Research Article

Population structure of the recent invader *Hemigrapsus takanoi* and prey size selection on Baltic Sea mussels

Ola Mohamed Nour[1,2,*], Meike Stumpp[3], Sonia C. Morón Lugo[1,4], Francisco R. Barboza[1] and Christian Pansch[1]

[1]GEOMAR Helmholtz Centre for Ocean Research Kiel, 24105 Kiel, Germany

[2]Department of Biology and Geology, Faculty of Education, Alexandria University, 21526 Alexandria, Egypt

[3]Institute of Zoology, Comparative Immunobiology, Christian-Albrechts University Kiel, 24118 Kiel, Germany

[4]Departement des Sciences Fondamentales, Universite du Quebec a Chicoutimi 555, Chicoutimi, Quebec G7H 2B 1, Canada

Author e-mails: *olasm.nour@gmail.com (OMN)*, *mstumpp@zoologie.uni-kiel.de (MS)*, *moronsonia@gmail.com (SCML)*, *fbarboza@geomar.de (FRB)*, *ch.pansch@gmail.com (CP)*

*Corresponding author

Abstract

The shore crab *Hemigrapsus takanoi* Asakura and Watanabe, 2005, native to the Northwest Pacific, was recorded in European waters about 25 years ago and it was first found in the Baltic Sea in 2014. Information on population structure of invaders and their new niche is needed in order to understand their biological impact. Over one year, we assessed temporal changes in relative abundance, size-class and sex ratio, as well as breeding season of *H. takanoi* in the Kiel Fjord (Western Baltic Sea). In addition, prey size preference and consumption rates on mussels (*Mytilus edulis* Linnaeus, 1758) were experimentally assessed in spring, summer and autumn. A total of 596 individuals were collected with highest and lowest abundances in June and February, respectively. Females were dominant over males (sex ratio 1.4:1), but males grew to larger sizes. *H. takanoi* reproduced between June and August with ovigerous females representing 30% of the entire female abundance registered over the entire year. Males were able to open larger mussels (due to larger claws) and consumed twice as many mussels when compared to females of similar size. Consumption rates for males were 6 and 2 times higher in summer (seawater temperature of 19 °C) compared to spring (8 °C) and autumn (13 °C), respectively. Females consumed 3 times more mussels in autumn than in spring. *H. takanoi* is an active predator, capable of reproduction in stressful brackish water conditions. Due to large abundances and high feeding pressure, this recently introduced species could play a key role in structuring post-settlement population dynamics of the dominant habitat builder *M. edulis*.

Key words: invasion ecology, non-native species, Asian brush claw shore crab, prey size selection, *Mytilus edulis*, Kiel Fjord

Introduction

Worldwide, crustaceans represent one of the most successful group of invaders (Devin et al. 2005; Galil 2008; Karatayev et al. 2009). The vectors for their dispersal are diverse but can be mainly attributed to ship transport via ballast water (Gollasch 2006; Ricciardi 2006). Natural and artificial canal systems can also facilitate their introduction to new habitats (Galil 2009), as does aquaculture and stocking translocation (Savini et al. 2010).

Advantageous biological and physiological characteristics, such as tolerance to environmental fluctuations, a broad variety of food choices, complex life-history traits, and modes of reproduction are generally thought to explain the invasion success of crustaceans (Hänfling et al. 2011). Crabs were described to largely contribute to the pool of invasions to the California Bay, the Laurentian Great Lake, as well as to the Baltic Sea (Cohen and Carlton 1998; Olenin and Leppäkoski 1999; Ricciardi and MacIsaac 2000).

The Baltic Sea is one of the largest brackish seas worldwide. This semi-enclosed basin, connected to the Atlantic Ocean only via narrow straits, is characterized by a significant salinity gradient, decreasing from south-west to north-east (Leppäkoski et al. 2002). According to their limited tolerance to low salinities, marine species are gradually replaced by freshwater species along this steep salinity gradient (Ojaveer et al. 2010). The Baltic Sea has a short geological age and is therefore thought to contain open niches for new species to arrive (Leppäkoski et al. 2002; Barboza and Franz 2016). Besides these natural environmental circumstances, human induced impacts, such as exploitation of living resources, land-based pollution, eutrophication and physical destruction impose a significant stress onto the Baltic Sea, an environment that is vulnerable to many invaders (Paavola et al. 2005; Ojaveer et al. 2016). To date, 152 non-native and cryptogenic species (34 species belong to crustaceans, among these 8 to decapods) have been recorded in the Baltic Sea (Casties et al. 2016; supplementary in Tsiamis et al. 2019). These non-native species compete for food with local native species (Kotta and Ólafsson 2003), and some of them have caused persistent restructuring and changed functioning of pelagic and benthic ecosystems (Ojaveer et al. 2015; Jormalainen et al. 2016; Tiselius and Møller 2017).

The Asian brush-clawed shore crab *Hemigrapsus takanoi* is a non-native species that recently arrived in the Baltic Sea. This species was recorded at the south-western coast of the Baltic Sea for the first time in 2014 (Geburzi et al. 2015). *H. takanoi* is native to the Northwest Pacific, and was initially identified as *H. penicillatus*, later being declared as a separate, but closely related, sibling of *H. takanoi* (Asakura and Watanabae 2005; Yamasaki et al. 2011; Markert et al. 2014). In 1993, *H. takanoi* was first observed in Bremerhaven, Germany (Gollasch 1999), only one year after a reproductive population of *H. takanoi* was recorded at La Rochelle at the Atlantic coast of France (Noël et al. 1997). From here, the species distribution extended along the Bay of Biscay from its southern part Laroda (Spain) to its northern part Formentine (France; Noël et al. 1997). Today, the recorded distribution of *H. takanoi* along the Atlantic coast of Europe spans from the northern coast of Spain to the southern North Sea coast of Denmark (Dauvin and Delhay 2010). *Hemigrapsus* spp., may have strong impacts on native crab populations in the invaded ecosystem (Jensen et al. 2002; Dauvin et al. 2009; Gothland et al. 2014; Geburzi et al. 2018). In addition,

significant ecological impacts on mussels (e.g. *Mytilus edulis*) were related to the occurrence of *H. sanguineus* after being introduced to the mid-Atlantic coast of North America, with likely consequences for the community structure (Gerard et al. 1999). However, to the best of our knowledge, no studies have been conducted on the predation impacts of *H. takanoi* on Baltic Sea mussel communities, and no information is available on seasonal differences in predation pressure.

In the present study, we assessed the population characteristics of *H. takanoi* in the Kiel Fjord (Western Baltic Sea). Biweekly semi-quantitative assessments of the relative abundance of this species were conducted over a full year cycle, which were used to determine size distribution, sex ratio and reproductive season of *H. takanoi*. In addition, feeding preferences (mussel-size selection) of both sexes of *H. takanoi* were investigated in repeated laboratory experiments in spring, summer and autumn. The results of this study provide valuable insights into possible ecological implications for the invaded habitat (Katsanevakis et al. 2013), and in particular insights into the potential impact of this non-native species on mussel (*M. edulis*) beds as well as mussels' size refuge from predation.

Materials and methods

Study area

Field monitoring and samplings for feeding assays were carried out in the inner most part of the Kiel Fjord (54°32.9′N; 10°14.8′E; Supplementary material Figure S1), where several mussel beds and aggregations at walls and pontoons (mostly harbour constructions) of the blue mussel *M. edulis* exist. In this habitat, *H. takanoi* is now co-occurring with the two main native predators, the European green crab *Carcinus maenas* and the common sea star *Asterias rubens* (Reusch and Chapman 1997).

Field monitoring and crab sampling

Females of *H. takanoi* were found to be less active in movement than males (personal observation), and they are known to bury themselves in the sediment, spending more time grooming their eggs than feeding during their reproductive period (Turoboyski 1973; Sumpton and Smith 1990). Therefore, relative abundance and size distribution for *H. takanoi* were determined by biweekly samplings between January and December 2017, using two separate methods: (1) active manual scraping of mussel beds for 20 min and (2) passive collection using traps. Scraping was conducted at a depth of 1.5–2 m, with ~ 35 bottom samples taken at each time point, using a scraper of 0.008 m² surface area and a mesh size of 0.5 mm (covering a total area of ~ 0.28 m²). The traps consisted of 50 × 50 × 20 cm PVC pipes covered entirely with a 1 mm mesh, with an entrance on one side (Figure S2). Traps were filled with crushed blue mussels as bait and deployed on the

bottom (1.5–2 m water depth) keeping a minimum distance of 1 m between traps (n = 5 traps). The traps were retrieved after 24 h. The two sampling methods were applied at the same location during the entire sampling period (Figure S1). After sampling, crabs were transported immediately to the near-by laboratory facilities of GEOMAR, Kiel, Germany, and kept in well aerated seawater. Samples obtained by the two sampling methods were pooled (Figures S3 and S4 for a detailed comparison of the results obtained with each sampling method) as this presumably reduced the bias from using only one of the sampling methods.

All sampled *H. takanoi* with a size (carapace width) larger than 5 mm were counted, sexed (based on their abdominal structure and claw morphology; after Asakura and Watanabae 2005), and ovigerous females were recorded. Reproductive season was determined as the period in which ovigerous females appeared in the population (Pinheiro and Fransozo 2002). Carapace width was measured using Vernier callipers to the nearest 0.1 mm, as the distance between the two second (middle) antero-lateral teeth (Mingkid et al. 2006a). Size classes were defined in 2 mm intervals, ranging from 5.1–7.0 to 27.1–29.0 mm. To study weight-size relationships, wet weight of collected individuals was recorded after blotting dry each crab with tissue paper to the nearest 0.001 g. For this, only crabs with complete and nearly equally sized appendages were used. Collected crabs were released into the Kiel Fjord after sampling and size measurements or used for the prey-size selection assays.

In addition to the biological samples, seawater temperature and salinity (WTW Cond 3110, Tetracon 325, Weilheim, Germany) were recorded weekly around midday at the monitoring site.

Prey-size selection assays

Adult males and females of *H. takanoi* (size-based definition: carapace width > 10 mm after Geburzi et al. 2015) were used in the assays. Males were measured and grouped into one of six size classes defined every 2 mm from 15.1–17.0 to 25.1–27.0 mm carapace width (n = 5 crabs for each class). Females were grouped into one of five size classes, from 11.1–13.0 to 19.1–21.0 mm carapace width (n = 5). Size classes used corresponded to those found in the field in the respective season. Crabs were then placed individually into covered transparent plastic aquaria (20 × 13 × 12 cm) filled with 1.5 l of aerated seawater. Experiments were conducted three times during the year with representative water temperatures of 8 ± 0.5 °C in early spring (starting 05/04/2017), 19 ± 0.5 °C in summer (starting 03/08/2017), and 13 ± 0.5 °C in early autumn (starting 07/10/2017), in constant temperature rooms of GEOMAR, Kiel, Germany.

All assays were run under LED light and a photoperiod of 12:12 h. Crabs were acclimated for a period of 5 days and fed daily with fresh mussel flesh. Crabs were starved for 7 days before the feeding assays in order to standardize

starvation levels (Elner and Hughes 1978; Jubb et al. 1983). All crabs used in the experiments had intact and equally grown claws. Because crabs stop feeding prior to moulting, and feed less while carrying eggs, ovigerous females as well as crabs that did not feed during the pre-experimental phase or moulted before or after the experiment, were excluded. Therefore, crabs were also monitored for moulting for a week after the feeding assay.

Individuals of *M. edulis* were collected by hand from the same site of crab collection, prior to each trial, and maintained in well aerated seawater under the same light and temperature conditions as the crabs. Only undamaged individuals were used as prey items. Mussels were cleaned from any epibionts prior to the experiment. The length of each mussel was measured to the nearest 0.1 mm using a Vernier calliper. Shell length was measured from the tip of the umbo to the edge of the margin at its greatest distance from the umbo. Mussels were then assigned into one of six size-classes defined every 3 mm from 3.1–6.0 to 18.1–21.0 mm. Each crab was offered 10 mussels of each size class. Since in a preliminary trial, none of the females were recorded opening mussels larger than 21.0 mm, the 18.1–21.0 mm size class was excluded in all female assays. After 24 h, shells of all mussels (eaten and non-eaten) were removed, tanks were cleaned and fresh seawater as well as new mussels were added. The assay lasted for 7 days. The mean number of each size class of mussels consumed by each size class of crabs was calculated for the overall experimental period.

In order to test for the effects of season and sex on the consumption rate, dry weights of mussels of all size classes consumed per day were calculated for males and females for spring, autumn and summer. Therefore, the number and shell length of mussels eaten by crabs were converted into dry weight. For this, a power function equation was calculated using data from Thomsen et al. (2013) to estimate the relationship between soft tissue dry weight and shell length of Kiel Fjord mussels (data obtained from Pangaea dataset: doi:10.1111/gcb.12109). Mean dry weight of mussels for the six size classes (3.1–21.0 mm) were 0.5, 2.3, 6.2, 12.8, 22.9, 37.2 mg, respectively. For consumed biomass, specific dry weight was multiplied with the number of eaten mussels in each size class.

To study the relation between crab size (carapace width) and claw height, crabs of both sexes, ranging in size from 11.5 to 20.2 mm, were used to calculate a claw height-crab size index (%):

$$\text{Claw height - crab size index \%} = \left(\frac{Mean\ claw\ height}{Mean\ carapace\ width} \times 100\right) \text{ (Equation 1).}$$

Previous measurements have shown that both left and right chela of *H. takanoi* have a monochealeous structure (i.e. claws of more or less similar shape and size). Thus, only the left claw height (mm) was measured as the highest vertical distance along the propodus.

Statistical analyses

Predefined functions from the *stats* package of the statistical software R (version 3.4.0, R Development Core Team 2016) were used to perform the analyses.

Based on the collected field data, descriptive bar-plots were produced to depict the size-class distribution and seasonal trends of abundance for males, females and ovigerous females. In addition, the carapace width to wet weight relationship was adjusted using a logarithmic transformation of the allometric growth equation:

$$\log \text{wet weight} = \log a + b \log \text{carapace width} \quad \text{(Equation 2).}$$

Where b is the slope and $\log a$ is the intercept of the regression. Differences in the allometric growth of males, females and ovigerous females were assessed by using an analysis of covariance (ANCOVA). Before the analysis, normality and homogeneity of variance assumptions were tested using Shapiro-Wilk and Fligner-Killeen tests, respectively. In the ANCOVA, log wet weight was included as response variable, while sex and log carapace width were included as explanatory variables. Potential changes in the slope of the partial regressions adjusted for each sex were expressed as the interaction between sex and log carapace width.

The effects of carapace width, sex and season on the consumption rate and total biomass of *M. edulis* consumed by *H. takanoi* were evaluated using generalized linear models (GLMs) with Gamma distribution and identity link function. The assumptions of GLMs were evaluated by a detailed visual inspection of the residuals' plots. Separated ANCOVA (see applied tests for evaluating normality and homogeneity of variances above) for males and females were used to analyse the main effects of season and carapace width, and their interactive effects, on the prey size preference of the crabs. In order to explain the observed differential capacity of males and females to open large mussels (see details in the Results), the relationship between claw height and carapace width was analysed for both sexes. The relationship for females was adjusted using a simple linear regression:

$$\text{Claw height} = a + b \text{ carapace width} \quad \text{(Equation 3).}$$

Where b is the slope and a is the intercept of the regression. For males, after unsuccessfully trying different non-linear functions, a segmented regression (package *segmented*; Muggeo 2017) was used. In addition, an ANCOVA (see the applied tests for evaluating normality and homogeneity of variances above), using only males and females in the range of sizes from 15.3–20.1 and 11.5–20.2 mm, respectively, was performed to evaluate the potential differential increase in claw height and carapace width in males over females.
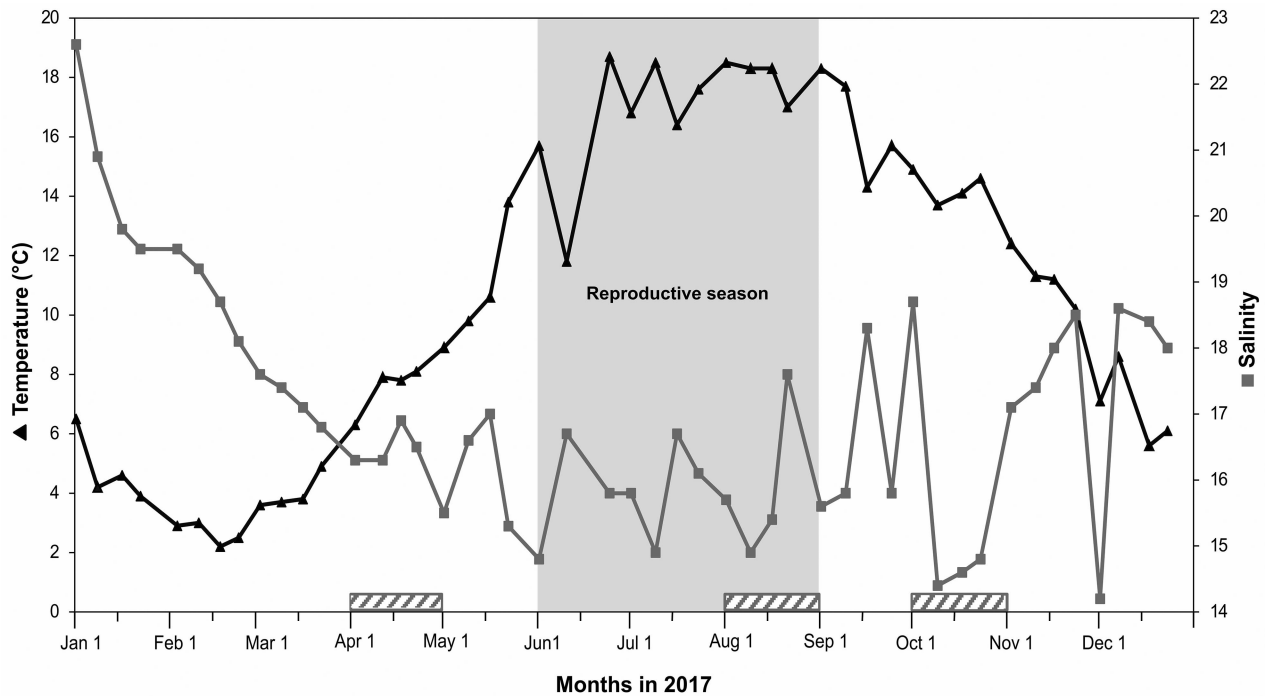
Figure 1. Kiel Fjord seawater temperature (°C; black triangle) and salinity (grey square) at a depth of 1 to 1.5 m during 2017. The grey shaded area indicates the reproductive season of *Hemigrapsus takanoi* (occurrence of ovigerous females) in the Kiel Fjord. The striped areas show when feeding assays were performed in spring (April), summer (August) and autumn (October).

Results

Field monitoring and crab sampling

Abiotic conditions, occurrence of *H. takanoi* and reproductive season

The study area is characterized by a strong seasonality. Seawater temperature varied between ~ 2 °C in mid-February and ~ 19 °C during June and August, while salinity varied between 14.2 and 22.6 (monthly extremes) with highest values in winter (Figure 1). Strongest changes occurred during early spring, with small-scale fluctuations in summer and autumn (Figure 1), reflecting the highly dynamic physical-chemical conditions at this site. A total of 596 individuals of *H. takanoi* were collected during the study period. Males represented 41% and females 59% of the total relative abundance. The sex ratio showed a dominance of females over males for most of the year, except for December (Figure 2A). During end of spring and beginning of summer, an increase in density of *H. takanoi* was recorded, with 17% (101 individuals) of the total counts recorded in June. The abundance declined towards winter reaching 1% of all counts in February. The reproductive seasons of *H. takanoi* started in early June, when ovigerous females were first observed, and ended in late August (Figure 1). A total of 106 ovigerous females was collected, representing 30% of the total female abundance registered over the entire year, with the highest abundance in July (48 individuals, 45% of the total of collected ovigerous females), when all females were found to be ovigerous (Figure 2A).
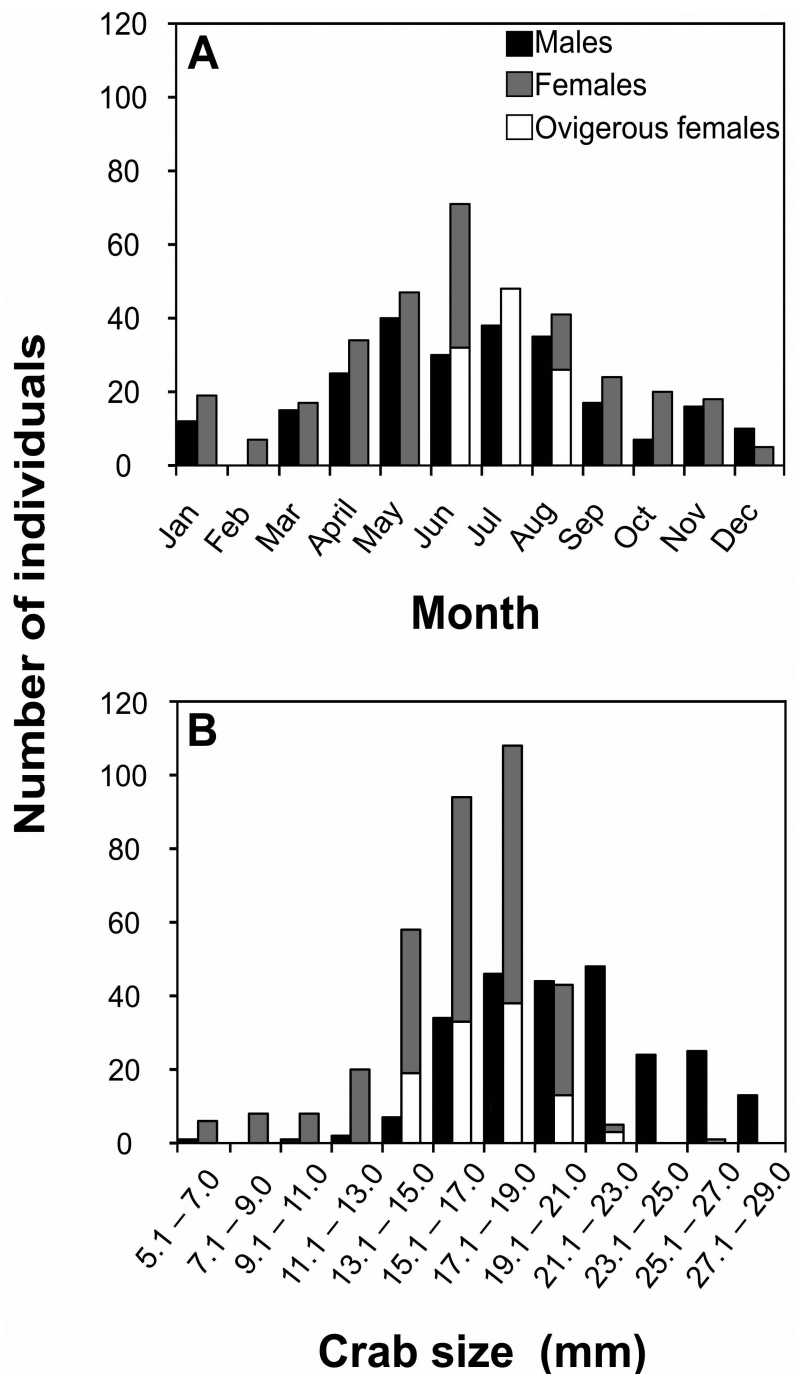
Figure 2. Relative abundance (A) and size (mm; B) of males (black), females (grey) and ovigerous females (white) of *Hemigrapsus takanoi*, sampled from January to December 2017 in the Kiel Fjord. Samples were obtained by scraping and traps (pooled in these plots).

<u>Biometric data of field-caught *H. takanoi*</u>

Smallest male crabs had a size of 6.5 mm and the largest individual a size of 29 mm. For females, the smallest and largest sizes were 5.5 and 25.5 mm, respectively. Smallest ovigerous females had a size of 13.5 mm, while the largest a size of 22.7 mm. Most ovigerous females were recorded in the size class 17.1–19.0 mm (38 individuals, 10.8% of all collected females; Figure 2B).

Differences in *H. takanoi* catches between the two sampling methods (scraping *vs.* traps) are illustrated in Figures S3 to S5. In general, the two

methods led to differences in both, numbers and sizes of crabs collected (Figures S3, S5). Scraping collected more females, while traps collected more males (Figure S3A, B). Scraping gathered more crabs and led to a better distribution of catches over the different size classes. Traps caught generally larger crabs compared to the scraping method. None of the small males (≤ 15.0 mm) and none of the large females or ovigerous females (≥ 21.1 mm) were collected by traps (Figures S3, S5).

The wet weight of crabs ranged from 0.11 to 11.41 g. There was a clear positive correlation between size and weight (males (n = 213): $R^2 = 0.91$, females (n = 234): $R^2 = 0.94$, ovigerous females (n = 100): $R^2 = 0.67$; Figure S6). Male crabs were heavier than both females and ovigerous females for a given size (ANCOVA: $F_{2,541} = 8.617$, $p < 0.001$; Table S1).

For individuals with sizes from 11.5 to 20.2 mm, a significant difference between claw height and size was observed between both sexes (ANCOVA: $F_{1,49} = 83.353$, $p < 0.001$; Table S2). Males had larger claws than females with a claw height-crab size index (39%) almost 2 times larger than that of females (21%). As shown by the segmented regression, the initial linear increase of claw height with body size for males reached a plateau (maximum claw height at about 9 mm) for individuals with a size larger than 20.5 mm (Figure S7). In the case of females, claw height increased linearly over the entire range of sizes registered (Figure S7). Considering only the range of sizes where both sexes overlap, the increase in claw height with body size was 3 times stronger for males than for females (Figure S7; Table S2).

Prey-size selection assays

Mussel size preference

When offering different size classes of mussels, *H. takanoi* males were recorded opening mussels of up to 18.1–21.0 mm during summer and autumn, while only mussels up to 15.1–18.0 mm were opened in spring (Figure 3A–C). In spring, no male crab fed on the smallest size class of mussels offered (3.1–6.0 mm). In contrast, all size classes of males opened the smallest mussels (3.1–6.0 mm) during summer and autumn, except for the largest size classes of crabs (21.1–23.0 and 25.1–27.0 mm) in autumn, in which crabs opened mussels larger than 6.1 mm (Figure 3A–C). All females opened mussels in the range of 3.1 to 12.0 mm, independently of their size and the season (Figure 3D, E). In general, female *H. takanoi* were not recorded opening mussels larger than 15 mm, and only females larger than 15.1 mm were recorded opening the largest mussels (12.1–15.0 mm; Figure 3D, E). Only small females of 11.0–13.1 mm failed to open mussels larger than 6.1–9.0 mm. Generally, crabs showed different optima in their mussel size class preference, depending on season and sex, which generally shifted towards larger mussel size classes with increasing crab size (Figure 3A–E).
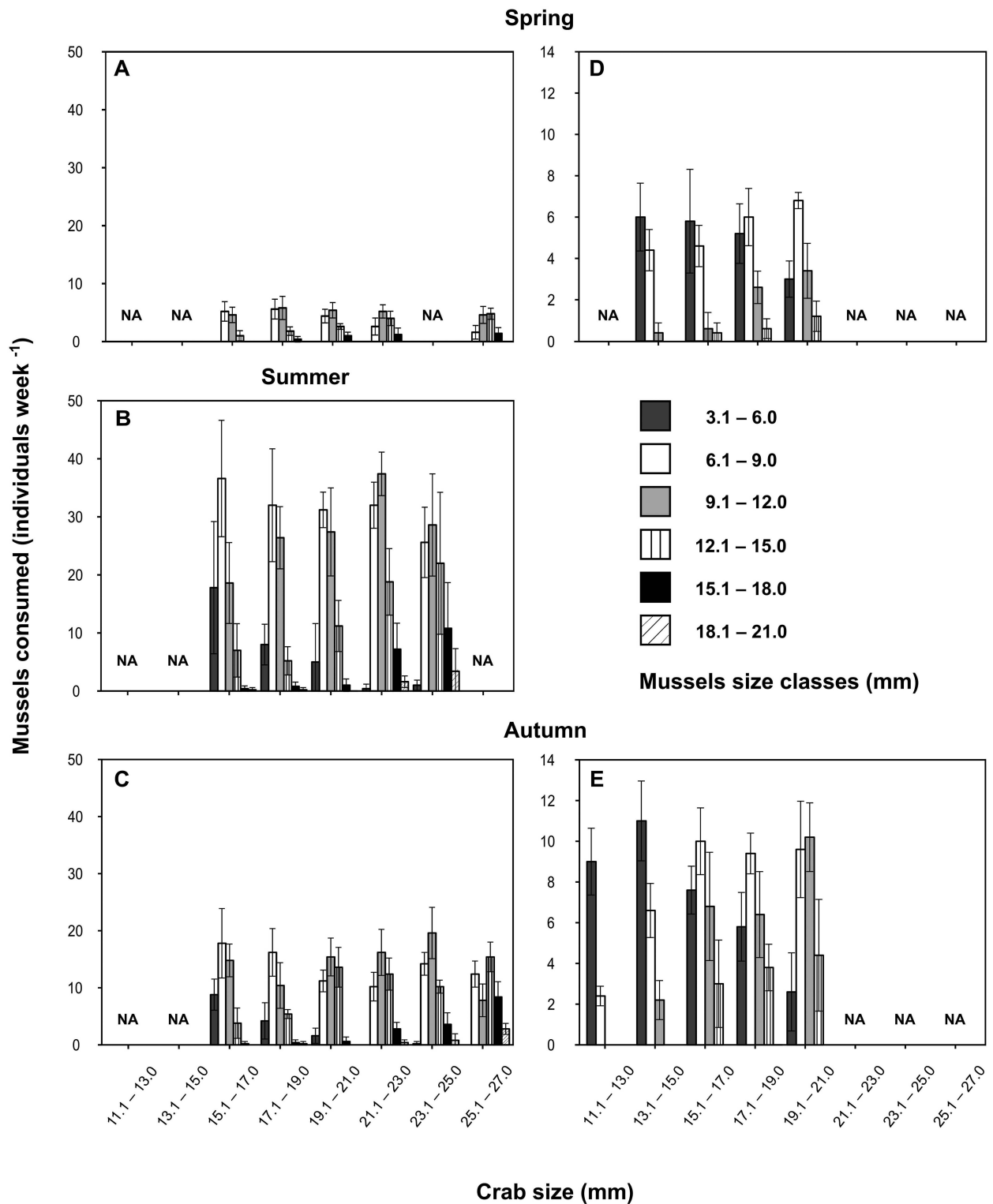
Figure 3. Mean consumption rates of mussels (*Mytilus edulis*) by different size classes of males (A, B and C) and females (D and E) of *Hemigrapsus takanoi* in different seasons (sums over 7 days). NA indicates size classes of crabs not found in the field when feeding assays were performed. Note that preferred mussel size classes can be observed within separate crab size classes. Error bars represent 95% confidence intervals.

The relation between *H. takanoi* size and shell length of mussels consumed showed that the chosen prey size increases with predator size (Figure 4A, B). The interaction effects between season and crab sizes showed no significant differences in the size of mussels opened by males in
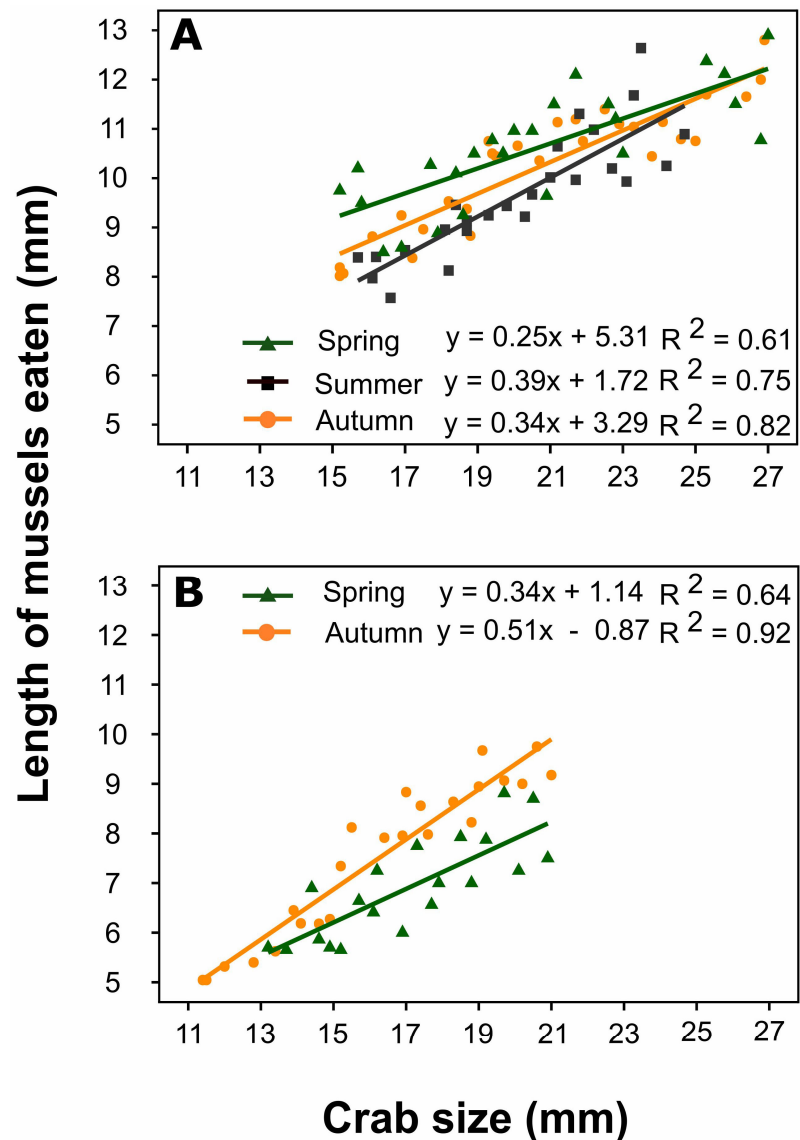
Figure 4. Relation between the mean length of mussels consumed and crab size for males (A) and females (B) of *Hemigrapsus takanoi* in different seasons (spring: green triangles, summer: black squares, autumn: orange circles). The slopes of all adjusted regressions were significantly different from zero. See statistical details in Table 1.

Table 1. Analysis of covariance (ANCOVA) testing the main and interactive effects of season and crab size on the length (mm) of *Mytilus edulis* eaten by males and females of *Hemigrapsus takanoi*. Significant results ($p \leq 0.05$) are highlighted in bold.

Dependent variable	Source of variation	SS	df	MS	F-value	p-value
Mussel length consumed by males	Season	11.972	2	5.986	14.033	**< 0.001**
	Crab size	88.942	1	88.942	208.505	**< 0.001**
	Season: Crab size	2.499	2	1.25	2.929	0.059
	Error	31.566	74	0.427		
Mussel length consumed by females	Season	2.975	1	2.975	10.264	**0.002**
	Crab size	66.873	1	66.873	230.694	**< 0.001**
	Season: Crab size	2.183	1	2.183	7.529	**0.008**
	Error	11.885	41	0.29		

the different seasons (ANCOVA: $F_{2,74} = 2.929$, $p = 0.059$; Figure 4A; Table 1). However, the slope of the regression for females in autumn was significantly higher than that for females in spring (ANCOVA: $F_{1,41} = 7.529$, $p = 0.008$; Figure 4B; Table 1).

Table 2. Generalized linear models (GLMs) testing the main and interactive effects of season and crab size on the dry biomass of *Mytilus edulis* daily eaten by males and females of *Hemigrapsus takanoi*. Significant results (p ≤ 0.05) are highlighted in bold.

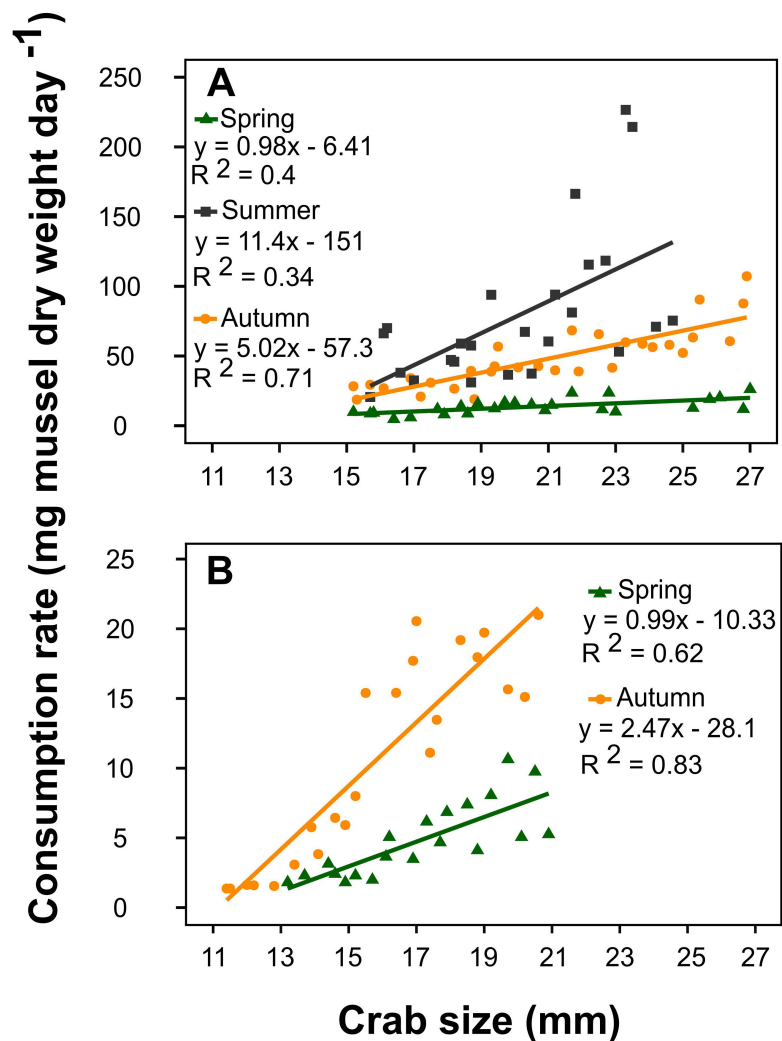| Dependent variable	Source of variation	SS	df	F-value	p-value
Mussels consumed by males	Season	29.277	2	116.173	**< 0.001**
	Crab size	4.750	1	37.702	**< 0.001**
	Season: Crab size	4.823	2	19.141	**< 0.001**
Mussels consumed by females	Season	5.939	1	56.599	**< 0.001**
	Crab size	15.520	1	147.917	**< 0.001**
	Season: Crab size	4.604	1	43.909	**< 0.001**

Figure 5. Dry weight of mussels eaten per day by males (**A**) and females (**B**) of *Hemigrapsus takanoi* in different seasons (spring: green triangles, summer: black squares, autumn: orange circles). The slopes of all adjusted regressions were significantly different from zero. See statistical details in Table 2.

Effects of season and sex on consumption rates

Seasonality (and/or temperature) significantly affected consumption rates for both sexes (p < 0.001; Table 2). Mussels (biomass) were more consumed in warmer than in colder seasons (see the statistic of GLMs in Table 2; Figure 5A, B). Comparing only similar size classes of crabs over the different seasons, feeding rates of males (15.1–23.0 mm) were 2 and almost 6 times higher in summer (mean ± SD, 66 ± 1.773 mg day^{-1}) than in autumn

(37 ± 6 mg day^{-1}) and spring (12 ± 2 mg day^{-1}), respectively. Feeding rates in autumn were 3 times higher than in spring. In addition, 3 times more mussel biomass was consumed by female crabs (13.1–21.0 mm) in autumn (14 ± 3 mg day^{-1}) than in spring (4 ± 1 mg day^{-1}). The interaction between season and crab size was statistically significant for both sexes (see statistics of GLMs Table 2). In addition, sex significantly affected feeding rates of crabs (p < 0.001; Table S3). When comparing male and female individuals of 15.1–21.0 mm in size, twice as much mussel biomass was consumed by males compared to females. Males consumed 33 ± 5 (mean ± SD) mg day^{-1} in spring and 12 ± 2 mg day^{-1} in autumn, while females consumed 5 ± 1 mg day^{-1} during spring and 17 ± 2 mg day^{-1} during autumn (see statistics of GLMs in Table S3; Figure S8A, B).

Discussion

This study aimed at elucidating the potential impact of the recent invader *H. takanoi* on a mussel-dominated benthic ecosystem, the Kiel Fjord, by describing its current relative field abundance and assessing the seasonality-dependent feeding pressure in laboratory-based experiments. Feeding rates were closely linked to season, likely due to seawater temperatures, and interrupted by the reproductive season in female individuals. Even though females were generally more abundant, males may have a stronger impact on the ecosystem as *per capita* feeding rates of males strongly exceeded those of females.

Kiel Fjord H. takanoi *exhibited a shortened reproductive season*

Female *H. takanoi* reached sexual maturity at a size (carapace width) of about 13.5 mm. Nevertheless, egg-carrying females as small as 10.2 mm were found in the Kiel Fjord during summer 2014 (Geburzi et al. 2015), which may be attributed to an unusual warm summer recorded during this particular year (see supplementary in Pansch et al. 2018; Pansch and Hiebenthal 2019), which might have led to early maturation at a smaller size in this non-native *H. takanoi* population. Long-term monitoring data, however, will be needed in order to correlate size at sexual maturity (and/or breeding season) with annual temperatures.

The duration of the reproductive period in brachyuran crabs may depend on latitude, and/or be related with seawater temperatures (McDermott 1998; Brousseau and McSweeney 2016). Ovigerous females were found in the Kiel Fjord over a period of three months, while in the native range the reproductive season lasts six months (Miyajima et al. 2012), and five months in the Dutch delta (van den Brink et al. 2013). In agreement with our study (with mean temperature of 15.4 °C), however, ovigerous females from the Oosterschelde estuary, Netherlands, have been observed in seawater temperatures above 15 °C (van den Brink et al. 2013). Consequently, the

H. takanoi population from the Kiel Fjord might be constrained by low-salinity stress, which may compress their breeding season.

Generally, egg production and successful embryonic and larval development of many Baltic Sea invertebrates (Kinne 1971), and in particular brachyuran crabs (Otto and Brandis 2011), decreases drastically with decreasing salinity. In the Kiel Fjord, salinities can be as low as 12 (Nasrolahi et al. 2016) compared to native and non-native habitats of *H. takanoi* populations with often much higher salinity regimes (Shinji et al. 2009; van den Brink et al. 2013; Wood et al. 2015; Ashelby et al. 2017). Ovigerous *H. takanoi* from Kiel Fjord were found in salinities down to 14.8, suggesting the capacity to successfully reproduce in these salinities. Despite the occurrence of ovigerous females at lower salinities, successful larval development from megalopae to juveniles required salinities higher than 25 in the native range of *H. takanoi* (Mingkid et al. 2006b). This may suggest that Kiel Fjord *H. takanoi* have already adapted to the prevailing environmental conditions.

While H. takanoi *females were more abundant, males reached a larger biomass*

In the Kiel Fjord, the observed sex ratio (1.4 females to 1 male) is in contrast to similar studies from non-native ranges in Europe, which recorded almost equal sexes abundance for this species (Noël et al. 1997; Dauvin et al. 2009), albeit using different methods and a shorter sampling duration (two months *vs.* twelve months in the present study; Dauvin et al. 2009).

Overall, males reached larger sizes than females, likely explained by differential reproductive and energy demands between sexes (Angeletti and Cervellini 2015). Larger body size increases the success rate in intra-specific competition, courtship, handling as well as protection of females during copulation (Araújo et al. 2012). Individuals' weight increased with size for both sexes, but males were heavier than females at a given size, being a well-known pattern in brachyuran crabs (Saher et al. 2016; Glamuzina et al. 2017).

Mussel size preference and overall energy uptake differed between sexes of H. takanoi

According to the optimal foraging theory, predators choose their diet to maximize the net rate of energy intake per unit foraging time (Emlen 1968; Charnov 1976; Elner and Hughes 1978; Hughes 1979), assuming that predators are able to rank prey in order of their profitability (Enderlein et al. 2003). Males of *H. takanoi* from Kiel Fjord (15 to 27 mm carapace width), opened a broad range of *M. edulis* individuals with shell lengths between 3 and 21 mm. Females of slightly smaller size (11 to 21 mm) were restricted to smaller mussels (3 to 15 mm). Generally, optimal sizes were

recorded around 6 to 15 mm and 3 to 12 mm, for males and females respectively. Males of *H. takanoi* (20–27 mm) from the native range (Japan) preferred to crush mussels (*Xenostrobus securis*) of 10 to 17 mm size, although these were occasionally found to open mussels up to 27 mm (Doi et al. 2009), as also observed in Kiel Fjord males. Smaller males (< 20 mm) preferred mussels between 5 and 12 mm while they were able to crush mussels of up to 17 mm (Doi et al. 2009).

Significant differences were present between sexes during autumn and spring, when males showed much higher feeding rates (energy uptake) than females. Elner (1980) explained this difference between sexes in *C. maenas* in the way that females rely more on other prey types than mussels. However, this aspect was not addressed within the present study. Claw size (propal height or gape) plays a critical role in prey size selection between crabs of similar sizes and/or weights (Yamada and Boulding 1998). In the present study, males of *H. takanoi* exhibited significantly larger claws than females of same sizes. Consequently, males of *H. takanoi* can feed on larger mussels than females of the same body size.

Seasonal temperature shifts determined feeding rates of H. takanoi

Feeding rates (and partly preferred prey size classes) for males and females of *H. takanoi* changed strongly with season. This might be directly linked to prevailing seawater temperatures during respective seasons when the assays were conducted, being highest in late summer (~ 19 °C) and early autumn (~ 13 °C), and lowest in spring (~ 8 °C). Observed increased feeding at higher temperatures has been described for other crustaceans as well. For example, *C. maenas* consumed about twice as much food at 24 °C than at 10 °C (0.2 times increased food uptake per °C; Wallace 1973). Moreover, consumption rates of *C. maenas* upon the cockle *Cerastoderma edule* increased by about 4-fold with increasing temperatures from 9.5 to 15.5 °C (0.6 times increasased food uptake per °C; Sanchez-Salazar et al. 1987). This shows the direct influence of seasonal temperature changes on feeding behaviour of crabs, which is likely related to increased metabolic rates and behavioural activity at warmer conditions (Thomas et al. 2000; Kemp and Britz 2008; Wang et al. 2016).

Interestingly, similar to *C. maenas* (Elner 1980; Sanchez-Salazar et al. 1987), equally-sized males of *H. takanoi* were unaffected by temperature and/or season when choosing their prey. In contrast, prey preference in females of equal sizes was significantly different between seasons. Females during spring chose to open smaller mussels than females of the same size in autumn. Female crabs require large amounts of energy to produce their eggs (Ruiz-Tagle et al. 2002). Presumably, females needed to accumulate energy during spring for the upcoming reproductive investment.

Possible ecological consequences

Overall, our data demonstrate that *H. takanoi* is an important predator particularly on small individuals of *M. edulis*, and especially so during the warmer seasons. Mussel recruitment occurs mainly from the end of May to September (Thomsen et al. 2010), with high biomass accretion during summer in this eutrophic area (Thomsen et al. 2013). However, growth of *M. edulis* is reduced in the presence of its two main predators: the green crab *C. maenas* and the sea star *A. rubens* (Dobretsov and Wahl 2001), and likely also in the presence of the recent invader *H. takanoi*, at the observed high abundances.

Adults of *C. maenas* in the western Baltic Sea show a preference for mussels smaller than 40 mm (Enderlein et al. 2003). Adults of *A. rubens* prey on mussels smaller than 33 mm in Kiel Fjord (Reusch and Chapman 1997). While in the Wadden Sea, *H. takanoi* and *C. maenas* individuals of the same size were recently shown to prey upon similar sized mussel prey (David Thieltges *personal communication*), *H. takanoi* exerts a significant pressure on smaller mussels (< 15 mm shell length) in the Kiel Fjord area. In turn, this might affect *M. edulis* recruitment patterns in the future. Once mussels reach a size of approximately 20 mm in the Kiel Fjord, they might be too large for *H. takanoi*, but continuing to be within the predation window of adult *C. maenas* or *A. rubens*. To what extent this pressure on smaller prey size will affect recruitment dynamics remains to be investigated by experimental and field studies on early post-settlement *M. edulis* individuals smaller than those examined in the present study. The results presented provide the first insights towards an understanding of the effects of *H. takanoi* predation on Western Baltic Sea mussel beds. Still, it remains to be addressed by what extent *H. takanoi* can further populate the Baltic proper. Adults and juveniles can tolerate salinities as low as 7 to 9 (Mingkid et al. 2006a; Gittenberger et al. 2010; Soors et al. 2010), and abrupt short-term changes in salinity regimes are not stressful to adult *H. takanoi*, unless salinities reach freshwater conditions (Shinji et al. 2009). This is considered an advantage to its invasion success and it is assumed that their current distribution is rather limited by cold temperature, not by low salinities (van den Brink et al. 2013). In contrast, higher salinities are required for *H. takanoi* larvae to develop (Mingkid et al. 2006b), and knowledge on the salinity tolerance of all life-history stages of Baltic Sea populations is needed to understand *H. takanoi's* invasion potential into the wider Baltic Sea.

Conclusions

Despite strong differences in feeding rates between males and females of *H. takanoi*, and a clear difference in prey size selection, *H. takanoi* will likely have a persistent impact on Western Baltic Sea mussel populations, with likely implications for mussel-associated communities (Koivisto and Westernbom

2012). The direct interactions with *C. maenas* and *A. rubens* and resulting changes in feeding pressure on mussel beds are not yet understood. The presence of *H. takanoi* will, however, most certainly increase predation pressure on small-sized mussels, with potential consequences for overall population dynamics. Clearly, the breeding season of Kiel Fjord *H. takanoi* is constrained, likely related to the prevailing seawater temperatures and/or the low-salinity regime. Therefore, a further spread of *H. takanoi* into the wider Baltic Proper might be restricted by low salinity, but be supported by favourable biological traits for dispersal (i.e. high fecundity, storing sperm for several broods, and high dispersal), all of which contribute to the overall invasion success of this species (Weis 2010). As both sexes recorded higher consumption rates in warmer temperatures, the impacts on the ecosystems as well as a potentially on-going invasion process will likely be favoured by future local and global warming trends.

Acknowledgements

Author contributions

OMN, MS and CP designed the study. OMN and SML performed the sampling and run the experiments. OMN, FRB, SML, MS and CP analysed and visualized the data. OMN, FRB, MS and CP wrote the manuscript. All co-authors contributed to the final draft of the manuscript.

Data availability

Data used in the present study are available at PANGAEA: https://doi.org/10.1594/PANGAEA. 905576

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Supplementary material

The following supplementary material is available for this article:

Table S1. Summary of the ANCOVA table showing the main and interactive effects of sex and carapace width on the body weight of males, females and ovigerous females of *Hemigrapsus takanoi*.

Table S2. Summary of the ANCOVA table showing the main and interactive effects of sex and carapace width on the claw height of males and females of *Hemigrapsus takanoi*.

Table S3. Generalized linear models (GLMs) testing the main and interactive effects of sex and crab size on the dry biomass of *Mytilus edulis* daily consumed by males and females of *Hemigrapsus takanoi* in spring and autumn.

Figure S1. Sampling site in the Kiel Fjord from which all *Hemigrapsus takanoi* individuals were collected during the sampling campaign in 2017 and for the feeding assays.

Figure S2. Trap design for catching crabs, consisting of 50 × 50 × 20 cm PVC pipes covered entirely with a 1 mm mesh, allowing mussel predators to enter on both sides.

Figure S3. Relative abundance and size for males, females and ovigerous females of *Hemigrapsus takanoi* collected by scraping and using traps in the Kiel Fjord during 2017.

Figure S4. Size class (mm) distribution of males, females and ovigerous females of *Hemigrapsus takanoi* collected in the Kiel Fjord during 2017.

Figure S5. Size class (mm) distribution of males, females and ovigerous females of *Hemigrapsus takanoi* collected by scraping and using traps in the Kiel Fjord during 2017.

Figure S6. Relationship between size (carapace width) and wet weight of males, females and ovigerous females of *Hemigrapsus takanoi* caught in the Kiel Fjord during 2017.

Figure S7. Relationship between size and claw height of males and females of *Hemigrapsus takanoi* caught in the Kiel Fjord during 2017.

Figure S8. Dry weight of mussels consumed per day by males and females of *Hemigrapsus takanoi* in spring and autumn.

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