



Warming, not acidification, favours survival of non-indigenous over native gammarid species

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Abstract Anthropogenic disturbances, including non-indigenous species (NIS) and climate change, have considerably affected ecosystems and socio-economies globally. Despite the widely acknowledged individual roles of NIS and global warming in biodiversity change, predicting the connection between the two still remains a fundamental challenge and requires urgent attention due to a timely importance for proper conservation management. To improve our understanding of the interaction between climate change and NIS on biological communities, we conducted laboratory experiments to test the temperature and $p\text{CO}_2$ tolerance of four gammarid species: two native Baltic Sea species (*Gammarus locusta* and *G. salinus*), one Ponto-Caspian

NIS (*Pontogammarus maeoticus*) and one North American NIS (*Gammarus tigrinus*). Our results demonstrated that an increase in $p\text{CO}_2$ level was not a significant driver of mortality, neither by itself nor in combination with increased temperature, for any of the tested species. However, temperature was significant, and differentially affected the tested species. The most sensitive was the native *G. locusta* which experienced 100% mortality at 24 °C. The second native species, *G. salinus*, performed better than *G. locusta*, but was still significantly more sensitive to temperature increase than either of the NIS. In contrast, NIS performed better than native species with warming, whereby particularly the Ponto-Caspian *P. maeoticus* did not demonstrate any difference in its performance between the temperature treatments. With the predicted environmental changes in the Baltic Sea, we may expect shifts in distributions of native taxa towards colder areas, while their niches might be filled by NIS, particularly those from the Ponto-Caspian region. Although, northern colder areas may be constrained by lower salinity. Additional studies are needed to confirm our findings across other NIS, habitats and regions to make more general inferences.

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Introduction

In the last century, anthropogenic activities, such as introduction of non-indigenous species (NIS; species moved by human activity outside their native region) and climate change, among other stressors, have significantly affected numerous ecosystems worldwide, leading to reductions in biodiversity, and occasionally, to losses of ecosystem functioning and services (Olden et al. 2004; Hawkins 2012; Simberloff et al. 2013; IPCC 2014; Linders et al. 2019; Pyšek et al. 2020). The rate at which NIS are introduced and detected is accelerating (Bailey et al. 2020; Seebens et al. 2021), directly mirroring increases in globalization of trade and travel, the development of new transport pathways, and the expansion of existing ones (Hulme 2009; Galil et al. 2015; Seebens et al. 2018, 2021). Predicted growth in global maritime trade may reach 240–1209% by 2050, with an associated 3–20-fold increase in invasion risk (Sardain et al. 2019). As the number of problematic NIS is positively correlated with the total number of established NIS (Ricciardi and Kipp 2008), the magnitude of adverse impacts associated with invasions is expected to increase rapidly (Blackburn et al. 2019; Essl et al. 2020; Pyšek et al. 2020; Cuthbert et al. 2021; Diagne et al. 2021).

The increase in gas emissions since the beginning of the eighteenth century, have caused persisting climatic changes, with rising temperatures and increase in greenhouse gases, such as methane and carbon dioxide (CO₂), being among the most prominent ones (IPCC 2014). Between 1880 and 2012, ocean surface temperature has risen 0.85 °C on average globally. More noticeable changes have been within the upper 75 m, where in the last 40 years temperature increased on average more than 0.1 °C per decade. Furthermore, the partial pressure of CO₂ has risen from ~316 to ~408 ppm since 1960 (Tans and Keeling 2019). This has resulted in an increased uptake of CO₂ by oceans and led to a lower pH value, a process commonly referred to as ocean acidification (Doney et al. 2009; NOAA 2018). Since carbonate ions are decreasing due to a higher uptake of CO₂ by the oceans, marine organisms may be directly affected by the change in this water chemistry parameter. In particular, calcifying organisms that need carbonate ions for growth (corals), building shells (mollusks) and exoskeletons (crustaceans) are considered to be

threatened the most by falling pH values (IPCC 2007, 2014; Whiteley 2011; Kroeker et al. 2013; Heuer and Grosell 2014; Waldbusser et al. 2015). Consequently, many studies have already observed shifts in migrations, geographic range changes and poleward movement of species due to increase in temperatures and changes to water chemistry (Chen et al. 2011; Lockwood et al. 2013; Poloczanska et al. 2013; VanDerWal et al. 2013; Bates et al. 2014; Holopainen et al. 2016; Smith et al. 2019; Pinsky et al. 2020).

Currently, the Baltic Sea is exposed to many anthropogenic stressors (IPCC 2014; Rutgersson et al. 2014; Andersson et al. 2015; Reusch et al. 2018; Meier et al. 2022). It is a geologically young, semi-enclosed brackish waterbody that was formed by glaciation (Leppäkoski et al. 2002). Interestingly, the system has the highest rate of temperature change in recent history, with an increase of more than 1 °C per decade, exceeding the global average seven times over (Belkin 2009; IPCC 2014; Reusch et al. 2018). Further increases by approximately 2–3 °C have been predicted for the end of the twenty-first century (IPCC 2007, 2014; Christensen et al. 2022). Likewise, ocean acidification corresponding to *p*CO₂ levels beyond those predicted under a 2 °C warming scenario has also been observed (Melzner et al. 2013; Rutgersson et al. 2014; Reusch et al. 2018; Christensen et al. 2022), and the system has already been invaded by at least 125 NIS (Casties et al. 2016; Cuthbert et al. 2022). Thereby, a potential synergy in environmental impacts between NIS and rapid environmental change may be forming. Native species in the Baltic Sea have a high phenotypic plasticity, but some populations already inhabit areas characterized by conditions at the limit of their environmental tolerance (Arndt 1989; Gräwe et al. 2013). Since anthropogenic impacts are still continuing to increase, it is of paramount importance to understand their effects on individual species as well as entire communities and ecosystems, with particular interest on both native and NIS (Kroeker et al. 2013; Lockwood et al. 2013; IPCC 2014; Gunderson et al. 2016; Reusch et al. 2018; Casties et al. 2019; Ricciardi et al. 2021). Anthropogenic stressors to the Baltic Sea have caused environmental changes exceeding the global averages (IPCC 2014; Rutgersson et al. 2014; Andersson et al. 2015; Reusch et al. 2018), thus the studies conducted there may not only provide important insight into resistance and resilience of the Baltic ecosystems to

those stressors, but also the understanding of future changes globally.

To improve our understanding on the interaction between climate change and NIS on biological communities, we conducted laboratory experiments to test the temperature and $p\text{CO}_2$ tolerance of four gammarid species. We used gammarid taxa as they are found globally and are recognised as important species in ecosystems due to their roles in the detritus cycle (e.g. litter breakdown processes) and food webs (e.g. providing prey for secondary consumers; Ruppert et al. 2004), and as they are adapted to various environmental conditions (Gerhardt et al. 2011; Cuthbert et al. 2020), are successful NIS and often cause declines in abundances of native gammarid species (Witt et al. 1997; Pinkster et al. 1992; Dermott et al. 1998; Grabowski et al. 2006; Kotta et al. 2013; Jänes et al. 2015; Cuthbert et al. 2020). Two Baltic (*Gammarus locusta* and *G. salinus*), one Ponto-Caspian (*Pontogammarus maeoticus*) and one North American species (*G. tigrinus*) were tested at two temperatures (i.e. 16 and 24 °C) and four $p\text{CO}_2$ levels (400, 1600, 2700, and 3500 ppm) factorially. To determine performances of the species during the experiments, we tracked mortality of individuals at different treatment conditions. We tested the hypothesis that climate change differentially affects native species and NIS. Our working hypotheses were that: (i) an increase in temperature causes higher mortality of native species than NIS; (ii) an increase in $p\text{CO}_2$ level causes higher mortality of native species than NIS; and (iii) combination of increases in temperature and $p\text{CO}_2$ causes higher mortality of native species than NIS.

Materials and methods

Organism collection and husbandry

Four gammarid species were collected for experimentation: two native (i.e. *Gammarus locusta* and *Gammarus salinus*) and two non-native (i.e. *Gammarus tigrinus* and *Pontogammarus maeoticus*) species. The two native gammarid species were collected from the Kiel Fjord in Kiel, Germany: *G. locusta* were collected at Falckenstein Beach (54° 23' 36.2" N 10° 11' 21.4" E) in February–April 2019; and *G. salinus* were collected at Kieler Meeresfarm (54° 22' 55.3" N 10°

09' 43.6" E) in July 2020. Collection of non-native *G. tigrinus* specimens was undertaken at Dassower Lake, Lübeck, Germany (53° 53' 52.1" N 10° 54' 54.0" E) in June 2020. Non-native *P. maeoticus* were collected near Jafrud, Iran (37° 29' 09" N, 49° 30' 20" E) in October 2014. Species were collected in these particular seasons due to these harbouring their highest abundance at the collection sites (E. Briski, personal observation), with different collection years owing to logistic practicality and space availability for the experiments. We emphasize, here, that the effect of time (i.e. different year and season) and acclimation to laboratory conditions (in the case of *P. maeoticus*) may have affected the response variable of our experiments (see further in the discussion section). Following collection, all species were transported in source water from their respective sampling sites to a climate chamber at GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany, and maintained at 16–18 °C under a 12:12 h light and dark regime. Animals were housed at their respective averaged ambient salinities (*G. locusta* = 14 g/kg; *G. salinus* = 14 g/kg; *G. tigrinus* = 10 g/kg; *P. maeoticus* = 10 g/kg) in 56 L glass aquaria (separately per species). Each aquarium contained an internal filtration system to maintain water quality, and was supplied weekly with a mixture of commercial crustacean food (Tetra Mix, Tetra Crusta, and Dr. Shrimp Healthy). The water used for housing was pumped from the Kiel Fjord, and 5 µm-filtered. Where necessary, ambient salinity was adjusted with Instant Ocean® artificial sea water or dechlorinated tap water.

Laboratory experimentation

Separate batches of trials according to species availability were performed in a climate chamber during April–May 2019 and July–November 2020 (i.e. *G. locusta* in April–May 2019; *G. salinus* in August–September 2020; *G. tigrinus* in July–August 2020; and *P. maeoticus* in October–November 2020). A crossed experimental design consisting of two temperature levels (16 and 24 °C) and four $p\text{CO}_2$ levels (400, 1600, 2700, and 3500 ppm) was used, yielding a total of eight treatment combinations per species (Bleich et al. 2008). Temperature conditions were based on the 15-year temperature observation data in the Kiel Fjord measured by GEOMAR and reported

in Pansch et al. (2018), while $p\text{CO}_2$ levels were based on Melzner et al. (2013) and HELCOM (2013).

One replicate of a given treatment consisted of a single 2 L aquarium and contained ten randomly selected conspecific adult individuals; each treatment combination was performed in triplicate, yielding a combined total of 24 replicates across the eight 'temperature \times $p\text{CO}_2$ ' scenarios per species. The 2 L aquaria were placed in water baths at the desired temperature in batches of six, with $p\text{CO}_2$ levels being randomly assigned within each water bath. Each 2 L aquarium contained artificial habitat, and the water was continuously infused with its determined $p\text{CO}_2$ level using an air stone; a fastened plastic cover stabilized the $p\text{CO}_2$ level of each container. One day prior to the start of experimentation, the aquaria were placed in the water baths and aerated at their assigned temperature and $p\text{CO}_2$ combination, to ensure the desired conditions were reached before the introduction of the animals. The salinity throughout the experiments was maintained at the ambient condition for each species, i.e. 14 g/kg for *G. locusta* and *G. salinus*, and 10 g/kg for *G. tigrinus* and *P. maoticus*. Raw data supporting the findings of this study are available as Supplementary Information (Appendix S1).

The experimental duration was 30 days, during which each aquarium was continuously aerated at its given $p\text{CO}_2$ level and animals were fed ad libitum with a ground mix of crustacean food (Tetra Mix, Tetra Crusta, and Dr. Shrimp Healthy). Mortality rates (i.e. number of dead out of the original ten supplied) were assessed daily to measure survival among species under each replicated temperature and $p\text{CO}_2$ combination. Salinity (WTW Cond 3110 with Tetracon 325 probe), pH (WTW pH 3110 with Sentix 81 pH electrode), and temperature were recorded daily, and dead individuals, molted exoskeletons, and newly emerged juveniles were removed at that time. A 50% water exchange was performed at most every ten days in each replicate. Water for the exchange was prepared in advance to meet the assigned temperature and $p\text{CO}_2$ levels.

Statistical analyses

Generalized linear models with binominal error distributions and logit links were used to test for differences in mortality with the raw data, with two

separate models used for the mid-point (i.e. day 15) and end-point (i.e. day 30) of the experiment. Each model considered mortality as a response variable (i.e. numbers dead out of original ten supplied) with species (i.e. four level factor), temperature (i.e. continuous term) and $p\text{CO}_2$ (i.e. continuous term) included as factorial explanatory variables. Residuals in each model were checked for over- and under-dispersion using simulations which were compared to fitted residuals (Hartig 2020). All possible two- and three-way interactions were included in a full model at each time point, which was reduced backward stepwise via analysis of deviance to obtain the most parsimonious structure that contained only significant terms (Crawley 2007). Complete separation was observed in some treatment groups at the end-point (i.e. owing to complete mortality across replicates in a group), and thus bias reductions were used for model coefficient corrections (Kosmidis 2020). Terms in the final models were computed using likelihood ratio tests via analysis of deviance, with Type III sums of squares incorporated in the presence of a significant interaction (Fox et al. 2019). *Post-hoc* comparisons were computed pairwise where a term yielded significance via Tukey tests (Lenth 2020). Significance was always inferred considering an alpha of 0.05. Generalized linear modelling was performed in R v4.0.2 (R Core Team 2020).

Then, we tested for differences in the onset and rate of mortality between species in each treatment over time. To test for differences between species, a mortality curve was constructed for each species for each treatment using data from the three replicates, described by the equation (Briski et al. 2008, 2011; Paiva et al. 2018):

$$y = 100 / [1 + e^{-Z(t-Q)}] \quad (1)$$

where Z is the slope of the mortality rate, t is temperature and Q is the onset of mortality. The model was then expanded to compare the slope and onset of the mortality rate between two curves using the equation:

$$y = 100 / [1 + e^{-(Z_1+Z_2)(t-Q_1-Q_2)}] \quad (2)$$

where Z_1 and Z_2 are the slopes of the mortality rates and Q_1 and Q_2 the onsets of mortality, for the first and second curves respectively. All pairs of curves were statistically compared by the fit non-linear model using generalized least squares. Significance levels

for statistical comparisons of estimated parameters Z_1 and Z_2 , and Q_1 and Q_2 , were adjusted for multiple pairwise comparisons by Bonferroni-type correction to guard against inflating the Type I error rate. The family-wise error rate of 0.05 was used (i.e. 0.001). All tests were performed using S-Plus 6.1 (S-Plus® 6.1, 2002; Insightful Corp., Seattle, WA, USA). Raw data are available as Supplementary Information.

Results

Species, temperature and their interactions were significant factors at both time-points of the experiment (i.e. the mid-point and end-point), while $p\text{CO}_2$ and any interactions involving it were not shown to be a significant driver of mortality of the tested species (Table 1). In general, the native gammarid species (i.e. *G. locusta* and *G. salinus*) had higher mortality compared to the two non-native species (i.e. *G. tigrinus* and *P. maeoticus*) in both tested temperatures (i.e. 16 and 24 °C; Fig. 1). *Gammarus salinus* had the highest mortality at 16 °C at both time-points of the experiment, whereas *G. locusta* at 24 °C for both time points (Fig. 1). *Gammarus locusta* was also the only species demonstrating 100% mortality at 24 °C; there was no 100% mortality for any

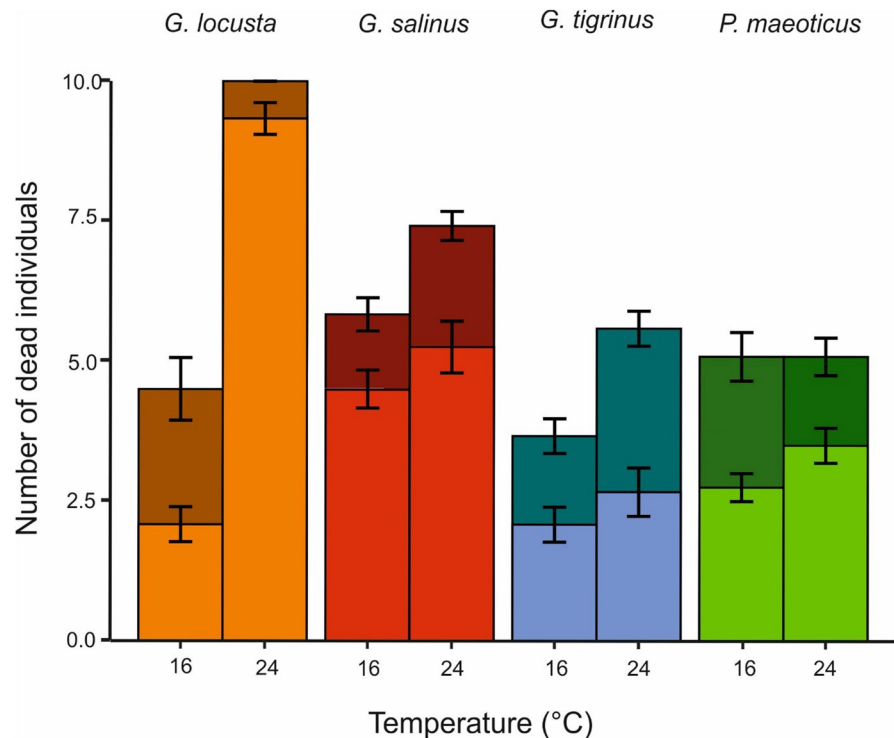
species at 16 °C (Fig. 2 panels e, f, g, and h). The onset of mortality was significantly different among the four species in all comparisons at 24 °C and in most comparisons at 16 °C (Fig. 2; Appendix S2). In all treatments, *G. salinus* began to die first, often followed by *P. maeoticus*. *Gammarus locusta* began to die last in most treatments. However, due to differences in mortality rate among species and treatments, our experiments resulted in *G. salinus* and *G. locusta* having the highest overall mortality at 16 and 24 °C, respectively (Table 1 and Appendix S2; Fig. 1). *Gammarus locusta* had significantly higher mortality in 24 °C than in 16 °C already at the mid-point of the experiment ($p < 0.001$; Fig. 1), while for *G. salinus* and *G. tigrinus* that was the case only at the end of the experiment ($p = 0.011$ and $p = 0.003$, respectively; Fig. 1). There was no difference in mortality of *P. maeoticus* in either of the time-points of the experiment considering temperature treatments ($p = 0.211$ and $p = 0.999$, respectively; Fig. 1). At the end of the experiment in both temperature treatments, there was no significant difference in mortality between *P. maeoticus* and *G. tigrinus* ($p = 0.131$ and $p = 0.872$, respectively; Fig. 1), whereas both of the species demonstrated significantly lower mortality at 24 °C than *G. locusta* and *G. salinus* ($p < 0.001$ and $p = 0.002$, respectively for *P. maeoticus*; $p < 0.001$

Table 1 Results of binomial generalized linear models with logit links used to test for differences in mortality rates for the mid-point (i.e. day 15) and end-point (i.e. day 30) of the experiment

	Day 15 (Type III tests)			Day 30 (Type II tests)		
	df	LR Chi-square	<i>p</i>	df	LR Chi-square	<i>p</i>
<i>Full model</i>						
Species	3	21.9064	< 0.0001	3	49.345	< 0.0001
Temperature	1	18.1881	< 0.0001	1	53.484	< 0.0001
$p\text{CO}_2$	1	0.4688	0.4935	1	0.170	0.6799
Species:temperature	3	29.2944	< 0.0001	3	79.431	< 0.0001
Species: $p\text{CO}_2$	3	1.2141	0.7496	3	1.056	0.7877
Temperature: $p\text{CO}_2$	1	0.5160	0.4725	1	0.166	0.6833
Species:temperature: $p\text{CO}_2$	3	2.0028	0.5718	3	-1.033	1.0000
<i>Most parsimonious model</i>						
Species	3	69.912	< 0.0001	3	62.367	< 0.0001
Temperature	1	64.771	< 0.0001	1	85.372	< 0.0001
Species:temperature	3	90.756	< 0.0001	3	78.470	< 0.0001

Results are shown from the full model (i.e. with all terms) and refined model (i.e. following backward stepwise deletion). Likelihood-ratio (LR) Chi-square values were computed from analysis of deviance with Type III (day 15) and Type II (day 30) sums of squares and significant terms are emboldened

Fig. 1 Means and standard errors of mortality in 16 and 24 °C treatments for four species (*G. locusta*, *G. salinus*, *G. tigrinus*, and *P. maeoticus*, in that order) at the mid-point and end-point of experiments (i.e. day 15 and day 30, respectively). Mortality in different $p\text{CO}_2$ treatments were used to calculate means and standard errors (i.e. 400, 1600, 2700, and 3500 ppm). Lighter colors denote values at the mid-point, while darker at the end-point



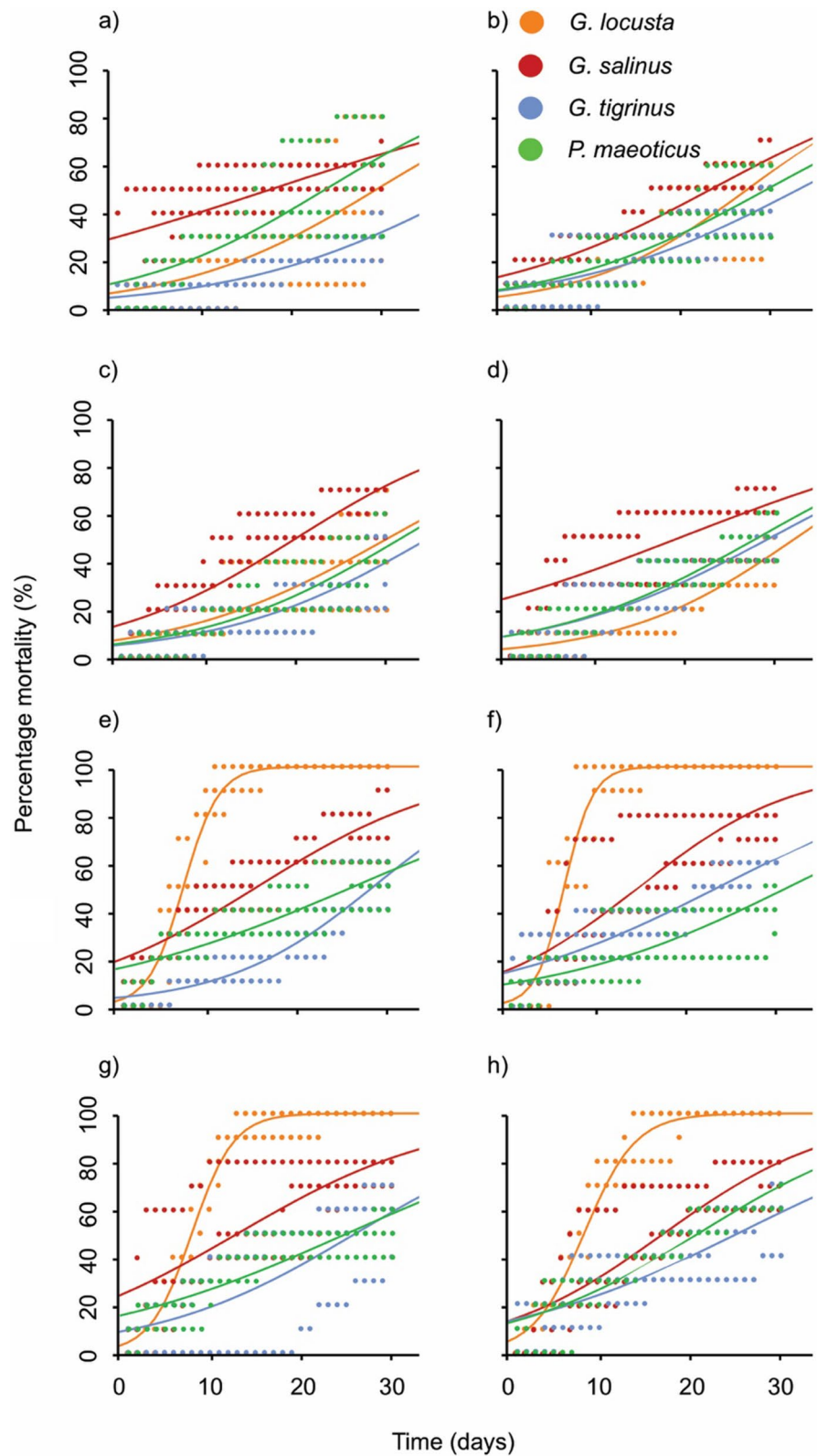
and $p=0.020$, respectively for *G. tigrinus*; Fig. 1). At 16 °C only *G. tigrinus* demonstrated significantly lower mortality than *G. salinus* by the end of the experiment ($p=0.006$); there was no significant difference in mortality among other species at 16 °C at this time-point (Fig. 1).

Discussions

Ecosystems worldwide are impacted by anthropogenic activities and globalization, with climate change and species introductions being among their greatest stressors (Olden et al. 2004; Hawkins 2012; Simberloff et al. 2013; IPCC 2014; Linders et al. 2019; Pyšek et al. 2020). In this study, we conducted laboratory experiments to compare temperature and $p\text{CO}_2$ tolerances of four gammarid species originating from three different regions—the Northern European, Ponto-Caspian and North American Atlantic regions—to detect interactions between climate change and NIS. Conversely to our expectations, our study demonstrated that an increase in $p\text{CO}_2$ level was not a significant driver of mortality, neither by itself nor in combination with increased temperature,

for any of the tested species. However, temperature was significant, and it affected the tested species to different extents, particularly favouring NIS over native species. The most sensitive was the native species *G. locusta* which experienced 100% mortality by the end-point of the experiment. The second native species, *G. salinus*, performed better than *G. locusta*, but was still more sensitive to temperature increase than any of the NIS. In contrast, *P. maeoticus*, the tested NIS from Ponto-Caspian, not only performed better than native species, but also did not demonstrate any difference in its performance between the temperature treatments. Consequently, if other native taxa and NIS would perform similarly to our studied species, the predicted environmental changes in the Baltic Sea, and in particular temperature increases, may lead to shifts in distributions among native gammarid taxa moving towards colder areas, while at the same time, their niches might be filled by NIS which exhibit better-suited environmental tolerances. In the best-case scenario, those NIS may take over roles of retreated native species and maintain ecosystem functioning. Nonetheless, as the chance that impactful NIS will arrive increases with the increased number of establishing NIS, the danger of negative impacts

Fig. 2 Mortality rates (%) of four gammarid species: *G. locusta* (orange), *G. salinus* (red), *G. tigrinus* (blue) and *P. maeoticus* (green) in experiments conducted in two temperature and four $p\text{CO}_2$ treatments: 16 °C and 400 ppm (a), 16 °C and 1600 ppm (b), 16 °C and 2700 ppm (c), 16 °C and 3500 ppm (d), 24 °C and 400 ppm (e), 24 °C and 1600 ppm (f), 24 °C and 2700 ppm (g), and 24 °C and 3500 ppm (h). The curves were constructed using pooled data from three replicates



connected with the new NIS may rise as well (Ricciardi and Kipp 2008; Blackburn et al. 2019; Essl et al. 2020; Pyšek et al. 2020; Cuthbert et al. 2021; Diagne et al. 2021).

Earlier studies reported that marine organisms, including crustaceans, experience negative effects on growth rate, moulting frequency and survival as a result of acidification, particularly in combination with elevated temperature (Whiteley 2011; Kroeker et al. 2013). In contrast to those studies, a recent review and meta-analysis based on 5153 observations from 985 studies, determined that many calcifiers (e.g. echinoderms, crustaceans, and cephalopods) are tolerant to acidification levels predicted for the year 2100, and the authors pointed out the underestimated calcifiers' phenotypic plasticity (e.g. physiological, mineralogical, structural, and molecular adjustments) and adaptability (Leung et al. 2022). That said, Leung et al. (2022) did not account for any additional stressors in their study, and emphasized crustaceans being underexplored compared to other taxa. Our study did not explore physiological consequences of elevated $p\text{CO}_2$, nor survival of gammarid taxa at juvenile stages, but survival of adults in our study was in concordance with Leung's et al. (2022) review, even when elevated temperature was considered. Interestingly, as stated above, this was not always the case, and there are many studies reporting contradictory results. For example, two Antarctic gammarid species, *Gondogeneia antarctica* and *Paradexamine fissicauda* have been significantly impacted by exposure to water with lower pH than that of their habitats (Schram et al. 2016). Survival for both species declined significantly at reduced pH and covaried with molt frequency. Schram et al. (2016) also specified that elevated temperature caused sub-lethal impacts on the species, while reduced pH caused significant mortality (Schram et al. 2016). As their findings are contradictory to ours and those of Leung et al. (2022), we point out that differences in robustness to certain stressors among taxonomic groups and species, or even at population levels, may relate to the species/population biogeographical origin and evolutionary history (Preisser et al. 2008; Kuo and Sanford 2009; O'Neill et al. 2008; Paiva et al. 2018). For example, in the case of Baltic Sea taxa, many species may have already been adapted to ocean acidification due to already decreased pH levels in the system (Melzner et al. 2013; Rutgersson et al. 2014; Reusch

et al. 2018; Christensen et al. 2022). However, these same species may still be sensitive to increased temperature as they live at their upper thermal tolerance limits. On the other hand, the opposite may be the case for Antarctic gammarid species. Consequently, we trust that further studies are needed using different crustacean taxa, ontogenic stages (e.g. larval stages), and populations originating from environmentally diverse ecosystems, to make more general conclusions on ocean acidification impacts, and its combination with other stressors, on this taxonomic group.

While predicted changes in $p\text{CO}_2$ concentrations and acidification turned out to be insignificant factors for the four tested species in our study, the temperature increase was especially detrimental for the native gammarid *G. locusta*, leading to mortality of all experimental individuals during our tests. Temperature was also a significant driver of mortality of the second native species tested, *G. salinus*, as well as of the North American NIS *G. tigrinus*, while it did not have a statistically clear effect on the Ponto-Caspian NIS, *P. maeoticus*. Casties et al. (2019) reported similar results for gammarid taxa originating from the same regions, with a Ponto-Caspian NIS being robust not only to temperature increase, but also to salinity changes. As mentioned above, the wider tolerance range to higher and/or lower temperature conditions is probably due to evolutionary history of the species (Cristescu et al. 2003; Preisser et al. 2008; Kuo and Sanford 2009; O'Neill et al. 2008; Paiva et al. 2018). Both native species colonized the Baltic Sea from the Atlantic Ocean after the last Glacial Maximum, where they evolved under colder conditions than the Ponto-Caspian taxa (Zenkevitch 1963; Björck 1995; Reid and Orlova 2002; Johannesson and André 2006). The North American NIS, *G. tigrinus*, originates from even colder areas of the North Atlantic coast, where the cold Labrador Current flows from the Arctic Ocean southwards along the coast of North America. Relative to the species' optimum temperature, environmental warming increases organism metabolism and energetic demands (Lemoine and Burkepile 2012; Bruno et al. 2015). However, based on metabolic theory of ecology, metabolism frequently increases more quickly with temperature than does food consumption, resulting in reduced ingestion efficiency and decreasing individual fitness (Pörtner 2010; Rall et al. 2010; Lemoine and Burkepile 2012). Consequently, while all four species in our study

had reasonable performance in the first few days of the experiment, as the experiment progressed, due to higher stress experienced by native species, they likely had no energy left for basic cell maintenance and physiological processes, leading to high mortality of tested individuals (Pörtner 2010; Rall et al. 2010; Lemoine and Burkepille 2012).

With the predicted temperature increases in the Baltic Sea, as well as globally in general, taxa unable to adapt to new conditions undoubtedly will shift in their distributions towards colder areas, as has already been observed (Chen et al. 2011; Poloczanska et al. 2013; Bates et al. 2014; Smith et al. 2019; Pinsky et al. 2020). However, in the case of the Baltic Sea, as the system becomes colder, it also becomes fresher due to the salinity gradient (Meier et al. 2022). Native species in the Baltic Sea are highly plastic towards salinity changes (Arndt 1989; Gräwe et al. 2013; Paiva et al. 2018; Casties et al. 2019). Still, some populations occupy areas characterized by conditions at the limit of their tolerance (Arndt 1989; Gräwe et al. 2013). Changes from optimal salinity require additional energetic costs because of osmoregulation, leading also to a decrease in organisms' fitness (Evens 2008; Rivera-Ingraham & Lignot 2017). Therefore, migration towards colder habitats may likewise lead to lower salinity and additional stress. Consequently, further studies combining effects of temperature and salinity, as well as oxygen depletion since deeper saltier areas contain lower oxygen levels (Meier et al. 2022), are needed for understanding the consequences of climate change on the ecosystems of the Baltic Sea.

Here, we emphasize that our findings should be taken with caution due to the temporal separation of experiments among different species and long-term laboratory maintenance of *P. maeoticus* before the experiments. We therefore acknowledge that there is a possibility that *P. maeoticus* might have had an advantage over other three species because it spent several years in laboratory culture before experiments started. Though, Casties et al. (2019) also demonstrated higher performance of the same laboratory population of *P. maeoticus* when compared to native *G. oceanicus* after species were laboratory cultured for one and a half and one year, respectively.

Previous studies conducted on *Fucus* communities from the Kiel Fjord reported that increasing $p\text{CO}_2$ concentrations had only minor effects, while warming

had strong and persistent effects on grazers (*Littorina littorea*, *Idotea* spp., and *Gammarus* spp.), with resulting consequences on population growth rate, biomass, and feeding rate of grazers among seasons (Werner et al. 2016; Wahl et al. 2020). However, interestingly, warming had detrimental consequences on grazers in the late summer (Werner et al. 2016; Wahl et al. 2020), which is opposed to the lowest performance of *G. locusta* in spring/early summer in our study, when grazers in Werner et al. (2016) and Wahl et al. (2020) demonstrated higher performance with warming. The same authors also reported similar results for filter feeders (*Amphibalanus improvises* and *Mytilus edulis*), predatory starfish (*Asterias rubens*), and brown alga (*Fucus vesiculosus*). Therefore, we trust that seasonal variation in our experimental testing probably did not affect the results of our study. Yet, annual effects are unclear and require further testing.

Changes in ecosystems due to climate change and other anthropogenic activities may enable or hinder introduction, spread and/or impact of NIS (Hufbauer et al. 2011; Holopainen et al. 2016). When focusing on gammarid taxa, and in particular on *G. tigrinus* and *P. maeoticus* tested in our study, we determined that these NIS are more resistant to predicted changes than their conspecific natives in terms of mortality. However, fecundity and other life history traits are also affected by temperature. Warmer temperature allows for more broods in amphipods due to the brooding period becoming shorter (Holopainen et al. 2016). However, because of differences in the upper thermal limits among diverse species and their resilience to temperature changes, we suspect even stronger effects of temperature on native gammarids tested than our study demonstrated. For example, life history of *G. locusta* at 20 °C, when compared to 15 °C, was characterized by at least a four-week reduction in the life-span and lower life expectancy (Neuparth et al. 2002). Though, a shorter generation time, faster individual growth, and interestingly, higher population growth rate were also observed (Neuparth et al. 2002). Furthermore, *G. locusta* produces two generations per year with a maximum of 65 eggs per clutch (Kolding and Fenchel 1981) and *G. salinus* tends to have their first clutch when they have reached an age of 3.5 months (Skadsheim 1990). In contrast, sexual maturity in *G. tigrinus* is

reached at a very small size, with females of 4 mm in length and one month of age being able to bear eggs. Their brooding time decreases at increased temperatures from 20 days at 10 °C to 9 days at 21 °C. Therefore, a newly hatched female could be brooding its first clutch in little over a month after hatching (Pinkster 1975). Ponto-Caspian gammarids have higher temperature tolerances than *G. tigrinus* and even more so than Northern European species (this study; Casties et al. 2019). Moreover, *P. maeoticus* has a two-month generation time and is able to reproduce throughout a year irrespectively of seasonality (personal observations; Nazarahighi et al. 2013). *Gammarus tigrinus* is able to reduce and replace local gammarid taxa through a combination of high reproductive potential and predation on their juveniles (Pinkster 1975; Jänes et al. 2015). *Pontogammarus maeoticus* is not yet established in the Baltic Sea, although other gammarid species from the Ponto-Caspian region are already in the system, and some of them are voracious predators capable of causing severe changes in local communities (Dick and Platvoet 2000; Grabowski et al. 2007; Gumuliauskaitė and Arbačiauskas 2008; Cuthbert et al. 2020). Accordingly, with the predicted changes in the Baltic Sea, there are greater chances that many native gammarid taxa will move towards colder areas of the system or their population would shrink, while their current habitats may be filled by NIS, and particularly those from the Ponto-Caspian region.

More broadly, these results exemplify how climate change and biological invasions can interact to mediate patterns of success of NIS. Whereas some effects of global change were found to be benign here even in the presence of other stressors (i.e. $p\text{CO}_2$), temperature was found to be a key determining factor that distinguished NIS from native species under changing climates. These results highlight the pertinence of considering multiple interacting stressors in the context of biological invasions, both for NIS success and impact prediction as environments change.

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Author contributions EB: Conceptualization. EB, CMR, RNC and LL: Investigation. LL, CMR and RNC: Formal

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Data availability Raw data supporting the findings of this study are available as Supplementary Information. There was no custom code or mathematical algorithm used in the study.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethics approval Ethical approval was not required for the nature of this work.

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