



Divergent desalination effects on alien and native gammarid functional responses

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Abstract

Climate change could shift the impacts of biological invasions on aquatic ecosystems. Sea freshening is an often-inconspicuous consequence of climatic change that may modify invasive alien species performance in enclosed seas. Several gammarid crustaceans have been particularly successful aliens across fresh, brackish, and marine waters. Here, we use comparative functional responses (feeding rates across resource densities) to examine the ecological impacts of an invasive alien (*Gammarus tigrinus*) and native (*Gammarus locusta*) gammarid, present in the Baltic Sea, under three different salinity regimes (14, 10, 6) toward larval chironomid prey. Feeding rates differed between the two species, but these differences depended on salinity, whereby at the lowest salinities, the invasive alien species showed significantly improved performance compared to the native species. Both gammarids exhibited hyperbolic Type II functional responses, with attack rates similar across salinity regimes. Handling times were significantly shortened, and maximum feeding rates heightened, in the alien under sea freshening scenarios compared to the native. These results have implications for enclosed sea systems, where projected freshening could shift the performance advantage toward invasive alien species over natives, thereby exacerbating their ecological impacts.

Keywords Baltic Sea · Biological invasions · Environmental change · Functional response · *Gammarus locusta* · *Gammarus tigrinus*

Introduction

Biological invasions represent one of the major ecological processes causing substantial environmental, social, and economic impacts (Pyšek et al. 2020; Diagne et al. 2021). Predictions of these impacts are challenged by context dependencies that alter alien success and impacts within invaded ecological communities (Catford et al. 2022). Rapid environmental shifts associated with climate change are particularly pertinent, representing a priority research

topic in the framework of bioinvasions science (Ricciardi et al. 2021).

While climate change is frequently associated with warming and heatwaves in aquatic systems, changes to the water cycle have also led to alterations of salinity regimes in aquatic environments which can be less conspicuous (Durack et al. 2012). Enclosed sea-basin systems are particularly prone to reductions in salinity, and these regime shifts could influence the impacts of invasive alien species (Kotta et al. 2019; Dickey et al. 2021). Broadly, salinity influences ecosystem functioning in aquatic habitats, such as by mediating trophic interactions (e.g., predation) and reproductive traits (e.g., fecundity), and reductions in salinity could mediate physiological or behavioral performances of alien species compared to natives (Paiva et al. 2018; Dickey et al. 2021).

Several species of gammarid crustaceans are relatively well-studied by invasion scientists [e.g., *Dikerogammarus villosus* (Sowinsky, 1894)], and these species have been characterized by several biological traits that promote widespread invasion success (Grabowski et al. 2007). Ecological impacts from gammarid invasions have arisen from

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processes such as benthic habitat modifications, competition with native gammarids, parasite transmissions, herbivory and predation (Conlan 1994; Kelly et al. 2006; Grabowski et al. 2007; Warren et al. 2022). Global flows of gammarid aliens have been dominated by movements toward fresher aquatic environments, and particularly from the extensively brackish Ponto-Caspian region to Eurasian waters (Cuthbert et al. 2020; Copilaş-Ciocianu et al. 2022). The Baltic Sea in northern Europe exhibits a strong natural salinity gradient, from around 0 to 24, and has received large numbers of invasive alien species (Leppäkoski et al. 2002; Casties et al. 2016). It has been proposed that native gammarid species in the Baltic Sea originate from fully marine conditions in the North Sea, whereas invading gammarid species tend to be more tolerant to reduced salinities (Paiva et al. 2018). Accordingly, potential future reductions in salinity in this sea system could exacerbate ecological effects of invasive alien species which have better performances at lower salinities, as well as their further spread.

One well-studied invasive alien gammarid in Europe is *Gammarus tigrinus* Sexton, 1939, originating from the Atlantic coast of North America. With a broad temperature and salinity tolerance (Casties et al. 2019; Paiva et al. 2018), this species has invaded many fresh and brackish waters of Europe, including inland waters and the Baltic Sea, where it is spreading (Rewicz et al. 2019). In this study, we compare the ecological impacts of *G. tigrinus* to a trophically analogous native species, *Gammarus locusta* (Linnaeus, 1758), whereby we employ a comparative functional response approach (Holling 1959). Functional responses have been identified as a useful experimental tool to measure and compare the ecological impacts of invasive alien and native species, through the use of rapid laboratory feeding experiments under standardized conditions (Dick et al. 2014). The type (i.e., linear Type I, hyperbolic Type II, and sigmoidal Type III; Dick et al. 2014) and magnitude of functional responses can be used to predict current and future impacts under changing environmental conditions. Particularly, invasive alien species tend to have a higher magnitude functional response than natives, characterized by higher efficiencies of resource exploitation and maximum feeding rates (Dick et al. 2017). Given the invasion success of *G. tigrinus* in European freshwaters (Cuthbert et al. 2020), we hypothesized that falling salinities would worsen the ecological impacts of this alien in the Baltic Sea, while those of the native *G. locusta* would show an opposite tendency. Therefore, *G. tigrinus* would become relatively more impactful as salinity fell, characterized by higher resource search efficiencies and maximum feeding rates than the native.

Methods

Animal collection and maintenance

Individuals of the alien, *G. tigrinus*, were collected from a population in Travemünde, Lübeck, Germany (53°83'N 10°64'E; site salinity range: 4–12): this site was situated at the river mouth, and was enclosed, receiving relatively low direct human disturbance. The native individuals of *G. locusta* were collected from Falkenstein Beach, Kiel, Germany (54°40'N 10°20'E; site salinity range: 12–18): this beach was situated in an open area with higher human activity, e.g., from bathers and boaters. Both were sampled using kicknets with 1 mm mesh around macroalgal assemblages of each site. The two species did not coexist at these sites at the time of collection. Sampling locations for both species were shallow littoral sandy-bottom substrates, with the *G. tigrinus* location characterized by reeds *Phragmites* sp. and brown algae *Dictyosiphon* sp., and that of *G. locusta* by brown algae *Fucus* sp. and blue mussels *Mytilus* sp. Both gammarid species were transported in source water to a controlled environment facility at GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany immediately after sampling.

In this laboratory, both species were maintained separately in 56 L aquaria, each with an internal filtration system and a mixture of Baltic Sea water and aged tap water (to allow chlorine to dissipate) to reach the ambient salinity of both species populations (*G. tigrinus*: 10 ppt; *G. locusta*: 13 ppt). Gammarids were fed weekly ad libitum with a mixture of crushed crustacean food (Tetra™ Mix, Tetra™ Crusta, and Aqua-Tropica™ Dr. Shrimp Healthy), with benthic habitat provided in each tank via sand and ceramic tubes. The laboratory was maintained at 18 °C under a 12:12 light and dark photoperiod, with both species kept there for a minimum of 10 weeks prior to experimentation. The prey, larvae of chironomids, were purchased commercially and were refrigerated until experimental use. Although purchased commercially, chironomids are major components of the benthic fauna in the Baltic Sea, comprising up to 30% of the macrozoobenthos taxa (Brodin et al. 2013).

Experimental design

The sizes of animals used in the experiments were (mean ± standard deviation): *G. tigrinus*, 10.6 ± 1.6 mm; *G. locusta*, 10.1 ± 2.0 mm; chironomids, 11.5 ± 1.2 mm. Seven days prior to the start of the experiment, each gammarid species was acclimated separately to one of three experimental salinities in 4 L aquaria. The salinity levels

in these aquaria were either 14, 10 or 6, with six aquaria in total between the two species. Each aquarium held 30 individuals of a species and contained ceramic tubes as benthic habitat. During this 1-week acclimation period, gammarids were fed ad libitum with chironomid larvae to standardize experimental prey familiarity. We compared these gammarid species across these three salinities to represent some of the natural variation in their sampled locations (4–12 for *G. tigrinus* and 12–18 for *G. locusta*), and also to capture current and future salinity regimes in other parts of the Baltic Sea where these species may occur (Meier et al. 2022). These species are also locally abundant and have the potential to coexist in future in the sampled locations. The ecological relevance of the range of salinities employed (6–14) is further underlined because they are well within the known salinity tolerances of both species, as shown among multiple populations (Paiva et al. 2018). Indeed, both species have exhibited survivability in fully marine conditions, as well as under regimes below the lowest salinity employed here. Although, *G. locusta* is better adapted to more saline conditions relative to *G. tigrinus*, and vice versa (Paiva et al. 2018).

Gammarids were starved for 24 h prior to the experiment to standardize hunger levels among individuals (as per Médoc et al. 2015). The functional response experiment was run in 500 mL arenas, filled with new water of the same salinity level (i.e., 14, 10, or 6) in a randomized array in the laboratory. Live chironomid prey were introduced into these arenas before the predators at one of five densities (2, 4, 8, 16, or 32 individuals) and allowed to settle for 3 h. After this settling time, individual gammarids of either species were introduced from the 4 L tanks and allowed to feed for 24 h, after which they were removed and remaining prey counted to determine those dead. Controls were run in the absence of gammarid predators ($n=3$ per prey density). Median levels of control mortality per salinity and prey density were subtracted from the prey numbers dead in the trials with predators under those same conditions to account for background mortality rates. In total, 135 experimental units were set up (i.e., 3 predator treatments \times 3 salinity levels \times 5 prey densities \times 3 replicates = 135 units).

Statistical analyses

Consumption rates (eaten, alive) were analyzed using generalized linear models assuming a quasi-binomial error distribution to account for overdispersion of residuals compared to the model degrees of freedom. These rates were analyzed as a function of predator species (two-level factor), salinity (three-level factor), and prey density (continuous numeric), as well as the interaction between predator species and salinity level, to test for differential responses to salinity between the alien and native. Analysis of deviance with F tests was

used to compute factor significance using Type III sums of squares (Fox and Weisberg 2019). Tukey comparisons were computed to examine the underlying pairwise drivers of significant factors (Lenth 2020).

For each of the six predator and salinity combinations, functional response types were inferred using logistic regression of the consumption rate as a function of prey density. A significant Type II functional response was determined by a significant negative first-order term, indicating that consumption rates fell consistently with increasing prey density (Juliano 2001). Since prey were not replaced as they were consumed, Rogers' random predator equation was fit to each dataset (Rogers 1972; Pritchard et al. 2017):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \quad (1)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack rate, h is the handling time (reciprocally the maximum feeding rate, $1/h$), and T is the total experimental period. The a corresponds to the rate of discovery of prey (i.e., functional response curve initial slope) and the h the time taken to capture, subdue, ingest, and digest the prey item (i.e., functional response curve asymptote).

The difference (delta) method was used to compare the attack rate and handling time of *G. tigrinus* and *G. locusta* pairwise at each of the three salinity levels (Juliano 2001; Pritchard et al. 2017). All statistical analyses were computed in R v4.0.2 (R Core Team 2020).

Results

Mean control mortality was 14%, 8%, and 12% at salinities 6, 10, and 14, respectively. Gammarid feeding rates differed significantly between the two species among the salinity levels, given a significant interaction term between the species and salinity terms ($F_{2,83}=9.15$, $p<0.001$). Specifically, feeding rates did not differ at salinities 14 ($p=1.00$) or 10 ($p=0.09$) between the two species, but *G. tigrinus* consumed significantly more prey than *G. locusta* at 6 ($p<0.001$), with fourfold higher consumption. Across species and salinities, feeding rates fell significantly with increasing prey density ($F_{1,83}=52.4$, $p<0.001$).

First-order terms were always significantly negative for the two species among the three salinities, indicating Type II functional responses (Table 1; Fig. 1). Functional response magnitudes of *G. tigrinus* tended to increase with falling salinity levels, whereas those of *G. locusta* showed the opposite tendency (Fig. 1).

Attack rates did not differ significantly between the species among any of the three salinity levels (Fig. 2). Contrastingly, handling time differences were statistically clear

Table 1 First-order terms and significance levels for the two gammarid species across three salinity levels

Taxon	Salinity	First-order term	<i>p</i> value
Alien	14	−0.082	<0.001
Native	14	−0.061	<0.001
Alien	10	−0.060	<0.001
Native	10	−0.081	<0.001
Alien	6	−0.058	<0.001
Native	6	−0.105	<0.001

Alien *Gammarus tigrinus*, Native *Gammarus locusta*

under 10 and 6 salinities between the two species, reciprocally reflecting reduced maximum feeding rates of the native compared to alien under desalination (Fig. 1). Handling time differences were not statistically clear between the species at salinity level 14 (Fig. 2).

Discussion

Seawater freshening constitutes a significant context dependency that can modulate the ecological impacts of invasive alien species (Dickey et al. 2021), but has been often overlooked in seas. Here, the functional response (feeding rate under different resource densities) of an invasive alien gammarid was improved by desalination, while the opposite effect was shown in the case of a native species comparator. Accordingly, impact assessments for biological invasions should consider a range of plausible salinity scenarios in aquatic systems, given the marked shifts in relative performance demonstrated here between aliens and natives. These results suggest that the *G. tigrinus* population sampled in the Baltic Sea has a propensity for improved feeding

performance under reduced salinities, which might become more frequent in future as climates changes or as the alien spreads (Meier and Kauker 2003; Rewicz et al. 2019). The repeatability of these effects remains to be elucidated across other populations of this invasive alien species.

While based on relatively short-term feeding intervals in simplified aquaria, functional responses have been shown to correlate tightly with metrics for ecological impacts in the field from invasive alien species (Dick et al. 2017). Consistent with other functional response studies on gammarids (e.g., Médoc et al. 2015; Dickey et al. 2021), there was a prevalence of hyperbolic Type II forms in the present study—for both species across all three salinity regimes. This suggests that seawater freshening does not dampen the feeding rate at low prey densities where gammarids are still able to successfully search for attack and handle prey with possible destabilizing effects owing to extirpation in the absence of alternative prey. This was further corroborated by the lack of significant differences in attack rates among treatment groups (i.e., functional response initial slopes), again suggesting that the efficiency of prey search at lower densities was not hampered.

In contrast, the handling time parameter, corresponding to the time taken to capture, subdue, ingest, and digest a prey item, was significantly affected by changes to salinity regime in the present study. Lower salinity levels significantly increased the handling time in the native species, which could indicate osmotic stress that hampered the feeding capacity. Indeed, marine organisms entering fresher waters must evolve to keep osmotic levels stable in bodily fluids, which requires high energetic costs (Schubart and Diesel 1999). This would often lead to higher food consumption. But in this case, we suspect that most energy is spent on osmoregulation, leaving not enough of it for efficient handling of prey. On the other hand, *G. tigrinus* exhibited

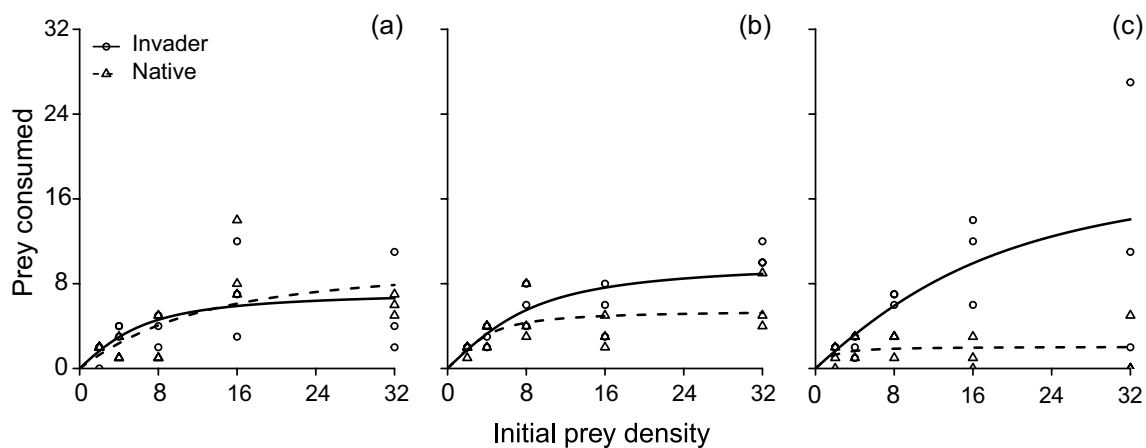


Fig. 1 Type II functional responses of invasive (*Gammarus tigrinus*) and native (*Gammarus locusta*) gammarids among 14 (a), 10 (b), and 6 (c) salinity levels toward chironomid prey after 24 h. Points represent raw data

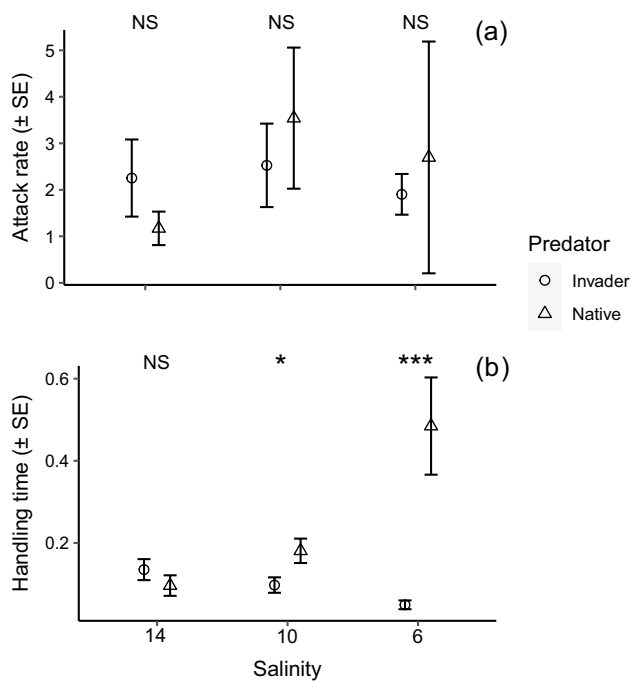


Fig. 2 Attack rate (a) and handling time (b) parameters of invasive (*Gammarus tigrinus*) and native (*Gammarus locusta*) gammarids among three salinity levels toward chironomid prey after 24 h. Parameter estimates are shown alongside their standard error (SE). Pairwise significance is shown above each predator pairing based on the difference method using SEs: NS, $p > 0.05$; * $p < 0.05$; *** $p < 0.001$

shorter handling times under the lower salinity levels. In turn, these shorter handling times translated to higher maximum feeding rates (i.e., functional response asymptotes) as salinity fell in the alien. Despite this, it is important to note the relatively short acclimation time to the experimental salinities in the present study (at least 1 week), as well as the particular salinity contexts of the sampling sites. Considering these contexts, it is possible that local adaptations and experimental holding protocols played a role in the responses exhibited here through short-term adaptations. It is also pertinent to consider whether these responses are population specific, and therefore vary among populations of the same species that are exposed to different ambient salinities (e.g., Howard et al. 2018)—despite some generalities in salinity tolerances already shown by the study species here among populations (Paiva et al. 2018). Furthermore, the effects of salinity on behaviors of the prey considered here should also be elucidated in future studies, since predators are only one side of the trophic interaction.

While the experimental salinities employed here (14, 10, 6) are well inside those known to be tolerated by the invasive alien *G. tigrinus* and native *G. locusta*, the latter has been shown to be particularly susceptible to reductions in salinity compared to existing and emerging invasive alien species (Paiva et al. 2018). *Gammarus locusta* is a

widespread and ecologically important species in European coastal systems (Costa and Costa 2020), but has not reportedly invaded any regions yet, despite the high level of interconnection of Europe to other parts of the world through shipping (Seebens et al. 2018). Curiously, while gammarid invasion dynamics have been dominated by brackish species moving into freshwaters, particularly from the Ponto-Caspian region (Cuthbert et al. 2020), *G. tigrinus* represents an anomaly to this trend, being among the few invasive alien gammarids from North America. This invasive alien gammarid has invaded many brackish and freshwater systems in Europe from a predominantly brackish native range on the Atlantic coast in North America, consequently demonstrating a very broad salinity tolerance.

Nevertheless, we cannot discount the importance of population-level variation in mediating salinity tolerances (Paiva et al. 2018), the uncertainties tied to future salinity estimates in the Baltic Sea (Meier et al. 2022), as well as the potential ecological oversimplification of laboratory conditions employed here. One interesting line of research would, therefore, be to disentangle the effects of these salinity shifts on the feeding performances in the native and invasive ranges of *G. tigrinus*, as has been examined for other alien species [e.g., European green crab *Carcinus maenas* (Linnaeus, 1758); Howard et al. 2018]. Furthermore, future research could examine the influence of salinity regimes on gammarid–gammarid interactions between these species, for example, by examining potential antagonistic or interference interactions that mediate feeding strengths (e.g., Sentis and Boukal 2018). Already, *G. tigrinus* has been found to be competitively superior over native species and displaces these in its preferred shallow, vegetated habitats with shelter (Orav-Kotta et al. 2009; Reisalü et al. 2016). Yet, *G. tigrinus* also displays a narrower niche space (Herkül et al. 2016). Further multiple predator and community-level experiments are needed to elucidate how these competitive biotic interactions manifest in terms of ecological impact.

While functional responses are a fundamental and long-standing measure of the *per capita* interaction strength of consumers in food webs, understanding the population-level responses of both predators and prey is critical under shifting environmental contexts (South et al. 2022). Although salinity regimes evidently mediated individual effects on prey here, the influence of salinity in terms of fecundity, abundance, and other areas of population performance should also not be discounted (Dickey et al. 2021). Future studies should, thus, ascertain whether the effects of freshening on ecological impact are accentuated or dampened at the population level in these species, by examining whether there are commensurate changes to reproductive output or survival as salinity levels change with future climate.

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Data/code availability Underlying data are available as supplementary material.

Declarations

Conflict of interest The authors declare no conflict of interest.

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

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