Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Prey size selection in invasive (*Hemigrapsus sanguineus* and *H. takanoi*) compared with native (*Carcinus maenas*) marine crabs

Mark M. Bouwmeester[1], Andreas M. Waser[1], Jaap van der Meer[1] and David W. Thieltges[1]

[1]Department of Coastal Systems, NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, Den Burg, The Netherlands

Original Article

Cite this article: Bouwmeester MM, Waser AM, van der Meer J, Thieltges DW (2020). Prey size selection in invasive (*Hemigrapsus sanguineus* and *H. takanoi*) compared with native (*Carcinus maenas*) marine crabs. *Journal of the Marine Biological Association of the United Kingdom* **100**, 73–77. https://doi.org/10.1017/S0025315419000985

Received: 24 April 2019
Revised: 26 September 2019
Accepted: 17 October 2019
First published online: 20 November 2019

Key words:
Invasive species; predator–prey interactions; prey size selection

Author for correspondence:
David W. Thieltges, E-mail: David.Thieltges@nioz.nl

Abstract

Introductions of predators can have strong effects on native ecosystems and knowledge of the prey size selection of invasive predators is pivotal to understand their impact on native prey and intraguild competitors. Here, we investigated the prey size selection of two invasive crabs (*Hemigrapsus sanguineus* and *Hemigrapsus takanoi*) recently invading European coasts and compared them with native shore crabs (*Carcinus maenas*) which are known to feed on similar prey species. In laboratory experiments, we offered different size classes of native blue mussels (*Mytilus edulis*) to different size classes of the crab species in an effort to identify the respective prey size preferences and potential overlap in prey size range of native and invasive crabs. In all three species, the preferred prey size increased with crab size reflecting general predator–prey size relationships. Prey size preference did not differ among the crab species, i.e. crabs showed similar mussel size preference in relation to carapace width. Given that additional morphological measurements showed that both of the invasive crab species have much larger claws relative to their body size compared with the native species, this finding was surprising and may relate to differential claw morphologies or structural strength. These results suggest that the invasive crabs exert predation pressure on the same size classes of native mussels as the native crabs, with potential effects on mussel population dynamics due to the high densities of the invaders. In addition, the overlap in prey size range is likely to result in resource competition between invasive and native crabs.

Introduction

Biological invasions are well recognised as one of the major drivers behind rapid ecological change worldwide (Pyšek & Richardson, 2010; Lowry *et al.*, 2013) and have in many cases led to vast impacts in recipient ecosystems (Asner & Vitousek, 2005; Ehrenfeld, 2010; Simberloff, 2011). The introduction of predators can have particularly devastating consequences (Clavero & García-Berthou, 2005; Ricciardi *et al.*, 2013; Doherty *et al.*, 2016). In general, the impact of an invasive predator on native prey will depend on its prey species range (i.e. the number of different species preyed upon), with generalist predators likely affecting a wider range of prey species than specialist predators. Predation impacts can further be expected to differ among life-history stages and size classes within specific prey species as predators typically show prey size preference depending on their own body size (Brose *et al.*, 2006; Brose, 2010). Apart from directly affecting native prey species, invasive predators may also indirectly affect native predators when prey spectra and preferred prey size ranges overlap, thus leading to inter-specific competition between native and invasive predators in invaded food webs (David *et al.*, 2017). Knowledge of the prey species range and prey size preferences of invasive predators and the identification of potential overlap of both with native competitors is thus pivotal in understanding the impacts of invasive predators on native communities.

In marine ecosystems, decapod crabs are among the most prominent invasive predators, often causing strong effects on recipient communities (Brockerhoff & McLay, 2011; Kotta *et al.*, 2018; Swart *et al.*, 2018). Arguably best studied in this respect is the invasion of European shore crabs (*Carcinus maenas*) along North American shores, where experimental work over the last decades has identified an overlap of the prey species spectrum and prey size preferences with native and other invasive crabs, with subsequent diverse effects on the invaded marine communities (see review by Klassen & Locke, 2007). In the native range of shore crabs in Europe, two species of Asian shore crabs (*Hemigrapsus sanguineus* and *Hemigrapsus takanoi*) have recently invaded coastal areas and now overlap in distribution and habitat with native shore crabs. The species were first sighted along the coast of northern France and in the south of the Netherlands around the turn of the century (Breton *et al.*, 2002; D'Udekem D'Acoz & Faasse, 2002; Dauvin *et al.*, 2009). Since then, both species have spread along the European coast and are currently found from Sweden to France (Dauvin *et al.*, 2009; Jungblut *et al.*, 2017). The invaders seem to be displacing native shore crabs *Carcinus maenas* and are now the dominant crab species at many coasts, with *H. takanoi* occurring in areas of low hydrodynamics while *H. sanguineus* can also be found in areas affected by stronger currents and hydrodynamics (Dauvin *et al.*, 2009; Van den Brink *et al.*, 2012). Research from North America, where *H. sanguineus* and *C. maenas* are both invasive, indicates that the general prey spectrum overlaps, with both species feeding on mussels and other invertebrates as well as algae (Klassen, 2012; Epifanio, 2013). In addition, American studies show that the prey size ranges of the crab species overlap, resulting in competition between the species (Ropes, 1968; Griffen *et al.*, 2008, 2012). In contrast, very limited data on prey range and prey size selection in invasive *Hemigrapsus* spp. compared with their native counterparts (*C. maenas*) exist from European coastal habitats (Epifanio, 2013). Like in America, the prey spectrum of the species seems to overlap, with invasive and native crabs being omnivores feeding on mussels, other invertebrates as well as on carrion and occasionally algae (Raffaelli *et al.*, 1989; Baeta *et al.*, 2006; Jungblut *et al.*, 2018). However, to date no studies exist on the prey size selection of invasive *Hemigrapsus* spp. crabs and whether there is an overlap with the prey size preferences of native crabs.

In this study, we investigated the prey size selection of the two invasive Asian crabs *H. sanguineus* and *H. takanoi* compared with native *C. maenas* in Europe. In laboratory experiments, we offered different size classes of blue mussel (*Mytilus edulis*) prey to different size classes of the crab species in an effort to identify the respective prey size preferences and potential overlap in prey size range between invasive and native crabs. In addition, we measured claw length and width of the different crab species to quantify difference in claw morphology among the three species. As the invasive crabs have relatively larger claws, we expected *Hemigrapsus* spp. to prefer larger prey than native *C. maenas* crabs of similar body size. Our experimental results contribute to the understanding of the impact of Asian shore crabs on native prey and potential competition with native crabs in European coastal waters.

Materials and methods

Sources of experimental organisms

The Asian shore crabs *Hemigrapsus sanguineus* and *Hemigrapsus takanoi* occur sympatrically with native shore crabs *Carcinus maenas* at coastal waters around the Dutch Wadden Sea island of Texel (Goedknegt *et al.*, 2017). Crabs of all three species were collected from the southern coast of Texel with baited traps and by hand in autumn 2017. Specimens were housed in aerated tanks and water was exchanged regularly. Crabs were fed a combination of blue mussels (*Mytilus edulis*), herring pieces and sea lettuce *ad libitum*. Juvenile blue mussels *M. edulis* were collected from groynes on the west coast of Texel in autumn 2017. If present, epifauna was carefully removed and mussels were then housed in aerated flow-through aquaria and fed with algae suspension (GroTech Plankto Marine P). All aquaria (crabs and mussels) were exposed to a 12-h photoperiod at ~16°C room temperature.

Experimental design

For the experiment, only males with intact claws were used because of the morphological differences between male and female crabs, as well as possible differences in foraging behaviour between the two sexes (Klassen, 2012). Using male crabs only is common practice in crab feeding experiments (e.g. Elner & Hughes, 1978; Smallegange *et al.*, 2006, Griffen *et al.*, 2008) and because we were only interested in differences between species and not between sexes, we also used male crabs exclusively. The carapace width of each crab was measured using callipers and crabs were assigned to one of the predetermined size classes which differed for each species based on the fact that *C. maenas* can reach a substantially larger size than either *Hemigrapsus* species. For *C. maenas* the size classes were: 12–15, 22–25, 32–35, 42–45 and 52–55 mm; for *H. sanguineus*: 12–15, 17–20, 22–25, 27–30 and 32–35 mm; and for *H. takanoi*: 12–15, 17–20, 22–25 mm (no larger individuals were found at the sampling locations). The maximum shell length of mussels to be served as prey to the crabs was measured using callipers and mussels were assigned to one of six size classes: 2–5, 7–10, 12–15, 17–20, 22–25 and 27–30 mm. Feeding trials were conducted in clear plastic tanks (21 × 13 × 12.5 cm) with opaque side walls. The tanks were filled up to 8 cm with filtered seawater and an air stone was added to each tank for aeration. We did not add structural elements such as larger mussels or oysters to mimic natural habitats to avoid confounding effects of mussel prey hiding behaviour on crab prey size selection. In addition, the lack of structural elements facilitated experimental handling (i.e. easier assessment of prey remains). A single crab of each species and size class was randomly added to each tank. Before adding a crab, its carapace width was measured. Tanks were covered with a lid to prevent crabs from climbing out via the aeration tubes. All crabs were introduced the day before the trial and were starved for 24 h prior to the start of the experiment to standardize hunger levels.

Due to logistical constraints, the experiment was conducted in two separate runs (2 and 3 replicates per crab size category, respectively) with two days in between. On the morning of each run the lids and air stones were removed to provide the observers a clear view into the tanks. The feeding trials began upon introduction of the prey. Five mussels of each size class (30 mussels in total) were added to each tank. Every 20 min we checked how many mussels had been consumed. When a crab had consumed ~50% of the available mussels, the trial was terminated for that tank by carefully removing the crab, as not to disturb the other crabs which still had not fed on approximately 50% of the mussels. The experiment was ended after 17 h (day 1) or 19 h (day 2) for all tanks in which the crabs had not yet eaten ~50% of the mussels. After the end of the trials, the surviving mussels were counted and the number of mussels consumed per size class was recorded.

Additional claw measurements

In order to quantify the relationship between claw size and body size in native and invasive crabs, we measured the carapace width and the claw (chelae) length and width of both claws using callipers for 30 additional individuals of *C. maenas*, *H. sanguineus* and *H. takanoi.*

Statistical analysis

Based on the number of mussels consumed per size class, we calculated a preference index for each individual crab using the following formula:

$$\mathrm{Pi} = \frac{\begin{array}{c}(n_1 \times 3.5\,\mathrm{mm}) + (n_2 \times 8.5\,\mathrm{mm}) + (n_3 \times 13.5\,\mathrm{mm}) \\ + (n_4 \times 18.5\,\mathrm{mm}) + (n_5 \times 23.5\,\mathrm{mm}) + (n_6 \times 28.5\,\mathrm{mm})\end{array}}{n_t} \tag{1}$$

Where Pi is the preference index score, n_a is the number of mussels eaten for size class a and n_t is the number of mussels eaten in total. The median mussel size per size class was used for each size category to allow for an intuitive understanding of the preference index score.

To investigate the relationship between crab body size and prey size preference index as well as to identify potential differences among the crab species, we used an ANCOVA approach, with crab species as fixed factor (3 levels) and crab carapace width as covariate (preliminary tests revealed no difference between the two runs so that a block factor was omitted). Likewise, the relationship between carapace width and claw size of the major claw (the larger chela of each individual's pair) was analysed using an ANCOVA framework. In both cases, we first tested for homogeneity of slopes. If the interaction term (crab species:crab size) was not significant, we dropped the interaction term and re-ran the analyses to derive at the minimum adequate model. Assumptions for all statistical analyses were inspected visually. All data analyses were performed using the R platform (R Core Team, 2017).

Results

Prey size preference

Out of the 65 crabs used for the experiments, four individuals (one *C. maenas* (32–35 mm), one *H. takanoi* (22–25 mm) and two *H. sanguineus* (22–25 and 27–30 mm)) did not consume any mussels at all and were thus excluded from the analysis. Although the prey size preference of *H. takanoi* appeared to increase more steeply with prey size than in the other two species (Figure 1), the slopes of all three species did not significantly differ (no significant interaction term; $P = 0.133$). In the minimum adequate model after dropping the insignificant interaction term, the preference index score of crabs was significantly positively correlated with crab carapace width in all three crab species (Figure 1; Table 1). In contrast, there was no significant difference in preference index among the crab species (Table 1; Figure 1). For raw data see Bouwmeester *et al.* (2019).

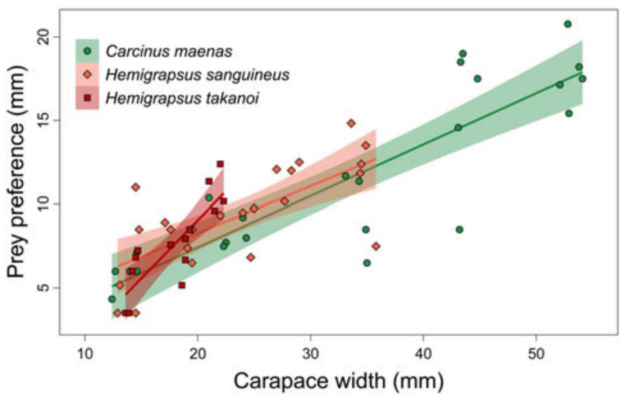

Fig. 1. Prey preference (mm) of invasive (*Hemigrapsus sanguineus* and *H. takanoi*) and native (*Carcinus maenas*) crabs in relation to crab carapace width (mm) in laboratory experiments offering five size classes of blue mussel (*Mytilus edulis*) prey to each crab. N = 5 replicates per crab size class. The shaded areas denote the 95% confidence intervals.

Table 1. Minimum adequate model after omission of the insignificant interaction term (species:crab size; $P = 0.133$) in the ANCOVA of the comparisons of prey preference index scores among crab species (invasive *Hemigrapsus sanguineus* and *H. takanoi*, and native *Carcinus maenas*), depending on the covariate crab size (carapace width)

Preference index	df	MS	*F*	*P*
Species	2	3.57	0.69	0.506
Crab size	1		118.81	<0.001

N = 5 replicates per crab species per crab size class.

Relative claw sizes

In all three crab species, claw length and width were significantly positively correlated with crab carapace width (Figure 2; Table 2). However, the intercept significantly differed among the three species, with both invasive crabs (*H. sanguineus* and *H. takanoi*) having much longer and wider claws in comparison with native *C. maenas* crabs of similar size (Figure 2; Table 2). In addition, the slopes were also significantly steeper in the invasive crabs compared with the native crabs as indicated by the significant interaction term (Figure 2; Table 2). For raw data see Bouwmeester *et al.* (2019).

Discussion

In contrast to our expectation based on morphological features, all three species of crabs showed similar mussel size preference in relation to carapace width. Given that our morphological measurements showed that both invasive crabs have much larger claws relative to their body size compared with the native *C. maenas*, this finding is surprising. Studies on crab predation have generally shown a strong link between claw size or claw morphology and preferred prey size (Elner, 1980; Sanchez-Salazar *et al.*, 1987; Mascaró & Seed, 2000) making it likely that the invasive crabs are more capable of opening larger mussels at a given crab size than the native crabs. The fact that they prefer relatively smaller mussels might stem from other differences in claw morphology and mechanics as well as related behavioural techniques (Elner, 1978) that further affect prey selection. According to this, it has previously been suggested that the slender claws of *C. maenas* may be better suited for opening bivalve shells than the more cumbersome claws of *Hemigrapsus* spp. (Jensen *et al.*, 2002). An alternative explanation could be that the claws of the invasive crabs are less sturdy than the ones of native crabs. Crabs are known to minimize the risk of claw damage by avoiding prey sizes that may inflict injuries during handling as this would have severe fitness consequences (Juanes, 1992; Smallegange & Van der Meer, 2003; Smallegange *et al.*, 2008). Hence, the relatively smaller prey sizes preferred by the invasive crabs may point to a higher relative vulnerability of their claws compared with the native crabs. Interestingly, *H. takanoi* in its native range in Japan shows a steeper increase in the maximum mussel size consumed by crabs with an increase in crab size compared with introduced Mediterranean *Carcinus aestuarii*, which has a very similar morphology compared with *C. maenas* (Doi *et al.*, 2009). This pattern of a steeper slope in *H. takanoi* resembles the pattern observed in our study (although it was not statistically significant). Further experiments with larger *H. takanoi*, which were not available in our study area and thus limit our inference, are needed to investigate potential differences in prey preference between the two *Hemigrapsus* species. In addition, more research into the mechanics of predation by the invasive crabs and their risk of claw damage in relation to native crabs would be insightful.

Our findings of similar mussel size preferences of the invasive and native crabs and a scaling of prey size preference with crab size have several important implications. First of all, they suggest that the invasive crabs exert predation pressure on the same size classes of native mussels as the native crabs. As the invasive *Hemigrapsus* species can locally reach much higher densities than the native *C. maenas* in the areas where they co-occur (Van den Brink *et al.*, 2012; Landschoff *et al.*, 2013; Jungblut *et al.*, 2017; Van den Brink & Hutting, 2017; Geburzi *et al.*, 2018), this is probably leading to an increased predation pressure on native mussels. This in turn may have effects on local mussel densities with subsequent repercussions for other species depending on mussels. However, whether such effects of increased

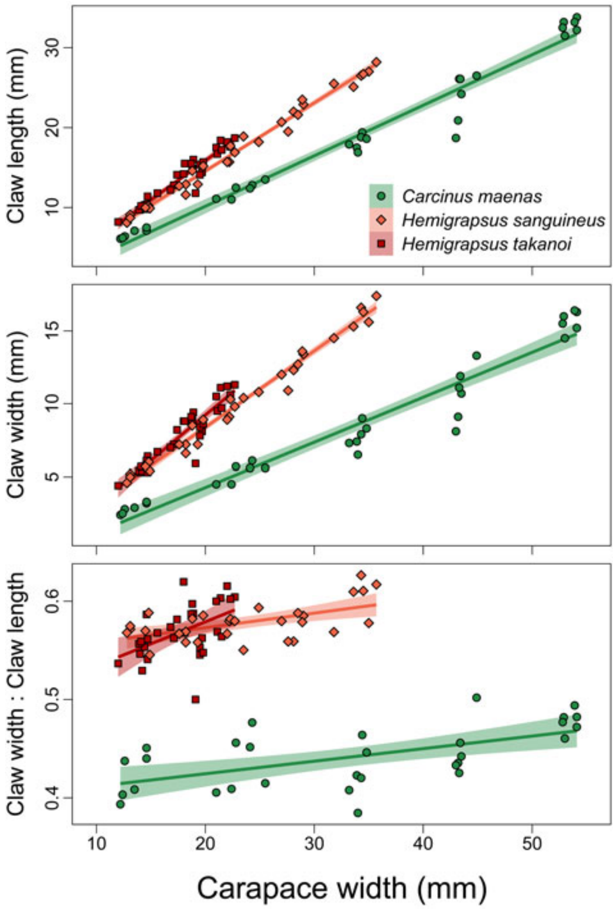

Fig. 2. Relationships between carapace width (mm) of invasive (*Hemigrapsus sanguineus* and *H. takanoi*) and native (*Carcinus maenas*) and major claw length (mm), major claw width (mm) and the ratio between the two. N = 30 replicates per crab species. The shaded areas denote the 95% confidence intervals.

Table 2. ANCOVA results of the comparisons of major claw length and major claw width among crab species (invasive *Hemigrapsus sanguineus* and *H. takanoi*, and native *Carcinus maenas*), depending on the covariate crab size (carapace width)

Response	df	MS	*F*	*P*
Major chelae length				
Species	2	204	139.5	<0.001
Crab size	1	3721.8	2545.2	<0.001
Species × Crab size	2	42.0	28.7	<0.001
Residuals	84	1.5		
Major chelae width				
Species	2	45.6	59.7	<0.001
Crab size	1	1029.3	1348.4	<0.001
Species × Crab size	2	38.3	50.1	<0.001
Residuals	84	0.76		

N = 30 per crab species.

predation on mussel populations exist remains to be investigated. The second implication of our findings is that the overlap in prey size range between invasive and native crabs is likely to result in resource competition between the invasive and native crabs. Such inter-specific competition may have contributed to the observed displacement of native *C. maenas* by the two *Hemigrapsus* species along European shores (Dauvin *et al.*, 2009; Van den Brink *et al.*, 2012). For both invasive crab species, intertidal mussel beds, rocky shores or dykes with loose rocks for shelter are the preferred habitat in Europe. These habitats generally harbour only small juvenile *C. maenas* (Thiel & Dernedde, 1994). Adult *C. maenas* may frequent these habitats occasionally during migrations from subtidal zones onto intertidal areas at high tide (Waser *et al.*, 2018). *Hemigrapsus* species seem to be superior to juvenile *C. maenas* in competition for shelter and adult crabs also predate more heavily on juvenile *C. maenas* than is the case the other way around (Jensen *et al.*, 2002; Griffen & Byers, 2006; Geburzi *et al.*, 2018). The negative effects on native crabs resulting from this interference competition and intra-guild predation may be exacerbated by additional resource competition. Our results suggest that this resource competition should be strongest in similar-sized crabs while in particular large adult *C. maenas* are probably released from resource competition with *Hemigrapsus* species. The extent of resource competition between invasive and native crabs can further be expected to depend on the availability and preference of other prey by the different crab species as indicated from studies in North America (Griffen *et al.*, 2008, 2012) and more research on the European side of the Atlantic is needed in this respect. Finally, the positive scaling of prey size preferences with crab size is important to take into account in studies investigating interactions between crabs and the resulting impact on the surrounding communities. Previous studies from North America have often compared *C. maenas* with *H. sanguineus* using their respective mean sizes at specific locations (e.g. Jensen *et al.*, 2002; Griffen & Williamson, 2008). While this gives good insight into the general impacts at natural crab size compositions, such approaches may mask the potential importance of competition. The mean carapace width of *C. maenas* can be twice as large as that of *H. sanguineus*, as *C. maenas* can grow much larger and our results demonstrate that resource competition will be small at large size differences between species.

While the results of our experiment contribute to the understanding of the impacts of the two invasive crab species on native communities along European shore lines, further research is needed to fully unravel the effects of the recent invasions. In particular, experiments on the potential role of resource competition for the invasion success of *Hemigrapsus* as well as its potential contribution to local declines of the native crab populations will be insightful. In addition, the impact on the wider community beyond single prey items still remains to be assessed. Given the rich literature from North America on the impacts of *C. maenas* and *H. sanguineus* on native ecosystems (see reviews by Klassen, 2012; Epifanio, 2013), such further studies would also be interesting in respect to comparing the impacts of the invasive crabs on both sides of the Atlantic.

Acknowledgements. We thank Nadine Bleile, Marvin Brandjes, David Bello Jimenez, Daisy ter Bruggen, Tomas van Elderen, Isabella Hofstede, Jeffrey Knol, Sascha Kuiper, Sil Piek, Enso van der Reep, Emma Verbeek and others for their help with collecting and sorting crabs and mussels, as well as setting up and running the experiments.

References

Asner GP and Vitousek PM (2005) Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences USA* **102**, 4383–4386.

Baeta A, Cabral HN, Marques JC and Pardal MA (2006) Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana* **79**, 1181–1193.

Bouwmeester MM, Waser AM, van der Meer J and Thieltges DW (2019) Prey size selection in invasive (*Hemigrapsus sanguineus* and *H. takanoi*) compared with native (*Carcinus maenas*) marine crabs. NIOZ Royal

Netherlands Institute for Sea Research. *Data set*. DOI 10.4121/uuid:bd70f097-6caf-4263-bfe6-297c6a3bf8a6

Breton G, Faasse M, Noël PY and Vincent T (2002) A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae). *Journal of Crustacean Biology* **22**, 184–189.

Brockerhoff A and McLay C (2011) Human-mediated spread of alien crabs. In Galil B, Clark P and Carlton J (eds), *In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts*. Dordrecht: Springer. pp. 27–106.

Brose U (2010) Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology* **24**, 28–34.

Brose U, Jonsson T, Berlow EL, Warren P, Banasek-Richter C, Bersier L-F, Blanchard JL, Brey T, Carpenter SR, Cattin Blandenier M-F, Cushing L, Dawah HA, Dell T, Edwards F, Harper-Smith S, Jacob U, Ledger ME, Martinez ND, Memmott J, Mintenbeck K, Pinegar JK, Rall BC, Rayner TS, Reuman DC, Ruess L, Ulrich W, Williams RJ, Woodward G and Cohen JE (2006) Consumer-resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.

Clavero M and García-Berthou E (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* **20**, 110.

D'Udekem D'Acoz C and Faasse M (2002) De huidige status van *Hemigrapsus sanguineus* (De Haan, 1835) en *H. penicillatus* (De Haan, 1835) in de noordelijke Atlantische Oceaan, in het bijzonder in Nederland, met opmerkingen over hun biologie (Crustacea, Decapoda, Brachyura). *Het Zeepaard* **62**, 101–115.

Dauvin JC, Rius AT and Ruellet T (2009) Recent expansion of two invasive crabs species *Hemigrapsus sanguineus* (de Haan, 1835) and *H. takanoi* Asakura and Watanabe 2005 along the Opal Coast, France. *Aquatic Invasions* **4**, 451–465.

David P, Thébault E, Anneville O, Duyck P-F, Chapuis E and Loeuille N (2017) Impacts of invasive species on food webs : a review of empirical data. *Advances in Ecological Research* **56**, 1–60.

Doherty TS, Glen AS, Nimmo DG, Ritchie EG and Dickman CR (2016) Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences USA* **113**, 11261–11265.

Doi W, Iinuma Y, Yokota M and Watanabe S (2009) Comparative feeding behavior of invasive (*Carcinus aestuarii*) and native crabs (*Hemigrapsus takanoi*). *Crustacean Research* **38**, 1–11.

Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics* **41**, 59–80.

Elner RW (1978) The mechanics of predation by the shore crab, *Carcinus maenas* (L.), on the edible mussel, *Mytilus edulis* L. *Oecologia* **36**, 333–344.

Elner RW (1980) The influence of temperature, sex and chela size in the foraging strategy of the shore crab, *Carcinus maenas* (L.). *Marine Behaviour and Physiology* **7**, 15–24.

Elner RW and Hughes RN (1978) Energy maximization in the diet of the shore crab, *Carcinus maenas*. *Journal of Animal Ecology* **47**, 103–116.

Epifanio CE (2013) Invasion biology of the Asian shore crab *Hemigrapsus sanguineus*: a review. *Journal of Experimental Marine Biology and Ecology* **441**, 33–49.

Geburzi JC, Brandis D and Buschbaum C (2018) Recruitment patterns, low cannibalism and reduced interspecific predation contribute to high invasion success of two Pacific crabs in northwestern Europe. *Estuarine, Coastal and Shelf Science* **200**, 460–472.

Goedknegt MA, Havermans J, Waser AM, Luttikhuizen PC, Velilla E, Camphuysen KCJ, van der Meer J and Thieltges DW (2017) Cross-species comparison of parasite richness, prevalence, and intensity in a native compared to two invasive brachyuran crabs. *Aquatic Invasions* **12**, 201–212.

Griffen BD and Byers JE (2006) Intraguild predation reduces redundancy of predator species in multiple predator assemblage. *Journal of Animal Ecology* **75**, 959–966.

Griffen BD and Williamson T (2008) Influence of predator density on non-independent effects of multiple predator species. *Oecologia* **155**, 151–159.

Griffen BD, Guy T and Buck JC (2008) Inhibition between invasives: a newly introduced predator moderates the impacts of a previously established invasive predator. *Journal of Animal Ecology* **77**, 32–40.

Griffen BD, Altman I, Bess BM, Hurley J and Penfield A (2012) The role of foraging in the success of invasive Asian shore crabs in New England. *Biological Invasions* **14**, 2545–2558.

Jensen GC, McDonald PS and Armstrong DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. *Marine Ecology Progress Series* **225**, 251–262.

Juanes F (1992) Why do decapod crustaceans prefer small-sized molluscan prey? *Marine Ecology Progress Series* **87**, 239–249.

Jungblut S, Beermann J, Boos K, Saborowski R and Hagen W (2017) Population development of the invasive crab *Hemigrapsus sanguineus* (De Haan, 1853) and its potential native competitor *Carcinus maenas* (Linnaeus, 1758) at Helgoland (North Sea) between 2009 and 2014. *Aquatic Invasions* **12**, 85–96.

Jungblut S, McCarthy ML, Boos K, Saborowski R and Hagen W (2018) Seasonal lipid storage and dietary preferences of native European *vs* invasive Asian shore crabs. *Marine Ecology Progress Series* **602**, 169–181.

Klassen G (2012) Biological synopsis of the Asian shore crab, *Hemigrapsus sanguineus*. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2978. Burlington, ON: Fisheries and Oceans Canada.

Klassen G and Locke A (2007) A biological synopsis of the European green crab, *Carcinus maenas*. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2818. Moncton, NB: Fisheries and Oceans Canada..

Kotta J, Wernberg T, Jänes H, Kotta I, Nurkse K and Pärnoja M (2018) Novel crab predator causes marine ecosystem regime shift. *Scientific Reports* **8**, 4956.

Landschoff J, Lackschewitz D, Kesy K and Reise K (2013) Globalization pressure and habitat change: Pacific rocky shore crabs invade armored shorelines in the Atlantic Wadden Sea. *Aquatic Invasions* **8**, 77–87.

Lowry E, Rollinson EJ, Laybourn AJ, Scott TE, Aiello-Lammens ME, Gray SM, Mickley J and Gurevitch J (2013) Biological invasions: a field synopsis, systematic review, and database of the literature. *Ecology and Evolution* **3**, 182–196.

Mascaró M and Seed R (2000) Foraging behavior of *Carcinus maenas* (L.): comparisons of size-selective predation on four species of bivalve prey. *Journal of Shellfish Research* **19**, 283–291.

Pyšek P and Richardson DM (2010) Invasive species, environmental change and management, and health. *Annual Review of Environment and Resources* **35**, 25–55.

Raffaelli D, Conacher A, McLachlan H and Emes C (1989) The role of epibenthic crustacean predators in an estuarine food web. *Estuarine, Coastal and Shelf Science* **28**, 149–160.

R Core Team (2017) *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Retrieved from http://www.r-project.org/

Ricciardi A, Hoopes MF, Marchetti MP and Lockwood JL (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs* **83**, 263–282.

Ropes JW (1968) The feeding habits of the green crab, *Carcinus maenas* (L.). *Fishery Bulletin* **67**, 183–203.

Sanchez-Salazar ME, Griffiths L and Seed R (1987) The effect of size and temperature on the predation of cockles *Cerastoderma edule* (L.) by the shore crab *Carcinus maenas* (L.). *Journal of Experimental Marine Biology and Ecology* **111**, 181–193.

Simberloff D (2011) How common are invasion-induced ecosystem impacts? *Biological Invasions* **13**, 1255–1268.

Smallegange IM and van der Meer J (2003) Why do shore crabs not prefer the most profitable mussels? *Journal of Animal Ecology* **72**, 599–607.

Smallegange IM, van der Meer J and Kurvers RHJM (2006) Disentangling interference competition from exploitative competition in a crab-bivalve system using a novel experimental approach. *Oikos* **113**, 157–167.

Smallegange IM, Hidding B, Eppenga JMA and van der Meer J (2008) Optimal foraging and risk of claw damage: how flexible are shore crabs in their prey size selectivity? *Journal of Experimental Marine Biology and Ecology* **367**, 157–163.

Swart C, Visser V and Robinson TB (2018) Patterns and traits associated with invasions by predatory marine crabs. *NeoBiota* **39**, 79–102.

Thiel M and Dernedde T (1994) Recruitment of shore crabs *Carcinus maenas* on tidal flats: mussel clumps as an important refuge for juveniles. *Helgoländer Meeresuntersuchungen* **48**, 321–332.

van den Brink AM and Hutting S (2017) Clash of the crabs: interspecific, inter-cohort competition between the native European green crab, *Carcinus maenas* and the exotic brush clawed crab *Hemigrapsus takanoi* on artificial oyster reefs. *Journal of Sea Research* **128**, 41–51.

van den Brink AM, Wijnhoven S and McLay CL (2012) Competition and niche segregation following the arrival of *Hemigrapsus takanoi* in the formerly *Carcinus maenas* dominated Dutch delta. *Journal of Sea Research* **73**, 126–136.

Waser AM, Dekker R, Witte JIJ, McSweeney N, Ens BJ and van der Meer J (2018) Quantifying tidal movements of the shore crab *Carcinus maenas* on to complex epibenthic bivalve habitats. *Estuaries and Coasts* **41**, 507–520.