UNIVERSITY OF CALIFORNIA SAN DIEGO

Assessment of ocean acidification and warming on the feeding behavior of the yellow rock crab
Cancer anthonyi

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

in

Marine Biology

by

Elizabeth Childers

Committee in charge:

    Professor Jennifer Taylor, Chair
    Professor Ryan Hechinger
    Professor Martin Tresguerres

2023

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

University of California San Diego

2023

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

First and foremost, I would like to thank Dr. Taylor. I am very appreciative of the guidance and mentorship you have provided me and others in your lab. You have been so thoughtful and caring. I am grateful to have you as an advisor.

Thank you to my sister, Victoria Childers, for always encouraging me to work towards the goals I thought I could not achieve. You are the standard I set for myself and I am fortunate to have you as an older sister.

Lastly, I would like to thank my grandparents, Paciencio and Clarita Guinto. You two are a constant inspiration for the selfless sacrifices you have made for others benefit. You two are a constant reminder to me that success comes with hard work. I would not be where I am now without them.

ABSTRACT OF THE THESIS

Assessment of ocean acidification and warming on the feeding behavior of the yellow rock crab
Cancer anthonyi

by

Elizabeth Childers

Master of Science in Marine Biology

University of California San Diego, 2023

Professor Jennifer Taylor, Chair

Many crustaceans are prodigious scavengers and predators whose feeding behavior may be sensitive to environmental change, such as ocean acidification (OA) and ocean warming (OW). In this study, I tested the hypothesis that the feeding behavior of the rock crab, *Cancer anthonyi*, is affected by OA and OW conditions. Adult crabs were exposed to the following treatments (N=12 per treatment) for 8 weeks: ambient pH/ambient temperature (8.1 pH, 12°C), reduced pH/ambient temperature (7.7 pH/12°C), ambient pH/increased temperature (8.1 pH/16°C), or reduced pH/increased temperature (7.7 pH/16°C). Crabs were given two similarly sized mollusk prey items (mussel, *Mytilus californianus* and snail, *Littorina* spp.) twice per week

and their feeding activity was video recorded for 5 minutes. A total of 14 feeding trials were performed in which multiple aspects of feeding behavior were recorded and compared across treatments: decision making time, prey handling time, prey preference, appetite (total number of prey consumed), prey consumption strategy, and shell damage to prey. Our results revealed sex-specific responses, whereby females had a lower appetite in the reduced pH/increased temperature treatment while males had a lower appetite in the reduced pH/ambient temperature treatment. All other feeding behaviors were unaffected by treatment. Two months of constant exposure to near-term OA and OW conditions are sufficient to alter some aspects of feeding behavior in adult *C. anthonyi*, despite natural exposure to environmental variations in upwelling regions of Southern California. The distinct responses observed in male and female crabs suggest that sex-based physiological differences should be considered in crustacean ocean acidification research.

INTRODUCTION

Crab feeding behavior renders them essential consumers and decomposers in their terrestrial and aquatic habitats. As opportunistic feeders, crabs prey on fish and invertebrates, but also clean the substrate of dead plant and animal matter. Consequently, crabs greatly affect ecosystem function and community structure. In some mangrove communities, for example, grapsid crabs process large quantities (as much as 28%) of leaf debris (Lee, 1998), contributing to ecological functions such as bioturbation, primary production turnover, and reduction of organic matter (Lee, 1998). These vital trophic roles and ecosystem services provided by crabs may be transformed if species distributions and/or feeding behaviors are impacted by climate change.

The climate change stressors of ocean acidification (OA) and ocean warming (OW) are major concerns for marine organisms because surface water pH is projected to decrease by 0.3-0.4 pH units and temperature is projected to increase up to 3°C by 2100 (IPCC, 2014). Such large changes in ocean temperature and carbonate chemistry have been shown to alter the physiological function, behavior, and productivity of diverse marine organisms (Doney et. al, 2012). Notably, OA and OW conditions can increase the energetic costs of physiological processes, thereby affecting energy allocation and metabolic activity across species (Doney et. al, 2012). These higher metabolic needs can lead to increased food consumption, as observed in the rocky intertidal crab *Acanthocyclus hassleri,* which was found to have a 94% increase in oxygen consumption and a 71% increase in mussel consumption when exposed to 20°C compared to 15°C (Manriquez et. al, 2021). Both warm seawater temperature and elevated pCO_2/reduced pH can affect crab citrate synthase levels, a proxy for ATP production capacity

and status of nutrition, decreasing it by 29% at increased pCO_2 levels (1400 µatm compared to 500 µatm) and by 25% at a temperature of 20°C compared to 15°C (Manriquez et. al, 2021). These findings indicate that changes in temperature and pH conditions can affect a crab's metabolic capacity to generate ATP (Manriquez et. al, 2021), and thus their nutritional state.

Environmentally induced increases in metabolic needs can drive observable changes in animal behavior, particularly in relation to foraging and feeding. Dodd et. al. (2015) studied the appetite and feeding behavior of mud crabs *Panopeus herbstii* under a series of pCO_2 levels and found significant treatment effects; the percentage of oysters consumed was highest in the control treatment (67.5% at 499 µatm), intermediate in moderate pCO_2 (41% at 785 µatm), and lowest in the extremely high pCO_2 treatment (1% at 9273 µatm). Additionally, crabs in the moderate pCO_2 treatment spent less time handling prey and gave up on failed predation attempts 84.6% faster (Dobb et. al, 2015). Thus, high pCO_2 levels affect the predator persistence of these crabs, which may be a response to increased metabolic stress (Dodd et. al, 2015). Likewise, elevated temperature also influences foraging strategies and appetite. For example, foraging behavior in the Asian paddle crab *Charybdis japonica,* is sensitive to temperature, whereby at a high temperature of 25°C, searching time, handling time, and time it took to consume prey after successfully breaking its shell, were significantly lower than at 18°C (Wu et. al, 2017). Similarly, the shore crab *Carcinus maenas* consumed more mussels and had a higher energy intake per day at 17°C compared to 10°C (Elner, 1979), while those acclimatized to 24°C ate 2.4 times more squid than crabs acclimatized to 10°C (Wallace,1973). Overall, these studies indicate that high levels of pCO_2 can reduce foraging and feeding activity, while high temperatures tend to stimulate these behaviors.

For crabs to successfully procure living prey and dead matter to meet higher metabolic needs under OA and OW conditions, it is essential that their chelae function properly. Chelae require fine motor control to sift through sediment and grasp organic matter, strong pinch forces to crush hard-shell prey, and fast movements to capture evasive prey (Vermeij, 1977). These actions depend on claw morphology and muscle physiology, as well as nervous system control. Crustacean neuromuscular function is known to be affected by environmental temperature (Blundon, 1989), but the effects of environmental pH are less studied (Stein & Harzsch, 2021). Despite this, many observed changes in locomotor activity and behavior under elevated pCO_2 could be attributable to effects on the nervous system (de la Haye et. al, 2011, Leduc et. al, 2013, Wittmann & Portner, 2013, Zittier et. al, 2013). Thus, there are multiple ways in which environmental conditions can influence crab chela function and feeding behavior.

Most often feeding performance in crabs is related to claw pinch force (Seed & Hughes, 1995), which is demonstrably affected by OA conditions in some species. The average pinching strength of the intertidal crab, *Acanthocyclus hassleri,* for example, ranges from 16 to 24 N in ambient pCO_2 conditions but was significantly reduced in high pCO_2 (1400 µatm) (Manriquez et. al, 2020). Additionally, blue crabs, *Callinectes sapidus*, exposed to low pH conditions (7.0 pH) had a decrease in claw pinch force of 26% (from 14.6 to 10.8 N) compared to crabs in ambient conditions (8.0 pH) (Longmire et. al, 2022). Likewise, the green shore crab, *Carcinus maenas*, also exhibited reduced claw strength under elevated pCO_2 (Landes & Zimmer, 2012). In general, warmer temperatures did not affect claw strength in these studies, but it did have some interactive effects with pH (Landes & Zimmer, 2012, Manriquez et. al, 2021), and warmer laboratory temperature was correlated with greater claw stresses (force per area) in the stone crab, *Menippe mercenaria* (Blundon, 1989). If OA and OW conditions alter crab claw force

production, species may require either more time to consume hard-shell prey or different strategies to break them. If unsuccessful, crabs may have to shift to weaker prey.

Studies so far have provided evidence that crustacean metabolism and feeding behavior are susceptible to changes in seawater temperature and pH/pCO$_2$ levels, but research on crustaceans is still limited and responses are highly species-specific. Thus, to understand the potential impacts on local communities, OA and OW research should be carried out on target species. Along the Southern California coastline, three species of rock crabs are abundant in shallow waters (from low intertidal to greater than 100 m) where they support valuable commercial fisheries and are key predators and scavengers in shallow water habitats. Rock crab commercial fishing has been rapidly expanding in California (Shanebeck et. al, 2020), with commercial fishing taking between 450 and 900 metric tons of crab annually (CDFW, 2019). Additionally, rock crabs play a prominent role in the food web, contributing as scavengers, predator and prey. As predators, red rock crabs, *Cancer productus*, help to control mussel populations (Hull & Bourdeau, 2017) and invasive ascidian species (Epelbaum et. al, 2009) that have been introduced to southern California harbors (Lambert & Lambert, 1998).

Objective

Considering the ecological and economic importance of rock crabs in Southern California and the growing concern of climate change impacts on local marine communities, we carried out an experiment to determine if OA and OW conditions affect the feeding behavior of the yellow rock crab *Cancer anthonyi*. Specifically, we tested the hypotheses that reduced pH would negatively affect feeding behavior, that warmer temperature would enhance crab feeding

behavior, and that the combined effects of reduced pH and warm temperature would mitigate one another.

MATERIALS AND METHODS

Animal acquisition and care

Adult yellow rock crab, *Cancer anthonyi*, were collected by hand from the Scripps Pier flume, La Jolla, CA from January to February 2023. Crabs were immediately brought to the experimental aquarium at Scripps Institution of Oceanography (SIO) where they were placed in individual plastic tanks (6.6 L) that each received flow-through seawater pumped from the SIO pier at ambient conditions (8.0 pH, 12°C). Crabs were fed mussels, *Mytilus californianus,* once a week prior to the start of the experiment.

Experimental setup

Crabs were exposed to a series of pH and temperature treatments using an experimental ocean acidification aquarium system. The system consisted of four large header tanks (150 L) that received filtered seawater pumped from the SIO pier, with each header tank feeding flow-through seawater to 12 smaller tanks (6.6 L) that housed individual crabs. Header tanks were adjusted for the following treatments: ambient pH/ambient temperature (8.0 pH/12°C), reduced pH/ambient temperature (7.7 pH/12°C), ambient pH/increased temperature (8.0 pH/16°C), and reduced pH/increased temperature (8.0 pH/16°C). Target pH and temperature values were selected based on current, seasonal ambient conditions and projections for the year 2100, which forecasts pH decreases of 0.3 - 0.4 and temperature increases of 3°C (IPCC, 2014).

Reduced pH conditions were achieved by bubbling 100% CO_2 directly into the respective header tanks. Increased temperature was achieved by placing three aquarium heaters (300-W) in

the respective header tanks. Both pH and temperature were controlled and monitored by an Apex Lite aquarium controller (data logged every 20 minutes) equipped with Apex Neptune pH and temperature probes (0.01 pH accuracy, 0.1°C temperature accuracy, Neptune Systems, Morgan Hill, CA, USA). Aquarium pumps were placed in each header tank to promote mixing.

Prior to the experiment, 48 crabs were semi-randomly assigned to each treatment (N=12) so that body size and sex were evenly distributed (Table 1). There was no statistical difference in either carapace width (Kruskal-Wallis, df = 7, f = 0.215, p = 0.98) or body mass (ANOVA, df = 8, h = 3.403, p = 0.91) between sexes and treatments. Some crabs initially were brooding eggs and were also divided equally across treatments. Experimental water parameters were gradually altered over three days in an effort to minimize stress. Once the parameters reached target levels, the experiment was run for eight weeks. Crabs were monitored daily for molting and mortality and fed twice per week (see feeding section below). Tanks were cleaned of food debris the day after each feeding.

Table 1. Body size and sex distributions of *C. anthonyi* across treatments.

		8.1 pH/12°C		7.7 pH/12°C		8.1 pH/16°C		7.7 pH/16°C
	N	mean ± s.d.	N	mean ± s.d.	N	mean ± s.d.	N	mean ± s.d.
carapace width(mm)								
female	7	66.12 ± 9.85	5	63.95 ± 12.20	7	67.61 ± 7.70	6	65.63 ± 10.42
male	5	58.73 ± 5.02	6	66.69 ± 8.37	4	60.72 ± 9.82	5	64.05 ± 7.97
mass (g)								
female	7	63.23 ± 26.51	5	62.77 ± 31.50	7	64.83 ± 22.96	6	62.56 ± 30.02
male	5	42.68 ± 9.68	6	68.45 ± 22.72	4	51.95 ± 25.32	5	55.62 ± 23.49

Water chemistry

A portable probe (HQ40d, probe PHC201, accuracy 0.01 pH, 0.1 temperature, Hach, Loveland, CO, USA) was used to collect daily readings of pH and temperature from each header and crab tank. In addition, water samples were collected once from each header tank following standard operating procedures (Dickson et. al., 2007) and submitted to the Dickson laboratory at SIO for analysis of pH, density-based salinity, and total alkalinity (A_T). These measurements are used to calculate the offset of the probe measurements with CO2SYS, but they were not available at the time of thesis submission.

Feeding behavior

Throughout the experiment, crabs were presented with specimens from two similar-sized mollusk species twice per week: California mussels, *Mytilus californianus,* and periwinkles, *Littorina* spp. Live mussels (25.64 ± 2.49 mm length) were collected from the Scripps Pier flume, La Jolla, CA while live periwinkles (23.21 ± 8.53 mm length) were purchased from a local market, San Diego, CA. Immediately after collection or purchase, prey items were placed in a -20°C freezer for approximately 24 hours before being thawed and fed to the experimental crabs. Both species were procured bi-weekly for the duration of the experiment.

For each feeding trial, individual crabs were kept in their experimental tank and moved to a table within the aquarium room to observe feeding behavior. Crabs were given one mussel and one snail simultaneously. Both prey items were positioned next to each other, equidistant and opposite to the crab. Once prey items were added to the tank, an iPhone 11 Pro was positioned in front of the tank to video record the feeding behavior. Video recording and assessment were limited to 5 minutes, as preliminary observations revealed that *C. anthonyi* typically feeds within

this time. Following the feeding trial, crabs were immediately returned to the experimental system. Feeding trials were conducted for each crab, twice per week for the duration of the experiment, but two feeding trials were missed, resulting in a total of 14 feeding trials per crab.

Feeding behavior was assessed for each feeding (n=14 feeding trials per crab) using the following metrics: 1. Decision time, 2. Handling time, 3. Prey preference, 4. Feeding strategy, 5. Appetite, and 6. Prey shell damage.

1. Decision time was defined as the time it took (in seconds) for a crab to decide on the preferred prey item. Crabs typically grabbed both prey items with their legs and assessed each before deciding which prey to consume. Decision time was therefore calculated from the video recordings as the time from the moment the crab makes contact with the prey to when it puts one down and begins actively trying to break and consume the selected prey. Mean decision time was calculated as an average for each crab over the 14 feeding trials.

2. Handling time was defined as the time it took (in seconds) for a crab to start consumption of the selected prey. This was calculated from the video recordings starting at the time when a crab selected a prey item and ending when it successfully ingested the first piece of soft tissue. Mean handling time was calculated as an average for each crab and prey item over the total number of feeding trials in which the crab consumed that prey.

3. Prey preference was defined as the first prey item consumed by a crab, which was documented from the video recordings. Prey preference for each crab was determined at the end of the experiment by calculating the total number of times that either the mussel or snail was chosen first divided by all 14 feeding trials.

4. Feeding strategy was defined as the technique that crabs used to access the soft tissue of the prey item. Crabs demonstrated multiple strategies for both the mussel and snail prey, so feeding strategy was divided into categories. For the snails, crabs were observed to use the following three strategies (Fig. 1): break (crabs use their chelae to break the shell), claw grab (crabs insert a chela into the aperture to pull the soft tissue out), and mouth grab (crabs bring the shell to their mouth and use their mouthparts to pull out the soft tissue).
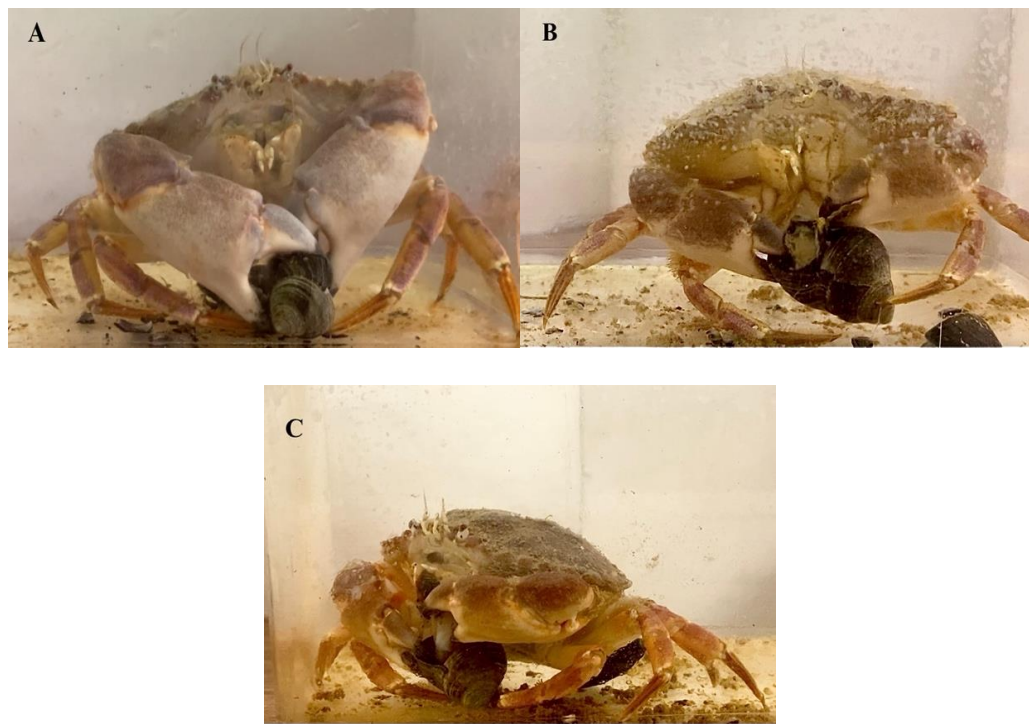
Figure 1. Representative categories for feeding strategy for the snail, *Littorina* spp. (a) break (b) claw grab, and (c) mouth grab.

For mussels, crabs used the following three strategies (Fig. 2): split (crabs use their chelae to split the mussel valves apart), crush (crabs use their chelae to crush the intact shell), and bite (crab brings mussel to mouth and uses its mouthparts to break the shell). Feeding strategies were documented from the video recordings. At the end of the experiment, the frequencies of each strategy used on both snails

and mussels were calculated for each crab out of the total number of feeding trials.

Figure 2. Representative categories for feeding strategy on the mussel, *Mytilus californianus.* (a) split, (b) crush, and (c) bite.

5. Appetite was defined as the number of prey items consumed within a 24-hour period. Crabs were given scores as follows: 2 if both prey were consumed, 1 if a single prey was consumed, 1.5 if one prey was consumed and the other partially consumed, and 0 if neither prey was consumed. The number of prey consumed was visually assessed at the end of the feeding period. A total appetite score was calculated for each crab by adding up the scores from all 14 feeding trials.

6. Prey shell damage was defined as the extent of shell breakage that occurred for each prey item. The remnants of each prey were assessed at the end of the 24-hour feeding period and damage was divided into multiple categories for each prey item. For snails, shell damage had three categories (Fig. 3): whole (no visible

damage), chipped (damage to the aperture), and crushed (shell broken into

multiple pieces).
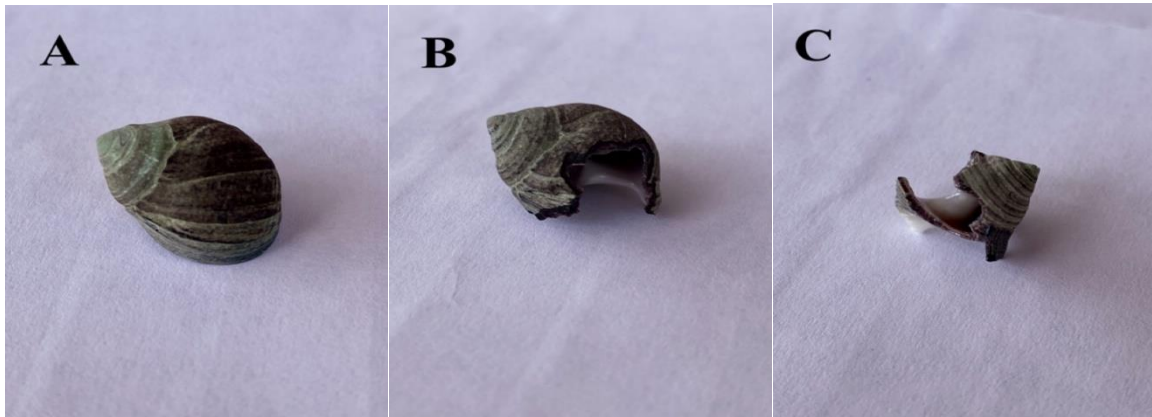
Figure 3. Representative categories of shell damage in the snail, *Littorina* spp. (a) whole, (b) chipped, and (c) crushed.

For the mussels, shell damage had two categories (Fig. 4): split (mussel valves are

split apart with little or no damage) and crushed (shell is broken into multiple

pieces). At the end of the experiment, the frequencies of each category of shell

damage observed from both snails and mussels were calculated for each crab out

of the total number of feeding trials.

Figure 4. Representative categories of shell damage in the mussel, *Mytilus californianus.* (a) split and (b) crushed.

Prey shell strength

Mussel and snail prey were chosen partly based on the assumption that they would differ in shell breaking strength, and thus might require different levels of effort to handle. We measured the shell breaking strength of 10 mussels, *Mytilus californianus,* (24.49 ± 1.767 mm shell length) and 10 snails, *Littorina* spp., (24.41 ± 2.059 mm shell length) using a universal testing machine (E1000, Instron, Norwood, MA, USA). Mussels were tested with a 250 N load cell and snails with a 2 kN load cell. Individual prey items were positioned horizontally between two steel compression plates and then compressed at a rate of 40 N per minute until shell fracture occurred. Mussels were compressed at the umbo, the widest and strongest part of the shell, while snails were compressed laterally at the widest whorl. The mean breaking force of mussels was 88.62 ± 33.35 N, which was significantly less than the 460.91 ± 60.21 N breaking force of snails.

Statistical analysis

All data, including handling time, decision time, prey preference, appetite, shell damage and feeding strategy, were tested for normality using Shapiro-Wilk tests and for homogeneity of variance using Bartlett's tests. ANCOVA with Tukey tests were used to compare handling time, decision time, prey preference, and appetite across treatments, with sex as a covariate. Feeding strategy and shell damage were compared across treatments for each prey type using a linear mixed model (LMM) with sex and carapace width as fixed effects and individual crabs as a random effect to account for repeated measures of individual crabs. AIC analysis of models with and without each of the fixed effects produced a best fit model with sex as the only fixed effect, so carapace width was excluded from the model. Tukey tests with adjusted p-values were used

for post-hoc comparisons. All statistical analyses were performed using R version 3.2.0 (R Core Team, 2015). All data in text are presented as mean ± s.d.

RESULTS

Survival and molting

While treatments were being adjusted to target pH and temperature conditions, one crab from each of the experimental treatments died, leaving a total of 45 crabs: 12 crabs in the ambient pH/ambient temperature treatment and 11 in each of the experimental treatments. All remaining crabs survived the experiment. Molting occurred in two crabs in the control (8.1 pH/12°C) treatment, three crabs in the 8.1 pH/16°C treatment, seven crabs in the 7.7 pH/16°C treatment, and no molting occurred in the 7.7 pH/12°C treatment.

Decision time

Treatment had no effect on the time it takes for crabs to decide on either mussel (ANCOVA, F = 0.383, p = 0.766) or snail (ANCOVA, F = 2.838, p = 0.062) prey items (Fig. 5, Table 2).
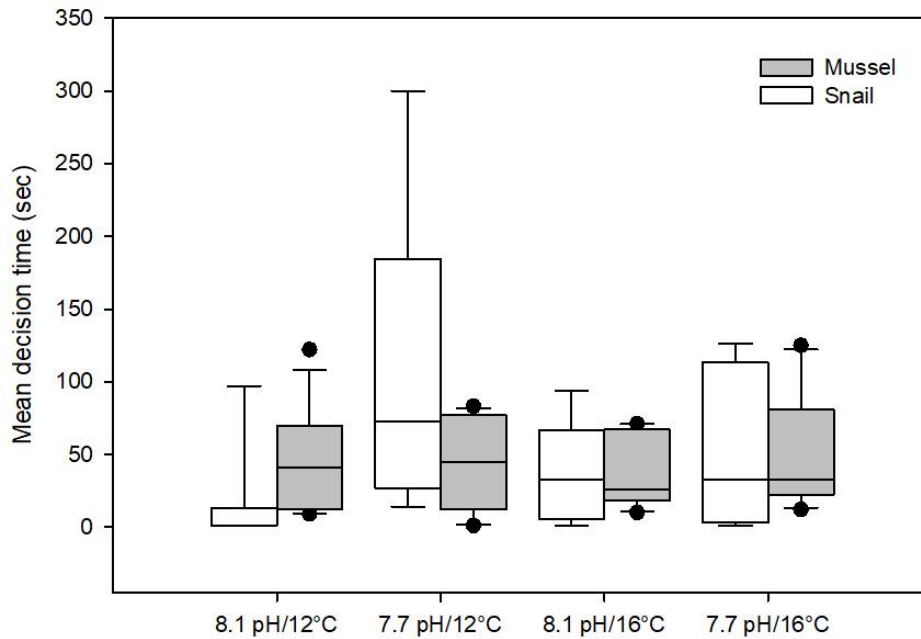
Figure 5. Mean decision time for mussels and snails across treatments. None of the pH or temperature treatments affected the time for crabs to choose a prey item. Box boundaries are the first and third quartiles, whiskers are 1.5 times the interquartile range, the center line is the median, and outliers are dots.

Handling time

After crabs select a prey item, the time spent handling it was no different among treatments for either mussels (ANCOVA, $F = 1.967$, $p = 0.136$) or snails (ANCOVA, $F = 2.177$, $p = 0.119$) (Fig. 6, Table 2).
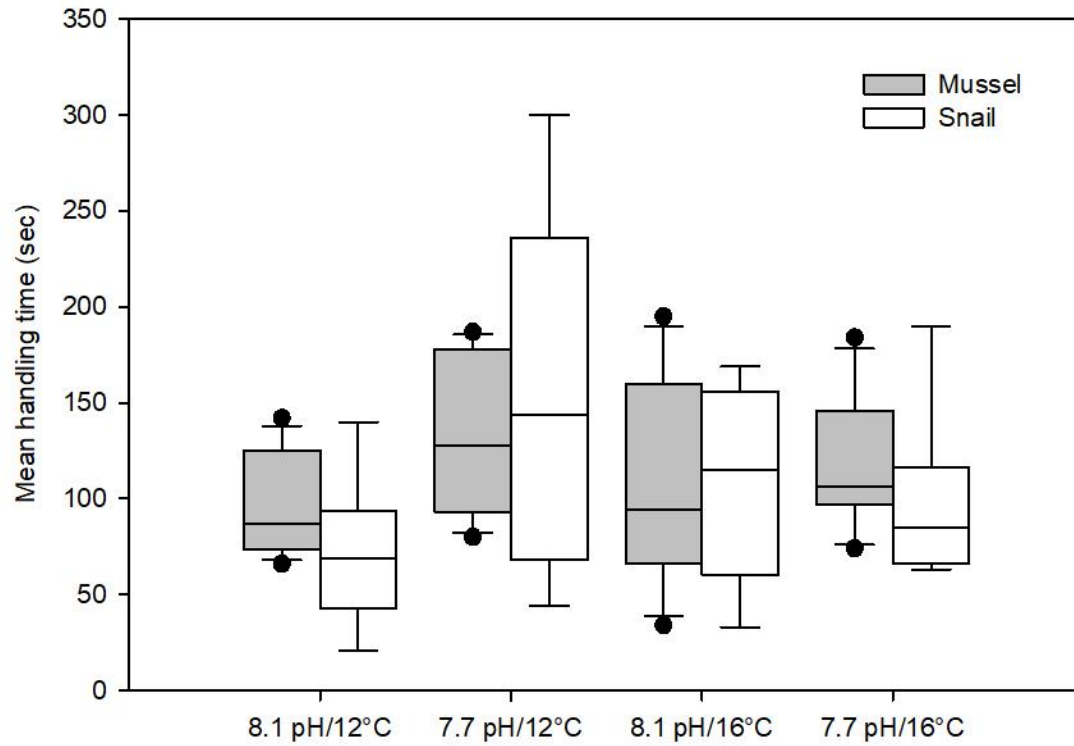
Figure 6. Mean handling time of mussels and snails across treatments. None of the pH or temperature treatments affected the time crabs spent handling prey items. Box boundaries are the first and third quartiles, whiskers are 1.5 times the interquartile range, the center line is the median, and outliers are dots.

Prey preference

Treatment had no effect on crab prey preference (ANCOVA, $F = 0.178$, $p = 0.911$) (Fig. 7, Table 2).
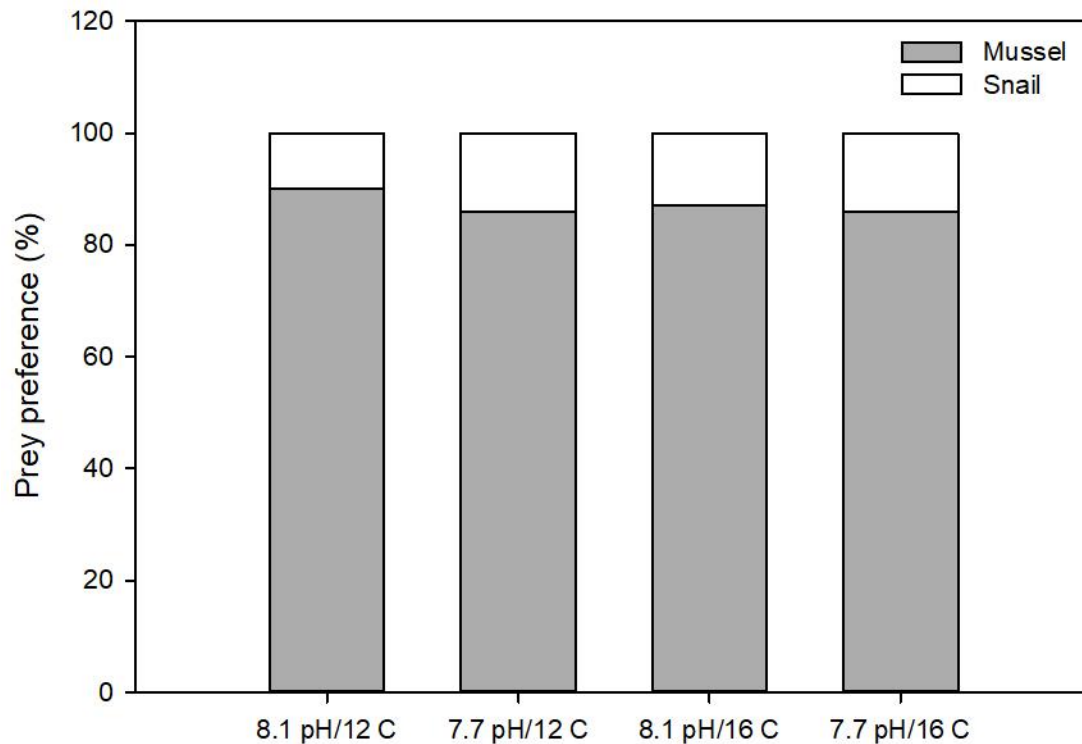
Figure 7. Prey preference of crabs across treatments. None of the pH or temperature treatments affected the preferred prey of crabs, which was consistently mussels.

Appetite

Crab appetite differed among treatments (ANCOVA, F = 5.009, p = 0.005) and between sexes (p = 0.005), with males having a consistently lower appetite than females (Fig. 8, Table 2). Female crabs in the reduced pH/increased temperature treatment (7.7 pH/16°C) had a significantly lower appetite compared to females in all other treatments (ANCOVA, F = 5.790, p = 0.005; Tukey, adj p < 0.05) (Fig. 8, Table 2). Male crab appetite was significantly lower in the reduced pH/ambient temperature treatment (7.7 pH/12°C) than the ambient pH/ambient temperature (8.1 pH/12°C) treatment (ANCOVA, F = 3.188, p = 0.051; Tukey, adj p > 0.05) (Fig. 8, Table 2).
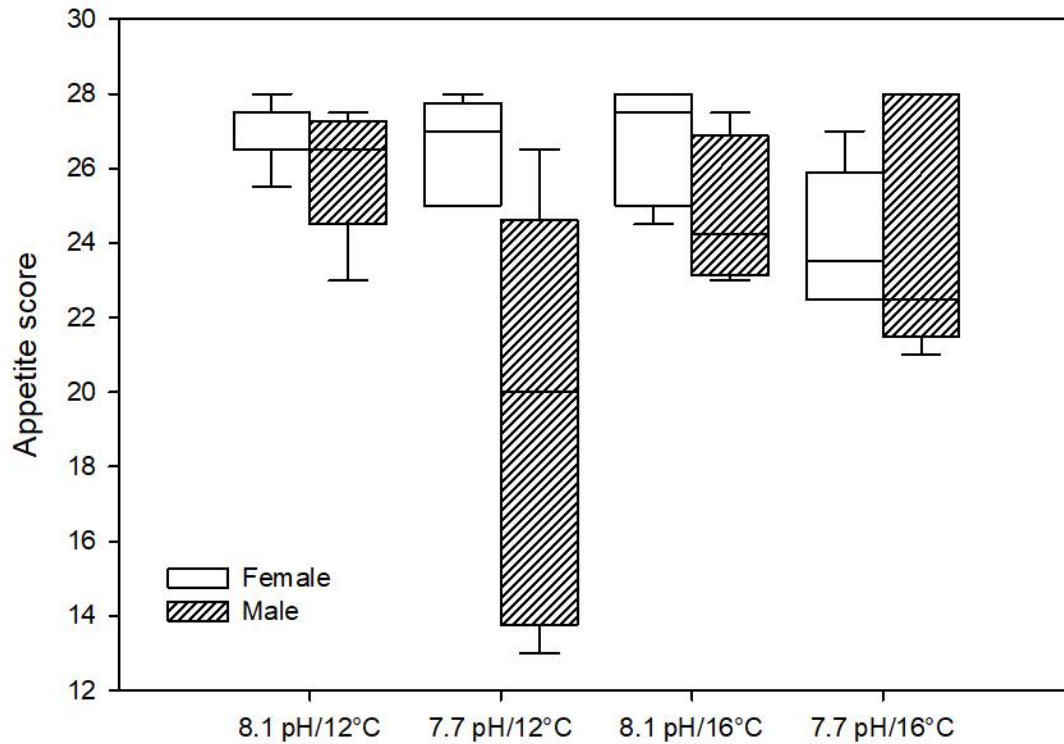
Figure 8. Appetite score of male and female crabs across treatments. Male crabs overall have a lower appetite score compared to females, with male crabs in the low pH/ambient temperature (7.7 pH/12°C) treatment having a significantly lower score than all other treatments. Female crabs in the combined low pH/high temperature (7.7 pH/16°C) treatment have a significantly lower appetite score compared to females in all other treatments. Box boundaries are the first and third quartiles, whiskers are 1.5 times the interquartile range, the center line is the median, and outliers are dots.

Feeding strategy

Crabs employed three strategies to feed on snails: using the chelae to break the shell, using the chelae to pull the soft tissue out of the shell, and using the mouthparts to suction the soft tissue out of the shell. While the frequencies with which crabs used these strategies differed (LMM, df=135, t=11.788, $p < 0.0001$), treatment had no effect on the frequency of any particular strategy (Tukey, all adj. $p > 0.05$) (Fig. 9, Table 2).
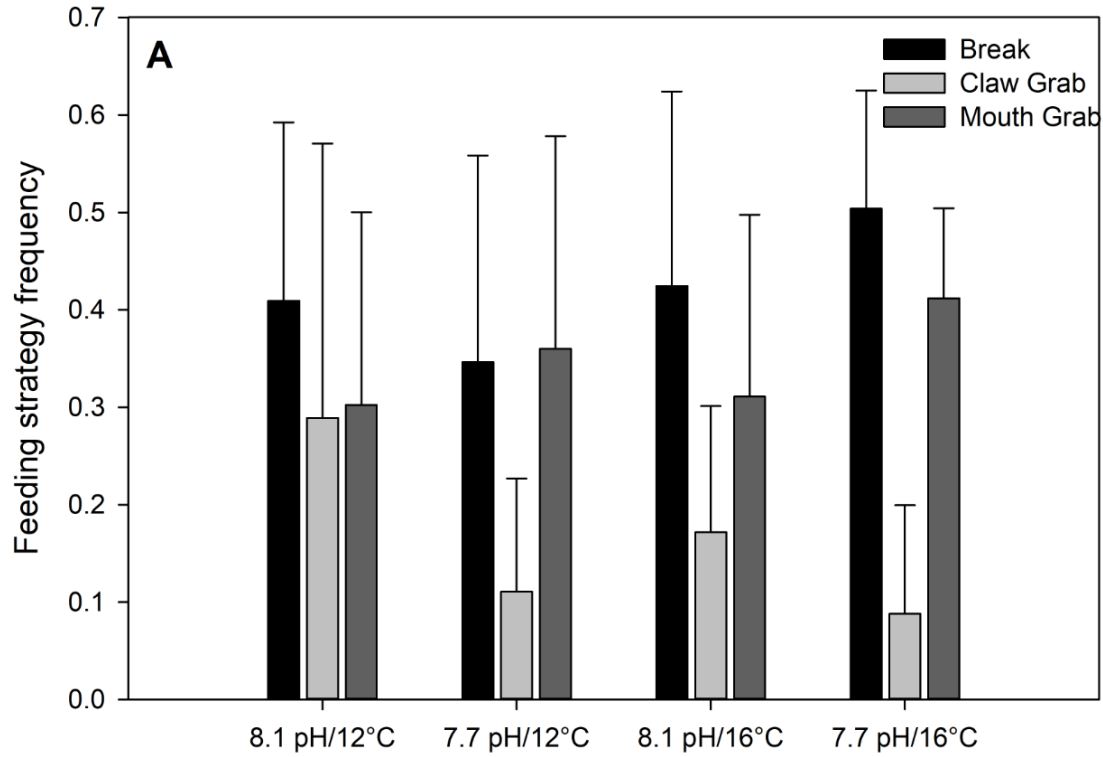
Figure 9. Feeding strategy used on snails across treatments. The frequency of strategies used to access snail tissue differed, but pH and temperature did not affect the frequency of any particular strategy. Error bars = standard deviation. Error bars = standard deviation.

Crabs employed three strategies to feed on mussels: using the chelae to split the valves, using the chelae to crush the shell, and using the mandibles to bite the shell. While the frequencies with which crabs used these strategies differed (LMM, df=135, t=5.585, $p < 0.0001$), treatment had no effect on the frequency of any particular strategy (Tukey, all adj. $p > 0.05$) (Fig. 10, Table 2).

Figure 10. Feeding strategy used on mussels across treatments. The frequency of strategies used to access mussel tissue differed, but neither pH nor temperature affected the frequency of any particular strategy. Error bars = standard deviation. Error bars = standard deviation.

Shell damage

After consumption, snail shells were either left whole, had chipping along the aperture, or were crushed into several pieces. While the frequencies of shell damage differed (LMM, df=135, t=6.440, p < 0.0001), treatment had no effect on the frequency of any particular type of damage (Tukey, all adj. p > 0.05) (Fig. 11, Table 2).
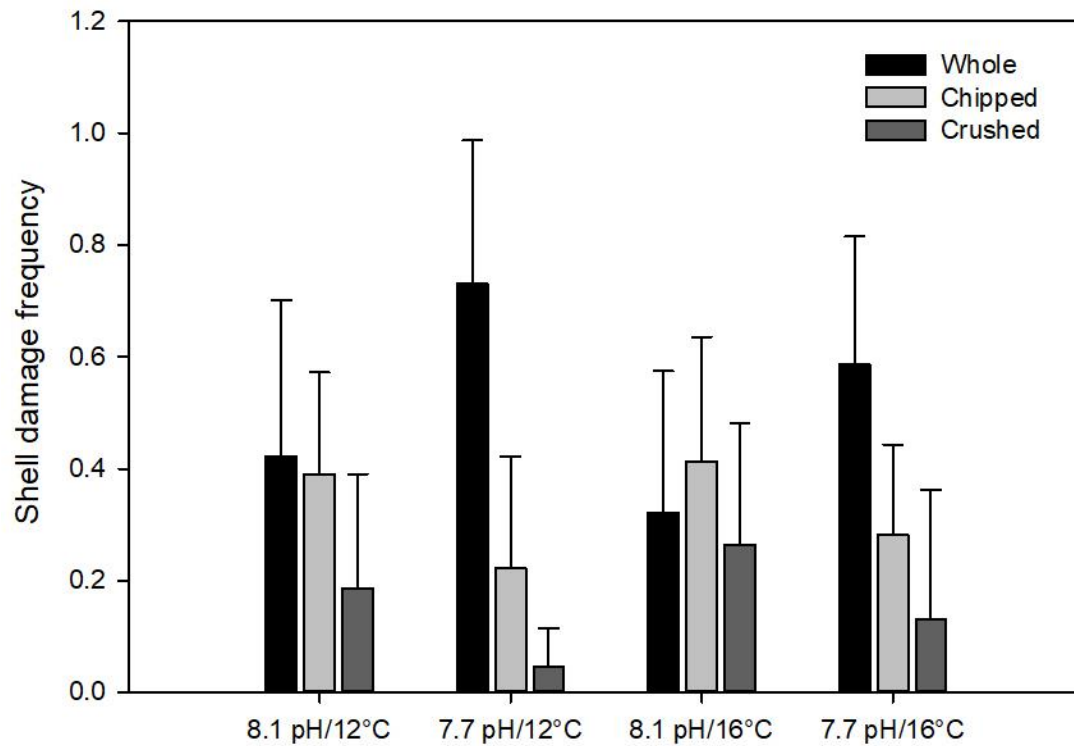
Figure 11. Snail shell damage frequency across treatments. While the frequency of the various categories of damage on snail shells differed, neither pH nor temperature affected the frequency of any particular type of damage. Error bars = standard deviation. Error bars = standard deviation.

After consumption, mussel shells were either left split but intact or were crushed into multiple pieces. The frequencies of mussel shell damage differed (LMM, df=135, t=9.363, p < 0.0001), but treatment had no effect on the frequency of any particular type of damage (Tukey, all adj. p > 0.05) (Fig. 12, Table 2).
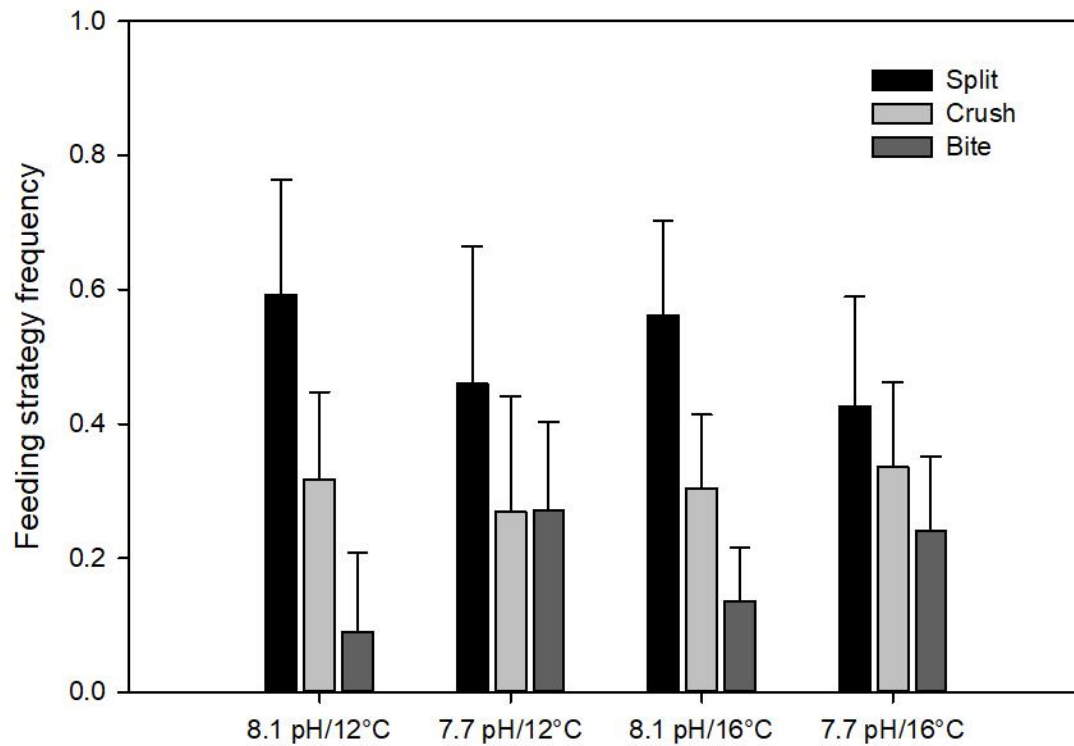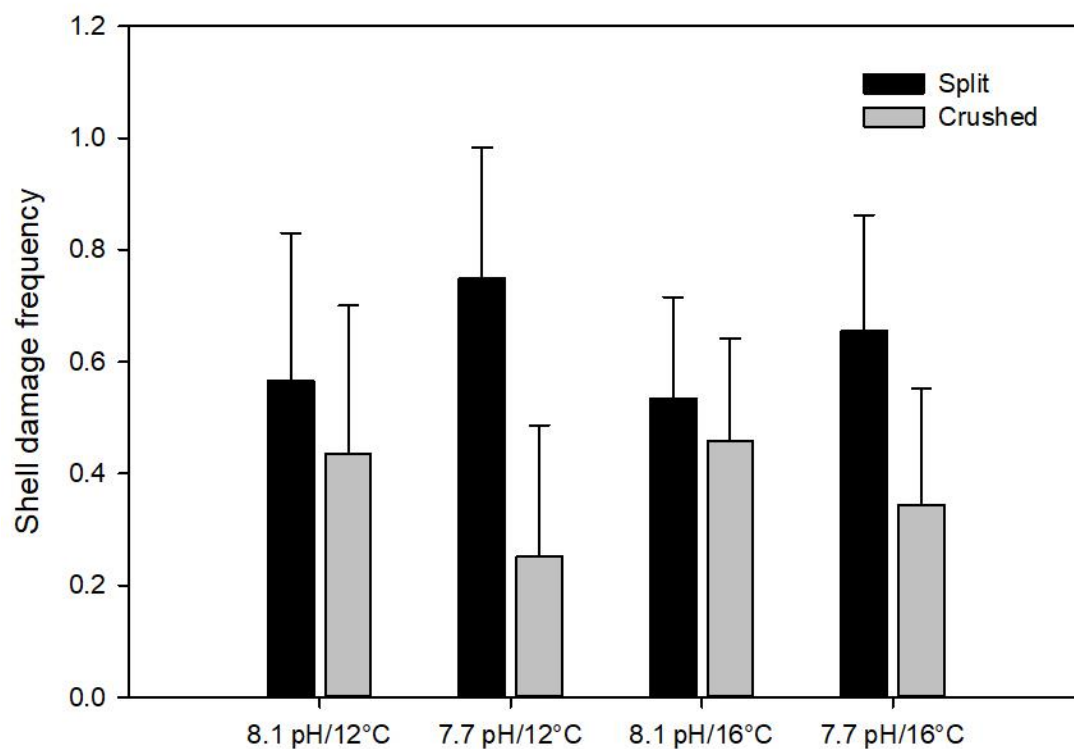
Figure 12. Mussel shell damage frequency across treatments. While the frequency of the various categories of damage on mussel shells differed, neither pH nor temperature affected the frequency of any particular type of damage. Error bars = standard deviation.

Table 2. Feeding behavior across treatments

		8.1 pH/12 °C		7.7 pH/12 °C		8.1 pH/16 °C		7.7 pH/16 °C	
Variable		N	mean ± s.d.	N	mean ± s.d.	N	mean ± s.d.	N	mean ± s.d.
Handling time(sec)									
	mussel	12	98.08 ± 27.17	11	135.18 ± 38.08	11	105.27 ± 50.91	11	119.91 ± 33.57
	snail	12	70.75 ± 36.90	11	153.83 ± 96.90	11	108.63 ± 49.66	11	98.38 ± 42.32
Decision time (sec)									
	mussel	12	45.17 ± 34.15	11	43.73 ± 30.88	11	36.27 ± 22.91	11	51.55 ± 39.99

Continued Table 2. Feeding behavior across treatments

		8.1 pH/12°C		7.7 pH/12°C		8.1 pH/16°C		7.7 pH/16°C	
	snail	12	15.63 ± 33.25	11	106.00 ± 105.42	11	37.50 ± 33.62	11	52.36 ± 54.31
Prey preference (%)									
	mussel	12	0.89 ± 0.093	11	0.86 ± 0.23	11	0.87 ± 0.10	11	0.86 ± 0.15
	snail	12	0.10 ± 0.093	11	0.14 ± 0.24	11	0.13 ± 0.10	11	0.14 ± 0.15
Appetite (total prey)									
	female	7	27.00 ± 0.87	5	26.50 ± 1.41	7	26.86 ± 1.46	6	24.08 ± 1.83
	male	5	26.00 ± 1.77	6	19.58 ± 5.48	4	24.75 ± 2.02	5	24.30 ± 3.42
Shell damage (freq)									
	snail								
	whole	12	0.42 ± 0.28	11	0.73 ± 0.26	11	0.32 ± 0.25	11	0.59 ± 0.23
	chipped	12	0.39 ± 0.18	11	0.23 ± 0.19	11	0.41 ± 0.22	11	0.28 ± 0.16
	crushed	12	0.19 ± 0.20	11	0.05 ± 0.07	11	0.26 ± 0.22	11	0.13 ± 0.23
	mussel								
	split	12	0.57 ± 0.26	11	0.75 ± 0.23	11	0.53 ± 0.18	11	0.66 ± 0.21
	crushed	12	0.44 ± 0.27	11	0.25 ± 0.23	11	0.46 ± 0.18	11	0.34 ± 0.21

Continued Table 2. Feeding behavior across treatments

		8.1 pH/12 °C		7.7 pH/12 °C		8.1 pH/16 °C		7.7 pH/16 °C	
Feeding strategy (freq)									
	snail								
	break	12	0.41 ± 0.18	11	0.35 ± 0.21	11	0.42 ± 0.19	11	0.50 ± 0.12
	claw grab	12	0.29 ± 0.28	11	0.11 ± 0.12	11	0.17 ± 0.13	11	0.088 ± 0.11
	mouth grab	12	0.30 ± 0.19	11	0.36 ± 0.22	11	0.31 ± 0.19	11	0.41 ± 0.09
	mussel								
	split	12	0.59 ± 0.17	11	0.46 ±0.20	11	0.56 ± 0.14	11	0.43 ± 0.16
	crush	12	0.32 ± 0.13	11	0.27 ± 0.17	11	0.30 ± 0.11	11	0.34 ± 0.13
	bite	12	0.09 ± 0.12	11	0.27 ± 0.13	11	0.14 ± 0.08	11	0.24 ± 0.11

DISCUSSION

The feeding behavior of rock crabs is a critical aspect of ecological dynamics in Southern California that may be affected by ocean acidification and warming as a result of physiological stress. Our hypotheses that OA and OW conditions would alter crab feeding behavior were only partially supported. We found that the appetite of *C. anthonyi* was responsive to pH, with the interaction of temperature affecting male and female crabs differently. All other metrics of feeding behavior were unaffected by either pH or temperature, indicating robustness to our experimental changes in environmental conditions.

Reduced pH decreases appetite

In this study, *C. anthonyi* consumed fewer total prey items (i.e. had a lower appetite score) when exposed to reduced pH (7.7) compared to ambient (8.1) pH conditions, which is consistent with observations made on mud crabs that consumed fewer oysters (Dodd et. al, 2015) and brown crabs, *Cancer pagurus,* that consumed fewer mussels (Wang et. al, 2018) with increasing pCO_2. Additionally, *C. pagurus* fed on smaller sized mussels in high pCO_2 conditions (10-30 mm shell length in 7.7 pH and 10-20 mm shell length in 7.4 pH) compared to ambient conditions (30-50 mm shell length in 8.1 pH) (Wang et. al, 2018). If metabolic rates are higher under reduced pH conditions, as consistently presumed for crustaceans and other invertebrates to maintain homeostasis (Doney et. al, 2012), then *C. anthonyi,* and other species, are not meeting these heightened needs with greater food intake. Suppressed appetite in these species may instead be correlated with reduced metabolic rates under elevated pCO_2 levels (Wang et. al, 2018), as has been observed in *Metacarcinus magister,* which exhibited a significant decrease in

oxygen consumption (Hans et al, 2014). This could explain why *C. anthonyi* consumed significantly less prey in the low pH treatments of this study.

Appetite and temperature/pH interactions differ between sexes

Male *C. anthonyi* had a significantly lower appetite than females, which contrasts with studies showing that for other crab species, like the Asian shore crab, *Hemigrapsus sanguineus* (Brousseau et. al, 2001) and the Japanese brush-clawed shore crab, *Hemigrapsus takankoi* (Theurich et. al, 2022). This genus of shore crabs, unlike rock crabs, are sexually dimorphic, with male crabs having larger claws than females, which may enhance prey capture, but also incur greater metabolic cost (Nour et. al, 2020). Crabs in the *Cancer* genus, on the other hand, show no sexual dimorphism in either claws or body size, but female crabs would require more energy, and thus more food consumption, to meet extra reproductive needs. Female blue crabs, *Callinectes sapidus*, invest more calories per gram into their somatic and reproductive tissues than male crabs (Turner, et. al, 2003), indicating that female crabs allocate more energy for individual maintenance in order to reproduce successfully. A greater appetite in female *C. anthonyi* is therefore not surprising, especially considering that several crabs were ovigerous at some point during the course of the experiment and the cost of carrying eggs increases metabolic rate in intertidal crabs (Taylor & Leelapivanart, 2001).

Despite having different baseline appetites, male and female crabs both demonstrated decreased appetites under one of the reduced pH treatments. Male crab appetite was approximately 19% lower in the reduced pH/ambient temperature (7.7 pH/12°C) treatment than in ambient conditions (8.1 pH/12°C), whereas female crabs had a lower appetite (by 9-11%) in the reduced pH/increased temperature treatment (7.7 pH/16°C) compared to all other treatments.

The results for male crabs support our hypotheses that reduced pH would suppress appetite and that this response would be mitigated when reduced pH was combined with warm temperature. These contrasting effects of pH and temperature on appetite are consistent with observations in other crabs. For instance, higher temperatures (20°C) significantly increased feeding (by 71%) in the crab *Acanthocyclus hassleri,* but when combined with elevated pCO_2 levels, these increases were abated (Manriquez et. al, 2020). Generally, higher temperature stimulates metabolism (Wallace, 1973), leading to greater consumption rates (Sanford, 1999), which could mitigate depressed metabolism and appetite often observed under reduced pH conditions.

Unlike male crabs, it was only the interaction of reduced pH and warmer temperature that affected female crab appetite, resulting in decreased prey consumption. Sex-specific responses to OA and OW conditions are rarely identified, but it is not unheard of that males and females react to their environment in different ways. Temperature is one factor has been shown to independently affect male and female crabs differently in other species due to sex-specific thermal tolerances (Edmands, 2021). For example, female shore crabs, *Pachygrapsus marmoratus,* have a greater thermal maxima and greater production of heat shock proteins than males (Edmands, 2021). If such sex-specific thermal physiology is widespread, it could help to explain why the feeding rates of female Asian shore crabs, *Hemigrapsus takanoi*, were unaffected by higher temperatures while males exhibited decreased feeding rates (Theurich et. al, 2022). It is possible that female *C. anthonyi* have broader pH and thermal tolerance than males, but when these stressors are combined, they act synergistically to decrease the aerobic scope and ability of female crabs to use energy for consuming prey. As seen in the shrimp *Metapenaeus joyneri*, reduced pH and increased temperature can act synergistically to reduce metabolic scope and swimming ability, among other physiological effects (Dissanayake & Ishimatsu, 2011).

The physiological differences driving these disparate responses between the sexes could also be related to imbalanced reproductive costs. Multiple female *C. anthonyi* were gravid and lost their eggs during our experiment. When gravid, female crabs have been shown to consume less food than males and non-gravid females (Choy, 1986), and this is potentially exacerbated by combined environmental stressors. The gravid state of female *C. anthonyi* was not continuously monitored throughout our experiment, but it did occur across all treatments and is therefore an unlikely explanation for the combined stressor effects. The reduced feeding rates of female *C. anthonyi* under combined stressors, but neither reduced pH nor increased temperature alone, requires deeper investigation into their metabolic rates, as well as other physiological aspects, to understand their distinct response.

Feeding behavior unaffected by OA and OW conditions

Foraging and feeding behaviors have been shown to be dependent on pCO_2 levels and temperature for multiple crab species. Under high pCO_2 levels, the dungeness crab, *Metacarcinus magister,* took significantly less time to handle and consume prey, and overall showed a reduced feeding performance with longer foraging periods (Wang et. al, 2018). Additionally, *Charybdis japonica,* the Japanese stone crab, showed a significantly increased foraging and feeding time when exposed to very low pH (7.3), while high temperatures (25°C) decreased their foraging and feeding time (Wu et. al, 2017). Unlike these species, most of the feeding behavior metrics measured for *C. anthonyi* were unaffected by the pH and temperature treatments used in our study. Notably, our treatment levels are not as severe as those used in other studies that uncovered changes in feeding behavior (Wu et. al, 2017; Wang et. al, 2018), but they revealed that a low pH of 7.7 and a temperature range of 12-16°C induce sufficient

stress in *C. anthonyi* to alter appetite, but not manifest in observable changes in other aspects of feeding behavior. *C. anthonyi* appears to have the regulatory capacity to accommodate near-term OA and OW conditions by adjusting only certain aspects their feeding behavior, though their pH and temperature thresholds are unknown. For blue crabs, *C. sapidus*, the pH threshold is very low: predation rates were only affected at a pH of 6.75 (Hidalgo et. al, 2022), which can be reached in marsh creeks of the Chesapeake Bay (Breitburg & Burrell, 2014). For *C. anthonyi* that live mostly between 18-55 m depth (Carroll & Winn, 1989), they only rarely experience pH levels as low as 7.69 during upwelling off of La Jolla, CA (Kekuewa et. al, 2022). Our experiment was conducted during the upwelling season and we exposed crabs to pH conditions slightly below the averages observed down to 40 m depth during this period (Kekuewa et. al, 2022), with ambient ocean temperature averaging 12°C. Our unseasonably warm temperature treatment (16°C) affected crab feeding behavior, even though *C. anthonyi* are likely to have higher temperature thresholds as they encounter temperatures above 20°C during the summer season (Smith lab data - SOAR). Assessing upper temperature thresholds for *C. anthonyi* would be beneficial for understanding their responses to increasingly warmer ocean temperatures.

Feeding behaviors of C. anthonyi

        Though the goal of this study was to assess the potential effects of OA and OW conditions on the feeding behavior of *C. anthonyi*, some of our observations enhance our understanding of their local ecology, which would be useful for understanding downstream impacts and managing this important fishery into the future. For instance, *C. anthonyi* showed a preference for mussel over snails and used different predation strategies for consuming different types of mollusks. The preference for mussels is consistent with the Atlantic rock crab, *Cancer*

irroratus, that also strongly preferred mussels over barnacles (Sungail et. al, 2013), quahog (Miron et. al, 2005) and sea urchins (Drummond-Davis et. al, 1982). If mussels are a primary food source for *C. anthonyi*, then their known susceptibility to OA conditions (O'Donnell et. al, 2013; Gazeau et. al, 2010; Fitzer et. al, 2014) could favor crab predation, but ultimately be problematic for crabs if their populations decline under future ocean conditions.

There is little known about the feeding behaviors and strategies of *C. anthonyi,* or rock crabs in general, but it has been observed that *C. irroratus* are more active and use a variety of handling strategies compared to other species of crabs (Moody & Steneck, 1992). Additionally, when offered larger mussels, *C. irroratus* would shift to a higher prevalence of strategies described in the study as "forces applied to the edge of the shell", such as prying and edge chipping (Moody & Steneck, 1992). We also observed that *C. anthonyi* mostly used their claws to chip the shells of snails to access the soft tissue but split the valves apart in mussels rather than breaking them. Consuming mussels in this way requires them to overcome the strength of the adductor muscles holding the valves together but does not require crabs to break the hard shell as it does for snails. This is despite our measurements showing that mussels have a much lower compressive breaking strength than snails (89 N vs 461 N). Changes in shell integrity of mollusk prey under OA conditions (Parker et. al, 2013; Coleman et. al, 2014) is more likely to have an impact on crab feeding behavior than direct effects on crab physiology.

CONCLUSION

The purported metabolic costs of survival in chemically altered environments can cause a reduction in energy availability for other behaviors, such as feeding (Briffa et. al, 2012). In our study, reduced pH conditions decreased the appetite of *C. anthonyi*. OA and warm temperatures did not affect most metrics of feeding behavior in *C. anthonyi,* but they did affect appetite in different ways for male and female crabs. Reduced pH at ambient temperature decreased appetite in male crabs, but female crab appetite decreased in combined reduced pH/increased temperature conditions. Such sex-specific responses highlight the need to consider potential sex differences in other environmental research on crustaceans. Furthermore, the results from our study show that *C. anthonyi* is not immune to OA and warming conditions in terms of feeding behavior, despite the fact that they already experience warmer temperatures due to El Niño events and low pH levels due to upwelling. Overall, this study adds new insights to our growing understanding of how OA and OW conditions affect aspects of ecological importance in crustaceans.

REFERENCES

Blundon J.A. (1989). Effects of temperature and thermal history on neuromuscular properties of two crustacean species. *J Comp Physiol B* **158**, 689–696. https://doi.org/10.1007/BF00693006

Breitburg D., Burrell R. (2014). Predator-mediated landscape structure: seasonal patterns of spatial expansion and prey control by *Chrysaora quinquecirrha* and *Mnemiopsis leidyi* . Mar *Ecol Prog Ser* **510**:183-200. https://doi.org/10.3354/meps10850

Briffa M., Haye K., Munday P. (2012). High CO2 and marine animal behaviour: Potential mechanisms and ecological consequences. *Marine Pollution Bulletin* **64**: 1519-1528. https://www.sciencedirect.com/science/article/pii/S0025326X12002524

Brousseau D., Filipowicz A., Baglivo J. (2001). Laboratory investigations of the effects of predator sex and size on prey selection by the Asian crab, *Hemigrapsus sanguineus. Journal of Experimental Marine Biology and Ecology* **262**: 199-210. https://www.sciencedirect.com/science/article/pii/S0022098101002908

Choy Satish C. (1986). Natural diet and feeding habits of the crabs *Liocarcinus puber* and *L. holsatus* (Decapoda, Brachyura, Portunidae). *Marine Ecology Progress Series* **31**: 87-99. https://www.jstor.org/stable/24817268

de la Haye K., Spicer J. I., Widdicombe S., Briffa M. (2011). Reduced sea water pH disrupts resource assessment and decision making in the hermit crab *Pagurus bernhardus. Animal Behaviour* **82**: 496-501. https://www.sciencedirect.com/science/article/pii/S0003347211002405

Dissanayake A., Ishimatsu A. (2011). Synergistic effects of elevated CO2 and temperature on the metabolic scope and activity in a shallow-water coastal decapod (Metapenaeus joyneri; Crustacea: Penaeidae). *ICES Journal of Marine Science* **68**: 1147-1154. https://doi.org/10.1093/icesjms/fsq188

Dodd L. F., Grabowski J., Piehler M., Westfield I., Ries J. (2015). Ocean acidification impairs crab foraging behaviour. *Proceedings of the Royal Society B: Biological Sciences* **282**: 20150333. https://royalsocietypublishing.org/doi/full/10.1098/rspb.2015.0333

Doney S., Ruckelshaus M., Emmett D., Barry J., Chan F., English C., Galindo H., Grebmeier J., Hollowed A., Knowlton N., Polovina J., Rabalais N., Sydeman W., Talley L. (2012). Climate Change Impacts on Marine Ecosystems. *Annual Review of Marine Science* **4**: 11-37. https://doi.org/10.1146/annurev-marine-041911-111611

Drummond-Davis N. C., Mann K. H., Pottle R. A. (1982). Some Estimates of Population Density and Feeding Habits of the Rock Crab, *Cancer irroratus*, in a Kelp Bed in Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **39**: 636-639. https://cdnsciencepub.com/doi/10.1139/f82-090

Edmands S. (2021). Sex Ratios in a Warming World: Thermal Effects on Sex-Biased Survival, Sex Determination, and Sex Reversal. *The Journal of Heredity* **112**: 155-164. 10.1093/jhered/esab006

Elner R., Jamieson G. (1979). Predation of Sea Scallops, *Placopecten magellanicus*, by the Rock Crab, *Cancer irroratus*, and the American Lobster, *Homarus americanus. Journal of the Fisheries Research Board of Canada* **36**: 537-543. https://cdnsciencepub.com/doi/abs/10.1139/f79-077

Epelbaum A., Pearce C. M., Barker D. J., Paulson A., Therriault T. (2009). *Marine Biology* **156**: 1311-1320. https://doi.org/10.1007/s00227-009-1172-7

Fitzer S. C., Phoenix V., Cusack M., Kamenos N. (2014). Ocean acidification impacts mussel control on biomineralization. *Scientific Reports* **4**: 6218. https://www.nature.com/articles/srep06218

Gazeau F., Gattuso J.-P., Dawber C., Pronker A. E., Peene F., Peene J., Heip C. H. R., Middelburg J. J. (2010). Effect of ocean acidification on the early life stages of the blue mussel *Mytilus edulis. Biogeosciences* **7**: 2051-2060. https://bg.copernicus.org/articles/7/2051/2010/

Hans S., Fehsenfeld S., Treberg J., Weihrauch D. (2014). Acid–base regulation in the Dungeness crab (*Metacarcinus magister*). *Marine Biology* **161**: 1179-1193. https://doi.org/10.1007/s00227-014-2409-7

Hidalgo F. J., Miller S. H., Borst K., Dozier J., Breitburg D. (2022). Context-dependent effects of ocean acidification on the interaction between a crab predator and its oyster prey. *Marine Ecology Progress Series* **693**: 39-54. https://ui.adsabs.harvard.edu/abs/2022MEPS..693...39H

Hull W. W., Bourdeau P. E. (2017). Can crabs kill like a keystone predator? A field-test of the effects of crab predation on mussel mortality on a northeast Pacific rocky shore. *PLOS ONE* **12**: e0183064. https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0183064

Kekuewa S. A. H., Courtney T. A., Cyronak T., Andersson A. J. (2022). Seasonal nearshore ocean acidification and deoxygenation in the Southern California Bight. *Scientific Reports* **12**: 17969. https://www.nature.com/articles/s41598-022-21831-y

Lambert C. C., Lambert G. (1998). Non-indigenous ascidians in southern California harbors and marinas. *Marine Biology* **130**: 675-688. https://doi.org/10.1007/s002270050289

Landes A., Zimmer M. (2012). Acidification and warming affect both a calcifying predator and prey, but not their interaction. *Marine Ecology Progress Series* **450**: 1-10. https://www.int-res.com/abstracts/meps/v450/p1-10/

Leduc A. O. H. C., Munday P. L., Brown G. E., Ferrari M. C. O. (2013). Effects of acidification on olfactory-mediated behaviour in freshwater and marine ecosystems: a synthesis.

Philosophical Transactions of the Royal Society B: Biological Sciences **368**: 20120447.
https://royalsocietypublishing.org/doi/10.1098/rstb.2012.0447

Lee S. Y. (1998). Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine and Freshwater Research* **49**: 335-343. https://www.publish.csiro.au/mf/mf97179

Longmire K. S., Seitz R. D., Seebo M. S., Brill M. S., Lipcius R. N. (2022). Biological responses of the predatory blue crab and its hard clam prey to ocean acidification and low salinity. *Marine Ecology Progress Series* **701**: 67-81. https://www.int-res.com/abstracts/meps/v701/p67-81/

Manríquez P. H., González C. P., Seguel M., Garcia-Huidobro M. R., Lohrmann K. B., Domenici P., Watson P., Duarte C., Brokordt K. (2021). The combined effects of ocean acidification and warming on a habitat-forming shell-crushing predatory crab. *Science of The Total Environment* **758**: 143587.
https://www.sciencedirect.com/science/article/pii/S0048969720371187

Miron G., Audet D., Landry T., Moriyaus M. (2005). PREDATION POTENTIAL OF THE INVASIVE GREEN CRAB (*CARCINUS MAENAS*) AND OTHER COMMON PREDATORS ON COMMERCIAL BIVALVE SPECIES FOUND ON PRINCE EDWARD ISLAND. *Journal of Shellfish Research* **24**: 579-586. https://bioone.org/journals/journal-of-shellfish-research/volume-24/issue-2/0730-8000_2005_24_579_PPOTIG_2.0.CO_2/PREDATION-POTENTIAL-OF-THE-INVASIVE-GREEN-CRAB-CARCINUS-MAENAS-AND/10.2983/0730-8000(2005)24[579:PPOTIG]2.0.CO;2.full

Moody K. E., Steneck R. S. (1993). Mechanisms of predation among large decapod crustaceans of the Gulf of Maine Coast: functional vs. phylogenetic patterns. *Journal of Experimental Marine Biology and Ecology* **168**: 111-124.
https://www.sciencedirect.com/science/article/pii/0022098193901188

Nour O. S. E. D. M., Stumpp M., Moron Lugo S. C., Barboza F. R., Pansch C. (2020). Population structure of the recent invader *Hemigrapsus takanoi* and prey size selection on Baltic Sea mussels. *Aquatic Invasions* **15** 297-317. http://dx.doi.org/10.3391/ai.2020.15.2.06

O'Donnell M. J., George M. N., Carrington E. (2013). Mussel byssus attachment weakened by ocean acidification. *Nature Climate Change* **3**: 587-590.
https://ui.adsabs.harvard.edu/abs/2013NatCC...3..587O

Parker L. M., Ross P. M., O'Connor W. A., Pörtner H. O., Scanes E., Wright J. M. (2013). Predicting the Response of Molluscs to the Impact of Ocean Acidification. *Biology* **2**: 651-692. https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3960890/

Sanford E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science (New York, N.Y.)* **283**: 2095-2097. 10.1126/science.283.5410.2095

Seed R., Hughes R. N. (1995). Criteria for prey size-selection in molluscivorous crabs with contrasting claw morphologies. *Journal of Experimental Marine Biology and Ecology* **193**: 177-195. https://www.sciencedirect.com/science/article/pii/0022098195001174

Shanebeck K. M., Presswell B., Lagrue C. (2020). Missing link: California rock crabs serve as intermediate hosts for the parasite *Helicometrina nimia*. *Journal of Helminthology* **94**: e143. https://www.cambridge.org/core/journals/journal-of-helminthology/article/missing-link-california-rock-crabs-serve-as-intermediate-hosts-for-the-parasite-helicometrina-nimia/BA695C9D36A2FC50FD0DE82BF3EBED68

Stein W., Harzsch S. (2021). The Neurobiology of Ocean Change - insights from decapod crustaceans. *Zoology (Jena, Germany)* **144**: 125887. 10.1016/j.zool.2020.125887

Sungail J., Brown A. C., Alpert K., Maurukas J. (2013). Prey selection by Gulf of Maine green crabs (*Carcinus maenas*), rock crabs (*Cancer irroratus*) and American lobsters (*Homarus americanus*): A laboratory study. *Journal of Experimental Marine Biology and Ecology* **449**: 294-303. https://www.sciencedirect.com/science/article/pii/S0022098113003614

Taylor H. H., Leelapiyanart N. (2001). Oxygen uptake by embryos and ovigerous females of two intertidal crabs, Heterozius rotundifrons (Belliidae) and Cyclograpsus lavauxi (Grapsidae): scaling and the metabolic costs of reproduction. *Journal of Experimental Biology* **204**: 1083-1097. https://doi.org/10.1242/jeb.204.6.1083

Theurich N., Briski E., Cuthbert R. N. (2022). Predicting ecological impacts of the invasive brush-clawed shore crab under environmental change. *Scientific Reports* **12**: 9988. https://www.nature.com/articles/s41598-022-14008-0

Vermeij G. J. (1977). Patterns in Crab Claw Size: The Geography of Crushing. *Systematic Biology* **26**: 138-151. https://doi.org/10.1093/sysbio/26.2.138

Wallace J. C. (1973). Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas*. *Marine Biology* **20**: 277-281. https://doi.org/10.1007/BF00354271

Wang Y., Hu M., Wu F., Storch D., Pörtner H.-O. (2018). Elevated pCO2 Affects Feeding Behavior and Acute Physiological Response of the Brown Crab *Cancer pagurus*. *Frontiers in Physiology* **9**. https://www.frontiersin.org/articles/10.3389/fphys.2018.01164

Wittmann A., Pörtner H.-O. (2013). Sensitivies of extant animal taxa to ocean acidification. *Nature Climate Change* **3**: 995-1001. 10.1038/nclimate1982

Wu F., Wang T., Cui S., Xie Z. Dupont S. (2017). Effects of seawater pH and temperature on foraging behavior of the Japanese stone crab *Charybdis japonica*. *Marine Pollution Bulletin* **120**: 99-108. https://www.sciencedirect.com/science/article/pii/S0025326X17303612

Zittier Z. M.C., Hirse T., Pörtner H.-O. (2013). The synergistic effects of increasing temperature and CO2 levels on activity capacity and acid–base balance in the spider crab, *Hyas araneus*.

Marine Biology **160**: 2049-2062.
http://www.springerlink.com/openurl.asp?genre=article&id=doi:10.1007/s00227-012-2073-8

California Department of Fish and Wildlife (2019).
https://wildlife.ca.gov/Fishing/Commercial/Landings