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Claw biomechanics and scaling in the brown box crab (Lopholithodes foraminatus)

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Claw biomechanics and scaling in the brown box crab (*Lopholithodes foraminatus)*

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Emily Lucas

Committee in charge:

Professor Jennifer Taylor, Chair
Professor Deirdre Lyons
Professor Martin Tresguerres

2025

The Thesis of Emily Lucas is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2025

DEDICATION

To my friends, family, and wonderful advisor Jennifer Taylor, ahi’yihe and thank you. I would have not made it this far alone. This thesis is dedicated to you, and to those who fight every day to protect Oak Flat/Chi’chil Bildagoteel and all other sacred spaces. Save Oak Flat.

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Thank you to my committee members, Dr. Martin Tresguerres, Dr. Deirdre Lyons, and most especially my wonderful and deeply patient advisor, Dr. Jennifer Taylor. Thank you to all the members of the Taylor Lab, to Dr. Carolynn Culver at California Sea Grant for sharing her expertise on brown box crabs and for coordinating with local fishers to collect animals, and to Phil Zerofski and Christine Steinke for animal husbandry and aquarium maintenance support. Lastly, thank you to all my family and friends who have been there for me throughout this journey, especially Summer Webb, for her words of wisdom and sharp editing, Andrew Yang, for his graphical prowess, and Will Lucas, for his skill with the finer arts of Powerpoint.

ABSTRACT OF THE THESIS

Claw biomechanics and scaling in the brown box crab (*Lopholithodes foraminatus)*

by

Emily Lucas

Master of Science in Marine Biology

University of California San Diego, 2025

Professor Jennifer Taylor, Chair

Crustacean claws can provide vital information about a species' lifestyle, including its feeding, agonistic interactions, defense strategies, and mating behaviors. Claw biomechanics are a good starting point for exploring the biology and ecology of a species, such as the brown box crab, *Lopholithodes foraminatus*. This species has an unusual morphology, a broad geographic and depth distribution, and is an experimental fishery in Southern California, yet little is known about their basic biology and ecology. Here we characterized claw scaling and biomechanics of *L. foraminatus* to establish fundamental traits associated with their feeding ecology. Specifically, we determined the scaling relationships of morphological (claw height, mechanical advantage) and mechanical (denticle hardness and stiffness, pinch force) claw properties of male and female crabs across a range of sizes (44.5-137.0 mm carapace width). We found that the crusher claw height scales with different allometries between sexes, while the cutter claw height scaled similarly, with slight negative allometry. This aspect of claw morphology does not appear to influence the biomechanics of the claws. Mechanical advantage did not scale with body size, though it was slightly larger for male crabs than female crabs. Neither the denticle mechanical properties nor the claw pinch force scaled with body size. Male crabs spanning a range of sizes generated large pinch forces that are sufficient to break hard mollusk shells. These results indicate that the claw biomechanics of *L. foraminatus* do not differ much between sexes nor do they change significantly as crabs grow larger, suggesting that they can support a consistently durophagous diet throughout their adult life.

INTRODUCTION

The brown box crab, *Lopholithodes foraminatus,* is a species of king crab (family Lithodidae) characterized by specialized morphology that permits their appendages to fold perfectly against the body, like a 3-dimensional puzzle. When folded, their chelipeds and adjacent pereopods (walking legs) join and form a circular opening, or foramen, on each side that is thought to enable flow to the gills for respiration when buried in sediment (NOAA, 2024). This tight ball or box-like structure, combined with a robust exoskeleton, affords protection against predators without having to use their claws. The claws, or chelae, may potentially be used primarily for feeding rather than defense, however, their proper fit against the body bestows a unique morphology that influences their biomechanics and function. The link between morphology and function is well-established in crustacean claws (Mariappan et al, 2000), and their biomechanics is a primary driver of a species' ecology, governing their diet, defenses, and how they interact with their physical environment (Schenk and Wainright, 2001). Therefore, study of the claw biomechanics of *L. foraminatus* can provide insights into the biology and ecology of this remarkable, yet poorly studied species.

Compared to other king crabs, *L. foraminatus* has a broad distribution along the Eastern Pacific, extending from the Aleutian Islands, Alaska to San Diego, CA. It is also eurybathic, occupying depths from 0 – 1795 m, though it is typically found between 18-574 m (Chevaldonné and Olu, 1996; Zhang et al., 2023). Other king crab species are known to locomote over large distances and depths (Alaska Department of Fish and Game, 2024), but the relatively stubby pereopods of *L. foraminatus* suggest that they may not travel as far, though little is known about their migratory behavior. Across their geographic and depth distribution, *L. foraminatus* encounters diverse predators and prey, although yet again, little is known about these interactions (Jørgensen and Spiridonov, 2013).

Like many other decapod crustaceans, the claws of *L. foraminatus* grow allometrically and differentiate into a major (“crusher”) and a minor (“cutter”) claw following an animal’s puberty molt. The asymmetrical claws are morphologically and functionally distinct. The crusher claw is specialized for generating large forces, so it tends to be taller, with longer in-levers and a greater closer muscle cross-sectional area (Schenk and Wainwright, 2001). In contrast, the cutter claw is generally specialized for tearing and is characterized by its smaller size, longer out-levers, and smaller closer muscle cross-sectional area (Schenk and Wainwright, 2001). Additionally, both claws have a series of denticles on the pollex, or fixed finger, of the claw. These irregularly spaced, toothlike structures help with prey handling and defense (Rosen et al, 2020), but also differ between claw types; the crusher has molariform denticles while the cutter claw has smaller and sharper denticles (Mariappan et al, 2000). Denticles on the crusher claws of durophagous species generally have a large surface area that is abrasion resistant and more phosphorous to increase hardness, both features that enable repeated shell-crushing (Inoue and Nakazato, 2023).

In crab claws, the dactyl (moveable finger) rotates at a fulcrum located at the proximal intersection of the dactyl and pollex (fixed finger), to close the claw and generate force (Fig. 1). The propodus makes up the majority of the claw and is composed of the pollex and the manus, or palm of the claw. Inside the propodus is the claw closer muscle. The workings of the claw rely largely on lever mechanics. The force is determined by geometry and can be measured in terms of mechanical advantage. The crusher claws can produce large pinch forces that frequently correlate with body size, with the largest crab species, the coconut crab, *Birgus latro*, producing forces up to 90 times its own body weight (Inoue et al, 2021), although this metric varies greatly from species to species. Notably, in species that generate large forces, the crusher claw develops to have a greater mechanical advantage (MA), which means that force output is amplified. Greater MA is achieved by having a longer input lever relative to output lever. The input lever is approximately the height of the dactyl at the fulcrum, while the output lever is the length of the dactyl (Fig.1). Thus, a relatively short dactyl with a thicker base will have a greater MA and thus generate a larger force. This is a simplification, however, as MA is also related to the cross-sectional area of the claw (Schenk and Wainwright, 2001). The physiological cross-sectional area of the closer muscle within the claw determines the force input, and the greater the area, the greater the force. This translates to a claw with larger external dimensions. Previous studies have demonstrated that claw dimensions, height in particular, are a good predictor of claw pinch force (Claussen et al, 2008).

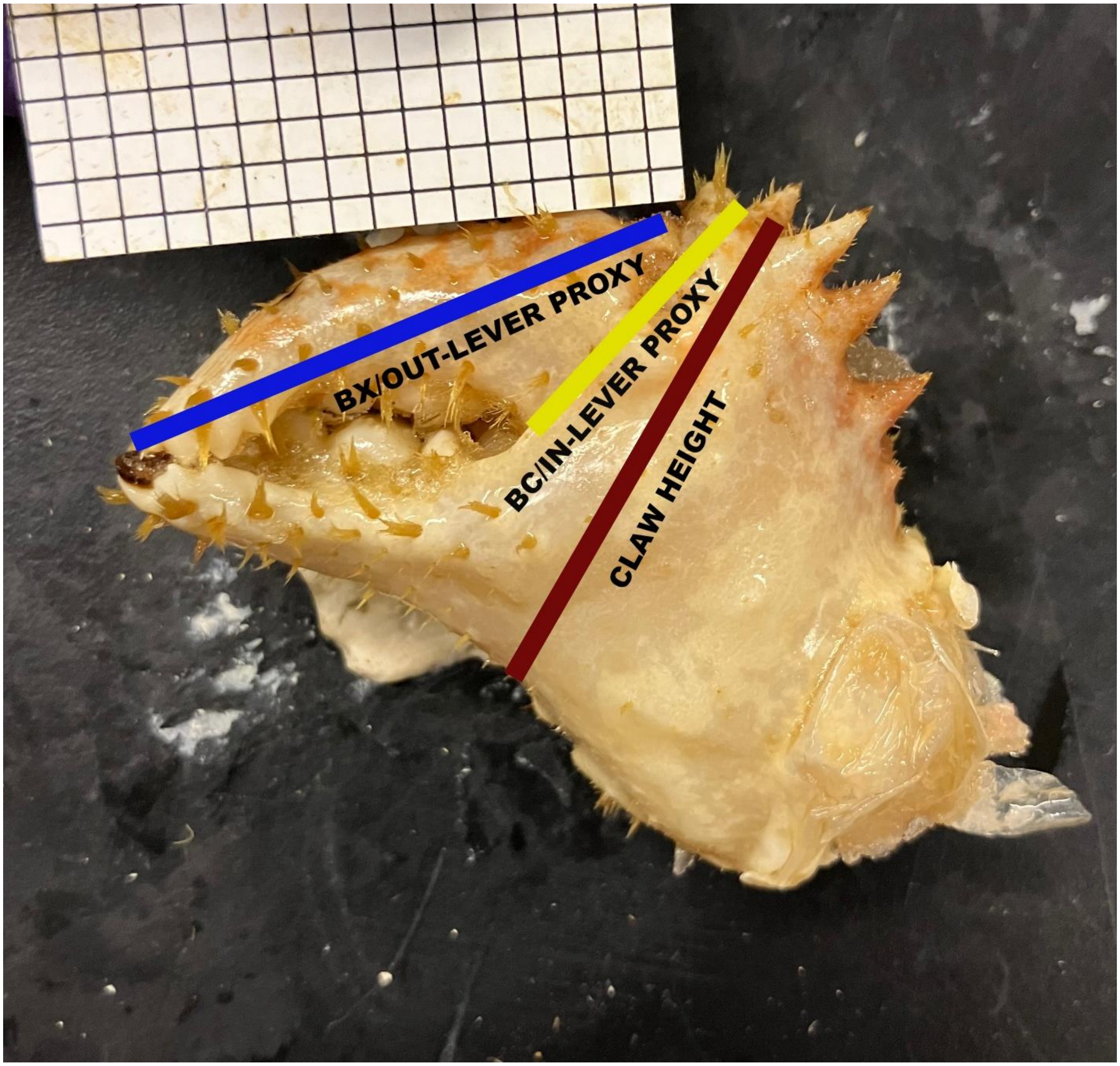

Figure 1: Internal side of a crusher claw showing measurements for claw height (red), BC/in-lever proxy (yellow), and BX/out-lever proxy (blue).

Because claw morphology dictates force production, it is also strongly linked to diet. In a study of six brachyuran crab species, Schenk and Wainwright (2001) found that the crusher claws of molluscivorous species, like xanthid crabs, were larger and stronger than those of non-molluscivores and had the largest mechanical advantages of the species being sampled.

Meanwhile, species with a more diverse diet, like the blue crab (*Callinectes sapidus*), had a more general claw shape, while the spider crab *Libinia emarginata*, which primarily consumes algae, had much smaller and weaker claws that showed little dimorphism (Schenk and Wainwright, 2001). Laboratory observations indicate that *L. foraminatus* primarily consumes hard-shelled mollusks (Stroud, 2022), and they readily consume mussels and clams in the lab, both of which have high crushing strength (Moretto, 2024). While the breadth of their diet in nature is unknown, it can be inferred that *L. foraminatus* crusher claw morphology facilitates the generation of large forces.

The strong selective pressures that shape the structure and function of crustacean claws make them an excellent proxy for studying the interplay between morphology and ecology (Schenk and Wainwright, 2001). Characterizing the claw biomechanics of king crab species, like the box crab, would generate new insights into the biology and ecology of these valuable fisheries species. Therefore, the objective of this study was to characterize the claw biomechanics of brown box crabs, *L. foraminatus,* to gain a better understanding of their ecological role in Southern California and contribute to their assessment as an experimental fishery (Southwest Fisheries Science Center, 2023).

MATERIALS AND METHODS

2.1 Animal Collection

Eighteen live brown box crabs, *Lopholithodes foraminatus*, were collected May -August 2022 by local fishers using baited traps at 100-250 m depth offshore of Cortes Bank, California, USA (32.4667° N, 119.1667°), where bottom temperatures ranged between 9-12°C (Southwest Fisheries Science Center, 2023). Crabs were immediately transported to the experimental aquarium at Scripps Institution of Oceanography (SIO), La Jolla, CA, where they were held in a large communal tank that received flow-through seawater pumped from the SIO pier and chilled to 9°C. Animals were fed live mussels (*Mytilus californianus*) once per week. These live crabs included 15 males (111.0 - 135.0 mm carapace width) and 3 females (96.0- 111.0 mm carapace width) and were used for claw pinch force measurements.

Morphological measurements were carried out on crabs that were previously collected by fishers off Cortes Bank, California, USA (32.4667° N, 119.1667°) and stored in a -20°C freezer. A total of 40 individuals were measured, including 20 male (47.0 - 137.0 mm carapace width) and 20 females (44.5 - 105.0 mm carapace width).

2.2 Morphological measurements

All crabs were fully defrosted prior to morphological measurements. Carapace width (CW) was measured at the widest part, to the nearest 0.05 mm using calipers. For claw measurements, both chelipeds were excised at the coxal-basal joint. Claw height (CH) was measured at the widest part of the propodus on both the crusher and cutter claws, also to the nearest 0.05 mm using calipers (Fig.1). Mechanical advantage (MA) was calculated by measuring the input (BC) and output (BX) levers for the external and internal sides of both claws and calculating BC/BX (Fig.1) (Schenk and Wainwright, 2001).

2.3 Denticle nano-mechanical properties

Denticle nano-mechanical properties were tested on 17 previously frozen crabs (male, N = 9, 44.5 mm- 94.0 mm CW; female, N = 8, 47.0 mm - 137.0 mm CW). Ideally, mechanical tests would be conducted on freshly euthanized samples, however, no degradation or effect of freezing on the exoskeleton was observed. Therefore, all samples were frozen for consistency. Additionally, initial tests on fresh, unfrozen samples showed that the nanomechanical properties were similar between fresh and frozen samples.

Once thawed, the pollex was cut from the propodus at the most proximal edge using a rotary tool (Dremel 4000, Robert Bosch Tool Corp., Mt. Prospect, IL, USA) with a 22 mm diamond cutting wheel. For larger crabs, the distal tips of the pollex were further cut with the Dremel to fit in the silicon bead molds (16 mm^3). Samples were carefully placed individually in square wells of the mold so that the largest, most proximal denticle was facing upward. Epoxy resin (EpoxiCure, Buehler, Lake Bluff, IL, USA) was added to the mold to a height below the base of the largest denticle. Samples were then covered in a seawater-soaked paper towel and stored in a sealed plastic container to keep damp while the epoxy cured for 24 hours. The next day, embedded denticles were sanded with 200 grit and 800 grit ultra-fine sandpaper to create a smooth, flat surface for nanoindentation. Embedded samples were kept hydrated with a seawater-soaked paper towel until testing.

Embedded denticles were affixed to an aluminum block using cyanoacrylate and then indented using a nanoindenter (Nanovea, Irvine, CA, USA) equipped with a Berkovich tip.

Indents were performed on the sanded surface of the denticle using a load of 80 mN at a loading and unloading rate of 160 mN/min. Each denticle was indented six times and the hardness and elastic modulus (GPa) were averaged for each sample.

2.4 Pinch Force

Pinch force measurements were taken from the crusher claw of 17 box crabs (male, N = 14, 111.0 mm - 135.0 mm CW, female, N = 2, 96.0 mm - 111.0 mm CW) following the methods of Singh et al. (2000). Crabs were situated on a wooden platform with their pollex placed underneath a curved metal bracket. The dactyl of the claw was then positioned on a hook connected to a force sensor (CI-6537, ± 50 N range, PASCO, Roseville, CA, USA). The force sensor was affixed to a ring stand so that the distance between the hook and the bracket could be adjusted to fit approximately 75% of maximum claw gape. The claw was positioned so that the pinch force was exerted from the middle of the pollex. Crabs readily pinched their claws and the force was recorded using the PASCO Capstone software. Peak pinch force was identified as the highest peak value on the force output curve. In addition, steady pinch force was calculated as the average pinch force exerted over 10 - 20 seconds of holding.

2.5 Statistical Analysis

All statistical analyses were conducted using R 4.3.1 (R Core Team, 2023) and RStudio (RStudio Team, 2023). The scaling relationship of each morphological (claw height and MA) and mechanical (denticle hardness and stiffness, peak and steady pinch force) variable was determined for male and female crabs using ordinary least squares regression on log-transformed data. Carapace width was used as the metric for body size, so the scaling exponents, or slopes, of linear dimensions are expected to be 1 for isometry. Each measurement variable, excluding claw pinch force, was compared between sexes using ANCOVA with sex as a covariate.

RESULTS

3.1 Claw Morphology

Claw height of the crusher claw scaled differently for male and female crabs (Fig. 2). For males, crusher claw height scaled with positive allometry (slope = 1.24, $R^2 = 0.955$, F = 315.89, $p < 0.001$) and for females it scaled with negative allometry (slope = 0.892, $R^2 = 0.884$, F = 91.10, $p < 0.001$). Despite these different scaling relationships, the relative size (claw height) of crusher claws was the same for both sexes (ANCOVA, df = 27, F = 3.527, p = 0.071) (Tables 1, 2). Cutter claws, on the other hand, scaled with negative allometry for both sexes (males: slope = 0.924, $R^2 = 0.731$, F = 40.68, $p < 0.001$; females: slope = 0.86, $R^2 = 0.721$, F = 36.139, $p < 0.001$) (Fig. 3) and the relative height of the cutter claw was the same for both male and female crabs (ANCOVA, df = 29, F = 0.716, p = 0.404) (Tables 1, 2).

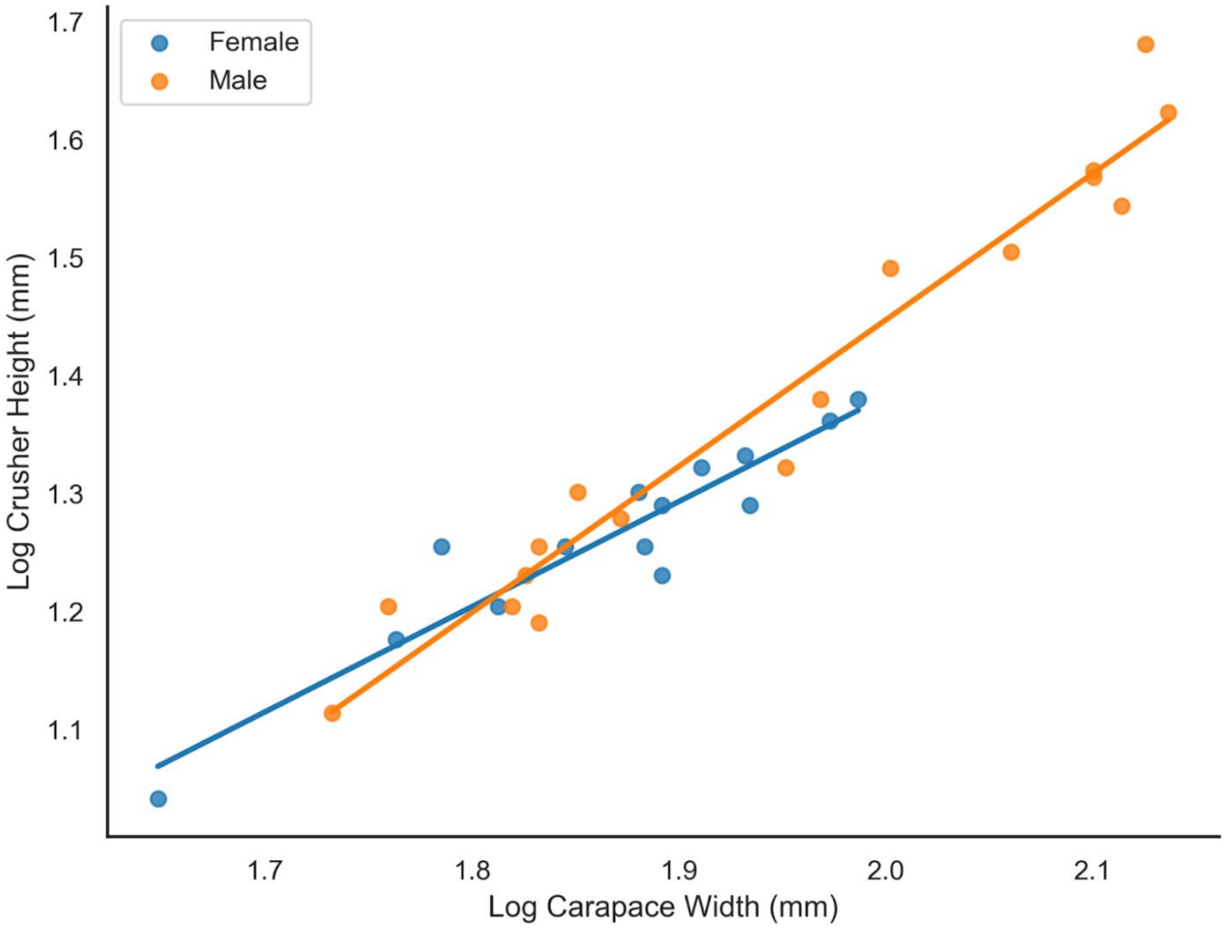

Figure 2: Crusher claw height scales allometrically and differs between sexes. It grows with slight negative allometry (slope = 0.89) in female crabs (blue), but with positive allometry (slope = 1.24) in male crabs (orange).

Table 1: Summary of mean values ± standard deviation of each variable measured for female and male crabs. N is sample size.

	Female		Male	
	N	mean ± s.d.	N	mean ± s.d.
Crusher				
Claw height (mm)	14	18.7 ± 3.4	17	26. 0 ± 10.8
Internal MA	14	0.42 ± 0.06	14	0.43 ± 0.07
External MA	14	0.39 ± 0.05	14	0.43 ± 0.05
Cutter				
Claw height (mm)	16	13.8 ± 2.9	17	17.0 ± 6.39
Internal MA	16	0.32 ± 0.04	17	0.34 ± 0.05
External MA	16	0.31 ± 0.04	17	0.34 ± 0.04
Denticle				
Hardness (GPa)	8	5.96 ± 2.88	9	6.75 ± 2.73
Stiffness (GPa)	8	80.8 ± 33.1	9	106 ± 35.4
Pinch force				
Peak (N)	2	37.2 ± 20.3	14	37.6 ± 13.5
Steady (N)	2	16.2 ± 0.60	9	27.1 ± 14.5

Table 2: Summary statistics of ANCOVA analyses. Carapace width (CW) was the predictor and sex was a covariate.

	df		**F**	**P**
Crusher				
claw height	27	CW	520.703	<0.001
		Sex	3.527	0.071
		CW:Sex	7.752	0.010
internal MA	24	CW	0.038	0.848
		Sex	0.300	0.589
		CW:Sex	1.78	0.193
external MA	14	CW	0.000	0.996
		Sex	6.175	0.020
		CW:Sex	4.205	0.051
Cutter				
claw height	29	CW	84.504	<0.001

Continued Table 2: Summary statistics of ANCOVA analyses. Carapace width (CW) was the predictor and sex was a covariate.

		Sex	0.716	0.404
		CW:Sex	0.074	0.788
internal MA	29	CW	0.308	0.583
		Sex	2.063	0.162
		CW:Sex	1.62	0.213
external MA	28	CW	0.885	0.355
		Sex	4.152	0.051
		CW:Sex	0.260	0.614
denticle stiffness	13	CW	1.066	0.321
		Sex	0.168	0.689
		CW:Sex	0.475	0.503
denticle hardness	13	CW	1.561	0.234
		Sex	1.397	0.258
		CW:Sex	0.704	0.417

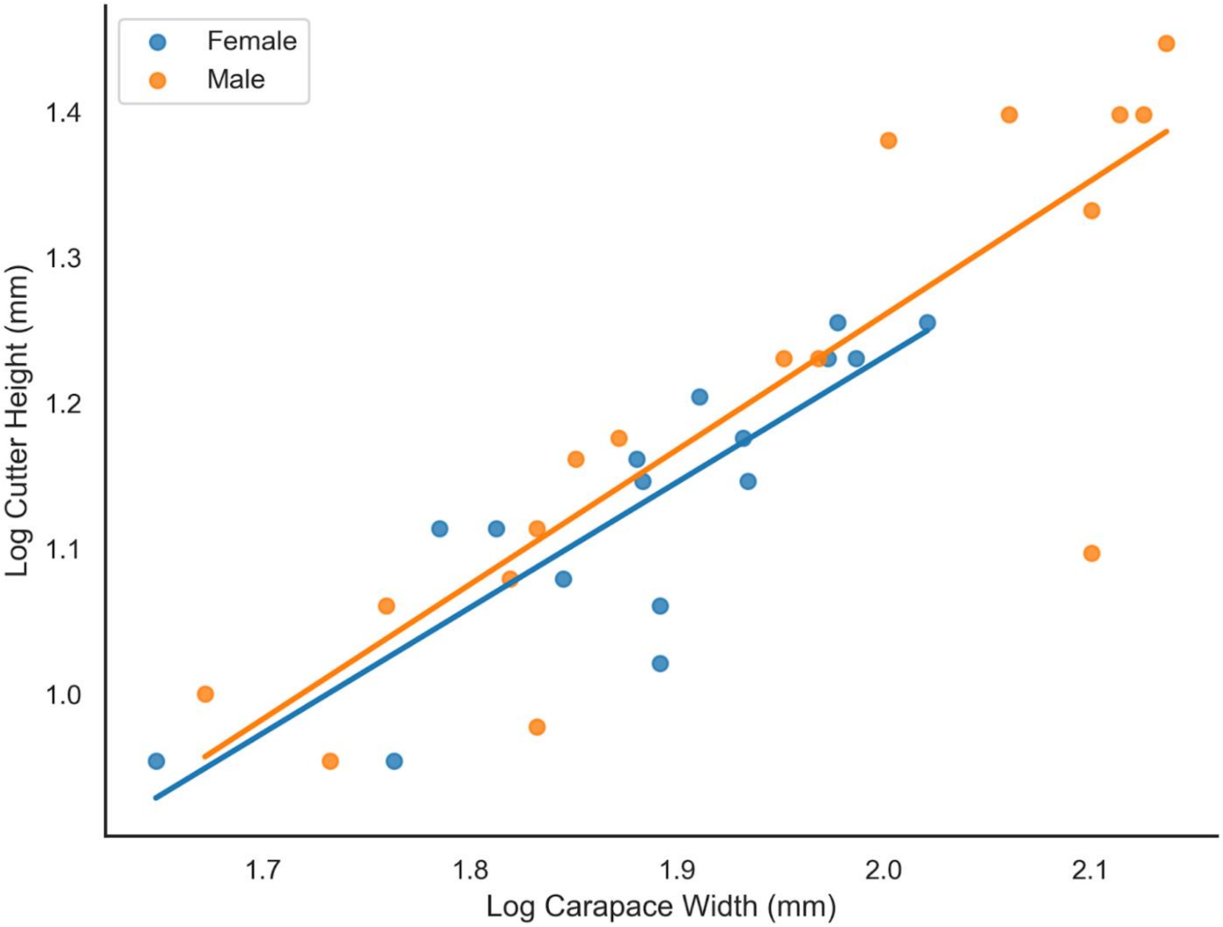

Figure 3: Cutter claw height scales allometrically and is similar between sexes. Both female (blue) and male (orange) crabs scale with slight negative allometry (slope = 0.86, 0.92, respectively).

Mechanical advantage (MA) of the internal side of the crusher claw was not predicted by body size for either sex (males: slope = 0.098, $R^2 = 0.039$, F = 0.490, p = 0.497; females: slope = 0.211, $R^2 = 0.113$, F = 1.522, p = 0.241) (Fig. 4), nor did it differ between males and females (ANCOVA, df = 24, F = 0.300, p = 0.589) (Tables 1, 2). The same was true for MA measured from the external side of the claw for males (slope = 0.057, $R^2 = 0.024$, F = 0.300, p = 0.594), but females had a near significant correlation with body size (slope = 0.319, $R^2 = 0.278$, F = 4.612, p = 0.053) and had a more widely ranging MA than males (ANCOVA, df = 14, F = 6.175, p = 0.020) (Tables 1, 2) (Fig.5).

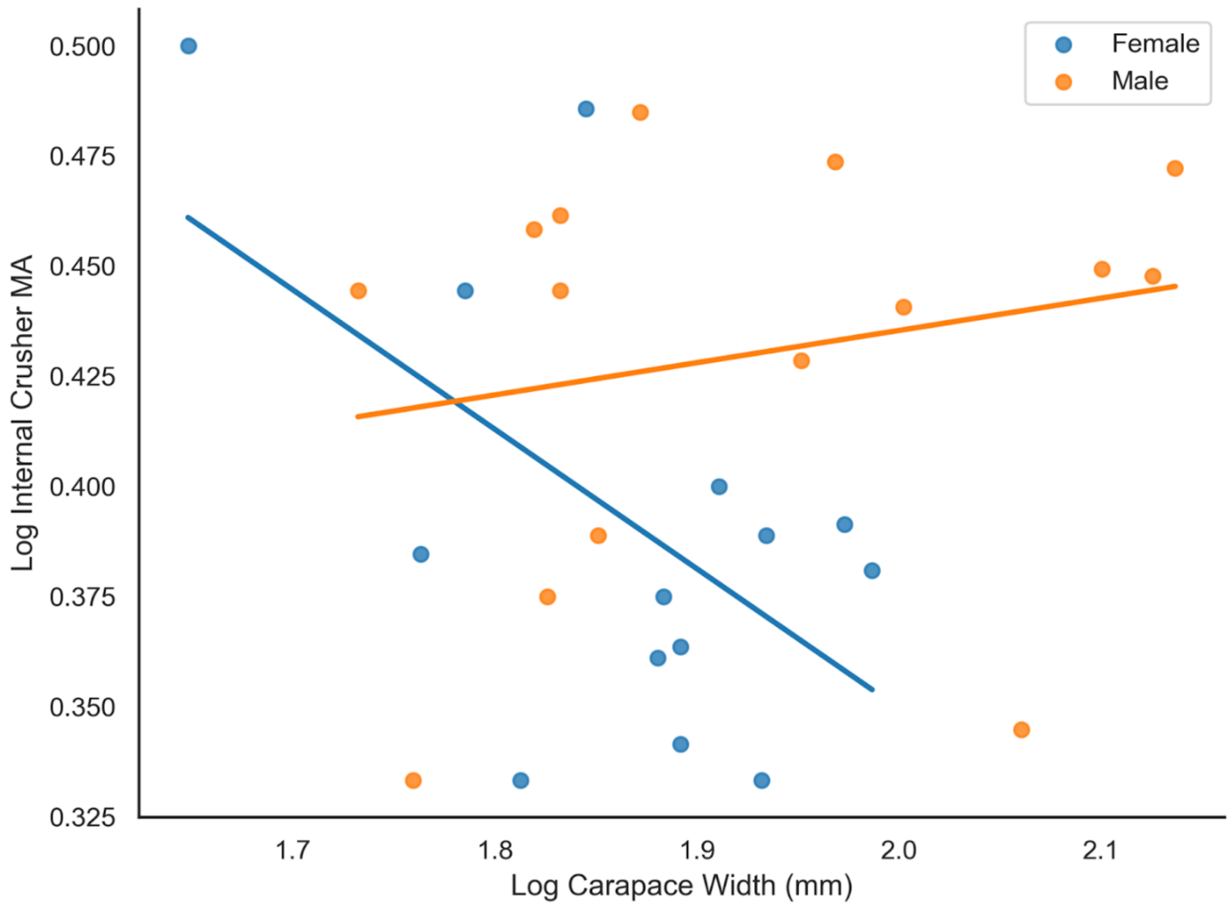

Figure 4: Crusher claw internal MA does not scale with carapace width and is the same for both female (blue) or male (orange) crabs.

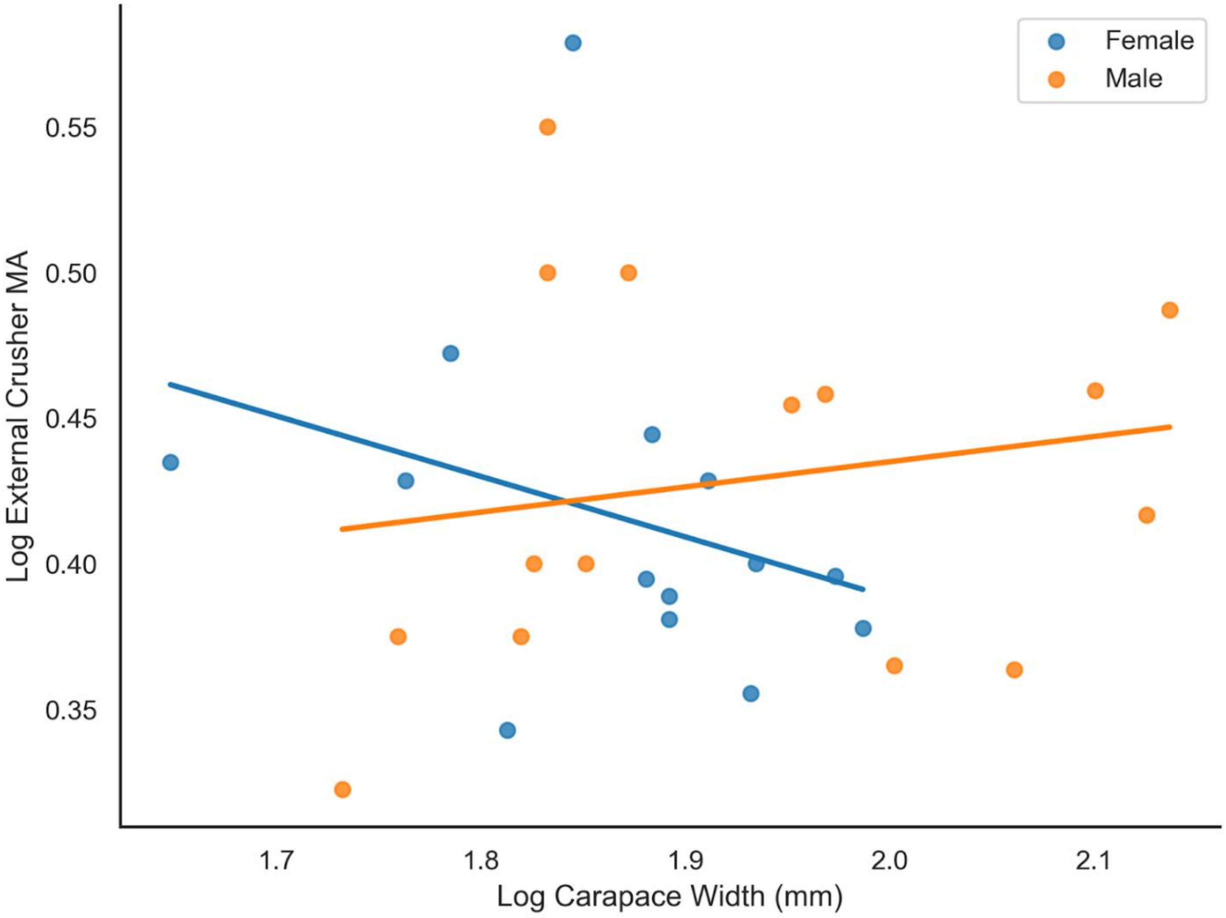

Figure 5: Crusher claw external MA did not scale with carapace width for males (orange), but had near significant negative allometry for females (blue). Female crabs had a lower MA than male crabs.

Cutter claw internal MA was not correlated with carapace width for either male or female crabs (males: slope = 0.220, R^2 = 0.072, F = 1.168, p = 0.297; females: slope = 0.169, R^2 = 0.087, F = 1.333, p = 0.268) (Table 2)(Fig. 6) and it did not differ between sexes (ANCOVA, df = 29, F = 2.063, p = 0.162) (Tables 1, 2). Similarly, MA measured from the external side of the cutter claw was not correlated with carapace width for either male or female crabs (males: slope = 0.011, R^2 = 0.001, F = 0.0169, p = 0.899; females: slope = 0.093, R^2 = 0.030, F = 0.438, p =

0.519), and there was a nearly significant difference between sexes, with female MA trending smaller than males (ANCOVA, df = 28, F = 4.152 p = 0.051) (Fig. 7) (Tables 1, 2).

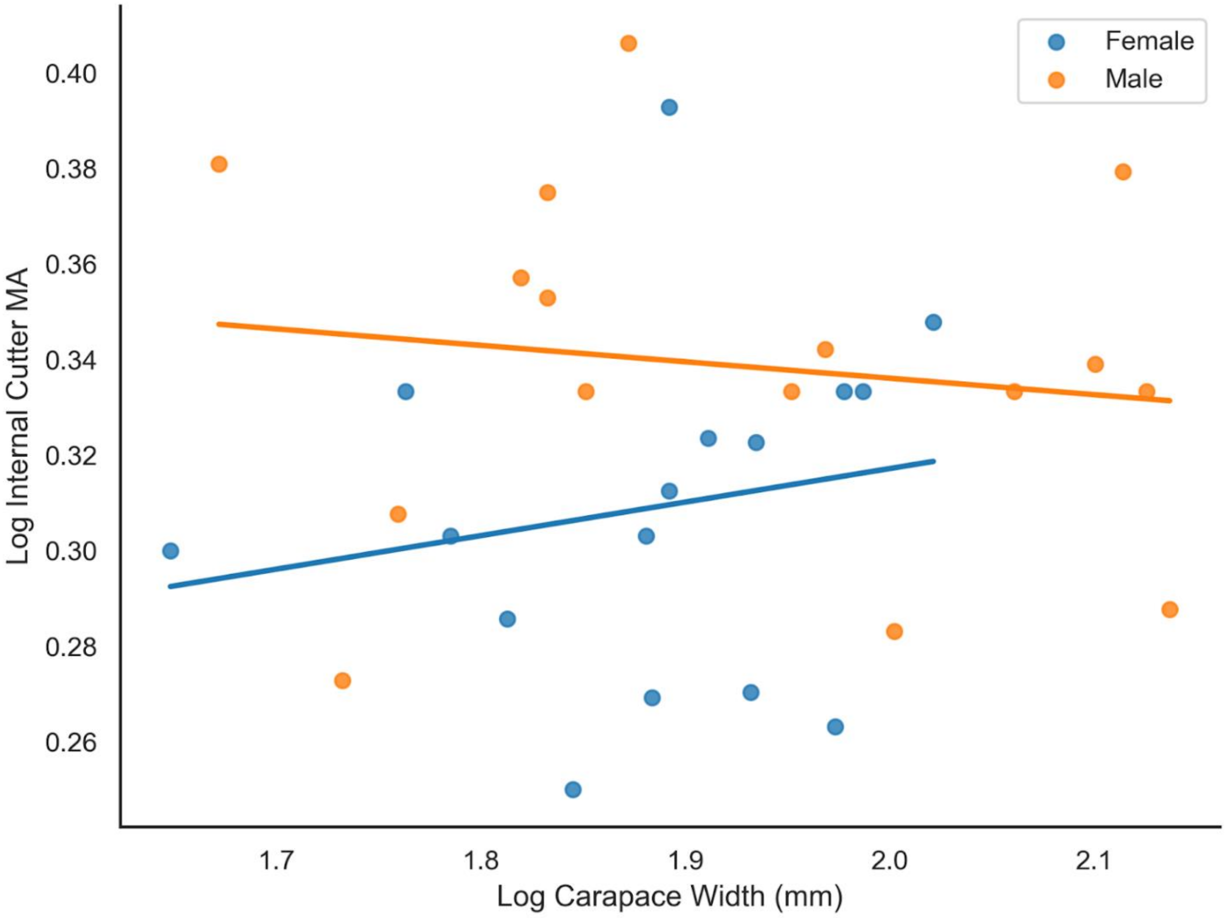

Figure 6: Cutter claw internal MA does not scale with carapace width and is the same for both female (blue) or male (orange) crabs.

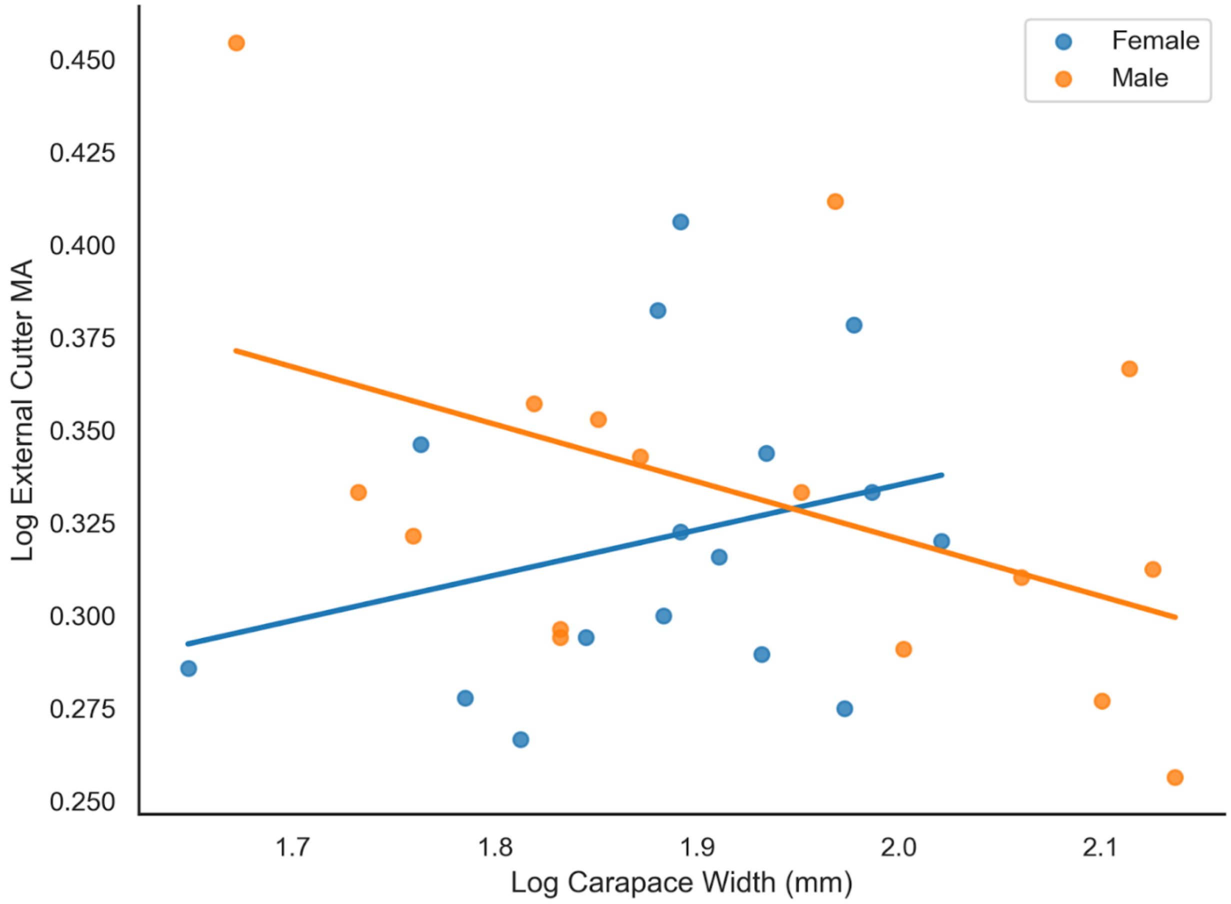

Figure 7: Cutter claw external MA does not scale with carapace width and trends smaller for female (blue) than male (orange) crabs.

3.2 Claw mechanics

Hardness of the large, proximal denticle on the crusher claw did not correlate with body size for either male or female crabs (males: slope = 0.201, R^2 = 0.033, F = 0.239, p = 0.640; females: slope = 0.948, R^2 = 0.101, F = 0.677, p = 0.442), nor did it differ between sexes (ANCOVA, df = 13, F = 1.397, p = 0.258) (Fig. 8). Denticle stiffness also showed no correlation with body size for either male or female crabs (males: slope = 0.903, R^2 = 0.015, F = 0.108, p =

0.752; females: slope = 0.752, $R^2 = 0.117$, F = 0.796, p = 0.407), nor did it differ between sexes (ANCOVA, df = 13, F = 0.168, p = 0.689) (Tables 1, 2).

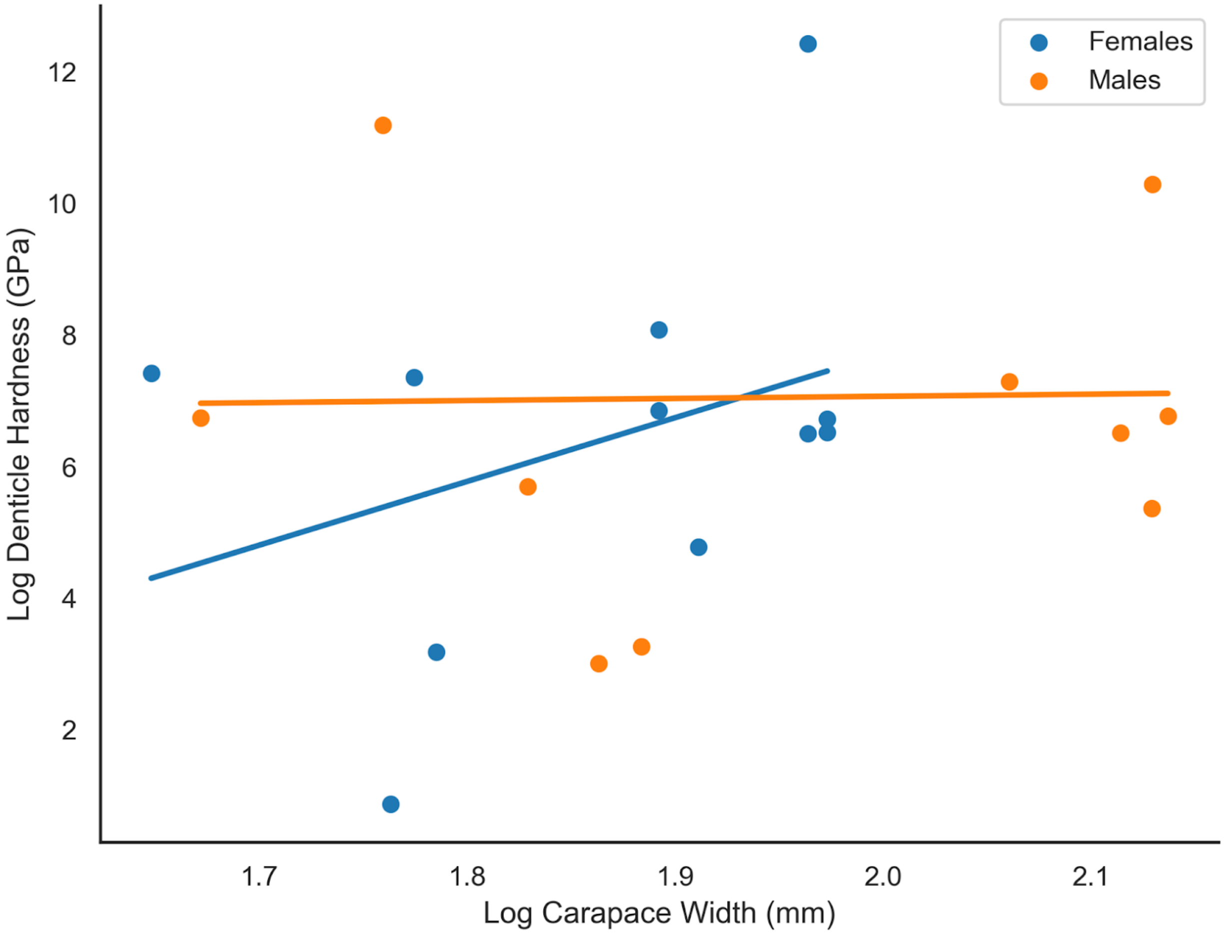

Figure 8: Denticle hardness does not scale with carapace width and is the same for female (blue) and male (orange) crabs.

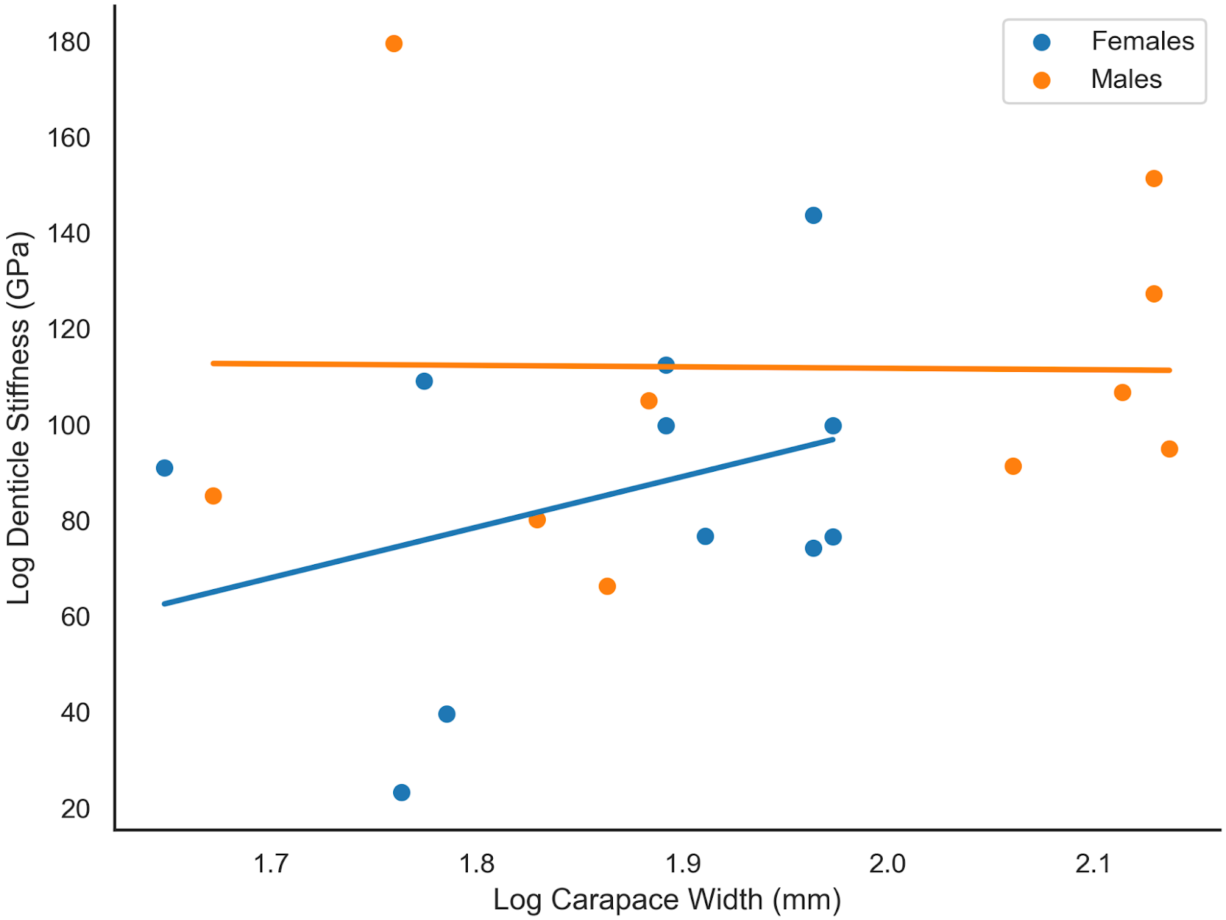

Figure 9: Denticle stiffness does not scale with carapace width and is the same for female (blue) and male (orange) crabs.

Neither peak nor steady pinch force by the crusher claw correlated with carapace width in male crabs (peak: slope = 0.449, R^2 = 0.007, F = 0.0818, p = 0.780; steady: slope = 0.047, R^2 = 0.000, F = 0.0002, p = 0.990) (Fig. 10). The sample size for female crabs was too low to assess scaling (N = 2), but the mean values were similar to those of male crabs (Tables 1, 2).

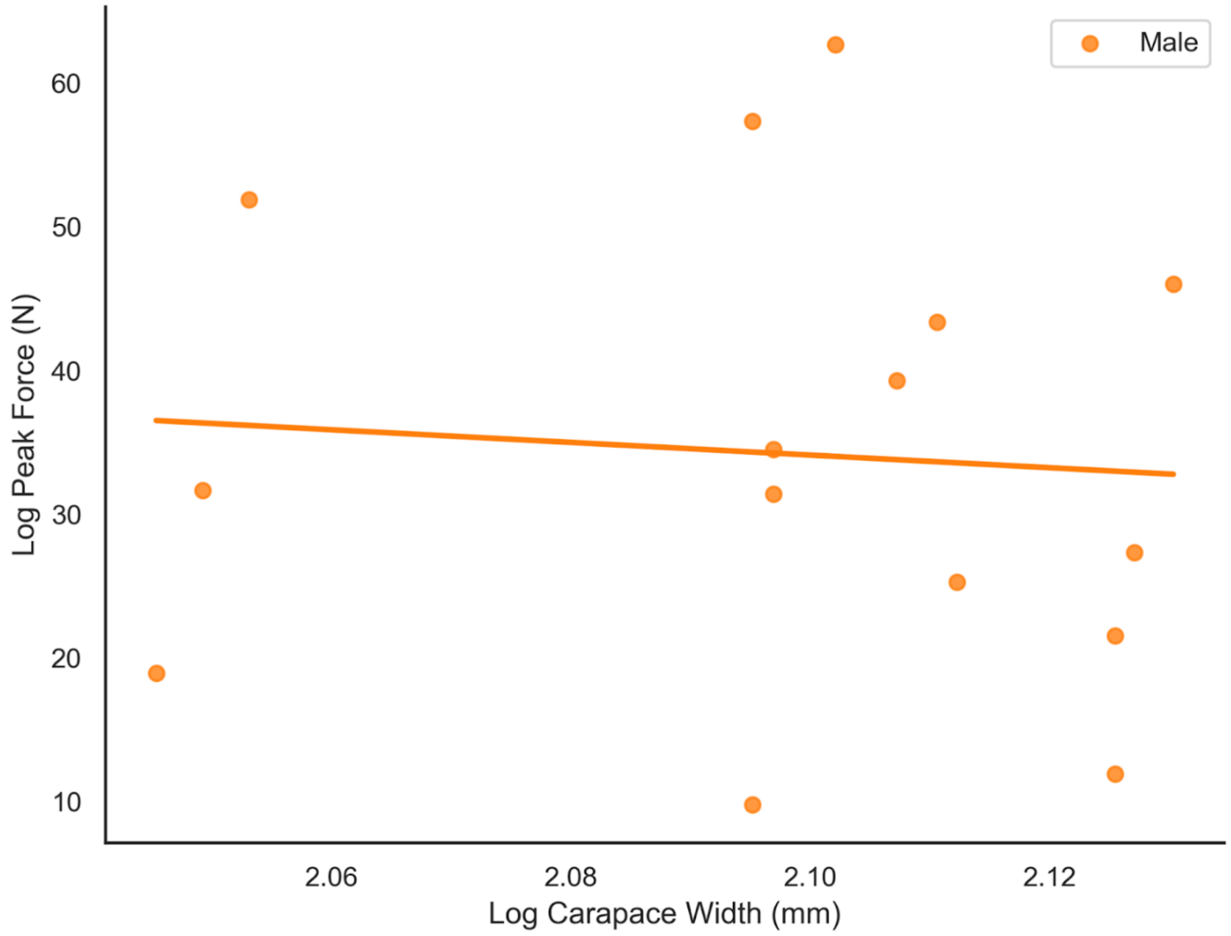

Figure 10: Peak pinch force does not scale with carapace width in male crabs.

DISCUSSION

Crustacean claws are an iconic example of the important link between form and function. They also provide fundamental insights into a species' ecology. With this in mind, we studied the claw biomechanics of the brown box crab, *L. foraminatus*, which has an unusual morphology, a broad distribution, and is of economic importance, yet our minimal knowledge about this species is derived from anecdotal observations and only a few published studies (Stroud et al, 2022; Moretto, 2023). Our analysis revealed a discrepancy between the morphology and mechanics of the claws, with some aspects of morphology scaling with body size, but the mechanics being independent of size.

Normally greater claw height corresponds to a greater physiological muscle cross-sectional area and thus greater force generation (Schenk and Wainwright, 2001). However, the height of both the crusher and cutter claws scale with body size in *L. foraminatus*, but the claw pinch force was independent of body size. Large crabs generated pinch forces equivalent to smaller crabs. One possible explanation is that the total claw cross-sectional area, including propodus width, is the primary correlate of force production, as observed in the fiddler crab *Uca pugilator* (Claussen et al, 2008). Propodus width was not measured in *L. foraminatus*, but it is observed to be relatively thin. Another possible explanation is that the greater propodus height in box crabs reflects their need to fold their claws tightly against their body. This possibility is supported by the presence of a thin carapace extension on the dorsal side of the crusher claw that increases its height but lacks internal muscle, and therefore doesn't contribute to the total muscle cross-sectional area and force production. External claw dimensions are not a good predictor of force production in *L. foraminatus*, possibly due to their folding capacity, so further study into the muscle physiology, such as sarcomere length, may be more explanatory (Taylor, 2000).

Unlike claw height, mechanical advantage of the claws did not scale with body size. This outcome was unexpected because we hypothesized that the lever components of the claws would scale allometrically to increase MA as crabs grew larger. Instead, the relative dimensions of the dactyl, and thus the ratio of input/output levers, remain the same. There is some precedence for this result: when comparing the crusher claws of six brachyuran species, Schenk and Wainright (2001) also found that MA did not scale with body size, suggesting that greater pinch forces in larger animals is driven by other factors, such as muscle physiology. Furthermore, most studies, including this one, calculate MA from the pivot point to the tip of the dactyl, yet most species generate maximal force closer to the pivot. Therefore, calculations of MA are likely not reflective of the standard use of the claw, and a more intricate measure of MA would be more informative and potentially influenced by size. Additionally, we measured crusher pinch forces of mostly male (N= 14), and only a couple of female (N = 2), crabs and peak forces ranged from 9.79 - 62.66 N. These forces are far below those generated by the large coconut crab, *Birgus latro*, which can generate forces of ~29 – 1765 N, but are surprisingly not much larger than the ~ 10-12 N of force generated by the small sand fiddler crab *Uca pugilator* (Oka et al, 2016; McLain et al, 2015). It is often a challenge to obtain maximum pinch forces from crustaceans due to force measurement techniques and issues with motivation, so we may not have measured maximum forces in *L. foraminatus*. Motivation is a major determinant of effort, which was observed in mantis shrimp that alter their strike forces when engaging with prey versus conspecifics (Green et al, 2019). Other studies have indicated that crustacean pinch forces are often related to diet, though mating behaviors can also have an impact (Claussen et al, 2007; Schenk and Wainwright, 2001). In this case, *L. foraminatus* appears to be molluscivorous, and large pinch forces are necessary for them to break open hard-shelled prey. Further studies on feeding behaviors, including prey size preferences and prey handling, would help shed light on how *L. foraminatus* use their claws and the forces that are required.

As discussed previously, the greatest pinch force is exerted at the base of the dactyl, adjacent to the pivot point, and this is typically where crusher claws have the largest denticles. Dentition plays an important role in claw function and individual denticles must resist wear and breakage at the same time as they concentrate force during claw closure. In our study, we found that neither hardness nor stiffness of the large denticle scaled with body size, indicating that the material remains consistent as animals grow. This may be explained by the specialized structure of the denticles, where the upper surface has a dense microstructure and more mineral that together afford greater abrasion resistance (Inoue et al, 2023). In this sense, the surface layer of the denticles may be a conserved material that provides a large safety factor for crabs at all body sizes. Denticle surface area may be a better proxy than material properties because as it increases with animal size, forces are applied over a larger area, resulting in decreased stresses.

Brown box crabs display sexual dimorphism in body size, with females reaching smaller maximum sizes than males (Stroud, 2022). We measured different scaling relationships in crusher claw height and females had a lower MA than males, yet these differences did not emerge in the mechanical functioning of the claw. Though only two female crabs were measured, they produced similar pinch forces as male crabs. Similar pinch forces suggest that female and male crabs can break shells of similar strength, but the differences in morphology may impart its effects on the size or shape of hard-shelled prey that they consume. If, for example, female claws have a shorter dactyl, they likely have a smaller gape that would limit them to smaller prey. This could potentially create diet partitioning between sexes based on size, but further study on prey preferences is needed.

It is important to note that this study on brown box crab claw biomechanics neglects the importance of environmental conditions in shaping claw morphology and feeding behavior. Aside from the important biological interactions that drive selection for claw morphology and function, abiotic conditions can influence the integrity of the exoskeleton and claw function over short time scales. For example, the composition and mechanical properties of crustacean exoskeleton are sensitive to environmental CO_2/pH. Multiple studies have demonstrated that reduced pH conditions can increase exoskeleton mineralization in some crustacean species (Taylor et al, 2015; Ries et al, 2009; Dickinson et al, 2021). This could render claws more brittle, causing them to be more susceptible to breakage under loading, but the structural integrity of *L. foraminatus* claws under reduced pH conditions has not been examined. Reduced pH conditions have been shown to decrease claw microhardness of red king crabs (Coffey, 2017) and negatively affect the crusher claw closer muscle strength increment in green crabs (Landes and Zimmer 2012), which could compromise the effectiveness of claws during feeding and defense.

Additionally, temperature is known to affect crustaceans at multiple physiological and behavioral levels. A temperature increase from 8 to 15°C caused *L. foraminatus* to alter their feeding preferences from clams to mussels (Moretto, 2023). Thus, crabs may be using their claws differently during predation events based on environmental temperature, which is variable across depths and seasons throughout their geographic range. This means that populations of *L. foraminatus* across their geographic and depth ranges may have environmentally driven feeding behaviors that can either affect or be affected by claw morphology and function.

CONCLUSION

This study provides the first biomechanical analysis of *L. foraminatus* claws and reveals that claw morphology may largely reflect their ability to fold appendages tightly to their body in their purported defense posture, but also enables them to produce large forces that permit a durophagous diet. Additionally, the size independence of MA, denticle properties, and force production suggest that the claws maintain similar function, and possibly diet, throughout their adult life. This information is a useful step toward understanding brown box crab ecology and ultimately constructing a sustainable fishery in Southern California.

REFERENCES

Alaska Dept. of Fish and Game. "Red King Crab Species Profile, Alaska Department of Fish and Game." Accessed June 13, 2024. https://www.adfg.alaska.gov/index.cfm?adfg=redkingcrab.printerfriendly.

Bentov, Shmuel, Eliahu D. Aflalo, Jenny Tynyakov, Lilah Glazer, and Amir Sagi. "Calcium Phosphate Mineralization Is Widely Applied in Crustacean Mandibles." Scientific Reports 6 (February 24, 2016): 22118. https://doi.org/10.1038/srep22118.

"California Cooperative Oceanic Fisheries Investigations (CalCOFI)Database | InPort." Accessed May 3, 2024. https://www.fisheries.noaa.gov/inport/item/20691.

Chen, Po-Yu, Albert Yu-Min Lin, Joanna McKittrick, and Marc André Meyers. "Structure and Mechanical Properties of Crab Exoskeletons." Acta Biomaterialia 4, no. 3 (2008): 587–96. https://doi.org/10.1016/j.actbio.2007.12.010.

Cho, Boongho, Dongsung Kim, and Taewon Kim. "Exceptional Properties of Hyper-Resistant Armor of a Hydrothermal Vent Crab." Scientific Reports 12, no. 1 (July 12, 2022): 11816. https://doi.org/10.1038/s41598-022-15982-1.

Coffey, William D., Jessica A. Nardone, Aparna Yarram, W. Christopher Long, Katherine M. Swiney, Robert J. Foy, and Gary H. Dickinson. "Ocean Acidification Leads to Altered Micromechanical Properties of the Mineralized Cuticle in Juvenile Red and Blue King Crabs." Journal of Experimental Marine Biology and Ecology 495 (2017): 1–12. https://doi.org/10.1016/j.jembe.2017.05.011.

Claussen, Dennis L., Gary W. Gerald, John E. Kotcher, and Courtney A. Miskell. "Pinching Forces in Crayfish and Fiddler Crabs, and Comparisons with the Closing Forces of Other Animals." Journal of Comparative Physiology B 178, no. 3 (March 1, 2008): 333–42. https://doi.org/10.1007/s00360-007-0226-8.

Currey, J. D., A. Nash, and W. Bonfield. "Calcified Cuticle in the Stomatopod Smashing Limb." Journal of Materials Science 17, no. 7 (July 1, 1982): 1939–44. https://doi.org/10.1007/BF00540410.

Dendinger, James E, and Alan Alterman. "Mechanical Properties in Relation to Chemical Constituents of Postmolt Cuticle of the Blue Crab, Callinectes Sapidus." Comparative Biochemistry and Physiology Part A: Physiology 75, no. 3 (January 1, 1983): 421–24. https://doi.org/10.1016/0300-9629(83)90104-4.

Dickinson, Gary H., Shai Bejerano, Trina Salvador, Christine Makdisi, Shrey Patel, W. Christopher Long, Katherine M. Swiney. "Ocean Acidification Alters Properties of the Exoskeleton in Adult Tanner Crabs, Chionoecetes Bairdi." The Journal of Experimental Biology 224, no. Pt 3 (February 5, 2021): jeb232819. https://doi.org/10.1242/jeb.232819.

Dutil, J-D., Claire Rollet, R. Bouchard, and W. T. Claxton. “Shell Strength and Carapace Size in Non-Adult and Adult Male Snow Crab (Chionoecetes Opilio).” Journal of Crustacean Biology 20, no. 2 (March 1, 2000): 399–406. https://doi.org/10.1163/20021975-99990051.

Fujiwara, Shin-ichi, and Hiroki Kawai. “Crabs Grab Strongly Depending on Mechanical Advantages of Pinching and Disarticulation of Chela.” Journal of Morphology 277, no. 10 (2016): 1259–72. https://doi.org/10.1002/jmor.20573.

Green, Patrick. A., M. J. McHenry, and S. N. Patek. “Context-Dependent Scaling of Kinematics and Energetics during Contests and Feeding in Mantis Shrimp.” Journal of Experimental Biology 222, no. 7 (April 4, 2019): jeb198085. https://doi.org/10.1242/jeb.198085.

Grunenfelder, Lessa Kay, Garrett Milliron, Steven Herrera, Isaias Gallana, Nicholas Yaraghi, Nigel Hughes, Kenneth Evans-Lutterodt, Pablo Zavattieri, and David Kisailus. “Ecologically Driven Ultrastructural and Hydrodynamic Designs in Stomatopod Cuticles.” Advanced Materials 30, no. 9 (2018): 1705295. https://doi.org/10.1002/adma.201705295.

Inoue, Tadanobu, Yuka Hara, and Koji Nakazato. “Mechanical Resistance of the Largest Denticle on the Movable Claw of the Mud Crab.” Biomimetics 8, no. 8 (December 2023): 602. https://doi.org/10.3390/biomimetics8080602.

Inoue, Tadanobu, Yuka Hara, and Koji Nakazato. “Mechanical Resistance and Tissue Structure of Claw Denticles of Various Sizes in the Mud Crab, Scylla Serrata.” Materials 16, no. 11 (January 2023): 4114. https://doi.org/10.3390/ma16114114.

Inoue, Tadanobu, Shin-ichiro Oka, Koji Nakazato, and Toru Hara. “Structural Changes and Mechanical Resistance of Claws and Denticles in Coconut Crabs of Different Sizes.” Biology 10 (December 9, 2021): 1304. https://doi.org/10.3390/biology10121304.

Jørgensen, Lis, and Vassily Spiridonov. “Effect from the King- and Snow Crab on Barents Sea Benthos.” 2013.

Landes, Anja, and Martin Zimmer. “Acidification and Warming Affect Both a Calcifying Predator and Prey, but Not Their Interaction.” Marine Ecology Progress Series, March 29, 2012. https://doi.org/10.3354/meps09666.

Lian, Jie, and Junlan Wang. “Microstructure and Mechanical Properties of Dungeness Crab Exoskeletons.” In Mechanics of Biological Systems and Materials, Volume 2, edited by Tom Proulx, 93–99. New York, NY: Springer, 2011. https://doi.org/10.1007/978-1-4614-0219-0_12.

Long, Christopher W., Katherine M. Swiney, and Robert J. Foy. “Effects of Ocean Acidification on the Embryos and Larvae of Red King Crab, Paralithodes Camtschaticus.” Marine Pollution Bulletin 69, no. 1 (April 15, 2013): 38–47. https://doi.org/10.1016/j.marpolbul.2013.01.011.

Lowder, Kaitlyn B., Michael C. Allen, James M. D. Day, Dimitri D. Deheyn, and Jennifer R. A. Taylor. “Assessment of Ocean Acidification and Warming on the Growth, Calcification, and Biophotonics of a California Grass Shrimp.” ICES Journal of Marine Science 74, no. 4 (May 1, 2017): 1150–58. https://doi.org/10.1093/icesjms/fsw246.

McLain, Denson, Jordan Logue, Ann Pratt, and Lance Mcbrayer. “Claw-Pinching Force of Sand Fiddler Crabs in Relation to Activity and the Lunar Cycle.” Journal of Experimental Marine Biology and Ecology 471 (October 1, 2015): 190–97. https://doi.org/10.1016/j.jembe.2015.06.008.

Melnick, C. A., Z. Chen, and J. J. Mecholsky. “Hardness and Toughness of Exoskeleton Material in the Stone Crab, Menippe Mercenaria.” Journal of Materials Research 11, no. 11 (November 1, 1996): 2903–7. https://doi.org/10.1557/JMR.1996.0367.

Moretto, Wave I., and Jennifer R. A. Taylor. “Temperature-Dependent Feeding Behavior in the Brown Box Crab, Lopholithodes Foraminatus.” Frontiers in Marine Science 10 (September 8, 2023). https://doi.org/10.3389/fmars.2023.1241950.

NOAA. “Alaska Marine Life and Ecosystem Science | NOAA Fisheries.” NOAA, April 26, 2024. https://www.fisheries.noaa.gov/region/alaska.

Oka, Shin-ichiro, Taketeru Tomita, and Kei Miyamoto. “A Mighty Claw: Pinching Force of the Coconut Crab, the Largest Terrestrial Crustacean.” PLOS ONE 11, no. 11 (November 23, 2016): e0166108. https://doi.org/10.1371/journal.pone.0166108.

Raabe, D., P. Romano, C. Sachs, H. Fabritius, A. Al-Sawalmih, S.-B. Yi, G. Servos, and H.G. Hartwig. “Microstructure and Crystallographic Texture of the Chitin–Protein Network in the Biological Composite Material of the Exoskeleton of the Lobster Homarus Americanus.” Materials Science and Engineering: A 421, no. 1–2 (2006): 143–53. https://doi.org/10.1016/j.msea.2005.09.115.

Raabe, D., C. Sachs, and P. Romano. “The Crustacean Exoskeleton as an Example of a Structurally and Mechanically Graded Biological Nanocomposite Material.” Acta Materialia 53, no. 15 (September 1, 2005): 4281–92. https://doi.org/10.1016/j.actamat.2005.05.027.

Ries, Justin, Anne Cohen, and Daniel McCorkle. “Marine Calcifiers Exhibit Mixed Responses to CO2-Induced Ocean Acidification.” Geology 37 (December 2, 2009): 1131–34. https://doi.org/10.1130/G30210A.1.

Roer, R. and R. Dillaman. “The Structure and Calcification of the Crustacean Cuticle.” American Zoologist 24, no. 4 (November 1, 1984): 893–909. https://doi.org/10.1093/icb/24.4.893.

Rosen, Miranda N., Kerstin A. Baran, Justin N. Sison, Brittan V. Steffel, W. Christopher Long, Robert J. Foy, Kathryn E. Smith, Richard B. Aronson, and Gary H. Dickinson. “Mechanical

Resistance in Decapod Claw Denticles: Contribution of Structure and Composition.” Acta Biomaterialia 110 (July 1, 2020): 196–207. https://doi.org/10.1016/j.actbio.2020.04.037.

Schenk, Steve C., and Peter C. Wainwright. “Dimorphism and the Functional Basis of Claw Strength in Six Brachyuran Crabs.” Journal of Zoology 255, no. 1 (2001): 105–19. https://doi.org/10.1017/S0952836901001157.

Stroud, Ashley M. “Size at Maturity, Reproductive Cycle and Fecundity of the Southern California Brown Box Crab, Lopholithodes Foraminatus, and Implications for Developing a New Targeted Fishery.” UC Santa Barbara, 2022. https://escholarship.org/uc/item/4w95d0r0.

Taylor, Graeme M. “Maximum Force Production: Why Are Crabs so Strong?” Proceedings of the Royal Society of London. Series B: Biological Sciences 267, no. 1451 (July 22, 2000): 1475–80. https://doi.org/10.1098/rspb.2000.1167.

Taylor, Jennifer R. A., Jasmine M. Gilleard, Michael C. Allen, and Dimitri D. Deheyn. “Effects of CO2-Induced PH Reduction on the Exoskeleton Structure and Biophotonic Properties of the Shrimp Lysmata Californica.” Scientific Reports 5 (June 1, 2015): 10608. https://doi.org/10.1038/srep10608.

Taylor, Jennifer R. A., Jack Hebrank, and William M. Kier. “Mechanical Properties of the Rigid and Hydrostatic Skeletons of Molting Blue Crabs, Callinectes Sapidus Rathbun.” The Journal of Experimental Biology 210, no. Pt 24 (December 2007): 4272–78. https://doi.org/10.1242/jeb.007054.

Verma, Devendra, and Vikas Tomar. “An Investigation into Mechanical Strength of Exoskeleton of Hydrothermal Vent Shrimp (Rimicaris Exoculata) and Shallow Water Shrimp (Pandalus Platyceros) at Elevated Temperatures.” Materials Science & Engineering. C, Materials for Biological Applications 49 (April 2015): 243–50. https://doi.org/10.1016/j.msec.2015.01.003.

Weaver, James C., Garrett W. Milliron, Ali Miserez, Kenneth Evans-Lutterodt, Steven Herrera, Isaias Gallana, William J. Mershon, Brook Swanson, Pablo Zavattieri, Elaine DiMasi, and David Kisailus. “The Stomatopod Dactyl Club: A Formidable Damage-Tolerant Biological Hammer.” Science 336, no. 6086 (June 8, 2012): 1275–80. https://doi.org/10.1126/science.1218764.

Weiner, Stephen. “Biomineralization: A Structural Perspective.” Journal of Structural Biology 163, no. 3 (2008): 229–34. https://doi.org/10.1016/j.jsb.2008.02.001.

Yoshida, Yutaka, Ken Yamauchi, Ryoma Hiraragi, Yutaka Kiyono, Seiichi Omori, and Jun-ichi Shibano. “Microstructures of Crab Chela: A Biological Composite for Pinching.” Journal of the Mechanical Behavior of Biomedical Materials 112 (December 1, 2020): 104071. https://doi.org/10.1016/j.jmbbm.2020.104071.

Zhou, Fei, Zhiwei Wu, Meiling Wang, and Kangmin Chen. “Structure and Mechanical Properties of Pincers of Lobster (Procambarus Clarkii) and Crab (Eriocheir Sinensis).” Journal of the Mechanical Behavior of Biomedical Materials 3, no. 6 (August 2010): 454–63. https://doi.org/10.1016/j.jmbbm.2010.05.001.