INVASION NOTE

# Predatory preferences of a non-indigenous crab do not depend on prey invasion scenarios

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**Abstract** Predatory non-indigenous species (NIS) have profound impacts on global ecosystems, potentially leading to native prey extinction and reshaping community dynamics. Among mechanisms potentially mediating predator impacts and prey invasion success are predator preferences between native vs. non-indigenous prey, a topic still underexplored. Using functional response and prey preference experiments, this study focused on the predation by the non-indigenous Japanese brush-clawed shore crab, *Hemigrapsus takanoi*, between the native gammarid *Gammarus duebeni* and the analogous non-indigenous *Gammarus tigrinus*. Although *H. takanoi* showed subtle differences in its functional response type between the two prey species, its preferences across their environmental frequencies were not strongly influenced by the prey invasion scenario. The findings highlight the need for a comprehensive understanding of interactions in ecosystems with multiple NIS, offering fresh insights into complex feeding interactions within marine environments.

## Introduction

Predatory non-indigenous species (NIS) have severely impacted ecosystems worldwide, including extinction of prey species (Nikolaou and Katsanevakis 2023). The extent of this impact is mediated by behavioural flexibility and prey preferences in complex ecological communities (Spilmont and Seuront 2023). A variety of hypotheses attempt to describe novel predator–prey dynamics, particularly the lack of a co-evolutionary history between native and NIS which can drive ecological novelty and naivete (Grosholz and Wells 2016). Non-indigenous predator preference towards naïve native prey could be one mechanism which promotes 'invasion meltdown', a process where non-indigenous species mutually facilitate each other's invasion, increasing their survival and impact on ecosystems (Simberloff and Von Holle 1999). This concept highlights the potential for a compounding effect, where introduced species collectively exacerbate ecological disruption, contrary to the slowing effect predicted by biotic resistance. However, evidence for this hypothesis remains equivocal, with only few studies having assessed interaction strengths and preferences between non-indigenous and native prey species from non-indigenous predators (Cuthbert et al. 2018).

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Functional responses are an important tool in ecological studies, delineating the relationship between resource availability and uptake by a consumer on a *per capita* basis. The concept of the functional response was pioneered by Solomon (1949) and provides a quantitative framework to analyse the feeding behaviours of a species as resource densities change. Historically, these responses were explored in the context of community ecology and biological control. However, in more recent years, they have been employed in invasion science as a tool to measure the ecological impact caused by both existing and potential invasive species (Dick et al. 2014; Dick et al. 2017; Cuthbert et al. 2018).

Since functional responses typically focus on pairwise predator–prey interactions, the method may be complemented by prey preference experiments, which offer insights into feeding behaviours in more complex prey communities (Cuthbert et al. 2018). In natural settings, resource communities are typically complex, with predators adjusting their feeding behaviour based on the ratio of available resources (i.e., 'ratio dependence'), thereby shifting from preferred sources to less preferred ones owing to mechanisms such as learning, spatial partitioning and visual cues (Oaten and Murdoch 1975; McCard et al. 2021). Prey switching is a particular form of ratio dependence, characterised by disproportionate preference for more abundant resources and disproportionate avoidance of rarer resources (Oaten and Murdoch 1975). Predators' prey switching behaviour can influence the stability of prey populations by regulating abundant prey species and, at the same time, offering protection to rarer prey species (Murdoch 1969). In the context of NIS, the concept can equally be used to explain and predict impact and invasion success. Thereby, if a predator displays ratio-independent preferences towards native over non-indigenous prey, impacts would be most severe towards the native while invasion success of the non-indigenous prey could be promoted (Cuthbert et al. 2018).

In marine ecosystems, the dominant mechanism through which biotic resistance operates is predation (Kimbro et al. 2013), making marine systems well-placed for examining density- or ratio-dependent trophic interactions. The Japanese brush-clawed shore crab *Hemigrapsus takanoi*, Asakura and Watanabe 2005 is a successful invader in European marine waters. In recent years, this species has spread further north and established populations in the Baltic Sea. It consumes algae, blue mussels, and, especially in females, preys on amphipods (Cornelius et al. 2021). Likewise, a new non-indigenous amphipod species, *Gammarus tigrinus* Sexton 1939, native to North America, is spreading in the Baltic Sea. This species is currently one of the most aggressive invaders in the Baltic (Ojaveer and Kotta 2015), serving as a potential prey analogue to the native *Gammarus duebeni* Lilljeborg 1852 for *H. takanoi*.

In this study, we therefore examine the predation by non-indigenous Japanese brush-clawed shore crabs on native gammarid *G. duebeni* and non-indigenous *G. tigrinus*, which often co-occur. We thus compare the functional responses, ratio dependent prey preferences of the non-indigenous predator towards both native *G. duebeni* and non-indigenous *G. tigrinus*.

## Material and methods

*Hemigrapsus takanoi* were sampled with a scrape net (mesh size 0.5 mm), in the innermost part of the Kiel Fjord (54°19′44.8″ N 10°08′55.5″ E), by dragging up ground material. Sexes were distinguished by their abdominal structure, with only non-gravid females selected for the experiments. Non-ovigerous females were selected owing to their preference for amphipod prey and to reduce potential effects of reproductive status (Cornelius et al. 2021). Two prey species, *G. tigrinus* and *G. duebeni* were sourced where they co-occur from Travemünde (53°83′ N 10°64′ E) and kept in 56 L holding aquaria with 10 g/kg salinity in an 18 °C climate chamber (8:16, light: dark rhythm) for multiple generations (1 + years). The collected crabs were placed into 56 L holding aquaria after initial collection and fed ad libitum with *Mytilus* sp.*,* a common prey of them in the Baltic that would mitigate predator learning. The gammarids were fed with crushed crustacean food (mixed Tetra™ Mix, Tetra™ Crusta, and Aqua-Tropica™ Dr. Shrimp Healthy). Prior to the experiments, the collected crabs were acclimatized to the laboratory conditions (16 °C 8:16 light–dark regime) and the desired salinity (10 g/kg) and temperature (16 °C) conditions for at least one week.

To prevent confounds related to size, all crabs and gammarids were measured such that predators and prey were each size matched as closely as possible within and between species. Crabs' carapace size

was measured with an electronic calliper (TRACE-ABLE® digital calliper), to ensure a range of carapace wide between 14 and 25 mm. Only gammarids with an anterior–posterior body length between 12 and 14 mm were used in these experiments, for both species.

In Experiment 1, we assessed the functional response of female *H. takanoi* towards the non-indigenous and native prey species. Five different prey densities (1, 2, 4, 8, 16) of each prey species were provided separately to individual crabs. Each combination was replicated three times, alongside three replicates of predator-free controls at each prey density to quantify background prey mortality. After acclimatization, individual crabs were housed in 2-L plastic aquaria (dimensions: $195 \times 130 \times 117$ mm), filled to 75% capacity with filtered Baltic seawater (salinity 10). All aquaria were located in the same climate chamber aforementioned set at 16 °C and were continuously aerated. The crabs were starved for 48 h to ensure a standardised hunger level of all individuals before adding gammarid prey at each nominal density. After the starvation period, the functional responses of *H. takanoi* towards live *G. tigrinus* (i.e., NIS) and *G. duebeni* (i.e., native species) were quantified. The crabs were allowed to feed for 6 h and prey were not replaced as they were eaten. After this period, the number of killed gammarids was assessed by counting the remaining living prey. Crabs were used only once to prevent habituation effects.

In Experiment 2, both prey species were offered simultaneously to individual female *H. takanoi*. The acclimatisation, starvation and feeding procedure was identical to Experiment 1. The prey species were offered at seven different ratios (2:14, 4:12, 6:10, 8:8, 10:6, 12:4, 14:2; n = 6 replicates per ratio). Prey were again not replaced in this experiment, and a predator-free control with one replicate per ratio was run to account for background prey mortality once more.

## Statistics

All data analyses were done using the statistical software R v.4.1.0 (RCore Team 2023). *P* values less than 0.05 were considered statistically significant. The functional response analysis for Experiment 1 was done using the R package "frair" (Pritchard 2017). First, the type of functional

response was assessed via logistic regressions, whereby a Type II functional response was indicated by a significant negative first order term. The experiment did not include prey replacement. Functional responses were fitted to the data using Type II, Type III, and flexible models (Pritchard 2017). Models were compared using the Akaike Information Criterion (AIC) if the logistic regression was not significant.

The type II model was chosen for *G. tigrinus* based on the logistic regression and modelled using Rogers random predator equation (eq. 1).

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

where $N_e$ is the number of killed prey, $N_0$ is the initial density of prey, $a$ is the attack rate, $h$ is the handling time and $T$ is the total experimental duration (i.e., 6 h).

Based on equivocal logistic regression, Hassell Type III was chosen for *G. duebeni* (Pritchard 2017) as it had the lowest AIC, and can be articulated as:

$$N_e = N_0 \left(1 - \exp\left(\left(d + bN_0\right)\left(hN_e - T\right) / \left(1 + cN_0\right)\right)\right) \tag{2}$$

with the additional constants *b, c* and *d.*

To calculate 95% confidence intervals (CIs) around the functional response curves, non-parametric bootstrapping was used with n = 2000 iterations. This method facilitates visual comparison of overlapping CIs (Pritchard 2017). Subsequently, estimates of handling time ($h$) were used to calculate daily maximum feeding rates ($1/h$).

For the prey switching experiment (Experiment 2), the numbers of prey consumed were examined using generalized linear mixed models (GLMM). The analysis used a Poisson error distribution and a log link, implemented via the 'lme4' package. The fixed effects in the model were prey, which denotes two distinct prey types (i.e. the two gammarid species), and supply, signifying the amount of prey provided. A random effect of '(1|unit)' accounted for repeated simultaneous measures of the two prey types per replicate (unit).

Subsequently, a selectivity index was calculated (Eq. 3) to measure the preference of the predator *H. takanoi* for non-indigenous *G. tigrinus* prey over native *G. duebeni*. Adjustments were made to account for the non-replacement of prey.

$$\alpha = \frac{\log\left(\frac{n_i - r_i}{n_i}\right)}{\log\left(\frac{n_i - r_i}{n_i}\right) + \log\left(\frac{n_{n0} - r_n}{n_{n0}}\right)} \quad (3)$$

where $\alpha$ is the selectivity index for non-indigenous *G. tigrinus*, $n_i$ is the number of the non-indigenous prey available at the start of the experiment, $r_i$ is the number of the non-indigenous prey consumed, $n_{n0}$ the number of native *G. duebeni* available at the start of the experiment and $r_n$ is the number of native prey consumed. The index ranges from 0 to 1, whereby 0 indicates complete avoidance, 0.5 neutral selectivity between native and non-indigenous prey and 1 indicates complete preference towards the NIS. Resulting $\alpha$ values were transformed (Eq. 4) to account for extreme data points (0,1) (Smithson and Verkuilen 2006).

$$\alpha t = \frac{((\alpha * (n-1)) + 0.5)}{n} \quad (4)$$

where $\alpha_t$ is the transformed selectivity index and $n$ is the sample size. Following this transformation, beta regression ('betareg' package, Grün et al. 2012) was used to compare indices over the different prey ratios.

## Results

Survival of the prey was high (> 95%) in the controls for both experiments, indicating that predation by *H. takanoi* was the primary cause of gammarid mortality and predation was observed frequently in situ. In Experiment 1, both prey received similar functional response magnitudes from crabs, but these differed subtly in type. A type II functional response was

detected for *H. takanoi* preying on *G. tigrinus*, with a significant negative first order term (Table 1). For *G. duebeni*, the logistic regression was not significant, but the type III FR model had the lowest AIC (type II: 63.67; type III: 49.67; flexible: 65.55) and so was selected.

Although the underlying FR types were different, the magnitude and confidence intervals of the curves almost entirely overlapped indicating statistically similar responses (Fig. 1). Estimates for handling time were shorter for *G. tigrinus*, than that of *G. duebeni* (Table 2). The derived maximum feeding rate towards *G. tigrinusr* was higher than the maximum feeding rate when *H. takanoi* preyed upon *G. duebeni* (Table 2).

In Experiment 2, there was no clear preference between the native and non-indigenous prey overall. There was thus no significant difference between prey types, indicating that the type of prey (native versus NIS) did not significantly affect consumption rates
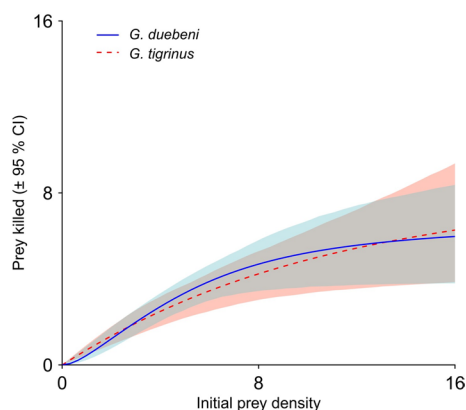


**Fig. 1** Functional response of female *Hemigrapsus takanoi* towards native *Gammarus duebeni* and non-indigenous *Gammarus tigrinus* prey with bootstrapped (*n*=2000) 95% CIs

**Table 1** First-order terms and significance levels from logistic regressions, with functional response type, z values, first order terms and *p* values for all experimental treatment groups with female *Hemigrapsus takanoi* feeding on *Gammarus tigrinus* (GT) *and Gammarus duebeni* (GD) prey

| Prey species | *z* Value | First order term, *p* value | Second order term, *p* value | FR type |
|---|---|---|---|---|
| GT | −2.312 | −0.092, 0.021 | | II |
| GD | −0.682 | −0.028, 0.358 | 0.010, 0.414 | III |

GT represents the non-indigenous prey species and GD the native

**Table 2** Female (F) *Hemigrapsus takanoi* functional response handling times (*h*), maximum feeding rates (1/*h*) and maximum feeding rated in one hour (1/*h*\*T) towards *Gammarus tigrinus* (GT) *and Gammarus duebeni* (GD)

| Prey species | Handling time (*h*), *p* value | Maximum feeding rate (1/*h*) | Maximum feeding rate per hour (1/*h* \*T) |
|---|---|---|---|
| GT | 0.098, 0.012 | 10.224 | 1.704 |
| GD | 0.163, 0.007 | 6.135 | 1.023 |

($z=0.419$, $p=0.675$). However, prey density positively influenced consumption, whereby the more that were prey supplied, the more that were consumed ($z=5.328$, $p<0.001$).

The selectivity indices toward the non-indigenous prey species were generally lower than the null preference of 0.5, except at the 50:50 ratio, where the index was slightly above the null preference (Table 3; Fig. 2). However, there was no evidence of frequency-dependent predation, and therefore the prey preference did not shift with prey ratios (Chi-square $=10.158$, $p=0.118$).

## Discussion

We compared the functional responses and prey preferences of a newly established non-indigenous predatory crab *Hemigrapsus takanoi* towards both a native

**Table 3** Selectivity indices ($\alpha\pm$ S.E.) for female *Hemigrapsus takanoi* towards non-indigenous *Gammarus tigrinus* over the native *Gammarus duebeni* at varying prey ratios. Selectivity indices above 0.5 indicate positive preference whilst indices below 0.5 indicate negative preference towards the invader

| Proportion available | $\alpha_t \pm$ S.E |
|---|---|
| 0.125 | $0\pm0$ |
| 0.25 | $0.281\pm0.128$ |
| 0.375 | $0.456\pm0.173$ |
| 0.5 | $0.531\pm0.148$ |
| 0.625 | $0.482\pm0.142$ |
| 0.75 | $0.263\pm0.100$ |
| 0.875 | $0.405\pm0.144$ |

prey species (*Gammarus duebeni*) and a non-indigenous prey species (*Gammarus tigrinus*) in the Baltic Sea context. The simultaneous occurrence of a native prey and a trophically-analogous non-indigenous prey species is becoming increasingly common, as NIS appear at all trophic levels, leading to potentially disrupted feeding interactions. However, many studies have assessed the effects of non-indigenous predators whereas relatively few have also considered non-indigenous and native resource contexts.

Our findings indicate that the predatory preferences of the non-indigenous crab *H. takanoi* are not influenced by the invasion scenario of the prey. There were nevertheless subtle differences in functional response shapes towards the two prey species. *Hemigrapsus takanoi* exhibited a potentially population-destabilizing type II functional response towards *G. tigrinus*. However, while the response towards *G. duebeni* was less statistically clear, a type III response had the best fit to the data. The type II model predicts higher rates of prey consumption at lower prey densities; these rates decrease as prey densities increase. This behaviour is linked to the exertion of potentially destabilizing forces on prey populations (Dick et al. 2014). In contrast, *G. duebeni* received lower predation pressure at low prey densities. The reduced foraging efficiency of *H. takanoi* towards *G. duebeni* could be linked to lower impact at low prey densities owing to a reduced encounter rate with the prey (Hassel et al. 1977; Vucic-Pestic et al. 2010). Whereas these underlying functional response types were different, the magnitude and confidence intervals of their curves always overlapped, with the functional response magnitude thus similar between prey

**Fig. 2** Prey switching propensities of female *Hemigrapsus takanoi* towards *Gammarus tigrinus* (red square) and *Gammarus duebeni* (blue triangle) prey. The solid line indicates the expected value in the case of no preference between prey types. Means are $\pm 1$ SE ($n=6$ per group)
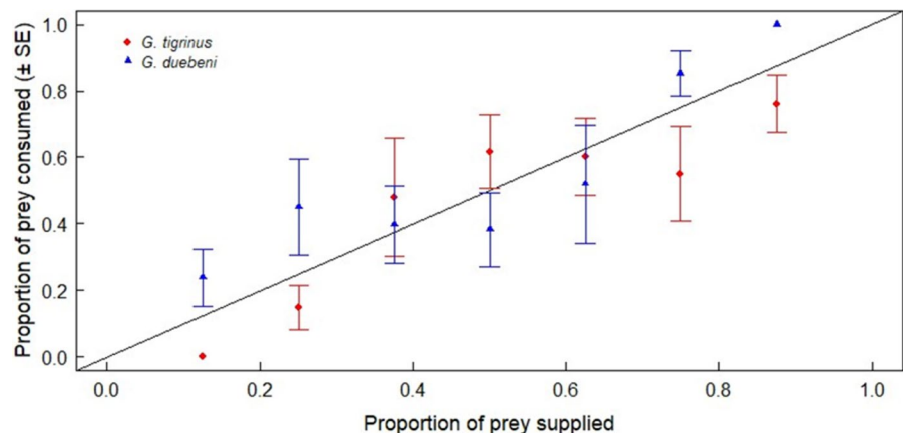
species. Thus, these two prey species were justified a priori for comparison in the prey preference trials, based on the interaction strengths they received from the non-indigenous predator.

When these native and non-indigenous gammarid prey were offered simultaneously, *H. takanoi* showed a slight preference for native *G. duebeni* at both high and low ratios of non-indigenous prey availability. Conversely, a slight preference for non-indigenous *G. tigrinus* was observed when both prey species were available in equal proportions. However, no statistically clear differences based on absolute consumption or ratio-dependent predation patterns were detected, indicating that *H. takanoi* does not currently show a preference for either of the offered prey species depending on the invasion scenario or relative availability in the environment. We also did not find evidence for a prey switching propensity, as has been evidenced in other NIS (McCard et al. 2021). The lack of preference by *H. takanoi* suggests that it does not mediate coexistence or extirpation of either gammarid species, indicating that the intraguild interactions between *G. duebeni* and *G. tigrinus* or interactions with other predators could possibly have a more profound impact on their populations within the ecosystem. The inherent competitive and predatory characteristics of *G. tigrinus* render ecosystems supporting both gammarids as potentially transient and unstable. Indeed, recent field surveys from the German part of the Baltic Sea already noted the absence of *G. duebeni* in this area after *G. tigrinus* was introduced (Briski E., personal observations). Ratios and occurrence of both gammarid species varied across years reflecting the dynamic in their abundance, where several years ago, the ratio of the two species was similar. However, two years ago, *G. tigrinus* abundance increased and the species became dominant almost the whole year except in the autumn when *G. dubenai* took over. Overall, *G. tigrinus* is already known for its ability to outcompete other native gammarids, and this may occur irrespective of higher predators (Ojaveer and Kotta 2015).

Prey preferences are influenced by a multitude of factors, including optimal foraging theory, species abundance, learning behaviour, physiological state, and the behaviour of the prey (McNair 1980). A comprehensive understanding of these underlying mechanisms is crucial for decoding the complex dynamics observed in this study. While requiring further

mechanistic study, the prey preference of omnivorous *H. takanoi* might be mostly influenced by the abundance of different prey types and may not necessarily be dependent on the invasion status of the prey. Therefore, feeding rates increase simply with rising encounter frequencies. The absence of adequate hiding substrates may have artificially increased the predation rate, as both types of gammarids typically seek shelter within such substrates. The lack of this habitat could have in turn resulted in their accumulation in the corners of the arenas, forming aggregations that would be easier for *H. takanoi* to prey upon. Although we used trophically analogous prey species, a study comparing the prey preferences of the sibling species *Hemigrapsus sanguineus* De Haan, 1835 between differing prey functional groups, native blue mussel *Mytilus edulis* Linnaeus, 1758 and introduced amphipod *Ptilohyale littoralis* Stimpson, 1853, also did not find a preference based on introduction status, but rather on encounter rates with the different prey types (Spilmont and Seuront 2023). As both gammarids were consumed relatively evenly, it could further indicate that neither of them has developed a behavioural defence against *H. takanoi* so far during this relatively recent invasion. The native shore crab, *Carcinus maenas* Linnaeus, 1758, was observed to consume a greater quantity of amphipods than mussels in the Wadden Sea, as reported by Cornelius et al. (2021). However, due to the lack of extensive studies, any inferences regarding the feeding preferences of *C. maenas* in comparison to the non-native *H. takanoi* remain speculative in the Baltic. Both experiments were nevertheless conducted under standardized laboratory conditions, which could affect consumption rates due to the lack of habitat complexity, little eco-evolutionary experience in lab-cultured gammarids and potential arena size effects (Vucic-Pestic et al. 2010).

Overall, this study shows that the non-indigenous *H. takanoi* does not exhibit a clear preference for either the native or non-indigenous prey species and has similar interaction strengths between them. The possibility of behavioural adaptations in both predator and prey species might change these observations over time. Nevertheless, this study offers a novel perspective by including a non-indigenous predator and analysing its interactions with both native and non-indigenous prey, diverging from other research that predominantly focused on binary choices between

prey types without referencing invasion scenarios. This distinctive approach adds insights into the complex feeding interactions under the presence of multiple non-indigenous species. In summary, *H. takanoi*, as a relatively new member in the Baltic Sea food webs, has various foraging options, potentially facilitating its further successful range extension without inhibiting other NIS prey.

**Declarations**

**Conflict of interest** The authors declare no conflicts of interest.

**Ethical approval** Ethical approval for the experimental project was granted by the Ministry for Energy Transition, Agriculture, Environment, Nature and Digitalization of the Federal State of Schleswig Holstein, Germany. All experiments were performed in accordance with relevant named guidelines and regulations.

## References

Asakura A, Watanabe S (2005) *Hemigrapsus takanoi*, new species, a sibling species of the common japanese intertidal crab *H. penicillatus* (Decapoda: Brachyura: Grapsoidea). J Crust Biol 25(2):279–292. https://doi.org/10.1651/C-2514

Cornelius A, Wagner K, Buschbaum C (2021) Prey preferences, consumption rates and predation effects of Asian shore crabs (*Hemigrapsus takanoi*) in comparison to native shore crabs (*Carcinus maenas*) in northwestern Europe. Mar Biodivers 51(5):75. https://doi.org/10.1007/s12526-021-01207-7

Cuthbert RN, Dickey JWE, McMorrow C, Laverty C, Dick JTA (2018) Resistance is futile: lack of predator switching and a preference for native prey predict the success of an invasive prey species. R Soc Open Sci 5(8):180339. https://doi.org/10.1098/rsos.180339

Dick JTA et al (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. Biol Invasions 16:735–753. https://doi.org/10.1007/s10530-013-0550-8

Dick JTA et al (2017) Functional responses can unify invasion ecology. Biol Invasions 19:1667–1672. https://doi.org/10.1007/s10530-016-1355-3

Grosholz ED, Wells EH (2016) Evolutionary novelty and the behaviour of introduced predators. In: Weis JS, Sol D (eds) Biological invasions and animal behaviour. Cambridge University Press, New York, pp 199–217. https://doi.org/10.1017/CBO9781139939492.013

Grün B, Kosmidis I, Zeileis A (2012) Extended Beta Regression in R: Shaken, Stirred, Mixed, and Partitioned. J Stat Softw 48(11):1–25. https://doi.org/10.18637/jss.v048.i11

Hassell M, Lawton J, Beddington J (1977) Sigmoid functional responses by invertebrate predators and parasitoids. J Anim Ecol 46:249–262. https://doi.org/10.2307/3959

Kimbro DL, Cheng BS, Grosholz ED (2013) Biotic resistance in marine environments. Ecol Lett 16:821–833. https://doi.org/10.1111/ele.12106

McCard M, South J, Cuthbert RN et al (2021) Pushing the switch: functional responses and prey switching by invasive lionfish may mediate their ecological impact. Biol Invasions 23:2019–2032. https://doi.org/10.1007/s10530-021-02487-7

McNair JN (1980) A stochastic foraging model with predator training effects. I. Functional response, switching, and run lengths. Theor Popul Biol 17:141–166. https://doi.org/10.1016/0040-5809(80)90003-9

Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. Ecol Monogr 39:335–354. https://doi.org/10.2307/1942352

Nikolaou A, Katsanevakis S (2023) Marine extinctions and their drivers. Reg Environ Change 23:88. https://doi.org/10.1007/s10113-023-02081-8

Oaten A, Murdoch WW (1975) Switching, functional response, and stability in predator-prey systems. Am Nat 109(967):299–318. https://doi.org/10.1086/282999

Ojaveer H, Kotta J (2015) Ecosystem impacts of the widespread non-indigenous species in the Baltic Sea: literature survey evidences major limitations in knowledge. Hydrobiologia 750:171–185. https://doi.org/10.1007/s10750-014-2080-5

Pritchard DW, Paterson RA, Bovy HC, Barrios-O'Neill D (2017) frair: an R package for fitting and comparing

consumer functional responses. Methods Ecol Evol 8:1528–1534. https://doi.org/10.1111/2041-210X.12784

R Core Team (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Simberloff D, Von Holle B (1999) Positive interactions of non-indigenous species: invasional meltdown? *Biol*. Invasions 1:21–32. https://doi.org/10.1023/A:1010086329619

Smithson M, Verkuilen J (2006) A better lemon squeezer: Maximum-likelihood regression with beta-distributed dependent variables. Psychol Methods 11:54–71. https://doi.org/10.1037/1082-989X.11.1.54

Solomon ME (1949) The natural control of animal populations. J Anim Ecol 18(1):1–35. https://doi.org/10.2307/1578

Spilmont N, Seuront L (2023) Aliens eating aliens: an introduced amphipod as a potential prey of an invasive rocky shore crab in laboratory experiments. Aquat Invasions 18:163–177. https://doi.org/10.3391/ai.2023.18.2.106252

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U (2010) Allometric functional response model: body masses constrain interaction strengths. J Anim Ecol 79:249–256. https://doi.org/10.1111/j.1365-2656.2009.01622.x