



# Seasonal changes in biodiversity of native and non-native amphipod taxa under diverse environmental contexts

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## Abstract

Anthropogenic disturbances are having strong, negative effects on aquatic systems globally, altering ecological communities and potentially creating vacant niches for both native and non-native species (NNS). Globalization and new trade routes have amplified the spread and establishment of NNS by connecting disturbed areas worldwide. In this study, we conducted a comparative assessment of seasonal variations in amphipod communities at three southeastern Baltic Sea locations – two anthropogenically impacted and one protected habitat – to determine if native and NNS diversity differed among these habitats. Our study revealed nine amphipod species - of which two were NNS - across all three habitats. The impacted habitats had significantly higher native species richness and lower NNS abundance. *Grandidierella japonica* was the only NNS found at the impacted habitats. In the case of the protected habitat, NNS *Gammarus tigrinus* was dominant for most of the year. In autumn, dominance shifted in favour of the native *Gammarus locusta* and *Microdeutopus* cf. *gryllotalpa*. *Grandidierella japonica* was not detected there. Although anthropogenically impacted habitats may be under higher invasion risk, other environmental factors, such as salinity and temperature, may be driving the establishment pattern of NNS and the resulting community structures. Furthermore, undisturbed and/or protected habitats may be highly vulnerable to invasions due to more tolerable environmental conditions, robust NNS populations and naïve native species to newcomers. Seasonality is an important aspect of ecological studies and must be taken into account, as omissions could potentially distort our understanding of the dynamics of ecosystems and prevent the detection of NNS.

**Keywords** Gammarids · Impacted habitat · Non-native species · Protected habitat · Species abundance · Species richness

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## Introduction

Marine habitats are facing strong, negative impacts due to anthropogenic disturbances, with coastal zones particularly threatened (Halpern et al. 2008). These regions receive land-derived pollutants from a variety of sources, including agriculture and livestock farming, urban development, tourism and industry. Ocean-based pollutants, on the other hand, arise from activities like shipping, fisheries, aquaculture, exploitation for fossil fuels (Halpern et al. 2008; Nogales et al. 2011), and – among others – the introduction of non-native species (NNS; Simberloff et al. 2013; Linders et al. 2019; Pyšek et al. 2020; Soto et al. 2024). The impacts of associated noise and light pollution are also being increasingly recognised (Davies et al. 2014; Di Franco et al. 2020). Such disturbances alter the composition of communities and may lead to vacant niches and habitats (Wilkinson 2002; Lockwood et al. 2013), potentially creating opportunities for both native species and NNS (Daehler 2003).

The majority of NNS are found in areas affected by human disturbances, and several instances showed that such disturbances foster their establishment (Smith and Knapp 1999; Minchinton 2002; Lockwood et al. 2013). This can be attributed to three main reasons. The first is high propagule pressure (i.e., introduction effort) between many anthropogenically disturbed areas due to strong interconnectivity (Briski et al. 2011, 2012a; Lockwood et al. 2013). For example, shipping ports are not only exposed to high levels of heavy metals, noise and light pollution, and contain huge amounts of artificial structures, such as pontoons, wharfs and buoys, but they also receive huge amounts of ballast water containing diverse taxa from viruses and bacteria to macroinvertebrates and fishes (Briski et al. 2012b, 2013; Lin et al. 2022). Furthermore, the equipment used during the construction of those ports is typically moved from site to site, often without biosecurity protocols to prevent the spread of “hitchhiking” species (Lockwood et al. 2013). The second reason is connected to the high environmental tolerance of NNS to diverse stressors when compared to species without an invasion record (Briski et al. 2018; Paiva et al. 2018, 2020; Casties et al. 2019; Martinez Reyes et al. 2024). This possibly stems from selection (i.e. survival of only prior-adapted individuals for particular environmental conditions) before and during the invasion process (Hufbauer et al. 2012; Briski et al. 2018). Finally, NNS may alter invaded habitats, causing an additional disturbance, and facilitate the establishment of more NNS. This phenomenon creates a positive feedback loop – known as “invasional meltdown” (Simberloff and Von Holle 1999; Light and Marchetti 2007; Lockwood et al. 2013).

The Baltic Sea is exposed to many anthropogenic stressors, including strong shipping activities (Kaluza et al. 2010;

Knebel 2021), introduction of NNS (Casties et al. 2016), and increases in temperature and  $p\text{CO}_2$  levels exceeding the global average seven times (Nikulina et al. 2008; Belkin 2009; Jutterström et al. 2014; Pachauri et al. 2014; Reusch et al. 2018). It is a large semi-enclosed brackish water system characterized by a strong salinity gradient ranging between 2 and 24 ppt (Casties et al. 2016). Seasonality in the system also strongly influences community compositions by affecting species behaviour, feeding, reproduction cycle, and even taxon survival (Fretwell 1972; Theurich et al. 2024). Yet, seasonality is rarely considered in ecological studies, particularly in connection to other anthropogenic activities and/or introductions of NNS (Wahl et al. 2020; White and Hastings 2020), and its omission could distort our understanding of ecosystem dynamics.

Amphipods are a globally distributed, diverse and widespread taxonomic group, spanning various aquatic habitats from freshwater to fully marine environments (Cuthbert et al. 2020). They are highly abundant, playing important roles in various ecosystem functions including the detritus cycle, the microbial loop, and as prey in the diet of many fish species (Grabowska and Grabowski 2005; Gerhardt et al. 2011). Due to their tolerance of environmental stressors, and in particular wide ranges of salinity, accompanied by foraging plasticity, migration ability and tendency to drift, they are also very successful and often notorious invaders (Grabowski et al. 2007; Gerhardt et al. 2011; Paiva et al. 2018; Cuthbert et al. 2020). Some well-known gammarid invaders include species such as *Dikerogammarus villosus*, *Gammarus tigrinus*, *Echinogammarus ischnus* and *Pontogammarus robustoides* that have spread throughout European and North American brackish and freshwater ecosystems (Grabowski et al. 2007; Cuthbert et al. 2020; Soto et al. 2022). Non-native species can outnumber and sometimes replace native species, exhibiting rapid growth, early maturation and high fecundity (Dermott et al. 1998; Grabowski et al. 2007; Soto et al. 2023).

With the Baltic Sea as our chosen study system, we therefore used amphipod taxa – an important taxonomic group in Baltic Sea ecosystems (Zettler and Zettler 2017) – to explore the effects of diverse environmental conditions on the biological communities. We conducted a comparative assessment of seasonal variation in amphipod communities from three Baltic habitats - two anthropogenically impacted and one protected, characterized by different salinity and temperature conditions. We expect that in impacted habitats native diversity will be lower than in protected ones, assuming native species unable to withstand disturbances have previously retreated to less affected areas. We also expect anthropogenic activities to provide more chances for NNS to be introduced into impacted habitats, and therefore we anticipate more NNS in these habitats than in the protected

site. The three null hypotheses that we tested were: (i) there is no difference in native diversity between impacted and protected habitats; (ii) there is no difference in NNS diversity between impacted and protected habitats; and (iii) there is no difference in gammarid communities across seasons.

## Methods

### Sample collection

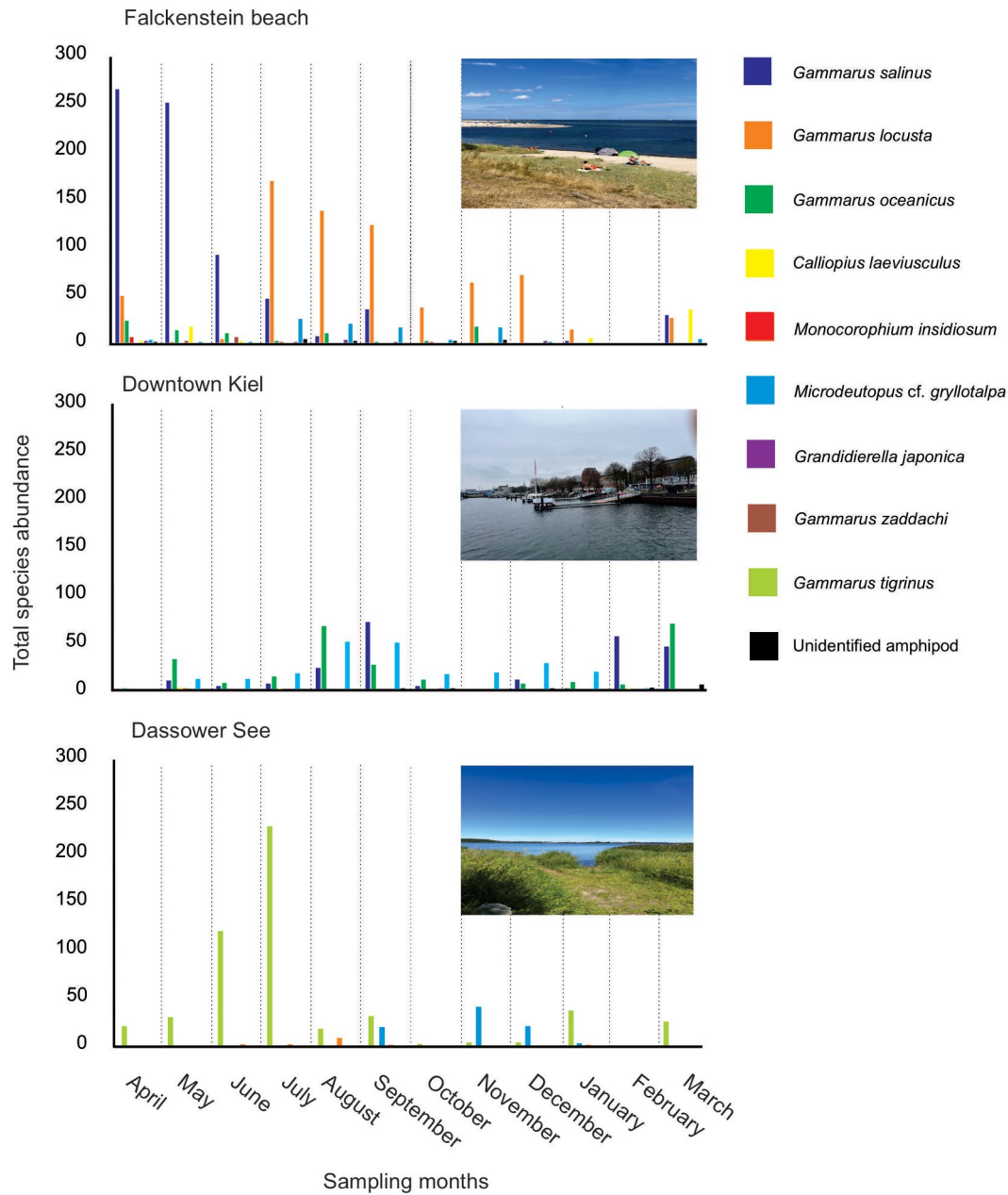
From April 2022 until March 2023, amphipod taxa were collected monthly at three locations in Schleswig-Holstein, Germany. Two locations were anthropogenically impacted habitats: (i) Falckenstein beach (54°39'04" N 10°19'24" E) and (ii) downtown Kiel (54°32'97" N 10°14'93" E), and one location was a protected area: (iii) Dassower See (i.e. Dassow Bay, 53°90'10" N 10°90'69"E; Supplementary Figure S1). Due to its proximity to the Nord-Ostsee-Kanal (i.e. North-Baltic Canal), one of the busiest canals in the world (Knebel 2021), Falckenstein beach is exposed to strong shipping activities and ballasting operations throughout the year, as well as being subjected to tourism activities during summer months (Fig. 1). Meanwhile, downtown Kiel faces numerous urban disturbances from light, noise, tourism and sailing activities to commercial shipping, ferry and shipyard activities. Both of these locations are also highly polluted by heavy metals, such as copper, zinc, tin and lead (Nikulina et al. 2008). Conversely, Dassower See has been a protected habitat since 1983, and is one of the largest bird reserves in Germany (Landkreis Nordwestmecklenburg, FD Bauordnung/Umwelt). However, it is also linked to the Trave River which connects the Baltic Sea with the Port of Lübeck; the Trave River catchment is polluted by diverse antifouling biocides (Mavchate et al. 2021). In addition, salinity conditions at Falckenstein beach and downtown Kiel fluctuate between 11 and 22 ppt, while those at Dassower See between 6 and 15 ppt (Supplementary Table S1). Temperature is similar throughout the year across locations (around 5 °C in winter and 20 °C in summer), except for Falckenstein beach where the temperature can rise to 30 °C during summer months (Supplementary Table S1).

Samples were collected during the first week of each month by intensive sampling of one person for an hour (April-July), or two persons for half an hour (August-March). At Falckenstein beach, *Fucus* spp. was collected using a 26×26 cm 500 µm mesh size landing net and shaken until the amphipods detached from the algae. In downtown Kiel, blue mussels, *Mytilus* sp., were scratched from the dock pilings with 16×11 cm 500 µm mesh size net and shaken to collect the amphipods hiding in between them. For Dassower See, a 26×26 cm 500 µm landing net was used to

collect plant debris and algae from the shallower parts of the lake near bulrushes and other vegetation. This debris was spread out on a sampling table allowing for amphipods to be collected. Slightly different sampling methods were used due to varying local conditions. At all three locations, only animals bigger than 2 mm in size were collected, as smaller individuals cannot be identified morphologically to the species level using conventional methods. Additionally, at each sampling location, salinity, pH, temperature, and oxygen were measured using WTW ProfiLine Cond 3110 m with TetraCon 325 probe and WTW ProfiLine pH 3110 m for salinity and pH, respectively, and WTW ProfiLine Oxi 3310 IDS meter for temperature and oxygen. Collected individuals were transferred in source water to GEOMAR in Kiel, preserved in 99% ethanol and stored at 4 °C until identification. All animals were identified morphologically following Zettler and Zettler (2017). At least five individuals of each morphologically identified species were further identified molecularly to confirm morphological identification (see below). Individuals that could not be visually identified to the species level were grouped morphologically, and again at least five individuals per group were taken for molecular identification.

### Molecular species identification

Total genomic DNA was extracted from the telson using the DNeasy Blood and Tissue kit (QIAGEN, Germany) following the manufacturer's protocol. Partial sequences of cytochrome *c* oxidase subunit 1 (*COI*) gene were amplified using several sets of primers to be able to obtain sequences for different gammarid species: LCO1490 and HCO2198 (Folmer et al. 1994), UCOIF and UCOIR (Costa et al. 2009), LoboF1 and LoboR1 (Lobo et al. 2013) and *G. tigrinus* species-specific primers (Kelly et al. 2006a). PCR reactions were performed in 20 µl volume including 9.8 µl of nuclease-free water, 2 µl of 10X PCR buffer (Invitrogen, USA), dNTPs, forward and reverse primer (5mM concentration) and 2 µl template DNA, and 0.2 µl of DreamTaq DNA polymerase (Invitrogen, USA). The amplifications using LCO1490 and HCO2198 and UCOIF and UCOIR sets of primers were performed with a denaturation step for 5 min at 94 °C, followed by 33 cycles of denaturation at 94 °C (35 s), annealing at 47 °C (45 s), extension at 69 °C (45 s) and a final extension step of 69 °C for 10 min. In the case of LoboF1 and LoboR1 primers, denaturation was performed at 94 °C for 1 min, followed by 5 cycles of denaturation at 94 °C (30 s), annealing at 45 °C (1 min 30 s) and extension at 72 °C (1 min), then by 44 cycles of denaturation at 94 °C (30 s), annealing at 54 °C (1 min 30 s) and extension at 72 °C (1 min), and finally ended with a final extension of 5 min at 72 °C. For *G. tigrinus* species-specific



**Fig. 1** Absolute monthly abundance of each amphipod species in three sampling locations from April 2022 until March 2023 with corresponding area images

primers, the protocol of Kelly et al. (2006a) was followed. The PCR products were sequenced on Sanger sequencing platform (Applied Biosystems, USA) at Eurofins Genomics (Kiel, Germany). Raw COI sequences were assembled and trimmed using CodonCode Aligner v 3.7.1 (Codon Code Corporation). Each sequence was blasted on NCBI (<https://www.ncbi.nlm.nih.gov/>). Sequences with  $\geq 98\%$  similarity were deemed a species-level identification, while those with  $< 98\%$  were grouped as unidentified; sequences with  $\geq 98\%$  similarity are shown in Supplementary Table S2.

### Statistical analyses

To compare species diversity among three sampling locations (i.e. Falckenstein beach, downtown Kiel, and Dassower See), Simpson's Diversity Index ( $D$ ) was calculated for each month (i.e. from April 2022 to March 2023), for each location, following the equation:

$$D = 1 - \left( \frac{\sum n_i (n_i - 1)}{N(N - 1)} \right) \quad (1)$$

whereby  $n_i$  was the number of amphipods that belong to species  $i$ , and  $N$  was the total number of amphipods. The value of  $D$  spans from 0 to 1, whereby 1 represents maximal diversity and 0 represents no diversity. For months where no species were collected from sampling, an index score of zero was assigned. To determine the effect of site on diversity, a non-parametric Kruskal-Wallis test was conducted, with a post-hoc Dunn's test to determine the pairwise differences between locations. A Benjamini and Hochberg  $p$ -adjustment was used to control the rate of false discoveries (Benjamini and Hochberg 1995).

To assess the variation in amphipod abundance and richness over a 12-month period across different locations we employed Generalized Additive Models (GAMs) at three locations due to non-linear relationship and non-constant variance. To account for the temporal patterns in the data across different locations, we first transformed the sampling dates into a continuous numeric variable, representing the number of days since the start of our sampling period. This transformation facilitated the use of GAMs to investigate temporal trends across locations. Subsequently, we applied a non-cyclic cubic spline (i.e., cs spline) with a maximum of five knots to avoid overfitting but allowing flexible modeling. We then evaluated the model by examining the distribution of the residuals using histograms, and determined that the negative binomial distribution with a log-link was the most appropriate distribution to use. Afterwards, we explored the population dynamic for native and non-native amphipod abundances across sites. However, due to the small number of NNS records at Falckenstein beach ( $n=5$ ) and downtown Kiel ( $n=1$ ), we were not able to create reliable models for these two locations, but only for Dassower See ( $n=11$ ).

Finally, we analyzed the influence of the four environmental predictors (i.e. pH, salinity, water temperature, and dissolved oxygen) on the temporal abundance of amphipod communities. For this purpose, we fitted a series of GAMs with individual predictors because the low number of sample points ( $n=12$  per location, i.e. one per month) generated the risk of overfitting across each site. Due to the multiple statistical tests conducted for each predictor across each location, we applied Holm's method for  $p$ -value adjustment to control the family-wise error rate. After visually inspecting the residual distribution of all models, we selected negative binomial distribution for all models. Additionally, Redundancy Analysis (RDA) was performed using the *rda* function of the *vegan* R package (Oksanen 2012). To assess the significance of the environmental variables in the RDA model, we conducted a permutation test using the *anova.cca* function with 999 permutations. The reproducible code and data used in this study are stored at <https://github.com/IsmaSA>.

## Results

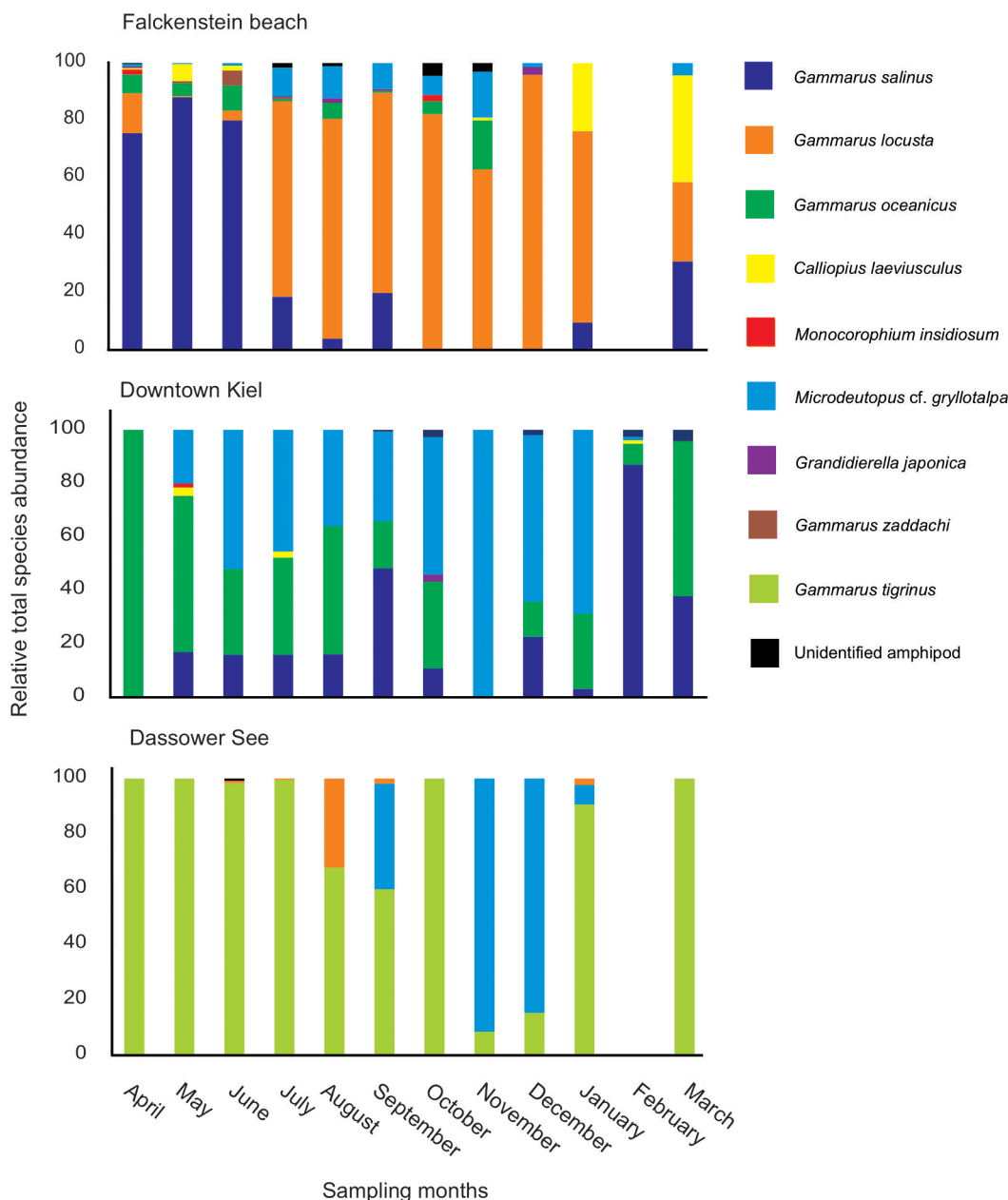
### Absolute and relative abundance and richness of amphipod communities

Across the three sampling locations, a total of nine species of amphipods were identified: *G. salinus*, *G. oceanicus*, *G. locusta*, *G. zaddachi*, *G. tigrinus*, *Calliopius laeviusculus*, *Monocorophium insidiosum*, *Grandidierella japonica*, and *Microdeutopus* cf. *gryllotalpa* (Figs. 1 and 2). All species except *M. cf. gryllotalpa* were identified both morphologically and molecularly; *Microdeutopus* cf. *gryllotalpa* was identified only morphologically due to the lack of the corresponding record of the species in GenBank (<https://www.ncbi.nlm.nih.gov/nuccore/>; accessed on March 20th, 2024). At all three locations, there were very few numbers of unidentified individuals (Supplementary Tables S1). *Grandidierella japonica* and *G. tigrinus* are NNS at the Baltic Sea, native to the North-West Pacific and the North-West Atlantic, respectively (Chapman and Dorman 1975; Kelly et al. 2006a, b; Soors et al. 2022).

At Falckenstein beach, the amphipod community was the most diverse and abundant with eight species present: *G. salinus*, *G. oceanicus*, *G. locusta*, *G. zaddachi*, *C. laeviusculus*, *M. cf. insidiosum*, and *G. japonica*. *Gammarus salinus* was the most abundant in spring, from April to June, when *G. locusta* took over (Figs. 1 and 2). *Grandidierella japonica* was present at low abundance. At downtown Kiel, six species were identified: *G. salinus*, *G. oceanicus*, *C. laeviusculus*, *M. insidiosum*, *M. cf. gryllotalpa*, and *G. japonica*. *Gammarus salinus*, *G. oceanicus* and *M. cf. gryllotalpa* were abundant species (Figs. 1 and 2). At Dassower See, three amphipod species were present: *M. cf. gryllotalpa*, *G. locusta*, and *G. tigrinus*, with *G. tigrinus* being the most abundant (Figs. 1 and 2). Indeed, *G. tigrinus* was dominant throughout most of the year, except November and December, when *M. cf. gryllotalpa* took over (Figs. 2 and 3). There was a significant effect of study location on Simpson's Diversity Index ( $\chi^2=12.764$ ,  $df=2$ ,  $p<0.005$ ). Both Falckenstein beach and downtown Kiel exhibited significantly greater diversity in comparison to Dassower See ( $Z=3.186$ ,  $p<0.005$ ;  $Z=2.994$ ,  $p<0.005$ ; Fig. 4).

### Seasonal effects on amphipod communities

Our models did not indicate any significant seasonal change in amphipod abundance over time across the three locations, though Falckenstein beach demonstrated slight seasonality but not significantly (all  $p>0.09$ ; Fig. 5; Table 1). The observed temporal patterns showcased considerable fluctuations among the period studied, with Falckenstein beach having the highest abundance of amphipods on average



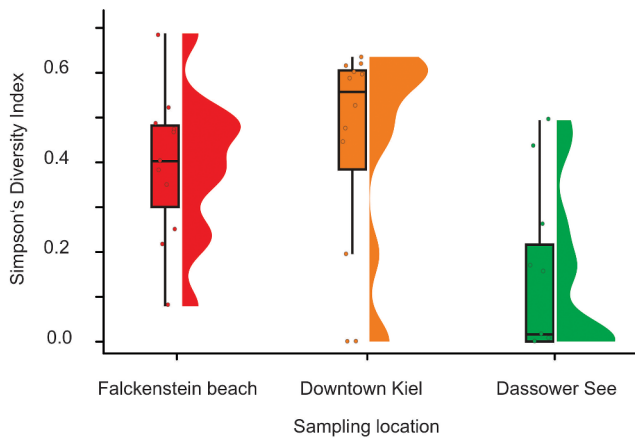
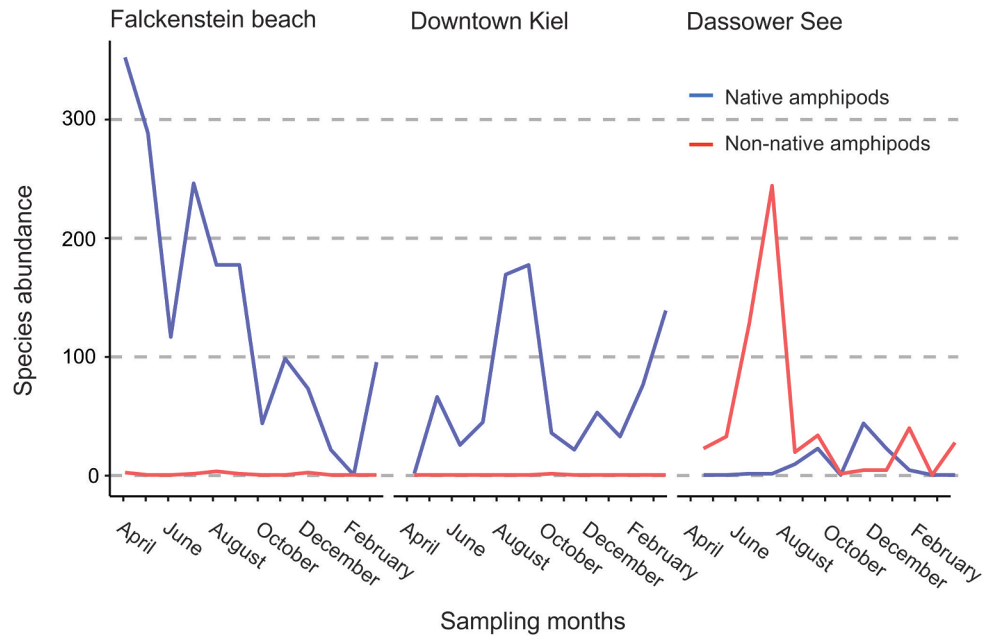
**Fig. 2** Relative monthly abundance of each amphipod species in three sampling locations from April 2022 to March 2023

(135.1 and 9.1 mean and standard error, respectively), followed by downtown Kiel (60.3 and 5.0, respectively), and lastly, Dassower See (43.4 and 5.3, respectively). The maximum abundance was recorded in Falckenstein beach during April with 351 individuals. Similar to abundance trends, we did not find any significant changes in the species richness over time across the three locations (all  $p > 0.12$ ; Fig. 5; Table 2). Model responses suggested high variability in species richness over time (all  $p > 0.12$ ), with Falckenstein beach displaying highest species richness variability (ranging from 3 to 8 species). On the other hand, Dassower See

exhibited the least variability, as well as the lowest amount of species richness (ranging from 1 to 3 species).

Following the above analyses, the abundance of native amphipods did not change over time in Falckenstein beach and downtown Kiel (both  $p > 0.15$ ; Fig. 6; Table 3). Though, in Falckenstein beach, slight decrease in abundance was noticeable during the winter months (Fig. 6). However, we found a significant change in Dassower See ( $p < 0.003$ ), with peak abundance during the fall months (i.e. October and November), followed by a decline in the subsequent months. A significant change was also observed in the abundance of NNS in Dassower See ( $p < 0.001$ ; i.e. *G. tigrinus*),

**Fig. 3** Absolute abundance of native and non-native amphipods at three sampling locations



**Fig. 4** Simpson's Diversity Index of amphipod species for each month in three sampling locations. Median values and interquartile ranges have been indicated in the box plots

with a peak during the summer months (i.e. June and July) followed by a sharp decrease until the end of the year, before a slight increase at the beginning of 2023 (January, February, and March).

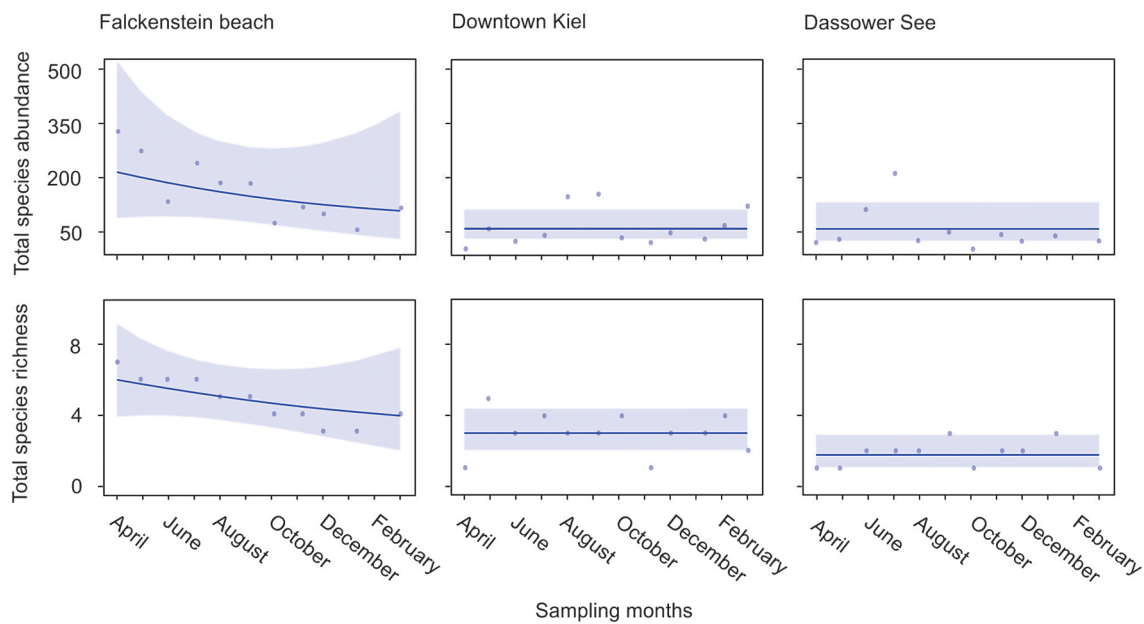
### Environmental effects on amphipod abundance

Over the study period, pH varied between 8.1 and 8.9, 7.8 and 8.2, and 7.9 and 9.1 at Falckenstein beach, downtown Kiel, and Dassower See, respectively (Supplementary Table S1). Salinity ranged from 11.1 to 20.4 ppt, 12.1 to 20 ppt, and from 6.2 to 15.1 ppt, respectively, while temperature ranged from 5.5 to 29.6, 4.6 to 20.9, and 4.2 to 20.8 °C. Dissolved oxygen measures were from 98.4 to 167.3, 84.0 to 107.2, and 93.1 to 122.4%, respectively (Supplementary

Table S1). Our analyses did not reveal significant impacts of pH or dissolved oxygen on amphipod abundance across the three locations (Supplementary Table S3). In the case of salinity, we observed a notable effect on the overall amphipod abundance at Falckenstein beach ( $p < 0.001$ ; Fig. 7), while no significant effect was found for downtown Kiel nor Dassower See ( $p > 0.55$ ); interestingly, an increase in salinity at Dassower See in November and December was associated with a decrease in abundance of *G. tigrinus* and increase of *M. cf. gryllotalpa*. Lastly, water temperature exerted a positive influence on the overall amphipod abundance in Dassower See ( $p = 0.04$ ) (Supplementary Table S3). The RDA plot revealed distinct clustering of samples based on location, indicating that species composition varied among the three studied locations. Salinity had an opposite effect on amphipod community than pH, oxygen and temperature (Fig. 8; Supplementary Table S4).

### Discussion

Anthropogenic disturbance is a major threat to ecosystem biodiversity, with NNS often establishing in habitats subject to high levels of human activity (Smith and Knapp 1999; Minchinton 2002; Halpern et al. 2008; Nogales et al. 2011; Lockwood et al. 2013; Linders et al. 2019; Haubrock et al. 2021). To assess the impacts of such activities on the diversity of native, as well as NNS, we monitored amphipod communities in two anthropogenically impacted and one protected habitat in the Baltic Sea for a whole year. Despite the higher invasion risk in the two anthropogenically impacted habitats, they experienced significantly



**Fig. 5** Model responses for the temporal trends in absolute abundance and richness over the study period across each site. Each dot represents the total species abundance or total species richness recorded for a given month

**Table 1** Results of the generalized additive models (GAMs) for the total abundance of amphipods at each location

Total abundance			
<b>Falckenstein beach</b>			
	Estimate	Standard Error	P value
Intercept	4.99	0.33	<0.001
Smooth terms:	edf	Ref.df	
Months	0.46	9	0.09
<b>Downtown Kiel</b>			
	Estimate	Standard Error	P value
Intercept	4.17	0.32	<0.001
Smooth terms:	edf	Ref.df	
Months	<0.01	9	0.53
<b>Dassower See</b>			
	Estimate	Standard Error	P value
Intercept	4.16	0.42	<0.001
Smooth terms:	edf	Ref.df	
Months	<0.001	9	0.54

edf and Ref.df denote estimated degrees of freedom and reference degrees of freedom, respectively

higher native species richness, as well as lower NNS abundance, when compared to the protected Dassower See. Out of nine amphipod species identified, only two were NNS, with *G. japonica* found strictly in the anthropogenically impacted habitats, and *G. tigrinus* in the protected habitat. Interestingly, *G. japonica* was also consistently recorded at low abundances, while Dassower See was dominated by *G. tigrinus* for the majority of the year. Similar results were also observed by Lin et al. (2022), where several NNS were highly abundant at an unpolluted oyster aquaculture site compared to a heavily polluted nearby shipping port.

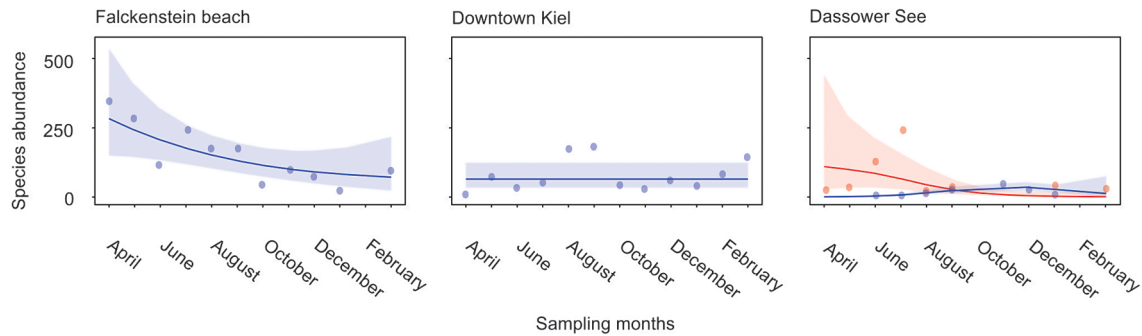
**Table 2** Results of the generalized additive models (GAMs) for the species richness of amphipods at each location

Species richness			
<b>Falckenstein beach</b>			
	Estimate	Standard Error	P value
Intercept	1.58	0.15	<0.001
Smooth terms:	edf	Ref.df	
Months	0.54	9	0.12
<b>Downtown Kiel</b>			
	Estimate	Standard Error	P value
Intercept	1.09	0.19	<0.001
Smooth terms:	edf	Ref.df	
Months	<0.001	9	0.79
<b>Dassower See</b>			
	Estimate	Standard Error	P value
Intercept	0.57	2.30	0.02
Smooth terms:	edf	Ref.df	
Months	<0.001	9	0.64

edf and Ref.df denote estimated degrees of freedom and reference degrees of freedom, respectively

Recent studies across a variety of taxa have revealed that species can adapt quickly in response to anthropogenically impacted environments (Johnson and Munshi-South 2017; Thompson et al. 2018; Santangelo et al. 2018; Borden and Flory 2021). The two anthropogenically impacted habitats in our study have already been affected by humans for centuries, and therefore the adaptation of native communities to numerous and diverse stressors may have already occurred or may currently be ongoing. However, we emphasize that our study does not provide evidence that adaptation of native taxa to anthropogenic conditions is the driver





**Fig. 6** Model responses for the temporal trends in absolute abundance of native and non-native species over the sampling period across each site. Each dot represents the total native species abundance (blue) and total non-native species abundance (red) recorded for a given month

**Table 3** Results of the generalized additive models (GAMs) for the abundance of native and non-native amphipods at each location

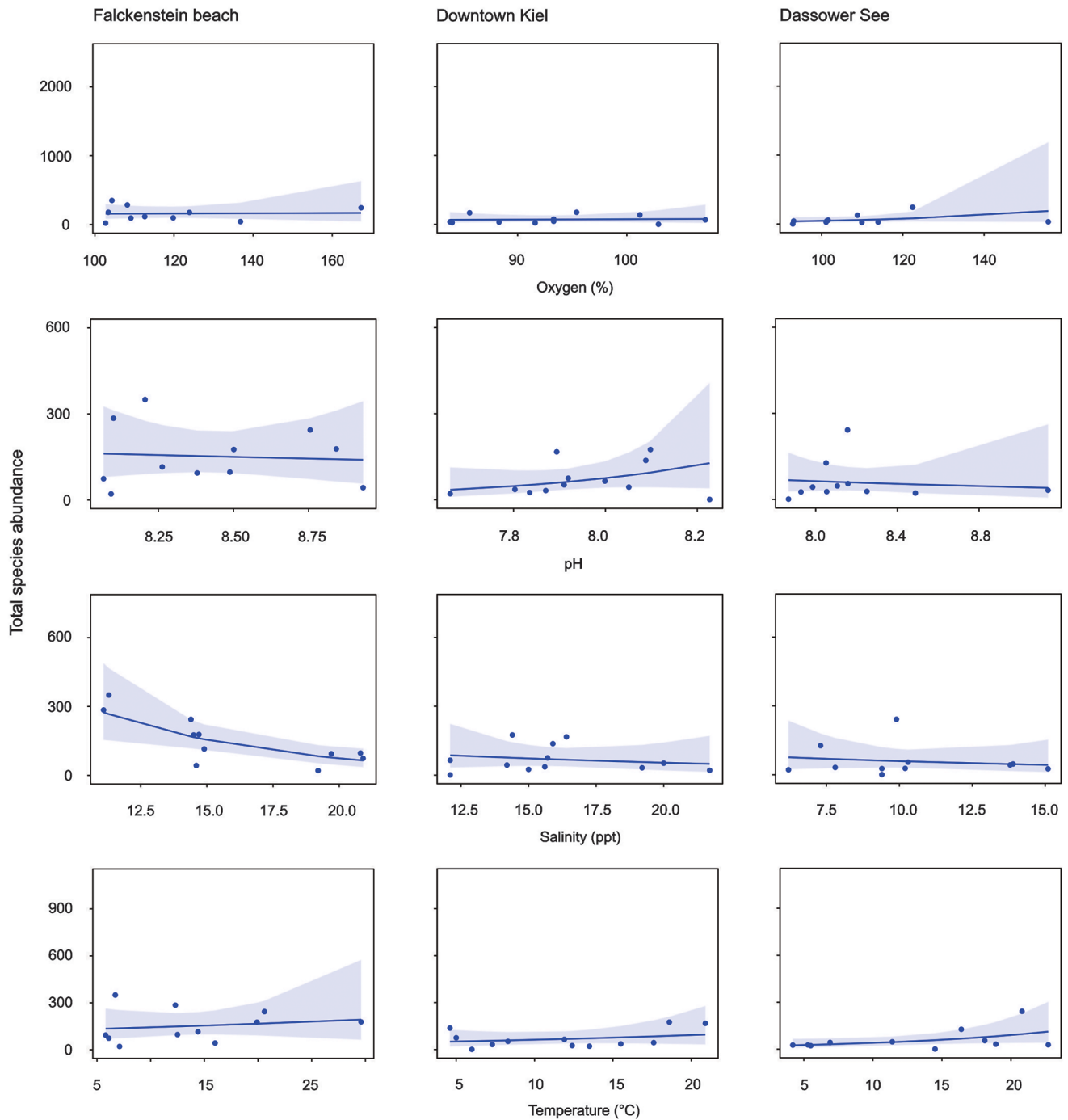
Native abundance			
<b>Falckenstein beach</b>			
	Estimate	Standard Error	P value
Intercept	4.97	0.33	< 0.001
Smooth terms:	edf	Ref.df	
Months	0.47	9	0.15
<b>Downtown Kiel</b>			
	Estimate	Standard Error	P value
Intercept	4.17	0.32	< 0.001
Smooth terms:	edf	Ref.df	
Months	< 0.001	9	0.53
<b>Dassower See</b>			
	Estimate	Standard Error	P value
Intercept	1.96	0.66	< 0.001
Smooth terms:	edf	Ref.df	
Months	1.35	9	0.003

edf and Ref.df denote estimated degrees of freedom and reference degrees of freedom, respectively

of differences of species abundances across sites. We also point out that newly arrived NNS might fail to establish, or persist only at low abundances, due to suboptimal environmental conditions. These NNS populations may be “sleeping populations” (Spear et al. 2021). Such populations can remain at low abundance for years, or even decades, until their population growth is triggered by a change in environmental factors, freshly introduced genetic material by newly arrived individuals from native or other non-native regions, or selection acting on the established population (Bock et al. 2015; Colautti and Lau 2015; Dlugosch et al. 2015; Spear et al. 2021). *Grandidierella japonica*, a NNS recorded at both anthropogenically impacted habitats in our study, was constantly detected at low density. For decades,

this species has already been spreading throughout North America and Northern Europe, where it has been reported at both low and high densities (Pilgrim et al. 2013; Soors et al. 2022). Though this species can colonise a variety of habitats, including harbours, marinas, and areas near sewage treatment plants (Chapman and Dorman 1975), it is sensitive to high metal concentrations (Lee et al. 2005). With both of the locations where we recorded the species being highly polluted by heavy metals (Nikulina et al. 2008), the heavy metal concentrations may prevent the species from becoming abundant.

Although the three locations sampled during this study are in close proximity, the highly invasive NNS *G. tigrinus* was observed only in Dassower See. One explanation for this could be the susceptibility of *G. tigrinus* to disturbances and habitat structural characteristics (Kotta et al. 2014), making the anthropogenically impacted Falckenstein beach and downtown Kiel environments possibly too disturbed for the species. Kotta et al. (2014) also reported that various forms of disturbance, such as the removal of plants and the mixing or removal of the sediment surface layer, can significantly affect its biomass in the Northeastern Baltic Sea. They suggested that while native species have already adapted to these disturbances, characteristic of the area, *G. tigrinus* has not. Another reason could stem from Dassower See having lower salinity compared to Falckenstein beach and downtown Kiel. Though *G. tigrinus*’ North American native-range salinity varies from 4 to 30 ppt, it has invaded only freshwater and brackish habitats (Sexton and Cooper 1939; Jazdzewski et al. 2002; Kelly et al. 2006b). Paiva et al. (2018) demonstrated that populations of gammarids from different regions have distinct salinity tolerances, suggesting local adaptation of populations to environmental conditions. Multiple introduction events of *G. tigrinus* to Europe promoted population admixture, increasing its genetic diversity (Kelly et al. 2006b). However, all established populations originated from freshwater and estuarine environments (Kelly et al. 2006b). *Gammarus tigrinus* established in European waters may therefore prefer lower saline habitats,



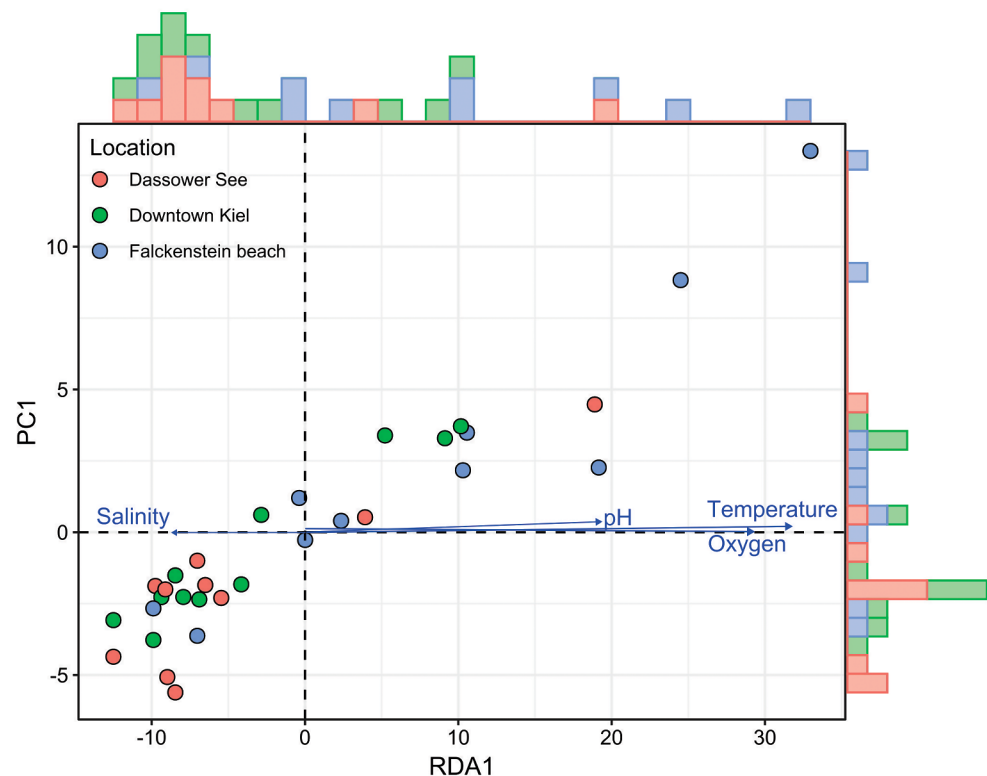
**Fig. 7** Model responses for the relationship among environmental conditions (i.e. oxygen, pH, salinity and temperature) and absolute amphipod abundance over the sampling period across each site. Each

dot represents the total species abundance recorded for a specific environmental conditions

as demonstrated for the Dassower See population by Dickey et al. (2021). Finally, a shift in the dominating population from *G. tigrinus* to native *M. cf. gryllotalpa* when salinity at Dassower See increased, further suggests that salinity may be one of the barriers preventing the spread of current *G. tigrinus* populations in European waters.

*Gammarus tigrinus* was the most abundant species in Dassower See, dominating over the native *G. locusta* and *M. cf. gryllotalpa*. Furthermore, the previously recorded native *G. duebeni* was completely absent during our sampling. With sampling in previous years showing similar abundances of *G. duebeni* and *G. tigrinus* (Zettler 2001; Briski, personal observation), the native species may have

**Fig. 8** Redundancy Analysis (RDA) plot showing the relationship between environmental variables and species composition across three locations: Falckenstein beach, downtown Kiel, and Dassower See. The marginal histograms on the top and right sides show the distribution of RDA1 and PC1 scores from each location



since been replaced by the NNS. Indeed, *G. tigrinus* has a long invasion history in Europe and has been identified as one of the most widespread and aggressive invaders currently in the Baltic Sea (Ojaveer and Kotta 2015). Its success may stem from traits such as higher fecundity, earlier sexual maturity and wider salinity tolerance when compared to native gammarid taxa (Pinkster et al. 1977; Grabowski et al. 2007; Orav-Kotta et al. 2009; Jänes et al. 2015; Paiva et al. 2018). The impact of this NNS is further enhanced by its aggressive and predatory behavior towards native amphipods and the propensity to attack and wound prey without consumption. This not only depletes potential food sources, but also introduces additional stress and vulnerability to native populations (Dick 1996; Dickey et al. 2021). Despite native gammarids occupying a wider ecological niche, they are limited by their attack and predation rates relative to *G. tigrinus* (Herkül et al. 2016; Cuthbert et al. 2022), which may also contribute to this NNS successfully outcompeting and replacing native species (Pinkster 1975; Pinkster et al. 1992; Szaniawska et al. 2003; Grabowski et al. 2006). After the decline of *G. tigrinus* abundance in late autumn, the abundance of native species increased, suggesting that *G. tigrinus* exerts strong competitive pressure on the native *G. locusta* and *M. cf. gryllotalpa*.

Though our model did not find significant seasonal differences for abundance nor species richness at Falckenstein beach when all gammarids were taken into account, the study demonstrated a clear shift in dominance from *G.*

*salinus* to *G. locusta* between spring and summer. There was also a significant change at Dassower See from summer to autumn, with the native *G. locusta* and *M. cf. gryllotalpa* replacing the non-native *G. tigrinus* as the most dominant taxa. Seasonality is rarely considered in ecology, but several recent studies have demonstrated its importance (Fuhrman et al. 2015; Needham and Fuhrman 2016; Wahl et al. 2020; White and Hastings 2020; Theurich et al. 2024). For instance, Fuhrman et al. (2015), Needham and Fuhrman (2016), Needham et al. (2017) determined prokaryotic and eukaryotic phytoplankton bloom species successions among seasons, while Theurich et al. (2024) revealed fluctuating feeding impacts of the non-native *Hemigrapsus takanoi* towards *Mytilus* sp. prey, with seasonality also mediating feeding responses between sexes of the predator. Our study correlates with these, further emphasizing the importance of seasonality in ecological studies, and in our case, its omission would have failed to recognize the seasonal succession. Further, failing to account for seasonality could lead to NNS being unrecorded from a study location should sampling be conducted when the NNS is at low abundance or absent.

Consequently, our study demonstrated that anthropogenically impacted habitats may be under higher invasion risk – serving as gateways for NNS (Smith and Knapp 1999; Minchinton 2002; Lockwood et al. 2013), but at the same time, they may not be the best environments for them to establish and flourish. In contrast, nearby undisturbed and/or protected habitats, such as Dassower See, may be highly

vulnerable to invasions due to more optimal environmental conditions, naïve populations, and robust, prior adapted populations of NNS (Kotta et al. 2014; Bock et al. 2015; Colautti and Lau 2015; Dlugosch et al. 2015; Briski et al. 2018; Lin et al. 2022). Although other factors, such as salinity, temperature, heavy metal concentrations, as well as stochasticity and randomness, may be affecting the establishment success of NNS and subsequently the community structures of the invaded habitats (Lockwood et al. 2013; Paiva et al. 2018; Casties et al. 2019; Briski et al. 2024; Martinez Reyes et al. 2024). Finally, our results show that seasonality is an important aspect of ecological studies and must be taken into account, as omissions could potentially distort our understanding of the dynamics of ecosystems, as well as lead to the unsuccessful detection of NNS (Wahl et al. 2020; White and Hastings 2020; Theurich et al. 2024).

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**Authors' contribution** EK: Sample collection, Data curation, Formal analysis, Visualisation, Writing – original draft, Writing – review & editing. JWED: Formal analysis, Visualisation, Writing – original draft, Writing – review & editing. IS: Formal analysis, Visualisation, Writing – original draft, Writing – review & editing. PJH: Formal analysis, Visualisation, Writing – original draft, Writing – review & editing. AK: Writing – review & editing. RB: Formal analysis, Visualisation, Writing – review & editing. GS: Sample collection, Writing – review & editing. EB: Conceptualisation, Data curation, Formal analysis, Visualisation, Writing – original draft, Writing – review & editing.

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**Data availability** The reproducible code and data used in this study are stored at [https://github.com/IsmaSA/Amphipods\\_Kiel](https://github.com/IsmaSA/Amphipods_Kiel).

## Declarations

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

**Conflict of interest** Elizabeta Briski is an associate editor of Marine Biology. The other authors declare no conflicts of interest.

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