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# Environmental tolerance of three gammarid species with and without invasion record under current and future global warming scenarios

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**Abstract**

**Aim:** Numerous regions worldwide are highly impacted by anthropogenic activities and globalization, with climate change and species introductions being among the greatest stressors to biodiversity and ecosystems. A main donor region of non-indigenous species (NIS) for numerous European water bodies, as well as in the North American Great Lakes is the Ponto-Caspian region (i.e., Black, Azov and Caspian Seas), with some of those species having significant impact on local communities and ecosystem functioning.

**Location:** Northern European, Ponto-Caspian and North American regions.

**Methods:** To determine environmental tolerance of native species and related NIS under current and future global warming scenarios of the Baltic Sea, we conducted common garden experiments to test temperature tolerance of three euryhaline gammarid species: one Baltic (*Gammarus oceanicus*), one Ponto-Caspian (*Pontogammarus maeoticus*) and one North American species (*Gammarus tigrinus*) in two different salinities.

**Results:** Our results determined that mortality of *P. maeoticus* in all temperature treatments (i.e., increased, control, and decreased) at the end of both experiments (i.e., conducted in salinities of 10 and 16 g/kg) was lower when compared to mortality of *G. oceanicus* and (c) *G. tigrinus*. The highest mortality was observed for *G. oceanicus*, reaching 100% in both experiments in the increased temperature treatment.

**Main conclusions:** Due to the high environmental tolerance of the Ponto-Caspian species tested in this study, as well as the fact that Ponto-Caspian species evolved in environmentally variable habitats and currently inhabit warmer waters than species from North America and Northern Europe, we suggest that species from the Ponto-Caspian region may benefit from global warming when invading new areas. Those new invasions may, in the best case scenario, increase biodiversity of the Baltic Sea. However, if notorious invaders arrive, they may have a significant impact on local communities and ecosystem functioning.

**KEYWORDS**

gammarids, non-indigenous species, RNA/DNA ratio, salinity, temperature tolerance

## 1 | INTRODUCTION

Ecosystems all over the world are progressively invaded by non-indigenous species (NIS) due to globalization and climate change (Capinha, Essl, Seebens, Moser, & Pereira, 2015; Hellmann, Byers, Bierwagen, & Dukes, 2008; Hulme, 2009; Hulme et al., 2008; Lockwood, Hoopes, & Marchetti, 2007). A main donor region of NIS for numerous European water bodies as well as in the North American Great Lakes is the Ponto-Caspian region (i.e., Black, Azov and Caspian Seas; Ricciardi & MacIsaac, 2000; Leppäkoski et al., 2002; Casties, Seebens, & Briski, 2016). As Ponto-Caspian species established in the North and Baltic Seas and Great Lakes-St. Lawrence River region in much higher numbers than expected based on introduction effort (i.e., shipping frequency) and environmental conditions between these regions, it has been suggested that Ponto-Caspian taxa are inherently better invaders than species from other regions (Casties et al., 2016; Leppäkoski et al., 2002; Ricciardi & MacIsaac, 2000). Some of those Ponto-Caspian species, such as the zebra mussel *Dreissena polymorpha*, the amphipod *Echinogammarus ischnus* and the round goby *Neogobius melanostomus*, can have high impact on local communities and ecosystem functioning (Charlebois, Corkum, Jude, & Knight, 2001; Dermott, Witt, Um, & González, 1998; Ojaveer et al., 2015; Ricciardi, Neves, & Rasmussen, 1998). Changes in species communities and environments may open new niche opportunities for continuously introduced species and might be enhanced by predicted future climate change (Holopainen et al., 2016; IPCC, 2014).

Beside introduction of NIS, other anthropogenic stressors have serious impact on biodiversity, ecosystems and environment, such as eutrophication and loss of habitats, as well as high emissions of greenhouse gases that change the global climate drastically (IPCC, 2014; Sala et al., 2000). Several previous studies determined temperature and salinity having strong influence on the distribution of organisms in aquatic environments (Delgado, Guerao, & Ribera, 2011; Einarson, 1993; Neuparth, Costa, & Costa, 2002; Sutcliffe, 1968). Therefore, one of the major concerns is the increase in sea surface temperature that potentially impairs growth, reproduction and survival of organisms and might lead to migrations of taxa to new and more favourable habitats (Bulnheim, 1979; Neuparth et al., 2002; Sainte-Marie, 1991). As global climate models predict warming and acidification of the oceans worldwide (IPCC, 2014) while species' resistance to multiple stressors facilitates establishment of NIS in new habitats, it is of great importance to investigate species' environmental tolerance limits, and in particular in regard to the introduction of NIS.

The Baltic Sea is a highly variable brackish water body which has already been invaded by 125 NIS (Casties et al., 2016) and will most likely be subject to future climate change. An increase in average surface water temperature by approximately 2–3°C and reduction in average salinity by approximately 2 g/kg have been predicted by the end of the twenty-first century (Gräwe, Friedland, & Burchard, 2013; Holopainen et al., 2016; IPCC, 2007, 2014). Native species in the Baltic Sea have a high phenotypic plasticity; however, some of

their populations often inhabit areas characterized by environmental conditions at the limit of their environmental tolerance (Arndt, 1989; Gräwe et al., 2013). Amphipods are important keystone species in the Baltic Sea and other aquatic ecosystems where they often appear in high abundance in shallow coastal zones (Gerhardt, Bloor, & Mills, 2011). They constitute a significant diet source for many zoobenthivorous fish and waterbirds. Furthermore, amphipods are successful invaders and known NIS in many regions worldwide due to their wide trophic range, high reproductive capacity and migration ability (Gerhardt et al., 2011). The decreased abundance of native amphipods due to establishment of a related NIS has been well documented in Europe and the Great Lakes (Dermott et al., 1998; Jänes, Kotta, & Herkül, 2015; Kotta, Orav-Kotta, Herkuel, & Kotta, 2011; Kotta et al., 2013; Pinkster, Scheepmaker, Platvoet, & Broodbakker, 1992; Pinkster, Smit, & Brandse-de Jong, 1977; Witt, Hebert, & Morton, 1997). They are osmoregulators able to maintain intracellular ion and osmolyte homeostasis at varying external water conditions, yet restricted by their individual salinity limits (Werntz, 1963).

To determine environmental tolerance, invasion success of the Ponto-Caspian taxa, and the probability of replacement of native species by related NIS under current and future global warming scenarios of the Baltic Sea, in this study, we conducted common garden experiments to test stress tolerance of three euryhaline gammarid species. We tested temperature tolerance of one Baltic (*Gammarus oceanicus*), one Ponto-Caspian (*Pontogammarus maeoticus*) and one North American species (*G. tigrinus*) in two different salinities (i.e., 16 g/kg – ambient salinity of *G. oceanicus*, and 10 g/kg – ambient salinity of *P. maeoticus* and *G. tigrinus*). To determine the performance of these species during the experiments, we followed mortality and conducted RNA/DNA ratio measurements as indicators for nutritional condition on randomly selected surviving individuals. We tested the hypotheses that there is no difference in mortality: (a) among different species in salinity of 10 g/kg (i.e., ambient salinity of NIS); (b) among different species in salinity of 16 g/kg (i.e., ambient salinity of native species); and (c) among different temperature treatments within each species (i.e., increased, control and decreased temperature treatments).

## 2 | MATERIALS AND METHODS

### 2.1 | Specimen collection

Three gammarid species were collected, transported in their ambient water to GEOMAR in Kiel, Germany, and acclimatized before the experiments were conducted. Two species were collected in their native range (*G. oceanicus* – Kiel Fjord, Western Baltic Sea, Germany and *P. maeoticus* – the South Caspian Sea, Iran), and one in its non-indigenous range (*G. tigrinus* – Dassow Bay, Germany). Specimens of *P. maeoticus* were collected in October 2014, while those of *G. oceanicus* and *G. tigrinus* in May 2015 and May 2016, respectively. The choice of the species was based on their native and non-indigenous status: (a) *G. oceanicus* is native to the Baltic Sea, where it occurs in its

entire area in salinities from 2 to 30 g/kg. It is also widespread along the coasts of the North Atlantic up to subarctic regions (Bulnheim, 1979; Segerstråle, 1947). It was not reported outside its native range (Paiva et al., 2018); (b) *P. maeoticus* is native to the Ponto-Caspian region in salinities from 0.5 to 30 g/kg (Paiva et al., 2018). It is NIS in freshwater areas of Turkey, but not in the Baltic Sea (Casties et al., 2016; Ozbek, 2011); and *G. tigrinus* is native to the Atlantic coast of North America in salinities from <0.5 to 30 g/kg (Paiva et al., 2018), while it is NIS in Northern Europe including the Baltic Sea (Daunys & Zettler, 2006). During the period until the experiments commenced, all three species were kept at the temperature and salinity of their respective collection sites (i.e., 16°C, 16 g/kg for *G. oceanicus*, 18°C, 10 g/kg for *P. maeoticus* and 16°C, 10 g/kg for *G. tigrinus*). The water used was filtered water from the surrounding area of the institute (i.e., Kiel Fjord; filtered through 5- $\mu$ m filter); salinity was adjusted by adding artificial seawater (Instant Ocean<sup>®</sup>) or potable tap water.

## 2.2 | Laboratory experiments

Two common garden experiments were performed in the GEOMAR facilities in June 2016 and September 2016. The first experiment was conducted in a salinity of 10 g/kg giving an advantage to *P. maeoticus* and *G. tigrinus*, while the second one was conducted in 16 g/kg giving an advantage to *G. oceanicus*. The experimental design of both experiments consisted of three temperature treatments: (a) control; (b) increased; and (c) decreased. Each temperature treatment in each experiment was tested in four replicates, containing 14 adult individuals of each species per replicate in the first experiment and 13 individuals in the second experiment. Number of individuals per replicate has been based on temperature experiments conducted by Tsoi, Chiu, and Chu (2005) and our previous experience with gammarid taxa where we were checking oxygen concentration. The size of the tested individuals was similar within each species, while sex was not determined. Three 1-litre beakers having mesh on two vertical sides to allow water exchange, each containing one species, were submerged in a common 8-litre tank (i.e., one replicate). Species were separated in 1-litre beakers to prevent cannibalism among different species. Both experiments started from 16°C. During the experiments, the temperature was increased/decreased by 2°C every 3 days until reaching 26 and 6°C, respectively. The 2°C step was based on the 15-year temperature observation data in the Kiel Fjord measured by GEOMAR and reported in Pansch et al. (2018). Mortality was checked daily throughout the experiments. When the values of 26°C and 6°C were reached, mortality was followed for two more weeks in these temperature conditions. This 20°C temperature range was tested as temperature of the Baltic Sea fluctuates greatly throughout the year (Pansch et al., 2018). Water in each 1-litre beaker and the common 8-litre tank was exchanged every 3 days for the first 2 weeks using temperature pre-equilibrated water. Afterwards, the water was exchanged once per week until the end of the experiments to reduce additional disturbance of the tested individuals; from previous personal experience with tested species, we observed that the change in water quality due to

rarer water exchange is negligible. During the experiments, each 1-litre beaker was continuously aerated, and animals were fed ad libitum with *Fucus vesiculosus*, *Ulva lactuca* and a mixture of algae flakes, while the light/dark cycle was 12:12 hrs. Temperature and salinity were measured daily using a WTW Cond 3110 salinometer and a Tetracon 325 probe (Xylem Analytics Germany Sales GmbH & Co. KG, WTW, Germany). The primary dataset containing experimental results is available at: <https://doi.org/10.1594/pangaea.890931>.

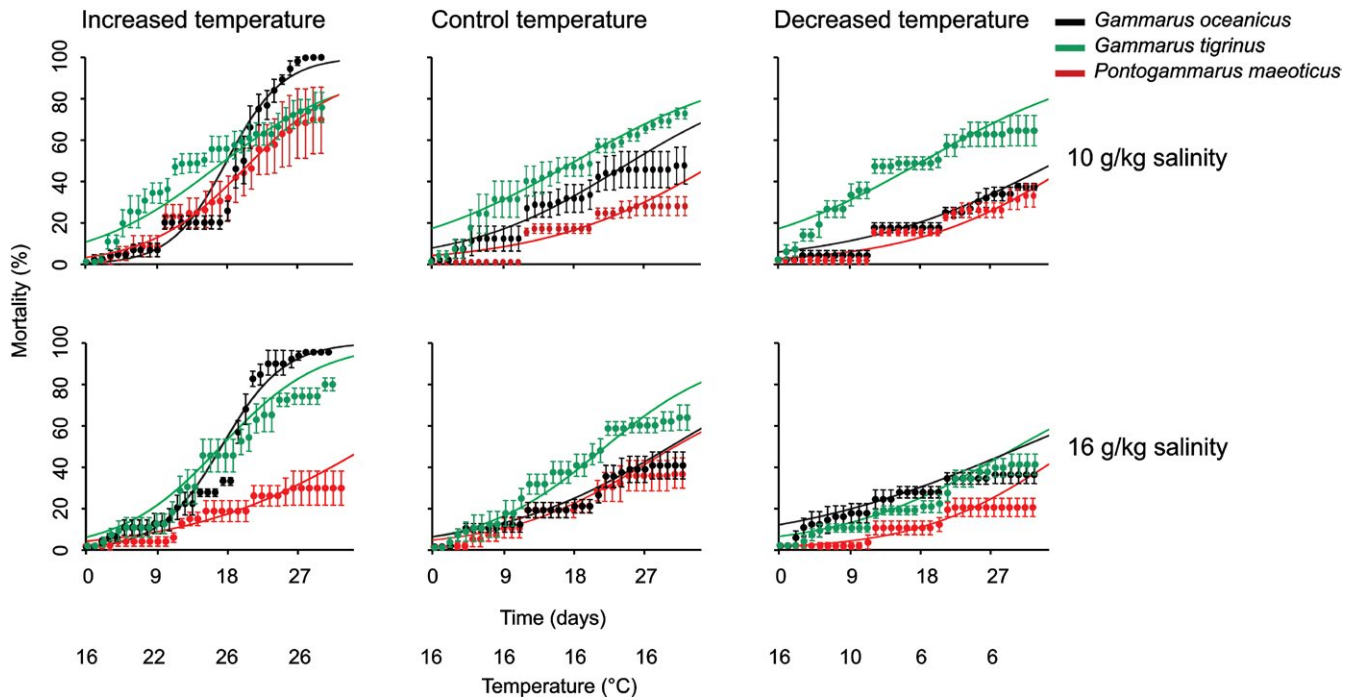
## 2.3 | RNA/DNA ratio measurements

As fitness level of animals under challenging environmental conditions can be characterized by the RNA/DNA ratio as a biochemical variable to measure growth and nutritional condition in many marine organisms including amphipods (Chícharo & Chícharo, 2008; Malzahn, Clemmesen, & Rosenthal, 2003; Moss, 1994; Tong, van de Merwe, Chiu, & Wu, 2010), beside mortality, we conducted RNA/DNA measurements to determine the performance of our species. Therefore, at the end of the experiments, all survived individuals were stored at -20°C. The specimen was prepared for the measurement by freeze drying for 18 h (Alpha1-4 freeze dryer; Christ GmbH, Germany) and subsequently weighed using a microbalance (SC2; Sartorius AG, Germany). Dried tissue was extracted from the exoskeleton, and quantification of RNA and DNA was performed following the method of Malzahn et al. (2003). To obtain reference values for the evaluation of the nutritional condition for each species, an additional food experiment was conducted where animals were kept in their natural salinity and either fed with algae ad libitum or kept under food deprivation for 18 days. This reference experiment was conducted in five replicates per species (i.e., one individual per replicate to prevent cannibalism among individuals), a temperature of 16°C and ambient salinity of each species. All surviving individuals were used for RNA/DNA measurements.

## 2.4 | Statistical analysis

Variation in mortality among species was compared using three-way factorial analysis of variance (ANOVA), where mortality was the dependent variable, and species (i.e., *G. oceanicus*, *P. maeoticus*, and *G. tigrinus*), salinity (i.e., 10 and 16 g/kg) and temperature treatment (i.e., increased, control, and decreased) were the independent variables. Two separate ANOVAs were performed, one for the middle and one for the end of the experiments. When significance was observed, additional Bonferroni multiple comparisons were conducted. Significance levels for statistical comparisons were adjusted for multiple pair-wise comparisons by Bonferroni-type correction with a family-wise error rate of 0.05, where the *p* value of 0.05 was divided by number of comparisons to calculate the  $\alpha$  value.

To test for differences in the RNA/DNA ratios among temperature treatments (i.e., increased, control and decreased), an additional one-way ANOVA was conducted. Four different tests were conducted, each for one experiment (i.e., conducted in salinities of 10 and 16 g/kg) and one species (i.e., *P. maeoticus* and *G. tigrinus*). In the



**FIGURE 1** Means, standard errors and the best-fitted curves of daily mortality (%) for three gammarid species (*Gammarus oceanicus*, *Pontogammarus maeoticus* and *Gammarus tigrinus*) in experiments conducted in 10 and 16 g/kg salinity in increased, control and decreased temperature treatments. The curves were constructed using pooled data from four replicates

case of *G. oceanicus*, independent *t* test was applied as all individuals in the increased temperature treatment died until the end of the experiments. Two separate tests were conducted, one for the experiment conducted in a salinity of 10 g/kg and one for the experiment in 16 g/kg. The RNA/DNA reference values of each species were tested using again independent *t* test. Two separate tests were conducted, each for one species (i.e., *G. oceanicus* and *P. maeoticus*). In the case of *G. tigrinus*, independent *t* test was not applied as only one individual survived at the end of the reference experiment in the food-deprived treatment. ANOVAs and independent *t* tests were performed using SYSTAT<sup>®</sup> version 11 (SYSTAT Software 2004).

Using data from the four replicates and following the equation:

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

where *Z* is the slope of the mortality, *t* is time and *Q* is the onset of mortality (Briski, Ghabooli, Bailey, & MacIsaac, 2011; Briski, Van Stappen, Bossier, & Sorgeloos, 2008), best-fitted curves for Figure 1. were constructed using S-Plus 6.1 (S-Plus<sup>®</sup> 6.1, 2002; Insightful Corp., Seattle, WA, USA). Sigmoid curves were fitted as they best describe mortality data (Lampl, 2012).

### 3 | RESULTS

#### 3.1 | Mortality in experiments

In general, average mortality of *P. maeoticus* in all temperature treatments (i.e., increased, control and decreased) at the end of

both experiments (i.e., conducted in 10 and 16 g/kg salinities) was lower when compared to average mortality of *G. oceanicus* and *G. tigrinus* (Table 1; Figure 1). The highest mortality was observed for *G. oceanicus*, reaching 100% in both experiments in the increased temperature treatment (Table 1; Figure 1). In general, mortalities of all three species were highest in the increased compared to the control and decreased temperature treatments (Table 1; Figure 1). Three-way ANOVAs determined that species and temperature treatment had significant effects on the mortality of species at the middle and end of the experiments ( $p < 0.05$ ; Table 2). Salinity had a significant effect on the mortality of species only at the middle of the experiment ( $p < 0.05$ ; Table 2) due to higher mortality of *G. tigrinus* in the decreased temperature treatment in 10 g/kg salinity experiment compared to that in 16 g/kg salinity ( $\alpha < 0.025$ ). However, the significant 3-way interaction showed that at both time points (at the middle and end of the experiments), the differences among species in any given temperature treatment depended on the salinity treatment ( $p < 0.05$ ; Table 2). *Gammarus tigrinus* had a significantly higher mortality than the other two species in all three temperature treatments at the middle of the experiments ( $\alpha < 0.016$ ). At the end of the increased temperature experiments, the mortality of *P. maeoticus* was significantly lower than those of the other two species ( $\alpha < 0.016$ ), while there was no difference between *G. oceanicus* and *P. maeoticus* in the control and decreased temperature treatments. *G. tigrinus* had also significantly higher mortality than *G. oceanicus* and *P. maeoticus* in the control and decreased temperature treatments at the end of the experiments ( $\alpha < 0.016$ ).

**TABLE 1** Annual salinity and temperature range of collection sites, and average percentage mortality of three gammarid species (*Gammarus oceanicus*, *Pontogammarus maeoticus* and *Gammarus tigrinus*) at the end of experiments conducted in 10 and 16 g/kg salinity in the increased, control and decreased temperature treatments

Species	Annual salinity range of collection site (g/kg)	Annual temperature range of collection site (°C)	Mortality after 32 days (%)			
			Salinity of the experiment (g/kg)	Increased	Control	Decreased
<i>Gammarus oceanicus</i>	12–18	1–23	10	100	48	38
			16	100	44	40
<i>Pontogammarus maeoticus</i>	9–11	7–28	10	70	29	34
			16	31	40	23
<i>Gammarus tigrinus</i>	6–10	1–23	10	75	75	66
			16	85	69	46

**TABLE 2** Results of three-way analyses of variance (ANOVAs) addressing differences in mortality among three gammarid species (*Gammarus oceanicus*, *Pontogammarus maeoticus* and *Gammarus tigrinus*) after 17 and 32 days of experiments in two different salinities (10 and 16 g/kg), and in three temperature treatments (increased, control and decreased temperature treatment)

	Day 17			Day 32		
	df	F	p	df	F	p
Species	2	48.597	<0.0001	2	37.101	<0.0001
Salinity	1	4.648	0.036	1	3.842	0.055
Treatment	2	5.689	0.006	2	45.790	<0.0001
Interaction: species – salinity	2	5.869	0.005	2	1.312	0.278
Interaction: species – treatment	4	1.397	0.247	4	8.499	<0.0001
Interaction: salinity – treatment	2	0.347	0.708	2	1.211	0.306
Interaction: species – salinity – treatment	4	4.010	0.006	4	4.344	0.004

df, F and p denote degree of freedom, F statistics and probability, respectively.

Temperature treatment had no effect on *P. maeoticus* either at the middle or at the end of the experiments ( $\alpha > 0.016$ ). In the case of *G. oceanicus*, there was no temperature treatment effect at the middle of the experiments ( $\alpha > 0.016$ ); however, at the end of the experiments, *G. oceanicus* had higher mortality in the increased compared to the control and decreased temperature treatments ( $\alpha < 0.016$ ). Finally, in the case of *G. tigrinus*, after Bonferonni corrections, there was no temperature treatment effect at the middle of the experiments ( $\alpha > 0.016$ ), but at the end of the experiment, *G. tigrinus* had higher mortality in the increased compared to the decreased temperature treatment ( $\alpha < 0.016$ ).

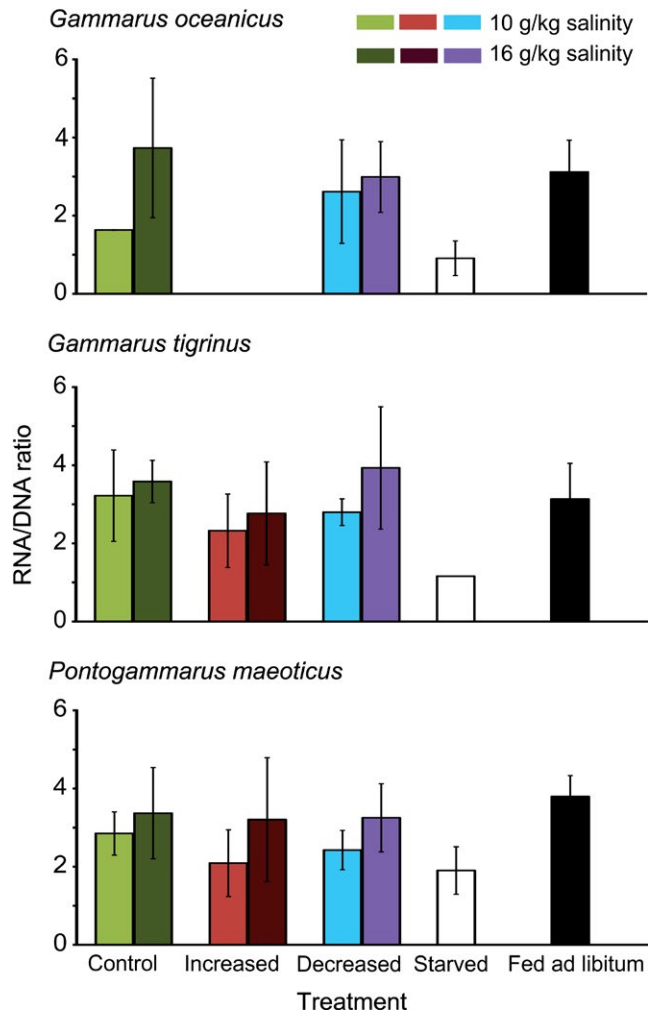
### 3.2 | RNA/DNA ratio measurements

At the end of the common garden experiments, the average RNA/DNA ratios ranged from 2.1 to 3.8, from 1.6 to 3.7 and from 2.4 to 3.9 in the increased, control and decreased temperature treatments, respectively (Figure 2). There was no significant difference among tested temperature treatments (i.e., increased, control and decreased) for any species in any experiment (i.e., conducted in 10 and 16 g/kg;  $p > 0.05$ ).

During the reference experiment, out of five individuals tested four, five and one individual of *G. oceanicus*, *P. maeoticus* and *G. tigrinus* survived in the food-deprived treatment, respectively. In the fed ad libitum treatment, five, four and five individuals of *G. oceanicus*, *P. maeoticus* and *G. tigrinus* survived, respectively. The average RNA/DNA ratio of *G. oceanicus* and *P. maeoticus* in the food-deprived treatment was 0.9 and 1.9, respectively, while those in the fed ad libitum treatment were 3.1 and 3.8 (Figure 2). The RNA/DNA ratio of *G. tigrinus* in the food-deprived treatment was 1.1, and the average RNA/DNA ratio in the fed ad libitum treatment was 3.1 (Figure 2). RNA/DNA ratios of the fed and starved treatments were significantly different ( $p < 0.05$ ) for *G. oceanicus* and *P. maeoticus*. The independent *t* test was not performed for *G. tigrinus* as only one individual survived the food-deprived treatment.

## 4 | DISCUSSION

Temperature and salinity are two important environmental parameters influencing life of aquatic organisms and limiting their distribution (Delgado et al., 2011; Einarson, 1993; Neuparth et al., 2002;



**FIGURE 2** RNA/DNA ratios of three gammarid species (*Gammarus oceanicus*, *Pontogammarus maeoticus* and *Gammarus tigrinus*) at the end of experiments conducted in 10 and 16 g/kg salinity in the increased, control and decreased temperature treatments, as well as in the reference treatment (i.e., Fed ad libitum and starved)

Sutcliffe, 1968). In this study, we compared temperature tolerance in two different salinities of three gammarid species originating from three different regions – Northern Europe, Ponto-Caspian and Great Lakes-St. Lawrence River regions – to determine if a native species would have environmental advantage over NIS under current and future global warming conditions. Our results demonstrated that the native species *G. oceanicus* performed well in the control and decreased temperature treatments, but was not able to survive in the increased temperature treatment. On contrary, the Ponto-Caspian species *P. maeoticus* not only performed well in the ambient salinity and temperature of the Baltic Sea and in the decreased temperature treatment, but also performed slightly better in those conditions than the native species and significantly better in the increased temperature treatment. The second NIS, *G. tigrinus*, did not perform well in any temperature treatment. If other species from the Ponto-Caspian region would

perform similarly to our tested species, we may expect new invasions from that region. Those invasions may, in the best case scenario, increase biodiversity of the Baltic Sea. However, if notorious invaders establish, they may have significant impact on local communities and ecosystem functioning (Charlebois et al., 2001; Dermott et al., 1998; Ricciardi et al., 1998).

The high mortality of the native species in the increased temperature treatment indicates that *G. oceanicus* probably would not be able to survive in some locations of the Baltic Sea where water temperature would increase due to future climate change (Holopainen et al., 2016; IPCC, 2014). In Kiel Fjord, the sampling location of *G. oceanicus*, water temperature fluctuates during different seasons, with summer temperatures currently reaching values between 18 and 21°C in 1.8 m depth (GEOMAR). In shallow coastal areas, however, where many gammarid species are found, temperature is reaching even higher values. Since a sea surface temperature rise of 2–3°C is predicted by the end of the century, the maximum tested temperature of 26°C is likely to be reached in many shallow locations in the future (Gräwe et al., 2013; Holopainen et al., 2016; IPCC, 2007, 2014). If such extreme temperatures only occur during heat waves for some days (Hobday et al., 2016) but not for an extended period of time, the tested species might be able to survive in those habitats. However, if those increased temperatures would last for a longer period of time, it is questionable if *G. oceanicus* would be able to withstand those stressful environmental conditions. The regional suppression of native gammarids by a related NIS has already been documented in the Baltic Sea (Jänes et al., 2015; Kotta et al., 2011, 2013). Therefore, we advice further comparative studies using different species and taxonomic groups are urgently needed for determining environmental tolerance and competitive ability of the Baltic Sea taxa, as well as of taxa in other regions, to be able to predict diversified anthropogenic impact on the ecosystems, and in general, to preserve biodiversity globally.

The wide temperature and salinity tolerance of the Ponto-Caspian species *P. maeoticus* (results of this study, Figure 1; Paiva et al., 2018), in addition to shipping and canal connectivity between Northern Europe and the Ponto-Caspian region (Bij de Vaate, Jazdzewski, Ketelaars, Gollasch, & Van der Velde, 2002; Kaluza, Kölzsch, Gastner, & Blasius, 2010), imply that there is a potential that this species, as well as some others from the Ponto-Caspian region invade the Baltic Sea under a future global warming scenario. Due to wide salinity and temperature tolerance, non-indigenous amphipods are predicted to become more widespread and abundant along the coasts of the northern Baltic Sea (Holopainen et al., 2016). Species originating from the Ponto-Caspian region are generally known to be successful invaders in freshwater as well as marine environments (Casties et al., 2016; Ricciardi & MacIsaac, 2000). In the Baltic Sea, the Ponto-Caspian region is one of the major donor regions of NIS, and out of seven non-indigenous gammarid species, six originate from the Ponto-Caspian area (Casties et al., 2016). In general, the likely reason for high environmental tolerance and amazing colonizing success of species evolved in the Ponto-Caspian region may be due to the geological history of the region (Cristescu, Hebert,

& Onciu, 2003; Dumont, 1998; Reid & Orlova, 2002; Zenkevitch, 1963). The region is geologically old and underwent numerous drastic changes in sea-level, salinity and temperature, with periods when it almost completely dried out during the Glacial Maxima (Zenkevitch, 1963; Dumont, 1998; Reid & Orlova, 2002; Cristescu et al., 2003). The species that have persisted and thrived despite these complex changes and successions over millions of years are probably highly adaptable to diverse environmental conditions, and in particular to environmentally fluctuating habitats, making them excellent candidates to become NIS.

The Northwest Atlantic species, *G. tigrinus*, did not perform well in our laboratory experiments, having high mortality in the control treatments as well. However, the species is a highly successful invader that established in the majority of Northern European freshwater and brackish habitats, where in some areas, it locally replaced or reduced abundance of native species, such as *G. duebeni*, *G. salinus* and *G. zaddachi*, and altered community compositions (Jänes et al., 2015; Kelly, Muirhead, Heath, & MacIsaac, 2006; Kotta et al., 2011, 2013; Pinkster et al., 1992). In addition, several previous studies reported that *G. tigrinus* can tolerate temperatures up to 30°C in brackish environments, and it thrives in heavily polluted waters (Pinkster et al., 1977; Ruoff, 1968; Savage, 1982; Wijnhoven, Van Riel, & van der Velde, 2003), while Paiva et al. (2018) determined different salinity tolerance among populations of that species and seven others. In the population used in our experiments, dark spots were regularly observed on animals. Paiva et al. (2018) reported the same problem suspecting that the population might be infected by parasite or some disease, reducing the immune system of individuals. Kestrup, Thomas, van Rensburg, Ricciardi, and Duffy (2011) observed high mortality of amphipods in the St. Lawrence River caused by parasitic oomycete (water mold), while microphallid trematodes and microsporidia were also reported in amphipods (MacNeil et al., 2003; Mouritsen, Tompkins, & Poulin, 2005). Another explanation could be cannibalism among individuals within replicates (Wijnhoven et al., 2003). However, the individuals were fed ad libitum to compensate for higher metabolic activity due to increased temperatures (Gillooly, Brown, West, Savage, & Charnov, 2001), and we did not detect any signs of cannibalism during the experiments. Consequently, based on our and previous studies, we are not able to provide clear conclusions considering environmental tolerance of this species.

Some gammarids are successful invaders and some are restricted to their native habitats (Baltazar-Soares, Paiva, Chen, Zhan, & Briski, 2017). Using the cytochrome c oxidase subunit I of mitochondrial DNA (mtDNA-COI), the same authors determined that genetic diversity did not differ between invasive and non-invasive species, but populations of non-invasive species showed a higher degree of genetic differentiation. They did not find any pattern when salinity of populations has been taken into account (personal observation, unpublished). However, Paiva et al. (2018) reported different salinity tolerance among populations for the same eight gammarid species indicating that neutral genetic markers, such as mtDNA-COI, are not able to detect population adaptation to different salinities and genome-wide screening, particularly of coding regions, is necessary to

determine adaptation to local environmental conditions. While, we are not aware of any study connecting temperature tolerance and populations for any species, we believe that the same would apply for adaptation to different temperature tolerance.

In this study, we tested two species with (*P. maeoticus* and *G. tigrinus*) and one without (*G. oceanicus*) history of invasions and revealed that one of the invaders performed much better in diverse temperatures and salinities than the other. While this finding may lead to the conclusion that just some, not all, invasive species might benefit from future global warming, we acknowledge that there is a possibility that in our study *P. maeoticus* might have had an advantage over the other two species because it spent a half and one and a half years longer in laboratory culture before experiments started than *G. oceanicus* and *G. tigrinus*, respectively. Furthermore, the former species has also been kept in two degrees higher temperature, as each species was kept in the temperature of the collection site at the time of collection. All of this might have led to selection and/or pre-adaptation of *P. maeoticus* to rearing laboratory conditions, or being simply due to transgenerational plasticity. Still, we emphasize that *P. maeoticus* came from the habitat with temperature variation from 7 to 28°C, while the maximum temperature of the habitats of the other two species is 23°C. This fact may further point that only species evolved in warmer habitats may benefit from future global warming scenario; however, this statement has to be proven using different species and taxonomic groups.

The amount of RNA is directly proportional to the rate of protein synthesis which is varying with changing environmental conditions, while the amount of DNA in a somatic cell is assumed to be constant (Bulow, 1987). In general, organisms in good conditions have higher RNA/DNA ratios than those in poor conditions (Bulow, 1987; Clemmesen, 1994). In our study, RNA/DNA ratios of all three species were similar among the temperature treatments and experiments, and corresponded to the fed ad libitum values of the reference experiment. One of the reasons that we did not detect any stress using RNA/DNA ratio measurements might be due to selection that occurred during the experiments leaving alive only the fittest individuals until the end of the experiments. In addition, the surviving individuals were exposed to the same environmental conditions in the last 2 weeks of the experiment (i.e., 6, 16 and 26°C), and probably acclimatized to the new environment, decreasing a chance of detecting temperature stress. Therefore, we assume that surviving individuals were in relatively good fitness and nutritional condition (Chícharo & Chícharo, 2008).

Numerous regions worldwide are highly impacted by anthropogenic activities and globalization, with climate change and species introductions being among the greatest stressors to biodiversity and ecosystems (Capinha et al., 2015; IPCC, 2014; Sala et al., 2000). Changes in ecosystems open new opportunities for continually introduced species, which are often more resistant to multiple stressors than many native species in an area, and probably preadapted to anthropogenically impacted habitats (Holopainen et al., 2016; Hufbauer et al., 2011; IPCC, 2014). Non-indigenous species often appear to occur with little impact

on the recipient community and may even increase biodiversity in some regions (Zettler, 2008). However, approximately 5%–20% of established NIS are predicted to have strong effects on recipient environments (Ricciardi & Atkinson, 2004; Williamson & Fitter, 1996). These species may act as predators, parasites, pathogens or competitors of native species, and their introduction can result in dramatic changes in ecosystems (Simberloff et al., 2013). Therefore, with global climate models predicting warming and acidification of the oceans worldwide (IPCC, 2014), it is of great importance to mitigate anthropogenic impacts and try to prevent new introductions of species. As Ponto-Caspian species evolved in environmentally variable habitats and currently inhabit warmer waters than species from North America and Northern Europe, we suggest that species from the Ponto-Caspian region may benefit from global warming in invading new areas. Identifying such donor region can be valuable for management strategies to prevent new species introductions.

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Author contributions: E.B. conceived the study; E.B. and I.C. designed the experimental set-up; I.C. carried out experimental work; I.C. and C.C. conducted RNA/DNA ratio measurements; and E.B. conducted statistical analyses. All authors were involved in writing the manuscript and gave final approval for publication.

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