

**CAN THE INVASIVE NEW ZEALAND MUD SNAIL (*POTAMOPYRGUS ANTIPODARUM*)
THREATEN FISHERIES OF TEMPERATE LAKES? A CASE STUDY
FROM LAKE DUSIA, LITHUANIA**

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Background. To date, numerous studies of the impact of snail *Potamopyrgus antipodarum* (Gray, 1843) on invaded ecosystems have been conducted. However, the majority of such studies intended to assess changes induced in macroinvertebrate assemblages, while the possible effects of *P. antipodarum* on higher trophic levels have not hitherto been studied. Of particular interest from the point of view of fisheries management is the elucidation of how this invasive snail can alter the energy flow towards higher trophic levels. When abundant, *P. antipodarum* consumes a substantial part of the primary production, but it is poorly consumed by native fishes. Consequently, part of its assimilated energy may become locked in lower trophic levels and fail to reach higher levels directly. Therefore, invasion of this snail may decrease fish production.

Materials and methods. Several years after establishment of *P. antipodarum* in a temperate mesotrophic Lake Dusia, we assessed: (1) changes in the biomass of littoral macroinvertebrates (proxy to secondary production), (2) assimilation of *P. antipodarum* by benthivorous fish (energy flow), and (3) changes in growth and catches of littoral benthivorous fish (fish production). All the analyses were based on a merger of “grey” literature and original data during the pre- and post-invasion periods.

Results. There was an evident increase in the biomass of littoral macroinvertebrates, and the assemblage changed from crustacean- to gastropod-dominated due to over-domination of *P. antipodarum*. However, *P. antipodarum* did not replace the native prey of fish. Moreover, a marked decrease was recorded in littoral fish growth and catches after the invasion of *P. antipodarum*.

Conclusion. Dense populations of *P. antipodarum* may reduce the channelling of primary production towards higher trophic levels and, consequently, the invasion may threaten fisheries of temperate mesotrophic lakes.

Keywords: Aquatic invasion, secondary production, fish diet, fish production, food webs.

INTRODUCTION

The New Zealand mud snail, *Potamopyrgus antipodarum* (Gray, 1843) (Mollusca: Tateidae) is one of the most widespread invasive species in the world. The snail is native to New Zealand and its adjacent islands (Winterbourn 1970) and exhibits all properties of an invasive species (Alonso and Castro-Díez 2008). Firstly, it is established in a wide variety of freshwater and estuarine habitats on all the continents except for Africa and Antarctica (Ponder 1988, Grigorovich et al. 2003, Collado 2014). Secondly, in invaded ranges, *P. antipodarum* reproduces parthenogenetically (Dybdahl and Drown 2011, Hamada et al. 2013). Thirdly, due to its hard shell, small size, and low nutritional value the species is avoided by the majority of native predators (Bersine et al. 2008, Brenneis et al. 2011, Rakauskas et al. 2013, 2016). Furthermore, if preyed upon by fish, some individuals of

P. antipodarum are able to survive the digesting process and fully recover after evacuation (Vinson and Baker 2008, Brenneis et al. 2011, Rakauskas et al. 2016). Up until now, only the tidewater goby, *Eucyclogobius newberryi* (Girard, 1856), were documented to prey upon and fully digest it under natural conditions (Hellmair et al. 2011). Overall, *P. antipodarum* usually reaches enormously high densities in invaded range (up to 800 000 ind. per m⁻²) causing drastic changes both at community and ecosystem levels (Hall et al. 2003, Kerans et al. 2005, Bennet et al. 2015).

Although present in Europe for more than 100 years (Nikolaev 1951), *P. antipodarum* is still undergoing its expansion further into the temperate freshwater ecosystems of the continent (Filippenko and Son 2008, Radea et al. 2008, Son 2008). For many years after its first record in Lithuania in 1954 (Gasūnas 1959), it was restricted

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only to the brackish waters of the Curonian Lagoon and the Baltic Sea coast (Šivickis 1960, Zettler and Daunys 2007). However, a rapid invasion into Lithuanian inland lakes and rivers has been observed since 2010 (Butkus et al. 2012, 2014).

Due to the high density of *P. antipodarum* during the initial invasion phase of population explosion, the most severe impact is suffered by recently invaded ecosystems (Hall et al. 2003, Kerans et al. 2005, Moore et al. 2012). Thus, studies of such ecosystems may reveal not only effects on invaded macroinvertebrate assemblages but also impacts on fish stocks. To date, numerous studies of the impact of *P. antipodarum* on invaded ecosystems have been conducted (e.g., Kerans et al. 2010, Moore et al. 2012, Bennett et al. 2015). However, the majority of such studies intended to assess changes induced in macroinvertebrate assemblages (e.g., Riley et al. 2008, Kerans et al. 2010, Rakauskas et al. 2018). If broader-scale impacts were studied, these studies were performed mostly in estuarine or riverine ecosystems (e.g., Brenneis et al. 2011, Moore et al. 2012, Bennett et al. 2015). Meanwhile, effects of *P. antipodarum* on higher trophic levels, especially in lakes, have not been studied so far. Understanding the propagation of *P. antipodarum* invasion impacts on higher trophic levels could help to predict the effects on ecosystems more accurately and develop more effective strategies for fisheries management and environmental protection.

This paper addresses the potential impacts of *P. antipodarum* on the fisheries in a temperate mesotrophic lake. A conjunction of the facts that (1) *P. antipodarum* may become abundant, (2) it consumes a substantial portion of lake primary production, and (3) it is not proportionally targeted by native predators, raises a legitimate concern that it may reduce the direct energy flow to higher trophic levels, leaving part of the primary production blocked from ascending further up the trophic chain (Rakauskas et al. 2016, 2018).

In the presently reported study, the recently invaded temperate mesotrophic lake, Dusia, Lithuania, became a model system for studying the impact of *P. antipodarum* on the natural environment. This is primarily due to a very rapid, strong, and rather well documented invasion of this snail (Butkus et al. 2012, 2014, Rakauskas et al. 2018). Secondly, the lake has been monitored by our research team for quite some time before the invasion, which allowed us to obtain the baseline macroinvertebrate and fish data. Lastly, frequent monitoring of water trophic parameters* and commercial fish catches** in this lake of high national importance allowed us to control for changes in important factors that could interfere with the outcomes of our study. While mesocosm experiments allow for better-controlled hypothesis testing, they are frequently disputed as unrealistic simplifications with limited relevance to natural ecosystems, especially when assessing broader-scale impacts (Carpenter 1996, Schindler 1998, Haag and Matschonat 2001).

To assess how *P. antipodarum* affects lake's secondary production we compared the biomass of littoral macroinvertebrates between the pre- and post-invasion periods. Seasonal diet analysis of benthivorous fish was performed to evaluate *P. antipodarum* integration into higher trophic levels. To determine its current effects on higher trophic levels, we also compared relevant fish community aspects between the pre- and post-invasion periods.

MATERIALS AND METHODS

Study site. Lake Dusia (54°17'N 23°41'E, South Lithuania, Baltic Sea drainage) is a post-glacial freshwater lake. It is a relatively large (23.3 km²), medium deep (mean and max. depths: 15.4 and 32.4 m, respectively) lake with annual water turnover of only 6% (Kilkus 1998). The lake has a wide sandy littoral, stretching 100–350 m offshore and covering 12% of the lake area. The hypolimnion starts at a depth of 12–16 m (Kilkus 1998). According to the prevailing indicator fish species, Lake Dusia should be considered a smelt lake (Virbickas 1988, Virbickas et al. 1996). The fish community is primarily composed of cold-water fish characteristic of ecosystems at early succession stages, i.e., *Osmerus eperlanus* (Linnaeus, 1758) and *Coregonus albula* (Linnaeus, 1758). In addition to these dominant species, the lake is inhabited by fishes of other ecological groups, i.e., *Perca fluviatilis* Linnaeus, 1758, *Gymnocephalus cernua* (Linnaeus, 1758), and *Rutilus rutilus* (Linnaeus, 1758) (see Virbickas 2013, Pilinkovskij et al. 2014).

The littoral macroinvertebrate assemblage of Lake Dusia had been enriched in the past with several Ponto-Caspian species. The zebra mussel *Dreissena polymorpha* (Pallas, 1771) is a historical invader with published records in the lake predating 1940s (Schlesch and Krausp 1938, Arbačiauskas et al. 2011). Later in the 1960s, amphipods: *Chaetogammarus warpachowskyi* Sars, 1897, *Obesogammarus crassus* (Sars, 1894), *Pontogammarus robustoides* (Sars, 1894) and mysid *Paramysis lacustris* (Czerniavsky, 1882) were introduced (Arbačiauskas et al. 2011). Due to particularly suitable conditions in this lake, it only took three years for these crustaceans to fully establish (Gasūnas 1970, 1975, Arbačiauskas 2005). Since then, these populations of Ponto-Caspian species are known to remain stable (Gasūnas 1975, Arbačiauskas 2002, Gumuliauskaitė unpublished***), serving as valuable prey for native fish (Gasūnas 1972, Arbačiauskas et al. 2010, Rakauskas et al. 2010). Several decades from these swift introductions until the invasion of *P. antipodarum* must have been sufficient for the ecosystem to reach an equilibrium state. Therefore, it is highly unlikely that these fully integrated Ponto-Caspian species could somehow interfere with the current study, and thus within this paper, they are treated as native.

During repeated macroinvertebrate surveys within 2003–2006 *P. antipodarum* was not detected in Lake Dusia (Gumuliauskaitė unpublished***), but when the

* Data on water trophic parameters in Lake Dusia during 2001–2016 kindly provided by the Ministry of Environment of the Republic of Lithuania.

** Data on commercial catches in Lake Dusia during 2001–2015 kindly provided by the Ministry of Environment of the Republic of Lithuania.

*** Gumuliauskaitė S. 2007. Ponto-Kaspijos šoniplaukos *Pontogammarus robustoides* gyvenimo ciklas ir poveikiai Lietuvos gelū vandenu bendrijoms. [Life cycle and impacts of Ponto-Caspian amphipods on the Lithuanian freshwater ecosystems]. Ph.D. thesis, Vilnius University, Vilnius, Lithuania. [In Lithuanian.]

surveys were renewed in 2010, the snail was already found to constitute over 30% of macroinvertebrate abundance and biomass (Butkus et al. 2012, Rakauskas et al. 2016, 2018). These findings indicated that *P. antipodarum* invaded the lake between 2007 and 2009, thus this period was excluded from our study. For the last three years (2014–2016), *P. antipodarum* remained a super-dominant macroinvertebrate species, with both abundance and biomass exceeding 70% and still showing a slight increase (Rakauskas et al. 2018).

Macroinvertebrate data. The pre-invasion macroinvertebrate assemblage could be well represented by data available from repeated surveys performed during 2003–2006 (Gumuliauskaitė unpublished*). We collected the post-invasion macroinvertebrate samples in 2014–2016 and supplemented them with available data from 2010 (Šidagytė, unpublished data), when *P. antipodarum* was also already established (Butkus et al. 2012). The macroinvertebrate data from 2011–2013 were not available.

For the pre- and post-invasion periods, the same lake site with sandy bottom and some macrophytes (*Potamogeton* sp., *Phragmites australis*) was sampled once per year, between late August and September. On each sampling occasion, three random replicates of quantitative macroinvertebrate samples were collected at a depth of 0.5–1.0 m using a custom-made “stovepipe” sampler with a cross-section area of 0.1 m². Preserved in 70% ethanol in the field, in the laboratory the samples were examined for macroinvertebrates that were sorted by family, and then counted and weighed (wet weight) to the nearest 0.1 mg (electronic balance, ABJ 120-4M, Kern and Sohn GmbH).

Seasonal diet of benthivorous fish. The diet was analysed using fish caught in spring, summer, and autumn of 2015 and 2016 (post-invasion period). Each season we analysed up to 70 fish individuals representing each of five fish species: *Perca fluviatilis*, *Rutilus rutilus*, *Gymnocephalus cernua*, *Tinca tinca* (Linnaeus, 1758), and *Abramis brama* (Linnaeus, 1758). In total, gut contents of 309 specimens were examined (fish with empty stomachs were excluded). As *P. fluviatilis* undergoes ontogenetic diet shifts (Hjelm et al. 2000, Horppila et al. 2000, Svanbäck and Eklöv 2002), the specimens were subdivided into two length groups: small (11–15 cm) and medium (17–21 cm).

After euthanizing the fish by immersing them into 1.5–2.0 mL·L⁻¹ solution of 2-phenoxyethanol for 5 min), their digestive tracts were immediately removed and preserved in 10% formaldehyde solution until the necropsy in the laboratory. Gut contents (found in the stomachs or the predetermined fore-/mid-gut sections of the stomach-less fish) were dissected out, and food items were identified, grouped, and weighed (wet-weight) to the nearest 0.1 mg (electronic balance, ABJ 120-4M, Kern and Sohn GmbH). Digested and thus unidentifiable particles were classified as ‘miscellaneous stomach content’, and their weight was proportionally distributed among identified food items.

Growth and standardised catches of littoral fish. Littoral fish were sampled from early July to late

September during the pre- (2001–2006) and post-invasion (2010, 2012–2015) periods. No fish data were available from 2011. At a depth of 2.0–5.0 m, fish were caught using multi-mesh benthic gillnets (30 to 60 m in length and 3 m in height). The mesh size varied and was 14, 18, 22, 25, 30, 40, 50, 60, and 70 mm. On each sampling occasion, net sets of length from 320 to 1840 m were used. Nets were positioned randomly to cover different parts and depths of the littoral zone, and left for at least 12 h overnight including the sunset and the sunrise.

In total, 9409 fish specimens were identified, measured to the nearest 1 mm, weighed to the nearest 0.1 g, and their age was determined from scales (Thoresson 1993) for growth assessment. As catches of other fish species were extremely sporadic (see Results), the growth of only *P. fluviatilis* (small – up to age 6+, 369 specimens in total) and *R. rutilus* (339 specimens) was assessed. Catch per unit effort (CPUE) of all fishes was estimated as biomass or a number of individuals (abundance) caught using a standard 30-m long gillnet in one night. If there were multiple sampling occasions per year, the estimates were based on the mean value.

Trophic state and commercial fishing data. Changes in productivity or commercial fishing may substantially affect standardised fish catches and growth (Virbickas and Stakėnas 2016), masking the effects of invasions. Thus, to legitimise the intended analysis of *P. antipodarum* invasion effects on fisheries of Lake Dusia, we also assessed changes in trophic state and commercial catches of littoral fish. To assess the trend in the trophic state, annual mean values of physicochemical parameters, such as Secchi depth, total N, total P, and chlorophyll *a* concentrations, were obtained for the period of 2001–2016*. The data for comparing the commercial fish catches were obtained for the pre- (2001–2006) and post-invasion (2010–2015) periods**. No commercial fishing occurred in 2016, as it was forbidden in all state inland waters since that year (Anonymous 2016).

Statistical analyses. To assess the impact of *P. antipodarum* invasion on total, native (excluding *P. antipodarum*) and relative macroinvertebrate biomasses, nested ANOVAs were fitted with the year factor nested within the invasion period factor (pre- vs. post-). These were followed by Fisher LSD post-hoc tests in cases of total and native biomasses to identify significant pairwise differences between years.

To test the *P. antipodarum* invasion effect (pre- vs. post-) on the growth of *R. rutilus* and *P. fluviatilis*, homogeneity of slopes (HOS) models were fitted to individual fish weights using fish age as a covariate. To assess the invasion impact on fish CPUEs (total catches and those of separate species) in terms of abundance and biomass, *t*-tests (pre- vs. post-) were used.

Temporal trends in lake trophic state were evaluated using Pearson’s correlations between each available physico-chemical parameter and the year variable.

* See the respective footnote on page 38.

** See the respective footnote on page 38.

Commercial fish catches before and after the invasion were compared using a *t*-test.

For the analyses, commercial fish catches, macroinvertebrate biomasses (total, excluding *P. antipodarum*, and relative), individual weights of *R. rutilus* and *P. fluviatilis*, as well as CPUEs of separate fish in terms of abundance and biomass were log-transformed. Such transformation ensured that model assumptions of data homoscedasticity and normality were met in all analyses. The homoscedasticity assumption was tested using Bartlett tests ($P > 0.093$) and the normality of model residuals was tested using Shapiro–Wilk tests ($P > 0.077$). The analyses were performed using STATISTICA 12.0 software. The significance level of $P < 0.05$ was specified for all statistical analyses a priori.

RESULTS

A shift in macroinvertebrate assemblage. Since its initial detection in 2010, the biomass of *P. antipodarum* in the littoral zone of Lake Dusia has been constantly increasing

(Fig. 1). Although total biomass of macroinvertebrates varied substantially between years (nested ANOVA, year effect: $F_{6,16} = 10.1$, $P < 0.001$; Fig. 1A), it was generally significantly larger during the post-invasion period (invasion effect: $F_{1,16} = 8.7$, $P = 0.010$; Fig. 1B). The between-year variation was also significant in case of native (excluding *P. antipodarum*) macroinvertebrate biomass (nested ANOVA, year effect: $F_{6,16} = 6.9$, $P < 0.001$; Fig. 1C). However, there was a significant decrease in it after the invasion (invasion effect: $F_{1,16} = 6.3$, $P = 0.024$; Fig. 1D).

Overall, the littoral macroinvertebrate community of Lake Dusia changed from being dominated by crustaceans to one dominated by gastropod molluscs, predominantly *P. antipodarum* (Fig. 2). After the invasion, the relative crustacean biomass significantly decreased from 46.8 ± 29.8 to $11.3 \pm 12.1\%$ (nested ANOVA, invasion effect: $F_{1,16} = 23.2$, $P < 0.001$). Conversely, the relative biomass of gastropods increased from 24.5 ± 25.7 to $75.7 \pm 20.6\%$ (nested ANOVA, invasion effect: $F_{1,16} = 28.9$, $P < 0.001$).

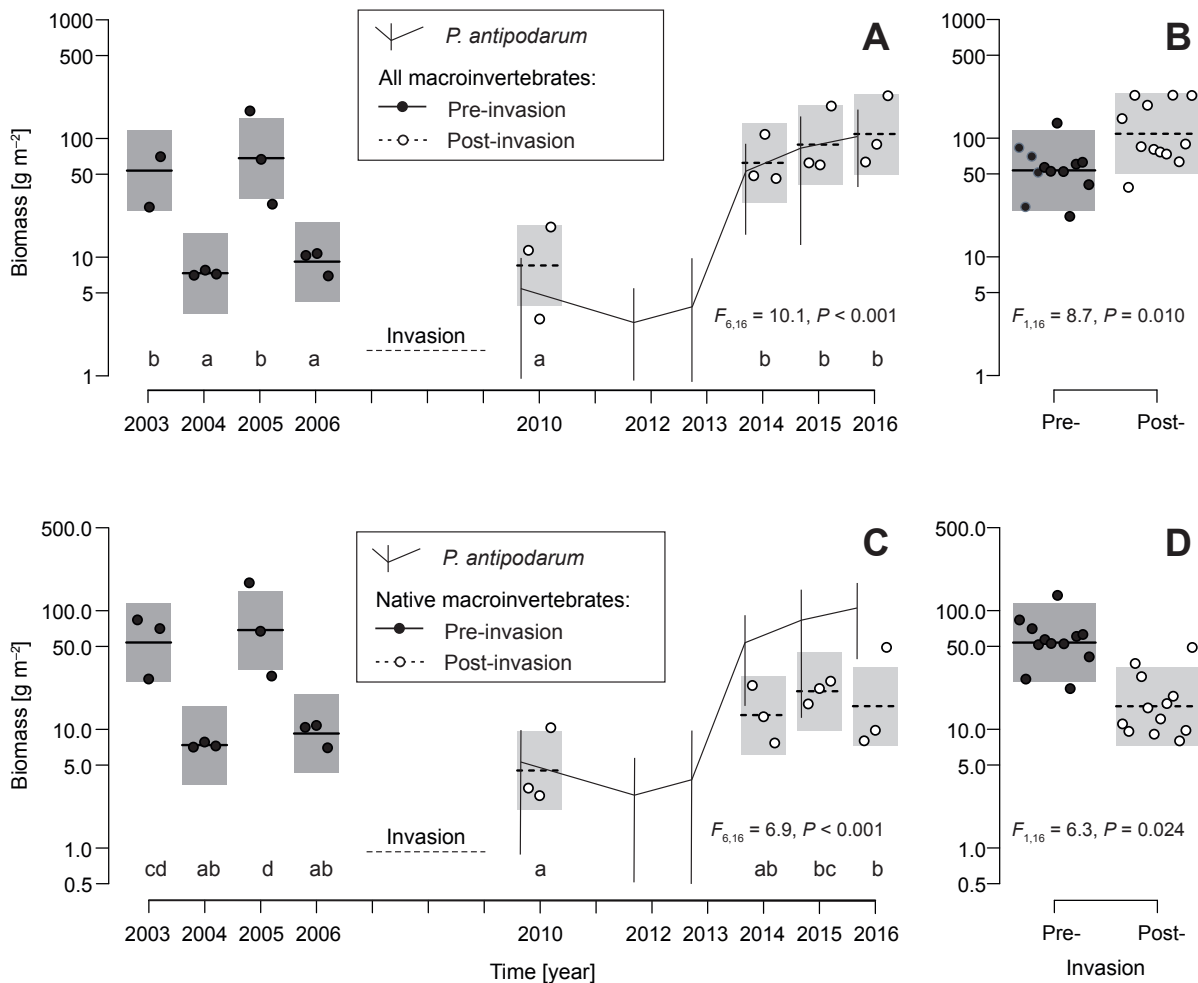


Fig. 1. Effects of between-year variation and *Potamopyrgus antipodarum* invasion on total (A, B) and native (excl. *P. antipodarum*; C, D) biomasses of littoral macroinvertebrates in Lake Dusia: predictions (with 95% confidence bands and partial residuals) made from nested ANOVAs; periods: before (Pre-) and after (Post-) the invasion; biomass (mean \pm SD) of *P. antipodarum* in the Lake Dusia littoral denoted by solid line; note the logarithmic scale of vertical axes; small letters (a, b, c, d) denote homogeneous year groups according to Fisher LSD tests

Seasonal fish diet. The analysis of fish diet during the post-invasion period (Fig. 3) showed that molluscs were the dominant prey item only in the diet of cyprinids (*T. tinca*, *A. brama*, and *R. rutilus*). The share of molluscs in the diet of these fish species varied from 40% to 95% with the exception of the spring and autumn diets of *A. brama*, which were dominated by insects. The share of molluscs in the diet of percids (*P. fluviatilis* and *G. cernua*) was generally negligible, but it was considerable (22%) within the autumn diet of *G. cernua*. However, bivalves (*Dreissena polymorpha*, *Pisidium* sp. and *Sphaerium* sp.) and native gastropods (*Bithynia* sp.) were the dominant molluscan prey, while the share of *P. antipodarum* in the diet of the studied fish species did not exceed 6% throughout all the seasons (Table 1).

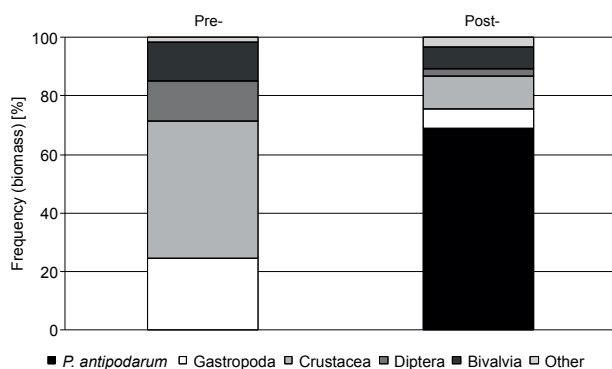


Fig. 2. Mean relative biomasses of littoral macroinvertebrate groups in Lake Dusia before (Pre-; 2003–2006) and after (Post-; 2010, 2014–2016) invasion of *Potamopyrgus antipodarum*

Changes in fish growth and CPUE. The comparison of *P. fluviatilis* and *R. rutilus* growth revealed marked differences between the pre- and post-invasion periods (Table 2). After *P. antipodarum* invasion, the growth of *R. rutilus* significantly decreased (HOS model, age \times invasion effect: $F_{1,335} = 9.6$, $P = 0.002$; Fig. 4A). The interaction term in the *P. fluviatilis* model was insignificant (HOS model, age \times invasion effect: $F_{1,365} = 0.4$, $P = 0.5$), but there was an overall significant decrease in size of small benthivorous *P. fluviatilis* during the post-invasion period (invasion effect: $F_{1,365} = 10.3$, $P = 0.001$; Fig. 4B).

After the invasion of *P. antipodarum*, CPUEs of littoral fishes, in terms of total biomass and abundance, significantly decreased (t -tests: $t_9 = 2.5$, $P = 0.031$ and $t_9 = 3.1$, $P = 0.012$, respectively; Fig. 5). However, when data for separate species (Table 3), such as *A. brama*, *P. fluviatilis*, *R. rutilus*, and *T. tinca*, were compared, no significant differences were revealed either in terms of biomass or abundance (t -tests: $P > 0.46$ and $P > 0.38$, respectively). Only CPUEs of *G. cernua* significantly decreased after the invasion (t -tests: for biomass, $t_9 = 7.2$, $P < 0.001$; for abundance, $t_9 = 4.6$, $P = 0.001$).

Trophic state and commercial fish catches. According to physicochemical parameters, Lake Dusia could be classified as mesotrophic with tendencies towards a eutrophic state. The ranges of the annual mean values of Secchi depth, total N, total P, and chlorophyll *a* concentrations were as follows: 2.9–7.0 m, 450–1146 $\mu\text{g} \cdot \text{L}^{-1}$, 20–54 $\mu\text{g} \cdot \text{L}^{-1}$, and 2.63–10.34 $\mu\text{g} \cdot \text{L}^{-1}$, respectively. No significant temporal trends in any of these parameters could be identified (Pearson's correlations: $r < 0.5$, $P > 0.21$). The pre- and post-invasion periods did not

Table 1

Seasonal prevalence of snail, *Potamopyrgus antipodarum*, in the diet of fish in Lake Dusia, Lithuania, within 2015–2016

Fish species	Season	<i>n</i>	TL [cm]	PR [%]	<i>I</i> [ind.]	<i>S</i> [%]
<i>Abramis brama</i>	SPR	2	53.2 \pm 13.4	50.0	9.0 \pm 0	1.0
<i>Gymnocephalus cernua</i>	SPR	42	13.5 \pm 2.9	23.8	4.1 \pm 8.8	4.2
<i>Perca fluviatilis</i> M	SPR	17	18.3 \pm 1.6	52.9	2.2 \pm 2.0	3.4
<i>Perca fluviatilis</i> S	SPR	12	14.8 \pm 0.6	41.7	1.0 \pm 0	3.0
<i>Rutilus rutilus</i>	SPR	8	22.5 \pm 6.4	25.0	2.0 \pm 1.4	1.6
<i>Abramis brama</i>	SUM	4	31.4 \pm 6.3	50.0	15.5 \pm 17.7	4.8
<i>Gymnocephalus cernua</i>	SUM	10	10.9 \pm 1.9	10.0	3.0 \pm 0	1.1
<i>Perca fluviatilis</i> M	SUM	4	17.3 \pm 0.5	25.0	6.0 \pm 0	2.5
<i>Perca fluviatilis</i> S	SUM	10	12.1 \pm 1.9	30.0	1.3 \pm 0.6	2.9
<i>Rutilus rutilus</i>	SUM	34	19.7 \pm 3.6	32.4	13.8 \pm 14.6	6.0
<i>Tinca tinca</i>	SUM	1	34.5	0	0	0
<i>Abramis brama</i>	AUT	12	34.7 \pm 3.5	41.7	3.6 \pm 2.4	0.2
<i>Gymnocephalus cernua</i>	AUT	43	12.3 \pm 1.7	20.9	2.6 \pm 2.4	3.9
<i>Perca fluviatilis</i> M	AUT	10	17.9 \pm 2.1	0	0	0
<i>Perca fluviatilis</i> S	AUT	24	12.8 \pm 1.8	4.2	7.0 \pm 0	0.05
<i>Rutilus rutilus</i>	AUT	70	21.1 \pm 5.4	28.6	10.6 \pm 18.3	4.4
<i>Tinca tinca</i>	AUT	6	26.8 \pm 6.8	60.0	0	0.3

n = number of fish specimens analysed, TL = total body length of fish (mean \pm standard deviation), PR = percentage of fish specimens that ingested *P. antipodarum*, *I* = number of ingested *P. antipodarum* individuals per fish specimen (mean \pm standard deviation), *S* = relative biomass (share) of *P. antipodarum* in fish diet; SPR = spring, SUM = summer, AUT = autumn; S = small, M = medium.

differ in commercially caught littoral fish biomass either (t -test: $t_9 = 1.2$, $P = 0.273$).

DISCUSSION

Impacts of invasive mollusc species on invaded ecosystems are usually major and cause significant shifts in diversity, abundance, and biomass of indigenous fauna (Nalepa 1994, Karatayev et al. 1997, Sampaio and Rodil 2014). Previous studies showed that *P. antipodarum*

frequently reaches enormously high densities in invaded ecosystems, causing changes in nitrogen and carbon cycling (Hall et al. 2003, Arango et al. 2009), consumption of primary production (Riley et al. 2008), and macroinvertebrate assemblages (Kerans et al. 2005, Moore et al. 2012). Furthermore, it has been shown that *P. antipodarum* may replace valuable food sources in the diet of benthivorous fish, and even reduce survivorship of fish that consume it (Vinson and Baker 2008). This study revealed changes in the ecosystem of Lake Dusia at several trophic levels, which coincided with the invasion of *P. antipodarum*. Firstly, the biomass and composition of littoral macroinvertebrate assemblage have changed. Moreover, a decrease in standardised littoral fish catches and growth rate of some benthivorous fish species was observed. These changes may be attributed to the negative *P. antipodarum* effects on the littoral macroinvertebrate community as trophic state and commercial fish catches did not change during the study, and there is no reason to believe that intensity of recreational fishing has changed. We suggest that *P. antipodarum* may decrease fish production by (1) over-domination and shifting the macroinvertebrate assemblage structure towards less favourable for fish feeding, (2) decreasing the biomass of native macroinvertebrates through competition, or (3) reducing the channelling of the energy stored in secondary production towards higher trophic levels due to its ability to avoid predation by benthivorous predators.

Changes in lake secondary production. Our study revealed a significant increase in the total macroinvertebrate

Table 2
Results of homogeneity of slopes models testing for impact of fish age and *Potamopyrgus antipodarum* invasion on body weight of *Rutilus rutilus* and *Perca fluviatilis* in Lake Dusia, Lithuania (see Fig. 4 for prediction plots)

Fish species	Effect	df	MS	<i>F</i>	<i>P</i>
<i>R. rutilus</i>	Age	1	194.38	3280.5	<0.001
	Invasion	1	0.07	1.2	0.282
	Age × Invasion	1	0.57	9.6	0.002
	Error	335	0.06		
<i>P. fluviatilis</i>	Age	1	124.97	3232.9	<0.001
	Invasion	1	0.40	10.3	0.001
	Age × Invasion	1	0.01	0.4	0.539
	Error	365	0.04		

df = degrees of freedom, MS = mean squares, *F* = *F*-statistic, *P* = probability; significant probabilities ($P < 0.05$) are set in bold type.

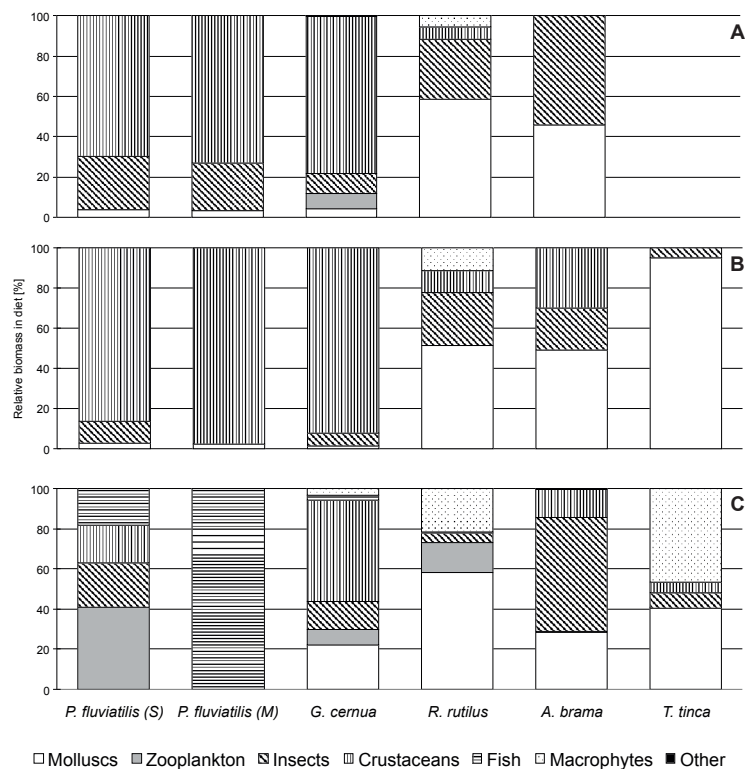


Fig. 3. Seasonal diet composition of fish in Lake Dusia during 2015–2016: spring (A), summer (B), and autumn (C); analysed fish: *Perca fluviatilis*, *Gymnocephalus cernua*, *Rutilus rutilus*, *Abramis brama*, *Tinca tinca*; size categories of *Perca fluviatilis*: S = small, M = medium; see Table 1 for fish numbers and sizes, and details on *Potamopyrgus antipodarum* within shown diets

biomass after the *P. antipodarum* invasion in Lake Dusia. Therefore, the conjecture that the *P. antipodarum* appearance supplements the littoral macroinvertebrate community and its total biomass increases due to the enhanced utilisation of primary production and detritus was confirmed. On the other hand, the total biomass of native macroinvertebrates was shown to significantly decrease indicating high *P. antipodarum* competition with native invertebrates. This result is in accord with previous studies which showed that *P. antipodarum* competition can be detrimental to native invertebrates (Múrria et al. 2008, Riley et al. 2008, Kerans et al. 2010). Overall, such a decline in native macroinvertebrates may imply that

P. antipodarum exerts negative impacts on the dominant forage base of benthivorous fish in the littoral zone of Lake Dusia.

Nevertheless, our analysis showed evident changes in the biomass proportions of some macroinvertebrate groups. The drastic increase in gastropods and the decrease in crustaceans were observed after *P. antipodarum* invasion. The relative biomass of gastropods grew up to 75%, while the relative biomass of crustaceans shrank and constituted less than 12%. Previous studies have also shown that *P. antipodarum* can both positively and negatively relate to densities of native macroinvertebrates

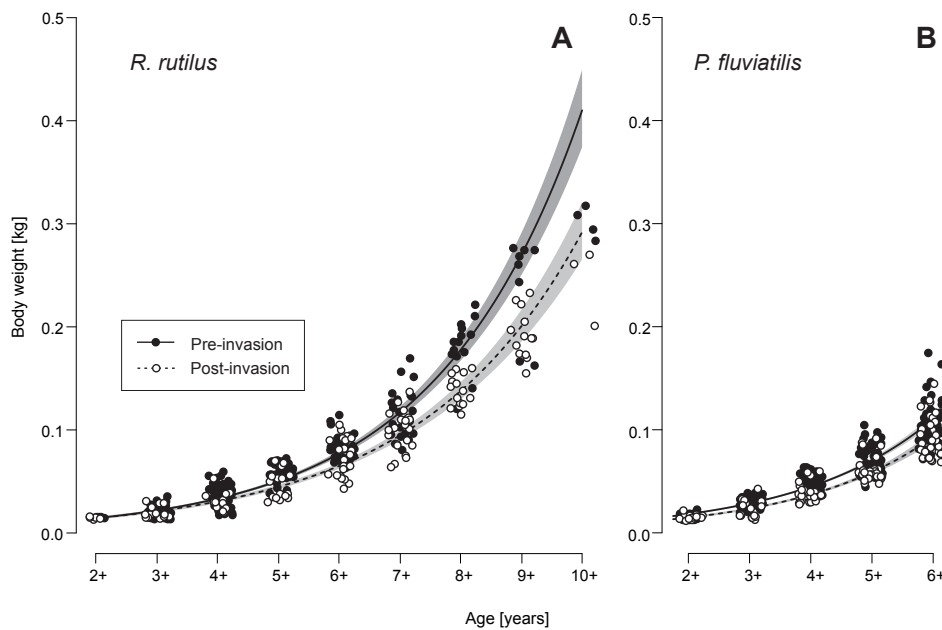


Fig. 4. Growth of *Rutilus rutilus* (A) and *Perca fluviatilis* (B) in Lake Dusia before (Pre-) and after (Post-) the invasion of *Potamopyrgus antipodarum*: predictions (with 95% confidence bands and partial residuals) of the homogeneity of slopes models (see Table 2 for effect tests)

Table 3

Standardised catches (catch per unit effort) of littoral fishes in Lake Dusia, Lithuania, before (2001–2006) and after (2010–2015) invasion of *Potamopyrgus antipodarum*

Year	<i>A. brama</i>		<i>G. cernua</i>		<i>P. fluviatilis</i>		<i>R. rutilus</i>		<i>T. tinca</i>		Other		Total	
	BM	AB	BM	AB	BM	AB	BM	AB	BM	AB	BM	AB	BM	AB
2001	0.0	0.0	0.7	30.3	1.2	20.0	0.1	1.7	0.0	0.0	0.1	1.1	2.0	53.1
2002	0.0	0.0	0.5	16.1	0.6	11.2	0.2	2.7	0.0	0.1	0.3	1.3	1.5	31.3
2003	0.0	0.3	1.0	43.6	0.6	14.2	0.5	7.9	0.2	0.3	0.2	1.8	2.5	68.1
2004	0.3	0.8	0.9	38.8	0.7	12.0	0.4	6.7	0.0	0.0	0.1	3.2	2.4	61.5
2005	0.2	0.4	0.7	22.6	1.6	19.5	0.1	1.3	0.0	0.0	0.1	0.6	2.6	44.4
2006	0.0	0.0	1.0	30.7	0.7	9.9	0.1	3.3	0.0	0.0	0.1	3.8	1.9	47.8
2010	0.1	0.1	0.2	7.9	0.7	8.2	0.1	0.9	0.0	0.0	0.0	0.2	1.1	17.3
2012	0.0	0.0	0.0	1.3	1.4	36.6	0.3	5.4	0.0	0.0	0.0	0.1	1.8	43.6
2013	0.1	0.0	0.2	11.8	1.3	16.6	0.1	1.4	0.1	0.3	0.2	2.9	1.9	33.1
2014	0.0	0.0	0.1	5.4	1.2	15.3	0.2	2.8	0.0	0.1	0.3	4.6	1.8	28.2
2015	0.3	0.2	0.1	6.3	0.3	3.9	0.4	4.7	0.1	0.1	0.2	0.5	1.3	15.6

BM = biomass (kg per year), AB = abundance (ind. per year); principal fish analysed: *Abramis brama*, *Gymnocephalus cernua*, *Perca fluviatilis*, *Rutilus rutilus*, *Tinca tinca*; other species: *alburnus alburnus*, *Anguilla anguilla*, *Blicca bjoerkna*, *Carassius gibelio*, *Esox lucius*, *Gasterosteus aculeatus*, *Scardinius erythrophthalmus*).

(Schreiber et al. 2002, Kerans et al. 2005, Rakauskas et al. 2018). A shift towards a macroinvertebrate assemblage dominated by gastropods may have effects on food webs of recipient ecosystems through both direct and indirect interactions. It may affect fisheries as previously dominant crustaceans are an important component in the diet of benthivorous fish species (Bubinas 1979, Kublickas and Bubinas 1985) and provide more energy per unit biomass than tiny, hard-shelled *P. antipodarum* (see Ryan 1982, McCarter 1986, Sagar and Glova 1995). Consequently, the establishment of a low-quality prey species such as *P. antipodarum* may displace more nutritionally valuable prey items in fish diet and reduce fish growth (Vinson and Baker 2008). Therefore, the rapid spread, population growth, and persistence of *P. antipodarum* in temperate lakes have the potential to affect food webs and fisheries.

Assimilation of secondary production. The increase of secondary production after supplementation by a new invasive primary consumer has a potential for increasing the production of secondary consumers, e.g., benthivorous fish (King et al. 2006, Watzin et al. 2008, Carlsson et al. 2009). However, such augmentation of fisheries could be expected only if channelling of the energy stored in increased secondary production (new primary consumers, e.g., *P. antipodarum*) toward higher trophic levels (secondary consumers, e.g., benthivorous fishes) is ensured. This requires that the invasive species would serve as high-quality, easily accessible and readily consumed fish-food (Arbačiauskas et al. 2010). If the invasion of *P. antipodarum* in temperate lakes meets this requirement, the growth rate and the standing stock of native benthivorous (and particularly molluscivorous) fish are likely to improve, and an increase in total fish production could be expected.

Benthivorous fish are considered to be the main molluscivores in temperate lake ecosystems (Wetzel

2001). Therefore the integration of secondary production accumulated in the standing stock of *P. antipodarum* towards higher trophic levels is mostly expected through fish predation on this invasive snail. Although the conclusions drawn from our fish diet analysis are limited due to a limited number of analysed fish specimens, some predictions (taking into account previous studies) about their ability to feed on *P. antipodarum* in Lake Dusia can be made.

This study showed that *P. antipodarum* share in the diet of studied benthivorous fish was very low throughout all seasons, although the contribution of other molluscs to the diet of some fish was significant. Similar results were obtained in previous studies of benthivorous fish performed during autumn in several Lithuanian lakes recently invaded by *P. antipodarum* (Rakauskas et al. 2016), or studies of various fish species in other regions (Bersine et al. 2008, Brenneis et al. 2011). Rakauskas et al. (2016) revealed that in temperate lakes the main benthivorous fishes actually avoid *P. antipodarum* as prey. However, at least in Lithuanian lakes, low integration of *P. antipodarum* into the fish diet may be explained by the fact that this invasive snail has established relatively recently, and native molluscivores may need some time to adapt to the exotic prey. Previous studies demonstrated a steady increase in numbers of *P. antipodarum* ingested by native fish species after its first appearance in the Green River, Utah; however, although a greater number of fishes consumed it, the proportion of this snail in the diet of an individual fish remained the same (Vinson et al. 2006). Thus, the importance of *P. antipodarum* in the diet of benthivorous fish in Lake Dusia may also remain negligible.

Previous studies also demonstrated that the majority of ingested *P. antipodarum* individuals remained intact after passing through the gastrointestinal tract of various fish species both in native and invaded ranges (McCarter

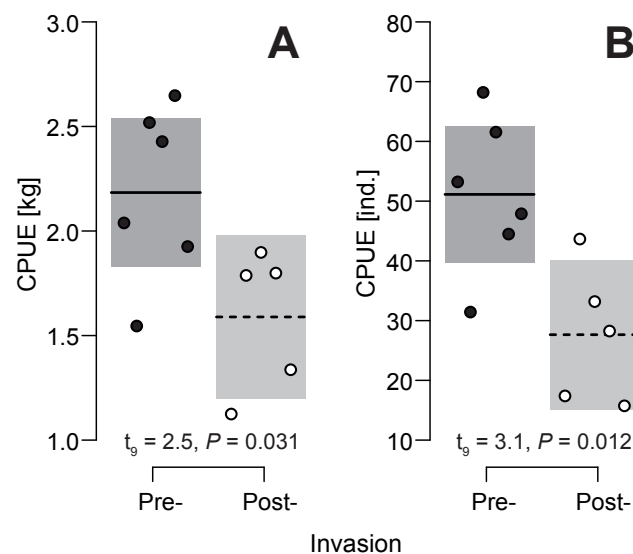


Fig. 5. Catch per unit effort (CPUE) of littoral fish in terms of biomass (A) and abundance (B) in Lake Dusia before (Pre-; 2001–2006) and after (Post-; 2010–2015) the invasion of *Potamopyrgus antipodarum* (means with 95% confidence bands)

1986, Jellyman 1989, Rakauskas et al. 2016). Additionally, earlier experiments revealed that *P. antipodarum* is able to survive after passing the guts of various benthivorous fish of temperate lakes (Rakauskas et al. 2016). Overall, compared to other macroinvertebrates *P. antipodarum* has been shown to provide little energy to fish (Ryan 1982, McCarter 1986). This has been confirmed by poor growth of fish fed on *P. antipodarum* (see Vinson and Baker 2008). Therefore, we conclude that *P. antipodarum* is a poor food source for secondary consumers such as fish, because it provides little energy and may pass through the gut undigested. Our study further suggests that the main benthivorous fish avoid consuming *P. antipodarum* in Lake Dusia throughout the season, though it is one of the most abundant macroinvertebrate species in the littoral zone. If native fish do not ingest, digest and assimilate *P. antipodarum*, part of lake primary production may get locked, and the energy flow towards higher trophic levels may be reduced.

Nevertheless, predatory macroinvertebrates may also contribute to the consumption of *P. antipodarum*. Previous studies showed that crayfish, dragonflies, and damselflies consume substantial numbers of *P. antipodarum* under experimental conditions (Brenneis et al. 2011, Bennet et al. 2015, Rakauskas et al. 2016). As these macroinvertebrates are valuable prey for benthivorous fish species they can link the secondary production of *P. antipodarum* with higher trophic levels. However, dragonflies and damselflies were very rare invertebrates in Lake Dusia, and crayfish density was below detection threshold throughout the study period (Rakauskas et al. 2018). Thus, in case of this lake, predatory macroinvertebrates are unlikely to transfer a considerable part of the energy accumulated in the standing stock of *P. antipodarum* towards higher trophic levels. However, the hypothesis warrants further investigation of field diet of other predatory macroinvertebrates, such as leeches, alderflies, or backswimmers in lakes invaded by *P. antipodarum*.

Fish production. Reduced growth of *R. rutilus* and *P. fluviatilis* in Lake Dusia in the post-invasion period, as demonstrated in our study, may be explained by *P. antipodarum* invasion. Although at some age these fish undergo a considerable ontogenetic diet shift, they are characterised as omnivorous benthic consumers with molluscs constituting a substantial part of their diet (Kublickas 1959).

Rutilus rutilus is generally known to change from a zooplanktivore into a benthic omnivore, which later becomes particularly molluscivorous (Hellowell 1972, Szczyglińska 1987, Specziár et al. 1997). In temperate lakes, large *R. rutilus* is also known to switch to molluscs, especially dreissenids (Kublickas 1959, Naddafi et al. 2010). In Lake Dusia, abundance and biomass of *D. polymorpha* halved after *P. antipodarum* invasion (Rakauskas et al. 2018); on the other hand, *R. rutilus* consumed some *P. antipodarum*. Therefore, the decreased growth of larger *R. rutilus*, could be mostly explained by the reduction of the proportion of suitable prey and high accessibility of low-value prey subsequent to the

domination of *P. antipodarum* in the macroinvertebrate assemblage.

Meanwhile, juvenile *P. fluviatilis* is a zooplankton feeder, which shifts to medium-sized macroinvertebrates during the second-third year (Hjelm et al. 2000, Rakauskas et al. 2010). When *P. fluviatilis* is large enough, its diet mainly consists of fish (Hjelm et al. 2000, Svanbäck and Eklöv 2002). Therefore, the slower growth of 3+ – 6+ age *P. fluviatilis* individuals during the post-invasion period could be also explained by the changes in the taxonomic structure of the macroinvertebrate assemblage after *P. antipodarum* invasion.

Results of this study also showed a marked decrease in the total CPUE of littoral fish after *P. antipodarum* invasion. However, species-specific comparisons did not reveal any significant differences except for a significant decrease of *G. cernua* during the post-invasion period. *Gymnocephalus cernua* was indicated as a very specific benthivorous predator consuming considerable amounts of molluscs, which constituted a significant part of its diet in Lake Dusia, especially in autumn (Pilinkovskij et al. 2014). This would suggest that *G. cernua* could benefit from a severe invasion of *P. antipodarum*. However, previous studies revealed low consumption of *P. antipodarum* by *G. cernua* in Lake Dusia and other Lithuanian lakes (Rakauskas et al. 2016). Thus, reduction in CPUE of *G. cernua* could instead be explained by changes in the structure of macroinvertebrate assemblage, i.e. decrease in the proportion of more desirable and nutritious macroinvertebrates, such as crustaceans, consequent to *P. antipodarum* domination.

Concluding remarks. The high abundance of *P. antipodarum* increased the total biomass of littoral macroinvertebrates probably due to the increased consumption of basal food sources (Rakauskas et al. 2018). However, it also changed the structure of fish food basis in Lake Dusia. Our results showed that benthivorous fish consumed negligible amounts of over-dominant *P. antipodarum* even after several years since the invasion, thus the channelling of energy stored in primary production towards certain fish may have been reduced. Consequently, the invasion may have negatively affected the growth of at least several fish species and reduced their production rates. Through such proliferating effects, *P. antipodarum* may have thus decreased the total littoral fish production in the lake. In extrapolation of our results, *P. antipodarum* invasion could threaten fisheries of temperate lakes. Therefore, the expansion of *P. antipodarum* across European waters has serious international implications that require awareness, cooperation, and support from concerned citizens and governments.

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