



Effects of perceived competition and water temperature on the functional responses of invasive and native crabs

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ABSTRACT: As the frequency of species introductions increases globally, the need for predicting the ecological impacts of invaders becomes ever more urgent. Functional responses, i.e. how resource uptake by consumers changes as a function of resource density, describe the species-specific ability to deplete resources under standardized conditions, and their shape has been used as a tool to predict the impact of non-native species. However, functional responses are usually derived from individuals foraging alone, which overlooks the important roles of intra- and inter-specific interactions in shaping per capita consumption rates. We tested the extent to which the functional responses of invasive European green crab *Carcinus maenas* and native graceful rock crab *Metacarcinus gracilis* are affected by the perceived presence of con- and heterospecific individuals. Overall, crabs did not consume significantly more prey in the perceived presence of either a conspecific or novel heterospecific, but did demonstrate significantly higher attack rates in warmer water in the presence of a conspecific. Regardless of competitor type, green crabs consumed, on average, 16% more prey than the native crabs. This was largely due to their higher attack rate and lower prey handling time in warmer water. Green crab prey consumption increased significantly with increasing water temperature while that of the native crab species was unaffected (12 vs. 3.5% per 1°C increase, respectively). Higher maximum feeding rates are congruent with green crab impacts throughout their invaded range and suggest that green crabs might be undeterred from feeding in the presence of this co-occurring native crab species.

KEY WORDS: Non-native species · Comparative functional response analysis · CFRA · Resource use · Impact prediction · Population stability · Climate change

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1. INTRODUCTION

A ubiquitous consequence of the globalization of trade and travel has been an increasing frequency of introductions of species outside of their natural ranges (Wonham & Carlton 2005, Simberloff 2013). While not all non-native species become established or threaten native populations and ecosystems, a common trait among successful non-native (i.e. inva-

sive) species is fast and efficient resource consumption. This often results in non-native species outcompeting similar native species for shared resources (Funk & Vitousek 2007, Catford et al. 2009, Shochat et al. 2010, David et al. 2017). For example, plant invaders can dominate ecosystems through rapid nutrient uptake and higher resource use efficiency (Vitousek 1990), and many mobile animal invaders are predators that can have immediate and observ-

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able detrimental impacts on native prey populations (Crooks 2005, Sih et al. 2010). Indeed, quantifying resource use by invasive species is at the heart of many hypotheses designed to explain and predict their impacts (e.g. Parker et al. 1999, Dick et al. 2017).

One such method for examining the patterns and rates of resource use by consumers is to consider relationships between resource availability and resource consumption rate, or ‘functional responses’ (Holling 1959). These often non-linear relationships between consumption and prey density describe fundamental aspects of resource consumption, attack rate, handling time, and maximum feeding rate (Holling 1959). More importantly, because a range of prey densities is used, the shape of a functional response curve can reveal whether a consumer is likely to regulate or destabilise resource populations, and the conditions under which local resource extinction may be possible (Oaten & Murdoch 1975). Comparative functional response analyses have been used to reveal relative differences in consumption rates between native species and invaders (e.g. Dick et al. 2013, Alexander et al. 2014, Hoxha et al. 2019). While these studies are typically framed around the question of how consumption rates will affect native prey populations, they can also provide information about the potential role of competition for a shared prey resource to either facilitate or mitigate (i.e. biotic resistance) the success of an invasive species.

Functional responses have also been used to demonstrate the effect of various context-dependent factors on per capita resource consumption. The shape, slope, and asymptote of functional response curves vary among species and populations (Howard et al. 2018, Dunn & Hovel 2020), and can depend on abiotic factors, like water temperature (Iacarella et al. 2015), or biotic factors, such as the presence of a competitor (Soluk 1993, Barrios-O’Neill et al. 2014, Hoxha et al. 2019). In uninvaded systems, the shared evolutionary history of native species leads to the expectation that competitive interactions among heterospecifics will have a less profound impact on consumption than interactions between conspecifics, as a result of resource partitioning among species (Peiman & Robinson 2010). In contrast, the lack of co-evolutionary history between some native and invasive species means that there is the potential for high resource overlap. In this context, interspecific interactions might be as detrimental to per capita consumption as intraspecific interactions. Importantly, this prediction depends on the ability of each species to recognize the other as a competitor.

Here, we compared the functional responses of a native and an invasive crab species that coexist in intertidal and shallow subtidal habitats of the north-east Pacific. Invasive European green crabs *Carcinus maenas* are well established along both the east and west coast of North America, as well as in areas of South America, South Africa, and Australia (Klassen & Locke 2007). They directly compete with native crustacean populations (McDonald et al. 2001, Hunt & Behrens Yamada 2003) and prey upon benthic invertebrates (Rossong et al. 2006). In British Columbia, Canada, green crabs are well established in mud flats and eelgrass beds (Klassen & Locke 2007), which are also important habitats for graceful rock crabs *Metacarcinus gracilis* (Orensanz et al. 1995), our focal native species. We examined the functional responses of both invasive and native species in the perceived presence of a conspecific and, separately, a heterospecific individual; in all cases, competitors were confined to prevent foraging but offered visual and olfactory cues that revealed their presence. Specifically, we tested whether the invader had a consistently higher consumption rate than the native species (e.g. Dick et al. 2013, Alexander et al. 2014), and whether the identity of the perceived competitor (i.e. heterospecific or conspecific) affected prey consumption (e.g. Rossong et al. 2006, Hoxha et al. 2019). Given the predatory impact of European green crabs elsewhere in their invaded range, we expected green crabs to have higher consumption rates than graceful rock crabs. In addition, we predicted that for both species, the perceived presence of a conspecific would elicit a greater increase in consumption than the perceived presence of a heterospecific, given the stronger potential overlap of resource use with conspecifics (Peiman & Robinson 2010).

2. MATERIALS AND METHODS

2.1. Study species and collection

We conducted these experiments over the course of 2 field seasons, the first in the summer of 2015 and the second in the winter of 2019. In each season, we collected 75 graceful rock crabs and 75 European green crabs from Barkley Sound, on the west coast of Vancouver Island, British Columbia, Canada. The native graceful rock crabs were captured at the head of Useless Inlet (48.993, –125.026) and Bamfield Inlet (48.815, –125.160), while the invasive green crabs were obtained at the head of Effingham Inlet (49.096, –125.198). Each species dominated the crab assem-

blage in the inlet in which it was collected, with too few individuals of the other species to permit collection from a single site. Both species are commonly found in the same habitats (e.g. soft bottoms) and at the same depths across Barkley Sound and actively forage during high tides. Whether either species is preferentially more active during the day or night is unclear, and likely depends on water temperature (Orensanz & Gallucci 1988, Orensanz et al. 1995, Klassen & Locke 2007, Behrens Yamada & Gillespie 2008, Young & Elliott 2020).

Animals were held at the Bamfield Marine Sciences Centre (BMSC) for 2–4 wk prior to the start of the trials and a total of approximately 8 wk including the completion of the trials. Because BMSC employs a flow-through water system, we only used male crabs of both species to reduce the risk of contributing to the spread of invasive European green crabs via gravid females. The notch-to-notch carapace width (CW) of green crabs ranged from 50 to 80 mm (mean \pm SD = 61 ± 8.4 mm), and the CW of graceful rock crabs ranged from 50 to 117 mm (71 ± 21.0 mm). Heights of the largest cheliped ranged from 10 to 20 mm (14 ± 2.5 mm) for green crabs and from 11 to 30 mm (16 ± 4.9 mm) for graceful rock crabs. We also collected juvenile California mussels *Mytilus californianus* (shell length: 25 ± 3 mm) from Dixon Island (48.852, -125.120) in 2015 and Prasiola Point (48.817, -125.168) in 2019. Although these mussels are uncommon in soft-bottom habitats, both crab species readily consumed them in the laboratory, making them suitable standardized prey.

Crabs were held in single-species sea tables (172 cm long \times 75 cm wide \times 16 cm deep) with flow-through seawater and were regularly fed equal amounts of frozen herring (2015) or hake and California mussels (2019). To standardize hunger levels, crabs were isolated in individual containers for 48 h prior to the beginning of a trial, during which food was withheld (Howard et al. 2018). For the 48 h before the trials began, and throughout the experimental trials themselves, crabs were held indoors under artificial lighting, which was turned off overnight to mirror the natural day–night cycle.

2.2. Experimental design

Each experimental enclosure consisted of a rectangular, opaque plastic container (61 \times 40.6 \times 22.2 cm) with a drainage hole on the side. Each enclosure had its own inflow, and water did not mix across enclosures. In the middle of each enclosure, we placed a

smaller, transparent container (14.5 \times 14.5 \times 9.7 cm) with mesh sides to hold the non-feeding competitor (total foraging area = 0.24 m²). Mussels were placed into the experimental enclosures 12 h before trials began. Although there was no sediment in the enclosures, mussels readily attached to the plastic surfaces. In each trial, one crab was allowed to feed on prey items scattered around the bottom of the enclosure while the other crab (i.e. the non-feeding crab) was placed within the transparent container such that visual and effluent cues were detectable to the feeding crab but direct competitive interactions (i.e. aggression, prey monopolization, kleptoparasitism, or depletion) between the 2 crabs could not occur. The feeding crab and the non-feeding crab were placed into each enclosure simultaneously, and each trial lasted 8 h. Trials were run indoors under artificial lighting, during daytime hours. During this time, access to the laboratory was restricted so crabs could forage without disruption.

Individual green crabs ($n = 72$) and graceful rock crabs ($n = 72$) were randomly assigned to an experimental trial, in which they were allowed to feed on 1 of 6 prey densities (i.e. 2, 4, 8, 16, 32, or 64 mussels per 0.24 m²) and paired with a conspecific or heterospecific non-feeding competitor. Individual crabs were only used as the feeding crab once and once as the non-feeding crab. All combinations of crab species, competitor type, and prey density were replicated 3 times during both the summer of 2015 and the winter of 2019, for a total of 6 replicates per treatment. Because outcomes of competitive interactions between crabs are dictated by the difference in claw size (Lee & Seed 1992), and crab foraging activity is often influenced by water temperature (Matheson & Gagnon 2012), we recorded measures for both in all trials. The difference in cheliped height between the feeding and non-feeding crab was calculated for each crab pair, based on the largest claw of each crab, and the average water temperature in each enclosure was calculated using measurements taken at the beginning and end of every trial (summer 2015 range: 11.0–14.0°C; winter 2019 range: 9.90–10.9°C).

At the end of each trial, we counted the number of mussels that were consumed. Trials where no mussels were consumed ($n = 31$) were omitted from the data set because we could not confidently attribute the failure to eat as a behavioural choice rather than a physiological response due to stress or to imminent moulting. Graceful rock crabs failed to feed 11 times in the presence of a heterospecific and 11 times when a conspecific was present. Green crabs failed to feed 5 times in the presence of a heterospecific and 4 times

in the presence of a conspecific. No mussel mortality was observed during no-predator control trials run for each prey density in Summer 2015 ($n = 18$ trials).

Note that we did not assess the effect of the perceived presence of a competitor compared to crabs foraging alone for several reasons. First, the functional responses of solitary green crabs foraging on small mussels and oysters have already been established, including for populations from our study region (e.g. Howard et al. 2018, Ens et al. 2021). Second, we were specifically interested in increasing the realism of functional response experiments by including potential competition. Finally, our main aim was to compare the foraging behaviour of these species in the perceived presence of a conspecific versus a novel heterospecific competitor, which does not require establishing a non-competitor baseline.

2.3. Data analysis

We first identified the most important factors and interactions driving foraging crab behaviour across all trials ($n = 113$). To do so, we modelled the proportion of prey consumed per trial using logistic regression, with the identity of the feeding crab species and the type of non-feeding competitor (heterospecific or conspecific) as categorical factors, and initial prey density, water temperature, and claw size difference as continuous, scaled factors. We initially fit a model that included all possible 2-way interactions between our predictor variables (Table S1 in the Supplement at www.int-res.com/articles/suppl/m684p069_supp.pdf). We then reduced the model using likelihood ratio tests to remove non-significant interaction terms (Tables S2 & S3) and added an observation-level random effect to correct for overdispersion (Browne et al. 2005). In plotting the results, the predicted values for significant terms in the final mixed-effects model were generated by holding all other model terms at their average (continuous variables) or proportional (categorical variables) values (Lüdecke 2018). We assessed all models for overdispersion and leverage by plotting the standardized quantile residuals against predicted values (Hartig 2021). We also confirmed that there was no significant multicollinearity among predictor variables, and linear relationships between the continuous predictor variables and the logit response variable were visually linear.

Based on the model output, we determined that water temperature significantly affected crab foraging behaviour (see Section 3). To investigate this further, we split the data into ‘cold’ ($n = 58$ trials) and

‘warm’ ($n = 55$ trials) subsets, based on the median water temperature (11.65°C), and fit functional response curves for each combination of temperature and foraging species. Although the interaction between competitor type and water temperature was not significant in the mixed-effects model (see Section 3), we fit functional responses to each combination of temperature and competitor type as well, as investigating the effect of competitor type on predator behaviour was the primary aim of the study, for a total of 8 functional response models. However, we did not generate species-specific functional response models for each competitor type (e.g. green crabs foraging in the presence of a conspecific, graceful rock crabs foraging in the presence of a conspecific, etc.).

For each of the 8 functional response models, we first determined the functional response equation that best fit the data by modelling the proportion of prey consumed (N_e) as a function of prey density (N_0) using logistic regression. All 8 models had a significant negative first-order term indicating Type II functional responses (Juliano 2001). We then used the Rogers’ Type II functional response equation:

$$N_e = N_0 \{1 - \exp[a(N_e h - T)]\} \quad (1)$$

where N_e is the number of prey consumed, N_0 is the initial prey density, and T is the duration of each trial, to estimate the attack rates (a) and handling times (h) of crabs foraging on mussels. Rogers’ random predator equation was used because prey was not replaced during trials.

To determine if there were significant differences in the behaviour of different feeding crab species or for different competitor types, we conducted pairwise difference tests on the attack rate and handling time parameter estimates. Difference tests fit the combined data from the 2 models (groups) being compared using the difference between the original parameter estimates of a and h from those 2 models. If the resulting model coefficients (D_a and D_h) are non-significant, then the null hypothesis that there is no difference between the 2 groups cannot be rejected (Juliano 2001, Pritchard et al. 2017). All models were built and analysed using the packages ‘lme4’, ‘frair’, ‘DHARMA’, and ‘ggeffects’ in R v. 3.6.3 (Bates et al. 2015, Pritchard et al. 2017, Lüdecke 2018, R Core Team 2020, Hartig 2021).

3. RESULTS

All of the factors and the interaction between water temperature and feeding crab species were re-

Table 1. Output of a mixed-effects logistic regression model, including an observation-level random effect, predicting the proportion of mussels consumed by crabs ($n = 113$). Feeding crab species were invasive green crab or native graceful rock crab; competitor type was either hetero- or conspecific; initial mussel prey densities were 2, 4, 8, 16, 32, or 64 mussels; claw size difference refers to the difference in height of the largest claw between the feeding and non-feeding crabs. Significant p -values ($p < 0.05$) are highlighted in **bold**

Model parameter	Coefficient	SE	t	p
Mussel prey density	-0.05	0.01	-10.21	<0.001
Feeding crab species	-0.56	0.23	-2.45	<0.001
Competitor type	-0.05	0.22	-0.23	0.82
Claw size difference	0.07	0.11	0.66	0.51
Water temperature	0.85	0.25	3.33	<0.001
Water temperature \times mussel prey density	-0.01	0.01	-1.87	0.06
Water temperature \times feeding crab species	-0.62	0.23	-2.63	<0.001
Water temperature \times competitor type	0.30	0.23	1.31	0.19

tained in the mixed-effects logistic regression model (Table 1). The proportion of mussels consumed by green crabs was on average 16% greater than that consumed by graceful rock crabs (Fig. 1a). Green crab foraging was also more sensitive to water temperature: the proportion of prey consumed by green crabs increased by an average of 12%, compared to 3.5% for graceful rock crabs, for every 1°C increase in water temperature (Fig. 1b). However, neither the type of competitor nor the difference in claw size between the feeding and non-feeding crabs significantly affected prey consumption (Table 1).

Difference tests performed on the functional response parameter estimates of attack rate (a) and handling times (h) of crabs under different contexts showed that green crabs attacked mussels 2.89 times

more often ($D_a = -28.6$, $z = -9653$, $p < 0.01$), and consumed mussels significantly faster ($D_h = 0.05$, $z = 2.19$, $p = 0.02$) in warm water than in cold water (Figs. 2a & 3a,c). In contrast, graceful rock crabs did not significantly alter their feeding behaviour under different thermal contexts (Figs. 2b & 3a,c). As a result of these species-specific differences in responses to temperature, green crabs consumed more mussels than graceful rock crabs in warm water due to having both significantly faster attack rates ($D_a = -26.2$, $z = -7025$, $p < 0.01$) and handling times ($D_h = 0.07$, $z = 3.20$, $p < 0.01$) (Figs. 2a,b & 3a,c). In cold water, we found no significant difference between these species, for either attack rate ($D_a = -0.38$, $z = -0.32$, $p = 0.75$) or handling time ($D_h = 0.00$, $z = 0.09$, $p = 0.93$) (Figs. 2a,b & 3a,c).

Although the interaction between water temperature and competitor type was non-significant in the mixed-effects model, we did observe temperature-dependent differences in attack rates due to competitor type. Crabs in the presence of a conspecific in warm water found and attacked mussels 2.2 times faster than crabs in the presence of a heterospecific crab in warm water ($D_a = -28.9$, $z = -3582$, $p < 0.01$) (Figs. 2c,d & 3b) and 3.6 times faster than in the presence of a conspecific in cold water ($D_a = -29.9$, $z = -3825$, $p < 0.01$) (Figs. 2d & 3b). All other pairwise comparisons were non-significant (Fig. 3).

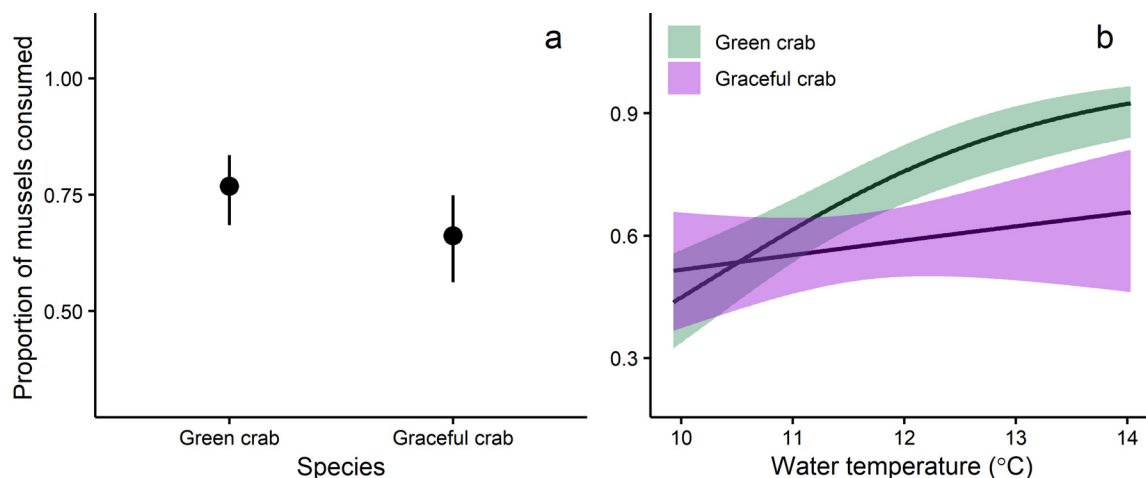


Fig. 1. Marginal effects plots determined from the mixed-effects logistic regression model (Table 1) predicting the proportion of mussels consumed by crabs for (a) feeding crab species (error bars, $\pm 95\%$ CI) and (b) the interaction between feeding crab species and water temperature (shaded areas, $\pm 95\%$ CI). Predicted values for each term were generated by holding all other model terms at their average (continuous variables) or proportional (categorical variables) values

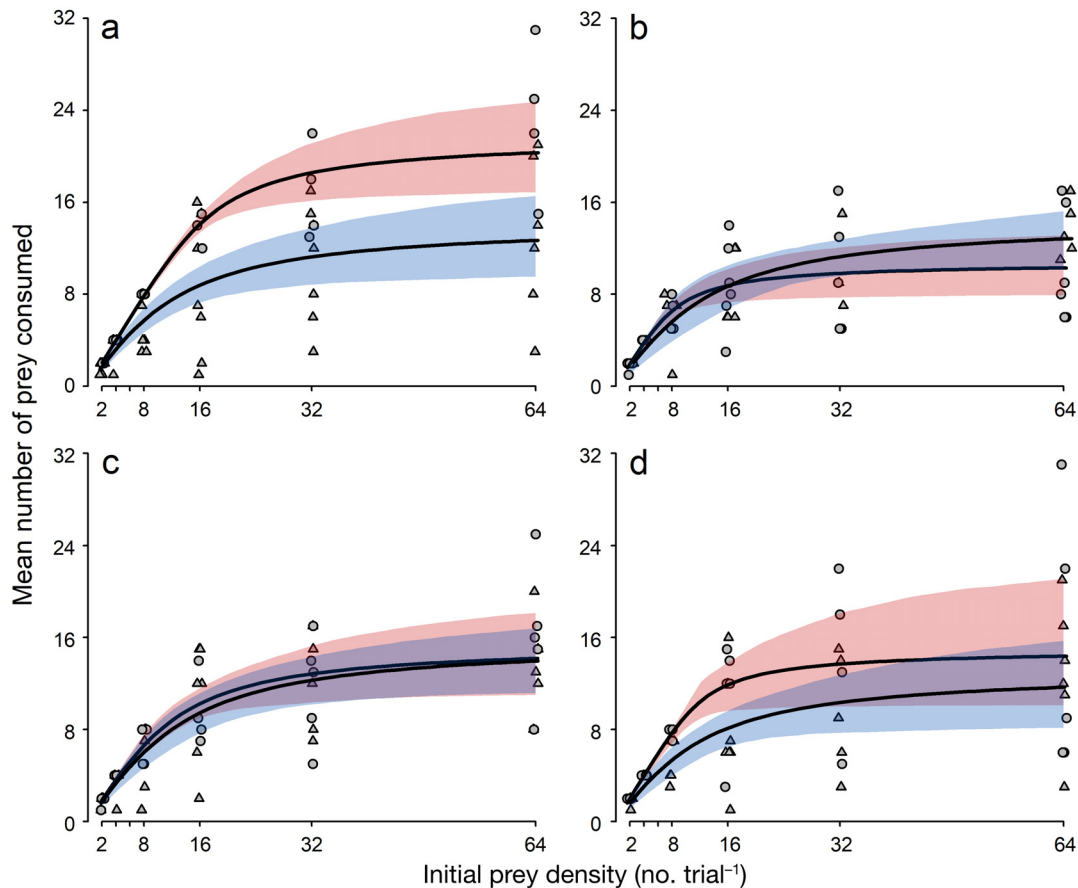


Fig. 2. Functional response curves showing the mean number of mussels (\pm bootstrapped 95% CI) consumed by crab species in warm water ($>11.65^{\circ}\text{C}$; red-shaded CI) and cold water ($\leq 11.65^{\circ}\text{C}$; blue-shaded CI). In all trials, the feeding crab was paired with a non-feeding competitor. Shown are the responses for (a) European green crabs and (b) graceful rock crabs, regardless of the species of the non-feeding competitor, and for (c) heterospecific and (d) conspecific crab pairs, regardless of species. Raw data are shown by circles (warm water) and triangles (cold water) and were intentionally offset for visualization purposes

4. DISCUSSION

The ability of an invasive species to recognize and respond to a novel competitor, and vice versa, can have significant consequences for the native competitor and its prey and may facilitate or inhibit the success of an invasive species. For example, on the west coast of North America, invasive European green crabs are competitively dominant over the native shore crab *Hemigrapsus oregonensis* (Jensen et al. 2002), but in both their native range in Europe and their invasive range on the east coast of North America, green crabs are outcompeted by invasive Asian shore crabs *H. sanguineus* (Jensen et al. 2002, van den Brink et al. 2012, Geburzi et al. 2018). Studies like these demonstrate the importance of investigating novel competitive interactions between invasive and native species, regardless of their perceived taxonomic or functional similarity (White et al. 2006,

Howard et al. 2017). At least 3 large native cancrid crab species commonly co-occur with green crabs on the west coast of North America, but published studies on their interactions are limited (McDonald et al. 2001, Hunt & Behrens Yamada 2003), or non-existent in the case of graceful rock crabs. To fill this gap, we examined the feeding behaviour of green and graceful rock crabs in the perceived presence of either a con- or heterospecific crab. Broadly, we found that green crabs typically consumed more prey than graceful rock crabs, but that neither species was more likely to increase its overall prey consumption in response to a perceived competitor. However, in warm water, attack rates of crabs feeding in the presence of a conspecific were significantly higher than those of crabs feeding in the presence of a heterospecific, which is consistent with our predictions. Additionally, we discovered that, for green crabs, the magnitude of the response was also significantly af-

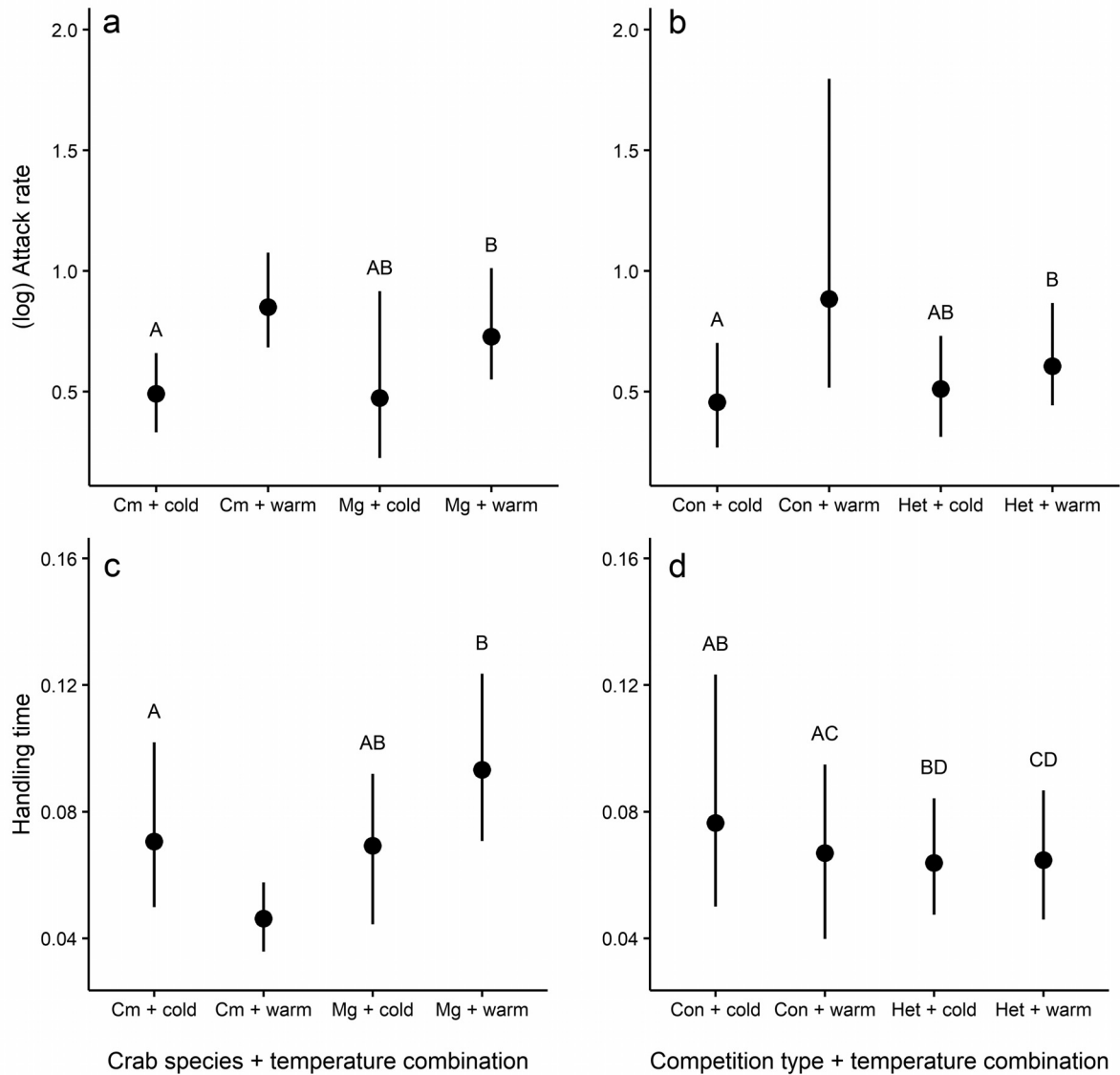


Fig. 3. Parameter estimates ($\pm 95\%$ CI) of (a,b) log attack rate and (c,d) handling time from bootstrapped Type II functional response curves of crabs foraging in warm water ($>11.65^\circ\text{C}$) or cold water ($\leq 11.65^\circ\text{C}$) in the presence of another, non-feeding crab. Shown are parameter estimates for different combinations of water temperature and (a,c) feeding crab species (Cm: green crab; Mg: graceful rock crab), regardless of the identity of the non-feeding crab, and (b,d) competitor type (Con: conspecific; Het: heterospecific), regardless of feeding crab species. Attack rates are presented on a log scale for visualization purposes only. Matching uppercase letters indicate that the parameter estimates are not significantly different, determined by a difference test. Comparisons were only run between pairs with a shared variable (e.g. the same crab species, temperature, or competitor type). The full output of these pairwise difference tests can be found in Table S4 in the Supplement

affected by water temperature, as prey consumption increased rapidly over comparatively small increases in temperature.

As expected, invasive green crabs preyed on mussels more effectively than native graceful rock crabs. Across all experimental conditions, green crabs consumed 16% more mussels than graceful rock crabs, despite the fact that graceful rock crabs were, on average, slightly larger than green crabs. Successful invasive species often exploit resources more effi-

ciently than ecologically similar native species (Funk & Vitousek 2007, Catford et al. 2009, Shochat et al. 2010, David et al. 2017, Hoxha et al. 2019, Ens et al. 2021). In our study, higher consumption rates were realised through both faster attack rates and lower handling times. However, these 2 functional response parameters have been shown to vary across invasive green crab populations, with sometimes just one of the parameters leading to higher prey consumption (Howard et al. 2018).

The presence of a potential competitor did not have a significant effect on overall prey consumption. However, we did detect a difference in attack rates depending on competitor type for crabs feeding in warm water, suggesting that crabs were responding to the visual and olfactory cues of their potential competitor to some extent. Specifically, crabs paired with a conspecific attacked prey 2.2 times faster than when paired with a heterospecific, which is consistent with our expectation that crabs should feed more in the perceived presence of a conspecific (Peiman & Robinson 2010). That we did not detect the same difference in handling times or in overall prey consumption may be because we did not allow the crabs to interact directly, thus eliminating the need to consume prey rapidly to avoid prey depletion or kleptoparasitism by a competitor (Chakravarti & Cotton 2014). Similarly, it may explain why the difference in claw size between the feeding and non-feeding crabs did not significantly affect overall consumption if crabs were not physically engaging in agonistic interactions (Smallegange et al. 2006).

Because we detected higher attack rates in response to conspecifics but not heterospecifics, our results suggest that green crabs and graceful rock crabs may not perceive the other as competitors. Lack of co-evolution could be one explanation. The 2 families to which these species belong were already separate by the end of the Cretaceous period, some 60 million years ago (Brösing 2008), and while the genus *Carcinus* evolved in the Atlantic basin, the genus *Metacarcinus* arose in the North Pacific Ocean (Schweitzer & Feldmann 2000). Naiveté has been suggested as an explanation for why invasive green crabs feeding in competition experiments with native American lobsters *Homarus americanus* did not display their claws aggressively when approached, and why the lobsters continued to unsuccessfully attempt to displace the crabs despite the risk of predation (Rosson et al. 2006). Similar failure to recognize a superior competitor was also observed between green crabs and invasive *Hemigrapsus sanguineus* (Jensen et al. 2002). While there is no information on interspecific recognition between green crabs and graceful rock crabs via visual or chemosensory cues or evidence for the ability of either species to learn these cues, learning has been observed for green crabs paired with other novel competitor species (Jensen et al. 2002, Rosson et al. 2012). If green and graceful rock crabs do recognize each other, then an alternative explanation for a lack of competitive behaviour is that there is limited prey resource overlap between them. It has been speculated that graceful crabs prefer soft-bodied

prey based on their chelae morphology (Orensanz & Gallucci 1988), and that the asymmetric morphology of green crab claws, i.e. having one 'cutter' and one 'crusher' claw, may give them access to a broader diet that includes hard-bodied prey (Elner 1981, Lee & Seed 1992). If this is the case, it would support the hypothesis that these 2 species do not compete for shared prey resources. However, in captivity, both species readily consumed soft tissues (i.e. fish carcasses) and hard-bodied prey that they may not otherwise encounter regularly. Understanding the extent to which resource overlap affects competition will require formal diet studies for both graceful rock crabs and green crabs in the northeast Pacific.

Activity levels, including feeding behaviour, in marine crabs usually increase with water temperature (McGaw & Curtis 2013). While experimental studies that focus on this relationship typically use temperature ranges of 10°C or more, we found that green crabs doubled their feeding rates over a mere 4°C temperature increase. This means that at the highest prey density, green crabs consumed, on average, 3.6 mussels h⁻¹ at 10°C and 7.4 mussels h⁻¹ at 14°C. By comparison, consumption by graceful rock crabs only increased from an average of 4.1 to 5.3 mussels h⁻¹ over the same temperature range. The difference is the result of green crabs increasing their attack rate and decreasing prey-handling time in warmer water, while these functional response parameters remained constant for graceful rock crabs. These interspecific differences were unexpected, since both graceful rock crabs and green crabs are temperate species capable of surviving in intertidal habitats year-round. Nevertheless, graceful rock crabs are not considered a 'shore' crab, and observations indicate that graceful rock crabs occur at their highest densities just below the low water mark, i.e. deeper than green crabs typically occur in the northeast Pacific (I. M. Côté pers. obs.). Graceful rock crabs may therefore have a narrower thermal niche than green crabs, not captured by the temperature ranges in our study, and undergo a larger tidal migration that allows them to follow their thermal optima (Orensanz & Gallucci 1988). Additionally, because our temperature trials were conducted several years apart, on different cohorts of crabs, we cannot exclude the possible role of temporal effects on crab behaviour. More studies on both the physiology and ecology of graceful rock crabs are needed to understand the role of water temperature on the foraging behaviour of this species.

The outlook for these 2 crab species in British Columbia appears to favour the invasive green crabs. The ef-

fect of water temperature in our study suggests that green crabs will likely benefit from warming as a consequence of climate change. There is anecdotal support for this prediction: following the El Niño/‘The Blob’ years (i.e. 2014 to mid-2016) in the northeast Pacific, new populations of green crabs appeared throughout British Columbia, and catch per unit effort for existing populations increased at several locations (Howard & Therriault 2021). These anomalously warm years likely enhanced larval survival, but also possibly adult survival and fitness, if green crabs were able to capitalize on warmer water temperatures by increasing their foraging efficiency. The impact of increasing temperature on green crab prey populations should not be directly estimated from functional responses, particularly in this instance where mussels were chosen as the prey species for experimental design reasons rather than for their ecological relevance as prey species for crabs in soft-sediment habitats. Moreover, we focussed solely on male crabs, which might not behave as females do in response to perceived competition or temperature (Christy 1987). Nevertheless, it may be that there is an increasing risk of overexploitation of prey, in general, as warm years become more frequent (Di Lorenzo & Mantua 2016), especially since green crabs consistently demonstrate destabilising Type II functional responses in experimental settings (Howard et al. 2018, Ens et al. 2021). Our study also suggests that competition with graceful rock crabs may not be a meaningful source of biotic resistance against green crabs, and that graceful rock crabs may be at risk of being increasingly outcompeted by green crabs for shared prey. However, more information on the dietary overlap and general foraging habits of these 2 species in shared soft-sediment habitats is still needed to confirm the impacts of invasive green crabs on the native graceful rock crab.

Acknowledgements. The authors are grateful to have been able to conduct this work on the traditional territories of the Nuuchah-nulth First Nations. They would also like acknowledge the many students and staff at the Bamfield Marine Sciences Centre who assisted with this study, particularly in the collection and care of our research animals. Funding was provided by a scholarship from the Second Canadian Aquatic Invasive Species Network (CAISN II) to B.R.H. and a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to I.M.C.

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Editorial responsibility: Rochelle D. Seitz,
Gloucester Point, Virginia, USA

Reviewed by: R. Dunn and 2 anonymous referees

Submitted: April 21, 2021

Accepted: December 6, 2021

Proofs received from author(s): February 3, 2022