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Ocean acidification reduces juvenile snow crab, *Chionoecetes opilio*, survival but does not affect growth or morphometrics

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ABSTRACT

Anthropogenic release of CO_2 and its subsequent dissolution in the oceans results in a decrease in the pH of seawater, known as ocean acidification, which can negatively affect marine organisms. Little is known about the response of snow crab, *Chionoecetes opilio*, to reduced pH. Juvenile snow crab were captured in the Bering Sea and exposed to three different pH treatments (Ambient (pH ~7.95), pH 7.8, and pH 7.5) for 396 days at a constant temperature of 4 °C with thirty crabs randomly assigned to each treatment. Crabs were checked daily for molting or mortality. Wet mass and carapace morphometrics were measured after every molt. Reduced pH did not affect the intermolt duration, the carapace width after each molt, or wet mass of the crabs after each molt, giving no indication that growth rate was changed by reduced pH. There also was no change in morphometrics caused by reduced pH. However, the mortality rate of crabs held at pH 7.5 was 40 % higher than those held at pH 7.8 or Ambient. Such a substantial increase in mortality without accompanying sublethal effects is surprising; individuals susceptible to reduced pH might have died early in the experiment, or that differences in growth rate might have become apparent with longer exposure. Regardless, juvenile snow crab are somewhat sensitive to ocean acidification, although, consistent with studies at other life-history stages, snow crab may be more resistant to changes in pH than other Alaska crab species.

1. Introduction

Since the advent of the Industrial Revolution, anthropogenic CO_2 emissions have caused an increase in the pCO_2 in the atmosphere and a commensurate increase in the oceans (Feely et al., 2004). Increasing pCO_2 in the oceans results in a lowering of the pH called ocean acidification (OA) becasue the CO_2 reacts with water to form carbonic acid; pH levels have dropped approximately 0.1 units over the last century (Caldeira and Wickett, 2003) with further reductions predicted and dependent on future CO_2 emission levels (Bopp et al., 2013; Pilcher et al., 2022). This gradual alteration of the carbonate chemistry of seawater affects a wide range of marine species, in part, due to the decrease in the saturation state of calcium carbonate, which is an important structural component for a wide range of organisms; however, the effects of OA differ greatly among species and OA is likely alter marine ecosystems through both direct and indirect mechanisms (Kroeker et al., 2013b; Kroeker et al., 2013a; Leung et al., 2022). Understanding how OA affects individual species is an important step to predicting how OA is likely to alter marine systems and the human fisheries dependent on them.

The snow crab, *Chionoecetes opilio,* is an important fisheries species that is distributed in Arctic and sub-Arctic waters in the Pacific, Atlantic, and Arctic Oceans (Jadamec et al., 1999). In the eastern Bering Sea, it has supported one of the largest crustacean fisheries in the world; however, the stock crashed in 2020 (Zacher et al., 2023), likely due to record-high water temperatures leading to mass starvation (Szuwalski et al., 2023), and the fishery was closed in 2022. Snow crab have life-history that is similar to many decapods. In the Bering Sea, eggs are incubated for 1 to 2 years, depending on water temperature (Gardner et al., 2021), before hatching (Webb et al., 2007). Larvae are planktonic and planktotrophic and pass through two zoeal stages before molting to the megalops stage and settling to the benthos and molting to the first crab stage (Kon, 1980).

Many decapod crustacean species are sensitive to ocean acidification (Bednaršek et al., 2021). An increase in ambient pCO_2 leads initially to higher pCO_2 and lower pH in the hemolymph (Pane and Barry, 2007). To return to homeostasis, crustaceans employ physiological mechanisms including decreasing basal metabolism (Pane and Barry, 2007; Small

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et al., 2016) and active ion transport at the gill (Whiteley, 2011; Harms et al., 2014); changes in gene expression suggest a wide range of other physiological changes (Harms et al., 2014; Niemisto et al., 2020; Spencer et al., 2024). These changes, however, have an energetic cost (Long et al., 2019) and physiological consequences such that long-term exposure can lead to decreased growth (Small et al., 2016; Long et al., 2021), increased mortality (Long et al., 2013a; Menu-Courey et al., 2019; Turra et al., 2020), reduced hatching success (Gravinese, 2018), hemocyte mortality (Meseck et al., 2016), reduction in cuticle physical and mechanical properties (Coffey et al., 2017; Dickenson et al., 2021), and changes in behavior (Durant et al., 2023; Ohnstad et al., 2024). Many species, however, are unaffected by low pH (Glandon and Miller, 2017; Glandon et al., 2018; Glandon et al., 2019; Gravinese et al., 2022). Snow crab mature females, embryos, and larvae are highly resistant to low pH (Algayer et al., 2023; Long et al., 2023), which stands in stark contrast with Tanner crab, *Chionoecetes bairdi,* a closely related congener with overlapping distribution in the Bering Sea (Long et al., 2016; Swiney et al., 2016). Nothing is known about the effects of OA on other life-history stages; however, this paper presents the results of a long-term experiment quantifying the effects of OA on the growth, morphometrics, and survival of juvenile snow crab.

2. Methods

Juvenile snow crab were captured by trawling in the Bering Sea and transported to the Kodiak laboratory in coolers filled with wet burlap and cooled with ice blocks. Upon arrival they were acclimated to the laboratory in tanks with flow-through sea water at ambient salinity (typical range ~ 30.5–32.5; see Table 1) from Trident Basin, Kodiak, chilled to 4 °C with a recirculating chiller and fed chopped fish and squid.

Experiments were performed in 380 L tanks with flow-through water at ambient salinity. Water was chilled with recirculating chillers to 4 °C throughout the experiment. Tanks were assigned randomly to 1 of 3 pH treatments: ambient pH, pH 7.8, and pH 7.5. Although average surface pH is not expected to reach a pH of 7.5 before the year 2200 (Pilcher et al., 2022), the pH in the eastern Bering Sea can seasonally drop down to ~ pH 7.5 for several months under current conditions (Mathis et al., 2014). The pH treatments were, in part, selected to allow for direct comparisons between this study and similar research on other Alaska crab species, including the Tanner crab, and to experiments on other life history stages of snow crab (Long et al., 2013b; Long et al., 2023). The pH in each tank was maintained by direct bubbling of CO_2 controlled via feedback from a Durafet III pH probe as per (Long et al., 2024). Temperature and pH were measured three times a week in three randomly selected inserts in each treatment and salinity was measured once a week using a Mettler Toledo InLab 731-2 m salinity probe. Alkalinity was calculated using the alkalinity-salinity relationship for the Gulf of Alaska (Evans et al., 2015) and other carbonate chemistry parameters were calculated using the seacarb package in R (R 4.2.3, Vienna, Austria). Propagated error to other carbonate chemistry parameters from using the alkalinity-salinity relationship has been shown to be very low (Evans et al., 2015). The average pH and temperatures in the tanks were close to the nominal targets and the water in the pH 7.8 treatment was undersaturated with respect to aragonite and the water in the pH 7.5 treatment was undersaturated with respect to both aragonite and calcite (Table 1).

Thirty crabs were randomly assigned to each treatment and placed in individual inserts made of 52 mm diameter PVC pipe with a mesh bottom. When a crab grew too large for its insert, it was transferred to a larger-sized insert 76 mm in diameter in order to avoid space-limited decreases in growth (Swiney et al., 2013). Water from within the tank was recirculated to each insert. This design does not allow for an estimate of tank effects, as all crabs within each treatment were housed in a single tank each; however, keeping the crabs in isolation substantially reduces the likelihood of tank effects. Crabs were fed 3 times a week to excess on a diet of Gelly Belly (Florida Aqua Farms, Inc., Dade City, Florida, USA) combined with Cyclopeeze powder or freeze-dried copepods, fish bone meal, astaxanthin, and krill and cod liver oils. Crabs were checked daily for molting or mortality. Exuvia and dead crab were carefully removed from the tanks and photographed using a stereo microscope. Images were calibrated using a 2 mm micrometer and the carapace width, carapace length, carapace length to the rostrum, carapace length to the eye orbit, rostrum base width, rostrum length, orbital spine width, and orbital spine length were measured using image analysis software for morphometric analysis (Fig. 1). Crabs were blotted dry and weighed at the beginning of the experiment and 7 days after each molt. At the end of the experiment the crabs were sacrificed by freezing them and then imaged and measured as above. The experiment began on April 23, 2021 and ran for 396 days.

Table 1
Average ± SD water chemical and physical properties in each of the three pH treatments. Temperature and pH were measured three times a week and salinity once every 2 weeks. Other parameters were calculated.

	Ambient	pH 7.8	pH 7.5
Temperature	4.1 ± 0.5	3.9 ± 0.3	3.9 ± 0.4
Salinity	31.73 ± 0.37	31.71 ± 0.34	31.75 ± 0.35
pH_T	7.96 ± 0.07	7.80 ± 0.02	7.50 ± 0.04
pCO_2 μatm	473 ± 97	702 ± 33	1415 ± 130
HCO_3^- mmol/kg	1.95 ± 0.042	1.953 ± 0.046	1.956 ± 0.048
CO_3^{-2} mmol/kg	0.081 ± 0.015	0.08 ± 0.016	0.079 ± 0.017
DIC mmol/kg	2.057 ± 0.034	2.059 ± 0.037	2.062 ± 0.038
Alkalinity mmol/kg	2.154 ± 0.018	2.154 ± 0.018	2.154 ± 0.018
$\Omega_{Aragonite}$	1.23 ± 0.23	0.84 ± 0.05	0.45 ± 0.06
$\Omega_{Calcite}$	1.96 ± 0.37	1.35 ± 0.08	0.72 ± 0.09

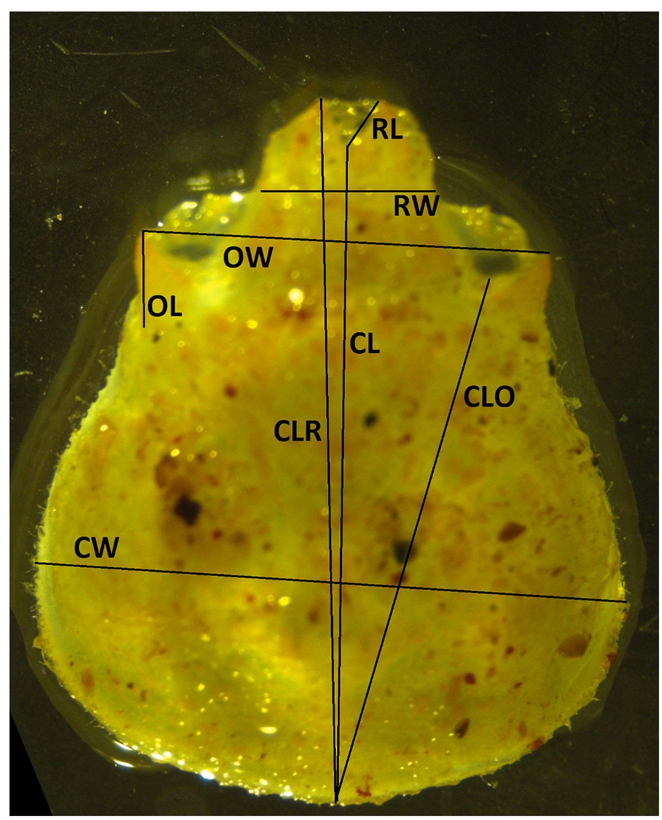

Fig. 1. Morphometric measurements made on juvenile snow crab. Measurements included carapace width (CW), carapace length (CL), carapace length to the rostrum (CLR), carapace length to the eye orbit (CLO), rostrum base width (RW), rostrum length (RL), orbital spine width (OW), and orbital spine length (OL).

The carapace width and wet mass of the crabs were analyzed with one-way ANOVAs with pH treatment as the factor. A separate analysis was performed for the sizes at the beginning of the experiment, after each molt, and at the end of the experiment. The assumption of homogeneity of variance was checked with Levene's test. The intermolt duration for each molt was calculated as the number of days between each subsequent molt and was analyzed with one-way ANOVAs with a separate analysis for each molt. Morphometric data were normalized and used in a permutational multivariate analysis of variance (PERMANOVA) based on a Euclidean distance matrix, with pH treatment fully crossed with molt stage, and crab identity nested within treatment as factors. Data were visualized using a non-metric multidimensional scaling plot.

Mortality was modelled assuming a constant rate of mortality over time such that

$$p = e^{-mt},$$

where p is the proportional survival, m is the mortality rate, and t is the time in days. Using maximum likelihood, a series of models was fit where m was allowed to vary with pH treatment with a binomial distribution of errors. Models considered included one where the treatments all had the same mortality rate, one where they all differed from each other, one where the ambient differed from the two low pH treatments, and one where the pH 7.5 treatment differed from the two others. The Akaike's Information Criterion corrected for small sample size (AICc) was used to select the best model (Burnham and Anderson, 2002).

All data from this project has been published and is freely available at the National Centers for Environmental Information (Long, 2025).

3. Results

Crabs molted up to 3 times during the experiment. Most of the crabs molted for the first time within the first month. At the end of the experiment, all but 2 crab, both in the pH 7.5 treatment, molted at least twice, and 12 crabs molted a third time. There was no difference among treatments in either the wet mass or the carapace width at the beginning of the experiment, after any molt, or at the end of the experiment (Table 2, Fig. 2). Likewise, neither the first (ANOVA, $F_{2,63} = 0.669$, $p = 0.516$) nor second (ANOVA, $F_{2,9} = 3.735$, $p = 0.066$) intermolt duration differed among the treatments (Fig. 3). Crab morphometrics differed among molt stages, reflecting expected growth, but not among pH treatments or their interaction (Table 3, Fig. 4).

In the best-fit model for crab mortality, the mortality rate was higher in the pH 7.5 treatment than in the other two treatments (Table 4). There was very limited support for the model in which all three treatments differed from each other, which had a ΔAICc of about 1.4. However, because that model only improved the −2 log-likelihood by 0.65 compared to the best model and the estimates for the mortality rate in the ambient and pH 7.8 treatments had strongly overlapping 95 % CIs, and the two treatments had the same overall percent survival at the end

Table 2
Summary ANOVA statistics for the effects of ocean acidification on snow crab wet mass and carapace width across multiple molts. Initial and Final indicate measurements at the beginning and end of the experiments. Molt 1–3 represent the measurements after the first through 3 molts, respectively. DF represents degrees of freedom.

	Wet mass			Carapace width		
	Error DF	F	p	Error DF	F	p
Initial	87	0.429	0.652	85	0.068	0.934
Molt 1	74	0.809	0.449	82	2.094	0.13
Molt 2	63	2.252	0.114	65	1.741	0.184
Molt 3	9	2.611	0.128	9	2.038	0.186
Final	57	1.893	0.16	57	1.447	0.244

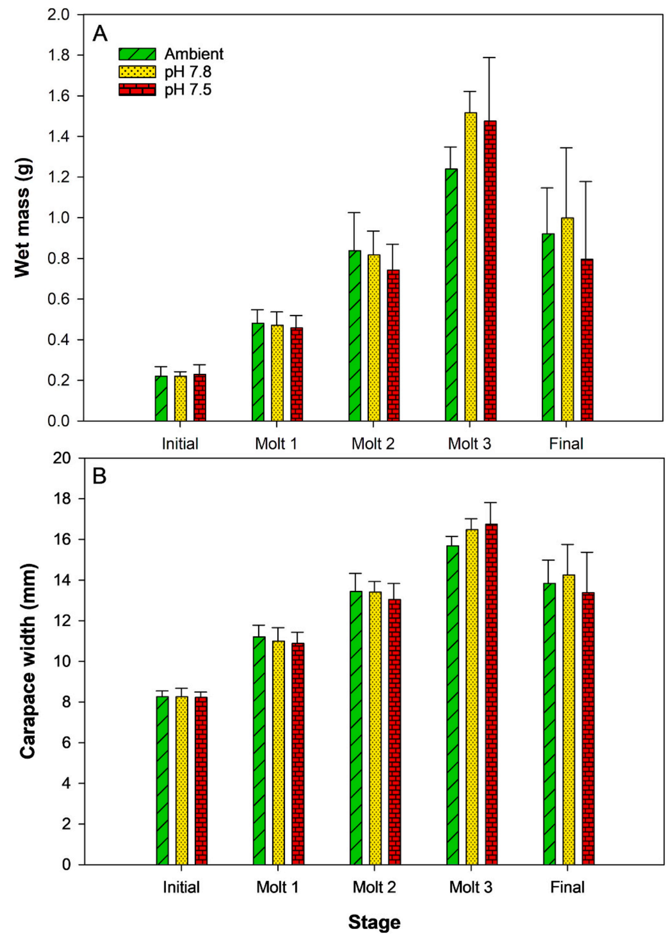

Fig. 2. Average wet mass and carapace widths of snow crabs held at three different pH treatments for multiple molts. Initial and Final indicate measurements at the beginning and end of the experiments. Molt 1–3 represent the measurements after the first through 3 molts, respectively. Error bars are one standard deviation. There were no differences among the treatments in either width or mass at any of the stages.

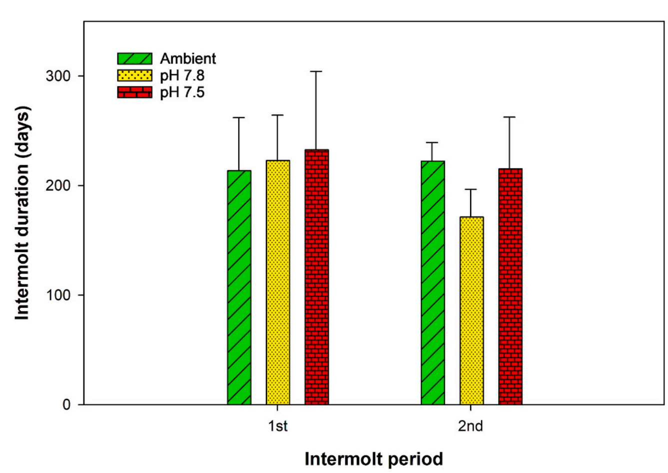

Fig. 3. Intermolt duration between the first and second (1st) and second and third molts (2nd) for snow crabs held in three different pH treatments. Bars are means and error bars one standard deviation. There was no difference among treatments for either intermolt duration.

Table 3
Permutational multivariate analysis of variance on juvenile snow crab morphometric measurements of crabs held at three different pH treatments over several molts. Tr represents pH treatment and St represent the molt stage.

Source	df	SS	MS	Pseudo-F	p
pH treatment	2	4.7635	2.3818	1.2082	0.2927
Molt stage	3	1235	411.67	245.23	0.00001
Tr x St	6	11.522	1.9203	1.1439	0.2931
Crab(Tr)	85	208.11	2.4484	1.4585	0.0001
Residual	145	243.42	1.6787		
Total	241	1928			

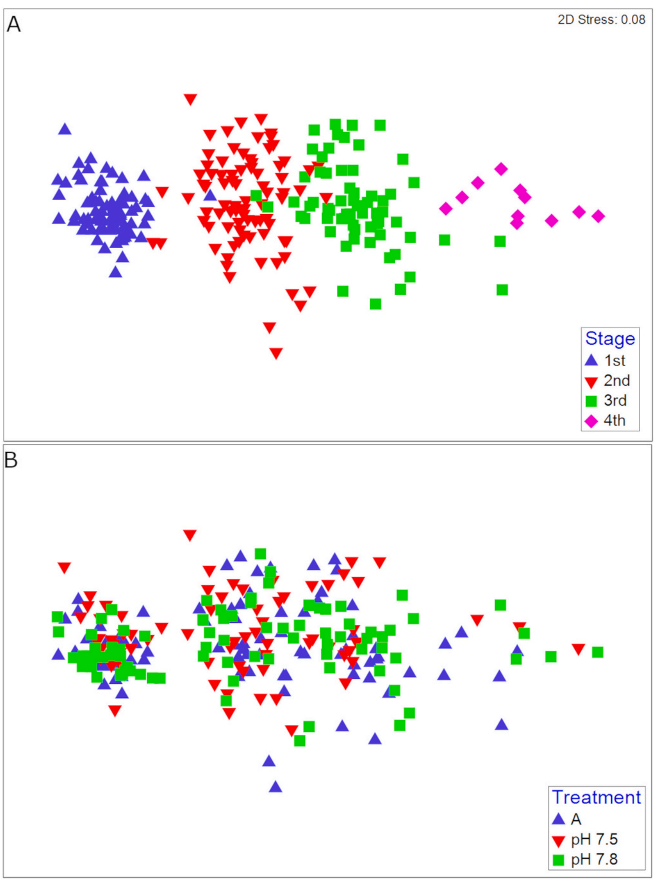

Fig. 4. Non-metric multidimensional scaling plot of the morphometrics of juvenile snow crab held at three different pHs over several molts. Stage represents the molt stage from the beginning of the experiment. Treatment is the pH treatment with *A* representing the ambient.

of the experiment, I make inferences from only the best-fit model (Burnham and Anderson, 2002). For completeness, the parameter estimates for both models are provided (Table 4). Both the ambient and pH 7.8 treatments had greater than 75 %survival (22 out of 30 crabs) at the end of the experiment whereas the pH 7.5 had only 50 % (15 of 30) survival (Fig. 5) and, in all treatments but particularly in the pH 7.5 treatment, mortality was associated with molting; that is, crabs tended to die during times of synchronized molting (cf. Figs. 3 and 5). The estimated mortality rate in the pH 7.5 treatment was 40 % higher than the other two treatments (Table 4).

4. Discussion

Snow crab juveniles may be moderately resistant to exposure to low pH. In this long-term study, snow crab mortality rates increased at the lowest pH tested but not at more moderate pHs. At the same time, no

Table 4
Model selection using Akaike's Information Criterion adjusted for small samples size (AICc) and parameter estimates (± 1 standard error) for the best fit models of the mortality rate of juvenile snow crabs held in three different pH treatments. Model indicates which treatments had the same mortality rates and K is the number of parameters. See text for model details.

Model	K	AIC_c	ΔAIC_c	Likelihood	AIC_c weight
All same	1	4699.00	158.56	0.00	0.00
All different	3	4541.80	1.36	0.51	0.34
Ambient, pH 7.8 = pH 7.5	2	4649.87	109.44	0.00	0.00
Ambient = pH 7.8, pH 7.5	2	4540.44	0.00	1.00	0.66
	Parameter estimates (days^{-1})				
	All different		**Ambient = pH 7.8, pH 7.5**		
$m_{Ambient}$	0.000845 ± 0.00002		0.000856 ± 0.000014		
$m_{pH7.8}$	0.000868 ± 0.00002		0.000856 ± 0.000014		
$m_{pH7.5}$	0.001194 ± 0.000024		0.001194 ± 0.000024		

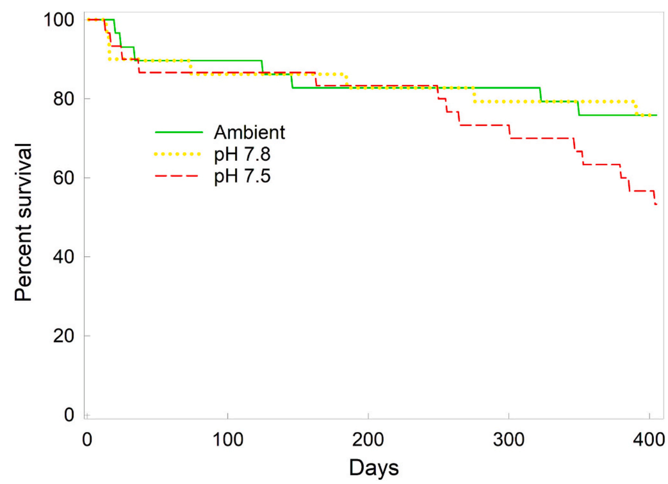

Fig. 5. Percent survival of juvenile snow crabs held in three different pH treatments over a 396-day experiment.

sublethal effects were detected. Growth rates, in terms of size and mass at molt stage and intermolt period, did not differ among treatments. Similarly, no change in morphometry over the course of several molts occurred. Overall, these results, especially when combined with other studies, suggest that snow crab will be resilient to pH conditions predicted over the next 50 to 100 years.

Mortality rates in snow crab were affected by pH and likely by molting. Almost all the crabs molted for the first time within the first 30 days and there was about 10 % mortality in all three treatments over this period. There was a second period of increased mortality at about the 250-day point, commensurate with the next round of molting, but this was only apparent in the pH 7.5 treatment and in the other two treatments the mortality rate was low and fairly constant. Molting is a physiologically stressful and energetically intensive period for crustaceans even in the absence of stressors (Roberts, 1957; Mangum et al., 1985; Chang, 1995). It is unsurprising that, under moderately stressful conditions, mortality would be associated with molting. In many species, including red king crab, *Paralithodes camtschaticus*, golden king crab, *Lithodes aequispinus,* (Long et al., 2021), Tanner crab, *Chionoecetes bairdi,* (Long et al., 2013b), and the European lobster, *Homarus gammarus*, (Small et al., 2016), mortality at low pH occurs at a higher rate during periods of molting. The mechanism leading to higher mortality is not clear; however, in order to maintain homeostasis crabs must regulate the pH of their haemolymph and this is most often done via active ion transport at the gills (Pane and Barry, 2007) which is an energy intensive process. In blue king crab juveniles, *Paralithodes platypus*, low pH at levels known to increase mortality (Long et al., 2017; Swiney et al., 2017), lead to higher basal metabolic rate with no increase in feeding, which leaves less energy available for processes such as growth and molting (Long et al., 2019). Similarly, although with a slightly different mechanism, European lobster juveniles are able to buffer hemolymph with bicarbonate, but basal metabolic rate stays the same while the feeding rate decreases (Small et al., 2020). In addition, reduced pH can alter hemocyte mortality which may result in increased susceptibility to diseases (Meseck et al., 2016); I did not see any evidence of disease in any of the crabs but, although some diseases like bitter crab syndrome have obvious external signs, that is not true of all (Shields, 2012) and thus cannot be ruled out.

Despite the increase in mortality, snow crabs suffered no change in growth; the size at molt and the intermolt period did not differ among the treatments. Many crustaceans are able to physiologically acclimate to a wide range of pH conditions. Blue crab, for example, show no difference in growth or mortality under even extremely low pH conditions (Glandon and Miller, 2017). However, given the higher mortality rate in the pH 7.5 treatment, this result is a little puzzling; if the snow crab in this experiment were stressed enough that mortality occurred, why were sublethal effects not detected? One possibility is that tolerance to low pH varied among the individuals such that individuals who were less resistant to low pH died, reducing the ability to detect sublethal effects. Alternatively, it may be that the effect on growth was subtle and undetectable after only 2–3 molts; there is limited evidence for this in that several of the crabs in the pH 7.5 treatment only molted once and so their intermolt period could not be calculated or included in the analysis. In other species, such as red king crab, differences in growth rates among pH treatments were detectable after 5 molts (Long et al., 2013b), but not after 3 (Swiney et al., 2017) even though differences in mortality rates were detected in both. Finally, there may have been sublethal effects on the crabs that were not measured in this experiment; low pH can affect behavior or the immune system, among other physiological processes (Ocampo et al., 2024) and crabs may have prioritized growth over those.

Low pH also did not affect the carapace morphology in snow crabs. Low pH can alter cuticle formation or maintenance in crustaceans and this can vary from one part of the cuticle to another which could affect external morphology. Red and blue king crab, for example, show differences in cuticle structure and function in their chelas but not in their carapace (Coffey et al., 2017). Low pH can also cause deformities in crustaceans (Kurihara et al., 2008; Agnalt et al., 2013; Ramesh et al., 2023), although the mechanism behind it is not clear. Direct external dissolution likely does not occur and, indeed, many species actually increase the calcium content of their cuticles in response to low pH (Ries et al., 2009; Long et al., 2013b). One of the mechanisms to adjust hemolymph pH when exposed to low pH is to actively transport bicarbonate into the hemolymph at the gills which makes the precipitation of calcium carbonate, an internal process in crustaceans, easier (Ries et al., 2009). Given that adult snow crabs do not show alterations in their cuticles in response to low pH (Algayer et al., 2023) the null effect on the carapace shape is unsurprising.

As is the case for a number of decapod species, the juvenile stage of snow crabs is the most sensitive. Adult females, embryos, and larvae showed no direct or, in the case of embryos or larvae, carryover effects of low pH even at pH 7.5 (Long et al., 2023). Red king crab juveniles (Long et al., 2013b) are more sensitive than embryos (Long et al., 2013a) or larvae (Long et al., 2024). Similarly, European lobsters suffer higher mortality at low pH at the juvenile (Small et al., 2016) than the larval (Small et al., 2015) stage. The American lobster, *H. americanus*, is likewise very tolerate of low pH at the larval stage, with larval growth rate, survival, and metabolism being unaffected by low pH (Waller et al., 2017), while the juveniles suffer increased mortality and decreased growth under the same conditions (Noisette et al., 2021). Why this is the case is not clear. Tolerance in larval American lobster is associated with extensive metabolic reprograming which is not present in juveniles, suggesting that a robust physiological response to low pH helps to impart tolerance (Noisette et al., 2021). In contrast, red king crab larvae do not alter gene expression in response to low pH and yet are highly tolerant, whereas juveniles greatly alter gene expression and are highly sensitive which suggests an opposite pattern (Swiney et al., 2017; Stillman et al., 2020; Long et al., 2024).

The results of this study also fall into the pattern of contrasting physiological responses to low pH with Tanner crabs. Snow crabs and Tanner crab are very similar species which have overlapping distributions in the Bering Sea (Zacher et al., 2024) and can produce fertile hybrids (Karinen, 1974; Johnson, 1976). Snow crab adults, embryos, and larvae are resilient to low pH down to at least pH 7.5 and juveniles to pH 7.8 (Long et al., 2023). Tanner crab embryos and larvae are unaffected by pH 7.5 water as well (Long et al., 2016; Swiney et al., 2016), but females are negatively affected at pH 7.5 (Swiney et al., 2016; Dickenson et al., 2021) and juveniles at pH 7.8 (Long et al., 2013b). A simple explanation for why snow crabs are more resilient is that, in the Bering Sea at least, snow crab may have evolved in waters that are naturally lower in pH. In the eastern Bering Sea, net bottom currents flow north along the shelf and out through the Bering Straits into the Arctic Ocean and, during the late spring and summer, water high in CO_2 from benthic respiration is advected northwards along the slope creating a south to north gradient in benthic pCO_2, and therefore benthic pH levels (Mathis et al., 2011). Tanner crabs are distributed in warmer waters in the southern part and snow crabs in colder waters to the north (Zacher et al., 2024). As different populations of *Hyas araneus* differ in their tolerance of low pH due to local adaptation (Walther et al., 2010), it is perhaps unsurprising that two similar species with different population-level exposure to low pH should likewise show differences in tolerance. The mechanisms behind this tolerance have yet to be elucidated, but future work should focus on determining how low pH tolerance is conferred.

Overall, this work suggests that snow crab will be resilient to pH levels predicted for the next 40 years. The Bering Sea shelf is predicted to start experiencing extended periods below pH 7.5 around 2060 (Pilcher et al., 2022) and effects on juveniles will be mild at first. Given that pH 7.5 is already experienced seasonally in Bering Sea, future work should consider including pHs lower than that. However, although the horizon is pushed off further than for other species, like Tanner and red king crab, this increased mortality would likely result in decreased stock productivity and fisheries (Punt et al., 2016; Punt et al., 2022). Indeed, for red king crab in Bristol Bay, there is evidence that decreasing pH levels may be partially responsible for decreasing recruitment in this stock (Litzow et al., 2025), indicating that even brief periods under known, species-specific thresholds may have a cumulative population-level effect. This work too, has major caveats that should be addressed in future work; crabs were reared on a high-quality diet enriched with essential fatty acids and fed to excess, and the crabs did not experience any other stressors. A recent crash in the snow crab population in the eastern Bering Sea was likely caused by starvation due to high temperatures (Szuwalski et al., 2023) and such conditions are predicted to become more frequent concurrently with decreasing pH. Future work should focus on how other stressors, especially increased temperature and food limitation, interact with low pH.measurements of crabs held at three

CRediT authorship contribution statement

W. Christopher Long: Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization, Writing – review & editing, Writing – original draft.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

William Long reports financial support was provided by NOAA Ocean Acidification Program. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

All data from this project has been published and is freely available at the National Centers for Environmental Information.

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