displacement, the per cent contribution of all food items to the whole gut content was estimated using a stereo microscope following the procedure by

McMahon et al. (2005) and Polačik et al. (2009). The contributions of individual food items were expressed as 'visually estimated proportion of volume [%]'. For methodological comparisons of fish stomach content analyses and visual estimation of volumes, see also Hynes (1950) and Hyslop (1980). In addition, we refer to Karlson et al. (2007), who showed that dry weight of food components can even be estimated with sufficient accuracy from only the numbers and maximum lengths of items by means of conversion factors available from the literature. Crushed bivalves and amphipods were reconstructed from the contents of the intestinal mucus hulls whenever possible to gather taxonomically relevant parts of the exoskeletons.

Statistical analyses

According to Herder & Freyhof (2006), the relative importance of a food item *i* among all items *j* for a

Table 2 Mean $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with corresponding standard deviations and ranges for *N. melanostomus*, *P. kessleri* and important prey items (with $^{\#}$ = pooled samples, $n^{\#}$ = size of pooled samples, na = not analysed) of early and late summer 2010

Species	Season	System	n	$n^{\#}$	$\delta^{15}\text{N}$ (‰)			$\delta^{13}\text{C}$ (‰)		
					Mean	SD	Range	Mean	SD	Range
<i>N. melanostomus</i>	Early summer	Pisces	61		15.07	0.48	13.65–16.24	–28.98	1.03	–30.74 to –26.67
	Late summer	Pisces	63		15.04	0.72	11.97–16.43	–28.98	0.94	–30.24 to –26.92
<i>P. kessleri</i>	Early summer	Pisces	57		13.78	0.68	11.60–15.19	–28.80	0.72	–30.62 to –27.30
	Late summer	Pisces	58		13.32	0.90	11.52–15.77	–28.58	0.87	–32.26 to –26.67
<i>Jaera sarsi</i>	Late summer	Pericarida	2 $^{\#}$	17, 26	12.95	0.85	12.10–13.81	–27.92	0.49	–28.41 to –27.44
<i>Leuciscus idus</i>	Late summer	Pisces	1		12.33	na	na	–27.45	na	na
<i>Dikerogammarus villosus</i>	Early summer	Amphipoda	6		11.55	1.04	10.03–12.86	–28.67	0.57	–29.25 to –27.67
<i>Potamopyrgus antipodarum</i>	Late summer	Gastropoda	2 $^{\#}$	19, 22	11.44	0.01	11.43–11.46	–17.59	0.11	–17.70 to –17.47
<i>Theodoxus fluviatilis</i>	Late summer	Gastropoda	2 $^{\#}$	3, 4	11.16	0.66	10.50–11.83	–31.16	0.74	–31.90 to –30.42
<i>Dreissena polymorpha</i>	Late summer	Bivalvia	2 $^{\#}$	3, 5	9.85	0.11	9.74–9.96	–31.22	0.54	–31.77 to –30.68
<i>Chelicorophium curvispinum</i>	Late summer	Amphipoda	1 $^{\#}$	11	9.75	na	na	–29.80	na	na
<i>Corbicula fluminea</i>	Late summer	Bivalvia	2 $^{\#}$	8, 20	9.74	0.23	9.51–9.58	–32.15	0.70	–32.84 to –31.45

population was calculated as the ‘index of food importance’ (I_{FI}) using visually estimated volumes and counted numbers of food items:

$$I_{\text{FI}}(i) = 100 O(i) V(i) \left(\sum_{n=1}^j O(i) V(i) \right)^{-1}$$

with O = % occurrence of prey i and V = visually estimated proportion of volume (%) of prey i . I_{FI} varies from 0 to 100, with higher values corresponding to a larger contribution of one food item compared with total gut content. As macrobenthos samples were treated like gut content samples, importance of naturally available prey was also calculated following the above mentioned formula as ‘index of environmental importance’ (I_{EI}) for each food item i .

Dietary overlap (O_{D}) between *N. melanostomus* and *P. kessleri* was calculated using the Schoener-Index (Schoener, 1970; see also Herder & Freyhof, 2006):

$$O_{\text{D}} = 1 - \left(0.5 \sum |p_{\text{a}} - p_{\text{b}}| \right) 100^{-1}$$

with p_{a} = percentage of a food item in species a, and p_{b} = percentage of a food item in species b. O_{D} ranges from 0 to 1, with 0 meaning total dissimilarity and 1 representing identical gut contents.

The Zihler index (Z_{I} ; Zihler, 1982) was calculated to assess digestive tract lengths as an indicator for diet adaptations according to Herder & Freyhof (2006):

$$Z_{\text{I}} = L(10M_{\text{f}}^{0.3})^{-1}$$

with L = length of the uncoiled intestinal tract (mm) and M_{f} = fish body mass (g).

The Z_{I} was used as it avoids body shape-dependent bias when comparing uncoiled digestive tract lengths. Bibliographical data (Karachile & Stergiou, 2010) displayed a range in Z_{I} for omnivores with preference to animal material of 1.5 to 12.7 ($n = 26$, mean $Z_{\text{I}} = 3.8$, SE = 0.5), whereas Z_{I} of herbivores ranged from 4.5 to 53.6 ($n = 5$, mean $Z_{\text{I}} = 20.3$, SE = 9.2).

Finally, a ‘prey-specific index of food importance’ was calculated (I_{P}) to obtain a prey preference analysis independent from benthic invertebrate sampling and therefore containing fish as prey. Only guts of specimens of a population in which a specific prey i occurred, were considered:

$$I_{\text{P}}(i) = (\sum I_{\text{FI}}(i)) n(i)^{-1}$$

with $I_{\text{P}}(i)$ = prey-specific index of food importance of prey i , $I_{\text{FI}}(i)$ = index of food importance of prey i , and $n(i)$ = number of guts containing prey i . The feeding strategies of gobies were then characterized in analogy to Costello’s method (Costello, 1990), modified by

Amundsen et al. (1996) by plotting I_P of each prey versus its frequency of occurrence, given by its relative proportion $n(i)$ %.

Fulton's condition factor [CF (g/cm³)] was calculated according to Anderson & Neumann (1996), subtracting the gut content mass:

$$CF = 100(M_f - M_g)L_T^{-3}$$

with M_f = fish body mass (g), M_g = gut content mass (g), L_T = total length (cm). The slope of the regression between length and weight for the selected specimens was 3.0 ($R^2 = 0.941$) for *N. melanostomus* and 3.3 ($R^2 = 0.949$) for *P. kessleri*, indicating completely isometric growth for *N. melanostomus* (Anderson & Neumann, 1996).

To assess food uptake and to test for the effects of the daytime of sampling on feeding behaviour, the index of stomach fullness (I_{SF}) was calculated following Moku et al. (2000) and Tudela & Palomera (1995):

$$I_{SF} = 100M_gM_f^{-1}$$

with M_g = gut content mass and M_f = fish body mass. Benthic invertebrates and food taxa were classified according to their biogeographical origin as 'indigenous' and 'invasive', species too small for taxonomic identification and species with non-allocatable biogeographical origin were classified as 'unassigned'. The proportions of these three classes were determined for the gut content samples of both goby species and for the benthic invertebrate samples.

For comparisons of mean values between species and seasons, One-Way ANOVA (SIA) or t tests (Z_1) were used if the criteria for parametric testings were fulfilled. Alternatively, non-parametric Mann–Whitney U -tests or Kruskal–Wallis tests (Bonferroni corrected) were applied (I_{FI} , I_{EI} , I_{SF} , CF, L_T , W). Significance was accepted at $P \leq 0.05$. Statistical analyses and plots were computed using SPSS 11.0 (IBM SPSS Statistics, NY, USA), PAST (Hammer et al., 2001) and Excel 2010 (MicrosoftTM).

Results

Both goby species were present throughout the sampling area, except for the most upstream sampling stretch where the first records were made in late summer 2010. The time elapsed as their first

recordings (Table 1) at downstream river stretches of the sampled river section were up to 6 years for *N. melanostomus* and up to 11 years for *P. kessleri*. Of all fishes captured, both goby species comprised 58% of all specimens in early summer (56% *N. melanostomus*, 2% *P. kessleri*) and 56% in late summer (52% *N. melanostomus*, 4% *P. kessleri*). Other species mainly comprised autochthonous cyprinids and percids, *Anguilla anguilla* (L., 1758) and to some extent *Lota lota* (L., 1758), *Silurus glanis* L., 1758 and *Esox lucius* L., 1758.

Stable isotope analysis

Highest $\delta^{15}\text{N}$ values of all investigated species were found in *N. melanostomus* with maximum values of 16.2‰ in early summer and 16.4‰ in late summer (Table 2). The mean $\delta^{15}\text{N}$ value in *N. melanostomus* of 15.1‰ significantly (ANOVA, $F_{1,116} = 142.630$, $P < 0.001$) exceeded that in *P. kessleri* in early summer by 1.3‰. A similar pattern was observed at the end of the growth period in late summer, when the mean $\delta^{15}\text{N}$ value in *N. melanostomus* (mean = 15.0‰, SD = 0.7) significantly (ANOVA, $F_{1,119} = 136.069$, $P < 0.001$) exceeded that in *P. kessleri* (mean = 13.3‰, SD = 0.9) by 1.7‰. Considering a constant enrichment of ^{15}N by maximum 3.4 ± 1.0 ‰ (Post, 2002) and by minimum 2.3 ± 0.2 ‰ (McCutchan et al., 2003) per trophic level (i.e. between prey and predator) in aquatic organisms, the significant differences in $\delta^{15}\text{N}$ values in both gobies (early summer $\Delta \delta^{15}\text{N} = 1.3$ ‰; late summer $\Delta \delta^{15}\text{N} = 1.7$ ‰) indicated a significantly lower trophic position of about half a trophic level in *P. kessleri* compared with *N. melanostomus*.

$\delta^{15}\text{N}$ values in the analysed benthic invertebrates ranged from 9.7 to 13.8‰. Filterfeeders like the amphipod *Chelicorophium curvispinum* Sars, 1895 as well as the bivalves *Dreissena polymorpha* Pallas, 1771 and *Corbicula fluminea* (O.F. Müller, 1771) had the lowest $\delta^{15}\text{N}$ values (means ranging from 9.7‰ to 9.9‰). Omnivorous *Dikerogammarus villosus* (Sovinskij, 1894) and the grazing gastropods *Theodoxus fluviatilis* (L., 1758) and *Potamopyrgus antipodarum* (Gray, 1843) had medium level $\delta^{15}\text{N}$ values (11.4–11.6‰). Highest invertebrate $\delta^{15}\text{N}$ values (12.9–14.3‰) were observed in the grazing isopod *J. istri* (12.1–13.8‰).

No differences in $\delta^{13}\text{C}$ values were observed in both gobies (means ranging from −28.6 to 29.0‰)

despite the large range found in benthic invertebrates (Table 2). $\delta^{13}\text{C}$ values of most food items ranged from -32 to -27‰ , except for *P. antipodarum*, which was less depleted (mean = $-17.6 \pm 0.1\text{‰}$).

The $\delta^{15}\text{N}$ values of muscle tissue and gut contents of the additional *N. melanostomus* sample set followed similar functions and were strongly dependent on L_T (Fig. 2). Both data were highly significantly ($r^2 = 0.82$; $P < 0.001$) described by a parabolic regression with size and a diet-tissue shift of 3.1‰ (SE 0.3‰). The residuals of the regression indicated that diet and muscle were predicted equally well with a slight parabolic trend in the residuals (Fig. 2, upper panel). The $\delta^{15}\text{N}$ value of the gut content of *N. melanostomus* changed with L_T during the observed growth-phase. Up to a L_T of 10 cm, $\delta^{15}\text{N}$ values increased by about 2.5‰ and then decreased again (Fig. 2, lower panel). Notably, the mean $\delta^{15}\text{N}$ value of the gut content was calculated from the mean $\delta^{15}\text{N}$ values of the detected species and thus reflects the change in the composition of the prey species but not an isotopic change within the individual prey species.

Diet and dietary overlap

Interspecific dietary overlap between both species was high and similar in early ($O_D = 0.66$) and late summer ($O_D = 0.69$). Crustacea were the dominant taxon consumed by *N. melanostomus* (about 2/3rd of total) and *P. kessleri* (about 3/4th of total) in both parts of the growth period (Fig. 3). *Dikerogammarus* spp. and invasive Amphipoda represented the most important food items, contributing, respectively, 73% (early summer) and 79% (late summer) of the total index of food importance in *P. kessleri*; 46% (early summer) and 60% (late summer) in *N. melanostomus*. Importance of Crustacea (amphipods) increased from early to late summer. To a lesser extent, insect larvae (mainly chironomids, but also Ephemeroptera, Plecoptera, Trichoptera (EPT) and other aquatic insects) were consumed by both fish species. Especially in *N. melanostomus*, consumption of chironomids was high in early summer (33%) and decreased to late summer (5%).

Only six out of 235 (2.1%) *P. kessleri* and two out of 283 (0.9%) *N. melanostomus* specimens had empty guts. Daytime did not affect the index of stomach fullness in *N. melanostomus* ($R^2 = 0.014$) and *P. kessleri* ($R^2 = 0.137$). The highest values of the

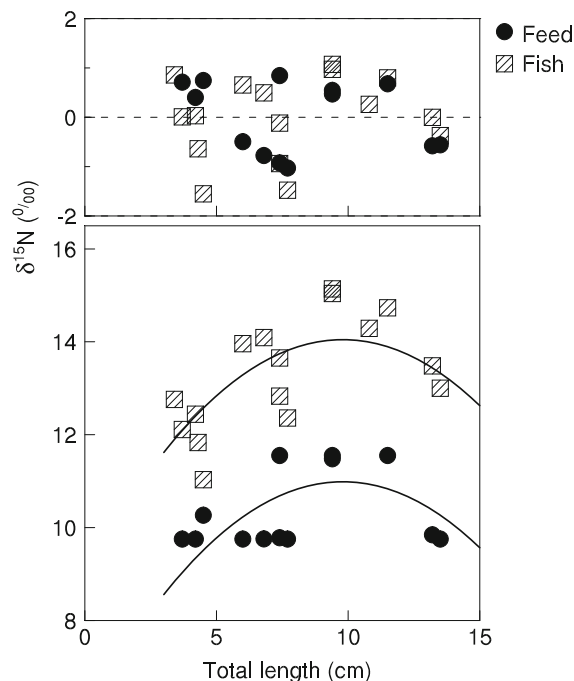
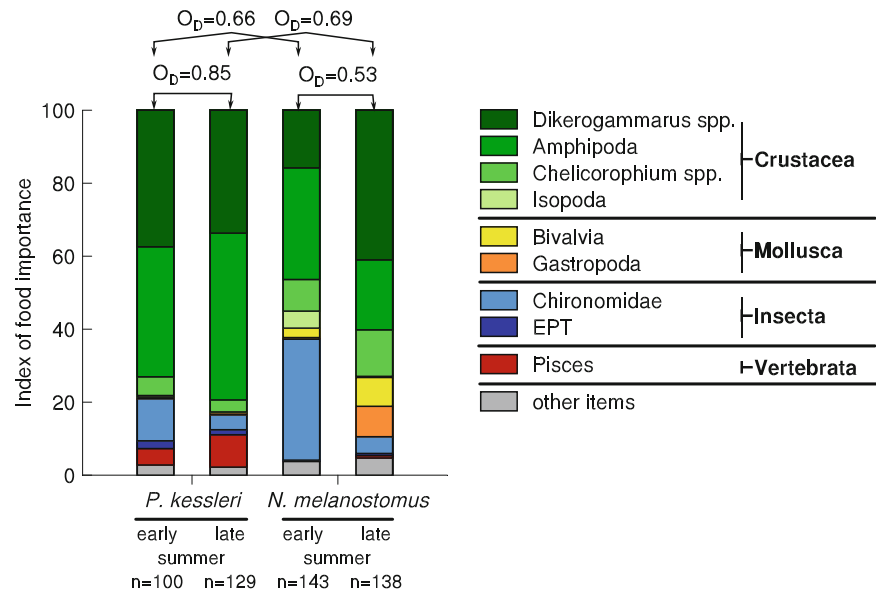


Fig. 2 Diet-tissue shift and ontogenetic diet shift in *N. melanostomus* (additional sample, $n = 16$) from sampling stretch no. 08_Regensburg ($49^{\circ}01'01.95''\text{N}$; $12^{\circ}09'21.09''\text{E}$), October 15, 2010. Lower panel: Change in the relative nitrogen isotope ratio of gut content (calculated, 'Feed', filled circles) and muscle tissue of *N. melanostomus* (measured, 'Fish', squares) in relation to total length; lines are a parabolic regression ($r^2 = 0.82$; $P < 0.001$) based on total length and the type of tissue. The $\delta^{15}\text{N}$ values of the gut contents (Feed) were calculated as averages weighted by their I_{FI} from mean $\delta^{15}\text{N}$ signatures of benthic invertebrates collected from the upper Danube River (Table 2). Upper panel: residuals of the parabolic regression

index of stomach fullness were found in *P. kessleri* with maximum values of 21.4 in early summer and 12.5 in late summer. The index of stomach fullness of *P. kessleri* (3.9 ± 2.6) significantly (Mann–Whitney U , $P < 0.05$) exceeded that of *N. melanostomus* (3.2 ± 1.5) in early summer but not in late summer. The intraspecific index of stomach fullness was seasonal in both species and additionally depended on sex in *P. kessleri* (Table 3). The index of stomach fullness of *N. melanostomus* in early summer was significantly (Kruskal–Wallis, $P < 0.01$) higher in females (3.6 ± 1.6) and (Kruskal–Wallis, $P < 0.001$) males (3.8 ± 1.7) than in late summer (females: 2.8 ± 1.2 , males: 2.8 ± 1.3). *P. kessleri* females revealed significantly (Kruskal–Wallis, $P < 0.05$) higher index of stomach fullness in early summer

Fig. 3 Mean seasonal dietary compositions of *N. melanostomus* and *P. kessleri*, as indicated by the index of food importance. Food items were combined to higher taxonomical groups. Ephemeroptera, Plecoptera and Trichoptera were combined to the group 'EPT', 'other items' consisted of debris, detritus, terrestrial insects, leaves and sand. Intra- and interspecific dietary overlaps (O_D) within and between seasons were calculated by the Schoener-Index (Schoener, 1970)



(4.7 ± 3.6) than in late summer (3.4 ± 2.0), whereas no significant seasonal difference in the index of stomach fullness was found in male *P. kessleri* (early summer: 4.0 ± 1.9 , late summer: 4.0 ± 2.4).

There was a distinct intraspecific seasonal shift in dietary composition of *N. melanostomus* ($O_D = 0.53$), as the index of food importance of molluscs in the diet significantly increased (Mann–Whitney U , $P < 0.001$) by a factor of five from early (3.1%) to late summer (16.2%), with a contrary picture in chironomids, where the index of food importance significantly decreased (Mann–Whitney U , $P < 0.001$) by a factor of 7. In *N. melanostomus*, significant changes between seasons were detected in 10 out of 14 food items (71%) resulting in a low seasonal dietary overlap ($O_D = 0.53$). In contrast, *P. kessleri* showed only significant changes in 4 out of 14 food items (29%) between seasons leading to a very high seasonal dietary overlap ($O_D = 0.85$). While intraspecific niche separation in *P. kessleri* remained stable from early to late summer, the trophic niche of *N. melanostomus* increased, as indicated by the decrease in niche overlap (O_D), demonstrating a greater plasticity in this species. The index of food importance of fishes as food items in *P. kessleri* was twofold higher in late summer (about 10%) than in early summer (about 5%), but this difference was not significant (Mann–Whitney U , $P < 0.7$). Considering only fishes as prey, *P. kessleri* consumed *N. melanostomus* (25%),

cyprinids (15%), *P. kessleri* (10%), European Perch (5%) and other fishes (45%). Consumption of Bryozoa was strictly limited to *N. melanostomus* and mysids were only consumed by *P. kessleri*, but contributed less than 2%. *Chelicorophium* spp., isopods, especially *Jaera sarsi* (Valkanov, 1938), zooplankton, oligochaetes and other items (terrestrial insects, debris, detritus, leaves, sand) were consumed by both species in overall low proportions.

Food availability and selection of food items

In early summer, abundance of benthic invertebrates was double the value from late summer (early summer: mean CPUE = 61 min^{-1} , SD = 68 min^{-1} ; late summer: mean CPUE = 35 min^{-1} , SD = 30 min^{-1} ; Kruskal–Wallis, $P < 0.01$). *Dikerogammarus* spp. and Amphipoda were dominant in benthic invertebrate samples in both parts of the growth period (Fig. 3). Their availability decreased most from early to late summer among all invertebrates ($\Delta \text{CPUE} = 18 \text{ min}^{-1}$; Mann–Whitney U , $P = 0.1$). Also the availability of Chironomidae significantly decreased from early to late summer ($\Delta \text{CPUE} = 13 \text{ min}^{-1}$; Mann–Whitney U , $P < 0.001$). The only significant increases from early to late summer in availability were detected in molluscs ($\Delta \text{CPUE} = 3.0 \text{ min}^{-1}$; Mann–Whitney U , $P < 0.001$) and *Chelicorophium* spp. ($\Delta \text{CPUE} = 7.5 \text{ min}^{-1}$; Mann–Whitney U , $P < 0.001$).

Table 3 Numbers and performance indicators of *P. kessleri* and *N. melanostomus* from the upper Danube River in early and late summer 2010: sex, mean and corresponding standard

deviation of total length (L_T), weight, index of stomach fullness (I_{SF}), Fulton's condition factor (CF)

Species	Season	Sex	n	L_T (cm)		Weight (g)		n	I_{SF}		n	CF (g/cm ³)	
				Mean	SD	Mean	SD		Mean	SD		Mean	SD
<i>P. kessleri</i>	Early summer	f	64	10.3	2.0	14.8	9.4	50	4.7	3.6	49	1.15	0.18
		m	39	9.7	1.5	12.1	6.1	31	4.0	1.9	31	1.15	0.14
	Late summer	f	75	10.2	2.1	14.6	9.9	75	3.6	2.0	75	1.17	0.32
		m	57	9.7	1.7	12.4	8.9	57	4.0	2.4	57	1.11	0.15
			235	10.0	1.9	13.7	9.1	213	3.9	2.6	212	1.15	0.23
<i>N. melanostomus</i>	Early summer	f	64	9.3	1.3	12.9	6.2	57	3.6	1.6	57	1.42	0.15
		m	80	9.3	1.7	12.6	6.1	67	3.8	1.7	67	1.38	0.11
	Late summer	f	71	9.7	0.8	13.3	4.0	71	2.8	1.3	71	1.41	0.14
		m	68	10.0	1.3	15.0	6.0	68	2.8	1.3	68	1.37	0.12
			283	9.7	1.3	13.4	5.7	263	3.2	1.5	263	1.39	0.13

In late summer, feeding on Gastropoda ($\Delta I_{FI}(\text{Gas}) = 7.9\%$; Mann–Whitney U , $P < 0.001$) and Bivalvia ($\Delta I_{FI}(\text{Biv}) = 5.3\%$; Mann–Whitney U , $P < 0.05$) significantly increased in *N. melanostomus* diet, while the increase was not significant in *P. kessleri* diet ($\Delta I_{FI}(\text{Gas}) = 0.2\%$; Mann–Whitney U , $P = 0.8$ and $\Delta I_{FI}(\text{Biv}) = 0.2\%$; Mann–Whitney U , $P = 0.8$). *Chelicorophium* spp. contributed 8.7% in early summer and 12.8% in late summer of *N. melanostomus* diet, but this increase was not significant (Mann–Whitney U , $P = 0.5$). The index of food importance of *Chelicorophium* spp. significantly (Mann–Whitney U , $P < 0.01$) decreased (early summer: 5.1%, late summer: 3.3%) in the diet of *P. kessleri*.

A comparison of the index of environmental importance with the index of food importance revealed seasonal changes of selectivity (preferences: ratio > 1 , avoidance: ratio < 1) in both fish species (Fig. 4). Even when environmental availability of food changed, *P. kessleri* maintained its dietary composition as indicated by almost horizontal arrows in Fig. 4a. *P. kessleri* positively selected *Dikergammarus* spp. both in early and late summer. The index of food importance of Amphipoda increased in *P. kessleri* (Mann–Whitney U , $P = 0.1$) and Amphipoda became the most selected food item in late summer. Consumption of fish doubled from early to late summer. Chironomids were consumed in either season, but were avoided in early summer (Mann–Whitney U , $P < 0.001$). Annelids and molluscs were almost completely refused. Other items were

consumed corresponding to their environmental availability.

In contrast, feeding behaviour of *N. melanostomus* was more opportunistic with a seasonal diet shift proportional to the changes in environmental availability as indicated by the arrows in Fig. 4b, which run almost parallel to the diagonal line. Nevertheless, *N. melanostomus* exhibited some selectivity. At the beginning of the growth period, chironomids were an important resource and the most preferred prey, but their index of food importance decreased significantly (Mann–Whitney U test, $P < 0.001$) in late summer. Low densities in late summer were compensated by significantly increased feeding on *Dikergammarus* spp. ($\Delta I_{FI}(\text{Dik}) = 25.2\%$; Mann–Whitney U , $P < 0.001$), while Amphipoda were sub-proportionally consumed. *Dikergammarus* spp. was an important resource and the most selected food item of *N. melanostomus* in late summer, while molluscs and *Chelicorophium* spp. were avoided (Fig. 4b). Annelids were rarely consumed. In spite of increasing importance due to higher availability in late summer, other food items were consumed in proportions mirroring their relative abundance in the environment.

Feeding strategies

The Costello's plot technique revealed similar generalized feeding strategies and a relatively wide niche with a broad diet spectrum for both investigated goby species (Fig. 5). *Dikergammarus* spp. and other

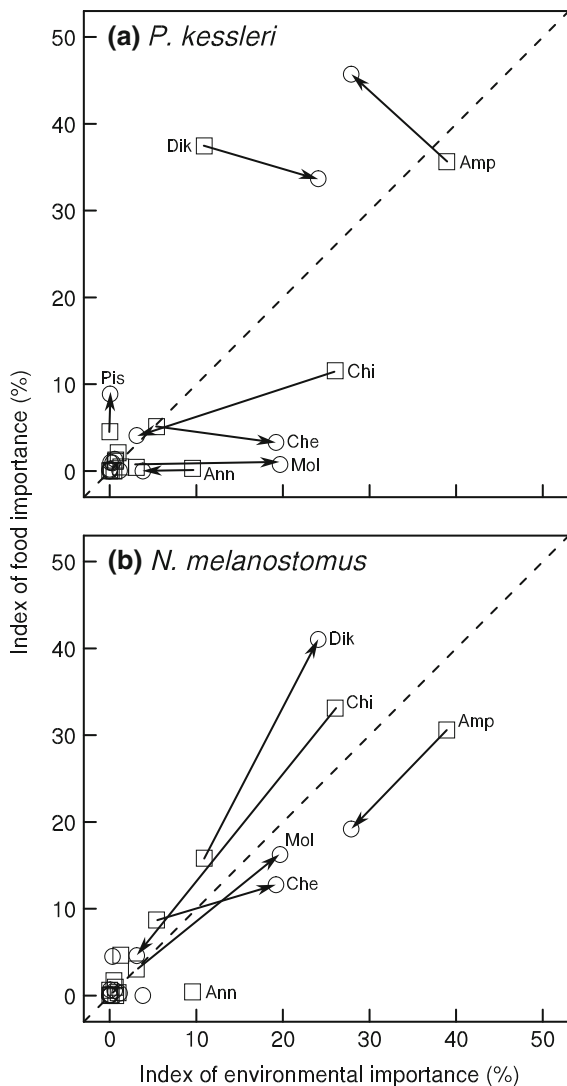


Fig. 4 Electivity plot displaying seasonal preferences of *P. kessleri* (a) and *N. melanostomus* (b) in early summer (squares) and late summer in (circles). Points beyond the angle bisector indicate preference (positive selection of food items), whereas points below indicate avoidance (negative selection of food items). Arrows denote the change of important items from early to late summer. *Dik* *Dikerogammarus* spp., *Amp* Amphipoda, *Chi* Chironomidae, *Mol* Mollusca, *Pis* Pisces, *Che* *Chelicorophium* spp., *Ann* Annelida

amphipods as prey were of high importance for both fish populations. Most of the individuals of the *N. melanostomus* population utilized many resource types simultaneously with a prey-specific index of food importance almost entirely below 40% (Fig. 5b), whereas different *P. kessleri* individuals specialized

on few resource types with prey-specific index of food importance >50% for *Dikerogammarus* spp., Pisces and Amphipoda (Fig. 5a). Fishes were consumed by 13 out of 100 (13%) *P. kessleri* in early summer and 19 out of 129 (15%) specimens in late summer. Also, the prey-specific index of food importance for fish increased about one third from early to late summer and reached 66% (Fig. 5a).

Invasive species as prey items

Invasive species dominated ($I_{FI} > 45\%$) the diets of *N. melanostomus* and *P. kessleri*, while indigenous ones only played a significantly (Mann–Whitney U , $P < 0.001$) minor role ($I_{FI} < 5\%$). The investigated Danubian invertebrate community consisted of a high fraction of invasive aquatic invertebrates ($I_{EI} = 39\%$) and a marginal fraction of indigenous ones ($I_{EI} = 3\%$). Considering taxa with unassigned origin ('unassigned'; Fig. 6) as missing values, ratios in indices of importance of invasive to indigenous species were 11:1 in *P. kessleri* ($I_{FI} = 92\%$), 14:1 in *N. melanostomus* ($I_{FI} = 93\%$), and 12:1 in benthic invertebrates ($I_{FI} = 92\%$). The dominant group within macroinvertebrate samples, the Gammaroidea, comprised 99.8% invasive taxa with Ponto-Caspian origin (*Dikerogammarus* spp. 90.2%, *Echinogammarus* spp. 7.5%, *Pontogammarus* spp. 1.9%, *Obesogammarus* spp. 0.2%) and only 0.2% autochthonous *Gammarus roeseli* (Gervais, 1835). Food resources utilized by gobies were not selected according to their biogeographical origin as no differences between the index of food importance and the index of environmental importance were observed in either category (Fig. 6).

Morphometric analyses

In line with the results of the gut content analyses, the Zihler-Index characterized both goby species as omnivores with preference for animal food items (predacious omnivores). The uncoiled intestinal tract in *P. kessleri* was significantly shorter (t test, $P < 0.001$) than in *N. melanostomus* ($n = 207$, $Z_I = 3.12 \pm 0.41$ and $n = 254$, $Z_I = 3.94 \pm 0.70$ for *P. kessleri* and *N. melanostomus*, respectively), indicating a slightly narrower niche by a higher adaptation of the digestive tract to animal food.

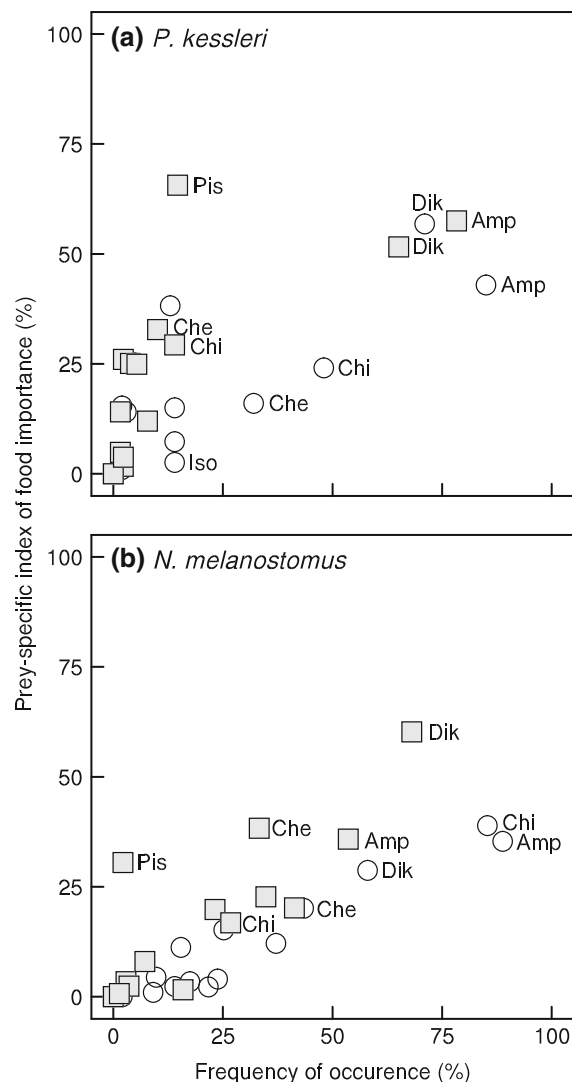


Fig. 5 Feeding strategies of *P. kessleri* (a) and *N. melanostomus* (b) in early (filled squares) and late summer (open circles) plotted according to Amundsen et al. (1996). The vertical axis represents the feeding strategy in terms of specialization or generalization, where specialization increases with increasing height. The proportion of goby individuals within the population preying upon a food item is explained by the horizontal axis. Thus, overall importance of a prey increases from the lower left to the upper right of the diagram. *Dik* *Dikerogammarus* spp., *Amp* Amphipoda, *Chi* Chironomidae, *Pis* Pisces, *Che* *Chelicerophium* spp., *Iso* Isopoda

Fulton's condition factor was significantly (Kruskal–Wallis, $P < 0.001$) lower in *P. kessleri* (1.15 ± 0.23) than in *N. melanostomus* (1.39 ± 0.14) in both seasons. Within species, no seasonal differences in L_T , weight and Fulton's condition factor were detected (Table 3).

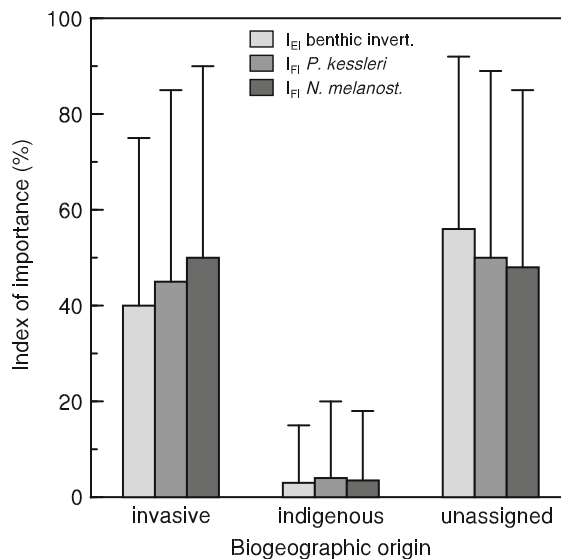


Fig. 6 Mean importance (and SD) of invasive species in the diets of *N. melanostomus* and *P. kessleri* compared with the mean environmental availability of benthic invertebrates as food resources in the headwater reaches of the Danube River, displayed by the index of food importance (I_{FI} , gobies) and the index of environmental importance (I_{EI} , benthic invertebrates). Species too small for taxonomic identification and species with non-allocatable biogeographical origin were classified as 'unassigned'

Discussion

Trophic relations and niche differentiation

This study characterized the trophic niches of two closely related goby species in the recently invaded headwater reaches of the Danube River. As evident from stable isotope, gut content and morphometric gut data, both species are predacious omnivores with similar trophic niches. As hypothesized, their great dietary breadths and opportunistic feeding strategies characterize both gobies as generalists, which may be important in explaining their invasive success. However, there are some important restrictions. Feeding on benthic invertebrates was not completely random, as amphipods, especially *Dikerogammarus* spp. were the most important and commonly preferred prey of both fishes and consumption of these taxa exceeded their environmental availability. The observed importance of amphipods may also be influenced by the size class (8–12 cm L_T) of fishes used to assess diets with the consequence of excluding the ontogenetic diet shift. This improved the detection of a seasonal diet shift in

N. melanostomus, highlighting their great plasticity, and a wide niche overlap between both gobiids. However, the transition from an amphipod-dominated diet to a mollusc-based feeding (found in this study for the additional sample of *N. melanostomus*) occurred at the chosen length and thus at least partly also captures the ontogenetically determined niche width. Also, the study design used herein was selected for the main purpose of comparing the same sizes of different species.

Ponticola kessleri showed a moderately higher degree of specialization and a more stable feeding pattern across seasons compared with *N. melanostomus*. In late summer, both gobies increased selective feeding. Although availability of *Chelicoropium* spp. and molluscs increased from early to late summer, *P. kessleri* food choice remained constant, as it strongly relied on *Dikerogammarus* spp. and amphipods during the whole growth period, while *N. melanostomus* increased feeding on items with increased availability. This indicates a narrower trophic niche in *P. kessleri* compared with *N. melanostomus*, feeding of which varied between seasons following resource availability leading to a niche expansion in this species from early to late summer. The increasing isotopic spacing ($\delta^{15}\text{N}$) between both species from early to late summer (by a factor of 1.3) corroborates the trophic niche expansion in *N. melanostomus*. As gut lengths depend on diet specification (Balfour, 1988), the longer digestive tract of *N. melanostomus* also suggests a more omnivorous generalist feeding than the more predacious niche associated with the shorter digestive tract of *P. kessleri*. This is corroborated by the observed wider spectrum of food items (including hard-shelled molluscs, even bryozoans and plant material) in *N. melanostomus*, while *P. kessleri* feeding is more restricted and contains a more carnivorous, easier digestible diet consisting mainly of amphipods and fish. The higher index of stomach fullness in *P. kessleri* indicates a generally higher food uptake in this species. Also, feeding behaviour of *P. kessleri* is more stenophag compared with the more euryphag *N. melanostomus*.

Neogobius melanostomus exhibits a pronounced and continuous ontogenetic diet shift, which determines a broad dietary niche at the population level. At a total length of about 10 cm, it switches from preying upon insects and crustaceans (increasing limb, Fig. 2)

to a mainly mollusc-dominated diet (decreasing limb, Fig. 2), which can also be interpreted as an increasing specialization at the individual level. The findings from the corresponding gut content analyses corroborate these results and mirror earlier findings from Campbell et al. (2009), who detected a diet shift from amphipods to molluscs at about 11 cm L_T in Lake Erie by mass balance simulation, assuming a fractionation of 3.4‰ (Post, 2002). Such dietary changes, based upon gut content analyses, have been also reported from other waterbodies in the Great Lakes area (French & Jude, 2001; Barton et al., 2005) and the Baltic Sea (Karlson et al., 2007) where this shift seems to occur between 6 and 11 cm L_T .

The trophic relations assessed by stable isotope analysis in this study are in line with the findings of Van Riel et al. (2006) from the lower River Rhine, where three trophic levels were distinguished with particular organic matter (POM) and phytoplankton as a base, primary and secondary consumers at medium level and top predators as highest level. Gobies were not considered in that study, as they had not invaded the River Rhine at that time.

The $\delta^{15}\text{N}$ values of the present study indicated a significantly lower trophic position (of about half a trophic level) of *P. kessleri* compared with *N. melanostomus* despite the fact that the gut content analyses would have predicted the opposite results as more fish (mainly *N. melanostomus*) was consumed by *P. kessleri* and more bivalves were consumed by *N. melanostomus*. This mismatch between the more predatory *P. kessleri* and one of their preys, *N. melanostomus*, could perhaps derive from differences in growth rates, excretion, digestive tract anatomy and physiology. In addition, digestibility of food, parasites and diseases might also play a role. The other $\delta^{15}\text{N}$ values of this study were within the range of values expected, with the bivalves as filter feeders at the lower end and both gobies as top predators at the upper end of the analysed trophic chain being about 3–4‰ above the bivalves. The $\delta^{15}\text{N}$ values of *N. melanostomus* were similar to those measured in the Gulf of Gdansk (about 14.2‰), where small *N. melanostomus* (L_T of 60–120 mm) tended to be more enriched in ^{15}N than medium-sized and large ones (Karlson et al., 2007). Analogously, $\delta^{15}\text{N}$ values clearly indicated an isotopic change with increasing L_T in *N. melanostomus* in this study. Both gut contents and muscle tissue exhibited the same behaviour, which indicates that the picture derived from the instantaneous

gut content analyses matches the long-term feeding picture derived from the muscle isotopic analyses. This interpretation is further supported by two findings: First, the diet-tissue shift is close to the expected diet-tissue shift for one trophic level with a consistent enrichment of ^{15}N within a range of 2.3‰ (McCutchan et al., 2003) to 3.4‰ (Post, 2002) per trophic level between prey and predator, which would not be true if the present food had differed from the previous food (Auerswald et al., 2010). Second, the residuals exhibited a slight parabolic trend as expected from the parabolic relations, consequently mirroring a low likelihood of a mismatch between the isotopic signatures of muscle tissue and stomach contents. Half-life times for marine goby muscles are reported to range around 25 days (Guelinckx et al., 2007, 2008) where new tissue contributes most to this fast apparent turnover (Maruyama et al., 2001). The increase by 2.5‰ when gobies grew from 4 to 10 cm may have occurred over a period of about 1 year assuming a growth rate of about 0.5 cm per month which agrees with the observations of this study. This provides sufficient time for equilibration.

Their flexible, generalist feeding strategy and the observed capability of an ontogenetic diet shift probably both contribute to a greater plasticity in realized trophic niche of *N. melanostomus*, which reduces intraspecific competition and which may add to the greater success (i.e. a factor of 25 greater abundance) of this species compared with *P. kessleri*. These specializing mechanisms, which increase resource utilization and thus reduced competition, have not been found in *P. kessleri*, which might cause a lower competitive ability against *N. melanostomus*. In addition, also interspecific competition (generally higher food uptake in *P. kessleri*) or lower habitat suitability can play a role.

Comparisons with other goby populations

In their native ranges, pronounced feeding on fish and amphipods has been observed in *P. kessleri*. Vasil'Eva & Vasil'Ev (2003) reported that in the Dniester estuary region, *P. kessleri* predominantly fed on small fishes, mainly small gobies (78–92%), and crustaceans (about 7%, mainly mysids and chelicorophiids), while molluscs, polychaetes and chironomids were less important. In addition, a seasonal variation in food composition with small fishes comprising one third in spring and up to

100% in summer and autumn was observed there for *P. kessleri*. The diet of native *P. kessleri* populations from the lower Danube was largely based on fish and amphipods (Polačik et al., 2009). A diet with a clear dominance of amphipods and low proportions of fish was found in non-native populations from the middle Danube River (Adámek et al., 2007; Borza et al., 2009; Polačik et al., 2009). Consequently, *P. kessleri* dietary niche is characterized by a restriction to fish and amphipods as prey, with a lower specialized feeding on fish in non-native populations, which is in line with the findings of this study from the headwater reaches of the Danube River.

The feeding behaviours of native and most invasive *N. melanostomus* populations differ from those of the non-native populations of the upper Danube River (analysed here), supporting their great dietary plasticity during invasion of new areas. A diet with an essential importance of molluscs (mainly bivalves) has been reported for *N. melanostomus* inside their native distribution range: Molluscs were most important food items (about 86% of gut contents) in the Sea of Azov area (Kovtun et al., 1974) and in Ponto-Caspian habitats such as the Bug estuary (~90%), the Grigoryevskiy estuary (~88%), the eastern Dnieper estuary (~83%) and the Azov Utlukskiy estuary (~68%), while crustaceans (gammarids, chelicorophiids), chironomids, annelids and fishes were of low importance (Pinchuk et al., 2003). Similarly, invasive *N. melanostomus* populations in the North American Laurentian Great Lakes (Ray & Corkum, 1997; French & Jude, 2001; Janssen & Jude, 2001; Barton et al., 2005; Johnson et al., 2005; Lederer et al., 2006; Kornis et al., 2012) and coastal waters of the Baltic Sea (Skóra & Rzeznik, 2001; Karlson et al., 2007) mostly fed on bivalves (*Dreissena* spp.) with occurrence of an ontogenetic diet shift. Shemonaev & Kirilenko (2008) observed intense molluscivory (~90% of diet by weight) for invasive *N. melanostomus* in a lentic reservoir of the River Volga.

In the lower Danube River, *N. melanostomus* preyed to a similar extent (prey specific importance) on molluscs and amphipods (Polačik et al., 2009). Simonović et al. (2001) observed pronounced molluscivory in *N. melanostomus* in the middle Danube. However, a great contribution of amphipods and chironomids to a broad diet were found in other non-native populations from the middle Danube River

(Polačik et al., 2009), even following a similar seasonal trend of chironomid depletion from early to late summer (Borza et al., 2009). Similarly, in Great Lakes tributaries, which did not contain *Dreissena* spp., Phillips et al. (2003) observed a diet without amphipods, instead being dominated by chironomids (up to 2/3rd of diet by volume, depending on fish size), while Pennuto et al. (2010) observed the opposite in this area (amphipods up to 2/3rd of diet by wet weight and nearly no chironomids). The results of these studies and those reported herein strongly suggest that feeding of *N. melanostomus* largely depends on availability and abundance of prey organisms in the ecosystem. It appears that in lotic habitats, diets of *N. melanostomus* are typically dominated by non-mollusc benthic invertebrates (~71% by mass, Laurentian Great Lakes tributaries) which mirrors the findings from our study, while in lentic or marine ones, molluscs are usually the primary diet component comprising 57–65% of the food biomass uptake (Kornis et al., 2012).

In addition to the differences according to various habitat types, time since invasion (in other words, ecosystem impact) also may be important. Most of the habitats in which *N. melanostomus* has been reported to primarily feed on molluscs and not on amphipods have been occupied for more than a decade, whereas their invasion in the upper Danube River (investigated herein) with an amphipod-based diet is a rather recent phenomenon. Similarly, in recently invaded areas of the Baltic Sea studied 2 years after first recordings, decapod shrimp (up to 72% of food biomass uptake) and snails were the most important food items (Azour, 2011) even in large *N. melanostomus*, whereas there was a shift towards bivalves in earlier colonized habitats of the Baltic sea, studied 5–14 years after invasion (Skóra & Rzeznik, 2001; Karlson et al., 2007). Consequently, the currently underestimated factor of time since invasion deserves better consideration in analyses of feeding habits of invasive Ponto-Caspian gobies and other invasive species as niche differentiation and effects of an invader can be modulated by evolutionary or ecological processes (Strayer et al., 2006).

In the recently invaded habitats studied herein, both goby populations probably have not yet reached maximum densities limited by the carrying capacity. It is therefore likely that the feeding ecology patterns found are close to their fundamental niches.

The role of invasive prey species in goby feeding and ecosystem impacts

As evident from this study, *D. villosus*, and few other invasive amphipods have already replaced native amphipods in the headwater reaches of the Danube River. Amphipods, especially invasive *D. villosus*, were identified as main energy suppliers for Ponto-Caspian gobies in the upper Danube River and thus seemed to facilitate the ongoing invasion. Invasive species contribute ten times more to the feeding of the gobies than indigenous species. Both goby species consumed mainly other non-native species (~92% of gut contents) and thus seem to benefit from previous invasions of prey species such as *D. villosus*, *C. curvispinum*, *Dreissena polymorpha* and *C. fluminea*.

According to Borza et al. (2009), the food web of the Danube River is currently approximating the Ponto-Caspian one, a process supporting the ‘invasive meltdown theory’ (Simberloff & Von Holle, 1999). This is also supported by our data and analogous predictions were made for the River Rhine (Van Riel et al., 2006). The benthic community of the analysed headwater reaches of the Danube River has been altered by invasions of benthic invertebrate species within the last two decades (see Tittizer et al., 2000), apparently indicating such an invasive meltdown. As a consequence, the indigenous, lotic invertebrate biocoenosis of Danubian headwaters has been altered to a non-native, lenitic one, now harbouring a major brackish and marine fauna. It is unlikely that this effect was primarily caused by the gobies, which have just arrived at the headwater reaches of the Danube. It is more likely that this alteration now provides food web conditions suitable for (further) Ponto-Caspian goby invasions, particularly as they almost entirely prey upon invasive species. However, given the differences in feeding strategies of the two goby species, their wide dietary niches and their plasticity regarding diet selection, it is likely that food is not the most important factor for the invasive success of the gobies. The success of the gobies and their prey rather reflects a change in environmental conditions favouring both prey and predator. The invasion of the gobies and their prey species may thus only mirror the fundamental ecological food web changes in large European freshwater ecosystems.

Also, invasions of the Ponto-Caspian gobiid fishes *N. melanostomus* and *P. kessleri* themselves are

suspected to cause serious regime shifts in freshwater ecosystems by, e.g. affecting fish diversity and benthic invertebrate community (see citations in the introduction). As these species continue to spread throughout European rivers, and, in the case of round gobies in North America, a new quality of potential threats can affect areas with high endemic aquatic biodiversity (Keller et al., 2011). As *N. melanostomus* has heavily invaded areas such as the Great Lakes tributaries despite of absence of *Dreissena* spp. in most of those systems (Kornis & Vander Zanden, 2010), early hypotheses that *N. melanostomus* would be largely limited to *Dreissena*-invaded systems have proven false on both continents. This fact, along with the great dietary plasticity complicates potential countermeasures. However, substantial populations of invasive species can occasionally collapse dramatically (Simberloff & Gibbons, 2004). Ontogenetically determined niche extension in *N. melanostomus* as well as intraguild predation and cannibalism in *P. kessleri* can be characterized as a feedback regulation process ('closed loop omnivory', Polis et al., 1989) which is likely to hamper spontaneous short-term population collapses of *P. kessleri* and *N. melanostomus*, potentially caused by overexploitation of food resources. Hence, these mechanisms are more likely to stabilize both fish populations and thus will consolidate their status quo by preventing from competitive exclusion or boom-and-bust.

Based on life history traits, *P. kessleri* is supposed to win the competition (Kovač et al., 2009). However, based on trophic interactions, *N. melanostomus* is likely to have advantages under changing food resource availabilities. A monitoring of the future success of both species in the Danubian headwaters may provide valuable insights into the relative importance of both factors.

Implications for future research and management

The observed feeding patterns of invasive gobies and their interactions with the Danubian food web support previous findings that both species are highly competitive because of their generalistic and opportunistic feeding strategies. At the same time, invasive gobies have a strong potential to alter current food web structures. Strategies to stop a further spread of both species are unlikely to be effective at this stage. Future research may be expanded to also address the feeding

patterns of different size classes, as well as different habitat types within the Danube River. Only recently, the arrival of another goby species, *Babka gymnotrachelus* (Kessler, 1857), was detected for the first time in Germany (Haertl et al., 2012) trophic interactions of which with the extant species and the aquatic food web will help us to compare the feeding plasticity and other factors which govern invasive success in these species.

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References

- Adámek, Z., J. Andreji & J. M. Gallardo, 2007. Food habits of four bottom-dwelling gobiid species at the confluence of the Danube and Hron Rivers (South Slovakia). *International Review of Hydrobiology* 92: 554–563.
- Ahnelt, H., P. Bañarescu, R. Spolwind, A. Harka & H. Waidbacher, 1998. Occurrence and distribution of three gobiid species (Pisces: Gobiidae) in the middle and upper Danube region – example of different dispersal patterns? *Biológia (Bratislava)* 53: 661–674.
- Amundsen, P. A., H. M. Gabler & F. J. Staldvik, 1996. A new approach to graphical analysis of feeding strategy from stomach contents data – modification of the Costello (1990) method. *Journal of Fish Biology* 48: 607–614.
- Anderson, R. O. & R. M. Neumann, 1996. Length, weight and associated structural indices. In Murphy, B. R. & D. W. E. Willis (eds), *Fisheries Techniques*, 2nd ed. American Fisheries Society, Bethesda, MD, USA: 732 pp.
- Auerswald, K., M. H. O. M. Wittmer, A. Zazzo, R. Schäufele & H. Schnyder, 2010. Biases in the analysis of stable isotope discrimination in food webs. *Journal of Applied Ecology* 47: 936–941.
- Azour, F., 2011. Fødebiologi hos den sortmundede kutling *Neogobius melanostomus* I danske farvande. Copenhagen: Biologistuderende ved Københavns Universitet (in Danish) [available on internet at http://snm.ku.dk/forskning/projekter/fiskeatlas/billeder/Sortmundet_kutlings_f_debiologi_i_DK.pdf/] (day of download: May 30th, 2012).
- Balfour, H., 1988. Nutrition of pond fishes. Cambridge University Press: 24–25.
- Barton, D. R., R. A. Johnson, L. Campbell, J. Petruniak & M. Peterson, 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.

- Beisel, J. N. & S. Devin, 2007. Biomonitoring: definition and assessment for macroinvertebrates in European running waters. In *Biological Invaders in Inland Waters: Profiles, Distribution, and Threats*. Invading Nature – Springer Series in Invasion Ecology, vol. 2. Springer, Netherlands: 369–379.
- Bij de Vaate, A., K. Jazdzewski, H. A. M. Ketelaars, S. Gollasch & G. van der Velde, 2002. Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174.
- Borcherding, J., S. Staas, S. Krüger, M. Ondračková, L. Šlapanský & P. Jurajda, 2011. Non-native Gobiid species in the lower River Rhine (Germany): recent range extensions and densities. *Journal of Applied Ichthyology* 27: 1–3.
- Borza, P., T. Erös & N. Oertel, 2009. Food resource partitioning between two invasive gobiid species (Pisces, Gobiidae) in the littoral zone of the River Danube, Hungary. *International Review of Hydrobiology* 94: 609–621.
- Bronnenhuber, J. E., B. A. Dufour, D. M. Higgs & D. D. Heath, 2011. Dispersal strategies, secondary range expansion and invasion genetics of the nonindigenous round goby, *Neogobius melanostomus*, in Great Lakes tributaries. *Molecular Ecology* 20: 1845–1859.
- Brooks, S., 1994. An efficient and quantitative aquatic benthos sampler for use in diverse habitats with variable flow regimes. *Hydrobiologia* 281: 123–128.
- Brown, A. V., M. D. Schram & P. P. Brussock, 1989. A vacuum benthos sampler suitable for diverse habitats. *Hydrobiologia* 153: 241–247.
- Campbell, L. M., R. Thacker, D. Barton, D. C. G. Muir, D. Greenwood & R. E. Hecky, 2009. Re-engineering the eastern Lake Erie littoral food web: the trophic function of non-indigenous Ponto-Caspian species. *Journal of Great Lakes Research* 35: 224–231.
- Charlebois, P. M., J. E. Marsden, R. G. Goettel, R. K. Wolfe, D. J. Jude & S. Rudnik, 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. INHS Special Publication No. 20.
- Corkum, L. D., M. R. Sapota & K. E. Skóra, 2004. The round goby, *Neogobius melanostomus*, a fish invader on both sides of the Atlantic Ocean. *Biological Invasions* 6: 173–181.
- Crossman, E. J., E. Helm, R. Cholmondeley & K. Tuininga, 1992. First record for Canada of the Rudd, *Scardinius erythrophthalmus*, and notes on the introduced Round Goby, *Neogobius melanostomus*. *Canadian Field-Naturalist* 106: 206–209.
- Costello, M. J., 1990. Predator feeding strategy and prey importance: a new graphical analysis. *Journal of Fish Biology* 36: 261–263.
- Dudgeon, D., A. H. Arthington, M. O. Gessner, Z. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A. Prieur-Richard, D. Soto & M. L. J. Stiassny, 2006. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 8: 163–182.
- French, J. R. P. III. & D. J. Jude, 2001. Diets and diet overlap of nonindigenous gobies and small benthic native fishes co-inhabiting the St. Clair River, Michigan. *Journal of Great Lakes Research* 27: 300–311.
- Freyhof, J., 2003. Immigration and potential impacts of invasive freshwater fishes in Germany. Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Annual Report 2002, vol. 17: 51–58.
- Geist, J., 2011. Integrative freshwater ecology and biodiversity conservation. *Ecological Indicators* 11: 1507–1516.
- Guelinckx, J., J. Maes, P. van den Driessche, B. Geysen, F. Dehairs & F. Ollevier, 2007. Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in different tissues of juvenile sand goby *Pomatoschistus minutus*: a laboratory diet-switch experiment. *Marine Ecology Progress Series* 341: 205–215.
- Guelinckx, J., J. Maes, B. Geysen & F. Ollevier, 2008. Estuarine recruitment of a marine goby reconstructed with an isotopic clock. *Oecologia* 157: 41–52.
- Gutowsky, L. F. G. & M. G. Fox, 2011. Occupation, body size and sex ratio of round goby (*Neogobius melanostomus*) in established and newly invaded areas of an Ontario river. *Hydrobiologia* 671: 27–37.
- Haertl, M., A. F. Cerwenka, J. Brandner, J. Borcherding, J. Geist & U. K. Schliwien, 2012. First record of Babka gymnotrachelus (Kessler, 1857) from Germany (Teleostei, Gobiidae, Benthophilinae). *Spixiana* 35: 155–159.
- Harka, Á. & P. Bíró, 2007. New patterns in danubian distribution of Ponto-Caspian gobies – a result of global climatic change and/or canalisation? *Electronic Journal of Ichthyology* 1: 1–14.
- Hammer, Ø., D. A. T. Harper & P. D. Ryan, 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 9.
- Herder, F. & J. Freyhof, 2006. Resource partitioning in a tropical stream fish assemblage. *Journal of Fish Biology* 69: 571–589.
- Hynes, H. B. N., 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the fishes. *Journal of Animal Ecology* 19: 36–58.
- Hyslop, E. J., 1980. Stomach content analysis, a review of methods and their application. *Journal of Fish Biology* 17: 411–430.
- Janssen, J. & D. J. Jude, 2001. Recruitment failure of mottled sculpin *Cottus bairdi* in Calumet Harbor, Southern Lake Michigan, induced by the newly introduced round goby *Neogobius melanostomus*. *Journal of Great Lakes Research* 27: 319–328.
- Jaroszewska, M., K. Dabrowski, B. Wilczyńska & T. Kakareko, 2008. Structure of the gut of the racer goby *Neogobius gymnotrachelus* (Kessler, 1857). *Journal of Fish Biology* 72: 1773–1786.
- Johnson, T. B., D. B. Bunnell & C. T. Knight, 2005. A potential new energy pathway in Central Lake Erie: the round goby connection. *Journal of Great Lakes Research* 31(Suppl. 2): 238–251.
- Jude, D. J., R. H. Reider & G. R. Smith, 1992. Establishment of Gobiidae in the Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 416–421.
- Jurajda, P., J. Černý, M. Polačik, Z. Valová, M. Janáč, R. Blažek & M. Ondračková, 2005. The recent distribution and abundance of non-native *Neogobius* fishes in the Slovak

- section of the River Danube. *Journal of Applied Ichthyology* 21: 319–323.
- Kakareko, T., D. Plachocki & J. Kobak, 2009. Relative abundance of Ponto-Caspian gobiids in the lower Vistula River (Poland) 3 to 4 years after first appearance. *Journal of Applied Ichthyology* 25: 647–651.
- Karachile, P. K. & K. I. Stergiou, 2010. Intestine morphometrics of fishes: a compilation and analysis of bibliographic data. *Acta ichthyologica et piscatoria* 40: 45–54.
- Karatayev, A. Y., S. E. Mastitsky, L. E. Burlakova & S. Olenin, 2008. Past, current, and future of the central European corridor for aquatic invasions in Belarus. *Biological Invasions* 10: 215–232.
- 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.
- Keller, R. P., J. Geist, J. M. Jeschke & I. Kühn, 2011. Invasive species in Europe: ecology, status, and policy. *Environmental Sciences Europe* 23: 23.
- 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.
- Kovač, V., G. M. Copp & R. P. Sousa, 2009. Life-history traits of invasive bighead goby *Neogobius kessleri* (Günther, 1861) from the middle Danube River, with a reflection on which goby species may win the competition. *Journal of Applied Ichthyology* 25: 33–37.
- Kovtun, I. V., M. Y. Nekrasova & N. I. Revina, 1974. On the diet of round goby (*Neogobius melanostomus*) and utilization of food supply in the Azov Sea. *Russian Journal of Zoology* 53: 728–736.
- Lederer, A., J. Massart & J. Janssen, 2006. Impact of round gobies (*Neogobius melanostomus*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and the associated macroinvertebrate community across an invasion front. *Journal of Great Lakes Research* 32: 1–10.
- Leuven, R. S. E. W., G. van der Velde, I. Baijens, J. Snijders, C. van der Zwart, H. J. R. Lenders & A. Bij de Vaate, 2009. The river Rhine: a global highway for dispersal of aquatic invasive species. *Biological Invasions* 11: 1989–2008.
- Lodge, D. M., 1993. Biological invasions: lessons for ecology. *Trends in Ecology & Evolution* 8: 133–137.
- Lynch, P. L. & A. F. Mensinger, 2011. Seasonal abundance and movement of the invasive round goby (*Neogobius melanostomus*) on rocky substrate in the Duluth-Superior Harbor of Lake Superior. *Ecology of Freshwater Fish* 21: 64–74.
- McMahon, K. W., B. J. Johnson & W. G. Ambrose, 2005. Diet and movement of the killifish, *Fundulus heteroclitus*, in a Maine salt marsh assessed using gut contents and stable isotope analyses. *Estuaries* 28: 966–973.
- Marentette, J. R., J. L. Fitzpatrick, R. G. Berger & S. Balshine, 2009. Multiple male reproductive morphs in the invasive round goby (*Apollonia melanostoma*). *Journal of Great Lakes Research* 35: 302–308.
- Maruyama, A., Y. Yamada, B. Rusuwa & M. Yuma, 2001. Change in stable nitrogen isotope ratio in the muscle tissue of a migratory goby, *Rhinogobius* sp., in a natural setting. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2125–2128.
- McCutchan, J. H. Jr., W. M. Lewis, C. Kendall & C. C. McGrath, 2003. Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* 102: 378–390.
- Miller, P. J., 1984. The tokology of gobioid fishes. In Potts, G. W. & R. J. Wootton (eds), *Fish Reproduction: Strategies and Tactics*. Wootton Academic Press, London: 119–153.
- Minchin, D., 2007. A checklist of alien and cryptogenic aquatic species in Ireland. *Aquatic Invasions* 2: 341–366.
- Moku, M., K. Kawaguchi, H. Watanabe & A. Ohno, 2000. Feeding habits of three dominant myctophid fishes, *Diaphus theta*, *Stenobranchius leucopsarus* and *S. nannochir*, in the subarctic and transitional waters of the western North Pacific. *Marine Ecology* 207: 129–140.
- Mooney, H. A. & E. E. Cleland, 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Science of the United States of America* 98: 5446–5451.
- Moyle, P. B. & J. E. Mount, 2007. Homogenous rivers, homogenous faunas. *Proceedings of the National Academy of Sciences of the United States of America* 104: 5711–5712.
- Paintner, S. & K. Seifert, 2006. First record of the round goby, *Neogobius melanostomus* (Gobiidae), in the German Danube. *Lauterbornia* 58: 101–107.
- Panov, V. E., B. Alexandrov, K. Arbačiauskas, R. Binimelis, G. H. Copp, M. Grabowski, F. Lucy, R. S. E. W. Leuven, S. Nehring, M. Paunović, V. Semchenko & O. M. Son, 2009. Assessing the risks of aquatic species invasions via European inland waterways: the concepts and environmental indicators. *Integrated Environmental Assessment and Management* 5: 110–126.
- Pennuto, C. M., P. J. Krakowiak & C. E. Janik, 2010. Seasonal abundance, diet, and energy consumption of round gobies (*Neogobius melanostomus*) in Lake Erie tributary streams. *Ecology of Freshwater Fish* 19: 206–215.
- Perga, M. E. & D. Gerdeaux, 2005. ‘Are fish what they eat’ all year round? *Oecologia* 144: 598–606.
- Phillips, E. C., E. Meaghan, A. Washek, W. Hertel & B. M. Niebel, 2003. The Round Goby (*Neogobius melanostomus*) in Pennsylvania Tributary Streams of Lake Erie. *Journal of Great Lakes Research* 29: 34–40.
- Pinchuk, V. I., E. D. Vasil’Eva, V. P. Vasil’Ev & P. J. Miller, 2003. *Neogobius melanostomus* (Pallas, 1814). In Miller, P. J. (ed.), *The Freshwater Fishes of Europe*. Vol. 8/I Mugilidae, Atherinidae, Atherinopsidae, Blennidae, Odontobutidae, Gobiidae 1. AULA-Verlag GmbH Wiebelsheim, Verlag für Wissenschaft und Forschung, Germany: 293–345.
- Poláčik, M., M. Janáč, P. Jurajda, Z. Adámek, M. Ondračková, T. Trichkova & M. Vassilev, 2009. Invasive gobies in the Danube: invasion success facilitated by availability and selection of superior food resources. *Ecology of Freshwater Fish* 18: 640–649.
- Polis, G. A., C. A. Myers & R. D. Holt, 1989. The ecology and evolution of intraguild predation: potential competitors

- that eat each other. *Annual Review of Ecology and Systematics* 20: 297–330.
- Post, D. M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703–718.
- Poos, M., A. J. Dextrase, A. N. Schwalb & J. D. Ackerman, 2010. Secondary invasion of the round goby into high diversity Great Lakes tributaries and species at risk hotspots: potential new concerns for endangered freshwater species. *Biological Invasions* 12: 1269–1284.
- Ricciardi, A., 2001. Facilitative interactions among aquatic invaders: is an “invasional meltdown” occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences* 58: 2013–2025.
- Ricciardi, A. & H. J. MacIsaac, 2000. Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. *Trends in Ecology & Evolution* 15: 62–65.
- Ray, W. J. & L. D. Corkum, 1997. Predation of zebra mussels by round gobies, *Neogobius melanostomus*. *Environmental Biology of Fishes* 50: 267–273.
- Sapota, M. R. & K. E. Skóra, 2005. Spread of alien (non-indigenous) fish species *Neogobius melanostomus* in the Gulf of Gdansk (south Baltic). *Biological Invasions* 7: 157–164.
- Schoener, T. W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408–418.
- Seifert, K. & F. Hartmann, 2000. Die Kesslergrundel (*Neogobius kessleri* Günther 1861), eine neue Fischart in der deutschen Donau. *Lauterbornia* 38: 105–108.
- Shemonaev, E. V. & E. V. Kirilenko, 2008. Some features of Biology of the Round Goby *Neogobius melanostomus* (Perciformes, Gobiidae) in Waters of the Kuibyshev Reservoir. *Journal of Ichthyology* 49: 454–459.
- Simberloff, D. & B. Von Holle, 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32.
- Simberloff, D. & L. Gibbons, 2004. Now you see them, now you don’t! – population crashes of established introduced species. *Biological Invasions* 6: 161–172.
- Simonović, P., B. Valković & M. Paunović, 1998. Round goby *Neogobius melanostomus*, a new Ponto-Caspian element for Yugoslavia. *Folia Zoologica* 47: 305–312.
- Simonović, P., M. Paunović & S. Popović, 2001. Morphology, feeding and reproduction of the round goby, *Neogobius melanostomus* (Pallas) in the Danube River basin, Yugoslavia. *Journal of Great Lakes Research* 27: 281–289.
- Skóra, 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.
- Stráňai, I. & J. Andreji, 2004. The first report of round goby, *Neogobius melanostomus* (Pisces, Gobiidae) in the waters of Slovakia. *Folia Zoologica* 53: 335–338.
- Strayer, D. L., V. T. Eviner, J. M. Jeschke & M. L. Pace, 2006. Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution* 21: 645–651.
- Tittizer, T., F. Schöll, M. Banning, A. Haybach & M. Schleuter, 2000. Aquatische Neozoen im Makrozoobenthos der Binnenwasserstraßen Deutschlands. *Lauterbornia* 39: 1–172.
- Tudela, S. & I. Palomera, 1995. Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the northwest Mediterranean Sea during the spawning period. *Marine Ecology* 129: 55–61.
- Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, E. L. Mills, K. T. Holeck, J. R. Liebig, I. A. Grigorovich & H. Ojaveer, 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1209–1228.
- Vander Zanden, M. J., G. Cabana & J. B. Rasmussen, 1997. Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 1142–1158.
- Van Riel, M. C., G. van der Velde, S. Rajagopal, S. Marguillier, F. Dehairs & A. Bij de Vaate, 2006. Trophic relationships in the Lower Rhine food web during invasion and after establishment of the Ponto-Caspian invader *Dikergammarus villosus*. *Hydrobiologia* 565: 39–58.
- Van Riel, M. C., E. P. Healy, G. van der Velde & A. Bij de Vaate, 2007. Interference competition among native and invader amphipods. *Acta Oecologica* 31: 282–289.
- Vasil’Eva, E. D. & V. P. Vasil’Ev, 2003. *Neogobius kessleri* Günther, 1861. In Miller, P. J. (ed.), *The Freshwater Fishes of Europe*. Vol. 8/I Mugilidae, Atherinidae, Atherinopsidae, Blennidae, Odontobutidae, Gobiidae 1. AULA-Verlag GmbH Wiebelsheim, Verlag für Wissenschaft und Forschung, Germany: 280–292.
- Zihler, F., 1982. Gross morphology and configuration of digestive tracts of cichlidae (teleostei, perciformes): phylogenetic and functional significance. *Netherlands Journal of Zoology* 32: 544–571.