

Warming effects on a nonindigenous predator are not conserved across seasons

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Abstract

The global proliferation of nonindigenous species remains a critical stressor driving both biodiversity loss and socioeconomic costs. These impacts frequently depend on environmental contexts, but few studies have investigated how seasonal variations coupled with climate changes, like warming, could modulate nonindigenous species ecological impacts. The Japanese brush-clawed shore crab *Hemigrapsus takanoi* is a successful nonindigenous species in northern European waters and is currently spreading in the Baltic Sea. In this study, we used generalized linear models and the comparative functional response approach to examine the predatory impact of *H. takanoi* toward blue mussels *Mytilus* sp. across four seasons under current and future temperature scenarios (i.e., ambient and + 6°C warming). We further integrated *H. takanoi* Q_{10} values and field abundances across seasons to examine population-level feeding impacts toward blue mussels. The nonindigenous species exhibited a consistent type II functional response (i.e., inversely prey density-dependent response) across all seasons, temperatures and sexes, with males consistently consuming more mussels than females across all seasons. Warming generally decreased handling times and increased attack rates, but these effects varied by season and sex, with the most pronounced temperature responses observed in autumn and spring. Population-level impact calculations integrating field abundance data of *H. takanoi* indicated that under ambient conditions, feeding impacts toward blue mussels currently peak in the summer months, but as temperature increases, this feeding impact is anticipated to shift later in the year into autumn. These findings underline the critical need for multifaceted research approaches to better understand and predict the context-dependent ecological impacts of nonindigenous species, particularly in the face of ongoing climate change and shifting population characteristics.

Environmental changes, such as the introduction of nonindigenous species (i.e., species established outside their native range), have significantly affected ecosystems worldwide, leading to reductions in biodiversity as well as losses of ecosystem functioning and services (Hawkins 2012; Linders et al. 2019; Pyšek et al. 2020). The nonindigenous species concern gains another layer of complexity with climate change, particularly the steady rise in mean annual sea surface temperatures

(IPCC 2014; Sawall et al. 2021; Meier et al. 2022). This warming expands the habitable zones for many nonindigenous species, intensifying their competitive advantage over native species in higher latitudes (Chan et al. 2019). This is particularly relevant in the Baltic Sea, with its sea surface temperature warming at over 0.35°C per decade — three times faster than the global average (IPCC 2014; Reusch et al. 2018; Meier et al. 2022). This persistent rise in temperature considerably impacts metabolic processes (Norin and Metcalfe 2019), potentially altering growth rates, reproductive cycles, oxygen demand, and overall physiological health of organisms (Lagos et al. 2017; Burraco et al. 2020; Fletcher et al. 2022). As nonindigenous species are often highly plastic and display a remarkable ability to adapt to new environments, including habitats with changing temperature regimes, they often have advantages compared to native species as environments change (Casties et al. 2019; Finch et al. 2021; Martinez Reyes et al. 2024).

Many systems such as the Baltic Sea experience significant seasonal temperature fluctuations (HELCOM 2018). Seasonality can profoundly affect species' behavior, reproductive

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cycles, and survival (Fretwell 1972). However, seasonality is rarely considered in ecological experiments, especially in interaction with temperature (Wahl et al. 2020; White and Hastings 2020). This omission could potentially skew our understanding of the dynamics of ecosystems in response to invasions and may lead to less effective management and conservation strategies.

Predatory brachyuran crabs have successfully invaded marine ecosystems worldwide, owing to their broad physiological adaptability and prolific reproductive traits (Geburzi et al. 2018). Successful nonindigenous species belonging to this group include the European green crab (*Carcinus maenas*, Linnaeus 1758) which is highly invasive in North America (Young and Elliott 2020), the Chinese mitten crab (*Eriocheir sinensis*, H. Milne-Edwards 1853) and the Harris mud crab (*Rhithropanopeus harrisi*, Gould 1841) that spread in both North America and Europe, and the Japanese shore crab (*Hemigrapsus sanguineus*, De Haan 1853) and the Japanese brush-clawed shore crab (*Hemigrapsus takanoi*; Asakura and Watanabe 2005) spreading in Europe (Epifanio 2013; Geburzi et al. 2015). *Hemigrapsus takanoi* spread throughout northern Europe over the last 25 yr and is currently reaching new areas in the Baltic Sea after arrival in the last decade (Geburzi et al. 2015). In its introduced range, the species can out-compete and outnumber *C. maenas* populations (van den Brink et al. 2012; O'Connor 2014; Geburzi et al. 2018). As an omnivore with a tendency toward predation, it affects the abundance of benthic taxa (Kraemer et al. 2007; Brousseau et al. 2014), potentially resulting in multifaceted consequences for the invaded ecosystem. Importantly, the predation pressure exerted by *H. takanoi* may be modulated by its sex demographics, with males exhibiting higher per capita feeding rates than females (Nour et al. 2020; Theurich et al. 2022). In addition, crustaceans are ectothermic organisms, and so their body temperature fluctuates according to the temperature in their environment (Alfonso et al. 2021), consequently affecting their feeding behavior and reproductive timing (Nour et al. 2019; Theurich et al. 2022).

To enhance our understanding of the combined effects of climate change and seasonality, we assessed the influence of seasonality under both current and projected future climate change temperature conditions in the Baltic Sea by determining the functional response of *H. takanoi*. As the functional response assesses the ecological per capita feeding rates of a species without accounting for population density of taxa (Dick et al. 2014, 2017; Faria et al. 2023), we further integrate seasonal field abundance data as a proxy for the numerical response (consumer aggregation as a function of prey density; Dick et al. 2017; Faria et al. 2023). Consequently, we investigated multiple facets of the predator–prey relationship between *H. takanoi* and *Mytilus* sp. Our objectives were to explore: (1) how the consumption rate of *H. takanoi* varies with the prey density of *Mytilus* sp.; (2) how this rate is influenced by the sex of *H. takanoi*; and (3) how increasing

water temperatures modulate these interactions across four seasons and at the population level.

Materials and methods

Animal collection and acclimation

Hemigrapsus takanoi were collected in the innermost part of the Kiel Fjord, Germany (54°19'44.8"N, 10°08'55.5"E). The animal collection was carried out on floating docks by dragging up benthic material from the ~2 m deep seabed with a scrape net (mesh size 0.5 mm) during four seasons. Individuals for the spring, summer, autumn, and winter experiments were collected between March and May, June and August, September and November, and December and February, respectively. Only individuals with intact claws, eight pereopods, and no visible damage were retained. In the laboratory, the collected individuals were morphologically identified, measured, and their sexes distinguished. Individuals with a carapace size between 16 and 28 mm (mean ± SD: 19.81 ± 2.9 mm) were kept. Males and females were placed separately in 56-L aquaria containing aerated filtered Baltic Sea water, stones and hard structure elements, under a 8 : 16 light : dark cycle. The temperature was configured in accordance with: (1) current seasonal mean temperature patterns (i.e., 7°C, 16°C, 13°C, and 5°C in winter, spring, summer, autumn, and winter, respectively); and (2) elevated temperature simulating climate change (i.e., 13°C, 22°C, 19°C, and 11°C in spring, summer, autumn, and winter, respectively). The elevated temperature scenario was selected as the Baltic Sea is a hotspot of sea surface temperature warming, especially in coastal areas. Mean sea surface temperature is predicted to increase by 3.5°C by the end of the century, but some areas in the Baltic are even expected to warm more than 6°C by 2100. We thus used +6°C as a worst-case scenario temperature increase, which also covers temperature gaps as they occur during marine heat waves (Pansch et al. 2018; Meier et al. 2022). During the acclimation phase, the crabs were checked biweekly and offered mussels *Mytilus* sp. ad libitum.

Experimental design

Prior to the experiments, the crabs were acclimatized for at least 1 week to the laboratory conditions under the two desired temperature conditions: (1) ambient; and (2) elevated. Our factorial design analyzed the functional response of *H. takanoi* under two different abiotic factors for both sexes across four seasons. Hence, two temperatures, two sexes, and eight different prey densities (i.e., 1, 2, 4, 6, 8, 16, 32, and 64 mussels) were crossed for each of the four seasons. Each factor combination was replicated five times, while three replicates of each factor combination, excluding sex, were run predator-free to assess the background prey mortality of *Mytilus* sp. Thus, our fully factorial experiment resulted in an overall number of 832 experimental units ([with predators: 5 (replicates) × 2 (temperature) × 2 (sex) × 8 (density)] + [controls: 3 (replicate) × 2 (temperature) ×

8 (density)] \times 4 (seasons); see Supporting Information Fig. S1 for a graphical illustration of all crossed parameters).

Prior the experiment, the crabs were measured at the widest part of their carapace with a caliper (TRACEABLE® digital caliper) to ensure they fit within the anticipated size range. Males had a mean size of 19.84 ± 2.99 mm and females of 19.79 ± 2.75 mm. Then, the crabs were placed individually into plastic aquaria with a capacity of 2 L ($195 \times 130 \times 117$ mm) situated in the same climate chamber. Six of these aquaria were placed in a 50-L water bath to regulate their temperature (Supporting Information Fig. S2). Separate water baths were used for the treatment groups with ambient and elevated temperatures to ensure uniform conditions across replicates. The water level was maintained at three-quarters of the height of the 2-L aquaria, while temperature was monitored inside the aquaria. For treatment groups exposed to elevated temperatures, a heater and pump were incorporated to ensure uniform temperature across all replicates in the water bath. Each of the small aquaria under both temperatures was aerated to avoid oxygen limitation, especially under the elevated temperature scenarios, as less oxygen dissolves in warmer waters, with implications for animal physiology (Keeling et al. 2010; Breitburg et al. 2018; Dickey et al. 2021). The aquaria were covered with a lid and no shelters were provided as the experiment's objective did not involve assessment of the impact of habitat complexity on feeding behavior. The climate chamber, being capable of accommodating eight water baths, allowed for simultaneous execution of up to 48 experimental units.

The experiments were started by a 48-h starvation period (Supporting Information Fig. S3). The starvation and feeding periods were chosen based on trial experiments, to ensure sufficient, but not too long, periods. Subsequently, a fixed number of mussels (between 1 and 64 nominal individuals) was added immediately to the respective aquaria. The mussels were collected prior to each feeding experiment at the same floating docks as the crabs. Those with size between 10 and 15 mm were cleaned and used for the experiments (Nour et al. 2019). At the end of the 72-h feeding period, the number of consumed mussels was determined by counting the number of intact mussels remaining. To prevent habituation effects, each crab was used only in a single experimental run. The order of experimental units was randomized to avoid positional and temporal biases during the experiment.

Statistical analyses

The data collected were analyzed using the statistical software R v.4.1.0 (R Core Team 2021). In all analyses, a p -value less than 0.05 was considered statistically significant. Generalized linear models were used to investigate the consumption rates of *H. takanoi*, as a function of temperature (two-level factor), sex (two-level factor), seasonality (four-level factor), size (continuous numeric), and prey density (continuous numeric). Interactions between temperature, sex, and seasonality were investigated, whereas size and prey-density were added solely as

fixed effects. The residuals of this model were assessed for overdispersion and zero-inflation by comparing them to simulated expectations using the “DHARMA” package (Hartig 2021). Due to overdispersion the quasibinomial family was chosen for these generalized linear models. Zero-inflation was not observed in this model. Nonsignificant terms were iteratively removed from the model using a backward, stepwise approach to create the most parsimonious model (Crawley 2007). The models were compared via F -tests to the stepwise reduced versions to compare deviances, using type III analysis of deviance through the “car” package (Fox and Weisberg 2019). Finally, post hoc tests for pairwise comparisons were carried out using the “emmeans” package in R (Lenth 2021).

Functional response analysis was done using the R package “frai” (Pritchard 2017). Before fitting the experimental data to a specific functional response equation, the type of functional response was assessed. Therefore, logistic regressions were used for each environmental condition and predator–prey combination. A type II response was marked by a significant negative coefficient in the first-order term, while a type III response was characterized by a significant positive first-order term followed by a significant negative second-order term (Juliano 2001). Locally Weighted Scatterplot Smoothing trend lines were plotted to further decipher the functional response type (Supporting Information Fig. S4). Since prey were not replaced after consumption and all treatments displayed a significant negative first-order term, type II functional response curves were modeled for each temperature, sex, and season treatment using Rogers random predator equation (Eq. 1).

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

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., 72 h). The equation provides results for a and h based on an optimization algorithm starting from predefined initial values (set by default to $a = 0.12$ and $h = 0.0015$) until the difference between the observed data and the model predictions is minimized and the best fitting values for a and h are found. Nonparametric bootstrapping ($n = 2000$) was then used on the resulting parameters to calculate 95% confidence intervals around the functional response curves. This approach allows for visual comparison by assessing the convergence or divergence in confidence intervals (Pritchard 2017). Estimates of the attack rate a and handling time h were used to further calculate daily maximum feeding rates ($[1/h] \times T$) (with $T = 3$ accounting for the 3-d experimental duration), as well as functional response ratios (FRRs; a/h) (Cuthbert et al. 2019).

To analyze how functional response parameters scale numerically with temperature, estimations for the parameters a and h were obtained through further bootstrapping, with $n = 20$ samples per parameter and sex. These bootstrapped a and h estimates were then analyzed with separate

polynomial mixed models for each sex and parameter, with season as a random effect. Estimates of a and h were \log_{10} -transformed. We used Akaike information criterion for model comparisons to choose between linear, quadratic, and cubic polynomial models for temperature effects under each sex and parameter. Delta Akaike information criterion's were calculated between the best model and the second best one, or the third best if delta Akaike information criterion was < 2 between the best and second best one.

Furthermore, Q_{10} values were calculated (Eq. 2) to quantify the effect of increasing water temperatures on the attack rate, maximum feeding rate, and FRR, and to assess how the effect varied between male and female *H. takanoi*. The Q_{10} value is a dimensionless coefficient which assesses how temperature increase of 10°C affect the rate of a biological process (Bennett 1990):

$$Q_{10} = \left(\frac{A_2}{A_1} \right)^{\left(\frac{10}{T_2 - T_1} \right)} \quad (2)$$

A_1 is a parameter at temperature T_1 and A_2 is the parameter at temperature T_2 . Values ranging between 1 and 1.5 indicate a thermal plateau, while values between 2 and 4 or above suggest considerable increases in activity as the temperature rises (Huey 1982; Bennett 1990).

Finally, per capita feeding rates from the seasonal functional response experiment were crossed with monthly recorded *H. takanoi* field abundances in the Kiel Fjord to calculate a population-level impact. For this analysis, we utilized population data collected by Nour et al. (2019), as our own net sampling efforts did not systematically record field abundances; our focus was solely on collecting the required number of crabs for the experiments. Nour et al. (2019) gathered field abundance data using both traps and net sampling techniques. By combining the results from these two methods, we calculated daily mean field abundances for *H. takanoi* in the respective month, covering a total area of $\sim 1.5 \text{ m}^2$ (1.25 m^2 from five traps and approximately 0.28 m^2 from net sampling).

The impact potential was calculated seasonally for each of males and females by.

$$\text{Impact potential} = \max_{\text{feeding}} \times n \quad (3)$$

where \max_{feeding} was the maximum feeding rate of *H. takanoi* per day at the given seasonal temperature and sex, and n is the daily field abundance in the respective month for that sex. The \max_{feeding} rates were obtained from the functional response parameter calculations ($[1/h] \times T$).

Results

Our analysis revealed significant temperature-dependent variations in the predatory behavior of *H. takanoi* toward blue mussels, which differed across seasons and sexes, underscoring

a complex interplay among sex, environmental conditions, and prey consumption. In particular, males consistently consumed more mussels than females and warming temperatures appeared to increase feeding activity, particularly in autumn and spring, but this trend was not equally strong across all seasons.

Consumption rates

Since the survival rate in the predator-free controls was over 99%, there was no need to adjust feeding rates for background prey mortality. Consequently, the observed mortality across all treatment groups was attributed to predation, an event often noticed in situ. Male crabs consumed almost twice as many mussels during the whole experimental period than the females, with a total consumption of 2116 and 1138 mussels, respectively (Supporting Information Table S1). Total prey consumption tended to differ across the four seasons, with autumn being the peak period for both sexes (Fig. 1).

Results from the complete and reduced generalized linear model indicated significant main effects for "Sex," "Temperature_{Category}," "Season," "Size," and "Density" (Table 1). While the Sex \times Season interaction was significant in the full model this effect was no longer significant in the reduced model; instead, the two-way interaction between "Temperature_{Category} \times Season" showed that temperature effects differed among seasons. A post hoc test on "Temperature_{Category} \times Season" revealed that the effect of warming was particularly strong in spring, autumn and winter (all p -values < 0.001), but less pronounced in summer ($p = 0.88$). Interestingly both males and females consumed less prey at 13°C in spring compared to the same temperature in autumn (Fig. 1a, c). Overall, temperature effects on consumption were mediated by seasonality while sex, size, and density effects were consistent.

Functional response

Seasonal and thermal variations played a pivotal role in modulating predation dynamics. The functional response analysis yielded significant negative first-order terms across all seasons, sexes, and temperatures, indicating a type II functional response under all examined conditions (Supporting Information Table S2). The magnitudes of these functional response curves varied substantially (Fig. 2). When comparing the confidence intervals of the functional response curves within sex groups and seasons, overlaps were common between temperatures (Fig. 2). For females, the functional response plots for ambient and elevated temperatures overlapped in spring and summer, but showed differences in autumn and winter at intermediate or high prey densities (Fig. 2a–d). In contrast, the functional response curves for males did not overlap in Spring and Summer at intermediate-high prey densities, but did overlap during autumn and winter (Fig. 2e–h). The magnitude of females' functional response was relatively low and similar during spring and summer (Fig. 2a, b). Moving toward autumn, the functional response

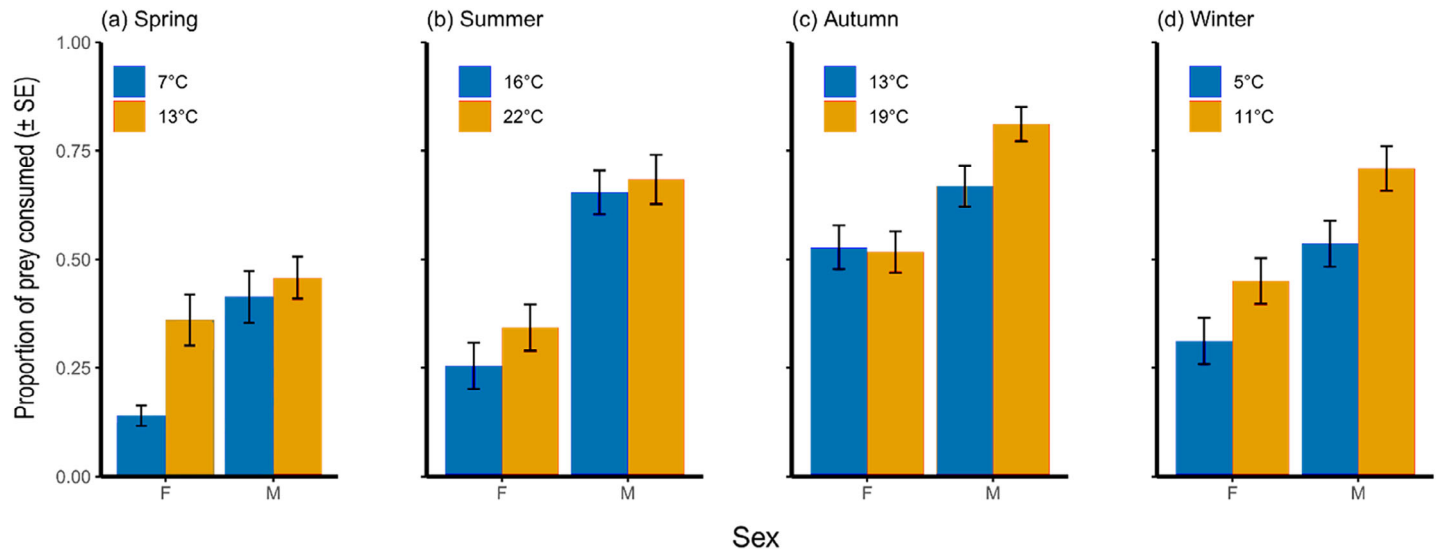


Fig. 1. The proportion of prey consumed (i.e., the average rate of mussels eaten, \pm SE) at two temperature levels per season (i.e., ambient and elevated temperatures). F and M indicate female and male individuals of *Hemigrapsus takanoi*, respectively.

of females reached relatively high values under both temperature scenarios, with even higher magnitudes in the elevated temperature scenario (Fig. 2c). The functional response curves decreased again toward winter generally (Fig. 2d). For males,

Table 1. Terms from the generalized linear model, with a quasibinomial error distribution after type III analysis of deviance, to determine differences in *Mytilus* sp. prey consumption rates by *Hemigrapsus takanoi* according to “Sex,” “Temperature_{Category},” “Season,” “Size,” and “Density.” The upper model includes all interactions, the lower one represents the most parsimonious one.

Predictor	F	df	p
Full model			
Sex	33.1	1	<0.001
Temperature _{Category}	16.46	1	<0.001
Season	6.28	3	<0.001
Size	66.86	1	<0.001
Density	358.21	1	<0.001
Sex × Temperature _{Category}	0.23	1	0.634
Sex × Season	4.04	3	<0.01
Temperature _{Category} × Season	1.16	3	0.324
Sex × Temperature _{Category} × Season	1.92	3	0.124
Reduced model			
Sex	197.4	1	<0.001
Temperature _{Category}	28.17	1	<0.001
Season	33.63	3	<0.001
Size	79.28	1	<0.001
Density	356.51	1	<0.001
Temperature _{Category} × Season	9.94	3	<0.001

the trend again indicated an increasing functional response magnitude toward autumn, followed by a slight decline moving into the winter temperature scenario. Intriguingly, the ambient temperature functional response curve for males in summer exhibited a greater magnitude than its elevated counterpart, marking the only instance where this occurred across all groups tested (Fig. 2f).

Functional response analyses consistently revealed significant estimates for both attack rate (*a*) and handling time (*h*) (Table 2). Both sexes exhibited higher attack rates and reduced handling times at the elevated temperature scenarios across the seasons, with an exception for females which had a reduced attack rate in the elevated autumn scenario and males in the elevated spring scenario (Table 2). Handling time was contrastingly not shortened in elevated temperature scenarios in spring for females and in summer for males. Females had their highest maximum feeding rate in the elevated autumn scenario and their lowest in the elevated spring scenario. Males’ maximum feeding rate was highest in elevated autumn also, while they showed their lowest maximum feeding rate in the ambient spring. The FRR was generally lower for females across all seasons compared to males, indicating a higher feeding impact of male *H. takanoi*. High FRRs were observed accordingly in autumn for both males and females and additionally in summer for males.

In females, the quadratic model was the best fit for attack rate, and the cubic model was the best fit for handling time (Supporting Information Table S3). In contrast, for males, cubic models had the lowest AIC for both attack rate and handling time. The findings thus showed that temperature had a nonlinear and varying effect on attack rates and handling times for both sexes. Female attack rates exhibited a unimodal trend, reaching a peak at intermediate temperatures (13–16°C)

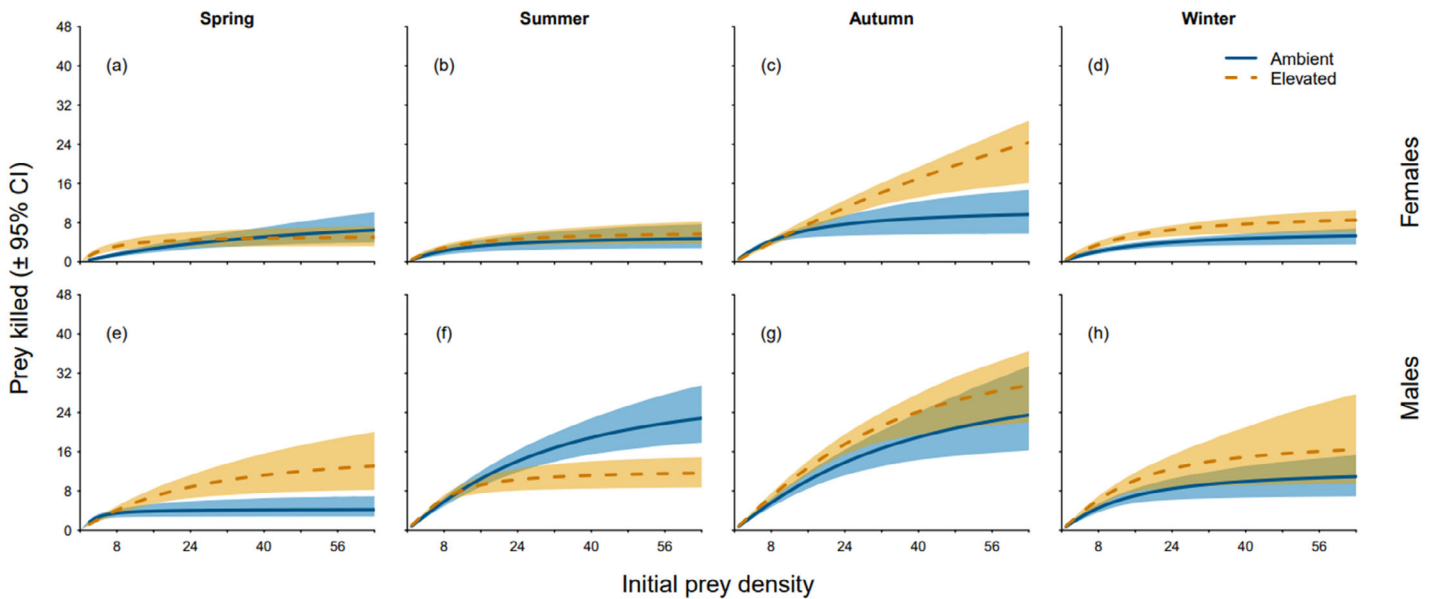


Fig. 2. Functional response curves for male and female *Hemigrapsus takanoi* preying upon *Mytilus* sp. at two temperature levels (i.e., ambient and elevated temperatures) across four seasons. (a) Females in spring (7°C and 13°C); (b) females in summer (16°C and 22°C); (c) females in autumn (13°C and 19°C); (d) females in winter (5°C and 11°C); (e) males in spring (7°C and 13°C); (f) males in summer (16°C and 22°C); (g) males in autumn (13°C and 19°C); (h) males in winter (5°C and 11°C). Shaded areas represent bootstrapped ($n = 2000$) confidence intervals. Lines represent the type II functional response models.

(Fig. 3). Conversely, the scaling of attack rate in males was nonlinear, displaying multiple peaks. Handling times in both females and males were slightly higher at the lowest and the highest applied temperatures, and lowest at temperatures just below 20°C.

The Q_{10} coefficient in the case of females in spring indicated that the attack rate was highly responsive to temperature increase from 7°C to 13°C (Table 3). In contrast, the Q_{10} based on maximum feeding rate was negatively affected, with a considerably affected FRR (overall impact) in that season.

Table 2. Female and male *Hemigrapsus takanoi* functional response parameter estimates (attack rate [a] and handling time [h]), maximum feeding rate per day ($[1/h] \times T$), and functional response ratio (FRR; a/h) for all experimental treatment groups toward *Mytilus* sp. prey. F and M denote females and males, respectively.

Season	Sex	Temperature	Attack rate (a), p -value	Handling time (h), p -value	Maximum feeding rate ($[1/h] \times T$)	FRR (a/h)
Spring	F	7	0.243, < 0.01	0.086, < 0.01	3.876	2.827
Spring	F	13	1.267, < 0.01	0.185, < 0.01	1.802	6.839
Spring	M	7	2.967, < 0.01	0.235, < 0.01	1.418	12.625
Spring	M	13	0.924, < 0.01	0.058, < 0.01	5.747	16.069
Summer	F	16	0.564, < 0.01	0.181, < 0.01	1.842	3.112
Summer	F	22	0.788, < 0.01	0.154, < 0.01	2.165	5.118
Summer	M	16	1.581, < 0.01	0.032, < 0.01	10.417	49.98
Summer	M	22	3.328, < 0.01	0.081, < 0.01	4.115	41.149
Autumn	F	13	1.130, < 0.01	0.086, < 0.01	3.876	13.168
Autumn	F	19	0.742, < 0.01	0.015, < 0.01	22.222	50.525
Autumn	M	13	1.384, < 0.01	0.028, < 0.01	11.905	48.758
Autumn	M	19	2.274, < 0.01	0.025, < 0.01	13.333	92.632
Winter	F	5	0.393, < 0.01	0.137, < 0.01	2.433	2.87
Winter	F	11	0.827, < 0.01	0.095, < 0.01	3.509	8.749
Winter	M	5	1.241, < 0.01	0.077, < 0.01	4.329	16.073
Winter	M	11	2.059, < 0.01	0.051, < 0.01	6.536	39.957

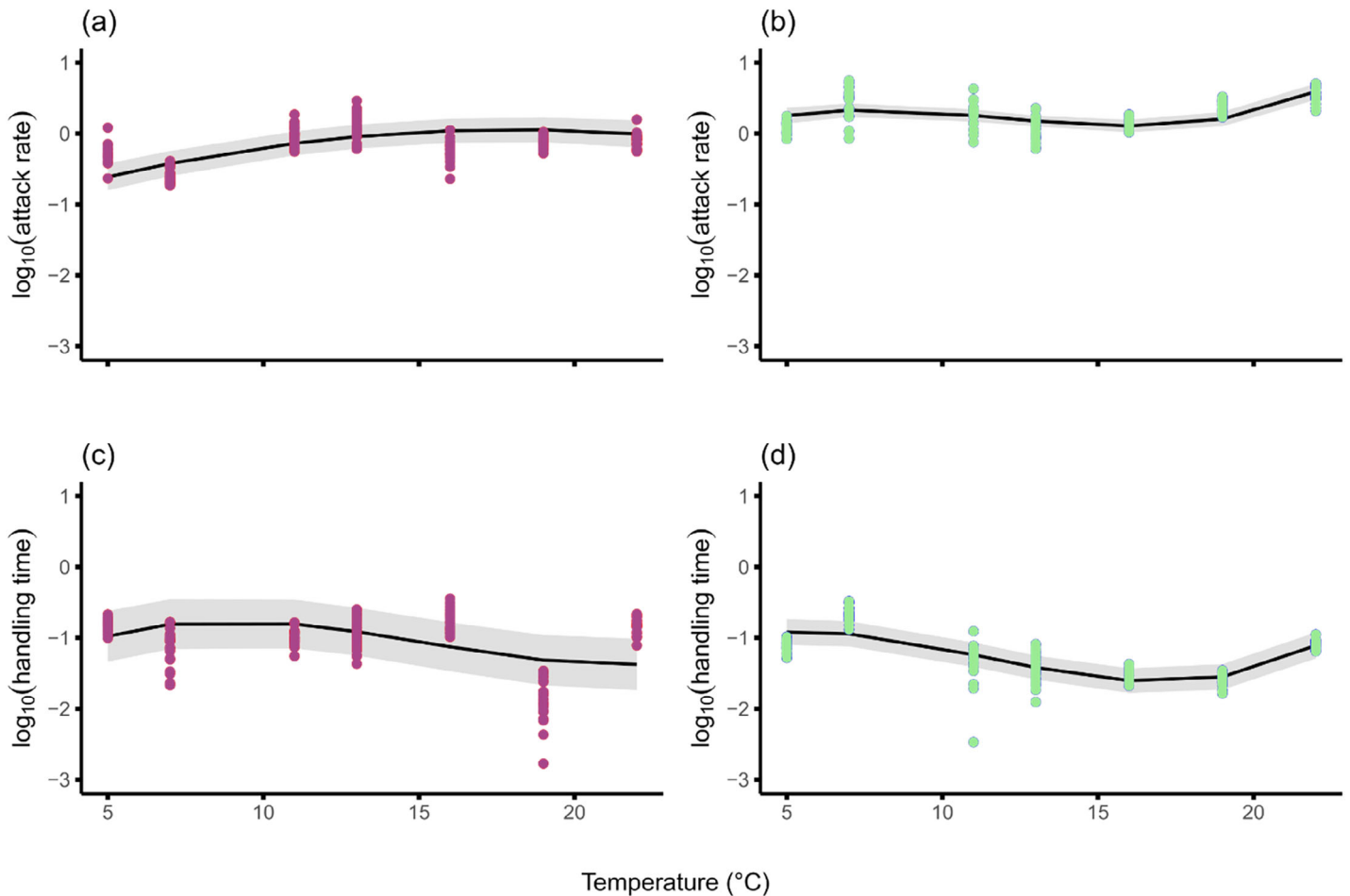


Fig. 3. Scaling of attack rates and handling times for female (a, c) and male (b, d) *Hemigrapsus takanoi* across temperatures, with data from all seasons combined for a numerical comparison of temperature values. Polynomial regression lines are presented alongside raw data points.

Reciprocally, male attack rate decreased substantially in spring, but their maximum feeding rate was strongly altered by rising temperature, and the FRR slightly increased with increasing temperature. In summer, females showed a thermal plateau in Q_{10} for attack rate and maximum feeding rate, with a considerably affected FRR, while males had substantially increased attack rates, but showed decreased performance with increased temperature for their maximum feeding rate and FRR. In autumn, the highest sensitivity in females was shown for maximum feeding rates and FRR, indicating that the activity of females is strongly influenced by temperature changes during this season, but an opposite effect was seen on attack rates. Males were less sensitive in autumn than females, although their attack rate and FRR were still substantially affected. In winter, both males and females showed strong sensitivity based on attack rates and FRR, and moderate sensitivity based on maximum feeding rates. Overall, seasonality moderated warming effects on interaction strengths differentially between sexes, with heightened maximum feeding rates with warming especially in females during autumn, and dampened feeding by males with warming in summer.

Population-level effect

The population-level feeding effects differed substantially between temperatures, seasons, and sexes (Fig. 4). Females exhibited a more consistent and lower feeding impact

Table 3. Q_{10} coefficient values associated with mean bootstrapped attack rates and handling times and therefrom derived functional response ratio (FRR) of *Hemigrapsus takanoi*. Q_{10} coefficient values were determined by Eq. 2.

Season	Sex	Q_{10} based on attack rate (a)	Q_{10} based on $([1/h] \times T)$	Q_{10} based on FRR (a/h)
Spring	F	15.634	0.279	4.36
Spring	M	0.143	10.302	1.495
Summer	F	1.746	1.309	2.291
Summer	M	3.458	0.213	0.723
Autumn	F	0.496	18.365	9.404
Autumn	M	2.288	1.208	2.914
Winter	F	3.455	1.841	6.409
Winter	M	2.326	1.987	4.566

throughout the year under ambient conditions, with slight peaks in the spring (Fig. 4a). In the elevated temperature scenario, the impact of females in spring diminished and shifted substantially toward autumn (Fig. 4b). Conversely, males displayed high feeding impacts during the summer and autumn in the ambient temperature scenario, and their impact was notably higher in the elevated spring scenario compared to the ambient spring scenario, while summer diminished. During low-impact periods in winter, both sexes showed decreased population effects, with negligible differences between ambient and elevated temperature scenarios (Fig. 4a, b).

Throughout the year, total impacts, aggregating both sexes, demonstrated significant fluctuations. In the ambient scenario, the impact peaked from June to August, reaching an impact potential of a consumption of up to 242 mussels per day per $\sim 1.5 \text{ m}^2$ by the crabs (Fig. 4c). The impact peak shifted to a later time in the elevated temperature scenario.

Here, the impact peaked from September to November, reaching a consumption of 268 mussels per day per $\sim 1.5 \text{ m}^2$ (Fig. 4d). Overall, warmer environments are anticipated to shift the greatest population-level impacts from summer to autumn, with a greater female contribution to impact during the autumn season.

Discussion

Our study provides valuable insights into the seasonal impacts of a nonindigenous species using a functional response approach under current and future predicted climate change conditions. We find here that seasonality mediates abiotic and biotic effects by altering temperature responses between sexes of the nonindigenous *H. takanoi* toward a predominant benthic prey—*Mytilus* sp. Using field abundance data recorded across seasons from the same population, we

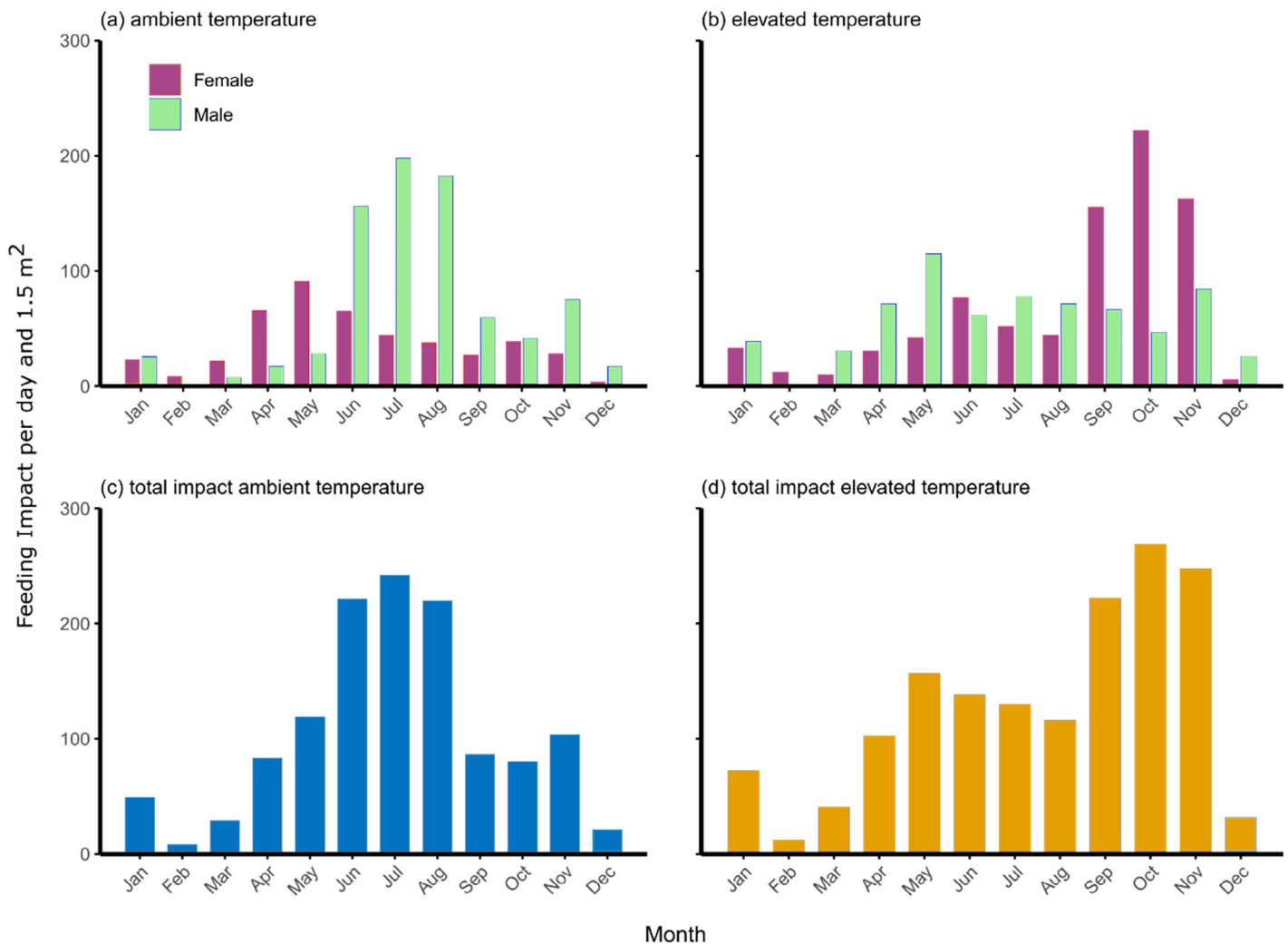


Fig. 4. Potential feeding impact of *Hemigrapsus takanoi* toward *Mytilus* sp. per day under current (a) and projected elevated (b) temperature conditions in the Kiel Fjord. Females and ovigerous females were pooled. Combined impact of males and females (total impact) for the ambient (c) and elevated (d) temperature scenario.

further identified impact peaks at the population-level between elevated temperature scenarios and sexes. Thus, our investigation not only quantified but also temporally resolved the predatory impacts of *H. takanoi*, shedding light on its feeding impacts under different climate change scenarios within one part of its non-native range. Similar principles could likely be applied to other nonindigenous species globally.

Consumption rates and prey preferences

Males consistently consumed more mussels than females across all four seasons, corroborating results of previous studies. One of these studies, conducted on a northern Wadden Sea population, directly compared the feeding of a fixed number of mussels for male and female and found males to consume more mussels than females in a no-choice laboratory setting (Cornelius et al. 2021). Similar results were also observed by Nour et al. (2019) in a laboratory experiment with a population from the Baltic. The difference in feeding between sexes can be attributed to different prey species or size preferences and foraging strategies of females and males, and may also be related to strong sexual dimorphism. Male *H. takanoi* have larger claws compared to the more filigree claws of females. Male claws can thus generate higher pressures than the claws of females allowing them to crush prey more easily (Brose 2010; Nour et al. 2019; Cuthbert et al. 2020). However, it is also important to note that the natural diet of *H. takanoi* is not limited to mussels; they also consume algae and amphipods. Female *H. takanoi*, in particular, appear to show a preference for amphipod prey (Cornelius et al. 2021), although they consume mussels in a similar size range than males (Nour et al. 2019).

Seasonality and temperature effects on predatory behavior

Temperature significantly affected the feeding rates of *H. takanoi*. With some exceptions, higher temperatures led to higher mussel consumption. This finding was also expected as crustaceans, being ectothermic organisms, are directly affected by temperature changes of their surrounding environment. Given that temperature influences the metabolic rate, growth, and reproduction, we expected a direct impact on their energy demand and thus consumption rate when temperatures change (Leffler 1972; Saucedo et al. 2004; Nie et al. 2016). Our results revealed that temperature effects vary between the sexes and are not consistent across seasons, thereby indicating a complex interplay among biotic and abiotic context-dependencies. For example, a 6°C temperature elevation in the autumn did not produce the same effects as the same increase in any of the other seasons. The sensitivity of both females and males to temperature changes was thus not uniform throughout the year. A study on *C. maenas*, a native crab in the Baltic Sea, also revealed a seasonal dependence on how the species copes with temperature after acclimatization, indicating that summer-acclimatized animals are more sensitive to heat shocks than winter acclimatized animals (Cuculescu

et al. 1998; Hopkin et al. 2006). A study on *Mytilus edulis* further demonstrated that their thermal tolerance varies with season (Jones et al. 2009). This fluctuation in thermal tolerance throughout the year may be connected to seasonal changes in the composition of plasma membrane lipids, which have been proposed to be associated with cellular heat injury (Manning and Bowler 1994). Such a seasonal variability in heat-shock proteins has also been shown in fish and mussels (Fader et al. 1994; Chapple et al. 1998), and was further linked to the overall thermal tolerance in two fish species (Nakano and Iwama 2002). Additionally, temperature fluctuations across seasons can lead to behavioral alterations in marine organisms (Moison et al. 2012; Godbold and Solan 2013). For instance, in certain marine vertebrates and invertebrates, their ability to move decreases when they are exposed to elevated temperatures (Moison et al. 2012; Kent and Ojanguren 2015).

In both sexes, consumption peaked in autumn, with a more than doubled mussel consumption compared to consumption in spring. Consumption in autumn also surpassed levels observed in summer. This is notable because the elevated summer temperature was higher than the elevated temperature in the autumn scenario. Normally, one would expect consumption to increase with rising temperatures due to higher metabolic rates (Hartnoll 1982; Sanchez-Salazar et al. 1987). Although, beyond their thermal optimum, species experience a decrease in their metabolism (Hartnoll 1982; Tattersall et al. 2012). The observed pattern here suggests a few possibilities which we cannot fully resolve: either the species reached a thermal optimum, beyond which consumption declined, or alternatively, the seasonal effects were more influential than the temperature increase. Adaptive shifts in the timing of seasonal events (e.g., reproduction period), could potentially precede adaptive shifts of their thermal optima. Moreover, processes like reproduction are highly seasonal in *H. takanoi*, although less so than in *C. maenas* (Geburzi et al. 2018), influencing the overall physiological reaction of *H. takanoi* to external stressors such as warming. Although only nonovigerous females were used in the experiment, summer is the reproduction season of *H. takanoi*, therefore providing a possible explanation for a reduced feeding behavior. Likewise, male crustaceans are more aggressive toward each other, which could reduce their feeding time and thus feeding impact during summer. We suspect that the high energy demand of *H. takanoi* in autumn could result from preparation for the coming winter season, where lower temperatures possibly limit the activities of the crabs. Studies on the impact of shifting seasons on marine species are nevertheless still rare, with more behavioral trends reported in terrestrial arthropods (Bradshaw and Holzapfel 2006).

Functional response and derived factors

Mytilus sp. density had a fundamental impact on the consumption rates of *H. takanoi*, as the feeding rates decreased toward higher prey densities in all temperature and season

scenarios. This trend is reflected in the type II functional response detected for all treatment groups. Such a response is associated with potential destabilizing pressure on prey populations (Dick et al. 2014). Functional response parameters were further found to be significantly affected by temperature. Both the attack rate and handling time trends varied across the seasons. An increase in temperature is expected to shorten the handling time (Jeschke et al. 2002; Dell et al. 2011), and was indeed found for the temperature increase in all seasons except spring in females, and summer in males. Additionally, higher attack rates are associated with a more significant ecological impact (Dick et al. 2013; Cuthbert et al. 2019). Consequently, attack rates increased in all elevated scenarios, except autumn in females and spring in males, and tended to decline at the highest temperatures. The observed unimodal attack rate response to temperature levels has been observed by other studies also (Tattersall et al. 2012). Beyond these thermal optima, functional responses may decline (Englund et al. 2011), which could be tested further in future studies with a higher temperature resolution.

The FRR (a/h) combines attack rate and handling time to a metric which can be attributed to overall impact (Cuthbert et al. 2019). Therefore, the FRR helped to resolve ambivalent temperature responses between attack rates and handling times here. The FRR significantly increased in almost all elevated temperature scenarios across the year compared to the ambient scenarios, with males during summer being the only exception. It is possible that males were disproportionately affected by the 22°C summer warming scenario than females, and their impact was reduced due to thermal stress reactions. This suggests a potentially greater overall impact of *H. takanoi* as climate change progresses and sea surface temperatures continue to rise until the species' thermal optimum is exceeded. We note that *Mytilus* sp. most likely did not alter encounter rates with *H. takanoi* in the different temperature scenarios, as they only passively escape by aggregating with conspecifics. Thus, *Mytilus* sp. is a prey which does not bring additional complications into the experimental setup, as could be the case with other free swimming prey species, such as gammarids. Overall, *Mytilus* sp. seems to be confronted with increasing feeding pressure by *H. takanoi* in the climate change scenario.

Functional response studies have regularly focused on nonindigenous/-native species comparisons (Faria et al. 2023); however, here we focus on the effects within a single nonindigenous species. The only co-occurring native crab species in the sampled location is the European green crab, *C. maenas*. While the per capita feeding of *C. maenas* is typically higher than that of *H. takanoi* (Cornelius et al. 2021), field observations show that the abundance of *H. takanoi* far surpasses that of *C. maenas*. This predominance suggests that the feeding impact of *H. takanoi* is likely more substantial in the field than that of its native counterpart. As female and males consume substantially different amounts of mussels, we

here emphasize the importance of considering intra-species variations, including demographics, when assessing the impacts of nonindigenous species populations. Data from both October 2019 and October 2021 revealed a pronounced disparity in the abundance of males and females of *H. takanoi*, with females being 2.8 times more prevalent (personal observations; Nour et al. 2019). This disparity means that the overall feeding impact of *H. takanoi* is not homogeneous across sexes, attributed not only to the different functional responses between male and female, but also to the variations in their demographics.

Limitations and considerations for future research

Despite strong effects, we caveat that the experimental conditions in our study were limited to a laboratory setting, and therefore naturally occurring prey selection, habitat complexity or the presence of multiple prey and predators were not captured (Cornelius et al. 2021; Dickey et al. 2021). The choice between different prey types potentially influences the feeding behavior substantially; however, since *Mytilus* sp. is a major prey resource in the Baltic, it served as a suitable choice for examining this specific predator-prey interaction. As Murdoch (1969) has shown, the occurrence of multiple prey species could trigger prey-switching behavior which could alter the type of functional response toward type III. Further, our experiments did not include ovigerous females during summer season, while population abundance data used to extrapolate our per capita consumption rates did (Nour et al. 2019). As ovigerous females tend to exhibit reduced feeding activities compared to their nonovigerous counterparts (Nour et al. 2019), our calculations may overestimate the feeding impact of the female group during the reproductive season. Moreover, it was not possible to assess field abundances in the elevated temperature scenario and sex ratios can differ through time in space. Estimates of crab density and therefore also field consumption rates might be overestimated, as Nour et al. (2019) used traps which could have attracted crabs artificially, leading to higher densities as naturally occurring in the same square area without a trap. However, traps might underestimate crab density as *H. takanoi* often hide below the surface in the mud, potentially escaping detection in turn. Lastly, environmental changes in aquatic environments are often simultaneously affected by multiple stressors, such as warming, pollution, and oxygen regimes. Here, we isolated temperature, but the responses of this predator-prey system to other regime shifts remain unclear.

A study in the Opal Coast France, in the North Sea, recorded an almost even sex ratio for *H. takanoi* (0.96; Dauvin et al. 2009), which deviates from our and Nour et al. (2019) estimates of 2.8 : 1 (female : male) ratio. While those differences may stem from different salinities between the study locations, we duly emphasize caution in generalizing impacts of *H. takanoi*, as it may differ across geographic locations or populations. Nevertheless, standardized conditions are a key

element of functional response studies to make them comparable to other studies under relevant contexts and to test context-dependencies in a controlled manner (Dick et al. 2014). We urge more robust and routine monitoring of nonindigenous species populations to infer robust impact assessments at the population level. Moreover, *H. takanoi* is not solely influenced by temperature changes; its potential predators in the Baltic, including various fish, other crustacean species and even seabirds, might also be impacted. These environmental shifts could in turn alter their predatory behavior toward *H. takanoi*. Furthermore, additional predators might establish in the Baltic Sea, due to constant propagule pressure of non-native species and climatic changes. However, the specifics of these potential changes in the system remain unknown at present, leading to uncertainties regarding future predation dynamics and the consequent alterations in the food web. Nevertheless, seasonal variability in feeding behavior suggests that *H. takanoi*'s impact on prey populations fluctuates throughout the year, complicating efforts to predict and mitigate its ecological effects. Higher predation pressure in autumn, for example, could deplete key benthic species like *Mytilus* sp. Management strategies should account for these temporal dynamics, rather than relying on annual averages. This information can help policymakers and conservationists to prioritize interventions during periods when the species' ecological impact is most severe or prior to their reproduction.

It was observed that *H. takanoi* males consistently consumed more mussels across all seasons than females, and the feeding rates of both sexes were notably influenced by temperature changes, but sometimes in opposite directions. Furthermore, this study illustrates that assessing warming effects is insufficient to infer the impact of nonindigenous species on an ecosystem, as their feeding impact is not a steady-state variable and it fluctuates across seasons. The results from our research unambiguously illustrate that *H. takanoi* exhibits a destabilizing type II functional response under elevated temperature scenarios across the whole year, with season and temperature having interactive effects. Our study calls for the integration of multiple factors—ranging from environmental conditions, individual behavioral traits, to population-level data—in future research to generate more accurate predictions of the ecological impact of nonindigenous species in general.

Data availability statement

The underlying data are available at PANGAEA (<https://doi.pangaea.de/10.1594/PANGAEA.966181>).

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Conflict of Interest

None declared.

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