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Does the Ice Age legacy end in Central Europe? The shrinking distributions of glacial relict crustaceans in Lithuania

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Abstract

1. Glacial relict crustaceans are characterized by their affinity for cold and well-oxygenated waters and their limited dispersal ability. They occur in large, deep lakes of Northern and Central Europe and North America, with their distributions shaped by glaciation events. In many countries and especially along the southern distribution edge, glacial relict populations are declining as a result of eutrophication, global warming, and possible adverse interactions with invasive Ponto-Caspian crustaceans.
2. This study assessed the status of three glacial relict malacostracan species (the amphipods *Monoporeia affinis* and *Pallaseopsis quadrispinosa* and the mysid *Mysis relicta*) in Lithuania and modelled their abundance across environmental variables, including the presence of Ponto-Caspian malacostracans.
3. The results showed that *M. affinis* is probably extinct in the country, whereas *M. relicta* was found in only nine out of 16 locations from which it was previously recorded. The distribution of *P. quadrispinosa* also seems to be shrinking.
4. The annual water renewal rate (*P. quadrispinosa* and *M. relicta*) and lake depth (*P. quadrispinosa*) were significantly and positively associated with the relative abundance of relict mysids and amphipods, but no association was found with lake size or with the presence of invasive Ponto-Caspian crustaceans. Both species were less abundant in samples collected in the 21st century compared with the 20th century.
5. Given the biogeographical and ecological importance of glacial relict crustaceans, their widespread declines are of concern and point to the deterioration of habitat quality, essential for other species with similar requirements. Urgent action is needed to improve water conditions and safeguard these communities. In cases where water quality improves, the reintroduction of extirpated relict populations should be considered. One example is Lake Drūkšiai, where these crustaceans became extinct during the operation of the Ignalina nuclear power plant but where conditions improved following the closure of the power plant in 2009.

KEYWORDS
biological invasion, climate change, eutrophication, glacial relicts, *Monoporeia affinis*, *Mysis relicta*, *Pallaseopsis quadrispinosa*, Ponto-Caspian crustaceans

1 | INTRODUCTION

Several species of malacostracan crustaceans, and mysids and amphipods in particular, have colonized the Baltic Sea and inland waters of Northern and Central Europe and North America through waterways created by post-glaciation events (Segerstråle, 1957; Holmquist, 1966; Väinölä, 1998; Audzijonyte, 2006). Their colonization history has been complex and most likely included several waves, facilitated by expanding and contracting ice sheets (Väinölä, 1990; Audzijonytė et al., 2005). For example, European and North American lakes are colonized by four closely related species of glacial relict mysids, formerly known as a single species, *Mysis relicta* Lovén, 1862, but now separated into morphologically, physiologically, and ecologically distinct species with different phylogenetic and colonization histories (Väinölä, 1990; Audzijonytė et al., 2005; Audzijonytė & Väinölä, 2005; Audzijonyte, 2006; Audzijonyte & Väinölä, 2006). These species cannot actively swim upstream, they brood live young, are confined mainly to deeper waters, and generally cannot be dispersed by birds or other natural external agents (Segerstråle, 1957; Väinölä, 1990; Väinölä, 1998). Their dispersal and present occurrences, naturally confined to the formerly glaciated areas, have contributed to the original idea that past glaciation events might have shaped the present distribution of species and populations (Lovén, 1862; Högbom, 1916). These crustacean species are characterized by a requirement for cold and well-oxygenated water (Suschenya, Semenchenko & Vezhnavets, 1986; Waterstraat, 1988), and are often referred to as glacial relicts (Lovén, 1862; Thienemann, 1925; Audzijonytė & Väinölä, 2005). They typically inhabit large oligotrophic and mesotrophic lakes of North America and Europe. In Europe, glacial relict species are common in Scandinavia and Northern Russia (Spikkeland et al., 2016; Berezina, Kalinkina & Maximov, 2021), with their southern distribution limit extending to Britain, Ireland, Germany, Poland, Lithuania, and Belarus (Gasiūnas, 1959; Köhn & Waterstraat, 1990; Żmudziński, 1990; Penk, 2011; Griffiths et al., 2015).

In suitable habitats, glacial relict crustaceans can be found in high abundance and play a significant ecological role in pelagic food webs, often comprising most of the diet of commercially valuable inland fish species, such as vendace, whitefish, and others (Lasenby, Northcote & Fürst, 1986; Sandlund, N sje & Jonsson, 1992; Scharf et al., 2008). In Lake Ontario, for example, the mysid *Mysis diluviana* (Audzijonytė & Väinölä, 2005) (formerly *M. relicta*) represents a third of all pelagic crustacean biomass and makes up to 60%–90% of the diets of pelagic fishes (Holda et al., 2019). Owing to diel vertical migration, glacial relict mysids also contribute to lake benthic food webs and benthic–pelagic coupling (Stockwell et al., 2020). However, during the 20th century and especially during the last few decades, glacial relict crustaceans face increasing human pressure, with extinctions or rapid declines in abundance reported in many locations. The rarest of these relict species is the amphipod *Monoporeia affinis* (Lindström, 1855), usually found only in the largest, deep lakes with low trophic levels (Ekman, 1953; Köhn & Waterstraat, 1990). This species is now considered extinct in Germany (Köhn & Waterstraat, 1990) and Poland (Żmudziński, 1995), but is still known to occur in one lake in Belarus (V.V. Vezhnavets, 2021, pers. comm.). Other glacial relict species are also declining in abundance. In the North American Lake Ontario, for example, the abundance and biomass of *M. diluviana* has more than halved over the last few decades (Holda, 2017). In Ireland, *Mysis salemaai* (Audzijonytė & Väinölä, 2005) (formerly *M. relicta*) is known to occur in 14 lakes in total, but between 1993 and 2012 its abundance in two major lakes (Lough Neagh and Lough Erne) declined by 96% and 58%, respectively (Griffiths et al., 2015). In Britain, the only known population of relict mysids (*M. salemaai*) was found in Ennerdale Water (Cumbria), but this population is now considered extinct (Penk, 2011). Even in Norway, *M. salemaai* is now elevated to 'Vulnerable' (Spikkeland et al., 2016).

Glacial relict crustaceans are often listed in national Red Lists, but more decisive action is required to safeguard their persistence. Two main factors implicated in the decrease of relict populations are the eutrophication of lakes and the increasing water temperatures caused by global heating (Griffiths, 2007; Penk et al., 2015). Eutrophication reduces the availability of oxygen in deeper and cooler water layers, whereas higher temperatures reduce relict crustacean reproduction and growth rates and body condition (Griffiths, 2007). Another potential but less studied factor is the introduction or invasions of mysids and amphipods from the Ponto-Caspian region. Ponto-Caspian malacostracans are among the major invaders of European inland ecosystems (Jażdżewski, 1980; Bij de Vaate et al., 2002), and are known to be highly successful competitors and predators (Dick & Platvoet, 2000; Arbačiauskas & Gumuliauskaitė, 2007). Invading Ponto-Caspian amphipods are out-competing native shallow-water amphipods in Lithuania (Arbačiauskas, 2005) and Germany (Meßner & Zettler, 2021), and it has been suggested that Ponto-Caspian amphipods and mysids are also likely to have competitive interactions with glacial relict mysids (Arbačiauskas, 2005; Penk, Donohue & Irvine, 2018) or affect their habitat quality and local distributions (MacNeil & Dick, 2012). Yet, to our knowledge, there are no formal statistical tests on the role of the Ponto-Caspian crustaceans in the disappearance of glacial relicts.

The decline and extinctions of glacial relict crustaceans are of concern for at least three reasons. First, from a biodiversity perspective, these species comprise a unique biogeographical element of freshwater fauna, closely linked to marine colonizations and glaciation events (Segerstråle, 1957; Audzijonyte, 2006; Väinölä &

Johannesson, 2017). From an ecological perspective, relict crustacean populations play an important role in aquatic food webs, both as predators and prey (see references in Stockwell et al., 2020). Finally, these crustaceans, being sensitive to low oxygen conditions (Thienemann, 1925; Griffiths, 2007; Paterson et al., 2022), serve as indicators of freshwater ecosystem status and reflect habitat quality for many other associated plant, invertebrate, and fish species that require cold and oxygenated waters. The rapidly accelerating impacts of global heating on freshwater ecosystems are likely to exacerbate the decline of glacial relict crustaceans and associated communities, yet recent data on population status in Europe remain scarce. To address this knowledge gap, this study presents information on the status of glacial relict malacostracan crustaceans in Lithuania, using data from both historical and recent records to model statistically the predictors of relict species abundance and address the potential role of Ponto-Caspian crustaceans in the decline of native glacial relict species.

2 | METHODS

2.1 | Species

The original investigations of glacial relict species distributions in Lithuania were conducted in the mid-20th century and were based on extensive sampling of all lakes potentially suitable for these species (Gasiūnas, 1959; Grigelis, 1980) (Appendix S1). The three glacial relict malacostracan species recorded in Lithuania and studied here are the relict mysid *M. relicta* and the amphipods *M. affinis* and *Pallaseopsis quadrispinosa* (G.O. Sars, 1867). Historically, *M. affinis* and *M. relicta* have been recorded in two and 16 lakes across Lithuania, respectively, whereas *P. quadrispinosa* was detected in 46 lakes (Appendix S1). Other glacial relict crustacean species occurring in Lithuania and elsewhere in Europe are the copepods *Limnocalanus macrurus* (G.O. Sars, 1863) and *Eurytemora lacustris* (Poope, 1887); their historical records and the latest data have been summarized in Arbačiauskas & Kalytytė (2010), and are not considered here. The introduced non-indigenous Ponto-Caspian crustacean species considered in this study include the mysid *Paramysis lacustris* (Czerniavsky, 1882) and the amphipods *Pontogammarus robustoides* (G.O. Sars, 1894), *Obesogammarus crassus* (G.O. Sars, 1894), and *Chaetogammarus warpachowskyi* (G.O. Sars, 1894). These species were first introduced into Lithuanian waters in 1960–1961 and are currently known in more than 30 lakes (Arbačiauskas et al., 2011; Arbačiauskas et al., 2017; this study).

2.2 | Sampling, occurrence, and relative abundance of malacostracan species

To assess recent changes in the occurrence of glacial relict species, 26 out of 46 lakes previously inhabited by glacial relicts were sampled from 1998 to 2021 (Figure 1; Table 1). This survey included all lakes known to have been inhabited by the mysid *M. relicta* and the amphipod *M. affinis*. The sampling for glacial relicts and Ponto-Caspian malacostracans was performed in depths between 5 and 30 m using a modified 70-cm-wide epibenthic dredge with a 0.5-mm mesh net. The dredge was slowly pulled (approx. 10 m min^{-1}) from a boat for 20–30 m, targeting, in separate trawling events, the deepest areas and shallower parts close to the thermocline. Depending on the sampling success, and especially if initial trawling did not yield any target species, the trawling was repeated in different parts of the lake, with at least five trawling events per lake during a survey day and, in some cases, subsequent sampling in several consecutive years. In three lakes where *M. relicta* and *M. affinis* were not known to occur, the presence of *P. quadrispinosa* was assessed by hand net sampling in wade-able depths late in the autumn season, when the species is known to occur at shallower depths because of decreased water temperatures (Table 1). The data on the presence of Ponto-Caspian crustaceans in lakes was based on the same sampling surveys and records from earlier studies (Arbačiauskas et al., 2011; Arbačiauskas et al., 2017).

During the sampling, the relative abundance of glacial relict crustaceans was assessed based on the number of individuals sampled in the trawling events. Four relative abundance categories were used: 'abundant' (scored as 3), when the number of individuals found in at least one trawling event at the site was >100; 'moderately abundant' (scored as 2), with 11 to 100 individuals from at least one trawling event; 'rare' (scored as 1), when no one trawling event yielded more than 10 individuals; and 'absent' (scored as 0), with no relict crustaceans captured. For the three lakes where *P. quadrispinosa* was assessed by hand net sampling (Table 1), ≤5 or >5 specimens per 5 minutes of sampling effort was roughly interpreted as indicating a moderate or abundant population. In historical data, the relative abundance was assessed according to abundances reported in literature records, aiming for approximate correspondence of abundance categories. There were no data to compare crustacean abundances between trawl and hand net sampling. However, as the abundance categories are broad, the potential difference between the two methods are likely to be slight. Yet, to assess whether the inclusion of these three lakes with different sampling methods affected the results, the analysis was repeated with these three lakes excluded. Sampling methods in earlier surveys also typically involved a dredge, although the tools were slightly different from those used in new samples. Nevertheless, abundance categories applied in this study are very broad (rare, moderate, abundant) and small deviations in the abundance category in some lakes (two instead of three, or vice versa) are unlikely to have effects on the statistical analyses, especially as repeated analyses with different subsets of lakes (e.g. all lakes or only those lakes that were sampled in both the 20th and the 21st centuries) gave identical final models and very similar final model coefficients.

2.3 | Statistical analysis

Five environmental variables were examined as predictors of glacial relict crustacean abundance: lake surface area, maximum lake depth, average lake depth, annual water renewal rate, and the presence of

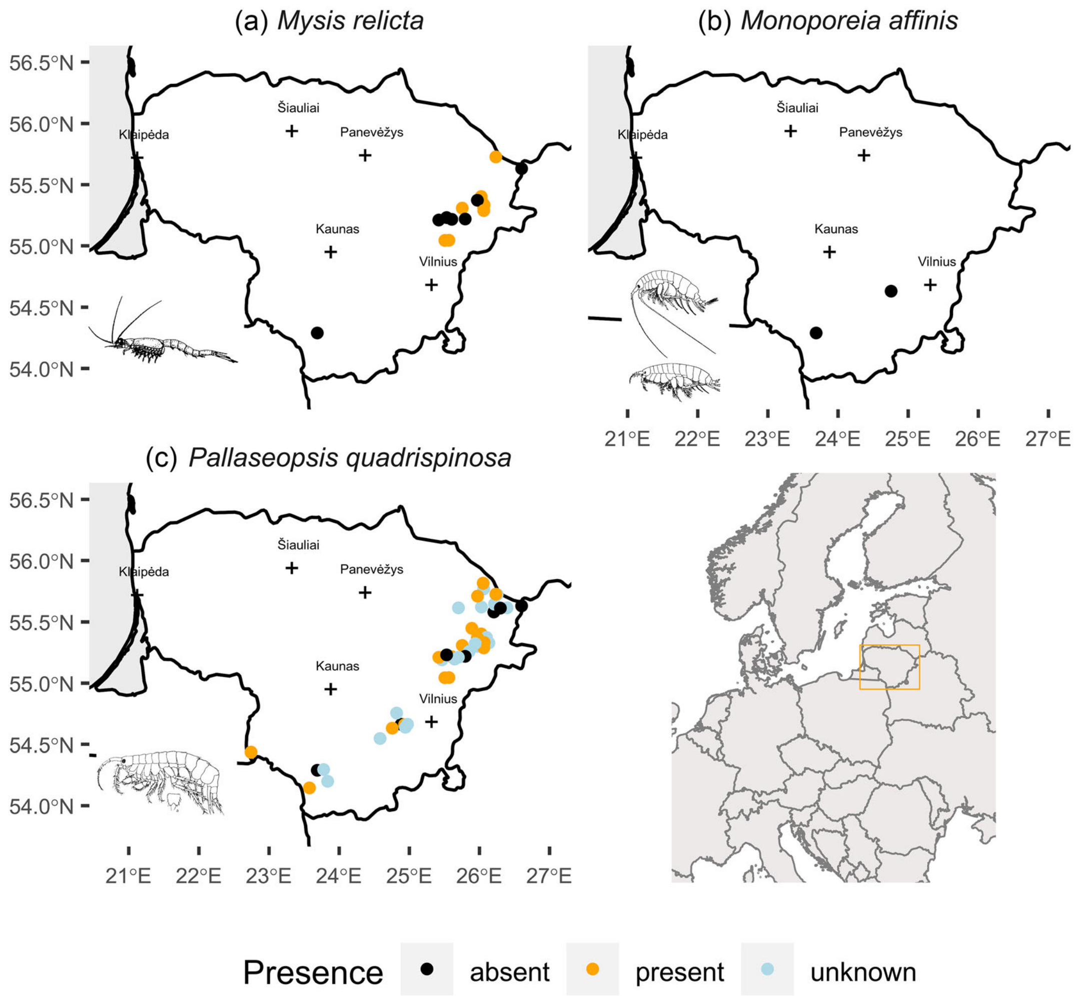

FIGURE 1 Location of Lithuanian lakes, including current knowledge about the occurrences of glacial relict crustaceans: (a) the mysid *Mysis relicta*; (b) the amphipod *Monoporeia affinis*; and (c) the amphipod *Pallaseopsis quadrispinosa*. The broader map shows the location of Lithuania in Europe. The amphipod *M. affinis* was known in two lakes, but is now considered extinct. The mysid *M. relicta* was known from 16 lakes and currently still occurs in nine lakes. The amphipod *P. quadrispinosa* occurred in 46 lakes, but currently appears to be absent from seven of these lakes, whereas 20 localities remain unchecked.

Ponto-Caspian crustaceans. The water renewal rate measures the proportion of water replaced annually by inflowing and outflowing rivers, and is an important contributor to the oxygenation of deeper water layers in the otherwise similar mesotrophic relatively deep lakes inhabited by the relict crustaceans (for a study exploring water renewal rates and deep-water oxygenation levels, see Fink, Wessels & Wüest, 2016). Consequently, the water renewal rate was used as a proxy for oxygen conditions in a lake, given that data on oxygen levels in deeper water layers were unavailable. Environmental variables for lake depth, area, and renewal rate were obtained from the data archive of the Institute of Geology and Geography (Geologijos ir Geografijos Institutas, 2002). Nutrient levels and primary productivity are also likely to affect water and habitat quality for the relict crustaceans. However, 20th-century data on nutrient levels and primary productivity were unavailable for the lakes included in this study. As a result, nutrient data were not included in formal statistical analyses but available data on current trophic status are provided in Appendix S2 for qualitative interpretation. Generally, lakes included in this study fall into the same category of deep, stratified, predominantly mesotrophic lakes.

Separate models were fitted to data for the relative abundance of *M. relicta* and *P. quadrispinosa*. To assess which variables predicted the relative abundance of these two species, generalized linear mixed models (GLMMs), as implemented in the libraries *nlme* (Pinheiro et al., 2020) and *glmmTMB* (Brooks et al., 2017) in R 4.2.1 (R Core Team, 2022), were fitted. Before model fitting, a data exploration was undertaken following the protocol described by Ieno & Zuur (2015). The data were examined for outliers in the response and explanatory variables, homogeneity and zero inflation in the response variable, collinearity between explanatory variables, the balance of categorical variables, and the nature of relationships between the response and explanatory variables. Sample variograms failed to show spatial dependency in the data, and an autocorrelation function plot failed to show temporal autocorrelation. As the sampling among years was

TABLE 1 New data on occurrences and relative abundances of the glacial relict malacostracans *Mysis relicta*, *Monoporeia affinis*, and *Pallaseopsis quadrispinosa* in the Lithuanian lakes investigated for this study during 1998–2021 (historical records and main lake characteristics are provided in Appendix S1).

No.	Lake	*Mysis relicta*	*Monoporeia affinis*	*Pallaseopsis quadrispinosa*	Ponto-Caspian
1	Aisetas	1999 (3), 2003 (3), 2021 (3)		1999 (2), 2003 (2), 2021 (2)	
2	Akmena			1998 (0)	
3	Asalnai	2003 (2)		2003 (2)	P.l., P.r.
4	Asveja	1999 (3), 2003 (3), 2021 (3)		1999 (3), 2003 (3), 2021 (3)	P.r., O.c.
5	Baltieji Lakajai	1999 (0)		1999 (3), 2003 (2),	
6	Baluošai	2003 (3), 2021 (3)		2003 (2), 2021 (2)	
7	Baluošas	1999 (3), 2003 (1), 2021 (1)		1999 (3), 2003 (3), 2021 (1)	P.l.
8	Čičirys			2003 (1)	
9	Drūkšiai	2003 (0)		2003 (0)	P.l.
10	Dusia	1999 (1), 2000 (1), 2002 (1), 2005 (0)	1999 (0), 2000 (0)	1999 (3), 2000 (2), 2002 (1), 2005 (0)	P.l., P.r., O.c., C.w.
11	Galstas[a]			2014 (2)	P.r.
12	Galvė[a]			2020 (1)	
13	Ilgai		1999 (0)	1999 (3)	
14	Luodis			1995 (1), 2008 (0)	
15	Luokesai	2003 (0)		2003 (2)	
16	Lūšiai	2003 (3), 2013 (3), 2021 (2)		2003 (3), 2013 (3), 2021 (3)	P.l., P.r., C.w.
17	Peršokšnai	2003 (2), 2021 (0)		2003 (1), 2021 (0)	
18	Siesartis	2003 (0)		2003 (0)	
19	Šakarvai	1998 (3), 2003 (3)		1998 (3), 2003 (3)	P.l., P.r., C.w.
20	Šventas			2018 (0)	
21	Tauragnas			1998 (3), 2003 (3)	
22	Ūkojas	1999 (3), 2003 (0)		1999 (2), 2003 (1)	
23	Vencavas			1999 (3)	
24	Vištytis[a]			2014 (2)	P.r.
25	Zarasas	2003 (3), 2021 (3)		2003 (3), 2021 (3)	
26	Žeimenys	2003 (3)		2003 (2)	P.l., P.r., C.w.

Note: For each species, the record indicates the year of sampling and the relative abundance (given in brackets). Abundance classes include: (0) absent; (1) rare; (2) moderately abundant; and (3) abundant. The last column lists the Ponto-Caspian crustacean species occurring in a lake: C.w., *Chaetogammarus warpachowskyi*; O.c., *Obesogammarus crassus*; P.l., *Paramysis lacustris* (P.l.); P.r., *Pontogammarus robustoides*.
[a]Lakes in which the glacial amphipod *P. quadrispinosa* was assessed by hand net sampling.

uneven, the year was treated as a category with two levels: samples from the 20th or 21st century. Maximum and average lake depths were strongly collinear, so should not both be included in the models owing to variance inflation. Initial models were run with either average or maximum depths, and the results of model selection were the same, but models with average depth had lower Akaike information criterion (AIC) values. Therefore, the final models included the average and not the maximum depth.

The relative abundance of relict crustaceans was modelled using a GLMM with Conway–Maxwell–Poisson distribution; this distribution, rather than a Poisson distribution, was used to accommodate underdispersion in the response variable. The initial full model was defined as:

$$Relict_{ij} \sim CMP(\mu_{ij}, \nu_{ij}),$$

$$E(Relict_{ij}) = \mu_{ij},$$

$$var(Relict_{ij}) = \mu_{ij} \times \nu_{ij},$$

$$square-root(\mu_{ij}) = \eta_{ij},$$

$$\eta_{ij} = \beta_1 + \beta_2 \times Period_{ij} + \beta_3 \times Flow_{ij} + \beta_4 \times AvDepth_{ij} + \beta_5 \times LakeArea_{ij} + \beta_6 \times PC_{ij} + Lake_j,$$

$$Lake_j \sim N(0, \sigma^2{}_{Lake}),$$

where $Relict_{ij}$ is the relative abundance of relict crustaceans (amphipod or mysid) in sample *i* from lake *j*, which was assumed to follow a Conway–Maxwell–Poisson distribution with an expected abundance (E) in each sample with mean μ_{ij} and variance $\mu_{ij} \times v_{ij}$ (where v is a dispersion parameter) and a square-root link function. The fixed effects were the period of sample collection ($Period_{ij}$), annual water renewal rate ($Flow_{ij}$), average lake depth ($AvDepth_{ij}$), lake area ($LakeArea_{ij}$), and presence of Ponto-Caspian crustaceans (mysids and/or amphipods) in the lake ($PC_{i,j}$) at the time of sampling, whereas β_1–β_6 are model coefficients to be estimated. To assess whether maximum depth provides a better fit for the models, alternative models with maximum depth instead of average depth were run, but the results of the final model selection were the same. As the maximum and average depth are strongly correlated, including both variables would inflate the explained model variance, so this was not done. To accommodate the fact that lakes were sampled repeatedly, and the abundance of relict crustaceans differed among lakes, the random intercept $Lake_j$ was included in models to introduce a correlation structure between observations for different samples from the same lake, with variance σ^2_{Lake} distributed normally and with a mean of zero (categorical, 26 levels). It was not possible to perform a time series or survival analysis on this dataset owing to the limited number of sampling years per lake. The optimal fixed structure of a model for each dataset was identified with a backward selection procedure using AIC (ΔAIC ≤ 2). All datasets and scripts used in these analyses are available from the GitHub repository https://github.com/astaaudzi/relictCrustaceans.

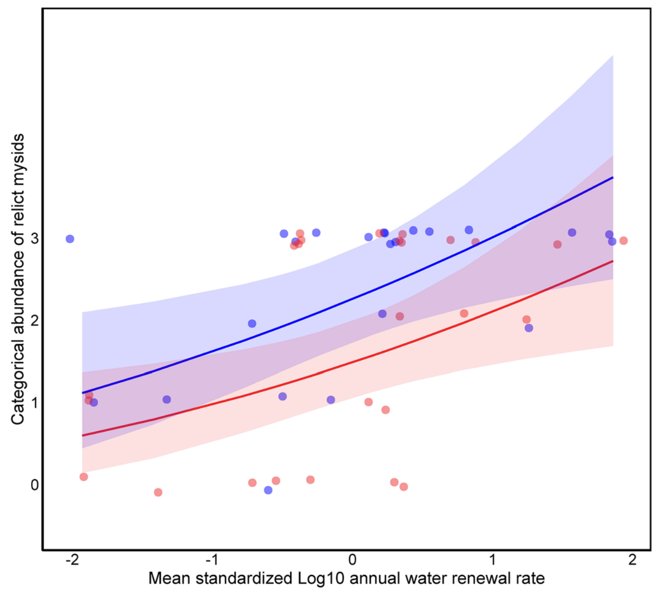

FIGURE 2 Results of the Conway–Maxwell–Poisson generalized linear mixed model (GLMM) analysis, showing relationships between the relative abundance of the relict mysid *Mysis relicta* against the mean standardized $\log_{10}$ annual lake water renewal rate during the 20th (blue) and 21st (red) centuries. Model predictions and 95% confidence intervals are shown with lines and shaded areas; raw data are shown as dots.

3 | RESULTS

Studies conducted in the 1950s reported the presence of glacial relict malacostracans in 46 Lithuanian lakes (Appendix S1; Figure 1). More recent sampling performed in 26 of these lakes, including all lakes with earlier records of *M. affinis* and *M. relicta*, showed that *M. affinis* was not found in either of the two lakes in which it was known to occur previously (Dusia 10 and Ilgai 13, Figure 1b), despite repeated sampling attempts over several years. In the mid-20th century, *M. relicta* was recorded in 16 lakes, whereas recent data suggest that the species now occurs only in nine lakes (Figure 1a; Table 1). The amphipod *P. quadrispinosa* was known to occur in all 26 studied lakes, but sampling failed to detect this species in seven of the lakes studied (Figure 1c).

Backward model selection showed that for relict mysids, the best-fitting model included two variables: annual water renewal rate and time period (20th or 21st century). For amphipods, the best-fitting model included three variables: average depth, annual water renewal rate, and time period (each step of the model selection process is illustrated in the supplementary GitHub code). Ten out of the 26 lakes investigated currently contain invasive Ponto-Caspian crustaceans, and in two of these lakes, extinctions of glacial relicts were observed (Figure 1; Table 1). Nevertheless, statistical analysis showed that removing the presence of Ponto-Caspian crustaceans from models improved the model fit (using the final models, this gives an AIC of 206 versus 295 for relict amphipods, and an AIC of 147 versus 177 for the relict mysid), suggesting that the presence of Ponto-Caspian crustaceans did not explain the relative abundance of glacial relict crustaceans.

The final models showed the relict crustacean relative abundance to be positively associated with the lake water renewal rate (for amphipods, $P = 0.002$; for mysids, $P = 0.007$), and with the average lake depth for amphipods only ($P < 0.001$) (Figures 2 and 3; Table 2). For both species, there was also a significant association with time period, with a consistent reduction in relative abundance associated with the 21st century compared with the 20th century (amphipods, $P = 0.007$; mysids, $P = 0.001$). For sensitivity analysis, model selection was repeated for relict amphipods excluding the three lakes that were sampled with the hand net only, but the final model selection was the same and the model-estimated parameter values were very similar (full details are available in Appendixes S1 and S2). Fixed effects explained 17%–24% of the relict crustacean relative abundance variance in both models (Table 2). In contrast, a lake effect, included as a random term in the models, explained approximately 9%–19% of the variance in both models; this is shown as the difference between conditional R^2, defined by fixed effects, and marginal R^2, defined by both fixed and random effects (Table 2).

4 | DISCUSSION

Investigations of glacial relict malacostracan crustaceans in the inland waters of Lithuania started in the middle of the 20th century (Gasiūnas, 1959), and historical records of their occurrence were

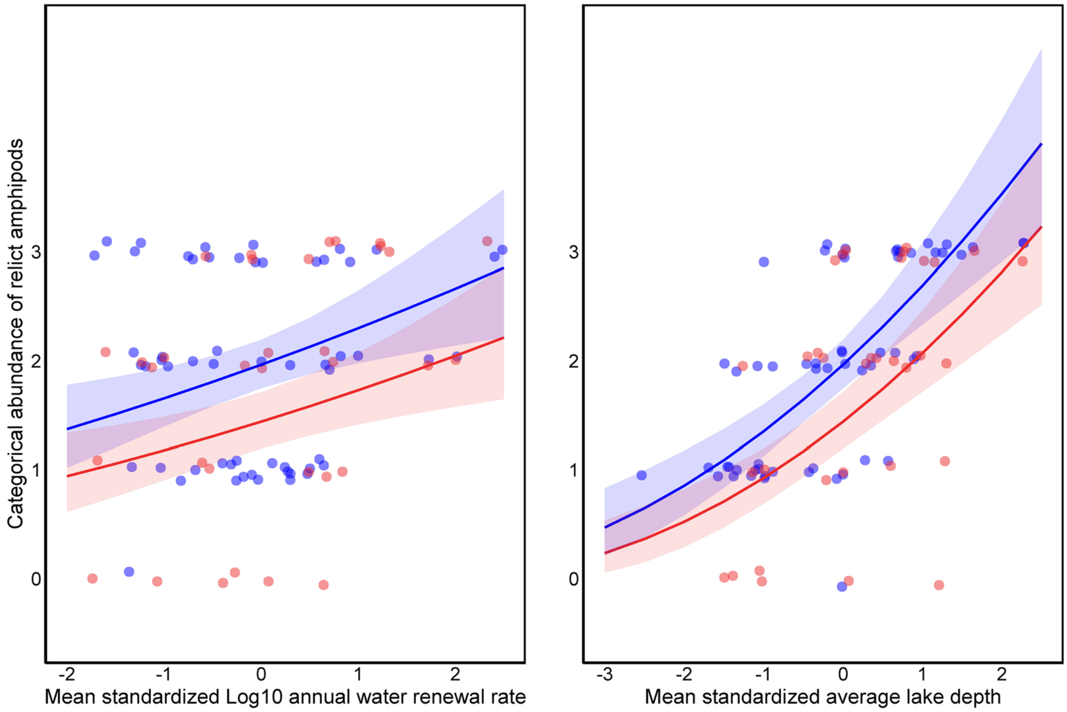

FIGURE 3 Results of the Conway–Maxwell–Poisson generalized linear mixed model (GLMM) analysis, showing relationships between the relative abundance of the relict amphipod *Pallaseopsis quadrispinosa* against the mean standardized $\log_{10}$ annual lake water renewal rate and the mean standardized average lake depth (m) during the 20th (blue) and 21st (red) centuries. Model predictions and 95% confidence intervals are shown with lines and shaded areas; raw data are shown as dots.

TABLE 2 Parameters of the final Conway–Maxwell–Poisson generalized linear mixed models for the relict mysid *Mysis relicta* and the amphipod *Pallaseopsis quadrispinosa* relative abundance analyses.

	Pallaseopsis quadrispinosa			*Mysis relicta*		
Coefficient	**Estimate**	**(95% CI)**	***P***	**Estimate**	**(95% CI)**	***P***
Fixed effects						
Intercept	1.40	(1.32, 1.48)	<0.001	1.50	(1.32, 1.69)	<0.001
Time period$_{(C21)}$	−0.20	(−0.31, −0.09)	0.001	−0.28	(−0.46, −0.11)	0.001
Water renewal rate	0.12	(0.04, 0.19)	0.002	0.23	(0.06, 0.40)	0.007
Average depth	0.24	(0.17, 0.31)	<0.001			
Random effects						
σ^2	0.17			0.28		
$\tau_{00\text{Lake}}$	0.02			0.08		
ICC	0.12			0.22		
N_{Lake}	45			16		
Other model statistics						
Observations	90			49		
Mar/Con R^2	0.24/0.33			0.17/0.36		

Note: Mar/Con R^2, marginal and conditional R^2 values; σ^2, mean random effect variance for each model; $\tau_{00\text{Lake}}$ is the model between-subject variance, indicating how much different levels of the random term 'Lake' differ from each other; ICC is the intraclass correlation coefficient, which is a measure of the degree of correlation within groups; *N* indicates the number of levels in the random effect 'Lake'. The water renewal rate is the $\log_{10}$ annual water renewal rate. Estimates are of relative relict crustacean abundance for model coefficients.

summarized by Grigelis (1980) and Grigelis & Arbačiauskas (1996, 1997). The latest published data on the abundance and ecology of glacial relict crustaceans in Lithuania are available in Audzijonytė (1999). The study presented here provides up-to-date information on the status of these Red List species. Recent results show a likely extinction of the glacial relict amphipod *M. affinis* in Lithuania, the likely disappearance of *M. relicta* in nearly half of the lakes in which it used to occur in the 1950s (seven out of 16), and the possible extirpation of *P. quadrispinosa* populations in about a third of the lakes studied. The amphipod *M. affinis* was originally found in only two locations in Lithuania and is now considered extinct in German and Polish waters (Köhn & Waterstraat, 1990; Żmudziński, 1995). The trends of declining glacial relict population status in Lithuania are consistent with observations from other countries, and are especially pronounced at the southern distribution limits, where lake eutrophication and increasing temperatures are the primary drivers (Ireland and BritainPenk, 2011; Griffiths et al., 2015; Germany – Scharf & Koschel, 2004; Rumpf et al., 2005). In some cases, and specifically in Northern Germany, strong water management and lake restoration efforts improved deep-water oxygen conditions and populations of glacial relicts have recovered (Scharf & Koschel, 2004; Rumpf et al., 2005). Yet, the increasing surface and deep-water temperatures and rapid changes in water mixing and water budgets driven by global heating (Shatwell, Thiery & Kirillin, 2019; Woolway et al., 2020) are likely to be putting further pressure on glacial relict populations. It is, therefore, even more important to ensure the regular monitoring of their status because of their ecological, biodiversity, and biogeographical importance, and as indicator species for the water quality conditions required by other species adapted to cold water and high oxygen. However, such monitoring efforts are limited, with little or no recent data about the population status available in Germany, Poland, Belarus, or Russia.

In addition to documenting the current status of glacial relict malacostracans in Lithuania, one of the key questions for this study was to assess whether Ponto-Caspian invaders are likely to be contributing to native relict population declines. Such adverse impacts of Ponto-Caspian invaders could be expected, given their widespread impacts on other native crustaceans (Arbačiauskas & Gumuliauskaitė, 2007; Meßner & Zettler, 2021) and the evidence for some negative interactions with glacial relicts (e.g. Arbačiauskas, 2005; Penk, Donohue & Irvine, 2018). Despite the initial predictions, however, no statistical evidence was found for the contribution of Ponto-Caspian crustaceans to the decreased abundance of relicts in Lithuania. None of the models tested selected Ponto-Caspian crustacean presence as an important variable explaining the categorical abundance of relict populations. Indeed, there are quite a few lakes where both glacial relict and Ponto-Caspian species coexist, at least for now (lakes 3, 4, 7, 16, 19, and 26 for *M. relicta* in Table 1), or where glacial relicts became extinct despite there being no Ponto-Caspian crustaceans (lakes 5, 15, 17, and 18). On the one hand, such a lack of invader impact may not be surprising because glacial relicts typically occur in deep waters, whereas the Ponto-Caspian species are primarily confined to the littoral zone. In another study, predatory interactions between an invasive American amphipod *Gammarus tigrinus* and the native glacial relict mysid *M. salemaai* in Northern Ireland also did not appear to have adverse effects on native mysids (Bailey et al., 2006). On the other hand, it is important to note that statistical analyses in our studies were inevitably limited owing to the small number of lakes where relict crustaceans occur (and even fewer lakes where relicts and Ponto-Caspian crustaceans co-occur), so the sample sizes were small. Moreover, assessing the abundance of bentho-pelagic crustaceans is difficult, and comparisons with historical data are also challenging (Scharf & Koschel, 2004). Hence, our comparisons with historical data sources must be viewed with caution, although to increase the robustness of the analyses we considered only broad crustacean abundance categories and used simple presence/absence scoring for Ponto-Caspian crustaceans. This treatment of the data provided the most robust statistical approach but may have missed species-specific nuances. Broader analysis across other European lakes should be conducted, although that would require an extensive collaborative effort to assess the current status of both relict and invading Ponto-Caspian populations.

Although Ponto-Caspian crustaceans seem to have a limited impact on glacial relict crustaceans, water quality and temperature, especially oxygen depletion in the deep cold-water layers, remain the main threat. Ultimately, it is the summer and autumn oxygen depletion in deep stratified layers of lakes that imperils glacial relict populations, either through the direct removal of their habitat or by pushing them to more shallow waters where crustaceans are exposed to intensive fish predation (Thienemann, 1925; Horppila et al., 2003; Paterson et al., 2011). Unfortunately, no long-term data on nutrient conditions or oxygen concentrations were available for the lakes studied in Lithuania, and hence the use of very general proxies such as lake depth and the annual water renewal rate (for a correlation between water renewal rate and deep-water oxygen conditions, see Fink, Wessels & Wüest, 2016). Naturally, oxygen conditions will also depend on vertical mixing and nutrient load. Still, both of these variables were broadly similar (Appendix S2), as these lakes are mostly deep and mesotrophic.

Although the legacy of the Ice Age has diminished in Central Europe, Lithuanian waters still support a rich glacial faunal heritage. Nine lakes in Lithuania still harbour *M. relicta*, compared with only three localities in Germany (Scharf & Koschel, 2004), up to three localities in Poland (Żmudziński, 1990), and only one in Belarus (V.V. Vezhnavets, 2021, pers. comm.). Moreover, the planktonic glacial relict species *L. macrurus* and *E. lacustris* seem to be surviving in the majority of historically recognized locations in Lithuania, with viable populations recorded in 13 and seven lakes, respectively (only in Lake Drūkšiai has *L. macrurus* vanished owing to the impact of the Ignalina nuclear power plant) (Arbačiauskas & Kalytytė, 2010). This glacial heritage in Lithuania warrants preservation and improvement. The management and restoration of northern German lakes, where glacial relicts were effectively extinct because of intensive eutrophication in the 1980s, but where population abundance rapidly increased once water quality improved, show that such efforts work and are worthwhile (Scharf & Koschel, 2004). These management efforts are especially urgent now, as global warming is increasing and will continue to increase surface and deep-water temperatures in lakes of the Northern Hemisphere (Schindler et al., 1990; Shatwell, Thiery & Kirillin, 2019; Stefanidis et al., 2022), and in this way, reduce the suitable habitats for relict crustaceans.

One notable example of glacial relict extinction was in the largest Lithuanian lake, Lake Drūkšiai (lake 9, Table 1). Since 1984, this lake has served as a cooling reservoir for the Ignalina nuclear power plant, with the lake temperature increasing by nearly 2°C, with the water eutrophication level increasing as a result of improper wastewater discharge from the town that served the nuclear power plant, and with oxygen concentrations decreasing in the lake profundal zone (Kesminas & Paškauskas, 2014; Vezhnavets & Škute, 2014). Consequently, our sampling in 2003 showed that all glacial relict species were also likely to be extinct in this lake (Table 1). However, the nuclear power plant was decommissioned in 2010, and environmental conditions in the lake are now improving, as is shown by the increasing abundances of two cold-water fish species: vendace (*Coregonus albula*) and smelt (*Osmerus eperlanus*) (Kesminas & Steponėnas, 2014; V. Kesminas, 2022, pers. comm.). As glacial relict species cannot naturally disperse and hence recolonize the lake, we recommend the reintroduction of *M. relicta* and *P. quadrispinosa* from nearby lakes, as previously suggested (Kesminas et al., 2014). Such introductions have been successfully conducted for many impounded lakes (Lasenby, Northcote & Fürst, 1986). Although relict crustacean introductions into new water impoundments often lead to unintended and adverse consequences (Lasenby, Northcote & Fürst, 1986), reintroduction into areas where these species already existed but became extinct owing to human impacts is warranted and necessary for conservation purposes. In the case of Lake Drūkšiai, a good source for translocations could be the nearby lakes of Lūšiai or Aisetas, where the population status of glacial mysids and amphipods is currently good. If successful, such reintroductions may increase the probability of these endangered species surviving in Lithuania. Nevertheless, the most urgent measure to ensure the survival of the Red List crustaceans and other aquatic species that rely on clear and oxygenated aquatic habitats is an urgent reduction of municipal and especially agricultural run-off into rivers and lakes.

AUTHOR CONTRIBUTIONS

Asta Audzijonyte: Conceptualization; investigation; formal analysis; writing—original draft; writing—review and editing; methodology; visualization; funding acquisition; supervision. **Kęstutis Arbačiauskas:** Conceptualization; investigation; writing—review and editing; data curation; methodology. **Carl Smith:** Formal analysis; writing—review and editing; software; visualization.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest associated with this work.

OPEN RESEARCH BADGES

This article has earned an Open Data Badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at DOI 10.5281/zenodo.8106730.

DATA AVAILABILITY STATEMENT

The original data used in this study, as well as all the relevant code for the analyses, are stored in GitHub (https://github.com/astaaudzi/relictCrustaceans) and have been archived within the Zenodo repository (https://zenodo.org/record/8106730).

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REFERENCES

Arbačiauskas, K. (2005). The distribution and local dispersal of Ponto-Caspian Peracarida in Lithuanian fresh waters with notes on *Pontogammarus robustoides* population establishment, abundance, and impact. *Oceanological and Hydrobiological Studies*, 34(Suppl. 1), 93–113.

Arbačiauskas, K. & Gumuliauskaitė, S. (2007). Invasion of the Baltic Sea basin by the Ponto-Caspian amphipod *Pontogammarus robustoides* and its ecological impact. In: Gherardi, F. (Ed.) *Biological invaders in inland waters: profiles, distribution and threats*. The Netherlands: Springer, Dordrecht, pp. 463–477. https://doi.org/10.1007/978-1-4020-6029-8_25

Arbačiauskas, K. & Kalytytė, D. (2010). Occurrence and interannual abundance variation of glacial relict calanoids *Limnocalanus macrurus* and *Eurytemora lacustris* in Lithuanian lakes. *Acta Zoologica Lituanica*, 20(1), 61–67. https://doi.org/10.2478/v10043-010-0009-4

Arbačiauskas, K., Šidagytė, E., Šniaukštaitė, V. & Lesutienė, J. (2017). Range expansion of Ponto-Caspian peracaridan crustaceans in the Baltic Sea basin and its aftermath: lessons from Lithuania. *Aquatic Ecosystem Health & Management*, 20(4), 393–401. https://doi.org/10.1080/14634988.2017.1328229

Arbačiauskas, K., Višinskienė, G., Smilgevičienė, S. & Rakauskas, V. (2011). Non-indigenous macroinvertebrate species in Lithuanian fresh waters, Part 1: distributions, dispersal and future. *Knowledge and Management of Aquatic Ecosystems*, 402, 12. https://doi.org/10.1051/kmae/2011075

Audzijonytė, A. (1999). Aukštesniųjų ledynmečio reliktinių vėžiagyvių gausumo ir populiacijos struktūros tyrimai Lūšių, Šakarvų, Akmenos ir Verniejaus ežeruose. *Ekologija*, 2(402), 36–41.

Audzijonyte, A. (2006). Diversity and zoogeography of continental mysid crustaceans (acad. diss. Univ. Helsinki). *Walter and Andrée de Nottbeck Foundation Scientific Reports*, 28, 1–46.

Audzijonytė, A., Damgaard, J., Varvio, S.L., Vainio, J.K. & Väinölä, R. (2005). Phylogeny of *Mysis* (Crustacea, Mysida): history of continental invasions inferred from molecular and morphological data. *Cladistics*, 21(6), 575–596. https://doi.org/10.1111/j.1096-0031.2005.00081.x

Audzijonytė, A. & Väinölä, R. (2005). Diversity and distributions of circumpolar fresh- and brakish-water *Mysis* (Crustacea: Mysida): description of *M. relicta* Loven, 1862, *M. salemaai* n. sp., *M. segerstralei* n.sp. and *M. diluviana* n. sp., based on molecular and morphological characters. *Hydrobiologia*, 544(1), 89–141. https://doi.org/10.1007/s10750-004-8337-7

Audzijonyte, A. & Väinölä, R. (2006). Phylogeographic analyses of a circumarctic coastal and a boreal lacustrine mysid crustacean, and evidence of fast postglacial mtDNA rates. *Molecular Ecology*, 15(11), 3287–3301. https://doi.org/10.1111/j.1365-294X.2006.02998.x

Bailey, R.J.E., Dick, J.T.A., Elwood, R.W. & MacNeil, C. (2006). Predatory interactions between the invasive amphipod *Gammarus tigrinus* and the native opossum shrimp *Mysis relicta*. *Journal of the North American Benthological Society*, 25(2), 393–405. https://doi.org/10.1899/0887-3593(2006)25[393:PIBTIA]2.0.CO;2

Berezina, N., Kalinkina, N. & Maximov, A. (2021). Distribution and functional ecology of malacostracan crustaceans in Russian northern and Arctic lakes. In: Shirokova, L.S., Pokrovsky, O.S., Vorobyeva, T.Y. & Bespalaya, Y. (Eds.) *Lake water: properties and uses (case studies of hydrochemistry and hydrobiology of lakes in northwest Russia)*. New York: Nova Science Publishers, pp. 229–248.

Bij de Vaate, A., Jażdżewski, K., Ketelaars, H.A.M., 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(7), 1159–1174. https://doi.org/10.1139/f02-098

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A. et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2), 378–400. https://journal.r-project.org/archive/2017/RJ-2017-066/index.html

Dick, J.T.A. & Platvoet, D. (2000). Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society B*, 267(1447), 977–983. https://doi.org/10.1098/rspb.2000.1099

Ekman, S. (1953). *Zoogeography of the sea*. London: Sidgwick & Jackson.

Fink, G., Wessels, M. & Wüest, A. (2016). Flood frequency matters: why climate change degrades deep-water quality of peri-alpine lakes. *Journal of Hydrology*, 540, 457–468. https://doi.org/10.1016/j.jhydrol.2016.06.023

Gasiūnas, I. (1959). Lietuvos ežerai, kuriuose gyvena reliktiniai vėžiagyviai. *Mūsų girios*, 3, 35–37.

Geologijos ir geografijos institutas. (2002). *Lietuvos ežerų klasifikacija pagal jų gamtines savybes*. Vilnius: Ataskaita.

Griffiths, D. (2007). Effects of climatic change and eutrophication on the glacial relict, *Mysis relicta*, in Lough Neagh. *Freshwater Biology*, 52(10), 1957–1967. https://doi.org/10.1111/j.1365-2427.2007.01824.x

Griffiths, D., Macintosh, K.A., Forasacco, E., Rippey, B., Vaughan, L., McElarney, Y.R. et al. (2015). *Mysis salemaai* in Ireland: new occurrences and existing population declines. *Biology and Environment: Proceedings of the Royal Irish Academy*, 115B(1), 59–65. https://doi.org/10.3318/bioe.2015.06

Grigelis, A. (1980). Bentosiniai ledynmečio reliktiniai vėžiagyviai, rasti Lietuvos TSR ledyninės kilmės ežeruose 1952-1978 m. *Lietuvos TSR MA darbai, C serija*, 2(90), 69–78.

Grigelis, A. & Arbačiauskas, K. (1996). Ledynmečio reliktiniai vėžiagyviai Baltijos aukštumų ežeruose. *Žuvininkystė Lietuvoje*, 2, 21–34.

Grigelis, A. & Arbačiauskas, K. (1997). Ledynmečio reliktinių vėžiagyvių būklė Lietuvoje ir antropogeninė tarša. *Ekologija*, 2, 25–27.

Högbom, A.G. (1916). Über die arktischen Elemente in der aralokaspischen Fauna, ein tiergeographisches Problem. *Bulletin of the Geological Institution of the University of Upsala*, 14, 241–260.

Holda, T.J. (2017). *Mysis diluviana in the Great Lakes: historic drivers of abundance and production, and current status in Lake Ontario*. M.S. Thesis, Ithaca: Cornell University.

Holda, T.J., Rudstam, L.G., Bowen, K.L., Weidel, B.C., Watkins, J.M., Sullivan, P.J. et al. (2019). Status of *Mysis diluviana* in Lake Ontario in 2013: lower abundance but higher fecundity than in the 1990s. *Journal of Great Lakes Research*, 45(2), 307–316. https://doi.org/10.1016/j.jglr.2019.01.007

Holmquist, C. (1966). Die sogenannten marin-glazialen Relikte nach neueren Gesichtspunkten. *Archiv für Hydrobiologie*, 62, 285–326.

Horppila, J., Liljendahl-Nurminen, A., Malinen, T., Salonen, M., Tuomaala, A., Uusitalo, L. et al. (2003). *Mysis relicta* in a eutrophic lake: consequences of obligatory habitat shifts. *Limnology and Oceanography*, 48(3), 1214–1222. https://doi.org/10.4319/lo.2003.48.3.1214

Ieno, E.N. & Zuur, A.F. (2015). *A beginner's guide to data exploration and visualisation with R*. Newburgh: Highland Statistics.

Jażdżewski, K. (1980). Range extensions of some gammaridean species in European inland waters caused by human activity. *Crustaceana. Supplement* (6), 84–107. https://www.jstor.org/stable/25027516

Kesminas, V. & Paškauskas, R. (2014). 1. Physical and geographical survey of Lake Drūkšiai. *Zoology and Ecology*, 24(2), 84–86. https://doi.org/10.1080/21658005.2014.925236

Kesminas, V. & Steponėnas, A. (2014). 8. Fish community. *Zoology and Ecology*, 24(2), 135–153. https://doi.org/10.1080/21658005.2014.925243

Kesminas, V., Vezhnavets, V.V., Kasperovičienė, J., Baichorov, V.M., Steponėnas, A., Rakauskas, V. et al. (2014). Recommendations on re-introduction of crustaceans and fish, use of fish stocks, and improvement of the state of Lake Drūkšiai. *Zoology and Ecology*, 24(2), 185–186. https://doi.org/10.1080/21658005.2014.925245

Köhn, J. & Waterstraat, A. (1990). Recent distribution of glacial relict Malacostraca in the lakes of Mecklenburg. *Annales Zoologici Fennici*, 27, 237–240. https://www.jstor.org/stable/23736039

Lasenby, D.C., Northcote, T.G. & Fürst, M. (1986). Theory, practice, and effects of *Mysis relicta* introductions to North America and Scandinavian lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 43(6), 1277–1284. https://doi.org/10.1139/F86-158

Lovén, S. (1862). Om några i Vettern och Venern funna Crustaceer. *Öfversigt af Kungliga Vetenskaps-Akademiens Förhandlingar*, 6, 285–314.

MacNeil, C. & Dick, J.T. (2012). Differential predatory and interference interactions between native and invasive freshwater amphipods and a co-occurring mysid (Crustacea). *Hydrobiologia*, 683(1), 35–42. https://doi.org/10.1007/s10750-011-0938-3

Meßner, U. & Zettler, M.L. (2021). Drastic changes of the amphipod fauna in northern Germany and the displacement of *Gammarus lacustris* G.O. Sars, 1864 to relict habitats/status. *Knowledge and Management of Aquatic Ecosystems*, 422, 17. https://doi.org/10.1051/kmae/2021016

Paterson, G., DeLuca, B., Bentzen, E., Lean, D.R. & Hickie, B.E. (2022). Lacustrine characteristics predict lipid contents of mysid shrimp (*Mysis diluviana*) populations. *Limnologica*, 92, 125942. https://doi.org/10.1016/j.limno.2021.125942

Paterson, M.J., Podemski, C.L., Wesson, L.J. & Dupuis, A.P. (2011). The effects of an experimental freshwater cage aquaculture operation on *Mysis diluviana*. *Journal of Plankton Research*, 33(1), 25–36. https://doi.org/10.1093/plankt/fbq096

Penk, M., Donohue, I., Récoules, V. & Irvine, K. (2015). Elevated temperatures interact with habitat quality to undermine survival of ectotherms in climatic refugia. *Diversity and Distributions*, 21(2), 200–210. https://doi.org/10.1111/ddi.12259

Penk, M.R. (2011). A review of the current distribution of the freshwater opossum shrimp *Mysis salemaai* Audzijonyte and Väinölä, 2005 in Ireland. *Biology and Environment: Proceedings of the Royal Irish Academy*, 111B(2), 107–115. http://www.jstor.org/stable/23033870

Penk, M.R., Donohue, I. & Irvine, K. (2018). Temporally variable niche overlap and competitive potential of an introduced and a native mysid shrimp. *Hydrobiologia*, 823(1), 109–119. https://doi.org/10.1007/s10750-018-3700-2

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2020). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-145. https://CRAN.R-project.org/package=nlme

R Core Team. (2022). *R: a language and environment for statistical computing, Version 4.2.1*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Rumpf, M., Krappe, M., Riel, P. & Waterstraat, A. (2005). Habitat shifts of *Mysis relicta* (Decapoda, Mysidacea) in the lakes Breiter and Schmaler Luzin (NE Germany). *Crustaceana*, 78(6), 685–699. https://doi.org/10.1163/156854005774353467

Sandlund, O.T., N sje, T.F. & Jonsson, B. (1992). Ontogenetic changes in habitat use by whitefish, *Coregonus lavaretus*. *Environmental Biology of Fishes*, 33(4), 341–349. https://doi.org/10.1007/BF00010945

Scharf, J. & Koschel, R. (2004). Distribution, abundance and life history of *Mysis relicta* (Loven) in the Feldberg Lake District, Germany. *Limnologica*, 34(3), 199–212. https://doi.org/10.1016/S0075-9511(04)80045-8

Scharf, J., Krappe, M., Koschel, R. & Waterstraat, A. (2008). Feeding of European cisco (*Coregonus albula* and *C. lucinensis*) on the glacial relict crustacean *Mysis relicta* in Lake Breiter Luzin (Germany). *Limnologica*, 38(2), 147–158. https://doi.org/10.1016/j.limno.2007.12.001

Schindler, D., Beaty, K., Fee, E., Cruikshank, D., DeBruyn, E., Findlay, D. et al. (1990). Effects of climatic warming on lakes of the central boreal forest. *Science*, 250(4983), 967–970. https://doi.org/10.1126/science.250.4983.967

Segerstråle, S.G. (1957). On immigration of the glacial relicts of Northern Europe, with remarks on their prehistory. *Societas Scientiarum Fennica, Commentationes Biologicae*, 16(16), 1–117.

Shatwell, T., Thiery, W. & Kirillin, G. (2019). Future projections of temperature and mixing regime of European temperate lakes. *Hydrology and Earth System Sciences*, 23(3), 1533–1551. https://doi.org/10.5194/hess-23-1533-2019

Spikkeland, I., Kinsten, B., Kjellberg, G., Nilssen, J.P. & Väinölä, R. (2016). The aquatic glacial relict fauna of Norway—an update of distribution and conservation status. *Fauna Norvegica*, 36, 51–65. https://doi.org/10.5324/fn.v36i0.1994

Stefanidis, K., Varlas, G., Papaioannou, G., Papadopoulos, A. & Dimitriou, E. (2022). Trends of lake temperature, mixing depth and ice cover thickness of European lakes during the last four decades. *Science of the Total Environment*, 830, 154709. https://doi.org/10.1016/j.scitotenv.2022.154709

Stockwell, J.D., O'Malley, B.P., Hansson, S., Chapina, R.J., Rudstam, L.G. & Weidel, B.C. (2020). Benthic habitat is an integral part of freshwater *Mysis* ecology. *Freshwater Biology*, 65(11), 1997–2009. https://doi.org/10.1111/fwb.13594

Suschenya, L.M., Semenchenko, V.P. & Vezhnavets, V.V. (1986). *Biologiya i produkciya lednikovykh reliktovykh rakoobraznykh [Biology and production of glacial relict crustaceans]*. Minsk: Nauka i technika.

Thienemann, A. (1925). *Mysis relicta*. Fünfte Mitteilung der "Untersuchungen über die Beziehungen zwischen dem Sauerstoffgehalt des Wassers und der Zusammensetzung der Fauna in norddeutschen Seen". *Zeitschrift für Morphologie und Ökologie der Tiere*, 3(2-3), 389–440. https://doi.org/10.1007/BF00408149

Väinölä, R. (1990). Molecular time scales for evolution in *Mysis* and *Pontoporeia*. *Annales Zoologici Fennici*, 27(3), 211–214.

Väinölä, R. (1998). A sex-linked locus (Mpi) in the opossum shrimp *Mysis relicta*: implications for early postglacial colonization history. *Heredity*, 81(6), 621–629. https://doi.org/10.1046/j.1365-2540.1998.00442.x

Väinölä, R. & Johannesson, K. (2017). Genetic diversity and evolution. In: Snoeijs, P., Schubert, H., & Radziejewska, T. (Eds.) *Biological oceanography of the Baltic Sea*, Dordrecht: Springer Netherlands, pp. 233–253. https://doi.org/10.1007/978-94-007-0668-2

Vezhnavets, V.V. & Škute, A. (2014). 2. The main characteristics of the habitat. *Zoology and Ecology*, 24(2), 87–91. https://doi.org/10.1080/21658005.2014.925237

Waterstraat, A. (1988). Zur Verbreitung und Ökologie der Reliktkrebse *Mysis relicta* (Loven), *Pallasea quadrispinosa* (Sars) und *Pontoporeia affinis* (Lindstrom). *Archiv fuer Naturschutz und Landschaftsforschung (German D.R.)*, 28, 121–137.

Woolway, R.I., Kraemer, B.M., Lenters, J.D., Merchant, C.J., O'Reilly, C.M. & Sharma, S. (2020). Global lake responses to climate change. *Nature Reviews Earth & Environment*, 1(8), 388–403. https://doi.org/10.1038/s43017-020-0067-5

Żmudziński, L. (1990). Past and recent occurrence of Malacostraca glacial relicts in Polish lakes. *Annales Zoologici Fennici*, 27, 227–230. https://www.jstor.org/stable/23736035

Żmudziński, L. (1995). Retreat of *Pallasiola quadrispinosa* (G. O. Sars) and *Monoporeia affinis* (Lindström) from the Polish lakes. *Polskie Archiwum Hydrobiologii*, 42(4), 401–407.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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