BIODIVERSITY RESEARCH

Diversity and Distributions WILEY

Sea freshening may drive the ecological impacts of emerging and existing invasive non-native species

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Abstract

Aim: The spread of invasive non-native species (INNS) will pose major threats to global biodiversity over the coming decades. However, predicting how key effects of climate change will influence the abilities of INNS to establish and exert ecological impact is a major challenge. One overlooked aspect of global change is the expected freshening of certain marine systems, which may interact with INNS and lead to drastic effects on community structure and stability.

Location: Baltic Sea, Europe.

Methods: Here, using three predatory amphipod crustaceans, we experimentally assessed how salinity reduction may affect the impacts of the emerging INNS, *Pontogammarus maeoticus*, relative to an existing INNS, *Gammarus tigrinus* and a trophically analogous native, *Gammarus salinus*. We quantified per capita impacts of the three species via the comparative functional response method (prey consumption over a range of prey densities) under a predicted seawater freshening scenario. We then combined amphipod functional responses with their life history traits to compare population-level relative impact potential (RIP) on prey of the three amphipod species across salinities.

Results: Freshening substantially altered the predicted relative ecological impacts of both the INNS compared with the native. First, the functional responses of invasive *P. maeoticus* and *G. tigrinus* increased under freshening, while that of the native *G. salinus* decreased. Second, RIP became consistently higher for both the INNS compared to the native with increased freshening.

Main conclusions: Our methods thus reveal potential for climate change via seawater freshening to drive large shifts in dominance and ecological impacts of INNS compared with natives. With the number of INNS introductions unlikely to saturate in the near future, we highlight the need to assess the impacts of potential future INNS, alongside established non-natives and native species, in combination with abiotic changes associated with climate change.

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1 | INTRODUCTION

With consensus being reached that a sixth mass extinction event is underway (Ceballos et al., 2015; Turvey & Crees, 2019), global biodiversity faces an uncertain future (Johnson et al., 2017). Invasive non-native species (INNS), those introduced outside of their historical ranges and found to cause negative ecosystem impacts, are major drivers of biodiversity loss (Courchamp et al., 2017), with increasingly connected transport networks facilitating invasions worldwide (Hulme, 2009; Seebens et al., 2019). While many INNS fail to establish (Williamson & Fitter, 1996), many spread and exert severe impacts, affecting biodiversity, ecosystem function, human, animal and plant health, and global food security (Laverty et al., 2015; Mazza et al., 2014; Paini et al., 2016). However, with the number of species introductions unabating (Seebens et al., 2018), predicting how such impacts are affected by other major threats to global biodiversity, particularly climate change (Thomas et al., 2004), and the vast associated suite of biotic and abiotic consequences (Brook et al., 2008), is a vital, albeit difficult task (Urban, 2015).

While warming, ocean acidification and changing weather patterns are widely studied and documented (Harley et al., 2006), the ecological effects associated with salinity shifts of sea water remain understudied (Illing et al., 2016). This has been described as a "rich get richer" mechanism (Chou et al., 2009), whereby highly saline marine regions are getting saltier, and relatively fresh regions are getting fresher (Durack et al., 2012). Such events could have severe consequences globally, with the greatest impact of freshening likely to occur in coastal and partially enclosed fjordic systems (Convey & Peck, 2019). Indeed, freshening has triggered mass mortality events for amphipods in Arctic waters (Eiane & Daase, 2002) and shifts from a krill-dominated system to a salp-dominated system off the West Antarctic Peninsula (Ballerini et al., 2014; Deppeler & Davidson, 2017). Further, periods of low salinity have in the past been shown to reduce the abundances and spatial distributions of a number of species in the Baltic Sea (e.g. Ojaveer & Kalejs, 2005). How physiological stress resulting from salinity changes will differentially affect INNS and native species is currently unknown and requires urgent assessment and prediction to forecast the identities of likely future INNS, their potential impacts and any effective mitigation strategies.

The Ponto-Caspian region is a donor hotspot for INNS (Cuthbert et al., 2020), with many euryhaline species deemed pre-adapted to invade and establish in new environments (Casties et al., 2016; Paiva et al., 2018; Pauli et al., 2018). Indeed, many Ponto-Caspian INNS can thrive in areas of anthropogenic alteration, including pollution and large salinity ranges, at the expense of natives (Den Hartog et al., 1992). Amphipod crustaceans are one group of particularly successful INNS, with many Ponto-Caspian species undergoing drastic range expansions over the last two decades (Clinton et al., 2018; Cuthbert et al., 2020; Grabowski et al., 2006). Amphipods are major drivers of disturbance through predation, herbivory, competition for substrate and modification of sediment (Conlan, 1994), and their invasions have lead to major changes in the faunal make-up of the systems in which they establish (Dick & Platvoet, 2000; Jazdzewski et al., 2004; Kelly et al., 2006). Predicting the likely identities of future INNS and recipient areas at risk are major goals of invasion ecology (Gallardo et al., 2016; Lucy et al., 2020; Peyton et al., 2019; Roy et al., 2014) and one Ponto-Caspian amphipod expected to spread through Europe in the near future is *Pontogammarus maeoticus* (Baltazar-Soares et al., 2017). Endemic to the Caspian, Black and Azov Seas (Stock et al., 1998), this species has a limited documented invasion history, with only some reports from Turkey and Ukraine in recent decades (Ahmet et al., 2003; Alexandrov et al., 2007). However, an INNS that has already arrived and established in Europe is *G. tigrinus* from North America, and it has been cited as a cause of reduced native species abundances (Grabowski et al., 2006). Relative to trophically analogous natives, *G. tigrinus* tends to have greater salinity tolerance (0–25 PSU: Grabowski et al., 2007), more generations per year and lower susceptibility to human impacts such as pollution and habitat degradation (Grabowski et al., 2007).

One representative system potentially at risk from *P. maeoticus*, and where *G. tigrinus* has already established, is the Baltic Sea in Northern Europe, which has been deemed especially sensitive to salinity changes (Meier & Kauker, 2003). The Baltic Sea has shorelines on nine countries and is subject to high volumes of shipping traffic, and approximately one hundred INNS have been recorded there (Casties et al., 2016; Leppäkoski et al., 2002). This large, semi-enclosed brackish-water sea area has a salinity range between 2 and 24ppt (Leppäkoski et al., 2002) due to a large freshwater supply, a narrow and shallow connection with the North Sea, and the mixing of outflowing brackish water with salty inflowing water (Rodhe & Winsor, 2002). Since the late 1970s, there has been a prolonged period of freshening (Ojaveer & Kalejs, 2005) and this is expected to continue, with salinities of 10ppt likely to become increasingly common (Vuorinen et al., 2015), and Kiel Fjord, to the west of the Baltic, predicted to see a ~ 2ppt decrease of salinity to less than 13ppt by the end of the century (Gräwe et al., 2013).

Here, we assess the effect of decreasing salinity on the predatory impacts of three focal amphipod species: the potential Ponto-Caspian INNS, *P. maeoticus*, and two of the most common amphipods in the northern Baltic, the established North American INNS, *G. tigrinus*, and the Baltic native and trophically similar *G. salinus* (Kotta et al., 2011). We use the comparative functional response method (CFR: Cuthbert et al., 2019; Dick et al., 2014; Dick, et al., 2017), which asseses ecological impact by quantification and comparison of the effect of prey density

on prey consumption rates (see Holling, 1959; Solomon, 1949), while allowing the incorporation of a wide range of biotic and abiotic contexts (e.g. oxygen: Laverty et al., 2015; habitat complexity: Cuthbert et al., 2019; temperature: Wasserman et al., 2018; parasites: Laverty, et al., 2017). We then use the Relative Impact Potential metric (RIP: Dick, et al., 2017; Dickey et al., 2020), which improves the predictive power of the CFR method by combining FR parameters with proxies of the consumer numerical response (NR), such as consumer abundance, density or certain life history trait-based measures (e.g. see Dickey et al., 2018), to establish present and future relative impacts of the three predator species under sea freshening.

2 | METHODS

2.1 | Specimen collection and maintenance

Specimens of *P. maeoticus* were collected in October 2014 in Jafrud, Iran (37°37' N 49°07' E), transported to Kiel, Germany, and kept in laboratory at 18°C and 10ppt. *Gammarus tigrinus* and *G. salinus* were collected in August 2017 in Travemünde, Germany (53°83' N 10°64' E) and Kiel, Germany (54°40' N 10°20' E), and kept at 16°C, and 10ppt and 16ppt, respectively. Salinities and temperatures were determined based on conditions of the collection sites. All three species were held in constantly aerated 56 L glass aquaria, filled with 5-µm filtered Kiel fjord water, with salinity being adjusted by adding artificial seawater (System Instant Ocean®) or potable tap water. Sand and artificial structure, such as ceramic tubes, were added to the tanks to simulate natural habitats. The animals were fed ad libitum with a mixture of commercial crustacean food (Tetra Mix, Tetra Crusta, and Dr. Shrimp Healthy), while the light/dark cycle was 12:12 hr.

2.2 | Functional response experiments

Experiments were conducted between 27 February and 6 March 2018, with the three amphipod species examined concurrently and with *Artemia franciscana* as prey. Two weeks prior to the experiments, 20 size-matched individuals of each of the three amphipod species were selected from their holding aquaria based on head to pleon length (mean ± SE: *P. maeoticus*, 13.602 ± 0.294 mm; *G. tigrinus*, 13.116 ± 0.331 mm; *G. salinus*, 13.273 ± 0.296 mm), and acclimated to a laboratory temperature of 17(±1)°C, which is currently common in shallow areas of the Baltic Sea and projected to become widespread by the end of the century (Holopainen et al., 2016). Two experimental salinities were chosen, that is 16ppt and 10ppt, to reflect a common current salinity on the western Baltic shoreline and an expected future freshened level, repectively (Vuorinen et al., 2015). Amphipod species were housed at densities of 10 individuals per 2 L plastic aquarium (i.e. two aquaria per species) with aerated water, with ceramic tubes for habitat. Each species was fed

twice per day with food pellets (see above), and given half water changes daily.

For *P. maeoticus* and *G. tigrinus*, individuals were adapted to 16ppt from initial holding salinities of 10ppt, and for *G. salinus*, individuals were adapted from 16ppt to 10ppt. In each case, salinities were changed by 2ppt per day towards the target salinities for three days. For individuals with an experimental salinity equal to their holding tank salinity, that is *P. maeoticus* and *G. tigrinus* at 10ppt, and *G. salinus* at 16ppt, water of the same salinity was added to standardise physical disturbance across species and salinities. The water used for experiments was a combination of water from Kiel Fjord and potable tap water, both filtered through a 5-µm filter and mixed to obtain allotted salinities.

The prey, *Artemia franciscana* (5–7 mm), was obtained commercially from Fischfutter Etzbach, Gemünd and maintained in the same laboratory as the predators (see before). Prey was collectively acclimated to the same conditions as predators from an initial salinity of 40ppt (i.e. supplier level) in two stages. First, all individuals were adapted to 30ppt on the day of purchase, 25ppt on the second day and 20ppt on the third day. Second, prey was then segregated, with half the supply acclimated to 16ppt and the other half to 10ppt via one further reduction each on the fourth day. All prey individuals were then given at least two days to acclimate to their experimental salinities. This prey was chosen as a commercially available species tolerant of a wide range of salinities, which had high survival and exhibited normal behaviour throughout experimentation and represented a general, readily consumed prey item (MacNeil et al., 1997).

Feeding experiments were conducted in 1L plastic jars filled with 700 ml of either 16ppt or 10ppt water that had been aerated for 24 hr prior and ordered at random. Five densities of prey were supplied, that is 2, 4, 8, 16 and 32 (n = 6 per prey density, per experimental group) and allowed to settle for 30 min, with trials commencing upon the addition of a single predator. Trials lasted for six hours and the number of live prey was recorded at the end of this time to enumerate numbers consumed, following removal of predators. Controls for each prey density at both salinities (n = 3 per prey density, per experimental group) were used to quantify any background mortality levels in the absence of amphipod predators. Remaining live prey after the experiment were further classified as "free-swimming" or "wounded" (i.e. at the bottom of the experimental arenas, moving thoracopods but unable to enter water column). Dissolved oxygen levels, measured using ProfiLine Oxi 3205 probe (WTW, Germany), did not fall below 85% saturation over the six-hour period. If any of the predators moulted during the experiments, the given treatment replicate was repeated with another inter-moult animal.

Due to the limited number of individuals of each amphipod species, size-matched individuals were re-used a maximum of three times (see Alexander et al. 2014). No individuals at either salinity were exposed to the same density of prey more than once, and a 48 hr recovery period was allowed between trials. To ensure no individuals were given the same prey density, all amphipods were held individually within the larger holding aquaria in 50ml test tubes with

TABLE 1 Calculations of amphipod Partial Fecundity Index (PFI) and Annual Partial Fecundity Index (APFI), with brood size, female size and generations per year figures

Species	(1) Brood size (mean no. eggs in brood pouch)	(2) Mean female breeding size (mm)	References	(3) Generations per year	PFI (1)/ (2)	APFI [(1)/ (2)]*(3)
Pontogammarus maeoticus[I]	24.75	6	Mirzajani (2003)	2	4.125	8.250
Gammarus tigrinus[I]	20.31	7.94	Grabowski et al. (2007)	3	2.558	7.674
Gammarus salinus[N]	25.53	10.62	Skadsheim (1984, 1989)	1	2.404	2.404

Note: [I] indicates INNS status, while [N] indicates native.

a mesh top (to facilitate dissolved oxygen diffusion), containing a ceramic tube for habitat, to track identity.

2.3 | Statistical analysis

All analyses were carried out in R v.3.2.2 (R Development Core Team 2015). Functional responses (FRs) were modelled using the "frair" package (Pritchard et al., 2017), and the type of curve (Type I, II or III) was derived through logistic regression of the proportion of prey consumed as a function of prey density. A significantly negative first-order term indicates a Type II FR, whereas a significantly positive first-order term, followed by a significantly negative second-order term, is indicative of a Type III response (Juliano, 2001). Functional responses of each species at each salinity were modelled using maximum likelihood estimation (MLE; Bolker et al., 2009) and the random predator equation (Rogers, 1972), due to prey not being replaced as they were consumed:

$$N_e = N_0 \left(1 - \exp\left(a\left(N_e h - T\right)\right)\right) \tag{1}$$

where N_e is the number of prey consumed, N_0 is the initial density of prey, a is the attack rate, h is the handling time and T is the total time available (i.e. six hours). A second FR was calculated whereby N_e represented the sum of the number of prey consumed and the number of prey wounded (described above), as such prey individuals are unlikely to survive and reproduce, that is are effectively removed from the prey population. Both models were fit to the data using the Lambert W function owing to the recursive nature of the random predator equation (Bolker, 2008). The initial a and h estimates were non-parametrically bootstrapped ($n = 2000$) to construct 95% confidence intervals around the functional response curve for each treatment.

The potential ecological impact of an INNS under context-dependencies can be predicted using the Impact Potential (IP) metric (Dick, et al., 2017; Dickey et al., 2020), calculated by taking the product of the predator FR and a proxy of the predator numerical response (NR):

$$IP = FR \times NRproxy \tag{2}$$

Here, we used the FR estimate of "maximum feeding rate" (curve asymptote), calculated as the inverse of handling time ($1/h$: Dick et al., 2014), as derived in the above experiment at salinities of 16ppt and 10ppt. This FR measure was combined with two life history trait proxies of the NR (see Table 1), deemed highly predictive of successful invasive gammarids (Grabowski et al., 2007). Firstly, IP was derived using the Partial Fecundity Index (PFI; Table 1):

$$IP_{PFI} = FR \times PFI \tag{3}$$

whereby PFI is calculated as follows:

$$PFI = \frac{\text{Mean brood size}}{\text{Female breeding size}} \tag{4}$$

Secondly, IP was derived using the Annual Partial Fecundity Index (APFI; Table 1):

$$IP_{APFI} = FR \times APFI \qquad (5)$$

whereby APFI is calculated as:

$$APFI = No.\ generations\ per\ year \times PFI \qquad (6)$$

Mean brood size, female breeding size and number of generations per year (Table 1) were taken from Mirzajani (2003) for *P. maeoticus*, Grabowski et al. (2007) for *G. tigrinus* and Skadsheim (1984, 1989) for *G. salinus*. Various studies have shown that salinity has little effect on these measures of fecundity of amphipods (see Maranhão & Marques, 2003; Neuparth et al., 2002; Xue et al., 2013), and thus these fecundity values were kept constant across the two salinities of the present study. RIP biplots (Cuthbert et al., 2018; Dickey et al., 2020; Laverty, et al., 2017) were created with "maximum feeding rate" on the *x*-axes and the above NR proxies (from Equations 4 and 6) on the *y*-axes for comparison among amphipod species at each salinity level, whereby ecological impact increases from the bottom left to top right.

3 | RESULTS

Prey survival in all controls was 100%, and thus experimental consumption did not require adjustment for background prey mortality. For both prey consumption alone and for prey consumption plus prey wounding, Type II FRs were exhibited by all three amphipod species under both salinity treatments, as determined by significantly negative first-order terms (Table 2, Figure 1). The functional response curves of *P. maeoticus* and *G. tigrinus* heightened under reduced salinities, while that of *G. salinus* lowered (Figure 1). This was driven by both INNS exhibiting lower handling times *h* (and hence higher maximum feeding rates, 1/*h*) with decreased salinity, whereas the native exhibited lower attack rates and higher handling times (and hence lower maximum feeding rates) with decreased salinity (Table 2; Figure 1; Figure 2). Of the three study species, the maximum feeding rate of *G. tigrinus* was most greatly heightened by accounting for prey wounding (Table 2; Figure 1; Figure 2).

The IP calculations, using both PFI and APFI, and firstly based on just "prey consumed," are shown in Table 3a. For 16ppt trials, IP_PFI scores were ordered *G. salinus* > *G. tigrinus* > *P. maeoticus* (Figure 3a), but for 10ppt trials, *P. maeoticus* and *G. tigrinus* had higher impacts than *G. salinus*, that is ordered *G. tigrinus* > *P. maeoticus* > *G. salinus* (Figure 3b). IP_APFI scores were ordered *G. tigrinus* > *P. maeoticus* > *G. salinus* at 16ppt and 10ppt respectively (Table 3a, Figure 3c-d).

IP calculations based on "prey consumed and wounded" are shown in Table 3b. For 16ppt trials, IP_PFI scores were ordered *G. tigrinus* > *G. salinus* > *P. maeoticus* (Figure 4a), but at 10ppt, *P. maeoticus* had a greater impact than the native, that is ordered *G. tigrinus* > *P. maeoticus* > *G. salinus* (Figure 4b). IP_APFI scores were ordered *G. tigrinus* > *P. maeoticus* > *G. salinus* at both 16ppt and 10ppt (Figure 4c-d).

4 | DISCUSSION

Understanding how the myriad consequences of climate change are likely to affect the ecological impacts exerted by invasive alien species (INNS) is a pressing concern for biodiversity conservation globally (Hellmann et al., 2008; Mainka & Howard, 2010). The ecosystem effects of INNS and climate change are, however, too often considered independently (Fey & Herren, 2014), and one major outcome of climate change, marine freshening, is often overlooked despite its potential significance globally (Bindoff & Hobbs, 2013; Constable

TABLE 2 First-order terms derived from logistic regression of a) the proportion of prey consumed, and b) the proportion of prey consumed and wounded, as a function of prey density, with parameter estimates from Rogers' random predator equation

	Species	Salinity (ppt)	First-order term	Attack rate (*a*)	Handling time (*h*)	Maximum feeding rate (1/*h*, prey per 6 hr)
a)	*Pontogammarus maeoticus*[I]	16	−0.056***	1.139*	0.247***	4.049
	Gammarus tigrinus[I]	16	−0.065***	1.918***	0.119***	8.403
	Gammarus salinus[N]	16	−0.096***	4.407***	0.108***	9.259
	P. maeoticus[I]	10	−0.038***	0.606**	0.145***	6.897
	G. tigrinus[I]	10	−0.038***	1.117***	0.078***	12.821
	G. salinus[N]	10	−0.096***	3.278***	0.126***	7.937
b)	*P. maeoticus*[I]	16	−0.044***	0.991**	0.157***	6.350
	G. tigrinus[I]	16	−0.044***	1.578***	0.055***	18.285
	G. salinus[N]	16	−0.087***	3.922***	0.087***	11.503
	P. maeoticus[I]	10	−0.032**	0.628***	0.099**	10.106
	G. tigrinus[I]	10	−0.033***	1.199***	0.039***	25.469
	G. salinus[N]	10	−0.083***	2.938***	0.104***	9.583

Note: Where a significant negative first-order linear coefficient was detected, a Type II functional response can be ascribed. Asterisks denote significance levels (*<0.05; **<0.01; ***<0.001). [I] indicates INNS status, while [N] indicates native.
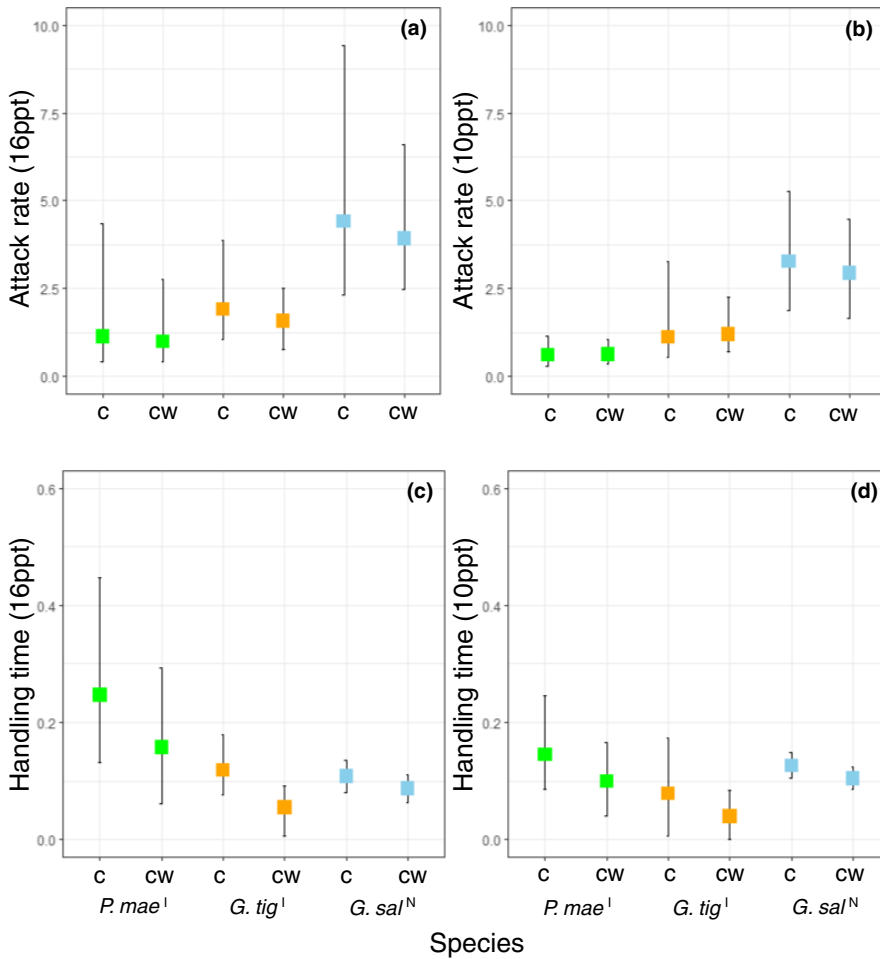
FIGURE 1 Functional response curves of *Pontogammarus maeoticus*, *Gammarus tigrinus* and *Gammarus salinus* consumption of prey at 16ppt (a) and 10ppt (b) salinities, and consumption and wounding of prey at 16ppt (c) and 10ppt (d) towards *Artemia franciscana* prey over 6 hr. Shading represents 95% confidence intervals. [I] indicates INNS status, while [N] indicates native
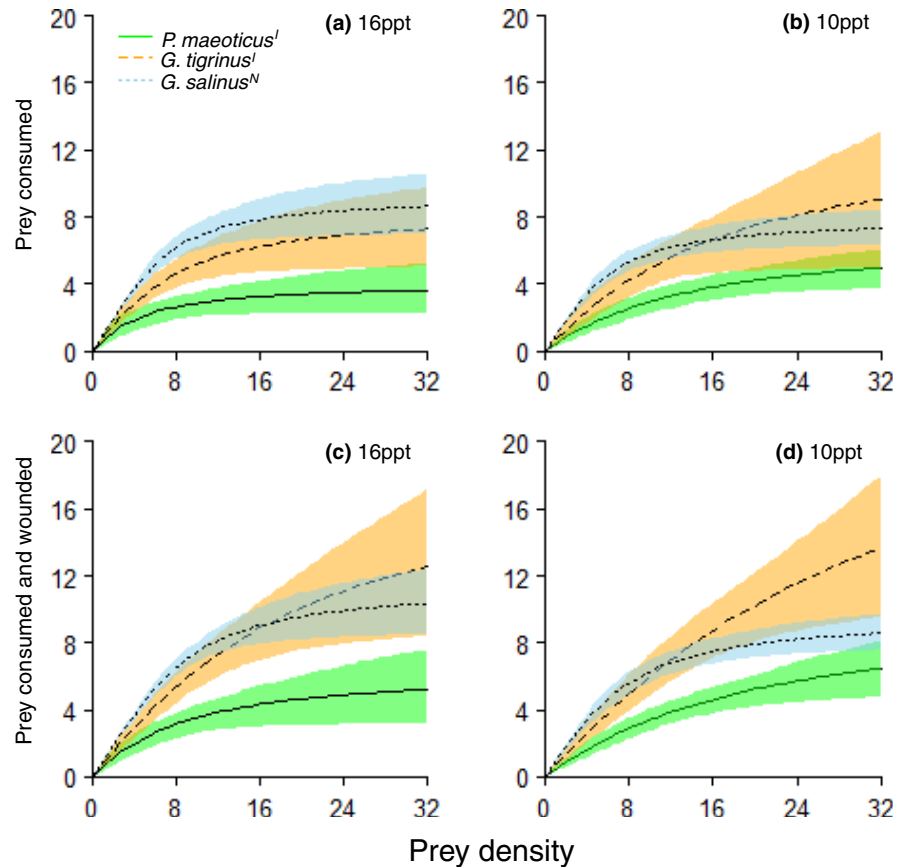
et al., 2014; Gattuso et al., 2018). In this study, we thus focused on a representative ecosystem affected by a wealth of established INNS, and predicted to experience significant future invasion and freshening—the Baltic Sea (Leppäkoski et al., 2002). Specifically, we quantified how two salinity levels, the current salinity of 16ppt, and a likely future salinity of 10ppt, affect the ecological impacts of a potential future INNS, the Ponto-Caspian amphipod, *P. maeoticus*, relative to the already established North American INNS, *G. tigrinus* and the native trophic analogue *G. salinus*. We used the novel approach of comparative functional responses (CFR), that is per capita effects, combined with proxies for the consumer numerical response (NR), to generate relative impact potentials (RIP: Dick, et al., 2017; Dickey et al., 2020).

From the CFR aspect of the experiment, we quantified both "prey consumed" and "prey consumed and wounded" across a range of prey densities. To date, FR experiments have tended to only quantify the number of prey killed (Dick et al., 2014), and this may underestimate the impact a predator exerts on prey populations as unaccounted wounded prey are unlikely to survive or reproduce in the long term. Here, using both FR measures, we found that both *P. maeoticus* and *G. tigrinus* had higher maximum feeding rates at the lower salinity, whereas the maximum feeding rate of *G. salinus* decreased with freshening. These results strongly suggest heightened predatory impacts of the potential and established INNS under future reduced salinity conditions, as differential laboratory FRs are strongly linked to differential ecological impacts in the field (Dick et al., 2013; Dick, et al., 2017).

While the above CFR method is highly effective at highlighting the role played by abiotic conditions on predatory impact, the need to incorporate proxies of the consumer numerical response (NR) into impact quantification has been highlighted (Dick, et al., 2017; Dickey et al., 2020), as their addition offers greater predictive power when assessing overall INNS impacts. That is, the total impact of a species is the product of the per capita effect of individuals and some measure of the number of individuals in the consumer population having those individual effects (Dick, et al., 2017; Dickey et al., 2020). For that reason, we compared the Impact Potentials of the three species, defining impact as the product of per capita effect (specifically the maximum feeding rates derived from the CFR experiments) and relevant life history traits related to the NR. While NR proxies such as abundance and density have been the default in the past (Dick, et al., 2017; Laverty, et al., 2017), this practice is all but impossible when potential INNS with limited invasion history are being assessed (see Dickey et al., 2018, 2020). While *P. maeoticus* have been found to live in extremely high densities in its native range (max. recorded density of 16,256m^{-2}: Mirzajani, 2003), this may not reflect abundance in invasive ranges, and thus we took measures of reproductive life history traits of the three species for more robust comparison. Such reproductive traits and ecological tolerance have been cited as key factors of amphipod success (Grabowski et al., 2007), and here our measure of impact combined both (i.e. life history traits as the NR proxy, tolerance for different salinities incorporated within the maximum feeding rates) to assess potential impact. We used the partial fecundity index (PFI) of Grabowski

FIGURE 2 Bootstrapped prey consumption (c) and prey consumption and wounding (cw) functional response parameter estimates (±95% BCa CIs) of: a) attack rate, *a*, at 16ppt; b) attack rate at 10ppt; c) handling time, *h*, at 16ppt; and d) handling time at 10ppt, of *Pontogammarus maeoticus*, *Gammarus tigrinus* and *Gammarus salinus*. [I] indicates INNS status, while [N] indicates native

	Species	Salinity	IP_{PFI} (ranking)	IP_{APFI} (ranking)
a)	*Pontogammarus maeoticus*[I]	16	16.702 (#3)	33.404 (#2)
	Gammarus tigrinus[I]	16	21.495 (#2)	64.485 (#1)
	Gammarus salinus[N]	16	22.259 (#1)	22.259 (#3)
	P. maeoticus[I]	10	28.450 (#2)	56.900 (#2)
	G. tigrinus[I]	10	32.796 (#1)	99.542 (#1)
	G. salinus[N]	10	19.081 (#3)	19.081 (#3)
b)	*P. maeoticus*[I]	16	26.192 (#3)	52.384 (#2)
	G. tigrinus[I]	16	46.774 (#1)	140.321 (#1)
	G. salinus[N]	16	27.654 (#2)	27.654 (#3)
	P. maeoticus[I]	10	41.687 (#2)	83.375 (#2)
	G. tigrinus[I]	10	65.150 (#1)	195.451 (#1)
	G. salinus[N]	10	23.037 (#3)	23.037 (#3)

TABLE 3 Impact Potential (IP) calculations accounting for a) prey consumed, and b) prey consumed and wounded, whereby IP_{PFI} = maximum feeding rate × Partial Fecundity Index, and IP_{APFI} = maximum feeding rate × Annual Partial Fecundity Index

Note: Partial Fecundity Index and Annual Partial Fecundity Index calculated as per Table 1.
[I] indicates INNS status, while [N] indicates native.

et al. (2007), that is mean brood size divided by female breeding size, and what we name the annual partial fecundity index (APFI), which takes into account the number of generations per year. Increased freshening clearly led to *P. maeoticus* having a higher IP_{PFI} and IP_{APFI} than *G. salinus*, and thus the INNS may exert a greater impact than

the native in the future, or in less saline parts of the Baltic Sea in the short term. We thus highlight *P. maeoticus* as being a species capable of exerting a greater ecological impact than the most common Baltic native, *G. salinus*, at decreased salinity levels, and one worthy of preventative action. Orav-Kotta et al. (2009) highlighted *P. robustoides*

and *O. crassus* as the most invasive Ponto-Caspian amphipods in the Baltic, and the fact *P. maeoticus* outnumbers the latter in the Caspian Sea (Mirzajani, 2003) may strengthen our assessment.

Gammarus tigrinus is regularly highlighted as a damaging INNS, with evidence suggesting it has been expanding its range rapidly over recent decades in the Baltic Sea (Herkül & Kotta, 2007) and beyond (Platvoet et al., 2009). Here, the ability of *G. tigrinus* to combine high feeding rates with high reproductive output means it had the highest IP_{PFI} and IP_{APFI} at both salinities, indicative of high impact in the Baltic Sea currently, and with increasing impact expected with freshening. While certain aspects of its success were not assessed in this study (e.g. aggressive and predatory behaviour towards native amphipods: Dick, 1996; Kotta et al., 2010), the high ecological impact displayed in our IP biplots corroborates its notoriety as a highly damaging INNS. Particular concern should surround its propensity to "wound" prey, and by accounting for this in our "consumed and wounded" biplots, we highlight the potential impact to prey species populations beyond direct consumption. Using both "consumed" and "consumed and wounded" measures, we see heightened predation rates at the lower salinity, indicating potential for enhanced impact in a freshening system for a species already linked to declining abundances of native amphipods, such as *G. salinus* (Orav-Kotta et al., 2009). Paterson et al. (2015), using the measure of "partial consumption", also found that different prey species can elicit different consumptive behaviours from amphipod predators, which they explained as interference caused by high densities of active prey interrupting predator feeding. However, that study did not attempt to assess a predator species effect. Here our "consumed and wounded" biplots demonstrate an enhanced disparity between *G. tigrinus* and the other study species, and highlight different species-specific foraging behaviours, possibly indicative of *G. tigrinus* selectively targeting the most nutritious parts of prey (Paterson et al., 2015).

Amphipod INNS are expected to continue to spread around the coastal areas of the Baltic Sea (Holopainen et al., 2016), and beyond (Grabowski et al., 2007; Son et al., 2020), with changing temperature and salinity conditions likely to further enhance ecological impacts. Intraguild predation is a common feature of coexisting amphipod species (Dick et al., 1999; MacNeil et al., 2004); however, the influence of climate change on intraguild predation has received little focus to date (Brambilla et al., 2019). While some studies have found differential effects of water conductivity on the degree of intraguild predation between amphipod species (Dick & Platvoet, 1996; Kestrup et al., 2011), there is a need to expand such studies to include other abiotic stressors associated with climate change, and to elucidate the associated effects of multiple predatory amphipod species on each other, as well as prey species. Indeed, while species replacements and exclusions often attract headlines, there is a need for future studies to account for the combined, total impact of trophically analogous INNS and native species on the ecosystem, and how those impacts might vary across abiotic contexts (see Relative Total Impact Potential: Dickey et al., 2020).

Salinity changes are affecting a host of aquatic ecosystems worldwide, with climate acting alongside human activities (e.g.

pollution from agriculture, salt mining: Velasco et al., 2018). The osmoregulatory abilities of organisms, both INNS and native species, to cope with such changes (alongside co-occurring stressors such as a temperature, ocean acidification and oxygen saturation levels) may have drastic consequences for biodiversity and ecosystem function. Many INNS arrive in recipient systems via ship ballast water exchanges between freshwater and sea water, and thus withstand selection pressure at an early stage of the invasion process (Briski et al., 2018; Piscart et al., 2011). However, a number of INNS are expanding their invaded ranges into areas of new salinities. For example, the invasive blue catfish (*Ictalurus furcatus*), deemed a freshwater species, has been infiltrating increasingly saline habitats in the Chesapeake Bay region and has been shown to be tolerant of higher salinities than most other freshwater fishes (Nepal & Fabrizio, 2019). Conversely, invasive lionfish (*Pterois volitans*), established throughout the western Atlantic and Carribean, have expanded their range into the estuaries of freshwater rivers (Jud et al., 2011). While the changing salinities of marine areas around the world are known to be affecting biodiversity and community composition, such as in polar seas (Convey & Peck, 2019; Doney et al., 2012), there is an increasing need to assess how such effects might interact with the presence of
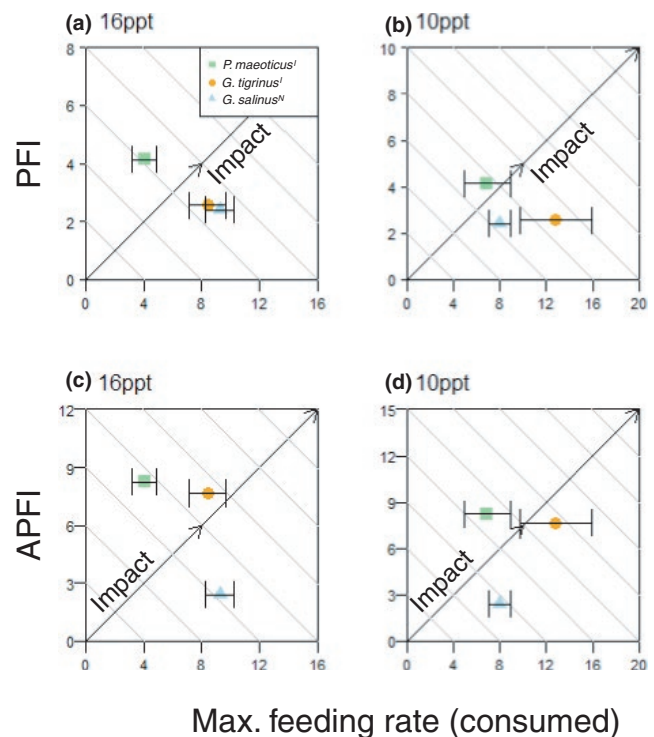
FIGURE 3 Biplots showing Relative Impact Potential of *Pontogammarus maeoticus*, *Gammarus tigrinus* and *Gammarus salinus* towards *Artemia franciscana* prey consumed. Impact potential is calculated as a product of maximum feeding rate and Partial Fecundity Index (PFI) at 16ppt (a), maximum feeding rate and PFI at 10ppt (b), maximum feeding rate and Annual Partial Fecundity Index (APFI) at 16ppt (c) and maximum feeding rate and APFI at 10ppt (d). Impact increases from bottom left to top right of each biplot, with error bars representing standard errors for maximum feeding rates. [I] indicates INNS status, while [N] indicates native
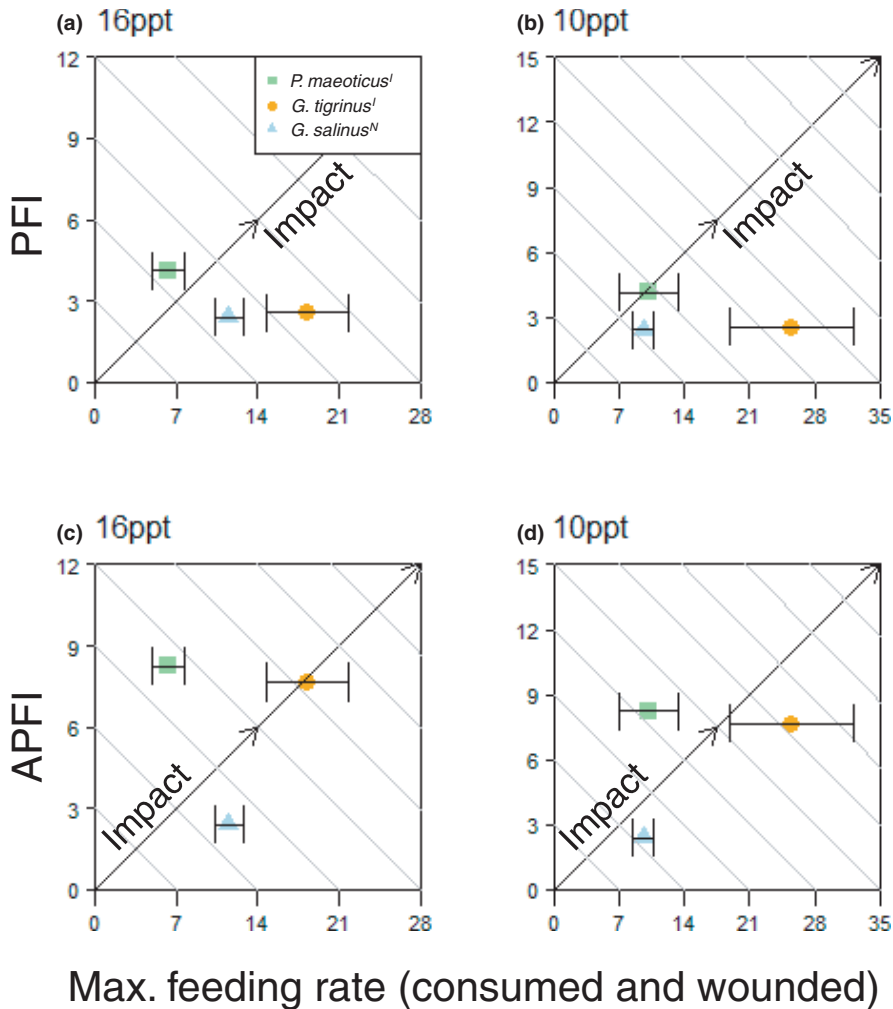
FIGURE 4 Biplots showing Relative Impact Potential of *Pontogammarus maeoticus*, *Gammarus tigrinus* and *Gammarus salinus* based on number of *Artemia franciscana* prey consumed and wounded. Impact potential is calculated as a product of maximum feeding rate and Partial Fecundity Index (PFI) at 16ppt (a), maximum feeding rate and PFI at 10ppt (b), maximum feeding rate and Annual Partial Fecundity Index (APFI) at 16ppt (c) and maximum feeding rate and APFI at 10ppt (d). Impact increases from bottom left to top right of each biplot, with error bars representing standard errors for maximum feeding rates.[I]indicates INNS status, while[N]indicates native

INNS, or species expanding their natural ranges through poleward migration (Aronson et al., 2015). The adaptability of certain INNS (Stern & Lee, 2020) combined with changing salinities in aquatic systems globally means that potential future INNS, as well as established non-natives and native species, need to be subject to relative impact assessments across further abiotic contexts, as per this study. Quantification of how INNS impacts is mediated by less conspicuous regime shifts associated with global climatic change requires urgent consideration by scientists and practitioners. We propose that our new metrics, such as the impact potential metric, offer user-friendly and informative means of assessing and, crucially, predicting said impacts, regardless of the invasion history of the species.

PEER REVIEW
The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13178.

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BIOSKETCH

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