

Fast and furious: shorter handling times reveal a foraging advantage of the invasive *Carcinus maenas* over its native competitor *Metacarcinus gracilis*

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Abstract

Invasive species have been shown to decrease the fitness of native species and reduce biodiversity. The European green crab (*Carcinus maenas*) is a prolific invasive crab species responsible for habitat degradation and biodiversity reduction across the globe, and has been present on Canada's southwestern coast since the late 1990's. Using feeding rates as a proxy for individual fitness, we examined how the rate of prey handling and consumption in *C. maenas* compares to that of the native graceful rock crab (*Metacarcinus gracilis*). The time required by *C. maenas* and *M. gracilis* to handle and consume a mussel (handling time) was compared at two flume velocities (10 and 19cm/s) to quantify feeding rates under differing flow conditions. These measurements have possible implications for how *C. maenas* populations may affect *M. gracilis* demography in coming years. At both flume speeds, *C. maenas* had a lower handling time than *M. gracilis*. At 10cm/s flow, *C. maenas* fed an average of 2 minutes faster than *M. gracilis*, whereas at 19cm/s they fed 5.2 minutes faster on average. These data suggest *C. maenas* is capable of more efficient foraging at a variety of current speeds. Handling time is widely recognized as an important influence on invasion success, and our findings thus suggest that *C. maenas* has a competitive advantage over *M. gracilis* across its native range. These results have implications for modeling the predicted spread of *C. maenas* along the coastal East Pacific.

Keywords — European green crab, competition, invasive species, resource use, feeding rate, handling time

1. INTRODUCTION

THE introduction of non-native species can negatively impact the fitness of native species, lower biodiversity, disrupt ecosystem function, and threaten human enterprise [1]. Studying species traits that have a direct impact on individual fitness is useful for understanding the competitive interactions between invasive and native species. Since a successful invasion is partially dependent on how efficiently

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an invasive species can compete with native species for resources [2, 3] and because invasive predators can reshape the community structure they inhabit depending on their ability to catch and consume prey items [4], studying the rate of resource consumption between an invader and a native competitor is helpful for predicting impacts. Handling time, the amount of time it takes a predator to handle its prey from initial contact to the time the prey item is eaten, can be used as a proxy for feeding rates [5]. Furthermore, handling time is a vital component of optimal foraging theory, which is a model that predicts how organisms search, compete, and consume resources [6]. According to optimal foraging theory, predators with shorter handling times are able to coexist with, or may even out-compete other predators [7]. These interactions have implications for a predator's ability to exploit prey items and are thereby important to shaping the ecosystem in which predators can reside [7].

The European green crab (*Carcinus maenas*), a native of Europe's Baltic Sea and English Channel, is a well-established invasive species of North America's east and west coasts, as well as areas of South America, southern Africa and Australia [8]. The origin of *C. maenas* on the west coast of Vancouver Island, located on the south coast of British Columbia, Canada, can be traced to a strong El Niño event in 1997/1998, when larvae were transported from established invasive populations in California [9]. *C. maenas* directly competes with other crustacean populations and is an aggressive predator of other benthic invertebrate species [10]. They exert significant top-down control on coastal marine food web, i.e. the structure of invaded communities becomes determined by the severity of *C. maenas* predation, not by the amount of nutrients or habitat available [11]. Despite earlier predictions that populations would eventually die out, *C. maenas* has persisted on Vancouver Island's west coast [9]. Studies suggest that *C. maenas* persistence seems to be partly dependent on the presence of relatively warm and sheltered water, where they feed at rates 2-3 times higher than exposed habitats [12, 8, 13].

The foraging time of *C. maenas* is increased with increasing flow velocity, while its feeding rate is decreased [14]. Consequently, *C. maenas* populations are highest in sheltered habitats with lower flow velocities, such as bays, and decline in higher velocity, exposed habitats [15]. A native competitor, the graceful crab (*Metacarcinus gracilis*) and *C. maenas* share habitats of sheltered, muddy or sandy bottoms with high eel grass coverage. However, *M. gracilis* also inhabit more exposed rocky shores [16]. Both populations of *M. gracilis* and *C. maenas* exist in the Pacific Northeast coastal regions and are present in Barkley Sound, an ocean inlet located in southwestern Vancouver Island, where *C. maenas* was first reported in Canada in 1999 [8, 16].

To assess the risk of *C. maenas* outcompeting *M. gracilis* in shared habitat, we compared the handling times of *C. maenas* and *M. gracilis* by measuring each species' handling times at two different flow rates. We hypothesized that at low levels of flow, *C. maenas* will have a similar or lower total mean handling time than *M. gracilis* since *C. maenas* populations have been well established in sheltered areas along the west coast [9]. At faster flows we expect the total handling time of *C. maenas* to increase at a greater rate than that of *M. gracilis*, and will therefore have a longer total handling time than *M. gracilis* at greater flows. These findings are important for predicting the future implications of *C. maenas* presence on *M. gracilis* populations and other native

crab species in the North-eastern Pacific. Furthermore, our description of *M. gracilis*' handling times is among the first information available in the literature describing its feeding behaviour.

2. RESULTS

At a flow rate of 10cm/s, mean handling time for *C. maenas* ($302.9 \pm 31.2s$) was 1.5 times faster than that of *M. gracilis* ($461.6 \pm 43.8s$) (Figure 2), although the difference was only marginally significant (Table 1; Linear Regression, $p = 0.077$, $df = 14$). Feeding rates of *M. gracilis* had a larger variance than those of *C. maenas*, with a difference of 312 seconds between the maximum and minimum feeding rates versus a difference of 290 seconds for *C. maenas*. Mussel size, crab size, and flume temperature were found to have no significant effect on the handling times of either crab species at the flow speed of 10cm/s, and were removed through the stepwise AIC process. However, the effect of water temperature varied depending on the species (Table 1; Linear Regression, $p = 0.058$, $df = 14$). Water temperature had a greater effect on *M. gracilis* compared to *C. maenas* (Figure 3).

Table 1: Linear regression table of parameter estimates, *t*-values, and their respective *p*-values for the handling times of *C. maenas* and *M. gracilis* with a flume speed of 10cm/s.

lm(formula= handling time ~ species + flume temp + species:flume temp)				
Parameter	Estimate	Std. Error	<i>t</i> -value	<i>p</i> -value
Intercept	2439.86	2391.00	1.020	0.32
Species	-2842.5	1486.84	-1.912	0.076
Flume Temp	-155.68	156.62	0.994	0.337
Species: Flume Temp	201.71	98.08	2.057	0.059

At the higher flow rate of 19cm/s the difference in total mean handling between the two species was significant (Figure 4) (Table 2; Linear Regression, $p < 0.001$, $df = 21$). The average handling time for *C. maenas* ($270.6s \pm 25.6s$) was 2.2 times faster than *M. gracilis* ($582.5s \pm 57.9s$) at the higher flume speed (Figure 4). Feeding rate variance for the *M. gracilis* was also shown to be higher than that of the *C. maenas* at the 19cm/s flume speed, with a difference of 565 seconds between the maximum and minimum feeding rates (Figure 4). Conversely, *C. maenas* feeding rates only differed by 299 seconds between the maximum and minimum handling times (Figure 4).

We found that at a high flow speed of 19cm/s, both mussel size and crab size were correlated with handling time (Figure 5). A significant positive correlation between crab size and total handling time was found across both species (Table 2, Linear Regression, $p = 0.027$, $df = 21$), with an increase in crab size associated with an increase in total handling time (Figure 5a). The same was found for mussel size (Figure 5b), with an increase handling time significantly correlated with an increase in mussel size (Table 2, Linear Regression, $p = 0.0057$, $df = 21$).

Table 2: Linear regression table of parameter estimates, *t*-values, and their respective *p*-values for the handling times of *C. maenas* and *M. gracilis* with a flume speed of 19cm/s.

lm(formula= handling time ~ species + flume temp mussel size + crab size)				
Parameter	Estimate	Std. Error	<i>t</i> -value	<i>p</i> -value
Intercept	-1298.51	530.61	-2.447	< 0.05
Species	480.54	97.73	4.917	< 0.001
Flume Temp	46.69	28.09	1.662	0.11
Mussel Size	396.42	125.37	3.082	< 0.01
Crab Size	-87.53	36.77	-2.381	< 0.05

3. DISCUSSION

The primary purpose of our study was to determine differences in handling time in varying flow conditions between *M. gracilis* and *C. maenas*. In our feeding trials, we were unable to detect statistical difference for total mean handling time at a flume speed of 10cm/s between the two species; however, we did observe a trend for *C. maenas* to have a faster handling time of ~1.5 minutes compared to *M. gracilis*. At higher flume speeds (19cm/s), *M. gracilis* had a much longer total mean handling time than that of *C. maenas*; *M. gracilis* fed an average of ~5.2 minutes slower than *C. maenas*. Mussel size and crab size were correlated with handling time at a flow speed of 19cm/s, which may explain the larger difference in handling time observed at 19cm/s compared to 10cm/s. At higher flow-speeds, dynamic pressure differences between the upstream side and downstream side are greater, thus the force of drag is greater than that of lower flow-speeds. As an organism increases in size, the difference in dynamic pressure also increases [17]; the much larger *M. gracilis* is therefore subject to greater drag forces, which should negatively affect their ability to handle food.

Rovero et al. [18] stated that for *C. maenas* the amount of time spent handling prey, and not energy expended, better represents the cost of prey-handling behaviour; it is reasonable to believe the same holds true for other shore crabs, including *M. gracilis*. Our results show that *C. maenas* feeding behaviour is more profitable at faster flow rates, suggesting the ability to obtain energy more efficiently may give *C. maenas* a fitness advantage over *M. gracilis* where distributions overlap in high flow environments [18]. While the unidirectional nature of flow inside the flume used in this study is rare in coastal marine systems, flow velocities upwards of 19cm/s in crab habitats are typical and likely highly directional in inlets and narrow channels. For example, in the many high flow inlets characteristic of the Barkley Sound region, our results suggest the efficient feeding behaviour of *C. maenas* may prove detrimental for local *M. gracilis* populations. Extirpation of the *M. gracilis* due to competition for food [7] and subsequent changes to community composition [19] are realistic outcomes of prolonged *C. maenas* presence in Barkley Sound.

Although the reduced efficiency of *M. gracilis* foraging could contribute to a competitive disadvantage that may threaten their existence in areas where *C. maenas* is present [7], additional competitive factors could moderate these species interactions. Direct confrontations between crustaceans are often decided in favour of the largest individual

[10], which, based on our sizing data, is likely to be the *M. gracilis*. Instead, the faster mean handling time suggests that *C. maenas* are more likely to consume resources at a faster rate than *M. gracilis* and as such, out-compete them in an indirect manner by diminishing food patches at a rate greater than *M. gracilis* can exploit them. This theoretical fitness advantage of *C. maenas* is dependent on whether they are equally capable as *M. gracilis* at finding patches of food. It is possible that *M. gracilis* are more sensitive to the olfactory cues given by local prey species than the recently-introduced *C. maenas*.

In our study both species of crab often did not react to the placement of a crushed mussel in the flume. It is possible that the size of the container did not allow for a demonstration of typical behaviours. Future studies should incorporate a larger flume to allow the crabs to behave more naturally. Another possibility is the unidirectional flow produced by the flume caused crabs to huddle down and become unresponsive. Wave exposure usually occurs in a back-and-forth motion and rarely exists as unidirectional flow in nature. Crabs of both species were more likely to become unresponsive at a higher flow velocity (pers. obsv.). As suggested by Robinson et al. [14], unresponsiveness to food may be due to increased mixing of the odour plume or increased dissipation of odour molecules at higher velocities. However, because of the small flume, effluent concentrations are more likely to have remained sufficiently high to initiate a response. Alternatively, it is possible that crabs are less likely to risk any movement at high unidirectional flows due to the perceived risk of being swept away [20]. Future studies should record the number of feeding trials that conclude with no response. These data may reveal the comparative vulnerability of each species to hydrodynamic forces.

Although we observed differences in handling times between the two species studied, there are several factors that may limit the interpretation of our findings. For example, we were not able to change flume water after every trial. This may have confounded our data due to a build-up of both crab feeding effluent and prey death effluent in the water, causing a decrease in handling times. Future studies, if unable to change the flume water after every trial, could include the trial number (1st after water change, 2nd, etc.) as a covariate to help standardize the data. Also, we did not standardize our design for starvation throughout experimental trials, which can have impacts on feeding rates. Future protocols should incorporate standardization of starvation periods by use of randomization of flume speeds, species used, as well as randomization of crab individuals for each trial. Lastly, although *C. maenas* and *M. gracilis* were subject to the same surface flow velocities, the actual flow velocity experienced by the crab would have differed slightly depending on height. As the distance from the bottom of the flume increases, so does the velocity of the water, owing to the no-slip condition, i.e. the zero-velocity condition of fluids adjacent to a solid boundary, and the subsequent gradient of increasing velocities as distance from the solid boundary increases [17]. With this in mind, the squat *C. maenas* would have been exposed to a slightly slower flow velocity compared to the more bulbous *M. gracilis*; this would have reduced drag and may have contributed to their comparatively quick handling times.

By determining how food handling times compare between a native crab and an

invasive crab species, this study elucidates an important piece of the puzzle in the prediction of how community structure may change due to the *C. maenas* invasion. Hampton and Griffiths [21] demonstrated that *C. maenas* is unlikely to out-compete local competitors in South African wave-swept shorelines owing to its lack of morphological adaptations suited to high-energy areas. An analysis of *M. gracilis*' morphological features could allow a similar comparison to be made for the Barkley Sound region. While our results imply the *C. maenas* is a better competitor in a fast, unidirectional-flowing environment, an in-depth comparative analysis of graceful and other crab morphologies would be useful in determining the relative structural advantages of each species, thereby helping to model the projected spread of the *C. maenas* across the Canadian Pacific. This information can then be used to assess which prey and competitor species are most vulnerable to the *C. maenas* invasion, and allow for the appropriate conservation measures to be taken.

4. METHODS

4.1. Experimental Design & Protocols

Thirty *C. maenas* with a carapace width of 6-7 cm were collected from Hillier Island (Figure 1) in Barkley Sound in July 2014 using Fukui crab traps. Only males were collected due to the fact that *C. maenas* is highly invasive and there are restrictions to their collection. Crabs were acclimated to a 12:12 hour light-dark cycle and fed with blue mussels (*Mytilus trossulus*) measuring 2-3 cm, collected by hand from Bamfield Inlet in Barkley Sound for 4 weeks before feeding trials. Thirty *M. gracilis* crabs with a carapace width of 6-10 cm were collected throughout the month of October 2014 from Burlo Island (Figure 1) in Barkley Sound using folding Fukui crab traps and were held in an identical manner to the *C. maenas* for 2 weeks before feeding trials began. Again, only males were collected to provide an appropriate comparison to the male *C. maenas*. Size measurements for crabs were taken using digital calipers at the widest point of the carapace. All crabs were held in sea tables with circulating seawater approximately 30 ppm and 14°C. To help initiate feeding behaviour during the trials, all crabs for the 10cm/s trials were deprived of food for 3.5 days and crabs for the 19cm/s trials for 4.5-5 days before feeding trials took place. This mismatch of starvation periods between 10cm/s trials and 19cm/s trials restricts the inferences that can be made; thus no comparisons were made between the two water velocities, only within.

A total of 46 feeding trials were conducted. Each feeding trial involved randomly selecting a flow-rate, species, and individual, placing the selected crab in a 75 cm long X 10 cm wide X 14 cm deep flume for 30 minutes. Each 30-minute feeding trial included a 7 minute acclimation period followed by a 3 minute effluent period, where a mussel was placed in the water but kept out of reach via a mesh gate. The length of each mussel was measured and mussels were cracked open with the palm of a hand against a flat surface to encourage feeding. Although cracking the shell is an important component of the handling time for mussel foraging, *C. maenas* scavenge a wide array of other food that does not require shell-cracking [22]; while the diet of *M. gracilis* is not well-described in the literature, given its morphology and life history typical of other shore crabs, it is reasonable to presume its diet is varied like other scavenging shore

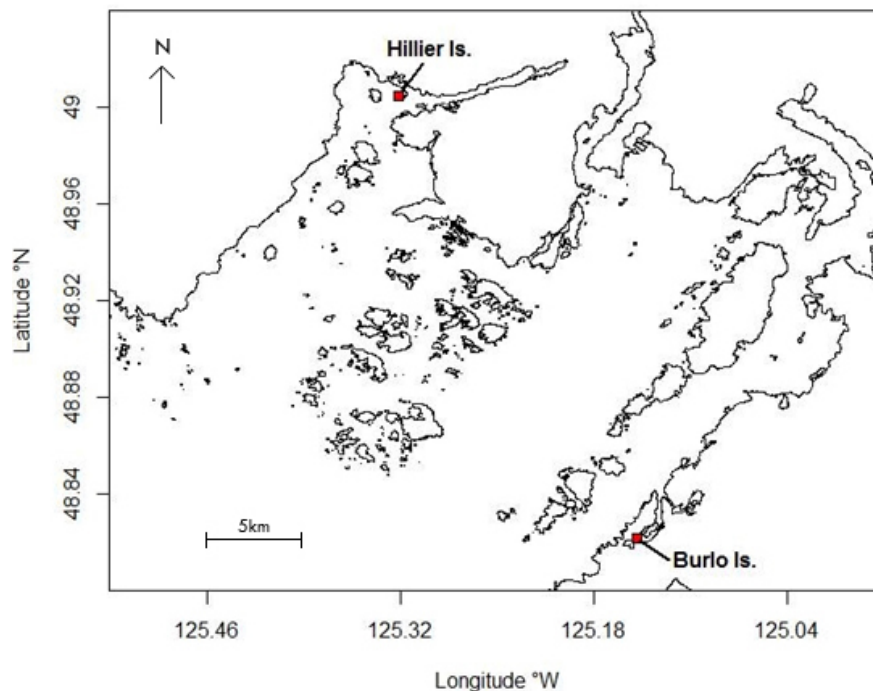


Figure 1: Map of Barkley Sound on Vancouver Island, British Columbia with the collection sites of *Carcinus maenas* and *Metacarcinus gracilis* labeled as Hillier Is. and Burlo Is. respectively.

crabs. We therefore argue that our results remain a relevant and useful comparison of *M. gracilis* and *C. maenas* food handling times.

The 20-minute feeding period followed where the gate separating the mussel and crab was removed. If a crab did not feed on the mussel during the allocated 20-minute feeding trial the crab was placed back into the holding tank and another crab was randomly selected. Feeding trials were recorded using a Sony Handycam HDR-CX55OV camcorder and the handling time (seconds from first touch of the mussel until completion of feeding) of each crab was quantified using a stopwatch.

The water in the flume was replaced after every three trials. For each trial flume depth and temperature were recorded. Ten feeding trials were conducted for each species at a flume velocity of 10cm/s, and 13 feeding trials tested at a flow rate of 19cm/s. No individual crabs were used more than once throughout the experiment. The chosen flume velocities were based on flow velocities of *C. maenas* habitat observed in other studies [16]. Flume velocities were calibrated by observing the average time it took a 1 cm-wide paper ball to float across a set distance. Water temperature in the flume increased a significant amount across the time span of 3 trials, and was therefore included as a test variable.

4.2. Data Analysis

Two separate generalized linear regression models were selected for each flume speed due to inconsistent starvation periods (see [Table 1](#) and [Table 2](#)). Therefore, no comparisons of handling times were made across flume speeds. Models were selected using stepwise AIC selection through removal of insignificant terms with removal priority on interaction terms. The variables considered were crab species, crab size (carapace width in cm), mussel size (shell length in cm), and water temperature (°C). A Shapiro-Wilk test was used to test for normality and the residuals were analyzed to check that the data meet the assumptions of generalized linear models. All data analyses were performed using the R statistical program [23].

5. CONCLUSION

By determining how food handling times compare between a native crab and an invasive crab species, this study elucidates an important piece of the puzzle in the prediction of how community structure may change due to the *C. maenas* invasion.

Future studies should conduct observations throughout the year to better understand differing handling times due to seasonal changes in metabolism and should also examine the difference in response to olfactory cues, or a comparison of search times required to find food. This would help determine how relatively capable *C. maenas* is at tracking down food patches consisting of prey species local to the *M. gracilis* range. Better control of starvation periods and flume temperature will also allow for comparisons between water velocities, which would increase the inferences that can increase the inferences made from the statistical model.

6. ACKNOWLEDGEMENTS

This student report is dedicated to River Sidley. He was kind, fun-loving, goofy, and had a curiosity that could not be satiated. His dedication to this project was admirable and it was nothing but an honour to be able to work alongside him not only as a colleague, but as a lifelong friend. He will be sorely missed.

We would also like to thank Kylee Pawluk, Alex Clifford, Allan Roberts, Anna Smith and Brett Howard for all their insight when approached for help. Their patience and kindness were highly appreciated, especially in times of frustration. We would also like to thank the Bamfield Marine Sciences Centre for their contribution of resources and facilities.

We would like to extend a big "thank-you" to everyone in Fall Program 2014 that helped us with our specimen collection. This project would not have happened without your generosity. The time you sacrificed to collect crabs with us in the worst weather was unbelievable and your company was well appreciated.

REFERENCES

- [1] Richard N Mack, Daniel Simberloff, W Mark Lonsdale, Harry Evans, Michael Clout, and Fakhri A Bazzaz. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecological applications*, 10(3):689–710, 2000. URL <http://www.esa.org/esa/science-resources/issues-in-ecology/>.
- [2] Colin W Clark and Marc Mangel. The evolutionary advantages of group foraging. *Theoretical Population Biology*, 30(1):45–75, 1986. doi:[10.1016/0040-5809\(86\)90024-9](https://doi.org/10.1016/0040-5809(86)90024-9).
- [3] Jennifer L Funk and Peter M Vitousek. Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446(7139):1079–1081, 2007. doi:[10.1038/nature05719](https://doi.org/10.1038/nature05719).
- [4] M Jake Vander Zanden, John M Casselman, and Joseph B Rasmussen. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401(6752):464–467, 1999. doi:[10.1038/46762](https://doi.org/10.1038/46762).
- [5] Crawford S Holling. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, 91(05):293–320, 1959. doi:[10.4039/Ent91293-5](https://doi.org/10.4039/Ent91293-5).
- [6] Robert H MacArthur and Eric R Pianka. On optimal use of a patchy environment. *American Naturalist*, pages 603–609, 1966.
- [7] Robert D Holt and Burt P Kotler. Short-term apparent competition. *American Naturalist*, pages 412–430, 1987. URL <http://www.jstor.org/stable/2461893>.
- [8] Gregory John Klassen and Andrea Locke. A biological synopsis of the European Green crab, *Carcinus maenas*. *Canadian Manuscript Report of Fisheries and Aquatic Sciences*, 2007.
- [9] Sylvia Behrens Yamada and Graham E Gillespie. Will the european green crab (*carcinus maenas*) persist in the pacific northwest? *ICES Journal of Marine Science: Journal du Conseil*, 65(5):725–729, 2008. doi:[10.1093/icesjms/fsm191](https://doi.org/10.1093/icesjms/fsm191).
- [10] MA Rossong, PJ Williams, M Comeau, SC Mitchell, and J Apaloo. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). *Journal of Experimental Marine Biology and Ecology*, 329(2):281–288, 2006. doi:[10.1016/j.jembe.2005.09.007](https://doi.org/10.1016/j.jembe.2005.09.007).
- [11] Edwin D Grosholz, Gregory M Ruiz, Cheryl A Dean, Kim A Shirley, John L Maron, and Peter G Connors. The impacts of a nonindigenous marine predator in a California bay. *Ecology*, 81(5):1206–1224, 2000. URL <http://www.esajournals.org/loi/ecol>.
- [12] Andrew N Cohen, JT Carlton, and MC Fountain. Introduction, dispersal and potential impacts of the green crab *carcinus maenas* in San Francisco Bay, California. *Marine Biology*, 122(2):225–237, 1995. URL <http://link.springer.com/journal/227>.

- [13] Bruce A Menge. Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia*, 58(2):141–155, 1983. URL <http://link.springer.com/journal/442>.
- [14] Elizabeth M Robinson, Delbert L Smee, and Geoffrey C Trussell. Green crab (*Carcinus maenas*) foraging efficiency reduced by fast flows. *PLoS one*, 6(6):e21025, 2011. doi:[10.1371/journal.pone.0021025](https://doi.org/10.1371/journal.pone.0021025).
- [15] ED Grosholz and GM Ruiz. Spread and potential impact of the recently introduced European Green crab, *Carcinus maenas*, in central California. *Marine Biology*, 122(2):239–247, 1995. doi:[10.1007/BF00348936](https://doi.org/10.1007/BF00348936).
- [16] JM Orensanz, AM Parma, DA Armstrong, J Armstrong, and P Wardrup. The breeding ecology of *Cancer gracilis* (Crustacea: Decapoda: Cancridae) and the mating systems of cancrinid crabs. *Journal of Zoology*, 235(3):411–437, 1995. doi:[10.1111/j.1469-7998.1995.tb01760.x](https://doi.org/10.1111/j.1469-7998.1995.tb01760.x).
- [17] Steven Vogel. *Comparative Biomechanics: Life's Physical World*. Princeton University Press, 2013.
- [18] Francesco Rovero, Roger N Hughes, and Guido Chelazzi. When time is of the essence: choosing a currency for prey-handling costs. *Journal of Animal Ecology*, 69(4):683–689, 2000. doi:[10.1046/j.1365-2656.2000.00426.x](https://doi.org/10.1046/j.1365-2656.2000.00426.x).
- [19] M Jake Vander Zanden, John M Casselman, and Joseph B Rasmussen. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature*, 401(6752):464–467, 1999. doi:[10.1038/46762](https://doi.org/10.1038/46762).
- [20] Marlene M Martinez. Running in the surf: hydrodynamics of the shore crab *Grapsus tenuicrustatus*. *Journal of Experimental Biology*, 204(17):3097–3112, 2001. URL <http://jeb.biologists.org/content/204/17/3097.full.pdf>.
- [21] SL Hampton and CL Griffiths. Why *Carcinus maenas* cannot get a grip on South Africa's wave-exposed coastline. *African Journal of Marine Science*, 29(1):123–126, 2007. doi:[10.2989/AJMS.2007.29.1.11.76](https://doi.org/10.2989/AJMS.2007.29.1.11.76).
- [22] Alexandra Baeta, Henrique N Cabral, João C Marques, and Miguel A Pardal. Feeding ecology of the green crab, *Carcinus maenas* (L., 1758) in a temperate estuary, Portugal. *Crustaceana*, 79(10):1181–1193, 2006. doi:[10.1163/156854006778859506](https://doi.org/10.1163/156854006778859506).
- [23] R Core Team. R: A language and environment for statistical computing. vienna, austria: R foundation for statistical computing; 2014, 2014. URL <http://www.R-project.org/>.

FIGURES

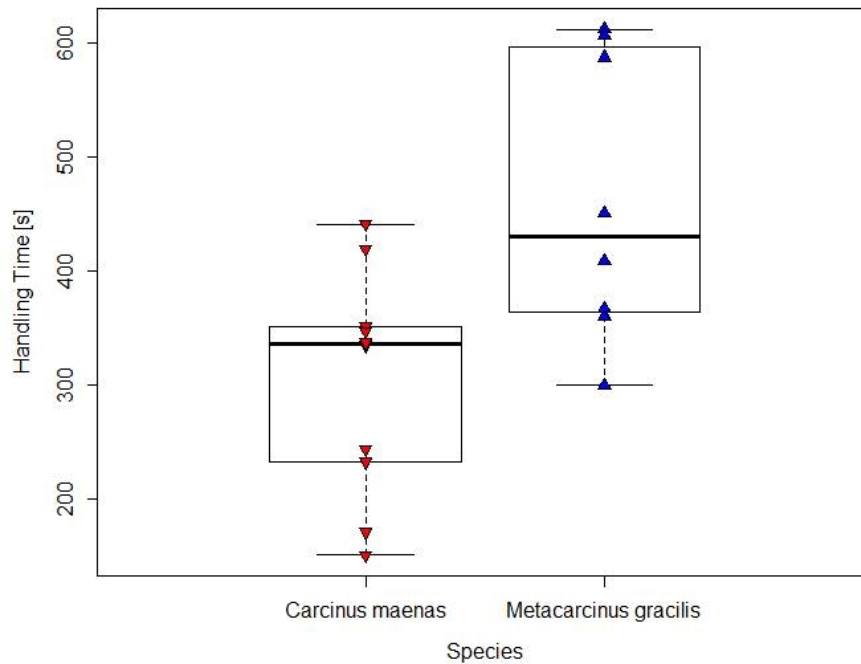


Figure 2: Handling times of *C. maenas* ($N = 10$) and *M. gracilis*, ($N = 8$) at a flume speed of 10cm/s with an overlaying scatterplot of the data points. Red, downward-facing triangles represent data points of *C. maenas* whereas blue, upward-facing triangles represent data for *M. gracilis*. Bold line represents the median, top and bottom of the box represent the location of the upper and lower quartile respectively. Whisker lines represent the maximum and minimum values, excluding outliers.

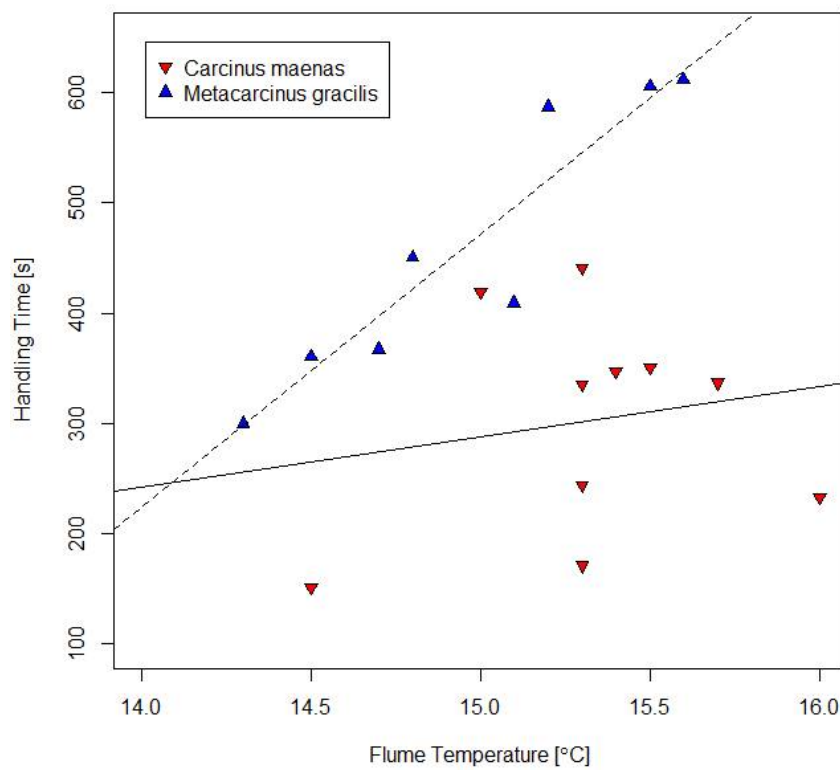


Figure 3: Handling times of both *C. maenas* and *M. gracilis* at a flume speed of 10cm/s as temperature increases. The dashed line represents the trend line for *M. gracilis* data ($r^2 = 0.034$, $Y = 46.03x - 402.68$), while the solid line represents the trend line for *C. maenas* data ($r^2 = 0.87$, $Y = 247.7x - 3245.2$).

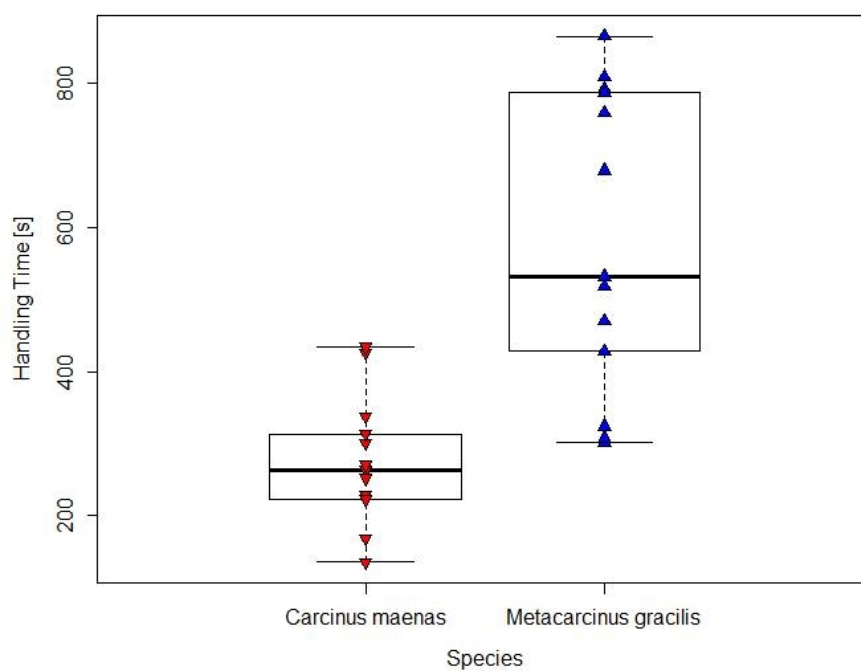


Figure 4: Handling times of *C. maenas* ($N = 13$) *M. gracilis* ($N = 13$) at a flume speed of 19cm/s with an overlaying scatterplot of the data points. Red, downward-facing triangles represent data points of *C. maenas* whereas blue, upward-facing triangles represent data for *M. gracilis*. Bold line represents the median, top and bottom of the box represent the location of the upper and lower quartile respectively. Whisker lines represent the maximum and minimum values, excluding outliers.

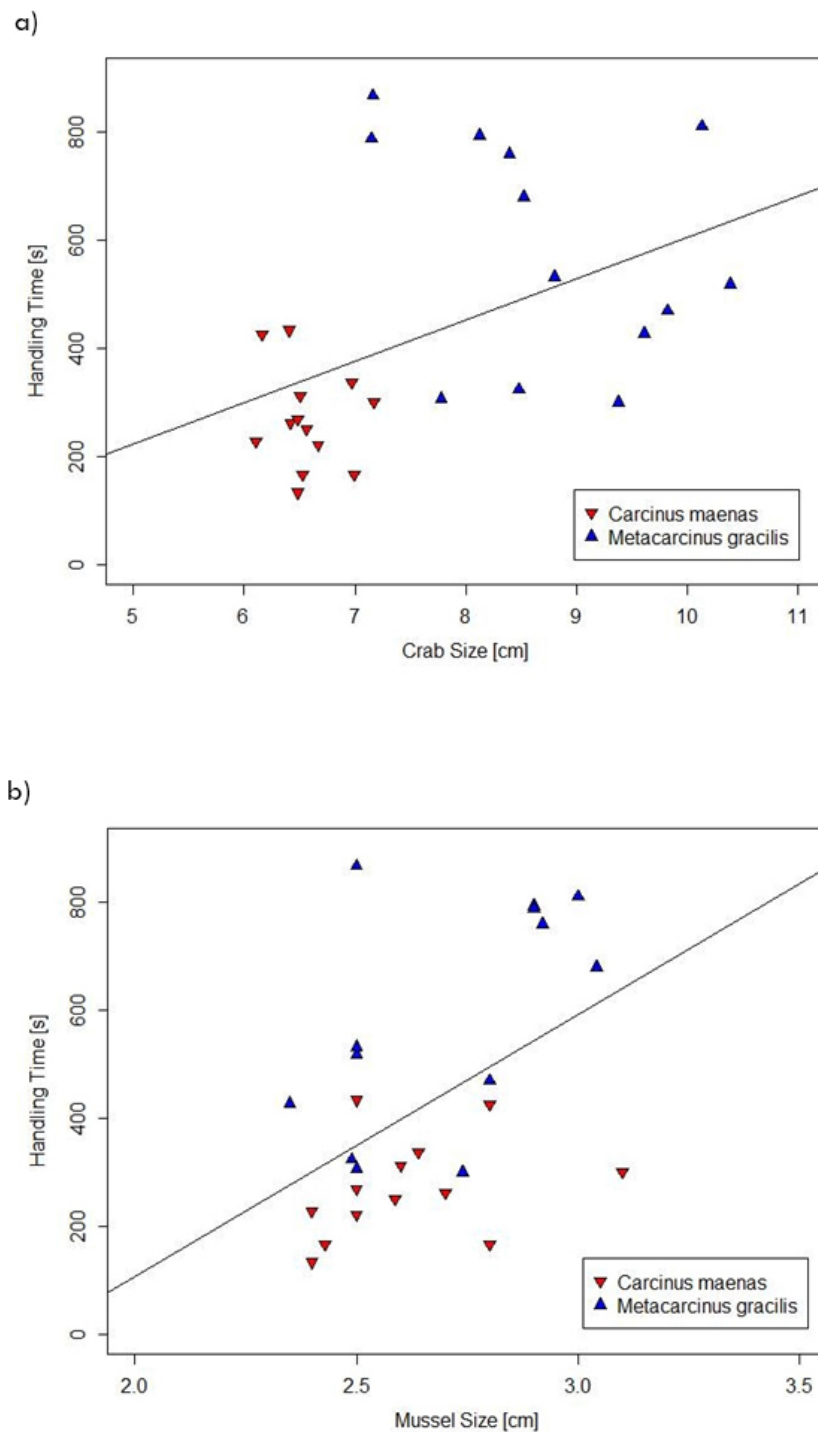


Figure 5: a) Scatterplot of the handling times of both *C. maenas* and *M. gracilis* at a flume speed of 19cm/s with crab size. The line represents the line of best fit ($r^2 = 0.21$, $Y = 76.37x - 158.59$). b) Scatterplot of the handling times of both *C. maenas* and *M. gracilis* at a flume speed of 19cm/s with mussel size. The line represents the line of best fit ($r^2 = 0.22$, $Y = 484.2x - 860.20$).