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Differences in stress tolerance and brood size between a non-indigenous and an indigenous gammarid in the northern Baltic Sea

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Abstract Differences in stress tolerance and reproductive traits may drive the competitive hierarchy between non-indigenous and indigenous species and turn the former ones into successful invaders. In the northern Baltic Sea, the non-indigenous *Gammarus tigrinus* is a recent invader of littoral ecosystems and now occupies comparable ecological niches as the indigenous *G. zaddachi*. In laboratory experiments on specimens collected between June and August 2009 around Tvärminne in southern Finland (59°50′N/23°15′E), the tolerances towards heat stress and hypoxia were determined for the two species using lethal time, LT_{50}, as response variable. The brood size of the two species was also studied and some observations were made on maturation of juveniles. *Gammarus tigrinus* was more resistant to hypoxia and survived at higher temperatures than *G. zaddachi*. Brood size was also greater in *G. tigrinus* than in *G. zaddachi* and *G. tigrinus* matured at a smaller size and earlier than *G. zaddachi*. Hence, there are clear competitive advantages for the non-indigenous *G. tigrinus* compared to the indigenous *G. zaddachi,* and these may be further strengthened through ongoing environmental changes related to increased eutrophication and a warming climate in the Baltic Sea region.

Introduction

Human-driven introductions of non-indigenous species into new biogeographical ranges are occurring worldwide at increasing frequency in both terrestrial and aquatic habitats (Lodge 1993; Ruiz et al. 2000; Occhipinti–Ambrogi and Savini 2003). It is therefore urgent to elucidate the mechanisms determining invasion success (McMahon 2002; Bruno et al. 2003; Stachowicz and Byrnes 2006; Lyons and Scheibling 2009). Generally, only a small number of introduced species become established and successfully invade their new habitat (Williamson and Fitter 1996). Knowledge about traits that turn a species into a successful invader is thus of great interest for ecologists and would help to predict and manage biological invasions. It is commonly assumed that a broad tolerance towards environmental stress, high reproductive rates, and plasticity (as capacity for change) increase invasiveness (Stachowicz and Byrnes 2006), although species' abilities to respond to natural selection have been suggested to be even more important (Lee 2002).

Even though many marine benthic habitats are inhabited by non-indigenous species that directly compete with indigenous species for common resources, the number of direct comparisons between both groups of organisms with

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regard to their performance in the face of stressors is low. Most previous studies (e.g. Wijnhoven et al. 2003; Kercher and Zedler 2004; Jewett et al. 2005; Schneider and Helmuth 2007; Lenz et al. 2011) point towards higher tolerance to stressors in non-indigenous species, although some results are ambiguous (Braby and Somero 2006; Thomsen and McGlathery 2007; Zardi et al. 2008; Bownes and McQuaid 2009, 2010). This apparent higher tolerance to stress may often be due to elevated growth and fecundity (McMahon 2002). However, comparisons of the reproductive performance between non-indigenous and related indigenous species are still rather rare (e.g. Peterson et al. 2004; Richard et al. 2006), with the possible exception of amphipods (Dick 1996; Bacela and Konopacka 2005; Grabowski et al. 2007a; Bacela et al. 2009; Pöckl 2009).

Non-indigenous marine species commonly reach new areas through vectors (mainly shipping), although they may also migrate into new ecosystems naturally, and this may be especially evident in young areas such as the Baltic Sea. This non-tidal, brackish water basin is geologically and hydrographically young, having undergone several dramatic shifts in salinity during the last 10,000 years, with its present state of low salinity (at the study site around 6) having prevailed for about 3,000 years (Voipio 1981). In consequence, relatively few species have adapted to the local conditions (Bonsdorff and Pearson 1999) and most Baltic Sea species are postglacial immigrants from the North Atlantic (Segerstråle 1957). Even though species diversity is low in the Baltic Sea, this brackish water area has faced many introductions of non-indigenous species in historical time, presumably due to many niches being unoccupied (Paavola et al. 2005). Today there are five indigenous *Gammarus* species in the northern Baltic: *Gammarus zaddachi*, *G. oceanicus*, *G. salinus*, *G. locusta* and *G. duebeni* (e.g. Fenchel and Kolding 1979; Kolding and Fenchel 1981; Packalén et al. 2008; Korpinen and Westerbom 2010); and one recently introduced species: *G. tigrinus*.

Gammarus tigrinus was first found along the southern coast of the Baltic Sea in northwestern Germany in 1975 (Bulnheim 1976) and apparently spread rather slowly initially, first along the coast eastwards and then northwards. A slow initial spread may be due to the species having to adjust to the new environment over a number of generations and similar time lags between initial establishment and documented effective spreads (invasions) have been observed for many non-indigenous organisms (e.g. Mack et al. 2000; Mooney and Cleland 2001). In the mid 1990s, however, *G. tigrinus* reached eastern Germany (Zettler 1995), a few years later, the Odra Estuary (Gruszka 1999) and then the Vistula Lagoon (Jazdzewski et al. 2002). Thereafter, observations of the invader were made in Puck Bay (Szaniawska et al. 2003), in the Gulf of Finland

(Pienimäki et al. 2004; Paavola et al. 2008), in the Curonian Lagoon in Lithuania (Daunys and Zettler 2006), in the Gulf of Riga (Herkül and Kotta 2007) and in the Neva Estuary (Berezina 2007). The Finnish, Estonian and Russian observations, revealing a wide geographical spread within a short time, indicate several introductions through ship ballast water and many successful establishments rather than gradual immigration. Recent dominance by *G. tigrinus* at inner archipelago sites in Helsinki, in the central Gulf of Finland (Packalén et al. 2008) was seen as an indication of change in the littoral communities, but still, the effects of *G. tigrinus* on the littoral ecosystem of the northern Baltic Sea are unclear. The question is, why was *G. tigrinus* so successful in its establishment and local performance?

To answer this question, we measured the tolerance of *Gammarus tigrinus* to commonly occurring stressors in the Baltic Sea, and compared the results with data on the locally most important competing species, *G. zaddachi*. *Gammarus zaddachi* occurs in the same habitats and at the same depths as *G. tigrinus* (Packalén et al. 2008; Korpinen and Westerbom 2010) and has similar reproductive periods (Kolding and Fenchel 1981) and food preferences (Sareyka and Kraufvelin unpublished). All of these criteria were not fulfilled by the other indigenous gammarid species in the area (Fenchel and Kolding 1979; Kolding and Fenchel 1981; Packalén et al. 2008; Korpinen and Westerbom 2010). We chose to study heat stress (occurring in sunny shallow rock pools and protected bays as a consequence of heat waves) and anoxia (following plankton and filamentous algal blooms or upwelling of anoxic water) and we hypothesised that both juvenile and adult *G. tigrinus* would be more resistant to these stressors than juveniles and adults of *G. zaddachi*. Additionally, we examined the brood size of both species as this factor may also be important for facilitating further invasion. We hypothesised that the non-indigenous *G. tigrinus*, by having a larger brood size, could be more effective in reproductive terms than the indigenous *G. zaddachi*. This assumption was further supported by Pinkster et al. (1977) who showed that *G. tigrinus* became sexually mature at about only half the size (and maturation time) as *G. zaddachi*.

Materials and methods

Sampling, identification and culture

Gammarus tigrinus and *G. zaddachi* were collected from three natural shores within 2 km of the Tvärminne Zoological Station in the western Gulf of Finland from June to August 2009. The gammarids were collected from bladderwrack, *Fucus vesiculosus*, at a depth of 0.5–1.0 m at mean

water levels and were transported to the laboratory in 80-l buckets with about 20 l of ambient water and 3 kg (wwt) of *F. vesiculosus*. After sampling, adult gammarids of both species, including ovigerous females, were classified and placed in separate aquaria. For identification, a Nikon stereomicroscope with up to $40\times$ magnification and the keys of Bousfield (1973), Lincoln (1979) and Köhn and Gosselck (1989) were used. The aquaria had a flow through (flow $\sim 5 \, \mathrm{l \, h^{-1}}$) of unfiltered brackish water, pumped directly from the sea and then distributed evenly from a water tower, and were placed in an outdoor greenhouse under natural light conditions and water temperatures of 16–20°C. The amphipods were fed pieces of *F. vesiculosus* and associated epiphytes and microalgae, but they also fed on food particles in the water.

The adult gammarids of both species were kept for at least 2 weeks in the aquaria before the experiments. To obtain juvenile gammarids of known species identity for the experiments, ovigerous females were kept in separate aquaria until they released their offspring, since species identification is difficult and time consuming for small gammarids. The hatched juveniles of each species were pooled (randomized mothers) in separate aquaria until the experiments began. Juveniles and adults of both gammarid species not used in the experiments were kept in separate aquaria under the same laboratory conditions and in these aquaria, the occurrence of newly hatched juveniles was observed daily.

Experimental set-up

Heat stress experiments with juveniles were run at three temperatures (30, 32 and 35°C) with ten replicate aquaria ($n = 10$) for each temperature and species. Temperatures ≥ 30°C were chosen, since heat waves were more frequent during the last decade than previously due to climate change (BACC Author Team 2008). Therefore maximum water temperatures in shallow rock pools and semi-isolated bays may rise considerably and even exceed 32°C in small rock pools (Ganning 1971), at least temporarily during sunny, calm summer days. Each replicate contained 10 juveniles of 2–3 mm telson length (TL) and 1–2 weeks of age. The experimental set-up consisted of a water bath (2 l) in which a container filled with 0.3 l of ambient seawater was placed. After 10 amphipods had been transferred to the inner container with a water temperature of approximately 18°C, the temperature was increased gradually (over 1.0–1.5 h) by heating the water bath using a Lifetech aquarium tube heater with 75 W, AC 220 V, 50–60 Hz and an integrated thermostat. Two thermometers were used, one for the inner and one for the outer container, to check the temperature constantly during the experiments. The respective experiments started when the water in the inner container had reached 30, 32 or 35°C, respectively. Time (in min) until the mortality reached 50% (the Lethal Time, LT_{50}) served as the response variable. Amphipods were considered dead when they had not moved any limbs for 2 min. Each experiment had a control consisting of 10 juveniles that were kept in a container of the same size and the same type of water at 18°C to account for background mortality.

Heat stress experiments were repeated with adult gammarids using the same number of individuals per replicate. The only difference was that the water basins for the adults were larger, with an outer tray of 5 l and an inner tray of 1 l volume. To heat the water in the outer basin, two Lifetech aquarium tube heaters were used. Both males and non-ovigerous females with a 10 mm TL were used. The sexes were not separated, because it was not possible to identify the sex of non-ovigerous *G. zaddachi*.

In the hypoxia experiment, ten specimens per replicate run (number of runs = 10) resulted in 100 juveniles of each species. The juveniles had a mean TL of 4.5 mm and were 4–6 weeks old. The experimental set-up consisted of a closed chamber ($100 \times 100 \times 40$ mm) with a volume of 0.3 l (see "Appendix"). The chamber had a plexiglass lid with a 4 mm diameter hole in the centre for the oxymeter electrode and a further hole for a nitrogen pipe. The water temperature was 20–22°C and the initial oxygen saturation around 100%. To reduce the oxygen concentration in the water, nitrogen was bubbled into the chamber until an oxygen saturation of 1% (0.09 mg $O_2 \, \mathrm{l^{-1}}$) was reached. After introducing 10 amphipods to the chamber, the oxygen level was adjusted to 1% and then monitored every 20th minute with an oxygen meter (Strathkelvin Instruments Model 782). Again, the response variable was LT_{50} (min). The controls consisted of the same number of juveniles (10 tray^{-1}), for a total of 100 of each species, which were kept in an open tray with seawater at 20–22°C and 100% oxygen saturation.

In the experiment on brood size, the number of juveniles released per ovigerous female of both species was assessed. For this, recently hatched juveniles from 23 ovigerous *Gammarus zaddachi* and 40 *G. tigrinus* were counted. The females were kept individually in small trays with 0.5 l of daily replaced seawater and containing 10 g wwt of *Fucus vesiculosus* as food. Only ovigerous gammarids with well-developed embryos were selected to keep the time until the release of juveniles short. The maximum time of observation was 14 days. All 63 trays were placed in an outdoor greenhouse under natural light and water temperatures of 16–18°C. The trays had a relatively even temperature due to a flow-through system of surrounding water pumped directly from the sea. Released juveniles were counted daily and removed from the tray. When all juveniles appeared to have been released, females were examined

under the stereomicroscope for remaining juveniles in the brood pouch, and in cases when more juveniles were found these were added to the total number per female. Finally, the females were gently blotted dry and weighed on a Mettler Toledo AX 205 precision balance ($d = 0.01$ mg, max 220 g).

Data analyses

Statistical analyses were performed using SPSS 18.0. A one-way ANOVA was used for testing differences in LT_{50} (min) in juvenile and adult gammarids under heat and hypoxic stress. A statistical comparison between *Gammarus tigrinus* and *G. zaddachi* was not realised for the same temperatures in the heat stress experiment, because *G. tigrinus* showed no mortality at 30 and 32°C, while all *G. zaddachi* died immediately at 35°C. For the brood size experiment, analysis of covariance (ANCOVA) was used with species as the factor, female weight as the covariate and species × female weight as the interaction. The number of juveniles released served as the dependent variable. All parametric tests were preceded by a test for normality (Kolmogorov–Smirnov's test) and a test for homogeneity of variances (Levene's test). If the assumptions were not met, an $\ln(x + 1)$ transformation was applied to the data.

Results

In a within-species comparison, no significant differences in heat tolerance were found between adult and juvenile gammarids (Table 1): *Gammarus zaddachi* at 30°C ($F = 0.78$, $p = 0.389$, $df = 1, 18$) and 32°C ($F = 0.90$, $p = 0.356$, $df = 1, 18$) as well as *G. tigrinus* at 35°C ($F = 2.24$, $p = 0.152$, $df = 1, 18$).

When comparing the heat tolerance of the two species, however, there were clear differences for both juvenile and adult specimens (Table 1). The non-indigenous *Gammarus*

tigrinus was more resistant to heat stress than the indigenous *G. zaddachi* and showed no mortality or stress-related symptoms even at temperatures causing many specimens of *G. zaddachi* to die rapidly (within 1 h). In our experiment, the time span to 50% mortality was the same for *G. tigrinus* at 35°C as for *G. zaddachi* at 30°C (no significant differences in gammarid LT_{50} between these temperatures). When subjected to 35°C, none of the indigenous gammarid individuals survived, but the juveniles and adults of the non-indigenous species tolerated these conditions even better than juvenile and adult *G. zaddachi* tolerated the 32°C treatment (Table 1). This pronounced difference in resistance to elevated temperatures is why no experimental temperature allowed a formal test of the null hypothesis. No gammarid died in the control groups, kept at ambient temperatures, during the experiment.

Hypoxic stress experiments at 1% oxygen saturation were only run for juvenile specimens. *Gammarus tigrinus* survived longer (Mean $LT_{50} = 211$ min, SE = 8.3), i.e. was significantly more tolerant towards hypoxia than *G. zaddachi* (Mean $LT_{50} = 184$ min, SE = 8.2), $F = 5.15$, $p = 0.036$, $df = 1, 18$ (Fig. 1). Under ambient oxygen concentrations, no gammarids died.

Bigger females had bigger broods, but the slopes were different for the two gammarid species, i.e. there was a steeper increase for *Gammarus tigrinus* than for *G. zaddachi* (Fig. 2). Thus, there was a significant interaction in the ANCOVA between female weight and species ($F = 4.755$, $p = 0.033$, $df = 1, 59$) (Table 2), expressed in such a way that the difference in brood size (bigger in *G. tigrinus*) increased with increased weight of the females (mothers).

Table 1 Effects of thermal stress on gammarid performance. LT_{50} (min) for *Gammarus tigrinus* and *G. zaddachi*, J = juvenile, A = adult

Gammarids	30°C Mean (SD)	32°C Mean (SD)	35°C Mean (SD)
G. zaddachi (J)	302.50 (63.34)	52.50 (24.75)	Died immediately
G. tigrinus (J)	All survived	All survived	402.00 (116.39)
G. zaddachi (A)	336.50 (103.98)	61.00 (13.09)	Died immediately
G. tigrinus (A)	All survived	All survived	335.00 (78.28)

All *G. tigrinus* survived at 30 and 32°C until the experiment was terminated after >10 h. All *G. zaddachi* died before the temperature reached 35°C
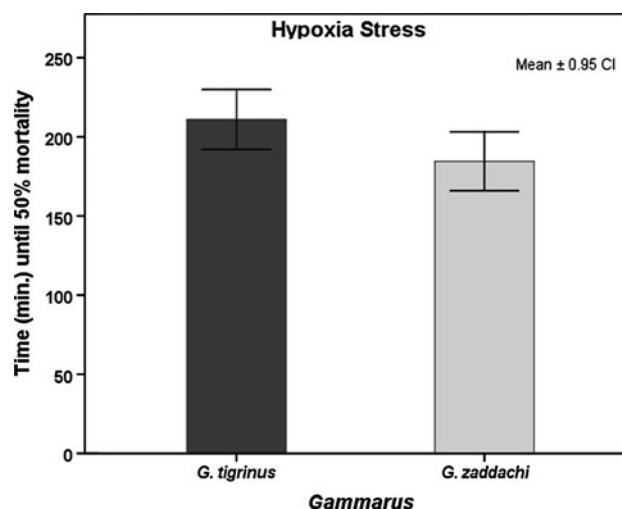

Fig. 1 Mean LT_{50} (min) (±95% CI) for *Gammarus tigrinus* and *G. zaddachi* under hypoxic conditions
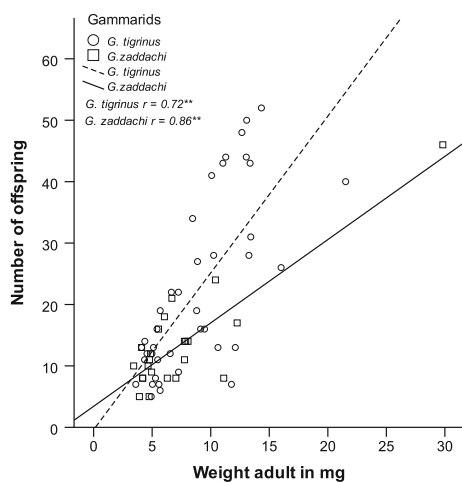
Fig. 2 Female brood size in relation to female wet weight (mg) in *Gammarus tigrinus* (*circles, dashed line*) and *G. zaddachi* (*squares, full line*)

Discussion

Our study shows that the non-indigenous *Gammarus tigrinus* resisted heat and hypoxia much better than the indigenous *G. zaddachi* and also that the brood size of the non-indigenous species was bigger. Both juveniles and adults of the non-indigenous *G. tigrinus* tolerated far higher temperatures (>5°C) than *G. zaddachi*. However, in both species there were no differences between juveniles and adults as could have been expected, since juveniles are generally considered to be more susceptible towards stress due to their smaller size, i.e. higher surface to volume relationship (Oksama and Kristoffersson 1979). *Gammarus tigrinus* juveniles also survived longer (on average 27 min or 15%) than juveniles of *G. zaddachi* under severe hypoxia. The brood size of *G. tigrinus* was significantly greater than for *G. zaddachi*, but the effects were an outcome of the species/female size interaction.

A central aim of the experiments was to identify responses of two closely related species to environmental conditions close to the limit of the species' stress tolerance range, although still using realistic conditions for the littoral zone of the northern Baltic Sea. With regard to the temperature experiments, *Gammarus tigrinus* showed no mortality at 30 and 32°C, clearly indicating that even these high values lay within the tolerance range of this species, as has previously been demonstrated for freshwater *G. tigrinus*, i.e. 32.2–34.2°C (Wijnhoven et al. 2003). The original distribution of *G. tigrinus* in North America, from Canada south to Florida (Bousfield 1958), also indicates a broad temperature tolerance. *Gammarus zaddachi*, on the other hand, died very rapidly at 32°C, indicating this species may be adapted only to colder environments. Concerning the hypoxia experiments, the shallow waters of the Gulf of Finland are normally not affected by hypoxia or anoxia, which occur frequently in deeper layers of the Baltic Sea as a consequence of its pronounced stratification and high nutrient input. However, increasing amounts of drifting algal mats may also induce periodic hypoxic events in shallow bays with clear effects on the composition and diversity of zoobenthic communities (Norkko and Bonsdorff 1996; Vahteri et al. 2000; Salovius and Kraufvelin 2004; Jewett et al. 2005). These events are likely to occur in late summer after massive macroalgal growth and they are expected to increase in frequency and extent in the coming years because of eutrophication. The effects of microbial activities on ambient oxygen concentrations may be amplified by elevated summer water temperatures and both processes, as well as their interaction, may result in dominance by species like the non-indigenous *G. tigrinus*.

Another aim of the experiments was to check for differences in brood size between *Gammarus tigrinus* and *G. zaddachi*, since this may also have implications for the invasive success of the non-indigenous species. Our results showed a steeper increase in brood size for *G. tigrinus* when plotted against the weight of the female, and thus a significant interaction between female weight and species, i.e. bigger broods for bigger *G. tigrinus* females.

In connection with the experimental results reported above, a couple of additional observations, which deserve further investigation, were made. While keeping the gammarids in the laboratory, it was observed that female *Gammarus tigrinus* started reproducing at a smaller size, 3 mm smaller TL, than corresponding *G. zaddachi* females (6 mm TL for *G. tigrinus* and 9 mm TL for *G. zaddachi*),

Table 2 ANCOVA on ln(*x* + 1)-transformed number of juveniles released per female for *Gammarus tigrinus* (*n* = 40, Mean 22.2, SD = 14.4) and *G. zaddachi* (*n* = 23, Mean = 13.5, SD = 8.6) in relation to female body wet weight (covariate)

Significant *p* values are in bold

Source	Type III sum of squares	df	Mean square	F	p value
Intercept	60.28	1	60.28	339.81	**<0.001*****
Female weights	9.50	1	9.50	53.53	**<0.001*****
Species	0.08	1	0.08	0.43	0.514
Female weights × species	0.84	1	0.84	4.76	**0.033***
Error	10.47	59	0.18		
Total	519.49	63			

thus indicating a shorter generation time. In this context, Pinkster et al. (1977) has also reported from the Netherlands that *G. tigrinus* has a higher reproductive capacity than indigenous species, since they become sexually mature at a total body length of only 4 mm (cephalic length of ca 0.6 mm) after 27–29 d at 20°C, while e.g. *G. zaddachi* must reach a total body length of 7–9 mm to become reproductive which takes 40–50 d at 20°C (Kinne 1961). During the heat stress experiments, at 30 and 32°C, *G. tigrinus* seemed unaffected and survived even without food supply, but after several hours (>10 h) they started to show cannibalistic behaviour (Christie and Kraufvelin 2004; MacNeil et al. 2008; Platvoet et al. 2009) by feeding on freshly moulted conspecifics. If this behaviour is more prominent among *G. tigrinus*, it could partly serve to control high population growth.

In addition to our findings, it is known from previous studies that *Gammarus tigrinus* can live and reproduce in a wide range of salinities (Lincoln 1979), and also in polluted waters. It was originally introduced to Germany in 1957 to serve as fish food in contaminated rivers, the Werra and Weser (Schmitz 1960), where the local gammarid fauna had completely disappeared due to inorganic and organic pollution (Pinkster et al. 1977), the latter leading to low oxygen. With respect to *G. tigrinus* in the northern Baltic Sea, we may have to deal with a highly tolerant, fecund species that in addition seems to have a short generation time.

Subsequent to the first observation of *Gammarus tigrinus* in the Baltic Sea (Bulnheim 1976), there have been various reports of its influence on the native fauna, and predictions that it may change benthic communities. In many parts of the Baltic Sea, indigenous gammarid populations have decreased and the non-indigenous *G. tigrinus* is now dominating, for example in the Vistula Lagoon and Puck Bay (Szaniawska et al. 2003, 2005; Grabowski et al. 2006) in Poland, and in the Curonian Lagoon in Lithuania (Daunys and Zettler 2006). These reports initially generated the idea that *G. tigrinus* may have a higher tolerance of abiotic stress than comparable indigenous species. However, its effective spread and dominance may also be due to earlier maturation and greater brood size (both traits were indicated in these experiments), faster juvenile growth, longer and more frequent reproductive periods, higher reproduction rates and greater longevity. Additionally, *G. tigrinus* predates on indigenous species (Grabowski et al. 2007b) as well as other non-indigenous species (Platvoet et al. 2009) and it is also said to be a strong competitor for food and habitat (Orav–Kotta et al. 2009). All these traits may further contribute to its dominance and success.

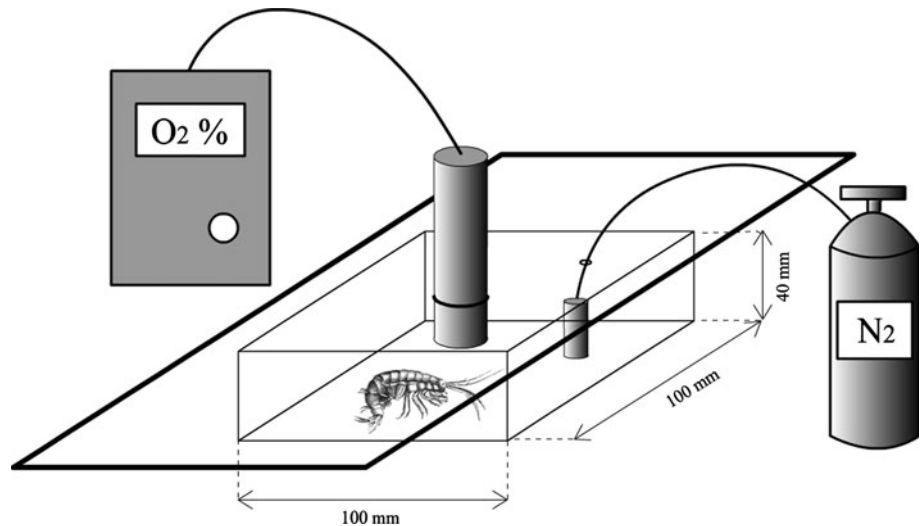Though large differences between the two investigated gammarid species with regard to their stress tolerance and reproductive performance were found in this study, it is too early to judge if these factors alone will lead to asymmetric competition between species belonging to the *Gammarus* complex. Other factors, such as the ability to use existing resources optimally, aggressive behaviour, competition, predation, facilitation or ultimate differences in habitat preference may play a role. Each of these traits needs further experimental investigation and the gammarid complex in the northern Baltic Sea in general may be well-suited for enhancing our understanding of invasion processes and its consequences for coastal ecosystems. Although our stress tolerance experiments only quantified lethal responses, sublethal effects may also be relevant for the success of a non-indigenous species with regard to e.g. reproduction, behaviour, foraging, growth, and competition in general. A 5°C lower lethal temperature, as for *Gammarus zaddachi* compared to *G. tigrinus*, may also indicate differences between the two species in the above mentioned traits at lower temperatures i.e. temperatures occurring during most summers. The same may apply for hypoxia, although the differences between the two species were not as great as for temperature. Hence, thorough investigations of sublethal differences between the gammarid species could be important future study areas. The higher tolerance to environmental changes due to eutrophication and a warming climate (BACC Author Team 2008) among non-indigenous *G. tigrinus* compared to indigenous *G. zaddachi* may also have implications for current and future large-scale changes in the Baltic Sea. Here, it should be emphasised that all changes and effects will not necessarily be negative. Gammarids may be quite effective in buffering the impact of eutrophication through grazing on macroalgae and changes in gammarid abundance, fitness and behaviour may partly counteract the effects of nutrient enrichment (Kraufvelin et al. 2006). Thereby, the non-indigenous *G. tigrinus* could have an important role in these processes, especially if the species continues to spread and increase in numbers.

Appendix

See Fig. 3.

Fig. 3 Schematic view of the study setup for the oxygen experiments

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