ARPHA Preprints

PENSOFT

PREPRINT

Author-formatted, not peer-reviewed document posted on 12/07/2023

DOI: https://doi.org/10.3897/arphapreprints.e109303

Mass invasion of the Ponto-Caspian amphipods in Masurian Lakeland associated with human leisure activities

Krzysztof Podwysocki, Tomasz Mamos, Andrea Desiderato, Tomasz Rewicz, Michał Grabowski, Alicja Konopacka, Karolina Bącela-Spychalska

Mass invasion of the Ponto-Caspian amphipods in Masurian Lakeland associated with human leisure activities

Krzysztof Podwysocki, Tomasz Mamos, Andrea Desiderato, Tomasz Rewicz, Michał Grabowski, Alicja Konopacka, Karolina Bącela-Spychalska*

*Corresponding Author

Abstract

Non-indigenous species (NIS) contribute to the decrease of native species' diversity on a local and global scale. One of Europe's most significant donors of freshwater invasions is the Ponto-Caspian region. Following the construction of artificial canals connecting isolated water bodies and resulting heavy boat traffic, the Ponto-Caspian Amphipoda started to spread in Europe. Four species: *Dikerogammarus haemobaphes*, *Dikerogammarus villosus*, *Pontogammarus robustoides* and *Chaetogammarus ischnus* invaded Masurian Lakeland (North-Eastern Poland). Based on the literature and our data, we studied their distribution in 14 lakes in the region in the years 2001 - 2016. We analysed their distribution against several water quality parameters and levels of anthropogenic pressure. Our results are also the first records of two new invaders - *D. villosus* and *C. ischnus* in the studied area. We show that the relative abundance and frequency of these two species rapidly increase, and simultaneously the populations of the older invaders, *D. haemobaphes* and *P. robustoides*, decrease. The native species - *Gammarus lacustris* - seems to be negatively affected by NIS richness as well as by the proximity of cities. The NIS found in the lakes appear to be facilitated by boating and the lower complexity of the shoreline. Our study shows how anthropogenic pressure and tourism in the specific, may directly aid bioinvasion, mining the survival of native biodiversity without proper regulation.

Keywords: biological invasions; lakes; recreational boating; tourist pressure; propagule pressure; time series; assemblage succession

Introduction

Biological invasions are among the most significant threats to biodiversity on a local and global scale (eg. Sala et al. 2000; Kettunen et al. 2009; Lambertini et al. 2011; Mačić et al. 2018). Many Non-indigenous species (NIS) cause a decline in abundance and diversity loss of native species, which is particularly witnessed in Europe and the USA (eg. Pinkster et al. 1992; Dick and Platvoet 1996; Ricciardi and Rasmussen 1998; Panlasigui et al. 2018) and is more prominent in freshwater ecosystems than in marine and terrestrial ones (Strayer and Dudgeon 2010). Many studies show high economic costs incurred by biological invasions on a global scale (Pyšek and Richardson 2010; Cuthbert et al. 2021a; Cuthbert et al. 2021b; Kouba et al. 2022). The average annual costs of preventing biological invasions and reversing their effects on the world reach $76 billion (Bradshaw et al. 2016), including $23 billion in aquatic ecosystems (Cuthbert et al. 2021b). However, the costs of pre-invasion management are 25 times lower than post-invasion management (Cuthbert et al. 2021a). The global economic costs of aquatic crustacean bioinvasions were estimated at $271 million, including around $179,800 for amphipods; nonetheless, it seems that the costs are underestimated (Kouba et al. 2022).

Despite the fact that surface freshwaters represent only 0.01% of the Earth's water resources and constitute 0.80% of the Earth’s surface, they are inhabited by ca. 6% of the world’s species (Dudgeon et al. 2006; Strayer and Dudgeon 2010). Therefore, freshwater ecosystems are precious from the environmental, economic, sanitary, cultural and scientific points of view (Dudgeon et al. 2006) and offer an especially important form of tourism (Hall and Härkönen 2006). Unfortunately, these ecosystems are in crisis, represented particularly by stronger biodiversity loss than in terrestrial ecosystems (Dudgeon et al. 2006). According to the Water Framework Directive (WFD, 2000) introduced in the European Union in 2000, until 2015 every water body in the EU should have achieved a high or at least good ecological and chemical status. However, the latest reports assume that only 40% of the waters achieved satisfactory, healthy status (State of Water Report, EEA, 2018). Land use and agriculture are among the most important factors which cause the decreasing conditions of aquatic ecosystems globally (Foley et al. 2005; Feld et al. 2016). Bioinvasions are perceived as a second (after habitat degradation) of the strongest threats to global biodiversity (Dudgeon et al. 2006; Kettunen et al. 2009; Strayer and Dudgeon 2010). In particular, invasions by Ponto-Caspian fauna threaten freshwater ecosystems worldwide (Ricciardi and MacIsaac 2000).

The Ponto-Caspian region covers the coastal area of the Caspian, Black, Aral, and Azov Seas and their brackish limans and deltas of rivers discharging into them (Jażdżewski 1980). This region is one of Europe's biggest sources of invasive species for inland waters (Bij de Vaate et al. 2002; Galil et al. 2008; Panov et al. 2009; Copilaș-Ciocianu et al. 2023a). The Ponto-Caspian Basin constitutes the hotspot of crustacean diversity (Cristescu and Hebert 2005; Väinölä et al. 2008; Copilaș-Ciocianu and Sidorov 2022; Copilaș-Ciocianu et al. 2022) with the emphasis on Amphipoda, as evidenced by around 10% of freshwater invasive species in Europe coming from this region (Pöckl et al. 2011). One of the main significant causes fueling the bioinvasions of Ponto-Caspian species is the construction of canals that connect previously isolated drainages (eg. Jażdżewski 1980; Bij de Vaate et al. 2002; Galil et al. 2008; Arbačiauskas et al. 2010; Minchin et al. 2019; Jażdżewska et al. 2020). Another important factor is species translocations in ballast waters (Jażdżewski 1980; Pinkster et al. 1992; Bij de Vaate et al. 2002; Zhulidov et al. 2018), on the submerged parts of tourist boats and barges (Bącela-Spychalska et al. 2013; Anderson et al. 2014; de Ventura et al. 2016; Rewicz et al. 2017) and with angling equipment (Anderson et al. 2014; Smith et al. 2020). Thus, although freshwater ecosystems occupy only a tiny fraction of Earth's surface, the high anthropogenic pressure results in a more pronounced negative impact of invaders on native species than in marine ecosystems (Ricciardi and Kipp 2008).

There are six Ponto-Caspian gammarids (Amphipoda, Gammaroidea) already recorded in Polish freshwaters: *Chaetogammarus ischnus* (Stebbing, 1899), *Dikerogammarus haemobaphes* (Eichwald, 1841), *Dikerogammarus villosus* (Sowinsky, 1894), *Obesogammarus crassus* (G.O. Sars, 1894), *Pontogammarus robustoides* (Sars, 1894) and *Spirogammarus major* (Cărăușu, 1943) comb. & stat. nov. (Konopacka 1998; Gruszka 1999; Jażdżewski and Konopacka 2000; Konopacka and Jażdżewski 2002; Jażdżewski et al. 2005; Grabowski et al. 2007; Rachalewski et al. 2013, Copilaș-Ciocianu et al. 2023b). These species are already widely distributed in the European inland waters, where they arrived through one of three well-defined migration corridors: the northern, the central and the southern ones (*sensu* Bij de Vaate et al. 2002). Not only did they colonise the major rivers and the canals constituting the invasions corridors, but also spread to the river systems and many European lakes, e.g. the Alpine Lakes (Rewicz et al. 2017) and the Great Masurian Lakes in Poland (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008). An extensive up-to-date description of the distribution of alien freshwater amphipods in Europe can be found in Copilaș-Ciocianu et al. (2023a). As the dynamics of invasion in terms of species and the ecosystem vulnerability varies and the impact of NIS depends on their invasion process (i.e. propagule pressure, species interactions), there is a constant need for monitoring and estimating the bioinvasion trends and threats. Their introduction leads to drastic changes in the macroinvertebrate community structure and affects the whole ecosystem's functioning (Jones et al. 1997; Lambertini et al. 2011). The lakes seem to be particularly impacted by biological invasions, as many of them are under high tourist pressure, resulting in a higher chance of introducing alien species, even if the lakes are not directly connected with the invasion corridor (Bącela-Spychalska et al. 2013; Bącela-Spychalska 2016; Rewicz et al. 2017).

The Masurian Lakeland is the most popular area for yachting in Poland and one of the main inland yachting regions in central Europe. Except for yachting, the region is extensively used by tourists for associated recreational activities (particularly angling and camping) (Kistowski and Śleszyński 2010; Ulikowski et al. 2021). In 2020, in the Warmian-Masurian Voivodeship (to which the Masurian Lakeland belongs) there were around 900,000 tourists served (Local Data Bank of the Warmian-Masurian Voivodeship, 2021, available at https://bdl.stat.gov.pl/bdl/dane/teryt/jednostka/2889). Between 2004 and 2008 the number of tourists was even three times higher than the number of inhabitants in the region (Kistowski and Śleszyński 2010). The Masurian Lakeland belongs to one of the five regions in Poland with the highest tourist pressure (Kistowski and Śleszyński 2010). Unfortunately, the knowledge about the spreading of the invasive Amphipoda in this region is poor and out of date (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008).

The aims of our study were: i) to update the knowledge on the distribution and expansion of the Ponto-Caspian amphipod fauna in the Masurian Lakeland; ii) to assess the distribution of native vs. invasive Ponto-Caspian gammarids in the context of biotic and abiotic characteristics of the lakes and anthropogenic pressure in this region, by using both historical and newly obtained data. Based on observed trends in other regions (Dick and Platvoet 2000, Grabowski et al. 2006, van Riel et al. 2006, Van der Velde et al. 2009), we assumed that some invasive gammaridean species are replaced by others and that native species are not able to coexist with the invasive ones. We hypothesise that the presence of invasive gammaridean species results from high tourist pressure while the existence of the native ones is associated with isolated and natural lakes. We tracked the distribution of invasive gammaridean species in the Masurian Lakeland since 2001 based on the literature and our data. To explore the relationship between the structure of amphipod assemblages and lake characteristics, including human tourist pressure in the years

2014 and 2016, we collected data on the relative abundance of amphipods, measured basic water parameters and estimated the tourist pressure.

Materials and methods

Study area

The Masurian Lakeland or Pojezierze Mazurskie [in Polish] is a lake district (macroregion) in northeastern Poland with a surface area of 52,000 km^2 including seven mesoregions i.a.: the Great Masurian Lakes Land and the Ełckie Lakeland (Kondracki 2002). The landscape was formed between 16,000-11,000 BP (at the end of the last glaciation) and is characterised by strong latitude differentiation, dominantly with moraine hills (Hillbricht-Ilkowska et al. 2000; Ulikowski et al. 2021) and with glacial tills as a dominant component of soil substratum (Hillbricht-Ilkowska et al. 2000). The lakes are mainly surrounded by a mosaic of agricultural areas and forests (Hillbricht-Ilkowska et al. 2000; Ejsmont-Karabin et al. 2020) giving similar input of allochthonous organic and mineral matter to every lake (Chróst and Siuda 2006). Most lakes of this region are dimictic with summer thermal stratification (Ulikowski et al. 2021) and are connected with main European watersheds via small rivers: the Pisa River (flowing into the Narew River and then into the Vistula River), and the Węgorapa River (flowing into the Pregolya River and then into the Vistula Lagoon) (Bajkiewicz-Grabowska 2008; Jażdżewska and Jażdżewski 2008; Ulikowski et al. 2021) and via the artificial canals (Ulikowski et al. 2021). This increase in the chance for invasive amphipods to spread in the region. For this study, we selected lakes with historical faunistic data based on Jażdżewski and Konopacka (1995) as well as along a gradient of tourist pressure, including also more natural and isolated lakes (Fig. 1).

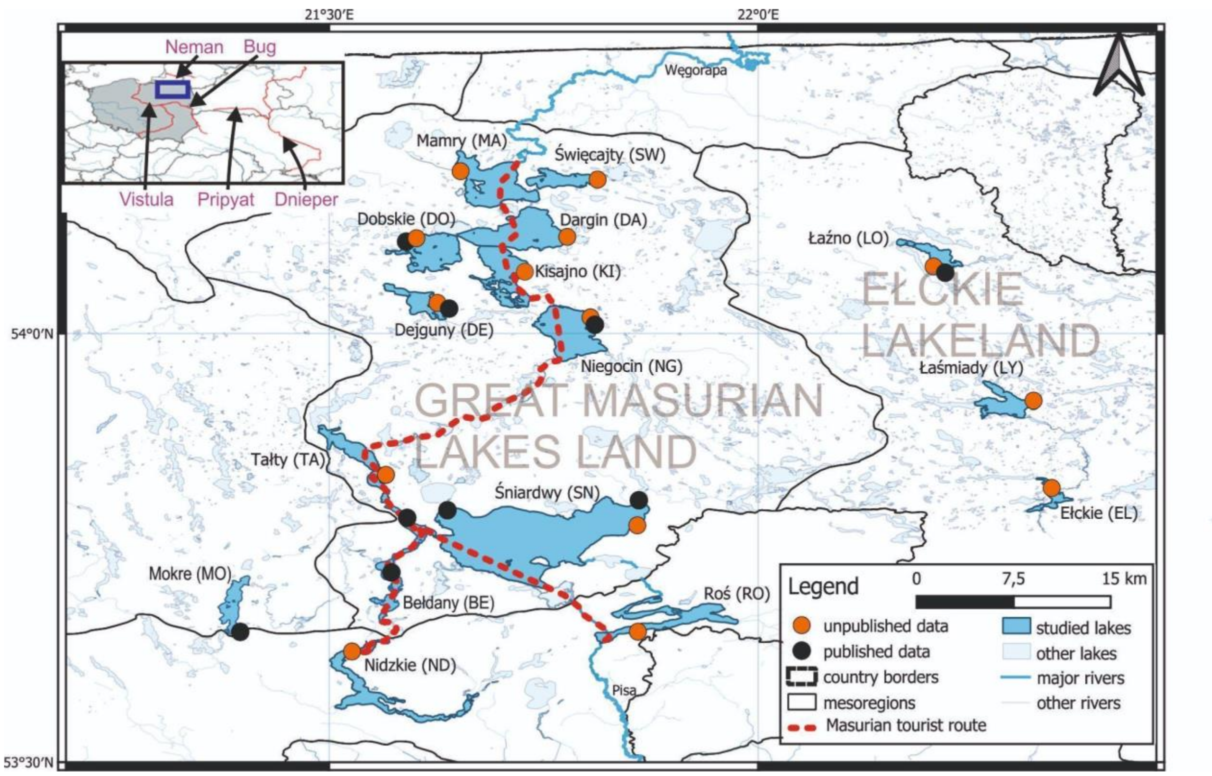

Figure 1. The sites in the Masurian Lakeland. The two-letter acronyms for particular lakes were used in further tables and figures.

Sampling and data collection

Our dataset consists of two types of data: (*i*) published, including the years between 2001 and 2007 (Jażdżewski 2003; Jażdżewska and Jażdżewski 2008) and (*ii*) new data coming from field surveys in 2008, 2009, 2014 and 2016 (See Supplementary Table 1). The studies between 2001 and 2009 have only qualitative character (i.e., presence/absence of amphipod species), while for 2014-2016 the species abundances are available. Generally, sampling was done through "kick-sampling" with a benthic hand-net with a mesh size of 0.5 mm for 45 min at each station, performed by two people with equal effort, from all available littoral habitats (sand, mud, gravel, stones, and submerged macrophytes) at depths from 0.05 to 0.5 m to collect all occurring Amphipoda species. Such a semi-quantitative method gives reliable and comparable results (Jażdżewski et al. 2002; Grabowski et al. 2006). The amphipods were preserved in 96% ethanol and then identified in the laboratory to the species level based on the available literature (Mordukhaj Boltovskoj 1964; Eggers and Martens 2001).

To detect the potential role of biotic and abiotic factors as well as human pressure on the presence of invasive amphipods in the lakes sampled between 2007 and 2016, we used topological and anthropogenic variables, such as the surface-volume ratio or the distance from the city listed in Table 1. As a proxy of lake naturality, we used the water quality index according to the Water Framework Directive 2000/60/EC. Environmental heterogeneity creates more niches that can be occupied by co-occurring species (Chesson 2000). Thus, we used two indexes: shoreline development and surface area to volume (A/V ratio). The shoreline development index is the ratio between the actual shoreline length of a lake and the circumference of a perfectly circular lake with the same area (Aronow 1982). High values indicate a more complex shoreline, retaining a higher load of nutrients from land (Cole 1975) and provide more niches for the biota (Chesson 2000). The surface area to volume ratio is providing information about the depth and size of the lake and can be inversely correlated to its productivity (Fee 1979). Smaller water bodies (lower A/V ratio) may play the role of refugia for native species (Grabowski et al. 2009). The density of boats (i.e. the number of boats divided by the lake surface in ha), assumed as a rough proxy of the maximum possible number of moored boats in marinas, was used to describe tourist pressure in the region (Johnson and Padilla 1996; Vander Zanden and Olden 2008, Bącela-Spychalska et al. 2013). Tourist infrastructure is mainly localised in urban areas (Kulczyk et al. 2016). Thus, we used the distance between the sampling point and the city (i.e., centroid) as an estimation of anthropogenic pressure. As a city, we used the settlement units characterised by dense urban development and non-agricultural functions, according to the Polish legislation (Dz. U. poz. 1612, z późn. zm., available at https://isap.sejm.gov.pl/isap.nsf/home.xsp). All spatial analyses and their visualisation were conducted using QGIS 3.10.13.

Table 1. Lake variables used in the analyses. In brackets, the names of variables are given.

Variable	Source of data
Water quality index (water QI)	Soszka et al. (2016).
Surface area to volume ratio (A/V ratio)	Soszka et al. (2016).
Shoreline length to surface area ratio (shoreline development)	https://mojemazury.pl
No. of boats per ha of lake surface (density of boats)	https://mazury24.eu; https://skorupki.mazury.info.pl
Distance of sampling point from urban area (distance from city)	Measured as linear distance in km from the closest city using QGIS software.

Data analysis

Using all the records since 2007, we modelled the presence of the only native gammarid (i.e., *Gammarus lacustris*) according to the number of NIS (Non-indigenous species) and the relative distance of each sampling site from a city. We included this variable as a proxy of the anthropogenic propagule pressure (i.e., the introduction of NIS by human activities) of NIS on the site (i.e., inversely correlated). We used generalised linear mixed models (GLMM) to include also the random variable of the sampling year. To account for spatial autocorrelation we included the product of Latitude x Longitude as a covariate. Given the presence/absence nature of the data, we used a Bernoulli distribution fitted with *glmmTMB* (link = logit) with the homonymous package (Brooks et al. 2017). The possible inclusion of the interaction between NIS richness (i.e. number of species) and the distance from the closest city was also tested using the Akaike information criterion (AIC; Bozdogan 1987). After fitting the model, we validated it by simulating its residuals using the package *DHARMa* (Hartig 2022).

Using samples collected between 2014 and 2016, we first explored the variability of the environmental parameters of the sites and lakes, grouping them according to their geographic position and connectivity (i.e., A: northern, B: southern, C: eastern; Fig. 2 B and See Supplementary Table 1). To explore and visualise the environmental variability of the study area, we used a principal component analysis (PCA) with standardised values with *prcomp* of the package *vegan* (Oksanen et al. 2022). We analysed the gammarid assemblage using a permutational multivariate analysis of the covariance (PERMANCOVA) with an orthogonal design with two fixed factors (i.e., lake groups with three levels; time with two levels), and five covariates: water QI, A/V ratio, shoreline development, number of boats, and distance from the city. To control the possible difference in sampling effort (i.e., the total number of individuals collected in each event) before calculating Bray-Curtis dissimilarities, we used Hellinger transformation on the abundances of the species. We used first *adonis2* of the package *vegan* with 9999 permutations and *pairwise.adonis* of the package *pairwiseAdonis*, with Bonferroni correction and 9999 permutations, for the postdoc analysis between levels of the significant factors (Martinez Arbizu 2020). To visualise and corroborate the results of the PERMANCOVA, we finally used a constrained ordination using distance-based redundancy analysis (dbRDA; based on Legendre and Anderson (1999) with *capscale* (package vegan) and

Bray-Curtis dissimilarities, including the covariates of the PERMANCOVA as constraining variables. All the analyses were performed in the R environment (R Core Team 2023).

Results

Generally, we found four invasive gammaridean species present in nine lakes and one native species present in five lakes. The first recorded invasive species was *Dikerogammarus haemobaphes* reported in 2001 (Jażdżewski 2003), and the second was *Pontogammarus robustoides* observed in 2007 (Jażdżewska and Jażdżewski 2008) (Fig. 2 A). The spread of invasive species can be observed over time. Between 2014 and 2016, *D. haemobaphes* spread to one more lake and is observed now in nine of them. *P. robustoides* did not colonise new lakes in 2016, compared to 2014. In 2014, we noticed the first appearance of the other two invaders: *C. ischnus* and *D. villosus*. *C. ischnus* was found in two lakes in 2014 and expanded to five further lakes in 2016. *D. villosus* was already found in five lakes in 2014 and expanded to two further lakes in 2016. Apart from Gammaroidea, another amphipod species - *Chelicorophium curvispinum* (G.O. Sars, 1895) - was recorded in 2014 and 2016 in one sampling point in the Narew River connected to the Masurian Lakeland. In Nidzkie Lake, we did not record any amphipod species.

Generally, the native species - *G. lacustris* - was not found in lakes inhabited by invasive species. Only in Dobskie Lake, the native and invasive gammarids co-occurred in 2014, but with a low number of *G. lacustris* (two individuals vs. 194 individuals of invasive species) (Fig. 2 A).

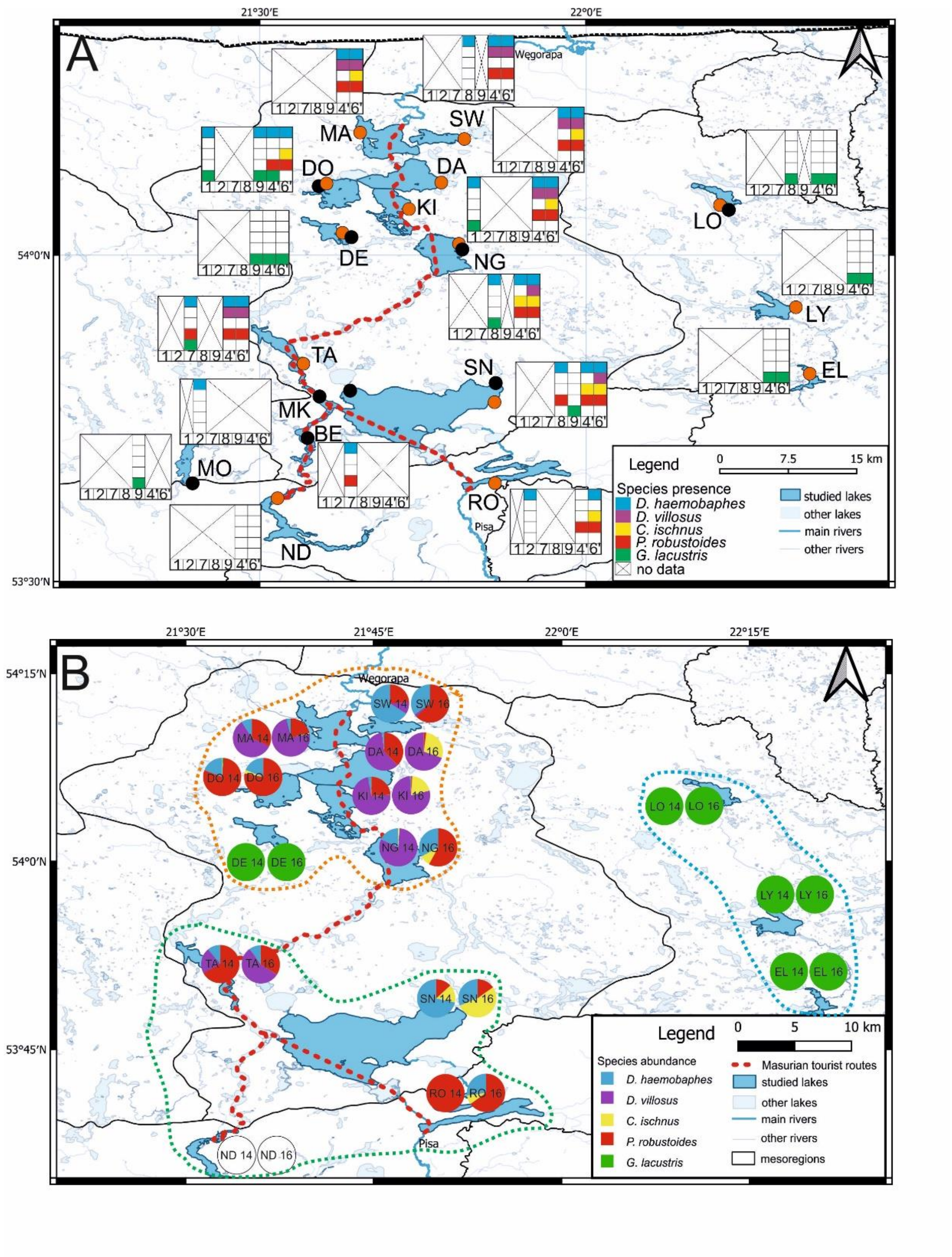

Figure 2. A. The distribution of invasive and native gammarid species in studied lakes since 2001 (based on published and new data). Table at each lake showing the assemblage (colours in rectangles according to different species, see legend) variation in time (symbols for sampling years: 1 - 2001; 2 - 2002; 7 - 2007; 8 - 2008; 9 - 2009; 4' - 2014; 6' - 2016). Circles corresponding to data points published (black) or unpublished (orange). Dashed black line: country borders; dashed red line: the Masurian tourist boat route. Black lines delimiting mesoregions according to Kondracki (2002). B. The assemblage composition of the gammarid fauna in studied lakes in the years 2014 and 2016 (locality codes according to Supplementary Table 1). Pie charts showing the relative abundances of each species. An empty circle means no amphipods recorded. A dashed black line means country borders; a dashed red line means the Masurian tourist boat route. Black lines delimiting mesoregions according to Kondracki (2002).

Coloured dotted lines surrounding the pie charts correspond to the lakes groups: orange – A, green - B, blue – C.

The GLMM for the presence of *G. lacustris* showed the significant negative effect of NIS richness (p-value=0.004) and the positive effect of the distance from an city (p-value= 0.042), but not their interaction (Fig. 3). The inclusion of the year as a random effect increased considerably the R^2 (Marginal 0.733 - Conditional 0.808), mostly because the sampling effort was different each year and mostly opportunistic (Table 2).

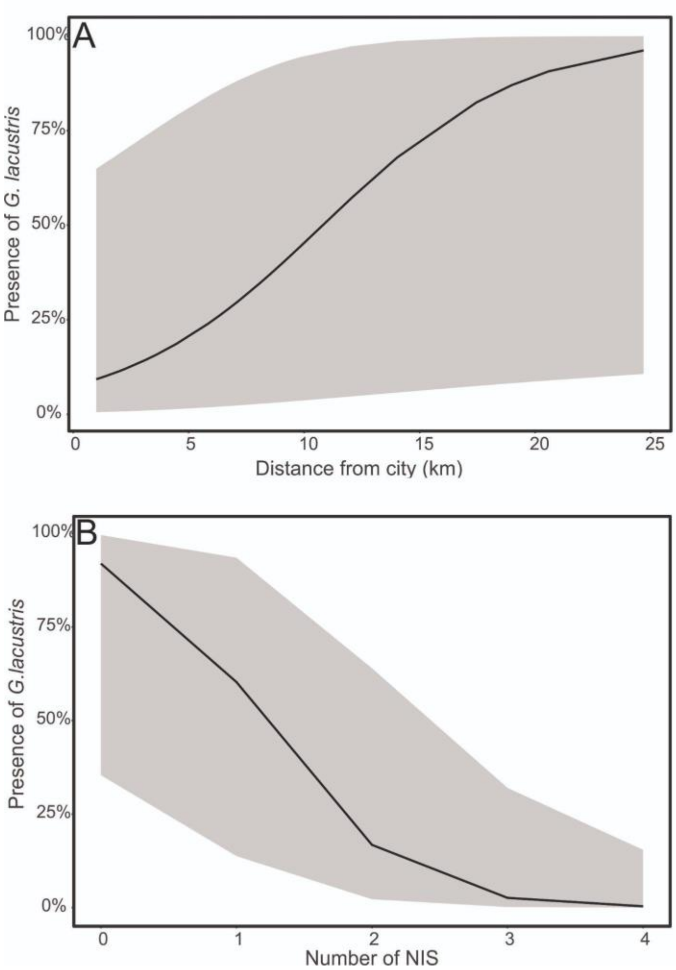

Figure 3. Predicted probability of occurrence of *G. lacustris* dependent on the distance of sampling point from a city (A) and richness of NIS (B).

Table 2. Summary of the best-fitting Bernoulli GLMM for the presence of native gammarid - *Gammarus lacustris*. A spatial variable representing the product between latitude and longitude, distance from a city in km, number of NIS as integer (i.e., 0-4) and year of sampling fitted as a random effect.

	Bernoulli GLMM (Presence of G.lacustris)		
Coefficient	*Log-Odds*	*Conf. Int (95%)*	*P-value*
(Intercept)	-5.71	-141.99 – 130.57	0.935
Spatial	0.01	-0.11 – 0.12	0.931
Distance from cities	0.23	0.01 – 0.46	0.042
Number of NIS	-1.97	-3.31 – -0.63	0.004
Random Effects			
σ^2	3.29		
$\tau_{00\ \mathrm{Year}}$	1.27		
ICC	0.28		
N_{Year}	5		
Observations	58		
Marginal R^2 / Conditional R^2	0.733 / 0.808		

The first three components of the PCA explained 85.5% of the variance among the environmental variables explored in the study (Fig. 4 A, B). According to PC1 and PC3 (~57% variance explained), the lakes further from the tourist route (i.e., group C) are indeed characterised by a lower number of boats, higher complexity of the shore, and a bigger distance from a city. The PC2 was more related to the water quality index and the surface-volume ratio showing a general trend of lower water quality and deeper waters for group A (highest quality for group B).

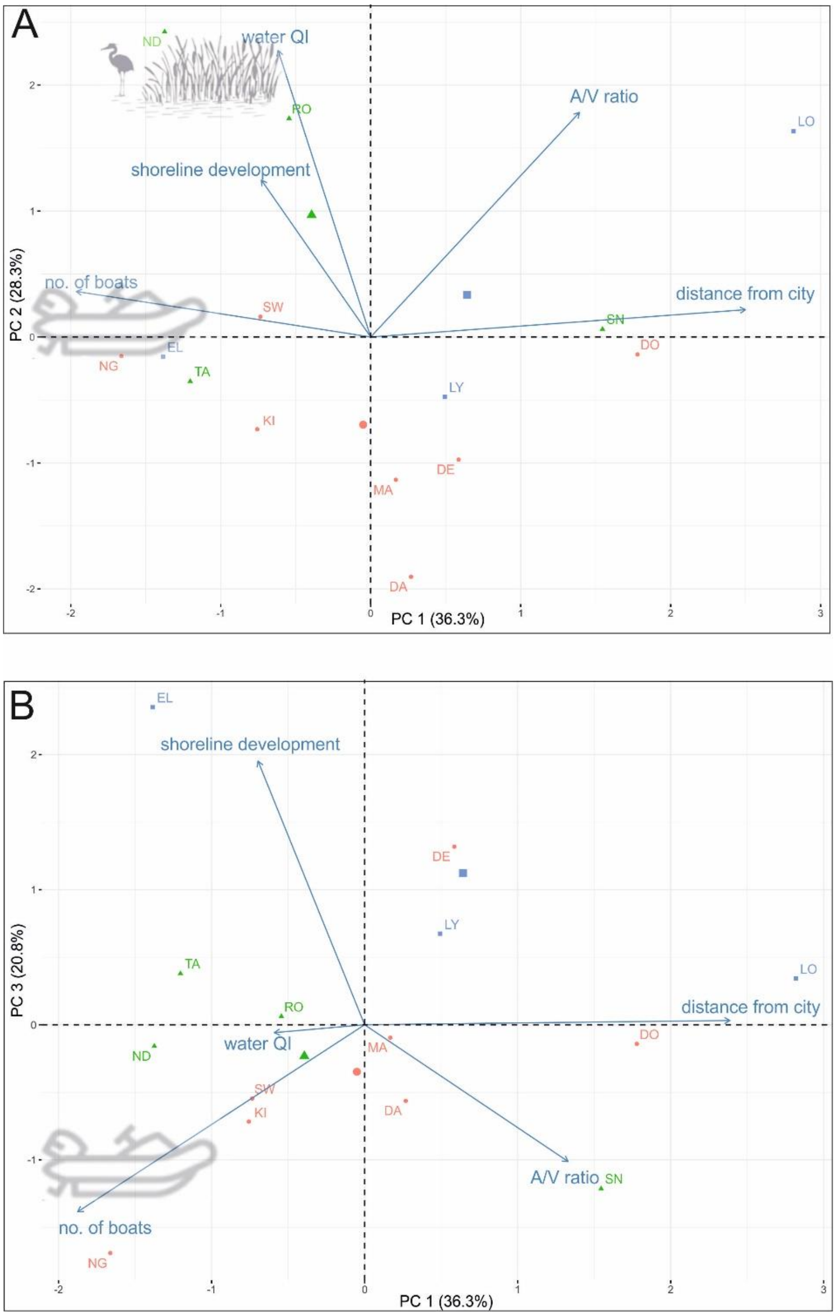

Figure 4. PCA biplot displaying the first three axes of the PCA of the environmental variables of the lakes sampled between 2014 and 2016 (A: PC1-2; B: PC1-3). The colours refer to the different lake groups: orange (A), green (B), and blue (C). Arrows proportional to the loading of each variable, Dashed lines = 0. Variables according to Table 1. The acronyms of lakes according to Fig. 1 and Supplementary Table 1.

The PERMANCOVA results showed a significant effect (p-values<0.05) of shoreline development, number of boats, and water quality on the assemblage of amphipods (Table 3). Even though the relative abundance of new invaders (*D. villosus* and *C. ischnus*) increased with time, while decreased for *D. haemobaphes*, *P. robustoides*, and *G. lacustris* (Fig. 2 B), the time factor was not significant.

Table 3. Results of PERMANCOVA test using 9999 permutations. Two fixed factors: lake group (lake: three levels) and year (time: two levels), and their interaction (time: lake). Five covariates: water quality index (QI), lake surface-volume ratio (A/R ratio), the complexity of the shoreline (shoreline development), and distance from the city. Significant p-values (<0.05) are in bold.

Predictor	Df	Sum of Sqs	R2	F	Pr(>F)
water QI	1	0.408	0.059	3.794	**0.035**
A/V ratio	1	0.179	0.026	1.661	0.195
shoreline development	1	2.376	0.346	22.096	**<0.001**
number of boats	1	1.16	0.1699	10.788	**<0.001**
distance from city	1	0.22	0.032	2.047	0.133
time	1	0.11	0.016	1.024	0.318
lake group	2	0.575	0.084	2.675	0.057
time: lake	2	0.016	0.002	0.075	0.991
residual	17	1.828	0.266		
total	27	6.871	1		

The first two axes of the dbRDA fitted 90.1% of 52.1% of the total variation explained. The presence of the native *G. lacustris* appeared more correlated to lakes with more complex shorelines (Fig. 5). The occurrence of *D. villosus* is mainly explained by the increasing number of boats and proximity to the city. The other three species (i.e., *P. robustoides*, *D. haemobaphes* and *C. ischnus*) seem to be related to simpler shorelines and average values for the other variables, generally opposite to *D. villosus*.

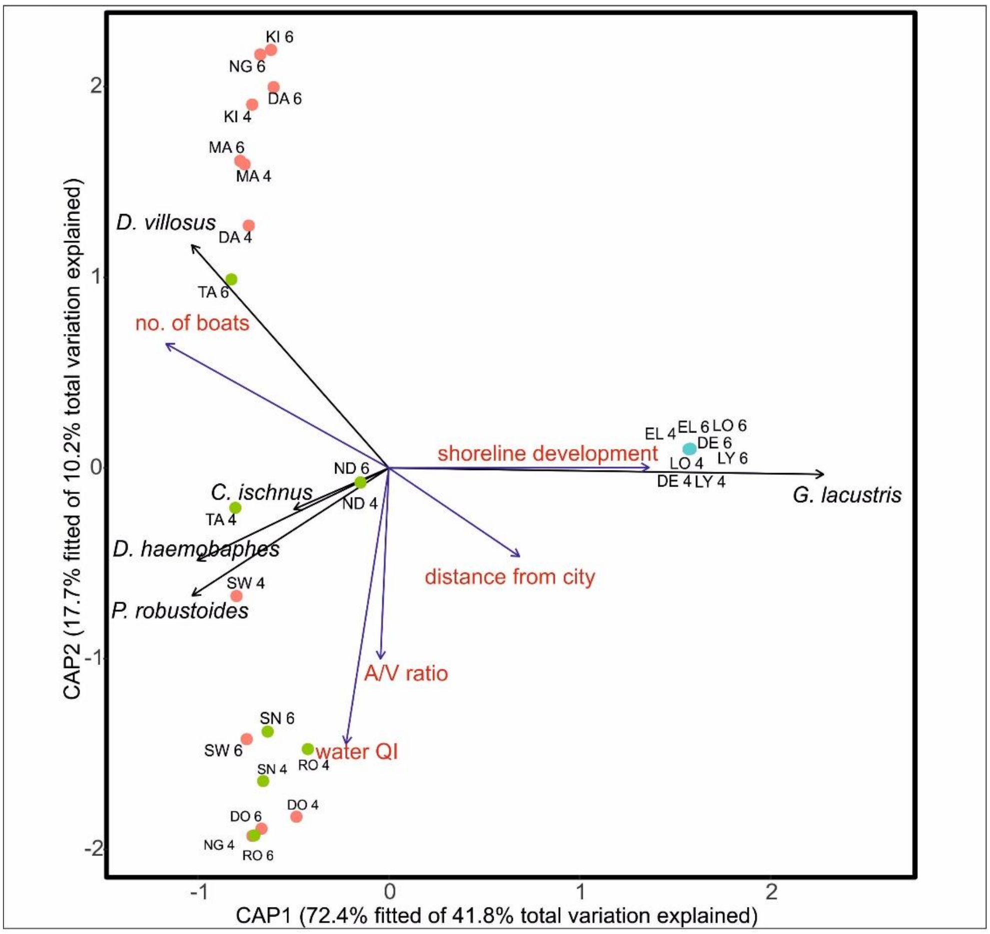

Figure 5. Canonical analysis of principal coordinates (CAPSCALE) derived from the Bray-Curtis dissimilarities of the gammarid assemblages and the environmental variables of the studied lakes in the years 2014 and 2016. Variables according to Table 1.

Discussion

Our study shows that between 2001 and 2016 the number of invasive amphipod species in the study area increased from one to five (including *C. curvispinum* in the Narew River). Simultaneously, the continuous decrease in the occurrence of *Gammarus lacustris* was recorded. Our study reveals that the presence of Non-indigenous species (NIS) in lakes is primarily facilitated by two key factors: recreational boating activities and simplified shorelines.

According to our results, NIS richness has a significant negative effect on the presence of *G. lacustris*. Indeed, this species seems to be one of the weakest competitors among European freshwater amphipod species giving way to Ponto-Caspian species of genera: *Chaetogammarus*, *Dikerogammarus* and *Pontogammarus* (Meßner and Zettler 2021). It occurs in a wide range of habitats, nevertheless, in the last few decades, the species has been pushed to the relict range of occurrence (Hesselschwerdt et al. 2008; Meßner and Zettler 2021). Nowadays, the species is present almost exclusively in isolated waterbodies and continues to decline (Meßner and Zettler 2021). The same tendency was observed in the study area. Once, the species was vastly present in the Masurian Lakeland. Among the studied lakes, *G. lacustris* was recorded in Mamry and Kisajno in 1975 (Jażdżewski and Konopacka 1995) but the last records in Kisajno comes from 2001, while the species was already not observed in Mamry at that time. The species' last records from Tałty Lake come from 2007 and from Śniardwy Lake from 2009. *G. lacustris* also disappeared from Dobskie Lake where the last record comes from 2014 (two individuals). The co-occurrence of *G. lacustris* with invasive species in 2014 in Dobskie Lake may be explained by low invasion and tourist pressures via the narrow connection of this lake with other lakes. In 2014, the invasion of this lake was still in its early stages. Among the studied water bodies, *G. lacustris* was present in 2016 only in four isolated lakes. Its presence in these lakes can be associated with low tourist pressure (low number of boats, long distance from the tourist route), long distance from invaded lakes and from the city (anthropogenic pressure). Instead, these lakes have higher shoreline complexity, which possibly increases the heterogeneity of the coastal ecosystems. Lack of direct connections between these lakes and Great Masurian Lakes (central part of the Lakeland), where all the invasive species are present, and low level of tourist pressure, create refuge for native species.

Freshwater NIS can easily spread with tourist activities. NIS usually have a broad tolerance to desiccation, improving their ability to overland invasion (Bącela-Spychalska et al. 2013; Glisson et al. 2020). In Alpine lakes, a significant positive relationship between the number of boats and the presence of *D. villosus* was observed (Bącela-Spychalska et al. 2013). Similarly, *P. robustoides* spread in Hungary (Csabai et al. 2020). We observed a similar tendency in the Masurian Lakeland. The density of boats had a significant effect on amphipod assemblage, especially on *D. villosus*. Yachting is a very significant component of tourism in the Masurian Lakeland, reaching 37% of total tourist activities in the region (Kulczyk et al. 2016). An example can be Niegocin Lake, with high tourist pressure and a large number of invasive species and rapid invasion of *D. villosus*, which was absent in 2014, while 2016 constituted 81% of all sampled gammarids. The lake is located between the other lakes with high tourist pressure, and the Masurian tourist route runs through the lake. It can also be characterised by a high number of car parks per km of shoreline and the highest number of beds in accommodation establishments in 2014, reaching more than five thousand for the area (i.e., community

Giżycko) (Kulczyk et al. 2016). Most of the marinas are located in the city with well-developed tourist facilities. We found a negative correlation between the number of boats and the distance of sampling points from the city. Indeed, the proximity to the city explains mainly the occurrence of *D. villosus*.

Distribution of other invasive species i.e. *P. robustoides*, *D. haemobaphes* and *C. ischnus* concern mainly the lakes with less developed shoreline and rather good water quality. Mainly, they are present in lakes with different conditions compared to those, where *D. villosus* was found. Especially two of these species - *D. haemobaphes* and *P. robustoides* - are weaker competitors than *D. villosus* and usually they occupy different niches (Bącela-Spychalska et al. 2012; Kobak et al. 2016). Records of *P. robustoides*, *D. haemobaphes* and *C. ischnus* in water bodies with good water quality are incompatible with the previous studies suggesting high ecological tolerance and the occurrence of invasive amphipods in polluted water bodies (Panov et al. 2009). Invasive species exhibit a broad tolerance to water quality, however, they tend to prefer waterbodies with high level of oxygenation and good overall water quality (Boets et al. 2010).

Expansion of the Ponto-Caspian amphipod fauna in Masurian Lakeland

One of the oldest Ponto-Caspian amphipod invaders in Europe and Poland is ***Chaetogammarus ischnus*** (see Grabowski et al. 2007). The species started spreading to the east reaching the Neman River and the Curonian Lagoon by the 1960s through the canal between the Bug and the Pripyat rivers (Bij de Vaate et al. 2002). In the western direction, *C. ischnus* colonised the Noteć River and the Oder River (Poland) before the 1970s (Grabowski et al. 2007). Our study is the first record of this species in the Masurian Lakeland. We suppose that *C. ischnus* has spread in this region from the Narew River and then from the Pisa River inasmuch as the species was not present in the Węgorapa River. The distribution of this species in the Masurian Lakeland is still low, similar to the general findings in Europe (Copilaș-Ciocianu et al. 2023a). However, small body size, ability to avoid bigger competitors (e.g. *Dikerogammarus* spp.) and occurring in different habitats may cause a further rapid expansion of this species (Borza et al. 2018). Interestingly, the abundance of *C. ischnus* is associated with *P. robustoides* and *D. haemobaphes*, suggesting the overlapping of their niches.

Dikerogammarus haemobaphes expanded in Eastern Europe very rapidly (Mordukhai-Boltovskoi 1964). Until 1980, the species was noticed in the lower and the middle Dnieper, the Dniester, the Don and the Volga rivers (Jażdżewski 1980). Since the 1990s the fast expansion of the species has begun (Jażdżewska et al. 2020). Species reached the Vistula River in 1997 (Konopacka 1998) and then the Oder River (Jażdżewski 2003). The species is currently present in almost every big European river (Jażdżewska et al. 2020). Also in the Masurian Lakeland, the species is common. Tourist activity could have promoted its further spread by sailing, angling, and diving equipment (Bącela-Spychalska 2016). Despite the high invasive potential, we observed a decrease in the abundance of this species in the studied area. For instance, compared to 2014, in 2016 the species almost disappeared from Dargin Lake (only two individuals found).

Another species, whose populations decline in the Masurian Lakeland, is ***Pontogammarus robustoides***. It has spread in Europe mainly by intentional introductions since the 1960s, e.g., in many Lithuanian and Ukrainian waters, including the Neman from where the species was able to reach the Baltic Sea (Mordukhai-Boltovskoi 1964; Arbačiauskas 2002). Two hypotheses exist regarding how the species arrived in Poland: one suggests it came from Lithuania through Belarus's rivers (Mastisky and Makarevich, 2007), while the other proposes its origin from the mesohaline coastal waters of the Baltic (see Grabowski et al., 2007). In 2007, Jażdżewska and Jażdżewski (2008) recorded *P. robustoides* for the first time in the Masurian Lakeland. Three hypothetical ways of invasion to this region were proposed - from Kaliningrad (Russia) via the Pregel and the Węgorapa rivers; from Lithuania via the Augustów Canal; from the Baltic Sea via the Vistula River and its affluents (Jażdżewska and Jażdżewski 2008). The appearance of *P. robustoides* in 2007 in the Masurian Lakeland started rapid expansions of this species which coincided with the significant decrease in the abundance of native *Gammarus lacustris* (Jażdżewska and Jażdżewski 2008). However, the invasions of *D. villosus* in 2014 caused a decrease in *P. robustoides* abundance. In 2016 this species disappeared from one lake compared to 2014 as well as in Niegocin the population was eradicating (only two individuals were found).

Dikerogammarus villosus seems to be the most successful invader in Europe (Rewicz et al. 2014; Rewicz et al. 2015) as well as in the studied area. The first records of the species beyond its native range come from 1926 from the Danube River (Nesemann et al. 1995). In 1999 the species was first time recorded in Poland in the Oder River (Gruszka 2000; Jażdżewski and

Konopacka 2002; Jażdżewski et al. 2002) and the Szczeciński Lagoon (Jażdżewski et al. 2005). The species also spread via the central corridor promoted by the Soviet intentional introductions to the artificial dam reservoirs on the Dnieper River (Rewicz et al. 2014). Nextly, it reached the Pripyat River, the Bug River and in 2007 the Vistula River in Poland (Konopacka 2004; Bącela et al. 2008). Our study shows the first species record in the Masurian Lakeland from 2014. The species was not recorded in rivers connecting the Masurian Lakeland with the Central invasion corridor (sensu bij de Vaate et al. 2002) i.e., the Vistula River, suggesting possible expansion by overland transport. The species was shown to utilise submerged parts of boats, ropes and diving gears (Bącela-Spychalska et al. 2013; Bącela-Spychalska et al. 2016; Minchin et al. 2019) to spread. *D. villosus* eliminates other invasive and native gammarids (Dick and Platvoet 2000; Platvoet et al. 2007, Bącela-Spychalska et al. 2012). Our results confirm these observations. *D. villosus* has become the most abundant gammarid in the Masurian Lakeland over two years. Between 2014 and 2016 the abundance of the species and area of occurrence significantly increased. This phenomenon may be more common in the future as a result of climate change (Hesselschwerdt and Wantzen 2018). Our study shows that new invaders in the Masurian Lakeland (i.e. *C. ischnus* and, particularly, *D. villosus*) are spreading in the studied area, while old invaders (*D. haemobaphes, P. robustoides*) possibly lose the competition with the newcomers.

The impact of invasive species on aquatic ecosystems is profound (Kurashov et al. 2012). NIS modify habitats as well as food chains. The presence of invasive amphipods, known to be ecosystem engineers, worsens the ecological state of lakes through ecosystem transformation (Jones et al. 1994; Jones et al. 1997). Invasions contribute to change in the energy flow - benthic communities are transformed from being energy suppliers to upper trophic levels i.e., major users of ecosystem energy (Nalepa et al. 2009; Kurashov et al. 2012).

Conclusions

The rapid expansion of the invasive Ponto-Caspian amphipods observed in this study aligns with a general trend along European freshwater basins. The contraction of the range and niche of native species when faced with more aggressive (e.g., *D. villosus*), generalist (e.g., *C. ischnus*), and even environmental engineering species (e.g., *C. curvispinum*) is something expected and confirmed by our findings. Even though many lakes seem to be still free from amphipod invaders, this may be for a short time considering the abrupt increase we registered in just two years.

In conclusion, our study emphasises the need for a comprehensive approach to understanding and addressing the dispersion of alien species through human activity. To gain deeper insights into these dynamics, we recommend the establishment of an inter-lakes traffic registry. This registry would provide crucial data on the movement of boats and potential pathways for the introduction of invasive species. Furthermore, it is essential to raise awareness among lake users about the negative consequences of biological invasions and the necessity of implementing such a registry. By educating and engaging lake users, we can foster a sense of responsibility and cooperation in preventing the spread of invasive species. Implementing these measures collectively will contribute to better biosecurity practices and safeguard the ecological integrity of lakes against invasive species.

Acknowledgements

We are grateful to the Committee on Scientific Research, Polish Ministry for Science and Higher Education grants, National Science Centre and the Department of Invertebrate Zoology and Hydrobiology of University of Lodz for funding. We would like to thank Krzysztof Jażdżewski, Ewa Janowska, Mariusz Surlejewski, Olga Antczak-Orlewska, Paula Krzywoźniak, Remi Wattier, Aleksandra Jabłońska and Anna Jażdżewska for help during sampling and suggestions and Antoine Fages for help with initial analysis.

References

Anderson LG, White PCL, Stebbing PD, Stentiford GD, Dunn AM (2014) Biosecurity and vector behaviour: Evaluating the potential threat posed by anglers and canoeists as pathways for the spread of invasive non-native species and pathogens. PLoS ONE 9: 1–10. https://doi.org/10.1371/journal.pone.0092788

Arbačiauskas K (2002) Ponto-Caspian amphipods and mysids in the inland waters in Lithuania: History of introduction, current distribution and relations with native malacostracans. In: Leppäkoski E, Gollasch S, Olenin S (Eds) Invasive Aquatic Species of Europe – Distribution, Impact and Managements, Kluwer Academic Publisher, Dordrecht, 104-115.

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: 28–37.

Aronow S (1982) Shoreline development ratio . In: Beaches and Coastal Geology. Encyclopedia of Earth Sciences Series. Springer, New York, NY. https://doi.org/10.1007/0-387-30843-1_417

Bajkiewicz-Grabowska E (2008) Obieg wody w systemie Wielkich Jezior Mazurskich [*Water circulation in the Great Masurian Lake System*]. In: Jasser I, Robak S, Zdanowski B (Eds), Ochrona i rekultywacja wód Wielkich Jezior Mazurskich narzędziem rozwoju naukowego, gospodarczego, społecznego i kulturowego regionu [*Protection and reclamation of water in the Great Masurian Lakes as a tool of scientific, economic social and cultural development of the region*]. IRS, Olsztyn, 19–29 [In Polish].

Bącela K, Grabowski M, Konopacka A (2008) *Dikerogammarus villosus* (Sowinsky , 1894) (Crustacea, Amphipoda) enters Vistula – the biggest river in the Baltic basin. Aquatic Invasions 3: 95–98.

Bącela-Spychalska K (2016) Attachment ability of two invasive amphipod species may promote their spread by overland transport." Aquatic Conservation: Marine and Freshwater Ecosystems 26 (1): 196-201.

Bącela-Spychalska K, Wattier RA, Genton C, Rigaud T (2012) Microsporidian disease of the invasive amphipod *Dikerogammarus villosus* and the potential for its transfer to local invertebrate fauna. Biological Invasions 14: 1831–1842. https://doi.org/10.1007/s10530-012-0193-1

Bącela-Spychalska K, Grabowski M, Rewicz T, Konopacka A, Wattier R (2013) The ‘killer Shrimp’ *Dikerogammarus villosus* (Crustacea, Amphipoda) invading Alpine lakes: Overland transport by recreational boats and scuba-diving gear as potential entry vectors? Aquatic Conservation: Marine and Freshwater Ecosystems 23: 606–618.

Bij de Vaate A, Jażdżewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. Canadian Journal of Fisheries and Aquatic Sciences 59: 1159–1174.

Boets P, Lock K, Messiaen M, Goethals PLM (2010) Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. Ecological Informatics 5: 133-139.

Borza P, Huber T, Leitner P, Remund N, Graf W (2018) How to coexist with the 'killer shrimp' *Dikerogammarus villosus*? Lessons from other invasive Ponto-Caspian peracarids. Aquatic Conservation: Marine and Freshwater Ecosystems 28: 1441–1450. https://doi.org/10.1002/aqc.2985

Bozdogan H (1987) Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. Psychometrika 52, 345–370. https://doi.org/10.1007/BF02294361

Bradshaw C, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Barbet-Massin M, Salles J-M, Simard F, Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. Nature Communications 7: e12986 doi: 10.1038/ncomms12986.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) "glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling." The R Journal, 9(2): 378–400. doi:10.32614/RJ-2017-066.

Chesson P (2000) General theory of competitive coexistence in spatially-varying environments. Theoretical Population Biology 58: 211–237.

Chróst RJ, Siuda W (2006) Microbial production, utilization, and enzymatic degradation of organic matter in the upper trophogenic layer in the pelagial zone of lakes along a eutrophication gradient. Limnology and Oceanography 51: 749–762.

Cole GA (1975) Textbook of Limnology. St. Louis, Mo.: C. V. Mosby Co., 283p.

Copilaş-Ciocianu D, Sidorov D (2022) Taxonomic, ecological and morphological diversity of Ponto-Caspian gammaroidean amphipods: a review. Organisms Diversity & Evolution 22: 285–315 https://doi.org/10.1007/s13127-021-00536-6

Copilaş-Ciocianu D, Rewicz T, Sands AF, Palatov D, Marin I, Arbačiauskas K, Hebert PDN, Grabowski M, Audzijonyte A (2022) A DNA barcode reference library for endemic Ponto-Caspian amphipods. Scientific Reports 12, 11332 https://doi.org/10.1038/s41598-022-15442-w

Copilaş-Ciocianu D, Sidorov D, Šidagytė-Copilas E (2023a) Global distribution and diversity of alien Ponto-Caspian amphipods. Biological Invasions 25: 179–195. https://doi.org/10.1007/s10530-022-02908-1

Copilaş-Ciocianu, D, Palatov D, Rewicz T, Sands AF, Arbačiauskas K, van Haaren T., Hebert PN, Grabowski M, Marin I (2023b) A widespread Ponto-Caspian invader with a mistaken identity: integrative taxonomy elucidates the confusing taxonomy of Trichogammarus trichiatus (= Echinogammarus) (Crustacea: Amphipoda). Zoological Journal of the Linnean Society 198 (3): 821–846.

Cristescu MEA, Hebert PDN (2005) The “Crustacean Seas” - An evolutionary perspective on the Ponto-Caspian peracarids. Canadian Journal of Fisheries and Aquatic Sciences 62: 505–517. https://doi.org/10.1139/f04-210

Cuthbert RN, Diagne C, Hudgins EJ, Turbelin A, Ahmed DA, Albert C, Bodey TW, Briski E, Essl F, Haubrock PJ, Gozlan RE, Kirichenko N, Kourantidou M, Kramer AM, Courchamp F (2021a) Biological invasion costs reveal insufficient proactive management worldwide, Science of The Total Environment 819, https://doi.org/10.1016/j.scitotenv.2022.153404.

Cuthbert RN, Pattison Z, Taylor NG, Verbrugge I, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Ells F, Gozlan RE, Haubrock PJ, Kourantidou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021b) Global economic costs of aquatic invasive species. Science of the Total Environment 775: e145238. DOI: 10.1016/j.scitotenv.2021.145238.

Csabai Z, Borza P, Rewicz T, Pernecker B, Berta BJ, Móra A (2020) Mass appearance of the Ponto-Caspian invader *Pontogammarus robustoides* in the River Tisza catchment:

Bypass in the southern invasion corridor? Knowledge and Management of Aquatic Ecosystems 421. https://doi.org/10.1051/kmae/2020003

de Ventura L, Wissert N, Tobias R, Kopp K, Jokela J (2016) Overland transport of recreational boats as a spreading vector of zebra mussel *Dreissena polymorpha*. Biological Invasions 18: 1451-1466.

Dick JTA, Platvoet D (1996) Intraguild predation and species exclusions in amphipods: The interaction of behaviour, physiology and environment. Freshwater Biology 36: 375–383.

Dick JTA, Platvoet D (2000) Invading predatory crustacean Dikerogammarus villosus eliminates both native and exotic species. Proceedings of the Royal Society B: Biological Sciences 267: 977–983.

Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: Importance, threats, status and conservation challenges. Biological Reviews of the Cambridge Philosophical Society 81: 163–182. https://doi.org/10.1017/S1464793105006950

Dz. U. poz. 1612, z późn. zm., available at https://isap.sejm.gov.pl/isap.nsf/home.xsp

Eggers TO, Martens A (2001) Bestimmungsschlüssel der Süßwasser-Amphipoda (Crustacea) Deutschlands. Lauterbornia 42: 1-68.

Ejsmont-Karabin J, Kalinowska K, Karpowicz M (2020) Structure of Ciliate, Rotifer, and Crustacean Communities in Lake Systems of Northeastern Poland. In: Korzeniewska, E., Harnisz, M. (Eds) Polish River Basins and Lakes – Part II. The Handbook of Environmental Chemistry 87. Springer, Cham. https://doi.org/10.1007/978-3-030-12139-6_4

Fee EJ (1979) A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments, Limnology and Oceanography 24. doi: 10.4319/lo.1979.24.3.0401.

Feld CK, Birk S, Eme D, Gerisch M, Hering D, Kernan M, Maileht K, Mischke U, Ott I, Pletterbauer F, Poikane S, Salgado J, Sayer CD, Van Wichelen J, Malard F (2016) Disentangling the effects of land use and geo-climatic factors on diversity in European freshwater ecosystems. Ecological Indicators 60: 71–83. https://doi.org/10.1016/j.ecolind.2015.06.024

Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JH, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. Science 309: 570–574. https://doi.org/10.1126/science.1111772

Galil BS, Nehring S, Panov V (2008) Waterways as Invasion Highways – Impact of Climate Change and Globalization. In: Nentwig, W. (Eds) Biological Invasions. Ecological Studies, vol 193. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-36920-2_5

Glisson WJ, Wagner CK, Verhoeven R, Muthukrishnan R, Contreras-Rangel R, Larkin DJ (2020) Desiccation tolerance of the invasive alga starry stonewort (*Nitellopsis obtuse*) as an indicator of overland spread risk. Journal of Aquatic Plant Management 58: 7-18.

Grabowski M, Konopacka A, Jażdżewski K, Janowska E (2006) Invasions of alien gammarid species and retreat of natives in the Vistula Lagoon (Baltic Sea, Poland). Helgoland Marine Research 60: 90–97.

Grabowski M, Jaździewski K, Konopacka A (2007) Alien crustacea in polish waters - Amphipoda. Aquatic Invasions 2: 25–38. https://doi.org/10.3391/ai.2007.2.1.3

Grabowski M, Bącela K, Konopacka A, Jażdżewski K (2009) Salinity-related distribution of alien amphipods in rivers provides refugia for native species. Biological Invasions 11: 2107–2117. https://doi.org/10.1007/s10530-009-9502-8

Gruszka P (1999) The River Odra Estuary as a Gateway for Alien Species Immigration to the Baltic Sea Basin. Acta hydrochimica et hydrobiologica 27: 374–382.

Gruszka P (2000) *Dikerogammarus haemobaphes* (Eichwald, 1841) (Crustacea:Amphipoda) – nowy gatunek w rzece Odrze. Materiały Zjazdowe: XVIII Zjazd Hydrobiologów Polskich, Białystok: 87. [in Polish]

Hall MC, Härkönen T (2006) Lake Tourism: An Integrated Approach to Lacustrine Tourism Systems, Channel View Publications, Bristol.

Hartig F (2022). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6

Hesselschwerdt J, Wantzen KM (2018) Global warming may lower thermal barriers against invasive species in freshwater ecosystems - A study from Lake Constance. Sci Total Environ 645: 44-50. doi: 10.1016/j.scitotenv.2018.07.078.

Hesselschwerdt J, Meeker J, Wantzen KM (2008) Gammarids in Lake Constance: Habitat segregation between the invasive *Dikerogammarus villosus* and the indigenous *Gammarus roeselii*. Fundamental and Applied Limnology 173: 177–186. https://doi.org/10.1127/1863-9135/2008/0173-0177

Hillbricht-Ilkowska A, Rybak J, Rzepecki M (2000) Ecohydrological research of lake – watershed relations in diversified landscape (Masurian Lakeland, Poland). Ecological Engineering 16: 91–98.

Jażdżewska A, Jażdżewski K (2008) *Pontogammarus robustoides* (G.O. Sars, 1894) (Crustacea, Amphiopoda), a new Ponto-Caspian invader in Great Masurian Lakes (NE Poland). Fragmenta Faunistica 51: 1–7.

Jażdżewska AM, Rewicz T, Mamos T, Wattier R, Bącela-Spychalska K, Grabowski M (2020) Cryptic diversity and mtDNA phylogeography of the invasive demon shrimp, *Dikerogammarus haemobaphes* (Eichwald, 1841), in Europe. NeoBiota 57: 53–86. https://doi.org/10.3897/neobiota.57.46699

Jażdżewski K (1980) Range Extensions of Some Gammaridean Species in European Inland Waters Caused by Human Activity. Crustaceana: 84–107.

Jażdżewski K (2003) An invasive Ponto-Caspian amphipod - *Dikerogammarus haemobaphes* (Eichwald, 1841) - conquers Great Masurian Lakes, north-eastern Poland. Fragmenta Faunistica 46: 19–25.

Jażdżewski K, Konopacka A (1995) Malacostraca prócz Oniscoidea. In: Mroczkowski M (Eds), Katalog Fauny Polskiej 13 (1): 1-165. [in Polish]

Jażdżewski K, Konopacka A (2000) Immigration history and present distribution of alien crustaceans in Polish waters. In: von Vaupel Klein JC, Schram FR (Eds), The biodiversity crisis and Crustacea, Proceedings of 4th International Crustacean Congress, Brill, Leiden, Crustacean Issues 12: 55-64.

Jażdżewski K, Konopacka A (2002). Invasive Ponto-Caspian Species in Waters of the Vistula and Oder Basins and the Southern Baltic Sea. In: Leppäkoski E, Gollasch S, Olenin S (Eds) Invasive Aquatic Species of Europe. Distribution, Impacts and Management. Springer, Dordrecht. https://doi.org/10.1007/978-94-015-9956-6_39

Jażdżewski K, Konopacka A, Grabowski M (2002) Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) recently invading Polish waters. Contributions to Zoology 71: 115–122.

Jażdżewski K, Konopacka A, Grabowski M (2005) Native and alien Malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century Oceanological and Hydrobiological Studies Vol . XXXIV , Supplement 1. Oceanobiological and Hydrobiological Studies 34: 175–193.

Johnson LE, Padilla DK (1996) Geographic spread of exotic species: Ecological lessons and opportunities from the invasion of the zebra musel *Dreissena polymorpha*. Biological Conservation 78: 23–33.

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69: 373–386.

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78 (7): 1946–1957.

Kettunen M, Genovesi P, Gollasch S, Pagad S, Starfinger U. Ten Brink P, Shine C (2009) Technical support to EU strategy on invasive species (IAS) - Assessment of the impacts of IAS in Europe and the EU (final module report for the European Commission). Institute for European Environmental Policy (IEEP), Brussels, Belgium. 44 pp. + Annexes

Kistowski M, Śleszyński P (2010) Presja turystyczna na tle walorów turystycznych Polski. Prace Komisji Krajobrazu Kulturowego Nr 14 [in Polish]

Kobak J, Rachalewski M, Bącela-Spychalska K (2016) Conquerors or exiles ? Impact of interference competition among invasive Ponto-Caspian gammarideans on their dispersal rates. 18: 1953–1965. https://doi.org/10.1007/s10530-016-1140-3

Kondracki J (2002) Geografia regionalna Polski, Warszawa, PWN, ISBN 83-01-13897-1. [in Polish]

Konopacka A (1998) Nowy dla Polski gatunek kiełża, *Dikerogammarus haemobaphes* (EICHWALD, 1841) (Crustacea, Amphipoda) oraz dwa inne rzadkie gatunki skorupiaków obunogich w Wiśle. Przegląd Zoologiczny 3-4: 211-218. [in Polish]

Konopacka A (2004) Inwazyjne skorupiaki obunogie (Crustacea, Amphipoda) w wodach Polski. Przegląd Zoologiczny 48: 141-162. [in Polish]

Konopacka A, Jażdżewski K (2002) *Obesogammarus crassus* (G.O. Sars, 1894) – one more Ponto-Caspian gammarid species in Polish waters. Fragmenta Faunistica 45: 19–26. https://doi.org/10.3161/00159301ff2002.45.1.019

Kouba A, Oficialdegui FJ, Cuthbert RN, Kourantidou M, South J, Tricarico E, Gozlan RE, Courchamp F, Haubrock PJ (2022) Identifying economic costs and knowledge gaps of invasive aquatic crustaceans. Science of the Total Environment 813. https://doi.org/10.1016/j.scitotenv.2021.152325

Kulczyk S, Derek M, Woźniak E (2016) Zagospodarowanie turystyczne strefy brzegowej jezior na potrzeby żeglarstwa - przykład wielkich jezior mazurskich. Prace i Studia Geograficzne 61 (3): 27–49. [in Polish]

Kurashov EA, Barbashova MA, Barkov DV, Rusanov AG, Lavrova MS (2012) Invasive amphipods as a factor of transformation of Lake Ladoga ecosystems. Russian Journal of Biological Invasions 3: 202–212. https://doi.org/10.1134/S2075111712030058

Lambertini M Leape J, Marton-Lefevre J, Mittermeier R, Rose M, Robinson J, Stuart S, Waldman B, Genovesi P (2011) Invasives: a major conservation threat. Science 333: 404–405.

Legendre P, Anderson MJ (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial ecological experiments. Ecological Monographs, 69: 1-24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Local Data Bank of the Warmian-Masurian Voivodeship, 2021, https://bdl.stat.gov.pl/bdl/dane/teryt/jednostka/2889

Mačić V, Albano PG, Almpanidou V, Claudet J, Corrales X, Essl F, Evagelopoulos A, Giovos I, Jimenez C, Kark S, Marković O, Mazaris AD, Ólafsdóttir G, Panayotova M, Petović S, Rabitsch W, Ramdani M, Rilov G, Tricarico E, Fernández TV, Sini M, Trygonis V, Katsanevakis S (2018) Biological invasions in conservation planning: A global systematic review. Frontiers in Marine Science 5. https://doi.org/10.3389/fmars.2018.00178

Martinez Arbizu P (2020) pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4

mazury24.eu, https://mazury24.eu

Meßner U, Zettler MB (2021) Drastic changes of the amphipod fauna in northern Germany and the displacement of *Gammarus lacustris* G.O. Sars, 1864 to relict habitats/status. Knowl. Manag. Aquat. Ecosyst 422 (17): 1-8.

Minchin D, Arbačiauskas K, Daunys D, Ezhova E, Grudule N, Kotta J, Molchanova N, Olenin S, Višinskienė G, Strake S (2019) Rapid expansion and facilitating factors of the Ponto-Caspian invader *Dikerogammarus villosus* within the Eastern Baltic sea. Aquatic Invasions 14: 165–181. https://doi.org/10.3391/ai.2019.14.2.02

mojemazury.pl: https://mojemazury.pl

Mordukhai-Boltovskoi FD (1964) Caspian fauna beyond the Caspian Sea. International Review of Hydrobiology and Hydrography 49: 139–176. https://doi.org/10.1002/iroh.19640490105

Nalepa TF, Fanslow DL, Lang GA (2009) Transformation of the offshore benthic community in Lake Michigan: Recent shift from the native amphipod Diporeia spp. to the invasive mussel Dreissena rostriformis bugensis. Freshwater Biology 54: 466–479. https://doi.org/10.1111/j.1365-2427.2008.02123.x

Nesemann H, Pöckl M, Wittmann KJ (1995) Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). Miscellanea Zoologica Hungarica 10: 49-68.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) vegan: Community Ecology Package. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>.

Panlasigui S, Davis AJS, Mangiante MJ, Darling JA (2018) Assessing threats of non-native species to native freshwater biodiversity: Conservation priorities for the United States. Biological Conservation 224: 199–208. https://doi.org/10.1016/j.biocon.2018.05.019

Panov VE, Alexandrov B, Arbačiauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RS, Nehring S, Paunović M, Semenchenko V, Son MO (2009) Assessing the risks of aquatic species invasions via european inland waterways: from concepts to environmental indicators. Integrated Environmental Assessment and Management 5: 110-126. https://doi.org/10.1897/IEAM_2008-034.1

Pinkster S, Scheepmaker M, Platvoet D, Broodbakker N (1992) Drastic changes in the amphipod fauna (Crustacea) of Dutch inland waters during the last 25 years. Bijdragen tot de Dierkunde, 61 (4): 193-204. doi: https://doi.org/10.1163/26660644-06104001

Platvoet D, Song Y, Shuqiang L, Van der Velde G (2007) Description of the lateral line organ of Dikerogammarus villosus (Sowinsky, 1894), with discussion on its function (Peracarida, Amphipoda). Crustaceana 80: 1373–1392.

Pöckl M, Grabowski M, Grabowska J, Bącela-Spychalska K, Wittmann KJ (2011) Large European rivers as biological invasion highways. In: Habersack H, Schober B Walling D (eds.), International Conference on the Status and Future of the World's Large Rivers, 11-14 April 2011, Vienna; Conference Abstract Book: 215

Pyšek P, Richardson DM (2010) Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35: 25–55. https://doi.org/10.1146/annurev-environ-033009-095548

R Core Team (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Rachalewski M, Grabowski M, Konopacka A, Bącela-Spychalska K (2013) *Echinogammarus trichiatus* (Martynov, 1932)' A new ponto-caspian amphipod invader in poland with remarks on other alien amphipods from the oder river. Crustaceana 86: 1224–1233. https://doi.org/10.1163/15685403-00003228

Rewicz T, Grabowski M, Macneil C, Bącela-Spychalska K (2014) The profile of a ' perfect ' invader – the case of killer shrimp, *Dikerogammarus villosus*. Aquatic Invasions 9: 267–288. https://doi.org/10.3391/ai.2014.9.3.04

Rewicz T, Wattier R, Grabowski M, Rigaud T, Bącela-Spychalska K (2015) Out of the Black Sea: Phylogeography of the Invasive Killer Shrimp *Dikerogammarus villosus* across Europe. *PLOS ONE* 10: e0118121.

Rewicz T, Wattier R, Rigaud T, Grabowski M, Mamos T, Bącela-Spychalska K (2017) The killer shrimp, *Dikerogammarus villosus*, invading European Alpine Lakes: A single main source but independent founder events with an overall loss of genetic diversity. Freshwater Biology 62: 1036– 1051. https://doi.org/10.1111/fwb.12923.

Ricciardi A, Rasmussen JB (1998) Predicting the identity and impact of future biological invaders: A priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55: 1759–1765.

Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great lakes by Ponto-Caspian species. Trends in Ecology & Evolution 15: 62–65.

Ricciardi A, Kipp R (2008) Predicting the number of ecologically harmful exotic species in an aquatic system. Diversity and Distributions 14: 374–380.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, et al. (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

skorupki.mazury.info.pl: https://skorupki.mazury.info.pl

Smith ERC, Bennion H, Sayer CD, Aldridge DC, Owen M (2020) Recreational angling as a pathway for invasive non-native species spread: awareness of biosecurity and the risk of long distance movement into Great Britain. Biological Invasions 22: 1135–1159. https://doi.org/10.1007/s10530-019-02169-5

Soszka H, Kolada A, Pasztaleniec A, Ochocka A, Kutyła S, Bielczyńska A (2016) Opracowanie zbiorczej oceny stanu jezior. Institute of Environmental Protection - National Research Institute [in Polish]

State of Water report, EEA, 2018

Strayer DL, Dudgeon D (2010) Freshwater biodiversity conservation: Recent progress and future challenges. Journal of the North American Benthological Society 29: 344–358. https://doi.org/10.1899/08-171.1

Ulikowski D, Traczuk P, Kapusta A, Kalinowska K (2021) New records of alien monkey goby, *Neogobius fluviatilis* (Pallas, 1814), in the waters of the Great Masurian Lakes system (northeastern Poland). BioInvasions Records 10 (4): 924–933, https://doi.org/10.3391/bir. 2021.10.4.17

Water Framework Directive (WFD, 2000)

Väinölä R, Witt JDS, Grabowski M, Bradbury JH, Jażdżewski K, Sket B (2008) Freshwater Animal Diversity Assessment. Hydrobiologia 595: 241–255.

Van der Velde G, Leuven RSEW, Platvoet D, Bącela K, Huijbregts MAJ, Hendriks HWM, Kruijt D (2009) Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. Biological Invasions 11: 2043–2054. https://doi.org/10.1007/s10530-009-9500-x

Van Riel MC, Velde G Van Der, Rajagopal S, Marguillier S, Dehairs F, Bij de Vaate A (2006) Trophic relationships in the Rhine food web during invasion and after establishment of the Ponto-Caspian invader *Dikerogammarus villosus*. Hydrobiologia 565: 39–58. https://doi.org/10.1007/s10750-005-1904-8

Vander Zanden MJ, Olden JD (2008) A management framework for preventing the secondary spread of aquatic invasive species. Canadian Journal of Fisheries and Aquatic Sciences 65: 1512–1522.

Zhulidov AV, Kozhara AV, van der Velde G, Leuven RSEW, Son MO, Gurtovaya TY, Zhulidov DA, Nalepa TF, Santiago-Fandino VJR, Chuikov YS (2018) Status of the invasive brackish water bivalve *Mytilopsis leucophaeata* (Conrad, 1831) (Dreissenidae) in the Ponto-Caspian region. BioInvasions Records 7: 111–120. https://doi.org/10.3391/bir.2018.7.2.02