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Seasonal abundance and feeding patterns of the invasive racer goby (*Babka gymnotrachelus*) in the littoral zone of a lowland European river

Alexander Didenko · Igor Buzevych · Yuriy Volikov · Svitlana Kruzhylina · Alexander Gurbyk · Vitaliy Bekh

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Abstract The racer goby (*Babka gymnotrachelus*), a Ponto-Caspian gobiid, has successfully established in several European rivers since the 1990s, and its range is expanding; however, information on its biology in invaded environments is still limited. Understanding the population dynamics and feeding ecology of this species may assist in predicting its potential impact on native ecosystems. The seasonal abundance and feeding of racer goby were studied in the littoral zone of a lowland river flowing into the Kaniv Reservoir (Dnieper River). The abundance of this goby in the sampling reach displayed significant inter-annual and seasonal fluctuations, which depended on water temperature. Mean lengths of racer goby also varied during the year, and the largest fish were observed mainly in January to April and in September to November. Age-0 fish started appearing in catches at the end of May. Almost all juveniles reached adult size in October of the same year. Overall, 72 prey organisms were identified in the gut contents of racer goby. The most abundant prey were chironomids followed by cladocerans, copepods, and water mites. Chironomids included 25 taxa, the most abundant of which were *Polypedilum convictum*, *Glyptotendipes* sp., and *Chironomus* sp. Among 18 identified cladoceran taxa, the most abundant were *Disparalona rostrata*, *Pleuroxus aduncus*, and *Alona affinis*. Based on the diet composition, which included both bottom-dwelling and macrophyte-associated organisms, it can be concluded that racer goby feeds in a large variety of microhabitats including open non-vegetated areas, on substrates near macrophyte beds, and possibly on macrophytes.

Keywords Gobiidae · Invasive species · Fish diet · Fish growth · Dnieper

Introduction

The racer goby (*Babka gymnotrachelus*) is a Ponto-Caspian euryhaline gobiid, the native range of which includes brackish waters of the Black, Azov, and Caspian Sea basins as well lower courses of their rivers (Kottelat and Freyhof 2007). During the 1990s, this species invaded several European rivers and successfully established in the Danube River (Kautman 2001; Bănăduc et al. 2014, 2016) upstream to its

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A. Didenko (✉) · I. Buzevych · S. Kruzhylina · A. Gurbyk
Institute of Fisheries of the National Academy of Agrarian Sciences of Ukraine, Obukhivska St. 135, Kyiv 03164, Ukraine
e-mail: al_didenko@yahoo.com

Y. Volikov
Institute of Hydrobiology of the National Academy of Sciences of Ukraine, Prospekt Geroiv Stalingradu, 12, Kyiv 04210, Ukraine

V. Bekh
Department of Aquaculture, National University of Life and Environmental Sciences of Ukraine, General Rodimtsev St. 19, Kyiv 03041, Ukraine

upper course in Germany (Haertl et al. 2012), and in the Western Bug and Vistula Rivers in Poland (Danilkiewicz 1996; Kostrzewa and Grabowski 2003; Grabowska 2005), the Rhine River in Germany (Borcherding et al. 2011), the Dnieper River upstream to Belarus, as well as the Pripyat River (Semenchenko et al. 2009). More recently, it was recorded in the Someş River in Romania (Cocan et al. 2016) and the Evros River in Greece (Zogaris et al. 2019). According to recent studies, racer goby is considered to be native in the Dniester River basin and in the submountain Strwiąż River in Poland (Grabowski et al. 2016; Kukuła et al. 2019). As for Ukrainian freshwaters, this species occurs in the Dnieper, Southern Bug, Dniester, and Siverskyi Donets rivers and some of their tributaries (Movchan et al. 2002; Movchan 2005; Shandikov and Goncharov 2008). In some waters (e.g. Dnieper reservoirs), it has become the most abundant gobiid together with the monkey goby (*Neogobius fluviatilis*) (Didenko et al. 2017).

Published data exist on some aspects of the feeding of racer goby in invaded freshwaters, but they are limited to studies conducted in Poland (Kostrzewa and Grabowski 2003; Grabowska and Grabowski 2005; Kakareko et al. 2005, 2013). Limited data are also available for some Ukrainian rivers and reservoirs (Smirnov 1986; Didenko et al. 2017). At the same time, information on seasonal population dynamics of the racer goby in invaded freshwaters is practically absent. When analysing the diets of gobiids, their preys are usually grouped to family or order level (Smirnov 1986; Kostrzewa and Grabowski 2003; Grabowska and Grabowski 2005) resulting in the loss of considerable information, therefore, a special attention was given to a very detailed description of prey organisms with a taxonomic resolution as high as possible (up to species level). Knowledge of the feeding patterns as well as the population dynamics of the racer goby in invaded freshwaters taking into account seasonal aspects and detailed description of prey taxa may assist in predicting its potential impact on native fish and aquatic invertebrates and their associated ecosystems around the world.

The aim of the study was to explore inter-annual and seasonal population dynamics and seasonal variation of the racer goby diet in a freshwater habitat located in the lower Stugna River (Ukraine) where this goby successfully established and became very abundant. This river flows into the Kaniv Reservoir, one of large reservoirs built on the Dnieper River. There is no information regarding when this species invaded the Kaniv Reservoir and particularly the Stugna River. According to available data, it was absent in the reach of the Dnieper River where the Kaniv Reservoir is located before its construction in 1965 (Sukhoyvan and Vyatchanina 1989) and was absent in the Stugna River in the beginning of 1970s (Poltavchuk 1976). However, the fish was reported as present during 1999–2004 (Sabodash and Tsyba 2006). Due to its high abundance, this species can potentially interact with native and other invasive fishes, shape local food webs, and affect local invertebrate communities.

Materials and methods

Fish sampling

Fish were captured in the littoral zone of the lower Stugna River within the city limits of the Ukrainka (Ukraine) at a single 70 m long sampling reach situated nearly 1100 m from the river's inflow to the Kaniv Reservoir along the right river bank (N 50° 08′ 57.16″, E 30° 43′ 55.05″). The river reach where sampling was performed was characterized by virtually absent current (velocity of which typically < 0.05 m/s). Substrate within the sampling reach was predominantly sand and muddy sand intermingled with patches of dense macrophyte beds consisting mainly of *Myriophyllum* sp., *Ceratophyllum* sp., and *Potamogeton* spp. Based on a visual assessment, the aquatic plants covered approximately 40% of the site area. River width in the sampling reach was nearly 85 m.

Samplings were conducted monthly from March 2015 to February 2016 and from March 2018 to November 2018, usually between the 15th and 20th days of the month and between 9:00 and 12:00 h. An additional sampling was conducted on May 31, 2018 to catch early age-0 fish.

Fish were captured by a beach seine made of mill sieve gauze (10 m long × 1 m high with 1.0 mm bar mesh size). Three adjacent hauls were made during each sampling event following the same pattern and covering approximately 30 m^2 each over both vegetated and non-vegetated substrates. The total hauled areas usually composed approximately 90–100 m^2.

However, additional hauls were carried out within or near the sampling reach, if too few individuals were caught in the first three hauls. The maximum depths covered by seining usually did not exceed 1.2 m. Fish from all hauls within one sampling event were placed into a 14-L plastic bucket with water. If few individuals were caught, they were all preserved in a 4% formaldehyde solution for further processing at the laboratory. In cases of large quantities of fish, they were randomly removed from the bucket using an aquarium net, visually identified and the first 30 to 40 specimens caught of each species including racer goby were preserved in formaldehyde solution for further processing. The remaining fish were counted, measured to the nearest 1 mm (total length, TL), and released. If extremely large specimens were found during counting, they were also preserved in formaldehyde solution. Most specimens were collected in 2015–2016 and additional fish were collected in 2018.

Water temperature in the sampling reach was measured using a digital thermometer “Digital Thermo” with an accuracy of 0.1 °C by placing the thermometer probe at a depth of approximately 0.5 m below the water surface.

Samples of benthic macroinvertebrates were collected from a depth of 1.0–1.2 m in 2015–2016 using an Ekman grab with a sampling area of 208 cm^2. Samples were sieved through a 0.5-mm mesh, individual macroinvertebrates were picked and preserved in a 4% formaldehyde solution for laboratory processing.

In the laboratory, fish were measured (TL) to the nearest 1 mm, weighed to the nearest 0.01 g using an electronic balance AXIS AD500, and eviscerated. The contents of the entire digestive tract were removed and examined in a counting chamber under a binocular microscope. Prey items were identified to the lowest taxon wherever possible and counted. In addition, up to ten fish, if available, were randomly selected from each sample and chironomid larvae from their stomachs were collected, pooled by a monthly sample, and preserved in Eppendorf tubes in a 4% formaldehyde solution. Later, they were separately identified to the lowest taxonomic level possible under a binocular microscope. Damaged and fragmented prey items were identified mainly based on their heads and corresponding fragments, if available. Damaged prey sizes were restored by juxtaposing corresponding fragments or approximately reconstructed by direct comparisons of prey heads or other fragments with intact or almost intact corresponding taxa. For zooplanktonic organisms, the lengths of at least 20 individuals of each identified taxa were measured with an ocular micrometre. The dry weights of prey organisms were estimated using published length-dry weight regression relationships (McCauley 1984; Culver et al. 1985; Benke et al. 1999; Watkins et al. 2011). The obtained dry weights were transformed into wet weights assuming the water content of 85.0% for zooplankton and 76.0% for benthic organisms (USEPA 2010).

Invertebrates from benthos samples were identified to the lowest possible level and counted under a binocular microscope in a counting chamber. The abundance of benthic macroinvertebrates was expressed as individuals per square metre.

Data analysis

Fish catch per unit effort (CPUE) in the sampling reach at each month was calculated as the mean number of individuals collected per 100 m^2 of a seine haul. Only fish caught in first three hauls were used for CPUE calculation because these hauls were carried out most regularly and covered exactly the same area. CPUEs were calculated for both 2015–2016 and 2018.

Only fish caught in 2015–2016 were used for diet analysis. Fish with no food in their stomachs were removed from the analysis.

Feeding activity was expressed as an index of stomach fullness (FI):

$$\mathrm{FI} = (\text{gut content weight})/(\text{fish weight}) \times 100$$

where gut content weight is the sum of the wet weights of prey items.

Diet compositions were described using following indices: frequency of occurrence (%F), relative abundance (%N), percentage of biomass (%W), index of relative importance (IRI), and percent index of relative importance (%IRI):

$$\%\mathrm{F} = f_i/\Sigma f \times 100$$

where f_i is the number of guts containing the prey item i and Σf is the total number of non-empty guts;

$$\%N = n_i / \Sigma n \times 100$$

where n_i is the total number of prey item i and Σn is the total number of prey items consumed by fish;

$$\%W = w_i / \Sigma w \times 100$$

where w_i is the total weight of prey item i and Σw is the total weight of prey items consumed by fish; and

$$IRI = (\%N + W) \times \%F$$
$$\%IRI = IRI_i / \Sigma IRI \times 100.$$

Only %N and %W were used for analysing individual chironomid taxa (Liao et al. 2001).

For some analyses, fish were divided into adults and juveniles, where adults were considered as specimens with sizes corresponding to those of age-1 or older fish, while juveniles were considered as specimens with sizes less than those of age-1 fish, and these two groups were analysed separately. All goby specimens caught in March to April were considered adults. Hence, the minimum length of this goby observed in catches in these months was set as approximately a threshold length for adult fish. The smallest fish caught in spring months was 51 mm; therefore, 50 mm was set as the approximate size when juveniles reached the length of adult fish and this threshold was used for dividing fish into adults and juveniles caught during summer and autumn. Juveniles and adults were hereinafter referred as < 50 mm fish and ≥ 50 mm fish, respectively. Diet compositions were additionally analysed in fish divided into three length groups: < 50 mm, 50–69 mm, and ≥ 70 mm as well as for pooled size groups.

One-way ANOVA with post hoc Tukey–Kramer test was used to compare mean lengths of fish sampled in different months, numbers of prey items in gut contents, and weights of gut contents of different length groups. Fish lengths, numbers of prey items, gut contents, stomach fullness values, and numbers of the most abundant prey items in fish stomachs were log-transformed to meet the assumptions of normality. Simple linear models (SLM) were used to find the relationships between the CPUE of the racer goby and water temperatures, stomach fullness index and water temperature, fish length and number of prey items in the stomach content, and numbers of the most abundant prey items in fish stomachs and their abundances in benthos samples.

Statistical analyses were performed in JMP 10 (SAS Institute).

Results

Seasonal abundance

Altogether, 574 racer goby specimens were captured during the study period and 258 of them were collected for the analysis of their stomach contents (Table 1). Fish total lengths ranged from 17 to 130 mm with mean length of 47.80 ± 1.11SE mm, while their weights after preservation in formaldehyde ranged from 0.05 to 21.28 g with mean weight of 2.75 ± 0.19SE g.

Mean CPUE of racer goby in beach seine catches varied significantly both during a year and between studied years (Fig. 1). No fish were caught in December and only one specimen was caught in January and one in February in samples collected in 2016. From March to November, mean CPUEs were higher in 2018 (57.7 ± 17.4SE fish/100 m^2) compared to 2015 (28.8 ± 12.3SE fish/100 m^2). The highest CPUEs in 2015–2016 were observed in July and September, while in 2018, they were in August and September. The lowest CPUEs were recorded in January to May in 2015–2016 and in March and May in 2018. Significant relationships were found between the CPUE of this

Table 1 Sample sizes and mean lengths of juvenile and adult racer goby used for diet analysis for each month in 2015–2016

Month	Juveniles		Adults	
	n	TL ± SE, mm	n	TL ± SE, mm
March	-	-	10	74.3 ± 3.2
April	-	-	15	65.3 ± 2.3
May	8	19.4 ± 0.7	4	63.7 ± 3.8
June	28	25.3 ± 1.0	6	82.0 ± 12.1
July	24	39.2 ± 1.3	18	58.1 ± 3.3
August	16	42.0 ± 0.8	19	63.1 ± 1.9
September	11	43.8 ± 0.9	44	69.4 ± 1.8
October	-	-	35	65.2 ± 2.1
November	-	-	18	67.3 ± 4.4
January	-	-	1	63.0
February	-	-	1	71.0

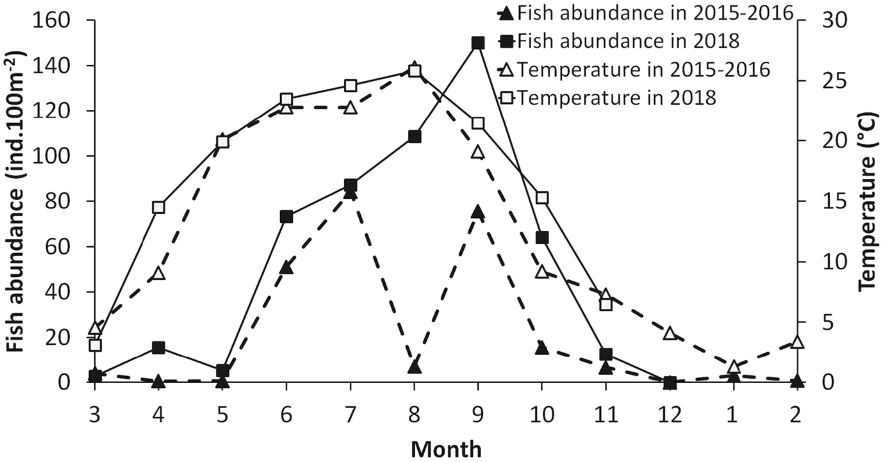


Fig. 1 Seasonal and inter-annual dynamics of racer goby abundance (CPUE) and water temperature in the sampling reach

species and water temperature for both studied years: LM: $F_{1,\ 10}=6.088$, $r^2=0.38$, $p=0.033$ (2015–2016); LM: $F_{1,7}=6.896$, $r^2=0.50$, $p=0.034$ (2018).

Mean lengths of racer goby in catches also varied significantly during a year (ANOVA: $F_{8,\ 523}=49.4$, $p<0.001$).The largest individuals were observed mainly from January to April and from September to November, while the smallest were observed from May to August (Fig. 2). Age-0 fish started appearing in catches at the end of May. No significant differences were observed among the mean lengths of racer goby sampled in March, April, October, and November (Tukey–Kramer test, $\alpha=0.05$). The average lengths were usually significantly different between each sequential month from May to September (Tukey–Kramer test, $\alpha<0.05$), except July and August. Practically all age-0 fish reached the size of adults (≥ 50 mm TL) in October.

Feeding patterns

The feeding activity of racer goby ≥ 50 mm showed clear seasonal dynamics, which depended on water temperature: $y=0.018(\pm 0.003\text{E})x+0.171(\pm 0.049\text{E})$; $n=11$; $r^2=0.80$; $p=0.0002$, where y is Stomach Fullness Index and x is water temperature (Fig. 3). The highest stomach fullness values were observed in May and in August–September, and the goby fed very little during winter months and late autumn. The highest stomach fullness values of individuals < 50 mm were observed in May–June and dropped as fish grew until August. In September, the stomach fullness values of < 50 mm fish almost reached those of ≥ 50 mm fish.

The numbers of individual prey items in the stomach contents ranged from 1 to 113 (mean = 17.5 ± 0.8E) and 0.40% of fish had empty guts. Mean numbers of prey items in gut contents were 16.4 ± 1.1SE, 17.3 ± 1.4SE, and 19.4 ± 1.7SE, respectively for < 50 mm, 50–69 mm, and ≥ 70 mm fish; however, this difference was not significant (ANOVA: $F_{2,\ 233}=0.63$, $p>0.05$). Almost a significant relationship was found between TL and the number of prey items in the stomach contents (LM: $F_{1,\ 257}=3.837$, $r^2=0.015$, $p=0.051$). Mean weights of gut contents significantly varied and were 3.4 ± 2.6SE, 11.2 ± 2.3SE, and 28.6 ± 2.8SE mg, respectively, for < 50 mm, 50–69 mm, and ≥ 70 mm fish (ANOVA: $F_{2,\ 233}=66.83$, $p<0.0001$).

Overall, 72 prey organisms were identified in the gut contents of racer goby in the littoral zone of the Stugna River (Table 2). The most abundant and most frequently encountered prey were chironomid larvae followed by cladocerans, copepods, and water mites. Chironomid larvae and fish dominated goby diet by weight. Chironomid larvae included 25 taxa, the most abundant being *Polypedilum convictum*, *Glyptotendipes* sp., and *Chironomus* sp. Copepods were represented mainly by Cyclopoidae. Among 18 identified cladoceran taxa, the most abundant were *Disparalona rostrata*, *Pleuroxus aduncus*, and *Alona affinis*. Among fish prey, the most common were gobiid juveniles such as Caucasian dwarf goby (*Knipowitschia caucasica*) and monkey goby, which were most abundant in the stomach contents in August. Much less frequently encountered were cyprinids and black-striped pipefish (*Syngnathus abaster*).

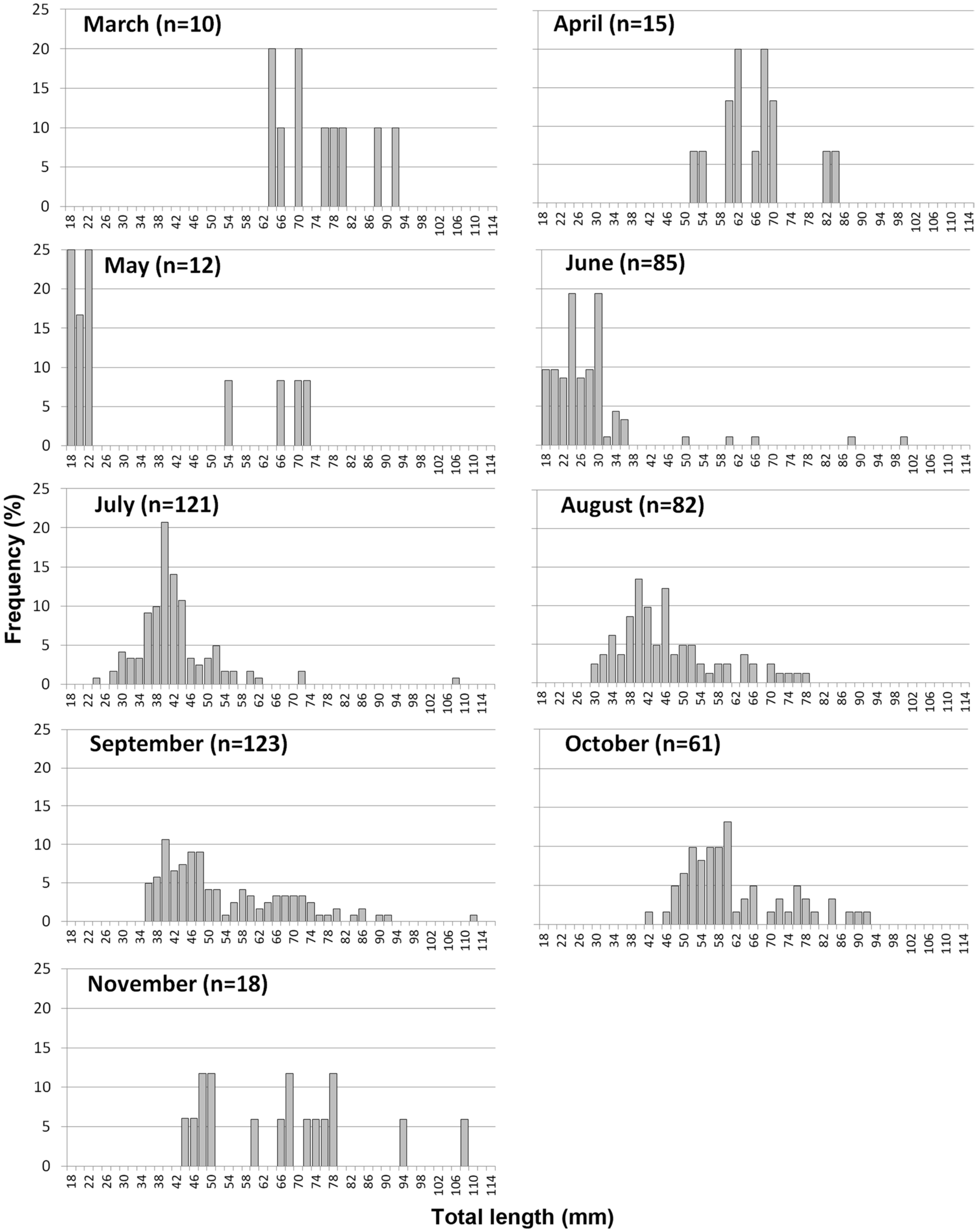


Fig. 2 Length-frequency histograms of racer goby caught in the sampling reach in different months in 2015 (n = number of measured fish)

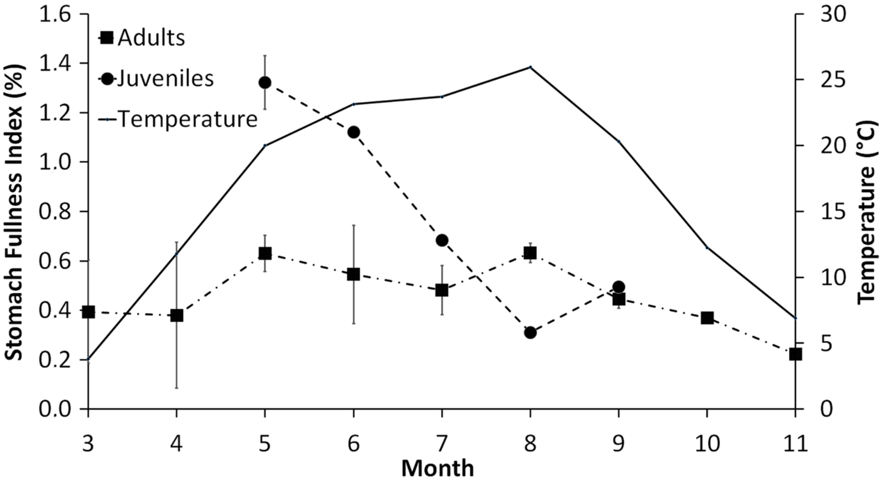


Fig. 3 Seasonal dynamics of the stomach fullness index (± SE) of racer goby and relationship with water temperature in the sampling reach in 2015

According to index of relative importance, chironomid larvae were the most important prey in the diet across all size groups of racer goby (Table 3 and Fig. 4). Cladocerans and copepods were the second and third most important prey in the diet of the smallest size group (< 50 mm), while *Dreissena* sp. and water mites were most important in the 50–69-mm-size group and *Dreissena* sp. and chironomid pupae followed by fish were most important in the ≥ 70-mm-size group. The 50–69-mm and ≥ 70-mm gobies consumed a somewhat higher diversity of prey organisms, which included 39 items (chironomid taxa pooled), compared to the < 50-mm-size group, the diet of which included 34 items.

The composition of prey items in the racer goby's diet showed seasonal dynamics; however, chironomid larvae predominated throughout the year in both < 50 mm and ≥ 50 mm fish (Fig. 4). They were somewhat less important in the diet of ≥ 50 mm fish in March and September and in the diet of < 50 mm fish in May and September. Copepods were most important in the gut contents of ≥ 50 mm fish in January-March, while they were most important in < 50 mm fish in May and September. Cladocerans were most important in the diet of < 50 mm fish in May–July and September. Other important prey items consumed by ≥ 50 mm fish were *Dreissena* sp. in July-November and especially in September (15.0% IRI), fish juveniles in August (11.8% IRI), and water mites in September (8.4% IRI). Other important prey items consumed by < 50 mm goby were Ephemeroptera (mainly *Caenis* sp.) in September (7.9% IRI) and water mites in May (5.2% IRI) and August (7.7% IRI).

Mean numbers of the most important groups of prey organisms in the stomach contents of ≥ 50 mm fish in the sampling reach varied by season. The highest abundances of chironomid larvae were observed in April to June with pronounced peaks in May as well as in October, copepods in January-March, and cladocerans in October (Fig. 5). The highest abundances of chironomid larvae in the diet of < 50 mm goby were observed in June to August and copepods and cladocerans in May and September. The highest diversity of prey organisms in the diet of both size groups was observed in September: 32 and 21 taxonomic groups, respectively.

In total, 34 taxa were identified in benthos samples in the sampling reach, among which chironomid larvae predominated throughout all months and their share by abundance varied from 89.6% in April to 62.2% in July. The most abundant chironomid species was *P. convictum* accounting for 55.0% of all chironomid taxa. Practically, all benthic taxa found in the benthos samples were observed in the racer goby diet. No significant relationship between the abundance of chironomids in the benthos samples and their number in fish gut contents was found (LM: $F_{1,8} = 3.799$, $r^2 = 0.35$, $p = 0.092$) nor were such relationships observed between the abundance of most abundant chironomid taxa (*P. convictum*, *Chironomus* sp., *Glyptotendipes* sp., *Cricotopus sylvestris*), some other benthic invertebrates (Gammaridae), and their numbers in the gut contents of this gobiid (LM: $p > 0.05$). Nevertheless, some common trends were observed in the monthly dynamics of the abundances of chironomid larvae in the benthos and fish stomach contents, as higher abundances usually occurred in spring and autumn (Fig. 6).

Table 2 Diet composition of racer goby at the sampling site (all length groups and seasons pooled) in 2015–2016, where %N = relative abundance of prey items, %W = percentage of biomass, %F = frequency of occurrence

Prey item	%N	%W	%F
Oligochaeta	0.03	0.10	0.43
Bryozoa statoblasts	0.30	0.39	0.86
Dreissena sp.	3.62	17.75	33.62
Gastropoda	0.18	0.14	3.02
Cladocera	14.44	1.21	62.5
Bosmina longirostris	0.10	< 0.01	0.86
Chydorus sphaericus	1.01	0.03	11.21
Ceriodaphnia sp.	0.36	0.02	3.88
Alona affinis	2.07	0.23	20.69
Alona sp.	0.65	0.04	10.34
Pseudochydorus globosus	0.96	0.09	11.21
Pleuroxus aduncus	2.53	0.19	21.12
Pleuroxus sp.	0.08	0.01	1.29
Disparalona rostrata	3.62	0.26	1.97
Graptoleberis testudinaria	0.15	0.01	2.59
Camptocercus sp.	0.96	0.11	12.50
Acroperus harpae	0.65	0.03	5.60
Eurycercus lamellatus	0.59	0.12	7.76
Ilyocryptus sp.	0.05	0.00	0.86
Leydigia leydigi	0.18	0.01	2.16
Simocephalus sp.	0.26	0.04	2.59
Anchistropus emarginatus	0.23	0.02	3.02
Copepods	7.93	0.76	40.09
Cyclopoida	7.52	0.75	37.93
Calanoida	0.03	< 0.01	0.43
Harpacticoida	0.39	0.01	4.74
Ostracoda	3.23	0.39	25.00
Mysidae	0.03	0.07	0.43
Asellus aquaticus	0.05	0.10	0.86
Amphipoda	0.77	1.33	11.21
Cumacea	0.03	0.06	0.43
Acari	4.75	2.34	31.90
Insects	64.43	48.59	100.00
Chironomidae larvae	53.78	40.08	97.41
Chironomus sp.	4.74	10.81	-
Cladotanytarsus mancus	1.77	0.24	-
Cricotopus algarum	0.09	0.02	-
Cricotopus sylvestris gr.	5.58	0.81	-
Cryptochironomus defectus	0.19	0.08	-
Cladopelma viridulum	0.37	0.05	-
Diamesa sp.	0.09	0.02	-
Dicrotendipes nervosus	4.00	1.12	-
Endochironomus albipennis	7.81	6.47	-
Eukiefferiella longicalcar	0.09	0.02	-
Glyptotendipes sp.	8.09	11.83	-
Microtendipes pedellus	0.19	0.04	
Parachironomus vitiosus	0.93	0.12	-
Paratanytarsus lauterborni	1.49	0.22	-
Polypedilum sordens	0.65	0.08	-
Polypedilum convictum	10.88	5.24	-
Polypedilum nubeculosum	0.47	0.12	-
Polypedilum scalaenum	1.49	0.51	-
Polypedilum sp.	1.21	0.38	-
Psectrocladius psilopterus	0.65	0.16	-
Procladius ferrugineus	0.09	0.01	-
Stictochironomus stictus	1.58	1.06	-
Tanytarsus gregarius	0.65	0.07	-
Tribe Chironomini	1.12	0.60	-
Tribe Tanytarsini	0.74	0.12	-
Chironomidae pupae	4.00	2.80	30.60
Ceratopogonidae larvae	0.10	0.49	1.72
Tipulidae larvae	0.03	0.42	0.43
Psychodidae larvae	0.13	0.08	1.72
Ephemeroptera larvae	0.90	0.49	13.36
Caenis sp.	0.70	0.39	10.78
Baetis sp.	0.21	0.10	3.02
Trichoptera larvae	2.51	0.66	23.28
Orthotrichia sp.	2.32	0.41	20.26
Other Trichoptera	0.18	0.25	3.02
Zygoptera larvae	0.52	2.72	7.33
Micronecta scholtzi	1.14	0.44	12.07
Lepidoptera larvae	0.05	0.19	0.86
Coleoptera larvae	0.08	0.12	1.29
Fish	0.21	26.75	3.45
Gobiidae	0.13	22.11	2.16
Cyprinidae	0.05	4.05	0.86
Syngnathus abaster	0.03	0.60	0.43

Discussion

Seasonal abundances

The seasonal dynamics of racer goby abundance showed patterns typical for gobiids and other fishes inhabiting temperate waters, the abundance of which in nearshore communities highly depended on water temperature (Young et al. 2010; Lynch and Mensinger 2012; Blair et al. 2019; Stacy-Duffy et al. 2020). The

Table 3 Diet composition of different length groups (TL) of racer goby in the Stugna River in 2015–2016: %F = frequency of occurrence; %IRI = percent index of relative importance

Prey item	< 50 mm		50–69 mm		≥ 70 mm	
	n = 74		n = 101		n = 62	
	%F	%IRI	%F	%IRI	%F	%IRI
Oligochaeta	-	-	0.99	< 0.01	1.61	< 0.01
Bryozoa statoblasts	-	-	-	-	3.23	0.05
Dreissena sp.	24.32	2.51	35.64	6.70	41.94	7.92
Gastropoda	-	-	4.95	0.02	3.23	0.01
Bosmina longirostris	2.70	0.01	-	-	-	-
Chydorus sphaericus	24.32	0.54	4.95	0.01	4.84	0.01
Ceriodaphnia sp.	9.46	0.09	1.98	< 0.01	-	-
Alona affinis	22.97	0.67	16.83	0.23	24.19	0.45
Alona sp.	22.97	0.33	4.95	0.01	3.23	0.01
Pseudochydorus globosus	12.16	0.14	11.88	0.11	12.90	0.11
Pleuroxus aduncus	37.84	2.03	13.86	0.16	11.29	0.10
Pleuroxus sp.	4.05	0.01	-	-	-	-
Disparalona rostrata	43.24	4.34	11.88	0.09	1.61	< 0.01
Graptoleberis testudinaria	6.76	0.03	0.99	< 0.01	-	-
Camptocercus sp.	5.41	0.02	18.81	0.25	9.68	0.06
Acroperus harpae	5.41	0.02	1.98	< 0.01	11.29	0.15
Eurycercus lamellatus	5.41	0.02	9.90	0.07	9.68	0.07
Ilyocryptus sp.	1.35	< 0.01	0.99	< 0.01	-	-
Leydigia leydigi	1.35	< 0.01	3.96	0.01	-	-
Simocephalus sp.	-	-	2.97	0.01	4.84	0.02
Anchistropus emarginatus	-	-	6.93	0.03	1.61	< 0.01
Cyclopoida	45.95	5.02	36.63	1.82	30.65	1.88
Calanoida	1.35	< 0.01	-	-	-	-
Harpacticoida	12.16	0.11	1.98	< 0.01	-	-
Ostracoda	18.92	0.45	24.75	0.76	30.65	1.08
Mysidae	-	-	-	-	1.61	< 0.01
Asellus aquaticus	1.35	0.01	-	-	1.61	< 0.01
Amphipoda	1.35	< 0.01	15.84	0.43	16.13	0.28
Cumacea	-	-	-	-	1.61	< 0.01
Acari	21.62	1.05	38.61	3.50	35.48	1.36
Chironomidae larv	95.95	82.01	99.01	82.85	96.77	78.29
Chironomidae pup	13.51	0.27	34.65	1.64	43.55	4.12
Ceratopogonidae larv	-	-	1.98	0.01	3.23	0.02
Tipulidae larv	-	-	-	-	1.61	0.01
Psychodidae larv	-	-	2.97	0.01	1.61	< 0.01
Caenis sp. larv	1.35	< 0.01	11.88	0.09	20.97	0.32
Baetis sp. larv	1.35	< 0.01	2.97	0.01	4.84	0.01
Orthotrichia sp. larv	1.35	< 0.01	21.78	0.48	38.71	1.63
Other Trichoptera larv	5.41	0.06	1.98	< 0.01	3.23	< 0.01
Zygoptera larv	-	-	7.92	0.31	14.52	0.39
Micronecta scholtzi	12.16	0.25	11.88	0.18	11.29	0.09
Lepidoptera larv	-	-	1.98	0.01	-	-

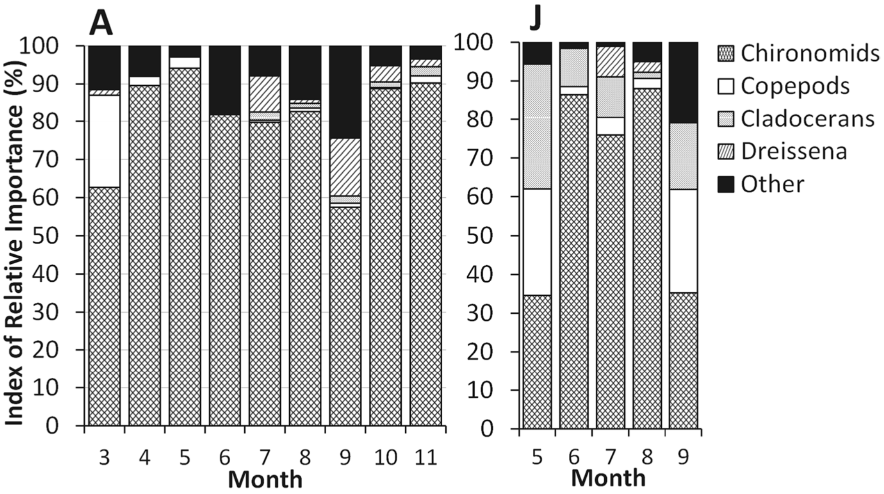
Table 3 (continued)

Prey item	< 50 mm		50–69 mm		≥ 70 mm	
	n = 74		n = 101		n = 62	
	%F	%IRI	%F	%IRI	%F	%IRI
Coleoptera larv	-	-	1.98	0.01	1.61	< 0.01
Gobiidae	-	-	1.98	0.15	4.84	1.45
Cyprinidae	-	-	0.99	0.03	1.61	0.08
Syngnathus abaster	-	-	-	-	1.61	0.02

paucity of racer goby individuals in the littoral zone of the Stugna River during winter suggests that this species winters offshore, probably in deeper waters, which is similar to other gobiids such as round goby (*Neogobius melanostomus*) (Sapota and Skóra 2005; Pennuto et al. 2010; Lynch and Mensinger 2012). Racer goby started migrating inshore in March and April with a rise in water temperature and their migrating activity also depended on it. For example, the CPUE of this species in March 2015 was higher than that in 2018 by 1.4 times and water temperature in the sampling reach in March 2015 exceeded that in 2018 by 1.5 °C. A similar picture but significantly more evident was observed in April, when CPUE in 2018 exceeded that in 2015 by 14.0 times, while water temperature in 2018 exceeded that in 2015 by 5.4 °C. A peak in the abundance of this goby in the sampling reach observed in April can be due to the arrival and concentration of brood fish on their spawning grounds. A positive correlation of goby occurrence with water temperature was also reported for round goby and bighead goby (*Ponticola kessleri*) in the invaded Rhine River (Baer et al. 2017).

A drop in racer goby abundance observed in May could be related to the end of spawning activity of this species. Such a decrease in the abundance of gobiids (e.g. round goby) after the spawning season can also result from postspawn mortality of large fish due to the physical stress incurred during their reproductive season (Lynch and Mensinger 2012). Additionally, females of this species can move to deeper waters after spawning for rest, while males remain near nests to guard them (Grabowska 2005). The first juveniles started appearing in catches in the end of May, when they reached an average length of 19.4 mm. This is similar to spawning of *B. gymnotrachelus* in the Włocławski Reservoir in Poland, where juveniles of an average length of approximately 18 mm also appeared in samples in the end of May (Grabowska 2005).

Fig. 4 Seasonal dynamics of the diet composition of racer goby in the sampling reach based on the percent index of relative importance (%IRI) in 2015: A, adult fish (≥ 50 mm); J, juveniles (< 50 mm)



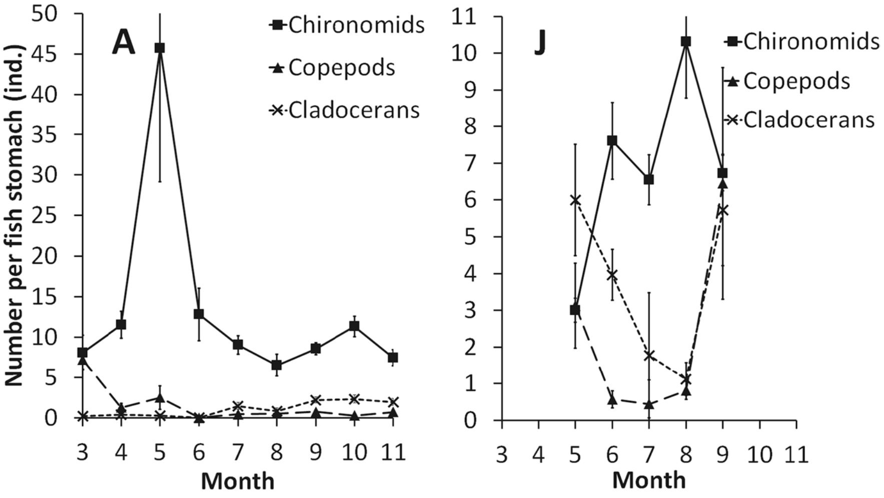


Fig. 5 Seasonal dynamics of mean abundances of most important groups of prey organisms in the stomach contents of racer goby in the sampling reach (N per fish ± SE) in 2015: A, adult fish (≥ 50 mm); J, juveniles (< 50 mm)

Increased abundance of racer goby in the sampling reach from May to June indicated recruitment of age-0. A sharp decline observed in August 2015 and then a subsequent increase might be due to very high water temperature observed during this month in 2015 compared to 2018. Although water temperature during the August 2015 sampling did not exceeded that of August 2018 substantially (26.1 °C versus 25.8 °C, respectively), the fish might left the littoral zone of the sampling reach earlier in 2015. The average air temperature according to archived data of the Ukrainian Hydrometeorological Centre at this location seven consecutive days before the sampling date was 32.0 °C in 2015 versus 27.9 °C in 2018, which might have resulted in a higher water temperature during these days in 2015 compared to 2018. Thus, racer goby might do not tolerate extremely high water temperatures. The preference for intermediate water temperature was also reported by Young et al. (2010) for the round goby. No data are available for the racer goby, but according to Hatton et al. (2018), the final temperature preferendum for this species (14.5 °C) is lower than that of the round goby (24.6 °C). Moreover, high water temperature, especially in macrophyte beds such as those found in the sampling reach, can lower dissolved oxygen content due to increased self-shading and respiration of aquatic plants (Carter et al. 1991; Chimney et al. 2006) affecting goby distribution. However, the above observations were available only for two years in a single site; therefore, additional studies are needed to determine factors, which affect the abundance of the racer goby during summer in the littoral zone of freshwaters.

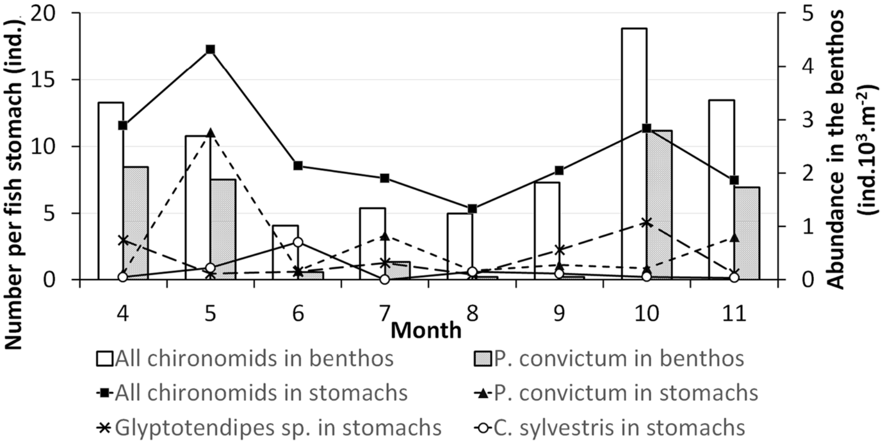


Fig. 6 Seasonal dynamics of some abundant chironomid taxa in the benthos and stomach contents of racer goby in the sampling reach in 2015

Racer goby juveniles were dominant in the total population in the sampling reach from the end of May to September and the majority of them reached the size of adult fish in October. In general, the growth pattern of age-0 fish in the Stugna River was similar to that described by Grabowska (2005) for the Włocławski Reservoir in Poland. The presence of small individuals and several peaks observed in the length frequency distribution of racer goby in the Stugna River in September to November may be better explained by the intrapopulation differentiation of individual growth rates than by extended spawning, because no early age-0 fish (18–25 mm) were found in samples from July to August. A multimodal distribution of length sizes of racer goby observed by Grabowska (2005) in the Włocławski Reservoir in Poland was explained by additional spawning events and it was concluded that spawning of this goby in this water body lasted from April to August. However, the author did not explain the absence of early age-0 fish (<20 mm) in samples in July and August, though they were abundant in May and June (Grabowska 2005).

Racer goby abundance in the littoral zone sharply declined after September. This could be due mainly to the migration of larger age-0 and older fish offshore for wintering; however, some fish were probably eliminated by predators. The outmigration to deeper waters coincided with a drop in water temperature and was correlated with it. For example, CPUE in October 2018 exceeded that in October 2015 by 4.1 times and water temperature in October 2018 exceeded that in 2015 by 6.1 °C suggesting that this migration in 2015 started earlier than in 2018 and more fish left the littoral zone by the sampling date in October in 2015 than in 2018.

Thus, seasonal changes in the abundances and average sizes of racer goby in the littoral zone of an invaded freshwater body are due to several casual mechanisms associated with water temperature. They include migrations of brood fish to the littoral zone before spawning resulting in an increase in their concentrations in April, then spawning in April–May and appearance of early age-0 fish in May–June, followed by the disappearance of the majority of brood fish in May–June. Additional spawning events probably occur later in June and July. An influx of small goby and increases in their average sizes during summer months indicated recruitment of new age-0 fish and their rapid growth, because the majority of the fish reached adult sizes by October. The outmigration of adult-sized goby from the littoral zone for wintering occurred in the October–November. This species can also leave the littoral zone in cases when water temperature exceeds some tolerance threshold and return later after the temperature drops below it.

Feeding patterns

Racer goby inhabiting the Stugna River consumed a broad spectrum of prey organisms and displayed distinct differences in feeding activities and diet compositions depending on both fish size and prey availability. The dependence of the feeding activity of this species on the season and water temperature is typical for fishes inhabiting temperate zone and was also reported for other gobiids (Borcherding et al. 2013; Všetičková et al. 2014).

Racer goby fed continuously throughout the year; however, their feeding activity during winter was very low. The stomach fullness of this goby started increasing in spring reaching a peak in May with a water temperature rise. Relatively low stomach fullness values observed in April compared to March despite the temperature rise may be because females during this period were filled with ripened eggs that could bias their total weights. Very similar dynamics of the stomach fullness with an increase from winter months to March, then some drop in April and a peak in May was also reported for the western tubenose goby (*Proterorhinus semilunaris*) in a lowland reservoir in the Czech Republic (Adámek et al. 2010). A drop in stomach fullness of racer goby observed from May to June and July was comparable to such a drop reported for other gobiids including western tubenose, round, and bighead gobies (Adámek et al. 2010; Borcherding et al. 2013; Vašek et al. 2014) and it can be connected with physical stress caused by extended reproductive activity and subsequent guarding of the eggs by males (Adámek et al. 2010). An increase in stomach fullness of ≥ 50 mm goby in August and September could be due to an increase in their feeding activity after recovery from the stress caused by reproductive activity, an increase in water temperature, and recruitment of actively feeding growing age-0 fish, which started reaching the size of adult fish. Later, from September to November, a second more significant drop in food consumption occurred, which followed a decrease in water temperature. This drop might be attributable to reduced feeding activity and not to a lack of available prey because chironomid abundance in benthos in the sampling reach during this period was higher than in other months. Early juveniles of racer goby were characterized by very active feeding during their first month of life and their feeding activity decreased with their growth and deceleration in their metabolism rate.

Besides seasonal differences in stomach fullness values, racer goby also displayed seasonal differences in diet composition that might be attributable to prey availability; however, chironomid larvae remained the most important prey of all size groups of this fish throughout each year.

Among the most abundant chironomid taxa recorded in the racer goby diet, *P. convictum* is predominantly a psammophilous species (Grzybkowska and Witczak 1990). *Glyptotendipes* sp. is usually associated with macrophytes and is a leaf miner (Koperski 1998), but can also inhabit various substrates such as plant tissues, plant detritus, wood debris, and mud (Kornijów 1986; Phillips and Kilambi 1994; Charbonneau and Hare 1998; Özkan et al. 2010). *Chironomus* sp. is a burrower in sand and mud (Özkan et al. 2010). *Endochironomus albipennis* and *C. sylvestris*, which also frequently occurred in the gut content, are phytophilous species, but can also occur in bottom sediments (Menzie 1981; Kornijów 1992). Thus, racer goby consumed a variety of chironomids taxa including macrophyte-associated and burrowers in sand and mud. A similar pattern was observed by Kakareko et al. (2005), where *Chironomus* sp. predominated, but phytophilous taxa were also very frequent among chironomid larvae consumed by racer goby inhabiting the Vistula River and Włocławek Reservoir in Poland. Chironomid larvae were also among the most important prey items in the diet of this gobiid in other freshwaters in Poland and Ukraine (Grabowska and Grabowski 2005; Didenko et al. 2017).

Another important prey group of racer goby were copepods, which were especially abundant in the diet of early juveniles in May and advanced juveniles in September. A drop in cyclopoid consumption observed in June to August might be due to a drop in their abundance in the sampling reach during these months. A decline in cyclopoids in June and July in the environment could be due to a combination of predation and diapausing, which they enter to avoid mid-summer predation (George 1973; Overgård Schou et al. 2009).

Cladocerans were quite important in the diet of early juveniles of racer goby in May–June and advanced juveniles in September. Among them, the most abundant and frequently encountered were chydorids (98.9% of all cladoceran according to %IRI), especially *D. rostrata*, *Chydorus sphaericus*, and *P. aduncus*, with the significant predominance of the first species. Benthic chydorids also composed a significant portion in the diet of fry of other gobiids in other invaded freshwaters, e.g. round goby in the Lake Michigan (Olson and Janssen 2017). Chydorids, however, in significantly lower abundances and mainly *A. affinis*, *P. aduncus*, and *Camptocercus* sp., were also found in the gut contents of ≥ 50 mm racer goby, especially in June to November. When comparing the species composition of consumed cladocerans, it seems that ≥ 50 mm goby consumed larger species than < 50 mm goby. Among the most abundant cladocerans found in the stomach contents of racer goby in the sampling reach, *D. rostrata* usually inhabits sites with little macrophyte growth, *P. aduncus* usually dwells among macrophytes and are rarely found on substrates devoid of plant cover, while *Alona affinis* and *C. sphaericus* can occur on different substrate types (Duigan 1992).

Other important prey in the diet of ≥ 50 mm racer goby in the sampling reach were *Dreissena* sp. and fish juveniles. *Dreissena* sp. was consumed mainly in the summer and autumn when small specimens with shell lengths of 2–5 mm were probably available. *Dreissena* sp. in the diet of the racer goby was also observed in the Vistula River in Poland (Kakareko et al. 2005). As for fish prey, the most important were gobiid juveniles, which were also observed in the diet of the racer goby during summer in the Dniprodzerzhynsk Reservoir (Didenko et al. 2017). Fish larvae and juveniles in the stomach contents of racer goby were also reported for the Włocławski Reservoir in Poland (Grabowska and Grabowski 2005; Kakareko et al. 2005). It should be noted that fish were usually relatively a larger prey than the majority of invertebrates, so they accounted for a large amount of food weight even if numbers were extremely low.

The stomach contents of ≥ 50 mm racer goby in September were characterized by a very high share of non-chironomid taxa (44.7% by %IRI), among which the most important were water mites, ostracods, and *Dreissena* sp. Racer goby consumed water mites relatively regularly throughout a year (7 months of 11) indicating that they can be one of favourite prey. Usually, fish do not consume water mites and rapidly reject them after accidental ingestion because of distasteful and unpalatable substances secreted by their idiosomal glands (Pieczynski and Prejs 1970; Kerfoot 1982). However, water mites also rarely occurred in the diet of other gobiids in freshwaters including round, monkey, and bighead gobies (Adámek et al. 2007; Borcherding et al. 2013).

As for < 50 mm racer goby, the most important prey in the group "others" were Ephemeroptera (mainly *Caenis* sp.) and Trichoptera (mainly *Orthotrichia* sp.) larvae, *Dreissena* sp., and water mites. As in the case of ≥ 50 mm fish, the share of "other" prey items was especially high in September. An ontogenetic diet shift from the consumption of predominantly benthic microinvertebrates such as cladocerans and copepods in the diet of early juveniles observed in May that is common for gobiid fry in invaded freshwaters (Olson and Janssen 2017) to predominantly benthic macroinvertebrates such as chironomids and *Dreissena* sp. observed in the diet of more advanced juveniles as soon as in June and July as well as in adults occurred in the Stugna River.

Comparison of diets of two size groups of adult racer goby (50–69 mm and ≥ 70 mm) showed a somewhat higher importance of non-chironomid taxa (e.g. Ephemeroptera, Trichoptera, Zygoptera) in the gut contents of the second group that might be related to larger sizes of these preys. Goby of the largest size group also consumed substantially more fish prey. An increase in the importance of fish prey in the diet was also observed in other gobiids including monkey and bighead gobies as they grew (Borcherding et al. 2013).

The absence of significant relationships between the abundances of prey organisms in benthos samples and fish stomach contents may be because benthos samples were point samples, which covered very small areas of the bottom, and thus, they may have not represented the entire benthic community in the sampling reach. It can be also be due to the fact that prey availability does not affect diets significantly or major prey preferred habitats, which were not sampled. Nevertheless, the common trends observed between the abundances of chironomids in the benthos and fish diets indicate that these point samples at least partially reflected the common picture. Moreover, racer goby also consumed macrophyte-associated prey organisms, which were not represented or underrepresented in the benthos samples (e.g. *C. sylvestris*, Ephemeroptera, Trichoptera).

Thus, racer goby seems to be an opportunistic feeder that consumes a broad variety of mainly benthic organisms. According to Kostrzewa and Grabowski (2003), this species selects prey that is probably the most abundant and therefore easily available in a particular locality and season. This confirms the work of other researchers who have found the prey of this goby varies across river systems. For example, the most important prey of this species in the lower Danube are copepods, chironomids, and molluscs (Petrusenko and Smirnov 1984); chironomids in the South Bug (Smirnov 1984); molluscs and amphipods in the middle Dnieper (Smirnov, 1984); molluscs, amphipods, and chironomids in the Włocławski Reservoir on the Vistula River (Kostrzewa and Grabowski 2003; Grabowska and Grabowski 2005); and chironomids and amphipods in the Vistula River (Kakareko et al. 2005). Based on the diet composition, which included both open-bottom-dwelling and phytophilous organisms, it can be concluded that racer goby in the Stugna River fed on a large variety of microhabitats including open non-vegetated areas with sand and muddy sand substrates and in benthic zones near or among macrophytes. The racer goby's opportunistic feeding strategy combined with high juvenile recruitment as well as with other attributes (e.g. euryhalinity and protection of laid eggs) can facilitate the successful establishment of this species in a variety of new environments and contribute to its wide distribution.

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Author contribution The study was designed by AD. Field data were collected by AS, AB, and VB. Identification and analysis of chironomid taxa was performed by YV, those of invertebrates by AD and SK. Population dynamics was analysed by IB. All authors contributed to data interpretation and manuscript preparation and editing.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Ethical statement Fish sampling and handling were performed according to the Ukrainian legislation. Fishing samples were collected under a permit issued by the State Agency of Fisheries of Ukraine.

Conflict of interest The authors declare no competing interests.

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