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Research Article

The role of invasive Chinese sleeper *Perccottus glenii* Dybowski, 1877 in the Ilgas Nature Reserve ecosystem: an example of a monospecific fish community

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Abstract

The Chinese sleeper, *Perccottus glenii*, is an invasive species that has spread into Eastern Europe from its natural geographic range in Far Eastern Asia. Here, we provide a complex hydrobiological study of a marsh waterbody in the Ilgas Nature Reserve Natura 2000 site (Latvia) where we registered a monospecific fish community comprised of Chinese sleeper. While benthic organisms were predominant in the diet of Chinese sleeper of < 70 mm, the diet of larger fish (particularly around 90 mm) included an increasing proportion of juvenile Chinese sleeper (cannibalism). In the case of the Ilgas marsh, we believe that medium natural production (mesotrophic waterbody), piscivory and high competition for food has resulted in a monospecific fish community represented by Chinese sleeper alone.

Key words: Natura 2000, invasive species, parasites, benthos, nutrition spectrum

Introduction

Following its introduction into a new area, an alien species may or may not become invasive, i.e. after becoming established, it may then spread to new areas and have a negative impact on native species and/or ecosystems. The degree to which an alien species becomes invasive is regulated by a range of internal (e.g. genetic diversity, ecological plasticity) and/or external (e.g. transformation of ecosystems or fish stocks) “trigger” mechanisms (Hauser and McCarthy 2009). Once it becomes invasive, an alien species can negatively influence local fauna through predation, food and spatial competition, hybridisation, the spread of parasites and pathogens or through modification of food webs or biochemical cycles (Leunda 2010; Cucherousset and Olden 2011).

Over recent decades, the Chinese sleeper, *Perccottus glenii* Dybowski, 1877 (Actinopterygii: Odontobutidae), a fish native to Far Eastern Russia, China, northwestern Korea and northern Sakhalin (Mori 1936; Bogutskaya

et al. 2008), has spread into Central and Eastern Europe, primarily through transportation of aquacultural fish stocks (Reshetnikov 2004; Kutsokon 2017). In Latvia, for example, local populations are most likely related to Baltic populations originating from an introduction by aquarists in St. Petersburg (Russia) in 1914 (Grabowska et al. 2020).

Over most of its new range, the Chinese sleeper is now recognised as a harmful invasive fish that competes aggressively with native fishes for food and spawning sites (Reshetnikov 2003; Kati et al. 2015; Grabowska et al. 2019). The species displays a generalist and flexible feeding strategy, typical of successful invaders (Rau et al. 2017), and shows relatively high tolerance to both anoxic and hypoxic environments (Chai et al. 2020), allowing the fish to attain high abundance in small waterbodies which otherwise support a poor ichthyofauna (Reshetnikov 2013). As such, the Chinese sleeper can harm small lentic waterbody ecosystems and, through interactions with eutrophication processes, affect waterbody regulation services (Reshetnikov 2003; Rechulicz et al. 2015; Rau et al. 2017). In isolated waterbodies such as marsh lakes, it has been shown to interact strongly with the local herpetofauna, changing food webs and parasitic life-cycles (Reshetnikov et al. 2013). In Europe, for example, the Chinese sleeper has altered amphibian food webs through both direct predation of tadpoles, which can form a major dietary item (Reshetnikov 2001; Plyusnina 2008), and as prey (Pupina et al. 2015; Pupins and Pupina 2018). As the diet of amphibian larvae consists primarily of benthic algae (Waringer-Löschenkohl and Schagerl 2001), they represent an important link for transmitting energy from freshwater to terrestrial ecosystems. As such, tadpoles can have an important impact on primary production, nutrient flux and competitive interactions within waterbodies (Brönmark et al. 1991; Kupferberg 1997). The Chinese sleeper is also known to have an impact on amphibian and reptile parasite life cycles by acting as a paratenic or intermediate host (Kvach et al. 2013; Reshetnikov et al. 2013).

The Ilgas Natura 2000 Nature Reserve, which is made up of a mosaic of marsh and forest habitats, was established in Latvia in 1999 in order to protect the northernmost population of the European fire-bellied toad (*Bombina orientalis* L., 1761), a protected species in both Latvia and Europe as a whole (Pupina and Pupins 2008). The Chinese sleeper became established in the marshes in 2004, though the actual vector of introduction still remains unclear (Pupina et al. 2015). In this study, we aim to i) provide a complex analysis of the marsh ecosystem (primary producers, zoobenthos, fish assemblage) in order to provide baseline data for future studies, and ii) to assess the role of Chinese sleeper within the ecosystem by examining its trophic status, dietary preferences and associated parasite assemblage.



Figure 1. Map of the study area.

Materials and methods

Sampling

The Ilgas Natura 2000 (code: LV0526300) Nature Reserve (area: 157 ha) is a natural protected area of European-wide importance located in the Silene Natura 2000 (code: LV0300400) Nature Park, south of the City of Daugavpils in Latvia (55.691217N; 26.771125E, Figure 1). Its marsh/forest ecosystem is primarily the result of Eurasian beaver (*Castor fiber* L., 1758) activity, which has produced an intricate system of shallow (up to 1m) natural and artificial waterbodies with silt and sand bottom sediments. The majority of the water surface (ca. 80%) is overgrown with aquatic and hydrophilic macrophytes, such as *Myriophyllum spicatum* L., *Phragmites australis* (Cav.) Trin. ex Steud., *Hydrocharis morsus-ranae* L., *Potamogeton* sp., *Carex* sp. and *Juncus* sp.

Sampling for this study took place at the Nature Reserve in August of 2019. Zoobenthos samples were taken using a 20 × 20 cm benthic frame (mesh size: 100 µm) at a depth of ca. 0.5 m. Three benthos samples were taken at each of three different sites (i.e. nine zoobenthos samples in total), with sites chosen based on technical feasibility. All samples were immediately transported to the laboratory in ice for further analysis.

Four qualitative microphytobenthos samples were collected from a depth of 0.5–1 m using a standard Ekman Grab and a 2 cm sediment slice taken from each grab sample using a 23 cm² aperture tube. In addition, phytoplankton were sampled by taking a 1 L water sample from the surface at the same site. All samples were immediately preserved in 4% formaldehyde and taken to the laboratory for further analysis.

Table 1. Size and weight parameters for Chinese sleeper (*Perccottus glenii*) used in the diet study (n = 70). SL = standard length; W = total body weight; W_{evi} = eviscerated body weight; above the line = Mean $\pm$ SD; below the line = min–max.

Length groups	SL (mm)	W (g)	W_{evi} (g)
< 70 mm (n = 42)	<u>39.3 ± 2.8</u>	<u>3.1 ± 0.5</u>	<u>2.7 ± 0.4</u>
	14.7–69.0	0.1–9.9	0.1–8.6
> 70 mm (n = 28)	<u>75.8 ± 1.3</u>	<u>11.7 ± 0.6</u>	<u>10.4 ± 0.5</u>
	70.0–86.0	8.7–16.2	7.9–14.4
All fish (n = 70)	<u>46.8 ± 2.8</u>	<u>4.9 ± 0.6</u>	<u>4.3 ± 0.5</u>
	14.7–86.0	0.1–16.2	0.1–14.4

Three periphyton samples were obtained from aquatic vegetation and, in addition, fresh fragments of semi-aquatic macrophytes were transported to the laboratory where they were studied under a light microscope.

Fish were sampled from a 100 m² area of water comprising both open and vegetated zones. In open water (free of macrophyte growth), fish were sampled by making two 5 m trawls with a 5 m beach seine (mesh: 5 mm). In vegetated zones, fish were sampled using a 0.5 cm mesh dipnet down to a depth of 1 m. All fish caught were measured (standard length [SL] in mm) directly at the sampling site. Of the 187 Chinese sleeper caught, 70 were placed into a container and kept on ice until transported to the laboratory for the diet study. A further 20 were transported alive to the laboratory in an aerated canister, where they were placed in an aerated aquarium for the parasite study.

Laboratory processing

Zoobenthos samples were washed through a series of standard benthic sieves with a minimum mesh size of 0.5 mm and the organisms collected were preserved in 4% formalin for further species identification. All benthic organisms were identified to the lowest possible taxonomic level and the number (N) and biomass (B) of each taxon was calculated to 1 m². The biomass of mass organisms, such as nematodes and ostracods, was not calculated.

The 1 L phytoplankton sample was concentrated using the sedimentation method, resulting in a final volume of 100 ml. Silt and clay were isolated from the sample using 35 kHz ultrasound over 10–20 min (Nevrova et al. 2015). Cells were counted under a Bresser $\times 400$ light microscope. For all primary producers, the number of cells was calculated using a Fuchs-Rosenthal counting chamber (0.012 ml volume) then calculated to cm² for phytobenthos and L² for phytoplankton. Biomass was calculated in accordance with the methods of Olenina et al. (2006) for real volume. Algae bioindication was based on Barinova et al. (2019); taxonomy given according to AlgaeBase (Guiry and Guiry 2019).

For the diet study, the 70 fish placed on ice were first measured (SL, mm) and weighed (total body weight [W, g]), then eviscerated and reweighed (W_{evi} , g) (Table 1). The eviscerated guts were then preserved in 70% ethanol for further identification of dietary items. Chinese sleeper diet was assessed

using the methods of Hyslop (1980) (see below), with dietary components identified taxonomically according to the World Register of Marine Species database (WoRMS 2020).

For the parasite study, the 20 living Chinese sleeper were measured (SL, mm) then sacrificed humanely (anaesthetising and subsequent overdosing by clove oil) and dissected within 48 hours of sampling, according to the recommendations of Kvach et al. (2016). The fins, skin, gills, eyes, muscles, body cavity and internal organs (gut, liver, gallbladder, spleen, swim bladder, kidneys, uterine bladder, gonads, mesentery and brain) were then examined for parasites. Unicellular parasites were immediately examined alive under light microscopy, while trematodes were first fixed in hot 4% formalin for further study (Cribb and Bray 2010).

Dietary analysis

Based on previous studies (e.g. Koščo et al. 2008), Chinese sleeper were divided into two groups according to expected ontogenetic dietary specialisation, i.e. benthophagous individuals of < 70 mm SL and piscivorous individuals of > 70 mm SL.

The reconstructed weights of dietary items were calculated based on the weights of similarly sized individuals of the same taxa in the benthos. The calorie content of different dietary items was assessed using the dependence method for calculation of the energy equivalent of body weight (Q, %) (Aleksandrov 2001a, b).

Prey item frequency of occurrence (O_i , %) was evaluated as $O_i = \frac{J_i}{P} \times 100\%$, where J_i is the number of fishes containing dietary item “I” and P is the number of fishes with food in their stomachs. The gut fullness index (FI) was calculated as the ratio of the weight of food (FW) and the total fish weight (W) using the formula $FI = \frac{FW}{W} \times 100\%$ (Hureau 1969). The significance of differences in gut fullness (FI) and energy equivalents (Q) between the stomach contents of small and large fish were determined using the nonparametric Mann-Whitney U-test. Cluster analysis based on Euclidean distance and complete linkage was used to evaluate similarity in diet composition between fish size groups. In order to test how the amount of food taken and its energetic value change with the fish size, Spearman correlations between fish size and FI and Q indices were calculated (standard

error of the correlation coefficient was calculated as: $SE_r = \sqrt{\frac{1-p^2}{n-2}}$).

Statistical analyses were performed using Primer v.5.0, Statistica v.12.0 (StatSoft, Inc.), the Microsoft Excel analysis package and Access 2010.

The index of the relative importance (IRI) of dietary items was calculated using the formula $IRI = (M + N) \times F$, where M represents the biomass of prey items (% of total restored biomass of all prey items in the diet), N represents the number of prey items (% of the total number of all

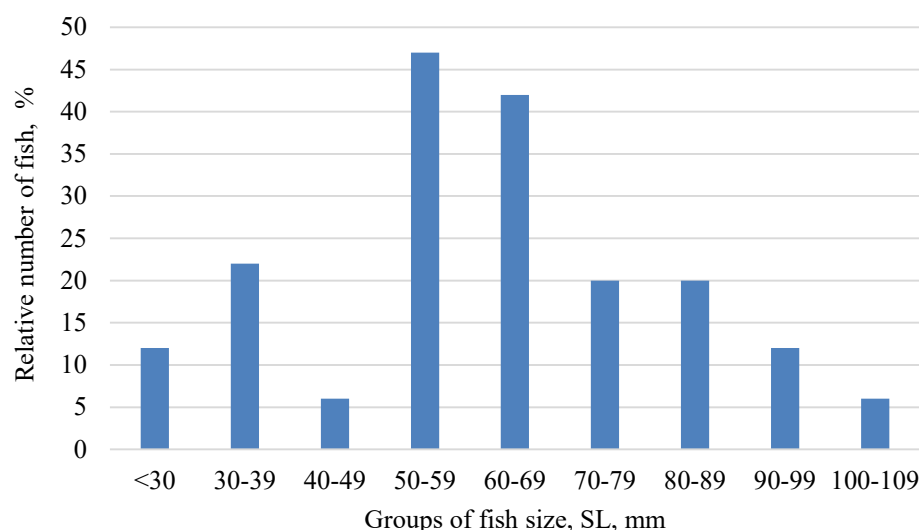


Figure 2. Percentage of different Chinese sleeper (*Perccottus glenii*) size groups at the Ilgas marsh.

prey items in the diet), and F represents the frequency that a prey item appears in the stomach contents (% of the total number of stomachs studied) (Pinkas et al. 1971).

Preference or avoidance of prey was assessed using Ivlev's index of electivity (EI) using the formula $EI = (s-b)/(s+b)$, where "s" is the percentage representation by weight of a food organism in the stomach and "b" is the percentage representation of the same organism in the environment (Ivlev 1961). Results > 0 suggest prey is taken preferentially and < 0 that prey is avoided, while results approaching 0 suggest prey is taken at a similar level to availability.

Parasite analysis

Based on the concept of Esch et al. (1990), the terms allogenic or autogenic were used depending on the environment from which the parasite originated. Indices of prevalence, mean intensity and mean abundance were calculated for each parasite species, according to Bush et al. (1997).

Results

Fish community

All of the 187 fish caught were Chinese sleeper, with no other species observed or caught, strongly suggesting that the Ilgas marsh has a monospecific fish community. Fifty-six of the 187 Chinese sleepers were adult specimens (30%) comprising 19 males and 37 females, giving a sex ratio of around 1:2. Fish of 50–70 mm SL dominated in the catch, with those < 70 mm SL representing 69% and those > 70 mm 31% (Figure 2).

Primary producers

A total of 82 microalgae species related to 31 genera (Supplementary material Table S1) were registered in different habitats at the Ilgas marsh.

Microphytobenthos total abundance reached $152\,000\text{ cells} \times \text{cm}^{-2}$, with phytoplankton reaching $940\,000\text{ cells} \times \text{l}^{-1}$, while microphytobenthos total biomass reached $161\text{ mg} \times \text{cm}^{-2}$ and phytoplankton biomass $42862\text{ mg} \times \text{m}^{-3}$.

Of the 82 species identified, 43 were diatoms (Ochrophyta), 11 green algae (Chlorophyta), 14 desmids (Charophyta), nine euglenoids (Euglenozoa, Euglenophyceae), two dinoflagellates (Miozoa, Dinophyceae), two golden algae (Ochrophyta, Chrysophyceae) and one yellow-green algae (Ochrophyta, Xanthophyceae). Of these, the genera *Navicula*, *Fragillaria* and *Cocconeis* were most numerous, while the genera *Pinnularia*, *Gomphonema* and *Epithemia* were the most diverse. The genera *Eunotia* and *Euglena* occurred at low frequency but at high biomass.

The greater part of phytoplankton biomass (98%) was represented by dinophytes, mainly *Peridinium cinctum* (O.F. Müll.) Ehrenb, while the euglenoid *Trachelomonas volvocinopsis* Svirenko represented up to 30% by frequency of occurrence. Diatoms represented between 86 and 97% of phytobenthos biomass, with euglenoids (8–12%) and desmids (1–5%) dominant (Table S2). In silt, three species, *Navicula radfiosa* Hustedt, *Epithemia turgida* (Ehr.) Kütz and *Pinnularia flexuosa* Cleve were dominant by frequency of occurrence.

Of the periphyton, green algae *Botryococcus braunii* Kütz, zygnematophytes *Spirogyra* sp. and the colonial diatoms *Fragilaria virescens* Ralfs were dominant, while euglenoids (genera *Lepocinclis* and *Phacus*), other green algae (*Pediastrum duplex*, *Ankistrodesmus falcatus*), desmids (*Staurodesmus* sp., *Cosmarium* sp.) and dinoflagellates (*Ceratium cornutum* (Ehr.) Claparède et J. Lachmann, *Peridinium cinctum*, were also numerous (Table S1).

Two interesting algal taxa were also noted, namely *Characium acuminatum* A. Braun and *Desmidium aptogonum* Bréb. ex Kütz, the latter species being rare in Latvian flora; indeed, this record is only the second since first being recorded by Skuja (1928).

Zoobenthos

A total of 12 zoobenthos taxa were identified in the Ilgas marsh, with Oligochaeta, Ostracoda and culicid larvae dominant by abundance (Table S3). Some taxa related to the zooplankton community were recorded in the benthos samples, e.g. Culicidae and Branchiopoda. Overall, total abundance reached $2109 \pm 552\text{ ind.} \times \text{m}^{-2}$, with biomass at $2.210 \pm 1.24\text{ g} \times \text{m}^{-2}$.

Chinese sleeper diet

Twelve prey taxa were identified from the alimentary tracts of Chinese sleeper in the Ilgas marsh (Table S4). We noted an increase in the number of food items taken as fish grew, with the food spectrum of the smallest fish (< 30 mm SL, age 0+) comprising 8–12 prey taxa and larger fish (70–90 mm SL, age 1–1+) taking 8–10 taxa (Tables S3, S4). There was a significant

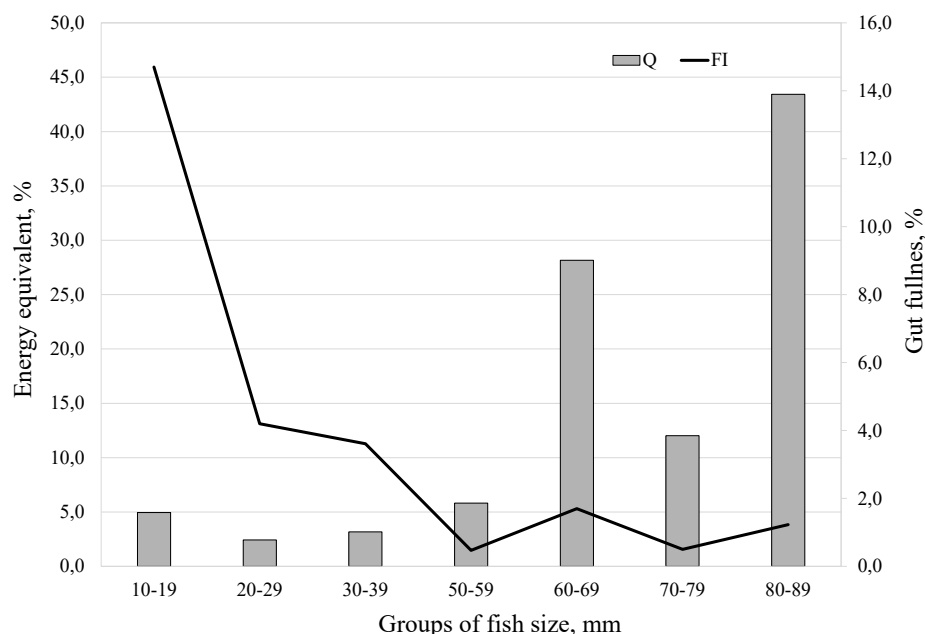


Figure 3. Dependence of gut fullness (FI, %) and energy equivalent of prey items from stomach contents (Q, %) of Chinese sleeper (*Perccottus glenii*) relative to size.

difference in FI and Q between small (< 70 mm) and large (> 70 mm) fish (Mann-Whitney test, both $n = 70$ and $p < 0.001$), with FI being greater in small fish (5.7%, compared to 1.1% in large fish) and Q greater in large fish (27.9% compared to 4.1% in small fish). The trend of increasing FI and decreasing Q with increasing fish size (Figure 3) was confirmed by a significant correlation between fish size and both FI (Spearman rank correlation, $r = -0.56 \pm 0.12$, $n = 70$, $p < 0.05$) and Q ($r = 0.58 \pm 0.12$, $n = 70$, $p < 0.05$).

By examining the composition of dietary items in fish stomachs in one-centimetre steps, it was possible to observe the transition from Gastropoda to fish. In smaller fish of < 70 mm, for example, micro-crustaceans (Ostracoda gen. sp.) dominated by both number and frequency of occurrence, though Insecta (Trichoptera gen. sp.) were more important by both biomass and energy equivalent (Table S4). In fish of > 70 mm, however, larger prey became more frequent, with the freshwater snail *Valvata cristata* Müller, 1774 appearing frequently in the diet of 70–79 and 80–89 mm fish, while juvenile Chinese sleeper began to be found in the stomachs of fish at around 60–90 mm, thereby confirming cannibalism in the Ilgas marsh population (Table S4).

The IRI index indicated Ostracoda, Insecta and *V. cristata* as an important prey item for all fish size groups (Table S3). Complete-linkage cluster analysis, based on a Euclidean distance between the diet composition of different size groups, showed a high similarity between groups 60–69 and 70–79 mm and lower similarity between groups 10–19 and 20–29 mm, with the 80–89 mm group showing least similarity with the other groups (Figure 4).

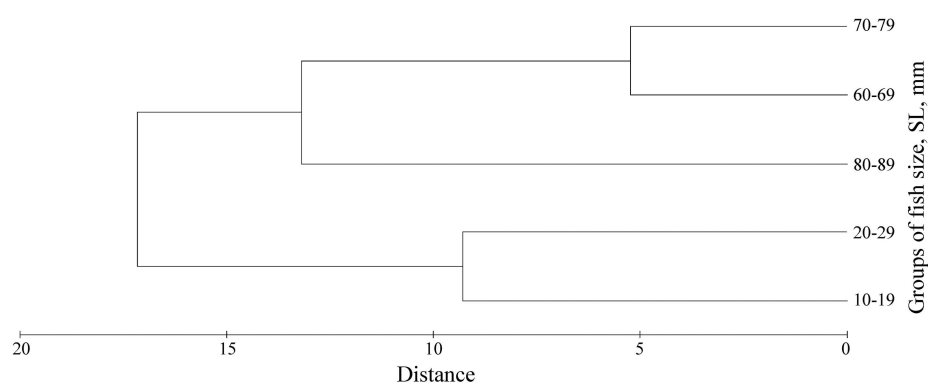


Figure 4. Complete-linkage cluster analysis (based on Euclidean distance) between diet composition in different size groups of Chinese sleeper (*Perccottus glenii*) at the Ilgas marsh.

Table 2. Selection and avoidance of benthic organisms in Chinese sleeper (*Perccottus glenii*) diet at the Ilgas marsh. N (ind. $\times$ m⁻²) = number in benthos; B (g $\times$ m⁻²) = biomass in benthos; EI, % = electivity index. N and B are presented as average and standard deviation.

Benthic taxa	Presence in benthos		EI, %		
	N	B	All fish	< 70 mm	> 70 mm
Oligochaeta	739 $\pm$ 358	0.322 $\pm$ 0.132	-0.72	-0.77	-0.77
Nematoda	11 $\pm$ 8	—	—	—	—
Gastropoda	109 $\pm$ 50	0.336 $\pm$ 0.159	-0.09	-0.24	-0.07
Bivalvia	14 $\pm$ 14	1.114 $\pm$ 1.114	-0.90	-0.92	-0.91
Ostracoda	496 $\pm$ 178	—	—	—	—
Hydrachnidia	113 $\pm$ 37	0.069 $\pm$ 0.023	—	—	—
Culicidae	371 $\pm$ 91	0.292 $\pm$ 0.090	—	—	—
Trichoptera	3 $\pm$ 3	0.008 $\pm$ 0.008	0.98	0.99	0.99
Odonata	62 $\pm$ 35	0.044 $\pm$ 0.023	0.84	0.85	0.81
Ephemeroidea	43 $\pm$ 27	0.025 $\pm$ 0.014	0.77	0.78	0.74
Branchiopoda	148 $\pm$ 64	—	—	—	—
Total	2109 $\pm$ 552	2.210 $\pm$ 1.240	—	—	—

By energy equivalent, Trichoptera larvae were dominant in the diet but displayed low number parameters (Table S4). Ivlev's index indicated that Chinese sleeper of both < 70 and > 70 mm fed on Trichoptera, Odonata and Ephemeroidea (Ephemeroidea) preferentially, but tended to avoid Gastropoda, Oligochaeta and Bivalvia (Table 2), with Gastropoda in particular apparently taken as a random food item, despite their relatively high numerical and weight characteristics (e.g. *V. cristata*).

Chinese sleeper parasites

Four of the 20 Chinese sleeper examined (20%) were infected with parasites. In three cases, just one parasite was found, while six parasites of two different taxa were recorded on the remaining fish.

Only three parasite taxa were recorded in the fish studies, one unidentified coccidian and two taxa of metacercariae (Table 3), all of which occurred sporadically. The coccidia were found in the mucosa of the rectum, while the metacercariae were encysted in tissues. Only *Metorchis xanthosomus* (Creplin, 1846) was identified to species level.

Table 3. Parasites registered in Chinese sleeper (*Perccottus glenii*) at the Ilgas marsh. P, % = prevalence, MI = mean intensity, IR = intensity range, A = abundance, met = metacercariae.

Parasite species	Location	P, %	MI $\pm$ SD	IR	A
Coccidia gen. sp.	Rectum	10.0	3.0 $\pm$ 2.8	1–5	0.3
<i>Metorchis xanthosomus</i> met	Muscles, mesentery	10.0	1.0 $\pm$ 0.0	1	0.1
Strigeidae gen. sp. met	Gills	5.0	1.0	1	0.1

Discussion

The Ilgas marsh was originally created through beaver activity which, over the years, has created an intricate system of shallow natural and artificial waterbodies characterised by a poor fish fauna. Between 1979 and 1984, just one fish species was registered in the marsh waterbodies, the naturalised Prussian carp *Carassius gibelio* Bloch, 1782 (M. Pupins *unpublished data*). In our own survey, presence of this species was unconfirmed; instead, we caught only Chinese sleeper, suggesting that Prussian carp have been totally replaced by Chinese sleeper since it invaded the system. As such, we believe that the Ilgas Natura 2000 Nature Reserve can now be classified as having a monospecific fish community represented by a single invasive fish species. This has significant implications for the status of the Natura 2000 site.

The marsh presently supports a relatively diverse microphyte community which effectively functions as the primary producer component of the ecosystem. Phytoplankton biomass was very high, probably due to sampling at the end of summer when autotrophic processes are at their highest (though the relatively low number of samples taken may also have played a role). Dinoflagellates were the main biomass component, though their abundance, at 601.3 thousand cells $\times$ l⁻¹, did not amount to a “bloom”. To the best of our knowledge, there have been no previous studies on microphytobenthos diversity from this site; hence, we can only compare microalgae diversity to that for phytoplankton. We identified seven species in all, which is on the low side compared with the 4–48 species known for 12 lakes in southeast Latvia (Gruberts et al. 2005b). Some of the species present in the epiphyton of the Ilgas marsh (i.e. *B. braunii*, *Dinobryon* sp.) are considered dominant species in brown-water lakes in Latvia (Klavins et al. 2003).

Klavins et al. (2003) distinguished two types of bog lake in Latvia, dystrophic and dyseutrophic. Dystrophic lakes are characterised by low species diversity and phytoplankton biomass (0.01–0.15 mg $\times$ l⁻¹), while dyseutrophic lakes support a comparatively high number of species and higher biomass, with chlorophyll-*a* levels of 2.3–6.25 mg $\times$ m⁻³. Very low biomass values are typical of lakes in the study region (Gruberts et al. 2005a) and, based on the ecological features of the species present, we can classify the Ilgas marsh as a mesotrophic type reservoir (Barinova et al. 2019). The relatively high level of primary production in the marsh provides favourable conditions for the development of algivorous amphibian larvae

(Waringer-Löschenkohl and Schagerl 2001). However, while this level of production is high for Latvia, it is very low compared to the southern part of the Chinese sleeper's European range. At Lake Kahul in Southern Ukraine (Danube basin), for example, total biomass varies from $10.2 \text{ g} \times \text{m}^{-2}$ in winter to $46 \text{ g} \times \text{m}^{-2}$ in autumn (Dzhurtubayev et al. 2013), which is higher than that found in the Ilgas marsh ($2.210 \pm 1.24 \text{ g} \times \text{m}^{-2}$).

The only parasite species identified to species level, metacercariae of *M. xanthosomus*, forms part of the allogenic fauna, the adults of which infest piscivorous birds (Sitko et al. 2016), as does the adult stage of a second metacercaria taxa identified, Strigeidae gen. sp. (Sudarikov et al. 2006). No parasite species/taxa related to amphibians was registered on Chinese sleeper in the Ilgas marsh, despite them frequently playing the role of an intermediate or paratenic host to amphibian parasites in other waterbodies. Metacercariae of *Opishyoglyphe ranae* (Fröhlich, 1791) and the nematode *Spiroxis contortus* (Rudophi, 1819), for example, have both been registered on this fish in Hungary, while the cestode *Ophiotaenia europaea* Odening, 1963 has been recorded in Ukraine (Kvach et al. 2013; Antal et al. 2015). Each of these parasites utilises semi-aquatic reptiles as definitive hosts and frogs as a secondary intermediate, or paratenic, host. In Russia, metacercariae of *Isthmiophora melis* (Schränk, 1788), a parasite with carnivorous mammals as definitive hosts and amphibians as a secondary intermediate host, have also been reported (Reshetnikov et al. 2013). In this study, we found no amphibian larvae in the diet of Chinese sleeper, which may be linked with the lack of amphibian parasites in this fish. As such, we suggest that Chinese sleeper predation on amphibians in the Ilgas marsh appears to be minimal.

Fish communities with low species diversity are typical for lakes of northern latitudes or higher altitudes, with just one or two species commonly dominating (Ponomarev 2019, and references therein). Occasionally, monospecific fish communities may occur, typically represented by predatory species (Ridgway and Chapleau 1994; Belk et al. 2014; Ortiz-Sandoval et al. 2015; Ponomarev 2019). Monospecific fish communities comprised of Chinese sleeper have also been recorded (Spanovskaya et al. 1964; Rafikov 2018). In such monospecific communities, two basic strategies are generally recognised. The first is cannibalistic, with small fish first eating plankton and then benthic organisms, while larger fish mainly eat small specimens of their own species. Our data on Chinese sleeper diet match those of Koščo et al. (2008), who observed high size-dependence in the food spectrum of Chinese sleeper, with an ontogenetic shift in diet at around 70 mm SL. Such systems may occur when the preferred habitats of the two groups are strongly separated. For example, small specimens of *Galaxias platei* (Steindachner, 1898) in the deep Thompson Lake in Chile live primarily in the littoral zone, while larger specimens concentrate in the benthic zone, only moving to the shallows to feed at night (Belk et al. 2014). The second strategy is represented by stunted populations, as

represented by the monospecific yellow perch, *Perca flavescens* Mitchill, 1814, population in a lake in Gatineau Park, Quebec, Canada (Ridgway and Chapleau 1994). While yellow perch are known to be cannibalistic in multi-species waterbodies, there was no evidence of fish in the stomachs of yellow perch in monospecific lakes (Ridgway and Chapleau, 1994); instead, the population tends to be stunted, with no large specimens present. The monospecific Chinese sleeper population in this study appears to be somewhat intermediate between the two strategies. While small Chinese sleeper were present in the diet of larger specimens, they were not found frequently (Table S3). A similar situation has been described in monospecific Chinese sleeper populations in ponds near Syktyvkar in Russia (Rafikov 2018) and for monospecific Creole perch, *Percichthys trucha* Valenciennes, 1833, populations in western Patagonian lakes in Chile (Ortiz-Sandoval et al. 2015). In the latter case, smaller fish were always present in the alimentary tracts of adults in multi-species populations, but only rarely in monospecific populations, these also displaying slower growth rates (Ortiz-Sandoval et al. 2015). In the Tarakanov pond near Moscow (Russia), adult Chinese sleeper appear to prefer invertebrates over juvenile Chinese sleeper, and only switch to eating small specimens when availability of invertebrates is extremely low (Spanovskaya et al. 1964). As the Tarakanov pond only became monospecific ten years after Chinese sleeper were introduced, cannibalism in this case appears to be forced (Spanovskaya et al. 1964). At the Ilgas marsh, Chinese sleeper showed a number of similarities with the first cannibalistic feeding strategy, with fish size groups of < 70 mm concentrating on benthic organisms, while fish of 80–89 mm or more included juvenile Chinese sleeper in the diet (Table 2, also see Table S4). Cluster analysis of dietary composition indicated high similarity between the 60–69 and 70–79 mm size groups, but low similarity between the 80–89 mm group and all other groups, mainly as the diet of this group was represented primarily (50%) by juvenile Chinese sleeper (Figure 4). This appears to be a characteristic path for this species owing to the lack of a forage base or difficulty in otherwise obtaining prey, e.g. through an inability to catch non-moving prey. Our study tends to confirm the findings of Reshetnikov (2008), who found that Chinese sleeper prefer moving over less motile prey, suggesting that juvenile fish are a more likely component of the diet. Such a strategy leads to a decrease in feeding efficiency, however, and a reduction in the gut fullness index. On the other hand this testifies that larger fish try to find more energetically capacious food, which is not easy in low productive reservoir.

Monospecific communities comprised of Chinese sleeper appear to be absent in more southern regions, where the species tends to form a component of relatively high diversity fish assemblages (Kutsokon et al. 2014; Kvach et al. 2018). It would appear, therefore, that the formation of monospecific Chinese sleeper fish communities is more likely in low production waterbodies such as the Latvian marshes; possibly because

competition for food resources between Chinese sleeper and other fishes is much lower in highly productive waterbodies, such as those found in the Black Sea drainage, than in the mesotrophic and dystrophic lakes and marshes typical at higher altitudes.

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Supplementary material

The following supplementary material is available for this article:

Table S1. List of microalgae genera and number of species registered in different habitats at the Ilgas marsh.

Table S2. Phytoplankton and microphytobenthos algal community structure at the Ilgas marsh.

Table S3. Abundance and biomass of zoobenthic taxa from the Ilgas marsh, along with their Index of relative importance in the diet of different sized Chinese sleeper (*Perccottus glenii*).

Table S4. Frequency of occurrence, number, biomass and energy equivalent of different prey items in the diet of different size cohorts of Chinese sleeper (*Perccottus glenii*) from the Ilgas marsh.

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