

VILNIUS UNIVERSITY
NATURE RESEARCH CENTRE

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TROPHIC POSITION AND FOOD WEB IMPACTS OF NON-INDIGENOUS
CRUSTACEANS IN LAKES

Summary of doctoral dissertation
Biomedical sciences, Ecology and Environmental science (03 B)

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GAMTOS TYRIMŲ CENTRAS

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INTRODUCTION

Relevance of the research

At present, there is no doubt that one of the main reasons causing the loss of biodiversity is the rapid spread of invasive species (Gherardi, 2007). Not only do invasive species reduce local biodiversity through competitive and predatory impacts on resident species, but they also significantly modify local ecosystem functioning by altering their food webs and may cause huge economic loss (Anonymous, 2005). Therefore the spread of alien species is now considered as international problem and local governments struggle to reduce the spread and impacts of alien species (Genovesi and Shine, 2004). However, further alien species spread is ongoing and their negative impact on local communities are still hardly predictable (Gherardi, 2007; Genovesi, 2007). It is still uncertain why some communities are able to retain native species diversity and maintain stability while others become unstable following the loss of biodiversity after new species invasions. Thus, it is very important to understand the alien species impact on the functioning of native food webs, because their organization and structure is related to community's ability to persist and preserve its constituent species. Understanding the pattern of alien species impacts on the structure and functioning of local communities' food webs can help us to predict the effects of alien species on native communities more accurately and build better strategies for protection of endangered species. Therefore, modern conservation and resource management of aquatic ecosystems warrant assessments of the trophic role of invading species and the community food web structure in order to predict newcomer impact on native communities.

Nowadays alien species have been spreading naturally or by random unintentional introductions as intentional introductions of non-native species are now strictly regulated by law (Genovesi and Shine, 2004). However, in the last century many species were intentionally introduced into inland waters for economical purpose (Gasiūnas, 1963, 1972; Lasenby *et al.*, 1986). Higher crustaceans were the main material of such introductions because they represent a significant proportion of freshwater fish diet or serves as a delicacy for humans (Бубинас, 1979; Bubinas, 1994; Кублискас and Бубинас, 1981, 1985; Lasenby *et al.*, 1986; Haertel-Borer *et al.*, 2005).

Currently, non-native crustaceans (amphipods, mysids and crayfish) constitute more than a half of all known higher crustacean fauna in Lithuanian lakes (Arbačiauskas *et al.*, 2012). Most of them were intentionally introduced to Lithuanian lakes in order to enhanced fish or crayfish production. In some lakes they constitute more than a half of all benthic macroinvertebrate biomass and clearly alter native communities in lakes. Although it passed more than 40 years after the initial introductions there are still many unanswered questions in relation to the introduced crustacean's impact on local communities. There is still unclear the trophic position of newcomers in a lake food web, especially when some authors underline their herbivory and detritivory (Юоффе and Максимова, 1968; Muller, 1973; Komarova, 1991; Gergs, 2008) while others, on the contrary, emphasise their carnivory and omnivory feeding (Prezant *et al.*, 2006; Lesutiene *et al.*, 2007; Grabowski *et al.*, 2007; Fink *et al.*, 2012). There is also still unclear do local fish species indeed feed selectively on the introduced peracaridans? May abundant populations of introduced alien crustaceans reduce the fish feeding niche breadth in lakes? Eventually there is still scarce quantitative data on the impact of alien

crustaceans on the structure of food webs in lakes. As it is known that alien higher crustaceans may impact both lower and higher trophic levels in lakes, it is very likely that they have a strong influence on the entire lake food web. Therefore, studies of alien crustaceans' impact on lake food webs are necessary in order to predict and reduce the negative impact of invasive crustaceans in lakes.

The aim and specific tasks of this study

The aim of this research was to evaluate the impact of alien peracaridans on fish diet and growth in lakes, to explore the trophic position of the alien higher crustaceans and to assess the impact of these crustaceans on the lake food web structure. The following tasks were set to achieve this aim:

1. to explore diet composition and feeding selectivity of 0+–3+ age perch (*Perca fluviatilis*), chosen as a model fish species, in lakes with and without alien peracaridans and to evaluate the impact of alien peracaridans on the perch diet;
2. to compare the growth of juvenile perch (*P. fluviatilis*) in lakes with and without alien peracaridans;
3. to compare the biomass of littoral fish in lakes with and without alien peracaridans;
4. to determine the trophic position of alien crustaceans (*Chaetogammarus warpachowskyi*, *Limnomysis benedeni*, *Obesogammarus crassus*, *Orconectes limosus*, *Paramysis lacustris* and *Pontogammarus robustoides*) in lake food webs;
5. to identify and to compare the isotopic niche structure of benthic macroinvertebrate and fish communities in lakes with and without alien crustaceans and to evaluate alien crustaceans impact on the isotopic niche structure of these communities.

Scientific novelty

Results of this study are of great scientific interest as it shows here for the first time:

1. the quantitative effects of alien peracaridans on perch diet content;
2. the trophic position of alien crustaceans (*C. warpachowskyi*, *L. benedeni*, *O. crassus*, *O. limosus*, *P. lacustris* and *P. robustoides*) in a lake food web;
3. the relation between the occurrence and abundance of alien crustaceans and the structure of isotopic niche of the macroinvertebrate or fish communities in lakes.

Practical value

Results of this study extended the scarce knowledge about the impact of alien crustaceans on the structure of lake food webs. This research expanded and advanced the use of stable isotope analysis in the assessing alien species impact on lake food webs. During this research, an extensive data set on the structure of Lithuanian mesotrophic lake food webs was collected which will allow a more accurate assessment of any changes in the future. Overall, the results of this research are of great applied interest and in the future may be applied in:

1. assessing individual trophic position of any hydrobiont in lake food web;
2. predicting the future impact of invasive hydrobionts on lake food webs;
3. assessing the impact of various factors (such as climate change, anthropogenic impact, etc.) on the lake food webs.

MATERIAL AND METHODS

Characteristics of investigated lakes.

a) **Physical characteristics.** In total 24 Lithuanian lakes were investigated for the impact of alien crustaceans on the fish diet, growth and various parameters of a lake food web (Fig. 1). Morphometric characteristics of lakes are presented in Tables 1.

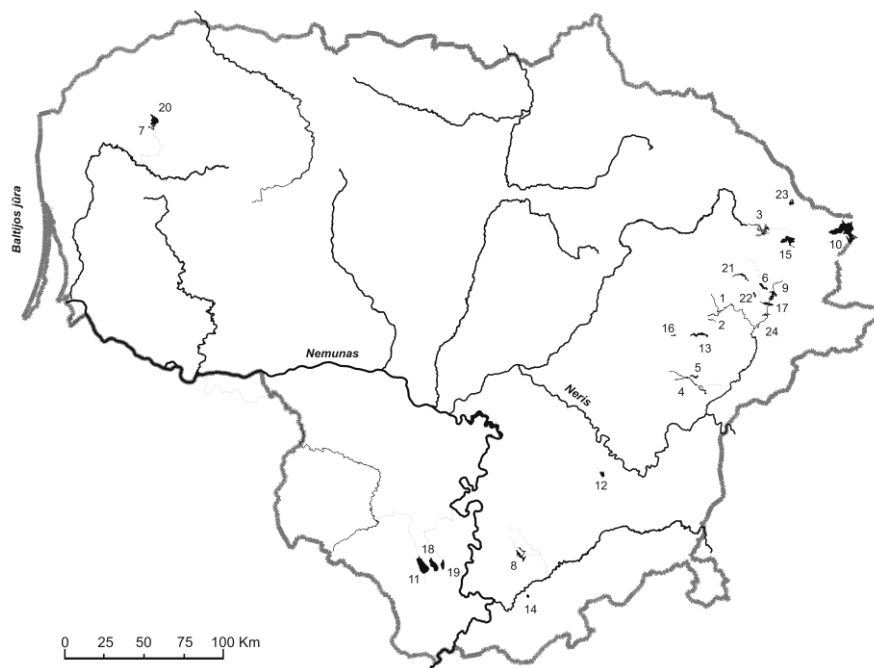


Figure 1. Locations of investigated lakes in Lithuania. Numbers correspond to water body names in Table 1.

Table 1. Morphometry of investigated lakes: area, ha (A); maximal depth, m (D_{max}); mean depth, m (D_{av}); volume, 10^6 m³ (V); retention time, % (R).

No.	Lake	A	D_{max}	D_{av}	V	R
1	Aisetas	501	40	10.4	52	123
2	Alnis	106	22	5.9	6	26
3	Antalieptės	1911	46	7.2	112	102
4	Asveja	978	50	14.7	149	46
5	Baluošai	245	38	12.5	31	52
6	Baluošas	426	34	10.7	44	103
7	Beržoras	52	6	4.6	2	36
8	Daugai	954	44	13.2	126	12
9	Dringis	721	24	8.4	61	72
10	Drūkšiai	4480	33	7.6	368	29
11	Dusia	2334	32	15.4	360	6
12	Galvė	371	47	13.6	50	20
13	Lakajai Baltieji	701	45	13.6	96	40
14	Lavysas	155	10	5.3	8	136
15	Luodis	1320	18	6.7	87	35
16	Luokesai	104	44	14.4	14	12
17	Lūšiai	391	37	13.9	54	249
18	Metelys	1290	15	6.8	88	12
19	Obelija	573	8	4.5	26	35
20	Plateliai	1182	46	11.4	136	12
21	Tauragnas	504	63	18.4	93	25
22	Ūkojas	210	31	11.3	24	155
23	Zarasas	323	37	11.5	38	124
24	Žeimenys	437	24	6.9	30	698

b) Trophic status. Investigated lakes differed in their trophic status. Four parameters which represent the trophic status of a water body were measured in September, 2010. Values of these measurements are presented in Table 2.

Table 2. Hydrochemical parameters of investigated lakes: Secchi depth, m (D_s); chlorophyll *a*, $\mu\text{g L}^{-1}$ (Chl); total nitrogen, $\mu\text{g L}^{-1}$ (N_T) and total phosphorus, $\mu\text{g L}^{-1}$ (P_T). Evaluation of trophic status with respect to parameter value is given in brackets: oligotrophic (O), mesotrophic (M), eutrophic (E), hypertrophic (H).

Lake	Date	D_s	Chl	N_T	P_T
Aisetas	2010.09.14	4.2 (M)	2.56 (M)	1280.7 (H)	22.6 (M)
Antalieptės	2010.09.15	5.8 (M)	3.56 (M)	786.9 (E)	24.0 (M)
Asveja	2010.09.02	3.6 (M)	4.92 (M)	854.4 (E)	28.2 (M)
Baluošai	2010.09.02	6.2 (M)	3.16 (M)	693.7 (E)	25.0 (M)
Baluošas	2010.09.14	4.3 (M)	4.56 (M)	796.6 (E)	23.2 (M)
Daugai	2010.09.09	4.0 (M)	4.55 (M)	928.3 (E)	28.6 (M)
Drūkšiai	2010.09.16	3.5 (E)	11.49 (E)	1144.8 (H)	70.4 (E)
Dusia	2010.09.10	7.0 (O)	2.86 (M)	717.9 (E)	22.4 (M)
Luodis	2010.09.15	3.4 (M)	9.67 (E)	805.3 (E)	29.5 (E)
Luokesai	2010.09.14	7.0 (O)	2.75 (M)	603.5 (E)	20.4 (M)
Lūšiai	2010.09.03	5.6 (M)	2.68 (M)	618.8 (E)	22.2 (M)
Metelys	2010.09.10	3.5 (E)	11.64 (E)	1009.4 (H)	36.2 (E)
Plateliai	2010.08.28	4.5 (M)	2.68 (M)	736.0 (E)	24.8 (M)
Tauragnas	2010.09.14	5.3 (M)	3.98 (M)	908.0 (E)	23.0 (M)
Zarasas	2010.09.16	4.0 (M)	5.56 (M)	1241.2 (H)	25.2 (M)
Žeimenys	2010.09.17	3.2 (E)	12.18 (E)	749.5 (E)	39.7 (E)

c) Biotic characteristics. Investigated lakes differed in respect of their crustacean species composition, their biomass or diversity of littoral macroinvertebrate community. Parameters of the macroinvertebrate communities were investigated in parallel with perch and stable isotope sampling in 2004–2006 and 2009–2012 year, respectively. Lakes varied in macroinvertebrate presence, biomass and abundance of introduced alien peracaridans in 2004–2006 year period (Table 3).

Table 3. Mean annual biomass (g m^{-2}) of littoral macroinvertebrates excluding molluscs (Macro), introduced amphipods and mysids (IntroAM), all amphipods and mysids including native species (AM) and their proportion in total biomass (Pro, %) in studied lakes during 2004–2006. Lakes with abundant populations of introduced species are indicated in bold (Gumuliauskaitė, unpublished data). Lake groups were separated in accordance with the proportion of peracaridans in the total biomass of littoral macroinvertebrates.

Lake group	Lake	Macro	IntroAM	AM	Pro
1	Dusia	18.03	10.19	10.19	56.5
	Daugai	8.13	3.40	3.40	41.8
2	Plateliai 1	8.31	3.28	3.28	39.5
	Plateliai 2	13.87	1.51	3.10	22.0
3	Baluošai	4.15	0	0.33	8.0
	Beržoras	6.57	0	0.32	4.9
	Asveja	10.50	0.01	0.29	2.8
	Lavysas	5.14	0	0	0

The results of the assessment of littoral macroinvertebrate fauna in 2009–2012 also revealed a gradient of total abundance and biomass of alien crustaceans in investigated lakes (Table 4).

Table 4. Mean annual biomass (B, g m⁻²), relative abundance (AB, ind. 10 min⁻¹) and Shannon-Wiener diversity index (H) of littoral macroinvertebrates (Invertebrate), alien mysids (Mysid), alien amphipods (Amphipod) and alien crayfish (Crayfish) and total alien crustaceans (Crustacean) in littoral zone of studied lakes (Šidagytė, unpublished data).

Lake	Invertebrate		Mysid		Amphipod		Crayfish		Crustacean	
	B	H	B	AB	B	AB	B	AB	B	AB
Aisetas	2.6	2.3	0	0	0	0	0	0	0.0	0
Antalieptė	5.7	2.1	0	1	1.0	116	0	0	1.0	117
Asveja	4.2	2.7	0	0	0	1	0	0	0.0	1
Baluošai	24.2	2.6	0	0	0	0	23.0	1	23.0	1
Baluošas	4.5	2.5	0	0	0	0	0	0	0.0	0
Daugai	2.5	2.1	0.020	171	0.4	191	0	0	0.4	362
Drūkšiai	10.9	2.2	0	0	0	0	0	0	0.0	0
Dusia	3.6	1.5	0.004	39	2.7	1104	0	0	2.7	1143
Luodis	4.2	2.3	0	0	0	0	0	0	0.0	0
Luokesai	1.2	2.3	0	0	0	0	0	0	0.0	0
Lūšiai	3.1	2.5	0.006	0	0.2	72	0	0	0.2	72
Metelys	3.9	2.1	0	0	2.2	523	0	0	2.2	523
Plateliai	4.4	1.8	0	0	2.3	288	0	0	2.3	288
Tauragnas	6.4	1.9	0	0	0	0	0	0	0.0	0
Zarasas	1.7	2.3	0	0	0	0	0	0	0.0	0
Žeimenys	14.5	2.4	0	0	0	8	0	0	0.0	8

Fish diet, growth and biomass analysis.

a) Diet analysis. To test if the introduction of Ponto-Caspian peracaridan species may affect the fish diet content a juvenile perch diet was investigated in Lakes Dusia, Daugai, Baluošai, Beržoras, Lavysas, Asveja and Plateliai during 2004–2006 year period (Fig. 1). For collation, these lakes were divided into three groups according to biomass proportion of amphipods and mysids within the total biomass of littoral macroinvertebrates (Table 3). Fish were caught using gill nets (5 and 10 m long and 10 and 14 mm mesh size, respectively) and 12 m long beach seine (bag of 3 mm mesh size). All specimens were measured to the nearest 1 mm (TL), weighed to the nearest 0.1 g, and their age was determined using *operculum* bones. The analysis of perch diet was performed following conventional methods. In total, food content of 537 specimens of 0+–3+ year perch was included in the analysis. To determine the age at which the perch changed its diet (i.e., the ontogenetic feeding shift) from zooplankton to macroinvertebrates, the diet was divided into three major resource types: zooplankton, macroinvertebrates, and fish. The age at which the perch switches from zooplankton to macroinvertebrates was defined as the age at which the percentage of macroinvertebrates in the total biomass of food consumed by the perch exceeded 50 % in most individuals of a given age (Hjelm *et al.*, 2000). For comparison of perch diet composition between the lakes, the average food item composition found in stomachs of perch of the same age was calculated. For presentation of food content, the identified items were grouped into five categories: zooplankton, mysids, amphipods, insects and other food. The biomass of peracaridans in perch stomachs was used as an indicator of their consumption by perch. The feeding niche breadth was estimated by Levins (1968) measure (B), which measures how uniformly the resources are being utilized. All specimens of the same age class were pooled to estimate the niche breadth. Feeding selectivity was calculated as the standardised alpha selectivity index measure (ϵ_i) by Chesson (1983). Proportions of various macroinvertebrate groups in lakes were derived from parallel assessments of macroinvertebrate communities in the littoral zone of lakes (Gumuliauskaitė,

unpublished data). Feeding selectivity was estimated for each sampling separately and based on average food composition of caught specimens. To receive comprehensive estimates of selectivity, two age groups of perch were analysed, 0+–1+ and 2+–3+ in particular, as the pattern of food composition within these age groups was similar within each sampling event in the same lake. For selectivity assessment of perch feeding on littoral macroinvertebrates, benthic diet components were divided into four categories: Diptera; other Insecta; Peracarida; and other food.

b) Growth analysis. To test if the introduction of Ponto-Caspian peracaridan species may affect the fish growth a juvenile perch growth was investigated in Lakes Dusia, Daugai, Baluošai, Beržoras, Lavysas, Asveja and Plateliai during 2004–2006 year period (Fig. 1). For collation, these lakes were divided into two groups according to the presence of abundant populations of alien peracaridans. First group was formed by Dusia, Daugai and Plateliai lakes, with abundant populations of alien peracaridans. While the second group was formed from Baluošai, Beržoras, Lavysas and Asveja lakes without alien peracaridans. In total, 654 specimens of 0+–3+ year perch were included in the analysis. Specific growth rates were calculated as coefficients of regressions of log-transformed weights on age (Winberg, 1966). Specific growth rate was assessed in two cohorts between 2004 and 2006 (cohort 1, hatched in 2004: from 0+ to 2+; cohort 2, hatched in 2003: from 1+ to 3+).

c) Fish biomass analysis. To test if the introduction of Ponto-Caspian peracaridan species may affect fish biomass in lakes, a catch per unit effort (CPUE) of littoral fish community was compared between four lakes with well-established populations of alien peracaridans: Dusia, Meletys, Obelija and Plateliai; and 11 lakes which lack introductions: Alnis, Asveja, Lakajai Baltieji, Baluošai, Baluošas, Dringis, Galvė, Luodis, Tauragnas, Ūkojas and Zarasas. These data came from the State Lake Monitoring Program. Lakes without alien peracaridans were selected with respect to their morphometry and trophic status to allow for comparison (to account fully for lake surface area was not possible as the most of large lakes harbour Ponto-Caspian peracaridan species due to introductions or recent invasions). Standardised surveys of littoral fish communities were performed using benthic multi-mesh gill nets (mesh size: 14, 18, 22, 25, 36, 40, 50, 60 mm, panel size 5 m, length 40 m, height 3 m; number of nets depended upon lake size, but no < 8 nets were used on each occasion) during July – early August, 2003–2008. If the fish community in a lake was sampled multiple times during this period, data were averaged prior to analysis to exclude pseudo-replication.

d) Statistical analyses. The effects of the presence of introduced peracaridans and perch age on the feeding niche breadth of perch were estimated by a two-way ANOVA, as the data satisfied requirements of parametric statistical methods. This test was also used to investigate the impact of introduced species on the specific growth of juvenile perch in the two cohorts. Mixed-model nested ANOVAs were used to show the effect of the presence of Ponto-Caspian mysids and amphipods in perch diet and lake factor on the body length and weight of perch. All other comparisons were made using non-parametric statistical methods, in particular the Kruskal-Wallis tests. The calculations were performed using Statistica 6.1 software.

Trophic position of the alien crustaceans in lake food web.

Trophic position was evaluated by calculating two metrics, *littoral reliance* (LR) and *trophic level* (TL), which indicate the occupied trophic position of a certain species

in a lake food web. The littoral reliance shows the percentage reliance of a certain species on littoral carbon source, while the trophic level indicates the trophic position occupied by a certain species in lake food chains. Both indices plotted in a bi-plot space are used to indicate the trophic position occupied by a certain species in a lake food web. The trophic level of alien and native higher crustaceans were investigated in Aisetas, Antalieptė, Asveja, Baluošai, Baluošas, Daugai, Drūkšiai, Dusia, Luodis, Luokesai, Lūšiai, Meletys, Plateliai, Tauragnas, Zarasas and Žeimenys lakes in both spring and autumn seasons.

a) Littoral reliance (LR) calculation. It is possible to quantify the relative use of prey dependent on littoral vs. pelagic carbon source using $\delta^{13}\text{C}$ measurements. This separation is based on littoral vs. pelagic isotopic enrichment of primary production: macrophyte or benthic algal forms vs. phytoplankton, respectively. Here, the littoral reliance was defined as the reliance on littoral benthic resources of each crustacean species estimated using $\delta^{13}\text{C}$ data in the two-source mixing model (Vander Zanden and Rasmussen 2001):

$$\text{LR} = (\delta^{13}\text{C}_{\text{peracaridan}} - \delta^{13}\text{C}_{\text{pelagic}}) / (\delta^{13}\text{C}_{\text{littoral}} - \delta^{13}\text{C}_{\text{pelagic}})$$

Here, $\delta^{13}\text{C}_{\text{peracaridan}}$, $\delta^{13}\text{C}_{\text{pelagic}}$, $\delta^{13}\text{C}_{\text{littoral}}$ are the mean $\delta^{13}\text{C}$ values of the peracaridan species, primary consumers that rely on the pelagic carbon source, and primary consumers that rely on the littoral carbon source, respectively. In this study, the mean $\delta^{13}\text{C}$ values of gastropod molluscs (*Lymnaea* sp., *Planorbarius* sp., *Radix* sp., *Viviparus* sp.) or amphipods (*C. warpachowskyi*, *G. lacustris*, *O. crassus*, *P. robustoides*) were used as littoral primary consumers, while unionid (*Anodonta* sp., *Unio* sp.) or dreissenid (*Dreissena* sp.) mussels were used as pelagic primary consumers.

b) Trophic level (TL) calculation. The calculation of the certain species trophic level was done in three steps. Firstly, the baseline of the second trophic level in a lake food web (TL 2 in Fig. 2) was described. In this study, to draw baselines of primary consumers (the second trophic level) a linear regression of mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of several genera of benthic invertebrates: gastropods (*Lymnaea* sp., *Planorbarius* sp., *Radix* sp., and *Viviparus* sp.), mussels (*Anodonta* sp., *Dreissena* sp., *Unio* sp.) and peracaridans (*A. aquaticus*, *C. warpachowskyi*, *G. lacustris*, *P. quadrispinosa*) was used. It was assumed that these benthic animals are the primary consumers in lakes. Secondly, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range (AG section, Fig. 2) of a certain consumer of interest from the baseline of the second trophic level was measured. And finally, knowing that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of a consumer are enriched per 1.0‰ and 3.4‰, respectively, relative to the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of its prey, the TL of a certain crustacean species was calculated as:

$$\text{TL} = 2 + \frac{|AG|}{f_{\text{NC}}}$$

where the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range of AG section was calculated as:

$$|AG| = \sqrt{(x_G - x_A)^2 + (y_G - y_A)^2},$$

given that the baseline of the second trophic level in a lake food web was described as:

$$y_{\text{base}} = kx + b,$$

and the integrated discrimination factor was calculated as:

$$f_{NC} = \sqrt{f_N^2 + f_C^2},$$

where f_N is the isotopic discrimination factor (enrichment per one trophic level) of $\delta^{15}\text{N}$ (3.4‰) and f_C is the isotopic discrimination factor of $\delta^{13}\text{C}$ (1.0‰) (Post, 2002). All the calculations were performed in R environment (R Core Team, 2012). The calculation of the trophic level is visualised in Fig. 2.

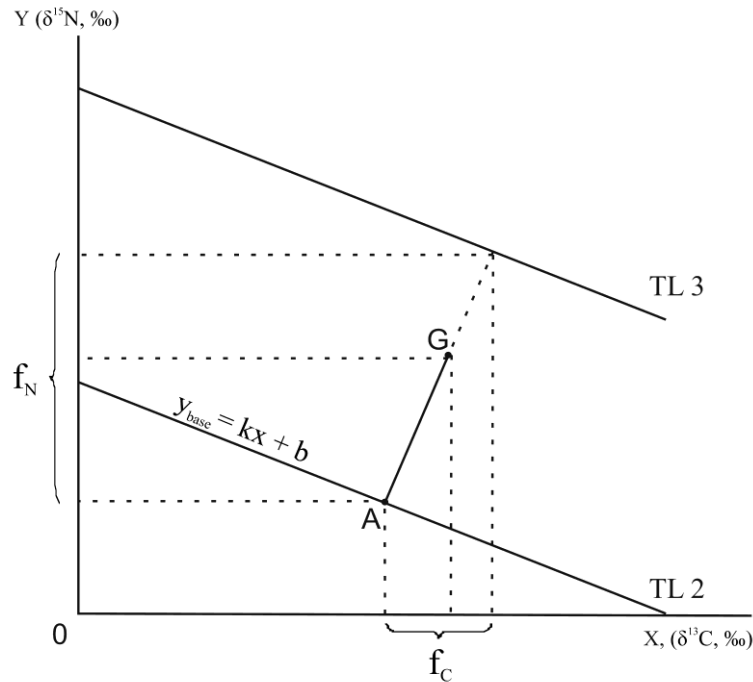


Figure 2. Visualised calculation of the trophic level of various crustaceans species in studied lakes: the baseline of the second trophic level in a lake food web (TL 2); the position of a certain crustacean species in the isotopic $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bi-plot space (G); the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ range of a certain consumer of interest from the baseline of the second trophic level (AG section); f_N and f_C are the enrichment of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values per one trophic level (3.4‰) and (1.0‰), respectively (Post, 2002).

c) Statistical analyses. *T*-tests were applied to reveal seasonal differences in the values of mean littoral reliance and trophic level indexes of crustacean species. To reveal the differences in mean littoral reliance and trophic levels of different crustacean species one-way ANOVAs were used. The Tukey HSD test was applied as an ANOVA post-hoc test.

The impact of alien crustaceans on lake food webs.

Most frequently, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are plotted in a bivariate fashion, a depiction that has been variously referred to as niche space, trophic space, isotopic space or the isotopic niche. In this research, the term “isotopic niche” was adopted. In this sense, the ecological information contained in stable isotope plots was used as a proxy for a subset of the Hutchinsonian *n*-dimensional hyper volume (Hutchinson, 1957). It was emphasized that the isotopic niche is distinct from, but in many circumstances should closely align with the aspects of an actual trophic niche, e. g. particular resource pools utilized or a relative trophic position within a web (Layman *et al.*, 2011). Therefore, the

structure of a community-wide isotopic niche was used to reveal the impact of alien crustaceans on lake food webs in this study.

a) Community-wide trophic niche metrics calculation. In total, six community-wide isotope metrics were used to reveal the changes in a community-wide isotopic niche (Layman *et al.*, 2007a).

1) $\delta^{15}\text{N}$ range (NR, ‰): the distance between the two species with the most enriched and most depleted $\delta^{15}\text{N}$ values (i.e., maximum $\delta^{15}\text{N}$ – minimum $\delta^{15}\text{N}$). NR is the only representation of the vertical structure within a food web. Trophic position of organisms must be calculated in relation to the $\delta^{15}\text{N}$ values of a standardised baseline (Post 2002), but, generally, a larger range in $\delta^{15}\text{N}$ among consumers suggests a larger number of trophic levels and, thus, a greater degree of trophic diversity.

2) $\delta^{13}\text{C}$ range (CR, ‰): the distance between the two species with the most enriched and most depleted $\delta^{13}\text{C}$ values (i.e., maximum $\delta^{13}\text{C}$ – minimum $\delta^{13}\text{C}$). A larger CR would be expected in food webs in which there are multiple basal resources with varying $\delta^{13}\text{C}$ values, providing for niche diversification at the base of a food web.

3) Total area (TA, ‰²): a convex hull area encompassing all the species in the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space. It represents the total amount of occupied niche space, and thus, a proxy for the total extent of trophic diversity within a food web. TA is influenced by species at extreme positions on either the $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ axis (or both), and thus, to some extent it is typically correlated with these two metrics.

4) Mean distance to centroid (CD, ‰): the average Euclidean distance of each species to the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ centroid, where the centroid is the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ value for all the species in a food web. This metric provides a measure of the average degree of trophic diversity within a food web. In cases where a few outlier species may differentially affect TA, CD may better reflect the overall degree of trophic diversity. However, this measure is also a function of the degree of species spacing (see the following metric).

5) Mean nearest neighbour distance (NND, ‰): the mean of Euclidean distances between each species and its nearest neighbour in the bi-plot space, and thus a measure of the overall density of species packing. Food webs with a large proportion of species characterized by similar trophic ecologies will exhibit a smaller NND (increased trophic redundancy) than a web in which species are, on average, more divergent in terms of their trophic niche.

6) Standard deviation of nearest neighbour distance (SDNND, ‰): a measure of evenness of species packing in the bi-plot space. It is less influenced by sample size than NND. Low SDNND values suggest a more even distribution of trophic niches.

The first four metrics are the measures of the total extent of spacing within the $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ bi-plot space, i.e., the community-wide measures of trophic diversity. The last two metrics reflect a position of each species relatively to other species position within the niche space and can be used to estimate the extent of trophic redundancy. The community-wide isotope metrics described herein were calculated using mean $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ values of multiple individuals for each species in a food web. The community-wide isotope metrics were calculated using SIAR package in R (Parnell *et al.*, 2010).

b) Testing the impact of alien peracaridans on lake food webs. The presence of alien crustaceans may have different affects on the macroinvertebrates and fish communities in lakes. Therefore the impact of alien crustaceans on the community-wide isotopic niche metrics was tested separately for littoral macroinvertebrate and fish

communities. In total 16 lakes (Aisetas, Antalieptė, Asveja, Baluošai, Baluošas, Daugai, Drūkšiai, Dusia, Luodis, Luokesai, Lūšiai, Meletys, Plateliai, Tauragnas, Zarasas and Žeimenys) were investigated for the of alien crustaceans impacts on macroinvertebrates and fish communities in lakes. The species or genera that represented macroinvertebrates and fish communities in this study are presented in Tables 5 and 6.

Table 5. Fish species used to calculate community-wide isotopic metrics in studied lakes.

Family	Species
Cyprinidae	<i>Abramis brama</i> , <i>Alburnus alburnus</i> , <i>Blicca bjoerkna</i> , <i>Rutilus rutilus</i> , <i>Sardinus erythrophthalmus</i> , <i>Tinca tinca</i>
Cobitidae	<i>Cobitis taenia</i>
Esocidae	<i>Esox lucius</i>
Gadidae	<i>Lota lota</i>
Percidae	<i>Gymnocephalus cernuus</i> , <i>Perca fluviatilis</i>

Table 6. Species or genera of benthic macroinvertebrates used to calculate community-wide isotopic metrics in studied lakes.

Class/Order	Genera/Species
Gastropoda	<i>Viviparus</i> sp., <i>Lymnaea</i> sp., <i>Radix</i> sp., <i>Planorbarius</i> sp.
Hirudinea	<i>Erpobdella</i> sp., <i>Haemopsis</i> sp., <i>Alboglossiphonia</i> sp., <i>Glossiphonia</i> sp., <i>Placobdella</i> sp.
Amphipoda	<i>S. ambulans</i> , <i>C. warpachowskyi</i> , <i>G. lacustris</i> , <i>P. robustoides</i> , <i>O. crassus</i>
Decapoda	<i>O. limosus</i>
Isopoda	<i>A. aquaticus</i>
Mysida	<i>L. benedeni</i> , <i>P. lacustris</i>
Ephemeroptera	<i>Centroptilum</i> sp., <i>Cloeon</i> sp., <i>Caenis</i> sp., <i>Ephemera</i> sp.
Megaloptera	<i>Sialis</i> sp.
Hemiptera	<i>Corixa</i> sp. <i>Ilyocoris</i> sp. <i>Nepa</i> sp. <i>Ranatra</i> sp. <i>Notonecta</i> sp. <i>Aeshna</i> sp., <i>Anax</i> sp., <i>Brachytron</i> sp., <i>Hemianax</i> sp., <i>Erythromma</i> sp., <i>Enallagma</i> sp.,
Odonata	<i>Ischnura</i> sp., <i>Cordulia</i> sp., <i>Epithea</i> sp., <i>Somatochlora</i> sp., <i>Gomphus</i> sp., <i>Onychogomphus</i> sp., <i>Sympecma</i> sp., <i>Libellula</i> sp., <i>Orthetrum</i> sp., <i>Platynemis</i> sp.
Trichoptera	<i>Goera</i> sp., <i>Leptocerus</i> sp., <i>Anabolia</i> sp., <i>Halesus</i> sp., <i>Limnophilus</i> sp., <i>Molanna</i> sp., <i>Agrypnia</i> sp., <i>Phryganea</i> sp.

Six community-wide isotope metrics were calculated separately for spring and autumn as for most of the species the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values significantly differed between the two seasons. Relations between the community-wide metrics and abiotic or biotic factors were tested. The abiotic factors were lake physical parameters such as the surface area (A), mean depth (D_{av}) or retention time (R), and lake measure of the trophic status such as the Secchi depth (D_S) and chlorophyll *a* (Chl), total nitrogen (N_T) and total phosphorus (P_T) concentrations in water. The seasonal factor was incorporated as a nominal factor (S). The biotic factors were the total biomass (MB) and diversity (the first Hill's number; H) of benthic macroinvertebrates, as well as the biomass (AB) and relative abundance (AA) of alien peracaridan species in the littoral zone of a lake. The presence of alien amphipods (A_P) and abundance classes of alien crustaceans (A_C) were incorporated as nominal factors.

c) Statistical analyses. To test for the relations between calculated community-wide metrics and abiotic or biotic parameters in studied lakes redundancy analysis and multiple regressions were applied. In order to reduce the impact of extreme values of the explanatory variables and improve homogeneity of variance the square root transformation for P_T , A, R, AA, AB and MB parameters was applied.

RESULTS AND DISCUSSION

Perch diet and growth analyses.

a) **Diet analyses.** The aim of these analyses was to evaluate how the introduced Ponto-Caspian peracaridans affect juvenile perch feeding in lakes, in particular their food content, feeding niche breadth and feeding selectivity. It was hypothesised that in lakes with abundant populations of Ponto-Caspian peracaridans perch juveniles should selectively feed on the introduced species, and due to the prevalence of the introduced peracaridans in the diet the juvenile perch would exhibit a narrower feeding niche in comparison to lakes devoid of these aliens where the food supply is more diverse.

The results showed that starting with the first year of life, the perch readily consumes the introduced mysids, when they are abundant. The Ponto-Caspian mysids formed a considerable part of the diet of 0+ and 1+ year perch in Lake Daugai and especially in Lake Dusia with abundant population of the mysid *P. lacustris* (Fig. 3). In contrast, it was the zooplankton that dominated in the diet of 0+ and 1+ year perch from other lakes without littoral mysids. Results showed introduced mysids' contribution to perch diet decreased from the third year of life, and since then the contribution of introduced amphipods started to increase. In general, the introduced mysids are an important prey during the first two years of perch ontogenesis, while amphipods' importance as food increases from the third year.

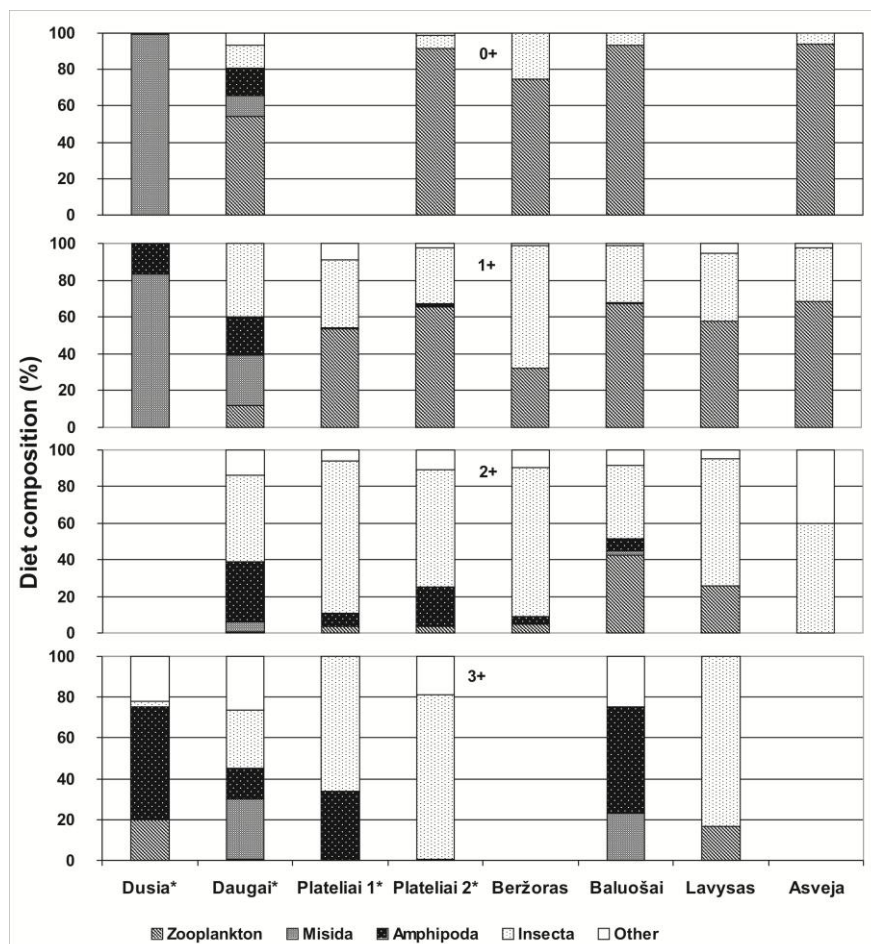


Figure 3. Diet composition of 0+–3+ year perch in studied lakes. Lakes with well-established populations of introduced Ponto-Caspian crustaceans are marked by an asterisk. Absence of data for an age class in a lake indicates that feeding of that perch age was not assessed.

Perch diet analysis also showed that the perch consumes more amphipods and mysids in lakes with numerous populations of these crustaceans (Fig. 3). The biomass (mean \pm SD) of consumed littoral peracaridans was 26.5 ± 27.4 and 5.4 ± 10.3 mg in 0+ year perch stomachs from lakes Dusia and Daugai, respectively, but they were absent in the stomachs of 0+ year perch from other lakes. The biomass of consumed peracaridans was 50.9 ± 35.3 and 19.6 ± 32.5 mg in the stomachs of 1+ year perch from lakes Dusia and Daugai, respectively, and they constituted less than 1 mg in other lakes. For the biomasses of consumed peracaridans in 2+ and 3+ year perch see Table 8.

Table 8. The biomass (mean \pm SD) of consumed littoral peracaridans in stomachs of 0+, 1+, 2+ and 3+ year perch in studied lakes. Lakes with introduced peracaridan species are indicated in bold.

Lake	0+	1+	2+	3+
Dusia	26.5 ± 27.4	50.9 ± 35.3	–	146.8 ± 189.9
Daugai	5.4 ± 10.3	19.6 ± 32.5	48.6 ± 64.9	56.8 ± 86.7
Plateliai 1	–	0.6 ± 1.4	8.5 ± 17.9	40.6 ± 42.3
Plateliai 2	0.0	0.9 ± 4.2	23.2 ± 33.8	9.2 ± 12.6
Beržoras	0.0	0.2 ± 1.2	4.5 ± 19.7	–
Baluošai	0.0	0.3 ± 1.8	3.3 ± 13.9	0.0
Lavysas	–	0.5 ± 2.4	0.7 ± 3.4	0.0
Asveja	0.0	0.0	6.6 ± 10.1	0.0

The available data allowed us to test the hypothesis statistically. A significant difference was observed in the diet of 0+ and 1+ year perch between the lakes of the first group (Dusia and Daugai) and the other lakes (Kruskal-Wallis test for 0+: $H(1, N = 6) = 4.8, p < 0.03$; for 1+: $H(1, N = 8) = 4.0, p < 0.05$). The diet of perch of other ages significantly differed between the lakes of the first and the second group and the lakes of the third group (Kruskal-Wallis tests: $H(1, N = 7) \geq 4.5, p \leq 0.03$).

It is known that the perch undergoes ontogenetic niche shifts during its life. When a juvenile, the perch is a zooplankton feeder, later it shifts to feeding on macroinvertebrates of an intermediate size and, when large enough, it shifts to a diet mainly consisting of fish (Hjelm *et al.*, 2000; Svanbäck and Eklöv, 2002). Our data suggest that its diet shift from zooplankton to macroinvertebrates occurs at an earlier age in the presence of the introduced Ponto-Caspian mysids, at least when the mysids are abundant. For the juvenile perch, the feeding shift from zooplankton to macroinvertebrates took place at an earlier age in lakes with numerous populations of the Ponto-Caspian mysids compared to lakes devoid of introduced mysids. The shift in perch diet from zooplankton to macroinvertebrates was observed during the first and the second year of perch life in lakes Dusia and Daugai, respectively, and during the third year in other lakes, which are devoid of littoral mysids (Table 9).

Table 9. Perch age (A), length (L) and weight (Q) related to the ontogenetic feeding niche shift from zooplanktivory to benthivory in studied lakes. Lakes with introduced mysids species are indicated in bold.

Lake	A	L (mean \pm SN)	Q (mean \pm SN)
Dusia	0+	7.2 ± 0.3	3.5 ± 0.6
Daugai	1+	8.4 ± 0.9	6.7 ± 2.5
Plateliai 1	2+	11.5 ± 0.9	17.9 ± 4.0
Plateliai 2	2+	10.9 ± 0.8	15.8 ± 3.4
Baluošai	2+	11.2 ± 0.6	15.1 ± 1.8
Lavysas	2+	11.4 ± 0.9	17.5 ± 4.0
Asveja	2+	11.4 ± 0.9	16.2 ± 2.7

The difference in the age of perch at which it undergoes the ontogenetic feeding shift appeared to be statistically significant between Lakes Dusia and Daugai (inhabited by the Ponto-Caspian mysids) and the other lakes (Kruskal-Wallis test: $H(1, N = 7) = 4.48, p = 0.034$). The pattern observed in the ontogenetic niche shift may be explained by the impact of the introduced mysids on the zooplankton. As the introduced mysids, at least *P. lacustris*, are partly carnivorous, they may prey on the formerly important fish prey items and reduce their availability for the juvenile fish. The predatory impact of the Ponto-Caspian mysids on the zooplankton in the Curonian Lagoon has been well-documented (Lesutienė *et al.*, 2007).

The feeding niche breadth of perch, indicating feeding specialization, varied among studied lakes and perch age groups (Fig. 4). It could be expected that the diversity of perch food should be lower; i. e. the feeding niche should be narrower, in lakes with abundant populations of the introduced amphipods and mysids. Firstly, the fish may specialise to feed on these readily available and valuable preys. Secondly, the introduced Ponto-Caspian peracaridans, at least the amphipods, may reduce species richness and the diversity of resident macroinvertebrate communities (Gumuliauskaitė and Arbačiauskas, 2008). However, this hypothesis was not supported by our results. The feeding niche breadth of the juvenile perch did not differ between lakes with abundant populations of introduced mysids and amphipods and lakes devoid of these peracaridans. The comparison of the three lake groups that differed in littoral peracaridan abundance did not reveal any differences in feeding specialisation; neither there was any differences observed in the feeding niche breadth among perch age groups (Table 10).

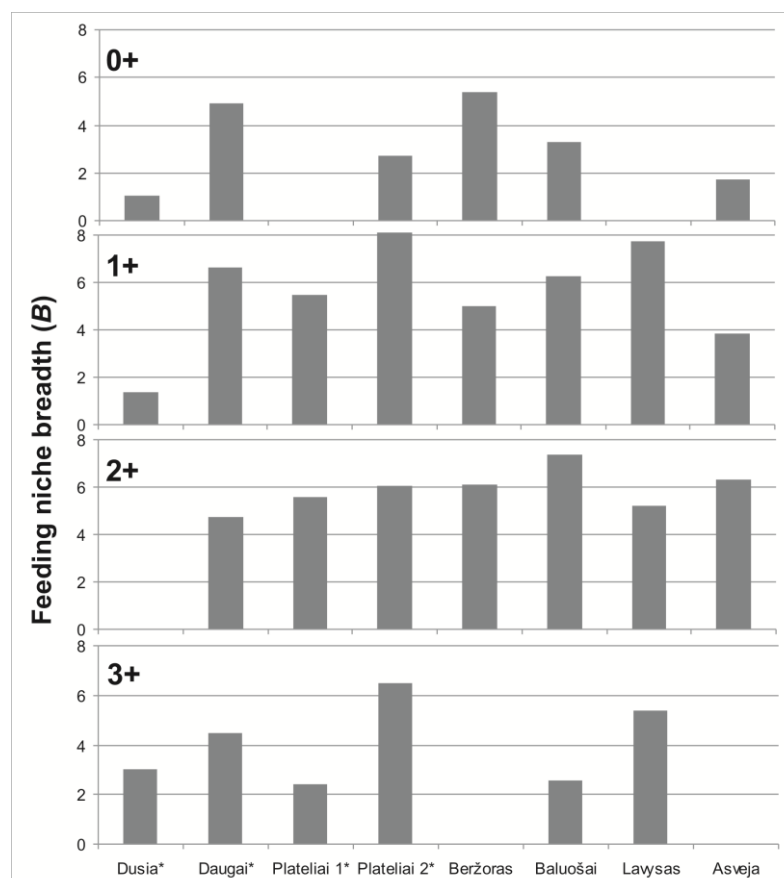


Figure 4. Feeding niche breadth (B) of 0+–3+ year perch in studied lakes. Lakes with well-established populations of introduced Ponto-Caspian crustaceans are marked by an asterisk.

Table 10. Results of two-way ANOVA testing for effects of lake group (differing in the presence and abundance of introduced peracaridans) and perch age on the feeding niche breadth of perch.

Factor	<i>df</i>	<i>F</i>	<i>p</i>
Lake group (<i>L</i>)	2	0.67	0.53
Age (<i>A</i>)	3	2.22	0.13
<i>L</i> × <i>A</i>	6	0.24	0.96
error	15		

The estimates of perch feeding selectivity for benthic animals were compared between lakes with and without the introduced Ponto-Caspian peracaridans. 0+ and 1+ year perch, as one age group, showed selective feeding on peracaridans in lakes with dense populations of introduced amphipods and mysids, but a negative preference for these crustaceans in lakes with only native peracaridans was observed (Table 11).

Table 11. Estimates of perch feeding selectivity (mean ± SD) for benthic macroinvertebrates divided into four groups in lakes with introduced amphipods and mysids (Ponto) and lakes devoid of these peracaridans (Native). Significant differences (Kruskal-Wallis test for 0+ and 1+: $H(1, N = 37) \geq 18.3$; for 2+ and 3+: $H(1, N = 19) = 4.9$) are highlighted in bold.

Age	Lakes	Diptera	Other Insecta	Other	Peracarida
0+–1+	<i>Ponto</i>	−0.68 ± 0.32	−0.07 ± 0.70	−1.00 ± 0.01	0.56 ± 0.44
	<i>Native</i>	0.61 ± 0.56	−0.31 ± 0.70	−0.95 ± 0.18	−0.88 ± 0.40
	<i>p</i>	< 0.001	0.34	0.35	< 0.001
2+–3+	<i>Ponto</i>	−0.74 ± 0.40	0.62 ± 0.59	−0.91 ± 0.14	−0.23 ± 0.55
	<i>Native</i>	−0.08 ± 0.72	0.15 ± 0.56	−0.89 ± 0.26	−0.32 ± 0.83
	<i>p</i>	< 0.03	0.09	0.83	0.80

The positive feeding selectivity of 0+ and 1+ year perch for introduced crustaceans was due to the high selectivity for mysids (0.98 ± 0.02), as compared with the negative selectivity for amphipods (-0.49 ± 0.39). In contrast, perch selectively fed on Diptera larvae (mainly Chironomidae) in lakes with only native peracaridans, but expressed a negative preference for dipterans larvae in lakes with introduced peracaridans. We did not observe any difference in feeding selectivity for peracaridans in 2+–3+ year perch in lakes with or without introduced amphipods and mysids. However, perch of this age showed differences in feeding selectivity for Diptera (Table 11).

b) Growth analyses. The aim of these analyses was to test if the introduction of Ponto-Caspian peracaridan species may affect the fish growth in lakes. Therefore a juvenile perch growth was investigated in seven lakes. Results showed that at the end of the same growing season, the size of 0+ and 1+ perch in lakes Dusia and Daugai, where the Ponto-Caspian mysids and amphipods substantially contributed to the diet (Fig. 3), did not differ from those in other lakes, where introduced peracaridans were absent or rare and thus were not recorded in fish stomachs used for the comparison. The variation in size depended only on the lake effect (Table 12).

Table 12. Summary of mixed-model nested ANOVAs testing for the effect of presence of Ponto-Caspian mysids and amphipods in the diet (PO) and the effect of lake as a random factor (LA) on body length (L) and weight (W) of 0+ and 1+ year perch at the end of the growing season (late October, 2004). Significant effects are highlighted in bold.

Metric	Source	Effect		Error		<i>F</i>	<i>p</i>
		<i>df</i>	MS	<i>df</i>	MS		
0+ L	PO	1	1.360	7.05	0.962	1.41	0.273
	LA	7	0.971	71.00	0.277	3.50	0.003
0+ W	PO	1	3.002	7.05	0.472	7.78	0.223
	LA	7	1.669	71.00	0.472	3.60	0.002
1+ L	PO	1	0.771	7.02	2.576	0.30	0.601
	LA	7	2.639	59.00	0.174	15.15	< 0.001
1+ W	PO	1	4.736	7.02	18.204	0.26	0.626
	LA	7	18.640	59.00	1.310	14.23	< 0.001

A three year data set of perch diet and size allowed us to track the juvenile perch cohorts. The assessment of specific growth rate of body weight in the two cohorts between 2004 and 2006 (cohort 1, hatched in 2004: 0+ to 2+; cohort 2, hatched in 2003: 1+ to 3+), calculated as coefficients of regressions of log-transformed weights on age (Winberg, 1966), also did not indicate any impact of introduced peracaridans on the growth of juvenile perch (Fig. 5; two-way ANOVA, introduction effect: $F_{1,10} = 1.1$, $p = 0.33$, cohort effect: $F_{1,10} = 13.6$, $p = 0.004$).

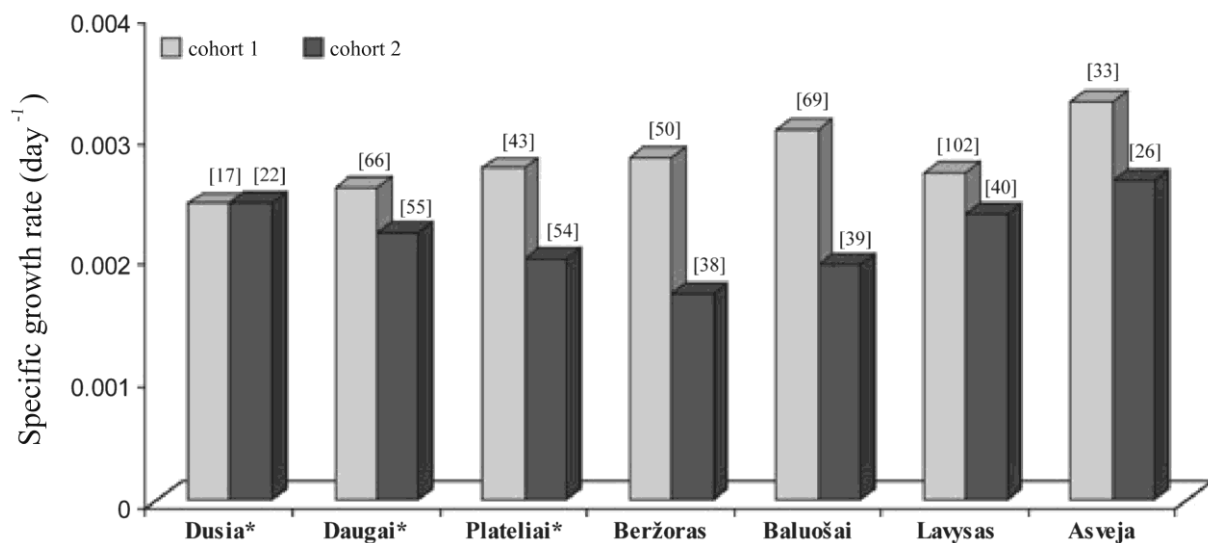


Figure 5. Mean specific body mass growth rate of two perch cohorts (cohort 1: 0+ to 2+; cohort 2: 1+ to 3+, 2004–2006) in lakes inhabited by abundant populations of Ponto-Caspian peracaridan species (denoted by asterisks) and lakes devoid of these species. Numbers of specimens used for estimates are given in brackets.

c) Fish catch analysis. Characteristics of littoral fish community were compared between four lakes with well-established populations of Ponto-Caspian peracaridan species and 11 lakes which did not experience introductions. No differences in the total littoral fish catch per unit effort (CPUE) or CPUE for perch under 8 years of age (the age when the perch is a benthivorous and is not subjected to commercial fishing) were found between lakes with and without introduced peracaridan species (Fig. 6).

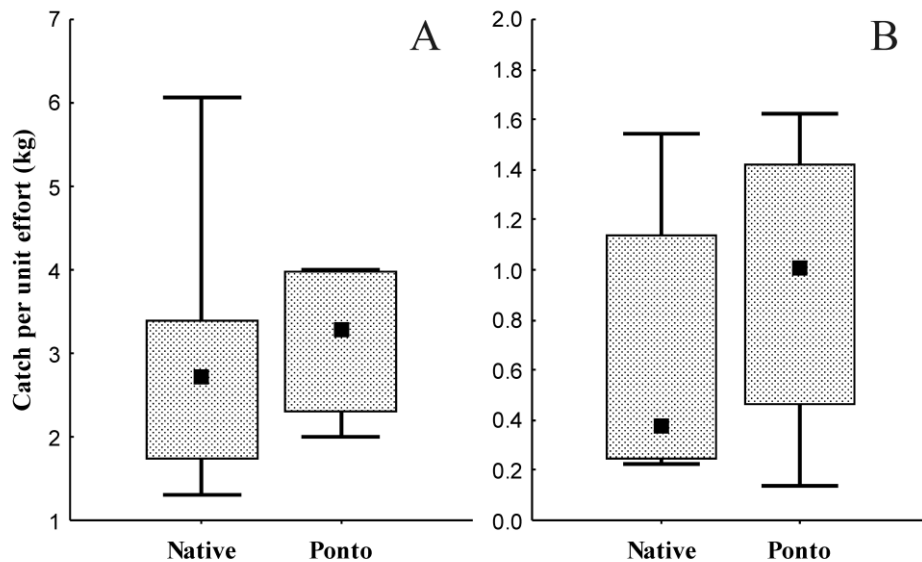


Figure 6. Catch per unit effort (biomass per standard 40 m length gill net per day; median, quartiles and range) of littoral fish community (*Abramis brama*, *Alburnus alburnus*, *Blicca bjoerkna*, *Esox lucius*, *Gymnocephalus cernuus*, *Perca fluviatilis*, *Rutilus rutilus*, *Scardinius erythrophthalmus* and *Tinca tinca*) (A) and 3+ to 7+ age perch (B) in lakes with (Ponto, four lakes) and without (Native, 11 lakes) Ponto-Caspian peracaridans in the benthic community. Differences are absent (Kruskal-Wallis tests, $p = 0.60$ and $p = 0.36$, correspondingly).

d) Conclusions. Results showed that introduced Ponto-Caspian amphipods and mysids, when abundant, are important food items in the diet of the juvenile perch, and the consumption of these food sources starts from the first year of perch life. In lakes with numerous populations of littoral mysids, perch underwent an earlier ontogenetic diet shift from zooplankton to macroinvertebrates due to the availability of mysids as prey and the probable reduction in the littoral zooplankton abundance. However, an impact of introduced peracaridans on the feeding niche breadth of perch was not recorded. Overall, the juvenile perch is an opportunistic feeder. It consumes preys that are available, easy to track and are of size suitable to ingest. Although perch assimilated the introduced peracaridans into their diet, as did some other fish species feeding in the littoral, the collation of available data does not support the enhancement of perch and other fish production in Lithuanian lakes. Thus, the original rationale for introduction of the Ponto-Caspian peracaridan species into Lithuanian waters appears misguided.

The position of alien crustaceans in lake food web.

Calculated littoral reliance and trophic level indices showed the trophic position of alien crustaceans in the food webs of studied lakes (Table 13, Fig. 7). The mean trophic level differed significantly among peracaridans species both in spring and autumn seasons (one-way ANOVAs: spring, $F = 26.1$; $p < 0.0001$; autumn, $F = 21.6$; $p < 0.0001$). There was also a clear statistical evidence of difference in mean littoral reliance indices (one-way ANOVAs: spring, $F = 33.6$; $p < 0.0001$; autumn, $F = 11.2$; $p < 0.0001$). However, seasonal differences in TL and LR indexes were only revealed for the alien mysid *P. lacustris* (t -test, $p < 0.03$), while for other crustacean species there were no significant differences of TL and LR values between spring and autumn seasons (t -tests, $p > 0.05$).

Table 13. Littoral reliance (LR) and trophic level (TL) of crustacean species in studied lakes in spring and autumn, 2009–2012. N represents the number of lakes sampled for a species. Significant seasonal differences (*t*-tests, $p < 0.05$) are indicated in bold.

Species	Spring			Autumn			Seasonal differences	
	N	LR \pm SE	TL \pm SE	N	LR \pm SE	TL \pm SE	LR	TL
AMPHIPODA								
<i>C. warpachowskyi</i>	5	0.88 \pm 0.1	2.0 \pm 0.1	5	0.84 \pm 0.2	1.9 \pm 0.1	$p = 0.73$	$p = 0.29$
<i>G. lacustris</i>	10	0.84 \pm 0.1	1.9 \pm 0.1	11	0.84 \pm 0.2	1.9 \pm 0.1	$p = 0.95$	$p = 0.87$
<i>O. crassus</i>	1	0.90	2.4	2	0.82 \pm 0.2	2.1 \pm 0.1	–	–
<i>P. quadrispinosa</i>	10	0.36 \pm 0.1	2.6 \pm 0.1	9	0.25 \pm 0.2	2.6 \pm 0.1	$p = 0.13$	$p = 0.51$
<i>P. robustoides</i>	7	0.88 \pm 0.1	2.4 \pm 0.1	8	0.90 \pm 0.2	2.4 \pm 0.1	$p = 0.99$	$p = 0.90$
<i>S. ambulans</i>	2	0.59 \pm 0.1	2.7 \pm 0.1	–	–	–	–	–
DECAPODA								
<i>A. astacus</i>	–	–	–	3	0.69 \pm 0.2	3.2 \pm 0.3	–	–
<i>O. limosus</i>	5	0.79 \pm 0.1	2.7 \pm 0.1	8	0.68 \pm 0.2	2.7 \pm 0.1	$p = 0.22$	$p = 0.75$
ISOPODA								
<i>A. aquaticus</i>	16	0.64 \pm 0.1	1.9 \pm 0.1	15	0.59 \pm 0.2	1.8 \pm 0.1	$p = 0.47$	$p = 0.08$
MYSIDA								
<i>L. benedeni</i>	1	0.60	2.8	1	0.51	2.2	–	–
<i>M. relicta</i>	5	0.05 \pm 0.0	3.3 \pm 0.2	5	0.11 \pm 0.2	2.7 \pm 0.2	$p = 0.58$	$p = 0.08$
<i>P. lacustris</i>	6	0.46 \pm 0.1	3.1 \pm 0.2	5	0.72 \pm 0.2	2.3 \pm 0.1	$p < 0.03$	$p < 0.004$

a) Amphipods. Study results showed that all the alien amphipod species highly depended on the littoral organic source (LR > 82%), thus, they should be attributed to the littoral food web. Results showed *P. robustoides* and *O. crassus* occupied higher trophic level than *C. warpachowskyi* in lake food chains (HSD test, $p < 0.05$, Fig. 7). However, all alien amphipods were plotted close to the second trophic level in the isotopic bi-plot and so should be attributed to the primary consumers in lakes (Fig. 7). This was coincident with pre-introduction hypothesis that the introduced alien amphipods would occupy the second trophic level and would function as primary consumers in lake littoral zones. The trophic position of the alien *C. warpachowskyi* was similar to that of the native amphipod *G. lacustris* (HSD test, $p > 0.05$), which was also a primary consumer. The other alien amphipods (*P. robustoides* and *O. crassus*) were plotted higher in lake food chains and did not overlap with the trophic position of any of the native peracaridan species (Fig. 7).

b) Mysids. Results showed both trophic position indices of alien mysids varied significantly between the spring and autumn seasons (*t*-test, $p < 0.05$, Fig. 7). In autumn they occupied second trophic level and were attributed to the primary consumers in a lake littoral. While in spring they occupied higher position in lake food chains and were attributed to the secondary consumers (Fig. 7). The results also showed that alien mysids depended on both the pelagic and the littoral carbon sources. Moreover, littoral reliance indices of alien *P. lacustris* mysids varied significantly between the spring and autumn seasons (*t*-test, $p < 0.03$, Fig. 7). *Paramysis lacustris* in spring relied on pelagic carbon source, while in autumn it consumed more than 70% of littoral carbon. In general, the revealed trophic position of alien mysids denies the pre-introduction hypothesis that introduced mysids would be primary consumers in lake littoral zone. Although alien mysids consumed pelagic carbon sources, however their trophic position did not overlap with the trophic position of the native pelagic *M. relicta* (HSD test, $p < 0.05$).

c) Crayfish. The performed analysis showed that the invasive crayfish *O. limosus* relied on the littoral organic carbon source (LR > 68 %) both in spring and autumn seasons and, as it was predicted earlier, it was attributed to the littoral food web of lakes.

The trophic position of *O. limosus* was closed to the third trophic levels and thus it was attributed to the secondary consumers in lakes. In the food chains of lakes, this alien species was plotted lower the native *A. astacus* (*t*-test, $p < 0.05$, Fig. 7). This indicates that *O. limosus* consumes less animal food source than the native *A. astacus*.

d) Conclusion. In general, most of alien crustacean species relied on the littoral carbon source and occupied the transitional position between the typical second and third levels in the lake food chains. Therefore, these species should be considered as omnivorous species in the lake littoral zone. Only the alien mysids occupied a unique transitional trophic position between littoral and pelagic food webs in lakes. Their reliance on the littoral carbon source significantly changes during the season, therefore alien mysids serve as a link between pelagic and littoral energy paths in lakes.

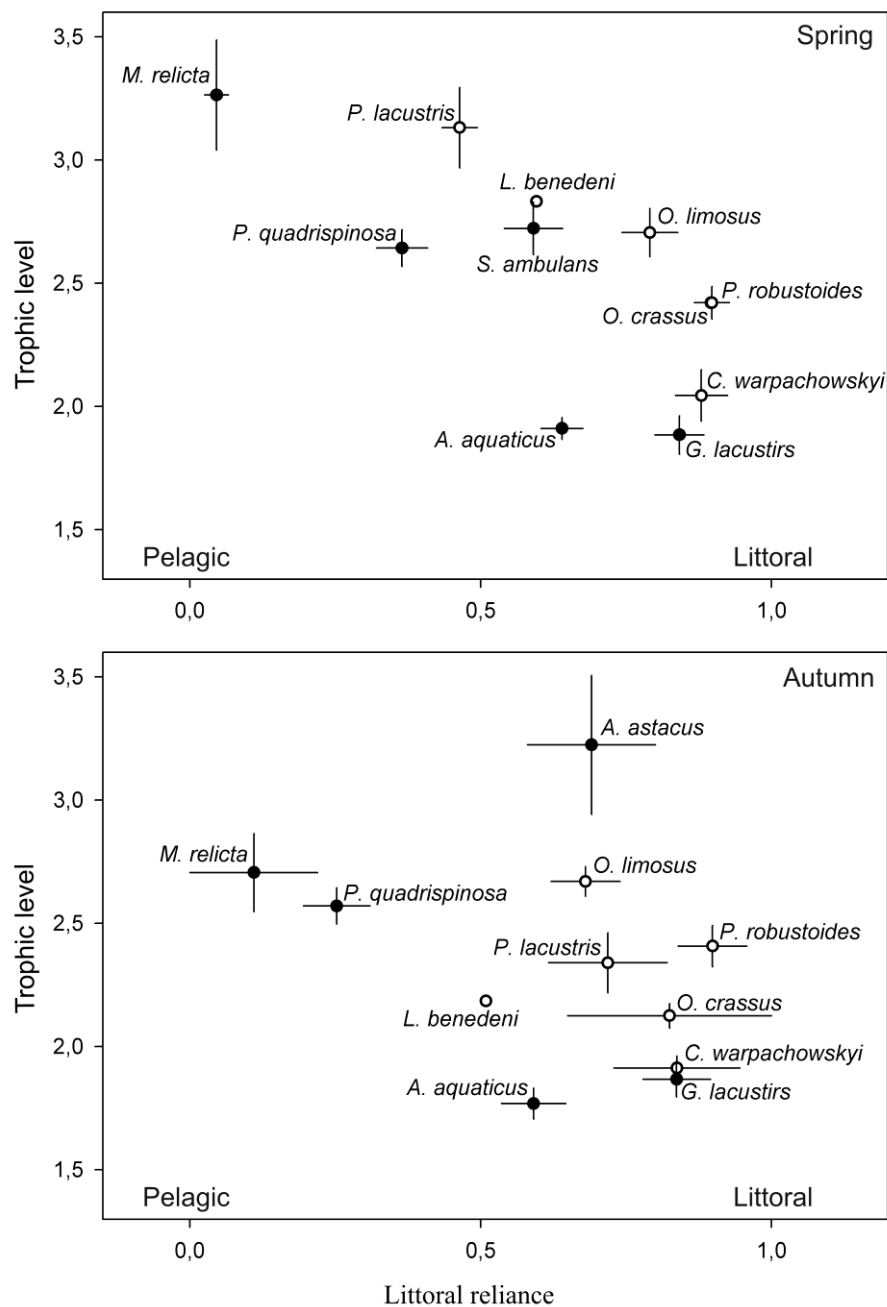


Figure 7. Isotopic bi-plot showing mean (\pm SE) littoral reliance and trophic level for different crustacean species throughout studied lakes in spring and autumn, 2009–2012.

The impact of alien crustaceans on a lake food web.

To show which abiotic or biotic factors were more related to the community-wide isotopic metrics of the benthic macroinvertebrate and fish communities' redundancy analysis was applied. To test if the presence and relative abundance of alien peracaridans were associated with calculated values of community-wide metrics in lakes multiple regressions were applied.

a) Impact on littoral macroinvertebrate community. Performed redundancy analysis showed that all explanatory variables explained 75 % of the variation in the benthic macroinvertebrate community-wide isotopic metrics data (Fig. 8).

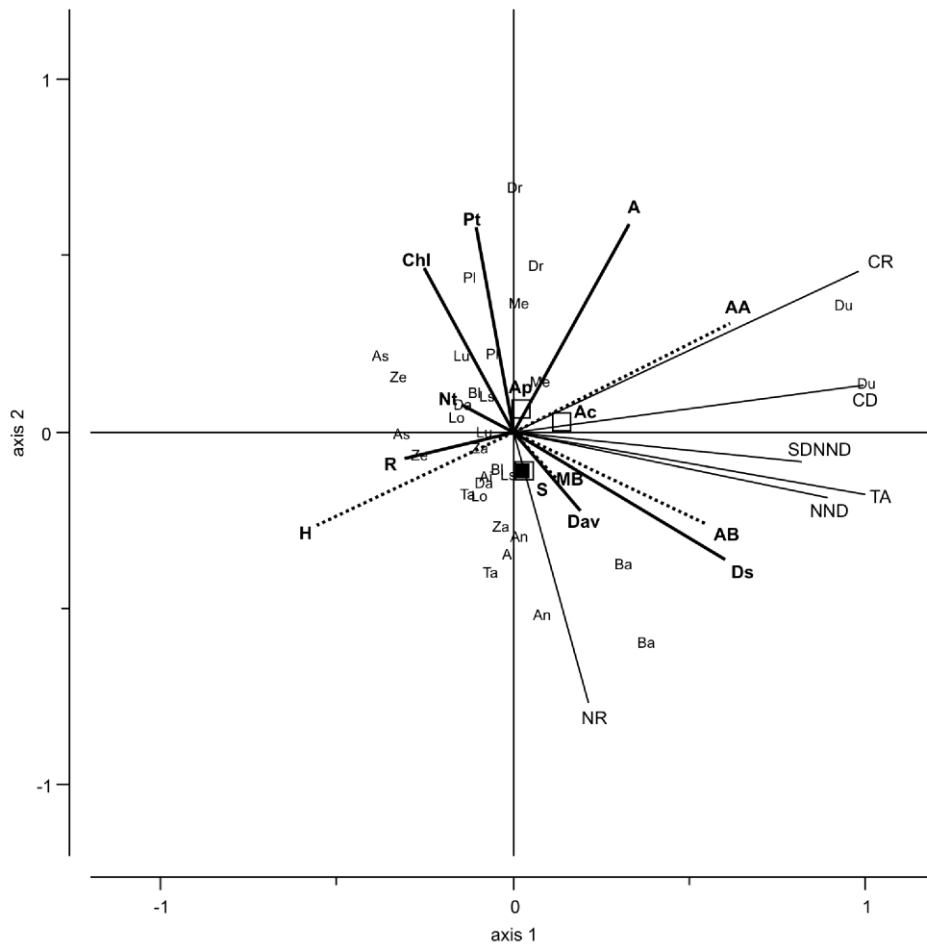


Figure 8. Redundancy analysis triplot for the macroinvertebrate community-wide isotopic metrics data. Square root transformation for AA, AB and MB parameters was applied. Response variables (grey lines): six community-wide isotopic metrics (CR, NR, TA, CD, NND, SDNND). Abiotic explanatory variables (bold lines): lake physical parameters such as the surface area (A), mean depth (D_{av}) or retention time (R), and lake trophic status parameters such as the Secchi depth (D_s), chlorophyll *a* (Chl), total nitrogen (N_T) and total phosphorus (P_T) concentrations in water. The seasonal factor (S) was incorporated as a nominal abiotic factor (filled square). Biotic explanatory variables (dotted lines): the total biomass (MB) and diversity (the first Hill's number; H) of benthic macroinvertebrates, as well as the biomass (AB) and relative abundance (AA) of alien peracaridan species in the littoral zone of a lake. The presence of alien amphipods (A_p) and abundance classes of alien crustaceans (A_c) were incorporated as nominal biotic factors (empty squares). Letter duplexes denote investigated lakes. Explanatory variables and the first two axes explain 75 % of the variation in the macroinvertebrate community-wide isotopic metrics data (Monte Carlo significance test of all canonical axes, 999 permutations using raw data, $F = 3.72$, $p = 0.001$).

Partial RDA results showed both abiotic and biotic explanatory variables were equally associated with variation in the macroinvertebrate community-wide metrics. Analysis showed abiotic and biotic factors explained 50 % and 52 % of the variation in

the benthic macroinvertebrate community-wide isotopic metrics data, respectively (Table 14).

Table 14. Results of RDA analysis for the benthic macroinvertebrate community-wide isotopic metrics data. Total variation is 1. Percentages are obtained by dividing the explained variance by total variance.

Explanatory variables	Explained variance	%
All variables	0.75	75
Abiotic	0.50	50
Biotic	0.52	52
Abiotic with biotic as covariable	0.23	23
Biotic with abiotic as covariable	0.25	25

The results of RDA analyses presented in table 14 let us to determine the pure effect of the used abiotic and biotic explanatory factors. Analysis showed that abiotic and biotic explanatory variables explained 23 % and 25 % of the pure (explained) variation in the benthic macroinvertebrate community-wide isotopic metrics data (Table 15).

Table 15. Variance decomposition table showing the effects of abiotic and biotic variables for the benthic macroinvertebrate community-wide isotopic metrics data.

Source	Variance	%
Pure abiotic	0.23	23
Pure biotic	0.25	25
Shared	0.27	27
Residual	0.25	25
Total		100

Performed multiple regression analyses showed that the presence and relative abundance of alien crustaceans were included in the best fit multiple regression models and significantly affected the isotopic niche metrics of the benthic macroinvertebrate communities in studied lakes, although the results were ambiguous (Table 16). On the one hand, isotopic niche metrics values were higher in lakes without alien amphipods. On the other hand, the isotopic metrics were positively correlated with the relative abundance of alien crustaceans in lakes where these crustaceans were present.

Table 16. Results of the best fitted multiple regressions of benthic macroinvertebrate community-wide isotopic metrics as dependent variables and abiotic or biotic explanatory variables in studied lakes. Regression coefficients of the intercept and explanatory variables: lake area (A), Secchi depth (D_S), total phosphorus (P_T), season factor (S), total biomass of benthic macroinvertebrates (MB), relative abundance of alien crustaceans (AA) and the presence of alien amphipods (A_p) in lakes littoral are given. Community-wide metrics (NR, CR, TA, CD, NND and SDNND) are explained in page 15. Significant ($p < 0.05$) regression coefficients are indicated by an asterisk.

Dependent variables	Explanatory variables							
	Intercept	A	D_S	P_T	S	AA	A_p	MB
NR	8.43	–	–	–0.83*	0.93*	–	–	0.49
CR	1.60	0.07*	0.47	–	–	0.23*	–2.59*	0.52
TA	0.45	–	2.89*	–	4.11	0.86*	–10.36*	3.49*
CD	0.90	0.007	0.11*	–	0.29*	0.04*	–0.39*	0.12
NND	0.44	0.003	0.08*	–	–	0.02*	–0.33*	–
SDNND	–0.15	0.005	0.13*	–	–0.11*	–	–	–

Overall, performed analyses showed the presence and relative abundance of alien crustaceans were associated with the variation in the benthic macroinvertebrate

community-wide isotopic metrics data and significantly correlated with the majority of calculated macroinvertebrate isotopic niche parameters in studied lakes.

b) Impact on fish communities. Performed redundancy analysis showed that all explanatory variables explained 79 % of the variation in the fish community-wide isotopic metrics data (Fig. 9).

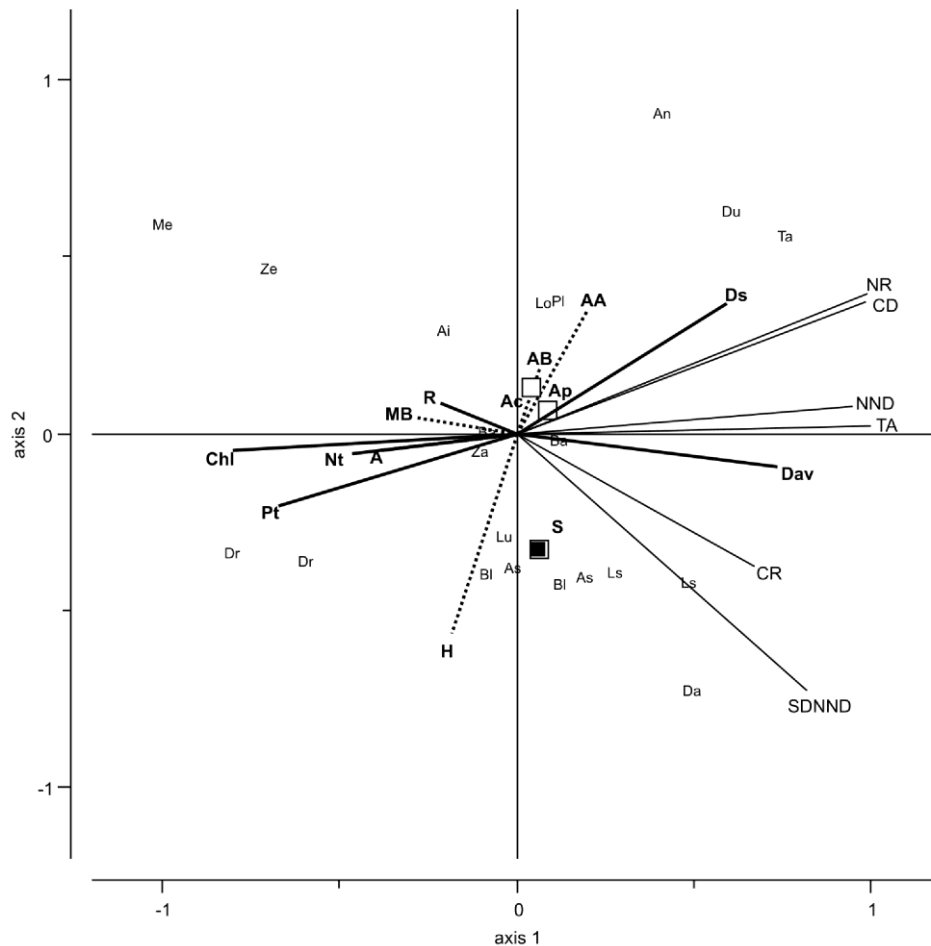


Figure 9. Redundancy analysis triplot for the fish community-wide isotopic metrics data. Square root transformation for AA, AB and MB parameters was applied. Response variables (grey lines): six community-wide isotopic metrics (CR, NR, TA, CD, NND, SDNND). Abiotic explanatory variables (bold lines): lake physical parameters such as the surface area (A), mean depth (D_{av}) or retention time (R), and lake trophic status parameters such as the Secchi depth (D_s), chlorophyll *a* (Chl), total nitrogen (N_T) and total phosphorus (P_T) concentrations in water. The seasonal factor (S) was incorporated as a nominal abiotic factor (filled square). Biotic explanatory variables (dotted lines): the total biomass (MB) and diversity (H) of benthic macroinvertebrates, as well as the biomass (AB) and relative abundance (AA) of alien peracaridan species in the littoral zone of a lake. The presence of alien amphipods (A_p) and abundance classes of alien crustaceans (A_c) were incorporated as nominal biotic factors (empty squares). Letters duplexes denote investigated lakes. Explanatory variables and the first two axes explain 79 % of the variation in the fish community-wide isotopic metrics data (Monte Carlo significance test of all canonical axes, 999 permutations using raw data, $F = 3.67$, $p = 0.20$).

Partial RDA results showed that variation in the fish community-wide metrics were more associated with abiotic explanatory factors than with biotic. Analysis showed abiotic and biotic factors explained 59 % and 39 % of the variation in the fish community-wide isotopic metrics data, respectively (Table 17).

Table 17. Results of RDA analysis for the fish community-wide isotopic metrics data. Total variation is 1. Percentages are obtained by dividing the explained variance by total variance.

Explanatory variables	Explained variance	%
All variables	0.79	79
Abiotic	0.59	59
Biotic	0.39	39
Abiotic with biotic as covariable	0.41	41
Biotic with abiotic as covariable	0.20	20

The results of RDA analyses presented in table 17 let us to determine the pure effect of the used explanatory abiotic and biotic factors. Analysis showed that abiotic explanatory variables explained 41 % of the pure (explained) variation in the fish community-wide isotopic metrics data; while biotic factors together explained only 20 % of the pure (explained) variation (table 18).

Table 18. Variance decomposition table showing the effects of abiotic and biotic variables for the benthic macroinvertebrate community-wide isotopic metrics data.

Source	Variance	%
Pure abiotic	0.41	41
Pure biotic	0.20	20
Shared	0.18	18
Residual	0.21	21
Total		100

Performed multiple regression showed there were no correlations between calculated fish community-wide metrics and alien crustacean parameters in studied lakes. Calculated fish community metrics were more related to abiotic than to biotic parameters of lakes (Table 19).

Table 19. Results of multiple regressions of fish community-wide isotopic metrics as dependent variables and abiotic and biotic explanatory variables in studied lakes. Regression coefficients of the intercept and explanatory variables: lake area (A), mean depth (D_{AV}), chlorophyll *a* (Chl) and total phosphorus (P_T), total biomass (MB) and diversity (H) of benthic macroinvertebrates in lake littoral zone. Community-wide metrics (NR, CR, TA, CD, NND and SDNND) are explained in page 15. Significant ($p < 0.05$) regression coefficients are indicated by an asterisk.

Dependent variables	Explanatory variables						
	Inter	D_{AV}	A	Chl	P_T	H	MB
NR	9,34	0,13*	–	–	–0,44*	–1,30*	–
CR	6,09	–	–	–0,21*	–	–	–
TA	16,17	–	–0,10	–1,07*	–	–	–
CD	3,15	0,04*	0,01	–	–0,24*	–0,35	–
NND	1,29	–	–	–0,03*	–0,0003*	–	–
SDNND	–0,54	0,05*	0,004	–	–	0,33*	–0,07

c) Conclusions. The results showed that alien crustacean species indeed influenced the isotopic niche of benthic macroinvertebrate assemblage in lakes. However, the isotopic niche of fish community was not influenced by these crustaceans. In general, food webs of these lakes were rich enough in members not to have substantial changes in the trophic niche of fish community after a few alien crustacean species appearance. The trophic niche structure of fish community was more dependent on abiotic factors such as size and average depth or trophic status of a lake.

CONCLUSIONS

1. Abundant populations of alien peracaridans composed a significant share of juvenile perch diet; however, there was no increase of perch growth in lakes inhabited by alien peracaridans.
2. There was no increase of the total littoral fish catch per unit effort in lakes inhabited by alien peracaridan species compare to the lakes without alien crustacean species.
3. There were seasonal significant differences in measured $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ values of most investigated macroinvertebrates genus and fish species in studied lakes.
4. Alien mysids (*P. lacustris* and *L. benedeni*) are omnivorous crustaceans in lakes littoral. Depending on the season, they may occupy the second or the third trophic level in lake food chains. In spring they are secondary consumers and rely more on pelagic organic source, while in autumn they are primary consumers and rely more on littoral organic sources.
5. Trophic positions occupied by alien (*L. benedeni* and *P. lacustris*) mysids were not similar to that occupied by native *M. relicta* mysid in both spring and autumn seasons, suggesting they explore different food source in a lake food web.
6. Alien amphipods (*C. warpachowskyi*, *O. crassus* and *P. robustoides*) are the primary consumers and rely on the littoral organic source in lakes food webs. There were no any significant seasonal changes in the trophic position occupied by these alien amphipods in the food webs of studied lakes.
7. Trophic position occupied by alien *P. robustoides* and *O. crassus* amphipods were not similar to that occupied by any of native peracaridan species in spring or autumn seasons. Meanwhile alien *C. warpachowskyi* and native *G. lacustris* amphipods occupied similar trophic position in studied lakes, suggesting these two amphipods species explore similar food source in lakes.
8. Alien crayfish *O. limosus* was a secondary consumer and relied on littoral organic source in lakes. There was no any significantly change in the trophic position occupied by *O. limosus* in a lake food web during the season.
9. The presence of alien crustaceans (*C. warpachowskyi*, *L. benedeni*, *O. crassus*, *O. limosus*, *P. lacustris* and *P. robustoides*) was significantly related to the isotopic niche structure of the benthic macroinvertebrate community in the lake littoral.
10. The presence of alien crustaceans (*C. warpachowskyi*, *L. benedeni*, *O. crassus*, *O. limosus*, *P. lacustris* and *P. robustoides*) was not significantly related to the isotopic niche structure of the fish community in the lake littoral.

LIST OF PUBLICATIONS

1. **Rakauskas, V.**, Ruginis, T., Arbačiauskas, K. **2010**. Expansion of the spiny cheek crayfish *Orconectes limosus* (Rafinesque, 1817) in the Nemunas River basin, Lithuania. *Freshwater crayfish* 17: 73–76.
2. Arbačiauskas K., **Rakauskas V.**, Virbickas T. **2010**. Initial and long-term consequences of attempts to improve fish-food resources in Lithuanian waters by introducing alien peracaridan species: a retrospective overview. *Journal of Applied Ichthyology* 26 (2): 28–37.
3. **Rakauskas V.**, Smilgevičienė S., Arbačiauskas K. **2010**. The impact of introduced Ponto-Caspian amphipods and mysids on perch (*Perca fluviatilis*) diet in Lithuanian lakes. *Acta Zoologica Lituanica* 20 (4): 189–197.
4. Arbačiauskas K., Višinskienė G., Smilgevičienė S., **Rakauskas V.** **2012**. Non-indigenous macroinvertebrate species in Lithuanian fresh waters, Part 1: Distributions, dispersal and future. *Knowledge and Management of Aquatic Ecosystems* 402 (12): 1–18.

CONFERENCE PRESENTATIONS

1. **Rakauskas V.**, Arbačiauskas K. **2010**. Can introduced Ponto-Caspian mysid *Paramysis lacustris* alter the littoral food web in lakes? 5-th International Student Conference “Biodiversity and Functioning of aquatic ecosystems in the Baltic Sea region”. Conference proceedings, 06–08 October, Palanga, Lithuania: 71–72.
2. Arbačiauskas K., **Rakauskas V.**, **2010**. Crayfish in Lithuanian waters: current states and perspectives. “European Crayfish Food, Flagships and Ecosystem Services”. 26–29 October, Poitiers, France: 50.
3. **Rakauskas V.**, Arbačiauskas K., **2013**. Trophic role of non-indigenous amphipod species in temperate lakes, Lithuania. 15th International Colloquium on Amphipoda. Book of abstracts, 2–7 September, Szczawnica, Poland: 80.

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REZIUMĖ

Jau Elton'as (1958) teigė, kad svetimkraštės rūšys, net ir esant negausioms jų populiacijoms, veikia vietinių bendrijų stabilumą. Šiuo metu nėra abejonės, kad viena pagrindinių priežasčių lemiančių bioįvairovės nykimą yra spartus invazinių rūšių plitimas (Gherardi, 2007). Invazinės rūšys ne tik reikšmingai mažina vietinių rūšių įvairovę, stipriai keičia vietinių bendrijų mitybos tinklų struktūrą bei funkcionavimą bet taip pat gali sukelti didelių ekonominių nuostolių (Anonimas, 2005). Dėl šių priežasčių, svetimkraščių rūšių invazijos yra tarptautinė problema, o šalių atsakingosios institucijos stengiasi užkirsti kelią nepageidaujamų organizmų plitimui bei kontroliuoti ir mažinti jų neigiamą poveikį (Genovesi ir Shine, 2004). Tačiau nepaisant minėtų pastangų svetimkraščių rūšių invazijos bei jų poveikis vis dar sunkiai prognozuojamas bei kontroliuojamas (Gherardi, 2007; Genovesi, 2007).

Lietuvos ežeruose svetimkraštės rūšys sudaro daugiau kaip pusę aukštesniųjų vėžiagyvių faunos (Arbačiauskas ir kt., 2012). Dauguma jų buvo tikslingai introdukuotos į Lietuvos ežerus siekiant padidinti žuvų produkciją ar atkurti sunykusias vėžių populiacijas (Arbačiauskas ir kt., 2012). Buvo tikimasi, kad svetimkraščiai vėžiagyviai sukurs gausias populiacijas ežerų litoralėse bei taps vertingu bei lengvai prieinamu žuvų maistu. Taip pat buvo tikimasi, kad svetimkraščiai vėžiagyviai padidins pirminės produkcijos įsisavinimą bei sutrumpins mitybos grandines ežerų litoralėse. Tuo būdu pagerės žuvų mityba, pagreitės jų augimas bei išaugs jų produkcija ežeruose (Гасюнас, 1963). Nors nuo pirmųjų tikslingų svetimkraščių vėžiagyvių introdukcijų jau praėjo daugiau kaip 40 metų iki šiol yra labai mažai žinoma apie svetimkraščių vėžiagyvių įtaką Lietuvos ežerų ekosistemoms. Iki šiol nėra vieningos nuomonės, kokią vietą ežerų mitybos tinkluose užima svetimkraščiai vėžiagyviai. Iki šiol galutinai nėra aišku, ar žuvys išties selektyviai maitinasi svetimkraštėmis vėžiagyvių rūšimis ežeruose? Ar dėl naujų vėžiagyvių rūšių atsiradimo gali reikšmingai pasikeisti žuvų mitybos racionas? Nors šiuo metu nėra abejonės, kad aukštesnieji svetimkraščiai vėžiagyviai įtakoja tiek žemesnius, tiek ir aukštesnius mitybinės grandinės lygmenis ežeruose bei daro stiprią įtaką visam ežero mitybos tinklui, iki šiol nėra atlikta jokių kiekybinių tyrimų, kurie įvertintų svetimkraščių vėžiagyvių įtaką ežerų mitybos tinklams. Į visus šiuos klausimus ir buvo bandyta atsakyti šio darbo metu.

Atlikti tyrimai nepatvirtino pirminės vėžiagyvių introdukcijos hipotezės. Darbo metu nebuvo rasta jokių faktų patvirtinančių, kad žuvys geriau auga svetimkraščiais vėžiagyviais praturtintuose ežeruose. Atlikta ešerio jauniklių, kaip modelinės žuvies, mitybos analizė parodė, kad nors ir svetimkraščių šoniplaukų bei mizidžių buvimas ežere reikšmingai pakeičia ešerio mitybą, tačiau ryškių ešerių mitybinės nišos skirtumų tarp svetimkraščiais vėžiagyviais praturtintų ežerų ir ežerų be jų nėra. Atlikta ešerių jauniklių augimo analizė taip pat nerodė jokių reikšmingų ešerių augimo skirtumų ežeruose, praturtintuose svetimkraštėmis rūšimis lyginant su kitais, svetimkraščių rūšių neapgyvendintais ežerais. Galiausiai žuvų sugavimai ežerų priekrantėse taip pat nebuvo reikšmingai didesni ežeruose su svetimkraštėmis vėžiagyvių populiacijomis lyginant su ežerais nepraturtintais svetimkraštėmis vėžiagyvių rūšimis.

Šio darbo metu taip pat buvo įvertinta svetimkraščių vėžiagyvių vieta ežerų mitybos tinkluose. Rezultatai parodė, kad daugelis svetimkraščių vėžiagyvių rūšių priklausė litoralės mitybinėms grandinėms. Kaip ir buvo galima tikėtis, aukščiausiai mitybinėse grandinėse stovėjo invaziniai vėžiai, kurie tirtuose ežeruose buvo priskirti

antriniams vartotojams. Tuo tarpu svetimkraštės šoniplaukos pagal savo užimamą padėtį mitybos tinkluose buvo priskirtos pirminiams vartotojams. Svetimkraščių mizidžių vieta mitybos tinkle sezono eigoje reikšmingai keitėsi, pavasario sezono jos buvo plėšresnės lyginant su rudens sezonu.

Šio darbo metu taip pat buvo nustatyta ar svetimkraščių vėžiagyvių buvimas ežere įtakoja ežero makrobentosinių bestuburių bei žuvų bendrijų mitybinio tinklo parametrų vertes ežeruose. Gauti rezultatai parodė, kad svetimkraščiai vėžiagyviai patikimai įtakoja tik makrobentosinių bestuburių bendrijų izotopinių nišų parametrus, tuo tarpu žuvų bendrijų mitybinio tinklo struktūros naujos vėžiagyvių rūšys ežeruose reikšmingai neįtakoja.

Šis darbas įvertino šiuo metu Lietuvos ežeruose gyvenančių svetimkraščių vėžiagyvių įtaką ežerų mitybos tinklams. Šio darbo metu buvo išstobulintas stabiliųjų izotopų metodas tiriant svetimkraščių hidrobiontų poveikį bendrijų mitybos tinklams ežeruose. Surinkti gausūs Lietuvos mezotrofinių ežerų mitybos tinklų duomenys ateityje leis tiksliau prognozuoti būsimų invazinių hidrobiontų poveikį ežerų mitybos tinklams bei vertinti įvairius mitybos tinklo pokyčius ežeruose.