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The impact of introduced Ponto-Caspian mysids (*Paramysis lacustris*) on the trophic position of perch (*Perca fluviatilis)* in European mesotrophic lakes

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Abstract – *Paramysis lacustris* was introduced into Lithuanian lakes in the middle of the 20th century. It was assumed that *P. lacustris* will enhance efficiency of primary production utilization and channelling of primary production towards higher trophic levels, *i.e.* commercially important fish species. However, at the time of *P. lacustris* introduction, there were no reliable data about its trophic position in lakes. Thus, *P. lacustris* was considered to have no or little impact on native ecosystems. Until now, there is a gap in the knowledge of the trophic role and potential impacts of *P. lacustris* on local food webs in lakes. Here we investigated the impact of *P. lacustris* on the food chain length of its potential predator *Perca fluviatilis* in temperate lakes. In this study, gut contents and stable isotope analyses were performed to assess the diet and trophic position of *P. lacustris* and *P. fluviatilis* in lakes with and without invasive mysids. The results obtained revealed that *P. lacustris* consumes a significant amount of animal prey and occupies the third trophic level in lake littoral zones. Furthermore, our results showed that *P. lacustris* might enhance the food chain length for at least some zooplanktivorous fishes. Overall, the assumption that *P. lacustris* invasion has no whole-ecosystem consequences, as it was thought before its introduction, is not correct.

Keywords: Aquatic invasion / food webs / fish diet / stable isotopes

Résumé – L'impact du mysidacé Ponto-Caspien introduit (*Paramysis lacustris*) sur la position trophique de la perche (*Perca fluviatilis)* dans des lacs mésotrophes européens. *Paramysis lacustris* a été introduite dans les lacs lituaniens au milieu du XX^{e} siècle. On a supposé que *P. lacustris* améliorera l'efficacité de l'utilisation de la production primaire et le transfert de la production primaire vers les niveaux trophiques supérieurs, c'est-à-dire les espèces de poissons commercialement importantes. Cependant, au moment de l'introduction de *P. lacustris*, il n'existait pas de données fiables sur sa position trophique dans les lacs. Ainsi, *P. lacustris* a été supposé comme n'ayant pas ou peu d'impact sur les écosystèmes indigènes. Jusqu'à présent, il y a une lacune dans les connaissances sur le rôle trophique et les impacts potentiels de *P. lacustris* sur les réseaux trophiques locaux dans les lacs. Nous avons étudié ici l'impact de *P. lacustris* sur la longueur de la chaîne alimentaire de son prédateur potentiel *Perca fluviatilis* dans les lacs tempérés. Dans cette étude, on a effectué des analyses du contenu gastrique et des analyses des isotopes stables pour évaluer le régime alimentaire et la position trophique de *P. lacustris* et *P. fluviatilis* dans les lacs avec et sans mysidacé envahissant. Les résultats obtenus ont révélé que *P. lacustris* consomme une quantité importante de proies animales et occupe le troisième niveau trophique dans les zones littorales des lacs. De plus, nos résultats ont montré que *P. lacustris* pourrait augmenter la longueur de la chaîne alimentaire pour au moins certains poissons zooplanctonivores. Dans l'ensemble, l'hypothèse selon laquelle l'invasion de *P. lacustris* n'a pas de conséquences sur l'ensemble de l'écosystème, comme on le croyait avant son introduction, n'est pas correcte.

Mots-clés : Invasion aquatique / réseaux trophiques / alimentation des poissons / isotopes stables

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1 Introduction

The problem of non-indigenous species invasion has persisted since the second half of the 20th century. Invasive species can cause food-web shifts that can have severe consequences for native species and ecosystems (David *et al.*, 2017; Jackson *et al.*, 2017). In aquatic ecosystems, Crustacea including Mysida, are the frequently observed groups of invasive species (Audzijonytė *et al.*, 2017; Arbačiauskas *et al.*, 2018; Borza *et al.*, 2019). Mysids are known to play a significant role in the diet of freshwater fish (Bubinas, 1979; Kublickas and Bubinas, 1985; Lasenby *et al.*, 1986). Therefore, several mysid species were intentionally released into water bodies throughout Eastern (Borodich and Havlena, 1973; Arbačiauskas *et al.*, 2018) and Northern Europe (Lasenby *et al.*, 1986; Ketelaars *et al.*, 1999) and North America (Lasenby *et al.*, 1986; Chess and Stanford, 1998) in order to increase fishery yields. The introduced mysids rapidly spread from original sites of introduction and are claimed to have caused perturbations in native food webs of the invaded habitats (Koksvik *et al.*, 1991; Langeland *et al.*, 1991; Spencer *et al.*, 1991). The mechanisms through which these invaders affect native communities are still poorly understood and quantitative data are scarce.

Similarly, *Paramysis lacustris* (Czerniavsky, 1882) was deliberately introduced into inland waters of Lithuania (Arbačiauskas *et al.*, 2018). Although *P. lacustris* failed to survive in most of the lakes into which it was introduced, it managed to establish sustainable populations in large lakes and water reservoirs. It was suggested that the best predictor of successful *P. lacustris* establishment in lakes was a larger surface area, faster water circulation and increased amount of total phosphorus (Arbačiauskas *et al.*, 2018). However, in the lakes in which they survived, *P. lacustris* produced very abundant populations (Arbačiauskas *et al.*, 2012).

When considering *P. lacustris* introductions, a major assumption of acclimatization was that there should be a free niche space. That was the case for introduction of *P. lacustris* to Lithuanian lakes, which were considered relatively poor in higher crustaceans due to geographical isolation (Gasiuūnas, 1963). Only one pelagic mysids species (*Mysis relicta* Lovén, 1862) was known from Lithuanian lakes before the introduction of *P. lacustris*. Thus, it was hypothesized that detritivorous and herbivorous littoral *P. lacustris* would obtain sufficient nutrition to develop high biomass and thus would supplement local invertebrate communities with high-value fish food items. The expectation that the introduced *P. lacustris* will acclimatize and will subsequently enhance fish production was underpinned by the following three assumptions. Firstly, the introduced mysids species will provide high quality (high calorie) and easily accessible food for fish. As a result, fish nutrition and subsequent growth will improve, and the standing stock will increase (Gasiūnas, 1963). Secondly, mysids will be an alternative food (substituting fish fry) for predatory fish species during their ontogenetic transition to piscivory and will increase the efficiency of energy transfer by shortening the food chain length (Vaitonis *et al.*, 1990). The third assumption was that the introduced mysids species would ensure constant food supply for benthivorous fish after hatching blooms of aquatic insects (Gasiūnas, 1963).

The introduction of novel species is always followed by consequences that are not necessarily such as expected. Previous studies showed that some introduced mysids species had a massive effect on plankton communities. Predation of mysids (Rieman and Falter, 1981; Koksvik *et al.*, 1991; Langeland *et al.*, 1991; Ketelaars *et al.*, 1999; Spencer *et al.*, 1999; Borcherding *et al.*, 2006) caused a significant decline in the abundance, species richness and diversity of cladocerans, which led to a notable change in the fish diet content (Lasenby *et al.*, 1986; Spencer *et al.*, 1991). These consequences show that the real impact of mysids introduction on native communities cannot be predicted without the knowledge of the trophic position of the introduced mysids. However, despite the rapid spread of *P. lacustris* in Europe, there is little knowledge about potential consequences of their invasion for the native ecosystems in temperate lakes. Therefore, the trophic role of *P. lacustris*, and its potential to lengthen the trophic chain in lakes are of great scientific and applied interest.

The present study was undertaken chiefly with a view to determine potential impacts of invasive *P. lacustris* on local food chains in temperate lakes. Here we investigated the impact of the introduced mysid species on the trophic position of zooplanktivorous perch juveniles in mesotrophic lakes. Studies of these covered the following aims: (1) to explore the trophic niche of invasive mysids by applying stable isotope (carbon $^{13}C/^{12}C$ and nitrogen $^{15}N/^{14}N$) analysis (2) to evaluate the diet and the trophic position of *Perca fluviatilis* Linnaeus, 1758 juveniles in lakes with and without invasive mysids.

2 Materials and methods

2.1 Studied lakes and sampling

The impact of the introduced *P. lacustris* on the trophic position of *P. fluviatilis* was studied in 12 mesotrophic lakes in autumn 2010–2012. Morphometric characteristics and trophic status of lakes are presented in Table 1. All studied lakes are similar in their littoral fish communities. *P. fluviatilis* together with roach, *Rutilus rutilus* (Linnaeus, 1758) is the most dominant fish species in the littoral zone of the studied lakes. In addition to these dominant fish species, the littoral zone of the studied lakes is inhabited by other fish species, *i.e.* *Gymnocephalus cernua* (Linnaeus, 1758), *Abramis brama* (Linnaeus, 1758), *Tinca tinca* (Linnaeus, 1758), *Blicca bjoerkna* (Linnaeus, 1758) or *Esox Lucius* (Linnaeus, 1758) (see Virbickas, 2013). However, the presence of the introduced *P. lacustris* in these lakes is different.

For diet analysis, perch were sampled with a beach seine in the shallow littoral zone (down to 2.0 m depth). A beach seine with 8- or 7-m long wings (mesh size 10 and 5 mm, respectively) was used; the opening of the seine bag was 1.2 × 1.3 m (width × height), and the length of 3 mm mesh-sized cod-end was 3 m. For gut content and stable isotope analysis, mysids were collected in the same littoral zone at 0.5–2.0 m depths using epibenthic sledge nets (opening 20 × 60 cm, mesh size – 500 µm). Molluscs (*Radix* sp.) were collected at the same time and the same place as mysids with a standard hydro biological hand net sampler (opening 25 × 25 cm, mesh size – 500 µm). Mesozooplankton samples (*Daphnia* spp.) were taken with 200 µm zooplankton net by

Table 1. Characteristics of the lakes and water reservoirs (WR) studied: surface area (S), mean depth (H), annual water circulation (AWC), annual average of chlorophyll a (Chl), total nitrogen (N_T), and total phosphorus (P_T) (Anonymous, 2015). The presence of *Paramysis lacustris* is indicated by an asterisk.

No.	Lake	S (ha)	H (m)	AWC (%)	Chl (μg/L)	N_T (μg/L)	P_T (μg/L)	*P. lacustris*
1	Aisetas	501	10.4	123	2.56	1280.7	22.6	–
2	Antaleptė WR	1911	7.2	102	3.56	786.9	24.0	*
3	Asveja	982	14.9	46	3.76	999.9	14.1	–
4	Baluošas	426	10.7	103	3.83	601.7	16.7	–
5	Daugai	911	13.2	12	4.55	972.8	28.6	*
6	Drūkšiai	4480	7.6	29	8.35	1026.2	70.1	*
7	Dusia	2334	15.4	6	6.56	903.2	34.4	*
8	Luodis	1320	6.7	35	9.67	805.3	29.5	–
9	Lūšiai	391	13.9	249	2.76	665.2	17.9	*
10	Plateliai	1182	11.4	12	2.65	593.5	21.8	–
11	Zarasas	323	11.5	124	4.98	1208.1	19.1	–
12	Žeimenys	436	6.9	698	12.18	749.5	39.7	*

filtering 30–500 L water from offshore stations (from 1.5, 2, and 3 m depths).

2.2 Diet analysis

The potential impact of *P. lacustris* on food chains of local fish was studied using 0+ juveniles of perch as a model fish species. Previous investigations showed that introduced mysids, when abundant, are important food items in the diet of perch juveniles, which start consuming them from the age 0+ (Arbačiauskas *et al.*, 2010; Rakauskas *et al.*, 2010). Furthermore, it was revealed that in lakes with numerous populations of littoral mysids, the ontogenetic shift in perch diet (from zooplankton to macro invertebrates) occurs earlier, which is because of the availability of mysids as prey (Rakauskas *et al.*, 2010).

Perch diet was studied in nine lakes, differing in the presence of *P. lacustris*. Up to 50 individuals of *P. fluviatilis* per lake were selected for diet analysis. In total, gut contents of 283 specimens were examined (fish with empty stomachs being excluded). After euthanization (by immersing into 1.5–2.0 ml L^{-1} solution of 2-phenoxyethanol for 5 min), digestive tracts of selected fish were immediately removed and preserved in 10% formaldehyde solution until necropsy in the laboratory. Before food content analysis, specimens were measured to the nearest 1 mm (TL), weighed to the nearest 0.1 g, their age being determined from *operculum* bones. Only first-year (0+) juveniles (<8 mm; 6.6 ± 0.7 mm) were used for gut content analysis. Gut contents were dissected out, and food items were identified to the lowest possible level, grouped and weighed (wet-weight) to the nearest 0.1 mg. Digested and thus unidentifiable particles were classified as separate ‘miscellaneous stomach content’ and their share in the fish diet was presented under the category of “*Other*” prey. The data from individual fish specimens were averaged to obtain estimates of mean proportions of various preys in *P. fluviatilis* diet in each lake.

The diet of mysids was studied only in Daugai, Dusia and Lūšiai lakes. For diet analysis, mysids were collected during the daytime. Up to 30 individuals of *P. lacustris* per lake were selected for diet analysis. In total, gut contents of 64 specimens were examined (mysids with empty stomachs being excluded). Before analysis, the body length of mysids (BL, mm) from the tip of the rostrum to the end of the telson was measured using an ocular micrometer (±0.1mm) under the stereomicroscope. Only large adults (>10 mm; 11.2 ± 0.8 mm) were used for gut content analysis. Gut contents were dissected out, and food items were identified to the lowest level possible, grouped, their volume proportion to the overall gut content being estimated (Hyslop, 1980). Digested and thus unidentifiable particles were classified as separate ‘miscellaneous stomach content’ and their share in mysids diet was presented under the category of “*Detritus*” prey. The data from individual mysid specimens were averaged to obtain estimates of mean proportions of various prey in *P. lacustris* diet in each lake.

2.3 Stable isotope analysis (SIA)

For stable isotope analysis, specimens of *P. fluviatilis* were taken from beach seine catches. Before analysis, selected perch specimens were measured. Only first-year juveniles (0+) (TL < 8 mm; 6.6 ± 0.7 mm) were used for SIA. The white muscle of fish was dissected from the dorsal part and placed into foil cups (three to six replicates per lake, 5 individuals per replicate). For SIA, live mysids were taken from epibenthic sledge catches and placed into filtered lake water. After transportation in coolers to the laboratory, the collected mysids were maintained alive for several hours to allow gut-content evacuation. Before analysis, the mysids were rinsed with distilled water and measured. Only large, whole-body adult mysids (BL > 10 mm; 11.2 ± 0.8 mm) were used for SIA. The mysids collected in each lake were divided into three to eight analytical replicates, with 5 individuals per replicate. The collected snails were frozen before dissection. The shell height (SH) was measured to the nearest millimetre. Only large adults (SH > 14 mm; 16.4 ± 0.9 mm) were used for SIA. Then the snails were separated from the shell material, their digestive gland was removed, and the remaining tissues were macerated.

The collected snails were divided into three replicates per lake, five individuals per replicate. Upon return to the laboratory, the bulk of zooplankton was manually separated into copepods, cladocerans (*Daphnia* spp, in particular) and large *Leptodora kindtii* (Focke, 1844) using carbonated water to narcotise the organisms. Then *Daphnia* spp. was placed into filtered lake water for several hours to reduce the influence of gut contents on stable isotope results (Feuchtmayr and Grey, 2003). The separated *Daphnia* spp. samples were filtered through 25 mm Whatman GF/C filter paper. The whole concentrated bulk of *Daphnia* spp. was divided into three analytical replicates per lake.

All samples were oven-dried at 60 °C for 48 h, ground to fine powder in an agate mortar. The samples were analyzed at Stable Isotope Facility, UC Davis, USA. Carbon and nitrogen stable isotope ratios were determined by continuous-flow isotope ratio mass spectrometry. Stable isotope ratios are given using the δ notation expressed in units per mil as follows: δ (‰) = $[(R_{\mathrm{sample}}/R_{\mathrm{standard}}) - 1] \times 1000$, and R = the $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The global references were atmospheric N_2 for the $^{15}N/^{14}N$ ratio, and Vienna Pee Dee belemnite for the $^{13}C/^{12}C$ ratio. Typical precision for a single analysis was ± 0.1‰ for $\delta^{13}C$ and ± 0.3‰ for $\delta^{15}N$. As lipids are depleted in ^{13}C (DeNiro and Epstein, 1977), any variation in lipid concentrations among fish replicates could influence comparisons of $\delta^{13}C$. However, in this study, the variation in mean C:N ratios (a correlate of lipid concentration) among fish replicates was very low (3.2 ± 0.1) and the correlation between C:N and $\delta^{13}C$ values of fish was insignificant (Spearmen rank order correlation: $\rho = -0.096$, $P > 0.1$). Therefore, fish $\delta^{13}C$ data were not arithmetically lipid-normalised. Macroinvertebrate $\delta^{13}C$ values were left uncorrected as well.

2.4 Trophic level calculations

Due to great temporal and spatial variability of stable isotope (SI) composition in primary producers in lakes, the trophic position (TP) of investigated consumers was reconstructed using SI signatures of several primary consumers (Post, 2002). Filter-feeding zooplankton is usually considered as an integrator of the pelagic phytoplankton signature and gastropods of benthic or littoral algal sources (Post, 2002). We used enriched pelagic primary consumer (zooplankton: *Daphnia* spp., Tab. 2) as a baseline (base 1) for the pelagic $\delta^{13}C$ signature. As a baseline (Base 2) for the littoral $\delta^{13}C$ signature, we used depleted littoral primary consumer (gastropods: *Radix* sp., Tab. 2). Overall, we used two isotopically distinct primary consumers to calculate the trophic position of the investigated consumers by the equation (Post, 2002):

$$\mathrm{TP} = 2 + (\delta^{15}\mathrm{N}_{\mathrm{consumer}} - [\delta^{15}\mathrm{N}_{\mathrm{base1}} \times \alpha + \delta^{15}\mathrm{N}_{\mathrm{base2}} \times (1 - \alpha)]) \times 2.9^{-1}$$

where $\delta^{15}N$ consumer is the nitrogen isotope ratio in a consumer of interest; $\delta^{15}N_{\mathrm{baseline}}$ is the nitrogen isotopic baseline of a primary consumer, corresponding to TP = 2; α is the proportion of nitrogen isotopes in a consumer, ultimately derived from sources similar to gastropods (base 1). Assuming that the rate of nitrogen and carbon flow from the diet to the predator is the same, α was estimated using $\delta^{13}C$ by the equation (Post, 2002):

$$\alpha = (\delta^{13}\mathrm{C}_{\mathrm{consumer}} - \delta^{13}\mathrm{C}_{\mathrm{base2}}) \times (\delta^{13}\mathrm{C}_{\mathrm{base1}} - \delta^{13}\mathrm{C}_{\mathrm{base2}}) - 1.$$

Table 2. Summary of the stable isotope analysis of the baseline organisms used for trophic position calculation (*Daphnia* spp., *Radix* sp.) from the lakes studied: stable isotope values ($\delta^{13}C$, $\delta^{15}N$, ‰).

Lake	*Daphnia* spp.		*Radix* sp.	
	$\delta^{13}C$	$\delta^{15}N$	$\delta^{13}C$	$\delta^{15}N$
Aisetas	–33.1	14.4	–31.9	11.8
Antalieptė	–32.9	7.1	–27.2	2.9
Asveja	–35.1	9.6	–29.8	7.0
Baluošas	–34.5	7.9	–29.3	5.7
Daugai	–29.6	7.1	–23.7	4.6
Drūkšiai	–28.0	2.2	–24.0	4.4
Dusia	–29.3	9.1	–23.8	3.3
Luodis	–31.3	10.3	–27.5	8.8
Lūšiai	–33.7	6.5	–30.7	5.5
Plateliai	–27.3	7.7	–23.3	4.2
Zarasas	–33.0	12.1	–27.1	10.3
Žeimenys	–34.9	7.7	–30.4	6.2

This two-end-member-mixing model allows differentiation between such two sources as littoral and pelagic food webs, and assumes that there is little trophic fractionation of carbon, and mixing is linear (Post, 2002). It also assumes that the fractionation factors between resources and consumers incorporated into the model were 0.39 ± 1.3‰ for $\delta^{13}C$ and 3.4 ± 0.98‰ for $\delta^{15}N$ (Post, 2002).

3 Results

3.1 Mysids diet

The analysis of *P. lacustris* diet showed that adults (11.2 ± 0.8 mm) mainly fed on phytoplankton (Fig. 1). On average, phytoplankton accounted for 40.7 ± 0.02% of the studied mysids diet. However, the gut content analysis showed that the share of zooplankton (Rotatoria, Cladocera, Copepoda) and benthic macroinvertebrates (Oligochaeta, Chironomidae) in the diet of mysids was also significant. Altogether, "animal" prey (primary consumers) accounted for 37.1 ± 0.1% of the mysids diet in the lakes studied (Fig. 1).

3.2 Variations in perch diet

Evident differences in the diet content of first-year (0+) *P. fluviatilis* were recorded in lakes with and without the introduced *P. lacustris* (Fig. 2). The diet of *P. fluviatilis* juveniles was clearly dominated by zooplankton in the lakes devoid of the introduced mysids. Zooplankton constituted more than 80% of the studied perch diet in theses lakes. Meanwhile, mysids were the dominant prey in the lakes where the introduced *P. lacustris* were present. The contribution of mysids to the diet of *P. fluviatilis* juveniles in these lakes reached more than 50% (Fig. 2).

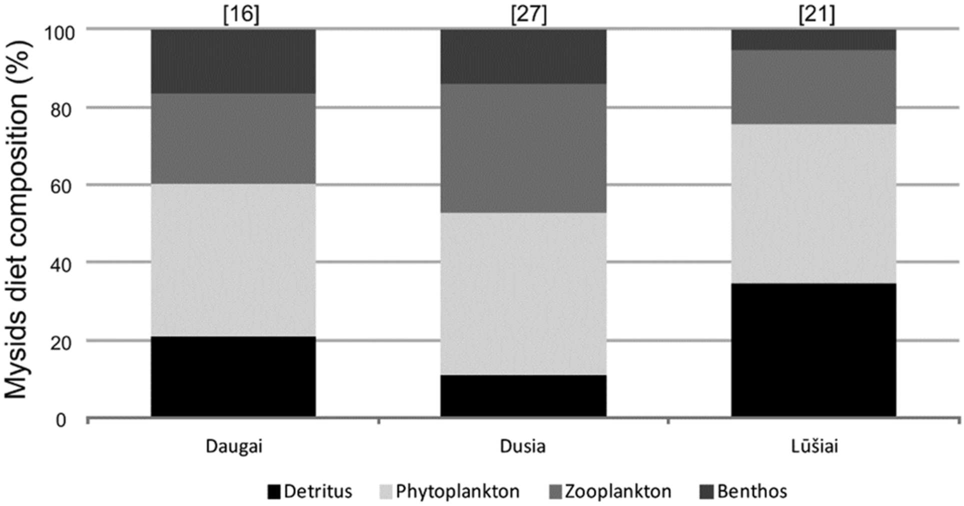

Fig. 1. Mean diet composition (volume percentage) of *Paramysis lacustris* from the lakes studied. Numbers of the specimens used for gut content estimates are given in square brackets.

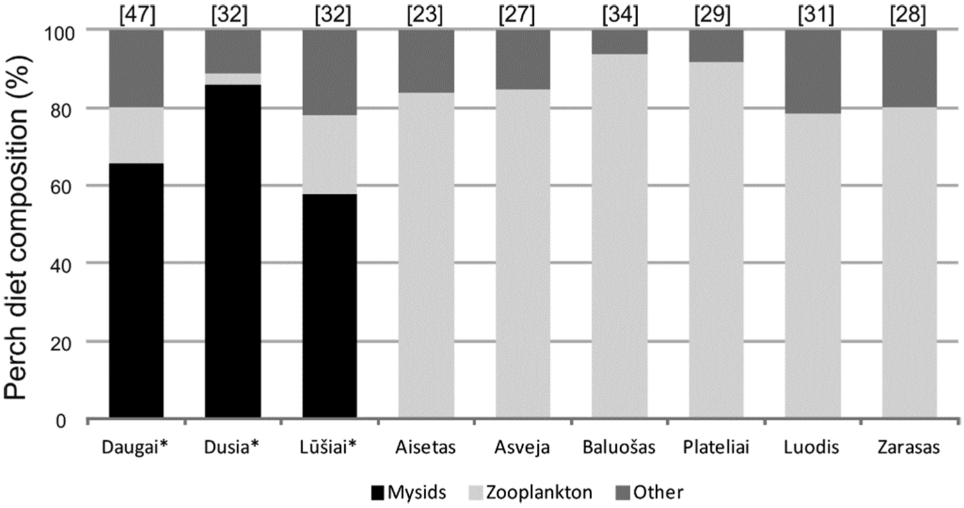

Fig. 2. Mean diet composition (weight percentage) of *Perca fluviatilis* juvenile from the lakes studied. Numbers of the specimens used for gut content estimates are given in square brackets. The presence of *Paramysis lacustris* is denoted by an asterisk.

In the lakes devoid of mysids, the mean share of consumed zooplankton in *P. fluviatilis* stomachs was 85.2 ± 6.1%. Meanwhile, the share of consumed zooplankton in stomachs of *P. fluviatilis* from the lakes inhabited by the introduced *P. lacustris* was only 12.4 ± 8.9%. Such a difference in zooplankton consumption between the lakes inhabited by the introduced mysids and the lakes devoid of them was statistically significant (Mann–Whitney *U* test: $Z = 2.32$, $P = 0.020$).

3.3 Stable isotope analysis (SIA)

The performed stable isotope analysis showed that in the lakes studied, zooplankton is a primary consumer. The mean trophic position (TP) of zooplankton was found to be 2.0 ± 0.02. It did not vary between the lakes (Kruskal–Wallis ANOVA test: H (5, $N = 18$) = 2.60, $P = 0.76$).

The summary of *P. lacustris* SIA results is presented in Table 3. According to SIA results, the mean TP of *P. lacustris* was 3.2 ± 0.2, which suggests that in the littoral zone of the lakes studied mysids are second-level consumers. The performed analysis also showed that *P. lacustris* occupied a higher trophic position in the lake food chain than zooplankton (Fig. 3). Their TP was significantly higher than that of zooplankton (Mann–Whitney *U* test: $Z = 2.88$, $P = 0.004$).

The summary of *P. fluviatilis* SIA results is presented in Table 4. The mean TP of perch juveniles (0+ age) was 4.1 ± 0.3 in the lakes containing *P. lacustris* populations, and it was significantly higher than that in the lakes devoid of invasive mysids populations – 3.4 ± 0.2 (Mann–Whitney *U* test,

Table 3. Summary of the stable isotope analysis of *Paramysis lacustris* from the lakes studied: number of replicates (*N*), stable isotope values (δ^{13}C, δ^{15}N, ‰), and trophic position (TP).

Lake	*N*	δ^{13}C	δ^{15}N	TP
		Mean ± SD	Mean ± SD	Mean ± SD
Antalieptė	3	–28.2 ± 0.1	8.2 ± 0.1	3.4 ± 0.1
Daugai	7	–28.3 ± 2.1	9.9 ± 1.8	3.0 ± 0.3
Drūkšiai	7	–26.2 ± 3.2	7.4 ± 3.3	3.2 ± 1.4
Dusia	6	–22.8 ± 3.1	7.6 ± 1.8	3.6 ± 0.4
Lūšiai	8	–32.1 ± 1.2	9.5 ± 1.7	3.0 ± 0.4
Žeimenys	3	–32.2 ± 0.5	10.7 ± 0.3	3.1 ± 0.1

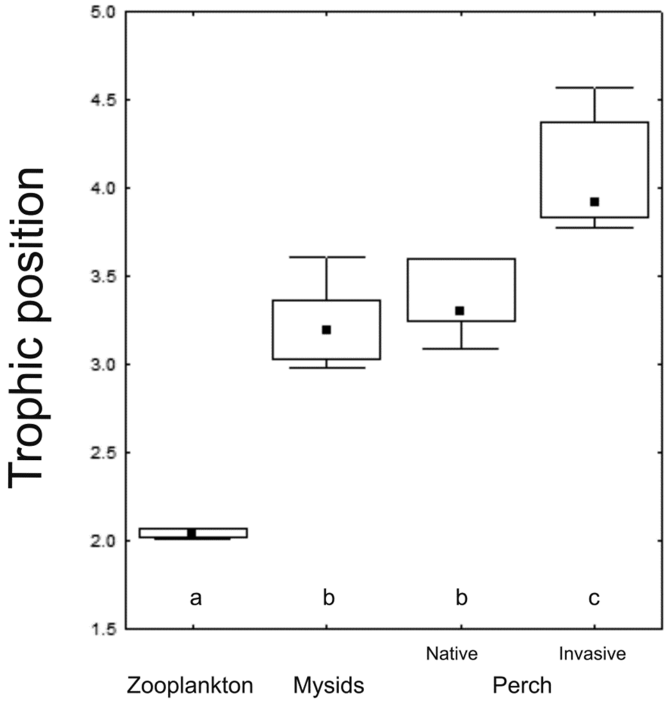

Fig. 3. The trophic position of zooplankton (*Daphnia* ssp.), Mysids (*Paramysis lacustris*) and juvenile perch (*Perca fluviatilis*) in the lakes studied. Differences in the trophic position of perch in the presence (*Invasive*) and absence (*Native*) of *P. lacustris* in lakes. Significant differences between the groups (Mann–Whitney U test: $P < 0.05$) are indicated by lowercase letters (a, b, c).

$Z = 2.88$, $P = 0.004$, Fig. 3). Furthermore, TP of perch juveniles from the lakes without invasive mysids was similar to that of *P. lacustris* from the lakes harbouring this invasive species (Mann–Whitney *U* test, $Z = 0.96$, $P = 0.33$, Fig. 3).

4 Discussion

In accordance with recent knowledge, *P. lacustris* is defined as an omnivore–herbivore species that feeds by gathering and filtering, although in some periods, zooplankton and other benthic invertebrates may constitute a significant part of these mysids' diet (Komarova, 1991; Jankauskienė, 2003; Lesutienė *et al.*, 2007). Such high dietary diversity of mysids implies a variety of possible functional roles in ecosystem food webs and difficulties in predicting their trophic linkages and extrapolating from one ecosystem to another. It is still not clear which trophic level *P. lacustris* occupy in temperate lakes. If zooplankton constitutes a significant part of their diet, *P. lacustris* may be a secondary consumer in the lake littoral. This fact suggests that adults of *P. lacustris* occupy a higher position in the trophic chain than zooplankton. Apparent predation of mysids on zooplankton may lengthen the food chain in lakes. If these mysids reduce zooplankton population density or induce changes in zooplankton species richness and diversity, zooplanktivorous fish may shift their diet from zooplankton to mysids, consequently, the food chain length will be increased. This study revealed that the introduction of *P. lacustris* may lead to the additional trophic level incorporation into the food chain of zooplanktivorous fish in temperate lakes.

Table 4. Summary of the stable isotope analysis of *Perca fluviatilis* from the lakes studied: number of replicates (*N*), stable isotope values (δ^{13}C, δ^{15}N, ‰), and trophic position (TP). The presence of *Paramysis lacustris* in the lakes is denoted by an asterisk.

Lake	*N*	$\delta^{13}C$	$\delta^{15}N$	*TP*
		Mean ± SD	Mean ± SD	Mean ± SD
Aisetas	4	–31.6 ± 1.0	15.7 ± 0.9	3.3 ± 0.6
Antalieptė*	3	–31.2 ± 0.1	12.3 ± 0.3	3.8 ± 0.1
Asveja	3	–32.3 ± 0.2	12.6 ± 0.2	3.3 ± 0.1
Baluošas	3	–31.0 ± 0.5	10.7 ± 0.5	3.2 ± 0.1
Daugai*	6	–27.4 ± 0.6	12.2 ± 0.6	3.8 ± 0.1
Drūkšiai*	6	–26.7 ± 1.5	11.0 ± 0.8	4.4 ± 0.5
Dusia*	3	–25.3 ± 0.7	13.6 ± 0.2	4.6 ± 0.3
Luodis	3	–28.2 ± 0.1	14.5 ± 0.1	3.6 ± 0.1
Lūšiai*	5	–30.7 ± 0.5	12.2 ± 0.7	4.0 ± 0.2
Plateliai	3	–23.0 ± 0.7	9.3 ± 0.5	3.6 ± 0.1
Zarasas	4	–31.7 ± 0.1	15.4 ± 0.1	3.1 ± 0.1
Žeimenys*	6	–31.9 ± 0.6	13.1 ± 0.9	3.9 ± 0.3

4.1 Trophic position of *P. lacustris*

The performed gut content analysis revealed that phytoplankton is the dominant prey for *P. lacustris*. However, prey of animal origin also contributed significantly to their diet in the lakes studied. Thus, according to the gut content analysis, the tropic position of *P. lacustris* is somewhere in-between the second and the third trophic levels. Meanwhile, SIA revealed *P. lacustris* as slightly more predaceous consumer (third trophic level) in studied lakes. Such a discrepancy may be explained by different methods employed for mysids diet analysis and the timing of mysids collection for their diet analysis.

Information on the diet of mysids is often obtained through gut content analysis (Mauchline, 1980; Johannsson *et al.*, 2001; Jankauskienė, 2003) or captive feeding trials (Komarova, 1991; Fink *et al.*, 2012). However, the diet of mysids cannot be accurately identified employing these direct methods because some of the prey get over-digested (mysids tend to macerate their prey beyond recognition) and such analyses reveal only undigested food remains or very recently ingested prey. Further disadvantages of gut content analysis include the following. Firstly, gut content analysis shows only what has been actually ingested rather than what has been assimilated and, secondly, it provides only a recent "snapshot" of the diet depending on the rate of digestion (Gearing, 1991). Meanwhile, stable isotopes signature integrates assimilated dietary source, providing time-integrated indication of the animal diet (Tieszen *et al.*, 1983; Grey, 2006). Body tissues of mysids contain the information on their diet accumulated over a period of several months (Gorokhova and Hansson, 1999; Johannsson *et al.*, 2001). Furthermore, some of the ingested prey might have higher nutritional value than others. For instance, Siegfried and Kopache (1980) revealed that *Neomysis mercedis* Holmes, 1896 gets 80% of all the energy from feeding on mesozooplankton. This fact suggests that animal prey might have higher nutritional value and, consequently a stronger influence on the isotope composition of *P. lacustris*. If correct, this assumption explains why the trophic level values obtained from SIA are a bit higher than those obtained from gut content analyses.

On the other hand, mysids are known for their diel vertical migration from the lake bottom to the water column (Gal *et al.*, 1999; Johannsson *et al.*, 2001; Lasenby and Shi, 2004). Previous studies showed that during the daytime, *P. lacustris* feed on detritus and phytoplankton near the sediment, and at night, migrate vertically to feed on mesozooplankton (Jankauskienė, 2003). In this study, for diet analysis, mysids were collected during the daytime, thus their gut content reflects rather a sedimentary diet that is dominated by detritus and phytoplankton. Meanwhile, SIA results represent the time-integrated diet content including a more predaceous nocturnal diet on mesozooplankton. Consequently, detritus and phytoplankton might be overrepresented in the mysids stomach content in comparison to the more predatory nocturnal feeding as indicated by stable isotope signatures. This fact could also explain the slightly higher trophic level values obtained from SIA than those obtained from gut content analyses.

Overall, this study revealed that in the lakes studied, *P. lacustris* is an omnivorous consumer with a propensity for carnivory. Therefore, it may affect local food webs both as a consumer (top-down effects) and novel prey for native predators (bottom-up effects). As an omnivorous consumer, *P. lacustris* can simultaneously act as a competitor of local zooplankton for resources (phytoplankton) and as a predator on small zooplankton. Our finding that *P. lacustris* consumes a significant share of secondary production in lakes is consistent with results of the similar studies conducted in lagoon ecosystems. The gut content analysis of *P. lacustris* showed that zooplankton crustaceans constitute a significant share of mysids diet in the Curonian Lagoon, especially at night when mysids migrate vertically (Jankauskienė, 2003). Previously performed stable isotope analysis also showed that zooplankton forms a very significant part of *P. lacustris* diet in the Curonian Lagoon (Lesutienė *et al.*, 2007). Furthermore, it showed that zooplankton dominate *P. lacustris* diet in summer when zooplankton are easily available and abundant (Lesutienė *et al.*, 2007). Overall, results of this study are in agreement with those of other studies performed in various habitats with *P. lacustris* featuring as a second order consumer (Lesutienė *et al.*, 2007; Arbačiauskas *et al.*, 2013). Furthermore, carnivory has also been indicated for other invasive mysids of Ponto-Caspian origin, *i.e. Hemimysis anomala*, G. O. Sars., 1907, *Limnomysis benedeni* Czerniavsky, 1882 (Ketelaars *et al.*, 1999; Borcherding *et al.*, 2006; Fink et al., 2012; Ricciardi *et al.*, 2012).

4.2 Changes in perch diet

The performed perch diet analysis revealed evident changes in proportions of the main prey organisms in the diet of juvenile perch at their zooplanktivorous feeding stage. A significant difference was observed in consumption of zooplankton and invasive mysids. This study revealed that in the presence of *P. lacustris*, perch juveniles mostly feed on mysids and in their absence, almost exclusively on zooplankton. In general, in the course of perch ontogeny, its feeding niche undergoes changes. When a juvenile, perch is a zooplankton feeder, later it shifts to feeding on macroinvertebrates of an intermediate size and, when large enough, to a diet mainly consisting of fish (Hjelm *et al.*, 2000). Meanwhile, other studies showed juvenile perch to be an opportunistic feeder. It was revealed that perch juveniles consume prey that is available, easy to cope with and suitable as food by their size (Svanbäck and Eklöv 2002; Rakauskas *et al.*, 2010). Furthermore, previous studies revealed that in the presence of introduced Ponto-Caspian mysids, at least when they are abundant, the shift in the diet of perch juveniles from feeding on zooplankton to macroinvertebrates occurs at an earlier age (Rakauskas *et al.*, 2010). Furthermore, perch juveniles were also found to show a strong feeding preference for invasive Ponto-Caspian mysids in Europe (Borcherding *et al.*, 2006; Rakauskas *et al.*, 2010). This fact suggests that littoral mysids are very important for perch juveniles at the transitional stage when their feeding shifts from zooplankton to benthos. Similar feeding trends were also revealed for pikeperch, *Sander lucioperca* (Linnaeus, 1758) another percid species of European lakes. It was revealed that pikeperch juveniles feed predominantly on Ponto-Caspian mysids during their ontogenetic feeding transition from feeding on zooplankton to fish fry (Ložys, 2003).

Overall, in the presence of invasive *P. lacustris*, secondary consumer prey (mysids) replaces the primary consumer prey (zooplankton) in juvenile perch diet. Consequently, *P. fluviatilis* juveniles become tertiary consumers (fourth trophic level) in lakes inhabited by *P. lacustris* (Fig. 4). Unfortunately, we failed to find any studies on the perch trophic level in temperate lakes with littoral mysids, although, other studies also showed perch juveniles to be secondary consumers in temperate lakes without littoral mysids. Surprisingly, Syväranta *et al.* (2011) indicated the same trophic position (TP = 3.4) of juvenile perch by SIA as the one determined in this study in lakes without invasive mysids. Therefore, our study clearly shows changes in the trophic level of perch juveniles associated with *P. lacustris* invasion and supports the

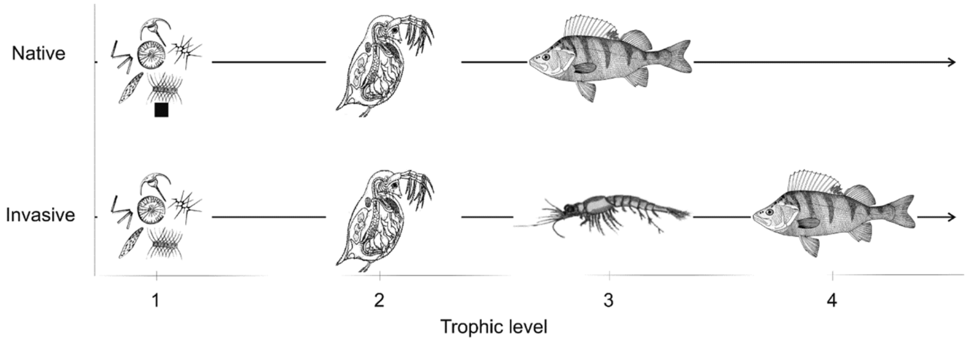

Fig. 4. Lengthening of the hypothetical food chain after *Paramysis lacustris* introduction into temperate mesotrophic lakes.

theory that invasion of non-indigenous mysids can arouse changes in the diet of native predators and alter local food webs (Lasenby *et al.*, 1986; Spencer *et al.*, 1991; Rakauskas *et al.*, 2010; Ricciardi *et al.*, 2012).

5 Conclusions

Before its introduction into water bodies, *P. lacustris* was thought to be a primary consumer. It was believed these mysids are herbivorous or detritivorous in the littoral zone of lakes (Gasiūnas, 1965, 1972; Vaitonis *et al.*, 1990). Thus, it was expected that their introduction would increase the consumption of detritus and plants and enhance incorporation of herbivorous production in food webs of mesotrophic lakes. However, this study revealed that *P. lacustris* are also potential predators of zooplankton and benthic invertebrates. As they consume a significant amount of animal-origin prey, *P. lacustris* constitute the third trophic level in the littoral zone of lakes. That is, probably, another important aspect of *P. lacustris* invasion into mesotrophic lakes. Being predacious enough to be a secondary consumer in lakes, *P. lacustris* may increase the food chain length at least for zooplanktivorous fish juveniles (Fig. 4). Such results are in line with the findings reported from other cases of mysid species introduction, which showed that mysid introduction could have profound impacts on fisheries. It was revealed that the introduced M. relicta are associated with declines in growth, abundance and productivity of planktivorous fishes in the lakes of North America (Lasenby *et al.*, 1986; Bowles *et al.*, 1991; Spencer *et al.*, 1991; Tohtz, 1993) or Scandinavia (Lasenby *et al.*, 1986; Langeland *et al.*, 1991). Furthermore, similar food chain lengthening for planktivorous fish species has been distinguished for another invasive mysid species of the Ponto-Caspian origin *i.e.*, *H. anomala* (Ricciardi *et al.*, 2012). Overall, the assumption that *P. lacustris* invasion may have no whole-ecosystem consequences, as it was though before their introduction, is not correct. The invasion of Ponto-Caspian mysids such as *P. lacustris* can affect the food web structure of invaded habitats at multiple levels and thus potentially have complex whole-ecosystem consequences.

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