1 Effects of ocean acidification on young-of-the-year golden king crab (*Lithodes*
2 *aequispinus*) survival and growth
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6 W. Christopher Long*, Katherine M. Swiney[1], and Robert J. Foy
7 Kodiak Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service,
8 National Oceanic and Atmospheric Administration, 301 Research Court, Kodiak, AK
9 99615 USA
10 *Corresponding author. E-mail: chris.long@noaa.gov, Telephone: 907-481-1715, Fax:
11 907-481-1701, Orchid ID: 0000-0002-7095-1245
12 [1]Present address: Fisheries Resources Division, Southwest Fisheries Science Center,
13 National Marine Fisheries Service, National Oceanic and Atmospheric Administration,
14 8901 La Jolla Shores Drive, La Jolla, CA 92037 USA
15
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26 **Abstract:**

27 Ocean acidification, a reduction in the pH of the oceans caused by increasing CO_2, can
28 have negative physiological effects on marine species. In this study, we examined how
29 CO_2-driven acidification affected growth and survival of juvenile golden king crab
30 (*Lithodes aequispinus*), an important fishery species in Alaska. Juveniles were reared
31 from larvae in surface ambient pH seawater at the Kodiak Laboratory. Newly molted
32 early benthic instar crabs were randomly assigned to one of three pH treatments: 1)
33 Surface ambient pH ~8.2, 2) likely *in situ* ambient pH 7.8, and 3) pH 7.5. Thirty crabs
34 were held in individual cells in each treatment for 127 days and checked daily for molting
35 or death. Molts and dead crabs were photographed under a microscope and measured
36 using image analysis to assess growth and morphology. Mortality was primarily
37 associated with molting in all treatments, differed among all treatments, and was highest
38 at pH 7.5 and lowest at ambient pH. Crabs at pH 7.5 were smaller that crabs at ambient
39 pH at the end of the experiment, both in terms of carapace length and wet mass; had a
40 smaller growth increment after molting; and had a longer intermolt period. Carapace
41 morphology was not affected by pH treatment. Decreased growth and increased
42 mortality in laboratory experiments suggest that lower pH could affect golden king crab
43 stocks and fisheries. Future work should examine if larval rearing conditions affect the
44 juvenile response to low pH.

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49 **Introduction**

50 Anthropogenic CO_2 is being released into the atmosphere and oceanic uptake of this CO_2
51 has resulted in a decrease of 0.1 pH in global mean surface waters over the last century
52 (Caldeira and Wickett 2003). This reduction in oceanic pH, known as ocean acidification
53 (OA), is predicted to reduce global ocean surface pH to ~7.8 by the end of the century
54 and pH ~7.5 by the end of 2200 (Caldeira and Wickett 2003; Bopp et al. 2013; IPCC
55 2014). The rate of pH change is expected to be higher in high latitude areas, including
56 Alaska waters, in part because CO_2 uptake is higher in cold waters (Fabry et al. 2009).
57 Within 50 years, waters around Alaska are predicted to be perennially undersaturated
58 with regard to aragonite (Mathis et al. 2015).

59 Ocean acidification has a negative effect on many marine species, although the
60 effects are highly variable among taxa, species, and even life history stages (Kroeker et
61 al. 2013). Within the decapod crustaceans there is is similar range of responses; ocean
62 acidification has a wide range of effects on a number of physiological parameters and can
63 increase mortality (Menu-Courey et al. 2019; Turra et al. 2020), decrease growth (Swiney
64 et al. 2017; McLean et al. 2018), cause morphological deformities (Kurihara et al. 2008;
65 Agnalt et al. 2013), change the metabolic rate (Hans et al. 2014; Long et al. 2019),
66 decrease reproductive output (Swiney et al. 2016), change exoskeleton properties (Coffey
67 et al. 2017), and alter hemolymph chemistry in many species (Pane and Barry 2007),
68 although some species are quite tolerant (deVries et al. 2016; Glandon and Miller 2017;
69 Glandon et al. 2019). This is of concern, both because crustaceans are an important part
70 of many ecosystems (Fabry et al. 2008) and because many species support high-value

71 fisheries, and OA is projected to decrease stock size and fishery yields (Punt et al. 2016;
72 Heinrich and Krause 2017; Punt et al. 2020).
73 Golden king crab (*Lithodes aequispinus*) is an ecologically important deep-water
74 species with a distribution range from Japan to British Columbia, Canada. In Alaska, they
75 are a commercially important species found in the Gulf of Alaska, Bering Sea, and
76 Aleutian Island waters (Donaldson and Byersdorfer 2005); the Aleutian Islands golden
77 king crab fishery had an ex-vessel gross revenue of $23.74 million in 2012 (Garber-Yonts
78 and Lee 2013). Golden king crab are found approximately 200 to 1,000 m depth
79 (Donaldson and Byersdorfer 2005), but data on the depth distribution is non-existent for
80 both larvae and newly settled young-of-the-year crab. Older juveniles, sub-mature but
81 CL > ~40 mm, are found on continental slopes between 350 and 400 m depth in the Sea
82 of Okhotsk, at approximately 500 m depth in the Bering Sea (Tarverdieva and Zgurovsky
83 1985), at depths greater than 548 m in the eastern Aleutian Islands (Blau et al. 1996), and
84 between 623 and 583 m depth on the Patton Seamount in the Gulf of Alaska (Shirley
85 2006). Shirley and Zhou (1997) hypothesized that golden king crab larvae occur at
86 depths greater than 200 m and remain near the benthic substrate; if this is true, then
87 juvenile settlement likely occurs at these depths. In contrast, juveniles in northern British
88 Columbia fjords are most commonly found in waters less than 100 m deep (Sloan 1985).
89 It is important to examine the effects of ocean acidification on different life stages
90 of the golden king crab since most if not all stages of this deep-water species are likely
91 already living in water at a pH well below surface oceanic pHs. Most carbon chemistry
92 data is limited to surface, shallow, and shelf waters, not the deep-waters that golden king
93 crab inhabit; we summarize the available information in the terms used in the studies

94 cited, but do not mean to imply that any one measure of the carbonate system (e.g., pH or
95 saturation state) is necessarily the driving factor in the crabs' physiological response.
96 However, the current calcite saturation horizon is approximately 250 m in the eastern
97 Bering Sea (Cross et al. 2013), and in September 2008 in the Gulf of Alaska, waters
98 deeper than approximately 175 to 225 m were undersaturated with regard to aragonite
99 (Fabry et al. 2009). These calcite and aragonite saturation horizons are shallower than
100 the depths that golden king crab of all life stages are generally thought to inhabit
101 (Donaldson and Byersdorfer 2005). In the Gulf of Alaska, the pH at the depths that adult
102 and older juvenile golden king crab inhabit are between about pH 7.7 and 7.8 (Byrne et
103 al. 2010). In this study, we reared young-of-the-year golden king crab in surface ambient
104 pH (~8.2, pCO_2 ~ 325 ppm), pH 7.8 (likely *in situ* pH, pCO_2 ~ 800 ppm), and pH 7.5
105 (pCO_2 ~ 1600 ppm) waters for 127 days to study the effects of ocean acidification on
106 survival, growth, and morphology.
107
108 **Methods**
109 **Sample Collection and Laboratory Study**
110 Ovigerous golden king crab were collected from the Aleutian Islands, Alaska
111 (51°18.30'N, 179º2.49'E and 52º17.47'N, 175º14.02'E), March and May 2013, and
112 shipped live to the Alaska Fisheries Science Center's Kodiak Laboratory seawater facility
113 in Kodiak, Alaska, where larval rearing took place from December 2013 to March 2014.
114 Larvae from two females were reared in surface ambient pH flow-through water
115 (temperatures 4-5 º C, Salinity ~31, pH ~ 8.0) and, because the larvae are lecithotrophic,
116 were unfed. The subsequent young-of-the-year crab were used in this study. Juveniles

117 were approximately 3 weeks after the molt to C1 and were likely all at the C1 or C2 stage
118 at the beginning of the experiment.
119 Ninety young-of-the-year crab were randomly assigned to one of three
120 acidification treatments based on projected global ocean surface pH levels: 1) surface
121 ambient (hereafter ambient) pH ~8.2, 2) pH 7.8 (c. ~2100), and 3) pH 7.5 (c. ~2200)
122 (Caldeira and Wickett 2003), for a total of 30 young-of-the-year crab per treatment. The
123 surface ambient treatment represents local ambient conditions, not the typical conditions
124 for young-of-the-year golden king crab; the pH 7.8 treatment is reflective of the *in situ*
125 pH in older juvenile golden king crab habitat and is likely similar to that of younger
126 juveniles (Byrne et al. 2010); the pH 7.5 treatment is acidified relative to both the current
127 surface ambient and *in situ* golden king crab conditions. Throughout this paper we refer
128 to pH because it is the parameter we were controlling for; however, we recognize that pH
129 is not necessarily the only or even main driver of the physiological response of marine
130 animals among the component of the carbonate chemistry of seawater. In this
131 experiment, because temperature, pressure, and salinity were all constant, by keeping the
132 pH within a narrow range we also kept each of the other components of the carbonate
133 system within a narrow range (Table 1). Each treatment was contained in a 53 (L) × 38
134 (W) × 23 (H) cm tub that was placed randomly in the experimental area. Each tub had a
135 flow rate of ~250 ml/minute and water was chilled to 5º C (Table 1). Although there was
136 not replication at the tub level, given the isolation of the crabs from each other combined
137 with a high flow rate, the effect of tub can reasonably be assumed to be negligible. A
138 temperature logger was placed into each tank and data recorded every 30 minutes. Tubs
139 were covered with 88.9 µm thick black plastic to minimize light penetration. Young-of-

140 the-year crab were reared in individual inserts constructed from PVC pipe 40 mm inner
141 diameter with 750 µm mesh attached to the bottom, and the inserts were placed inside the
142 treatment tub. This size insert was determined to be the optimal size for individual
143 rearing of juvenile red king crab larger than the crab in this study (Swiney et al. 2013);
144 therefore, it was assumed that this size insert was more than adequate for this study.
145 Inserts were raised off the bottom of the tub by placing them on plastic grating. Water
146 was delivered into each insert via a submersible pump connected to a manifold. Crab
147 were fed three times per week to excess on a gel diet of Gelly Belly (Florida Aqua Farms,
148 Inc., Dade City, FL, USA) enhanced with Cyclop-eeze powder (Argent Laboratories,
149 Redmond, WA, USA), pollock bone powder (US Department of Agriculture, Agricultural
150 Research Service, Kodiak, AK, USA), and astaxanthin. Old food was removed prior to
151 feeding.

152 Each insert was checked daily for molts and mortalities, and exuvia and
153 mortalities were removed for growth and morphometric analysis. At the end of the
154 experiment, the remaining crab were carefully blotted dry with a tissue, weighed, and
155 placed in a -80º C freezer. Carapaces from exuvia, mortalities, and from the live crabs at
156 end of the experiment were photographed under a dissecting microscope. Carapace
157 width, carapace length, rostrum base width, orbital spine width, and the first spine length
158 (Fig. 1) were measured using Image Pro Plus v. 7.0.1.658 imaging software (Media
159 Cybernetics, Inc., Bethesda, MD, USA) (Long et al. 2013b). All these measurements
160 were included in the morphometric analysis (below). Throughout this paper "initial"
161 refers to the size of the crabs at the beginning of the experiment, "final" refers to the size
162 of surviving crabs at the end of the experiment, and "1st molt" to the size of crabs after

163 molting the first time. No crabs molted more than once. The experiment began April 15,
164 2014, and ran for 127 days.
165

166 **Seawater Acidification**

167 Sand filtered seawater was acidified using the same methods described in Long et al.
168 (2013a). Ambient treatment water was pumped into the laboratory from 15 and 26 m
169 depth intakes. In short, a tank of pH 5.5 was established by bubbling CO_2 into ambient
170 seawater. This pH 5.5 water was mixed with ambient seawater in the treatment head
171 tanks via peristaltic pumps controlled by Honeywell controllers and Durafet III pH
172 probes. The ambient head tank did not receive any pH 5.5 water. Waters from the
173 treatment head tanks were then supplied to the treatment tubs. pH_F (free scale) and
174 temperature were measured daily in each experimental tub using a Durafet III pH probe
175 calibrated with a TRIS buffer, and when the pH deviated from the target pH by more than
176 ±0.02 pH units, the Honeywell controller set points were adjusted to bring the pH back to
177 the target value. Weekly water samples from the treatment tubs were taken and poisoned
178 with mercuric chloride unless they were analyzed the same day as collection. Total
179 alkalinity (TA) was determined at the Kodiak Laboratory using a VINDTA 3S
180 (Marianda, Kiel, Germany), and dissolved inorganic carbon (DIC) was determined at an
181 analytic laboratory using a VINDTA 3C coupled to a 5012 Coulometer (UIC Inc., Joliet,
182 IL). Both laboratories used Certified Reference Material from the Dickson Laboratory
183 (Scripps Institute, San Diego, CA) and the procedures in DOE (1994). The other
184 components of the carbonate chemistry in the seawater were calculated using the seacarb
185 package in R (V 3.6.1, Lavigne and Gattuse 2012)

186

187 **Statistical Analysis**

188

189 Differences in growth, expressed as carapace length (CL), were analyzed with
190 separate ANOVAs for mean initial size, size after molting, and percentage increase in
191 size ($100\frac{CL_{initial}-CL_{final}}{CL_{initial}}$) in Systat (v13.2.01, San Jose, CA). The number of days from
192 the beginning of the experiment until molting was also analyzed with an ANOVA. Wet
193 weight at the end of the experiment for crab that had all of their limbs was analyzed with
194 a fully crossed ANOVA. Carapace length and percentage increase in size or wet weight
195 were the dependent variables and pH the factor. When significant differences were
196 detected, Tukey's HSD post-hoc pairwise comparison was run to examine differences
197 among treatments. Levene's test for homogeneity of variance and the Anderson-Darling
198 test for normality were used to determine if data met the assumptions of ANOVA; data
199 were found to meet the assumptions, except initial size was not normally distributed.
200 Morphometric measurements were normalized (expressed in terms of their z-
201 values) prior to analysis to ensure that measurements of larger features did not dominate
202 the analyses. Morphometrics were analyzed with a fully crossed 2-way permutational
203 analysis of variance (PERMANOVA) with pH treatment and molt number (initial
204 measurements and measurements taken after the 1st molt) as factors in Primer 6.1.13
205 (Plymouth, UK). The assumption of homogeneity of dispersion was verified with the
206 permutational dispersion test. The data was visualized using a nonmetric
207 multidimensional plot.

208 Survival in each treatment was fit to a set of models using maximum likelihood
209 and assuming a binomial distribution of errors in R. In the first set of models developed
210 *a priori,* we assumed a constant mortality rate such that: $p_m = e^{-mt}$, where p_m is the
211 cumulative probability of mortality, m is the mortality rate and t is the time in days. We
212 included models where m was constant among the treatments and where it differed
213 among the three treatments. However, these models proved a very poor fit to the data
214 based on visual assessments of the predictions compared to the data; on closer
215 examination, it appeared that mortality increased substantially in the later part of the
216 experiment at about the same time that molting was occurring. Since molting was
217 relatively synchronous within each treatment (as expected given the crabs were all from
218 the same batch of larvae), this led us to include logistic (sigmoidal) models such that:
219 $p_m = s + \frac{1-s}{1+(\frac{t}{t_{50}})^b}$, where s is the predicted final survival, t_{50} is the time in days to 50%
220 mortality, and b is a slope parameter. We fit two logistic models to the data, one in
221 which the three parameters were the same among the treatments and one in which they all
222 differed. Although these models were an improvement over the constant mortality
223 models visual assessments of the fits indicated they too were unsatisfactory, in part
224 because they failed to capture mortality at times other than molting. In order to
225 accommodate mortality during both molting and during the intermolt, we considered a
226 series of models where the mortality rate was allowed to vary over time such that $S_t =$
227 $S_{t-1}(1 - m_t)$ where S_t is the cumulative survival at time = t and m_t is the daily mortality
228 rate at time = t. Note that when m_t is constant for all t the model is identical to the
229 constant survival model above. We then modeled m_t as a combination of base, constant
230 mortality and mortality during molting such that $m_t = m + E_t m_{molt}$ where m is the base

231 mortality rate for all causes except molting, E_t is the probability of molting (ecdysis) at

232 time = t, and m_{molt} is the probability of death during molting. As above, because molting

233 was synchronous, we considered that the cumulative probability of molting could be

234 modeled as a logistic equation $p_{molt} = \frac{1}{1+(\frac{t}{t_{molt50}})^b}$ where t_{molt50} is the time at which 50%

235 of the crabs had molted. The rate of molting is then proportional to the slope of this

236 logistic curve such that $E_t = c\frac{dp_{molt}}{dt} = c\frac{bt_{molt50}^b t^{b-1}}{(t^b+t_{molt50}^b)^2}$ and where c is a constant of

237 proportionality. Thus, $m_t = m + cm_{molt}\frac{bt_{molt50}^b t^{b-1}}{(t^b+t_{molt50}^b)^2}$. In this model c and m_{molt} cannot

238 be estimated independently so we substituted in a combined constant d such that $d =$

239 cm_{molt}. We then fit three models, one where the three pH treatments were the same,

240 one in which m was constant among the three pH treatments and b, t_{molt50}, and d varied,

241 and one where m, b, t_{molt50}, and d all varied among the pH treatments. We calculated the

242 Akaike's Information Criterion corrected for sample size (AIC_c) for each model and used

243 it to select the best one. Models with a ΔAICc of < 2 were considered to explain the data

244 equally well (Burnham and Anderson 2002).

245

246 **Results**

247 The data and metadata underlying this article are included as a supplement ((Online

248 Resource 1).

249 Target temperature and pHs were achieved through the experiment. DIC increased with

250 decreasing pH, pCO_2 increased with decreasing pH, and alkalinity did not vary with

251 treatment. Aragonite was supersaturated in the ambient treatment but undersaturated in

252 the pH 7.8 and pH 7.5 treatments. Calcite was supersaturated in the ambient and pH 7.8
253 treatments, and undersaturated in the pH 7.5 treatment (Table 1).
254 At the end of the experiment all crabs that had not died had molted once. Overall
255 17 crabs successfully molted in the ambient treatment, 20 in pH 7.8, and 14 in pH 7.5.
256 Young-of-the-year crab golden king crab mean initial size was 2.68 (SE = 0.009) mm CL
257 and did not differ with pH treatment (ANOVA, $F_{2,74} = 0.290$, $p = 0.749$), but after
258 molting CL differed with treatment (ANOVA, $F_{2,46} = 4.742$, $p = 0.013$; Figure 2). Crab
259 from the pH 7.5 treatment were on average smaller than crab from the ambient treatment
260 (Tukey's HSD, $p = 0.010$); average size did not differ among the other treatments (Figure
261 2). On average, crab CL increased by 6.0 % (SE = 0.614) after molting, and the percent
262 increase varied with pH treatment (ANOVA, $F_{2,43} = 4.690$, $p = 0014$; Figure 3). The
263 average percent increase in CL was higher for the ambient treatment than the pH 7.8
264 (Tukey's HSD, $p = 0.031$) and pH 7.5 (Tukey's HSD, $p = 0.027$) treatments, which did
265 not differ from each other (Figure 3). Crabs in pH 7.5 water took longer to molt than
266 those in ambient or pH 7.8 water (ANOVA, $F_{2,48} = 16.189$, $p < 0.0005$; Figure 3).
267 Average wet weight at the end of the experiment also differed with treatment (ANOVA,
268 $F_{2,20} = 7.978$, $p = 0.003$); on average, pH 7.5 treatment crab weighed less than ambient
269 (Tukey's HSD, $p = 0.027$) and pH 7.8 (Tukey's HSD, $p = 0.002$) treatment crab, which
270 did not differ from each other (Figure 4).
271 Morphology of golden king crab juveniles did not vary with pH treatment
272 (Pseudo-$F_{2,73} = 0.686$, p = 0.697) but did with molt number (Pseudo-$F_{1,73} = 15.388$, p <
273 0.00005) and with their interaction (Pseudo-$F_{2,73} = 2.243$, p = 0.030). Post-hoc
274 PERMANOVA pairwise comparisons indicated that the morphology of both the ambient

275 and pH 7.8 crabs changed between the initial morphology and after the first molt
276 (ambient: $t = 4.074$, $p < 0.00005$, pH 7.8: $t = 2.660$, $p = 0.0004$), but this was not true of
277 the pH 7.5 crabs ($t = 1.237$, $p = 0.194$; Fig. 5). Despite this, there were no differences in
278 morphology among the pH treatment groups either initially or after the first molt ($p >$
279 0.10 in all cases).

280 In the best-fit model of mortality, mortality was treated as a combination of
281 baseline mortality (i.e., not associated with molting), which was constant over time, and
282 mortality during molting Both types of mortality differed among pH treatments; no other
283 models had any support at all (Table 2). In all three treatments, there was a low baseline
284 mortality rate throughout the experiment with a substantial increase in mortality rate
285 during the time molting was occurring (Fig. 6). Both baseline mortality and the mortality
286 during molting were lower in the ambient treatment than in the pH 7.8 and pH 7.5
287 treatment. Baseline mortality was similar between pH 7.8 and pH 7.5, but mortality
288 during molting was higher at pH 7.5 (Fig. 5, Table 2). There was a high degree of
289 correspondence between successfully molting and mortality risk; in the ambient and pH
290 7.8 treatment no crab that successfully molted subsequently died and in the pH 7.5 only
291 three crabs that successfully molted later died. In addition, of the 60 crabs that died, 12
292 died while in the process of molting. The sigmoidal models predicted peak mortality a
293 little after the peak in molting in all three treatments (Fig. 6). At the end of the
294 experiment there were 12 crabs surviving in the ambient treatment, 8 in the pH 7.8, and 8
295 in the pH 7.5.

296

297 **Discussion**

298 Juvenile golden king crabs exposed to pH levels below surface ambient had
299 significantly lower growth and survival than those exposed to surface ambient water.
300 These results suggest that population dynamics of golden king crab could be affected by
301 ocean acidification within this century and are similar to the effects of ocean acidification
302 on other species of king crab in Bering Sea (Long et al. 2013b; Long et al. 2017). Higher
303 mortality and slower growth would decrease population abundance and productivity and
304 have a corresponding effect on the directed fisheries.

305 Juvenile golden king crab showed decreased growth under low pH conditions.
306 Time to first molt was increased by 34% in pH 7.5 compared to surface ambient pH and
307 the growth increment was 49 and 45% lower in pH 7.5 and 7.8 compared to surface
308 ambient. Overall, this resulted in crabs that were larger in the surface ambient treatment
309 than in the other two by the end of the experiment. This is similar to what has been
310 observed in other lithodid species; both red and blue king crabs (*Paralithodes*
311 *camtschaticus* and *P. platypus*) have slower growth under reduced pH (Long et al. 2013b;
312 Long et al. 2017). Likewise, other crustacean species, such the American lobster
313 (*Homarus americanus*), exhibit decreased growth under ocean acidification (Small et al.
314 2016; McLean et al. 2018). In golden king crab, however, the change in growth was not
315 accompanied by changes in morphology. Both *H. americanus* and the shrimp *Palaemon*
316 *pacificus* exhibit deformities under low pH (Kurihara et al. 2008; Agnalt et al. 2013),
317 suggesting that low pH can interfere with cuticle formation or hardening. Similarly, red
318 and blue king crab did not exhibit any morphological change associated with pH (Long et
319 al. 2013b; Long et al. 2017), although the micromechanical properties of their
320 exoskeletons were affected (Coffey et al. 2017).

321 Decreased growth could have several effects at the population or ecological scale.
322 Slower growth would either increase the time it takes for crabs to reach maturity or
323 decrease the size-at-maturity. The longer it takes to achieve maturity the more likely a
324 crab is to die prior to that, and a decrease size-at-maturity would decrease fecundity.
325 This would likely correspond with lower stock productivity. Further, for most species of
326 crabs, smaller crabs are more vulnerable to predation. Red king crab juveniles have a
327 decreasing chance of being predated upon as they get larger (Pirtle et al. 2012; Long et al.
328 2018), and juvenile blue crab, *Callinecetes sapidus*, suffer high predatory mortality when
329 small, but get a partial size refute from predation once they reach 40 mm carapace width
330 (Johnson et al. 2008). Thus, decrease growth could indirectly increase predatory
331 mortality for juvenile crabs.

332 Mortality of golden king crab juveniles was increased at both pH 7.8 and 7.5.
333 This is a common response among crustaceans; red and blue king crab (*Paralithodes*
334 *camtschaticus* and *P. platypus*), Tanner crab (*Chionoecetes bairdi*), the European lobster
335 (*Homarus gammarus*), and the shrimps *Metapenaeus joyneri* and *Palaemon pacificus* all
336 suffer increased mortality under acidified conditions (Kurihara et al. 2008; Dissanayake
337 and Ishimatsu 2011; Long et al. 2013b; Small et al. 2016; Long et al. 2017). The best- fit
338 model of mortality split the mortality between molting and all other sources and was an
339 excellent fit to the data (as estimated visually, Fig. 6). Both sources of mortality were
340 increased under reduced pH. For golden king crab, the majority of the mortality in all
341 treatments was associated with molting. The peak in mortality rate in all three treatments
342 occurred just slightly after the average time-to-molt (Fig. 6, Table 2), suggesting that
343 many of the crabs which died were those that did not molt successfully, and many crabs

344 died while trying to molt. Molting is a physiologically complicated and energetically
345 expensive process in crustaceans (Roberts 1957; Mangum et al. 1985; Chang 1995), so it
346 is not surprising to see elevated mortality prior to molting under physiologically stressful
347 conditions. A similar association between mortality and molting under acidified
348 conditions occurs in juvenile *H. gammarus*, mature female red king crab, and adult *M.*
349 *joyneri* (Dissanayake and Ishimatsu 2011; Long et al. 2013a; Small et al. 2016).
350 The decreased growth and increased mortality in golden king crab in acidified
351 waters suggests that the crabs are responding physiologically to the decreased pH. Most
352 decapod species respond to increased pCO_2 by increasing bicarbonate transport into the
353 hemolymph, which in turn reduces or completely eliminates the change in hemolymph
354 pH (e.g., Pane and Barry 2007; Appelhans et al. 2012; Knapp et al. 2016). This active
355 transport is likely energetically expensive; juvenile red and blue king crabs both greatly
356 increase respiration rates immediately after exposure to acidified water: 73% for red king
357 crab and 178% for blue (Long et al. 2019). If the energetic costs of maintaining acid-
358 base homeostasis are higher under reduced pH conditions, then that would leave less
359 energy available for other biological functions, such as growth, and indirectly cause an
360 increased morality rate during energetically expensive life-history events such as molting.
361 Alternatively, as it the case for other deep water species (Pane and Barry 2007), golden
362 king crab may not be able to regulate their hemolymph pH or may only be able to
363 partially compensate for reduced environmental pH. Altered hemolymph and
364 intracellular pH would have a suite of physiological consequences including decrease
365 enzymatic actives (Tanner et al. 2006) which would could also explain the decreased
366 growth and increased mortality observed.

367 That juvenile golden king crab should be negatively affected at a pH they are
368 known to live at naturally is a surprising result; one would presume that the animals are
369 well adapted to those conditions. There are several non-exclusive possibilities that may
370 explain these patterns. It is possible that the growth and mortality rates that we observed
371 at pH 7.8 are reflective of what actually occurs *in situ.* This is possible, but it seems
372 unlikely that a species would not be better adapted to its local environment.
373 Alternatively, it could be that laboratory rearing of larvae at surface water pH resulted in
374 juveniles that were physiologically adapted or acclimated to surface pH, either through
375 selection of individuals adapted to surface pH, phenotypic plasticity induced at the larval
376 stage, or a combination of these mechanisms. Species including the Sydney rock oyster
377 (*Saccostrea glomerata*), the calanoid copepod (*Pseudocalanus acuspes*), and the Manila
378 clam (*Ruditapes philippinarum*) show high evolutionary potential in selective breeding
379 and transgenerational experiments (Parker et al. 2012; Parker et al. 2015; Thor and
380 Dupont 2015; Zhao et al. 2018), although other species do not (Langer et al. 2019).
381 We hypothesize, therefore, that golden king crab have a potential for
382 acclimatization or adaptation to a range of pH conditions at least within the range of pHs
383 that occur along their depth distribution; though this may not extend to lower pHs.
384 Although juveniles in the Aleutian Islands population of golden king crab, where the
385 crabs in this study came from, occur at depths greater than 500 m (Blau et al. 1996),
386 populations in British Columbia fjords occur at depths from 50-400 m (Sloan 1985).
387 Given that pH is highly depth dependent in such systems, this suggests there is wide
388 variance in golden king crab tolerance for a range of pH conditions both with and among
389 populations.

Future work should focus on examination of carryover effects on juveniles from the embryo and larval stages. If, as hypothesized above, the response of juvenile golden king crab is determined by the pH at larval stage, a fully crossed experiment would test this effectively. Further, a comparison of gene expression and hemolymph chemistry among the treatments could help to pinpoint the underlying biochemical mechanisms. Finally, understanding the interactive effect of other potential co-stressors, including increased temperature and low dissolved oxygen is essential for this deep dwelling, cold-water species (Breitburg et al. 2015).

Declarations and compliance with ethical standards:

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Availability of data and materials: The datasets generated during and/or analyzed during the current study included as a supplement to this paper.

Code availability: The code generated during the current study is available from the corresponding author on reasonable request.

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Table 1. The mean and standard deviation (SD) of water chemistry parameters in the three treatments. pH_F (free scale) and temperature were measured daily, DIC, salinity, and alkalinity were measured weekly, and all other parameters were calculated.

Treatment	Temp °C	Salinity PSU	pH_F	pCO_2 µatm	HCO_3^- mmol/kg	CO_3^{-2} mmol/kg	DIC mmol/kg	Alkalinity mmol/kg	$\Omega_{Aragonite}$	$\Omega_{Calcite}$
Ambient	5.05(0.28)	31.30(0.28)	8.15(0.07)	326.28(54.25)	1.88(0.03)	0.11(0.02)	2.00(0.03)	2.15(0.02)	1.67(0.23)	2.67(0.37)
pH 7.8	5.26(0.49)	31.34(0.30)	7.80(0.03)	779.20(30.74)	2.01(0.03)	0.05(0.00)	2.11(0.03)	2.14(0.01)	0.80(0.04)	1.27(0.06)
pH 7.5	5.11(0.34)	31.32(0.29)	7.52(0.05)	1561.76(65.62)	2.06(0.01)	0.03(0.00)	2.17(0.01)	2.14(0.02)	0.41(0.02)	0.66(0.03)

Table 2: AIC model selection table for models of golden king crab mortality at three different pHs. Models include constant (baseline) mortality rate models (m), sigmoidal models (Sigmoid) to capture mortality during molt, and models including both constant (baseline) mortality and mortality during molt (m_{molt}). (T) indicates that the model was allowed to vary with pH treatment. See Methods for details on model development. (K) indicates the number of parameters. The best fit model is indicated in bold. Parameter estimates with the standard errors included parenthetically are given for the best-fit model.

Model	K	AIC_c	ΔAIC_c	Likelihood	AIC_c weight
m	1	1932.32	710.21	0.00	0.00
m(T)	3	1820.89	598.79	0.00	0.00
Sigmiod	3	1458.36	236.25	0.00	0.00
Sigmiod(T)	9	1340.59	118.49	0.00	0.00
m, m_{molt}	4	1451.20	229.10	0.00	0.00
$m, m_{molt}(T)$	10	1228.16	6.05	0.05	0.05
$m(T), m_{molt}(T)$	**12**	**1222.10**	**0.00**	**1.00**	**0.95**

Parameter estimates for best-fit model				
Treatment	m	**T_{50}**	**b**	**d**
ambient	0.0016(0.0006)	86.39(9.29)	5.95(3.45)	0.66(0.25)
pH 7.8	0.0027(0.0003)	94.61(3.44)	9.24(1.93)	0.97(0.13)
pH 7.5	0.0026(0.0001)	115.38(1.83)	30.5(7.93)	0.78(0.13)

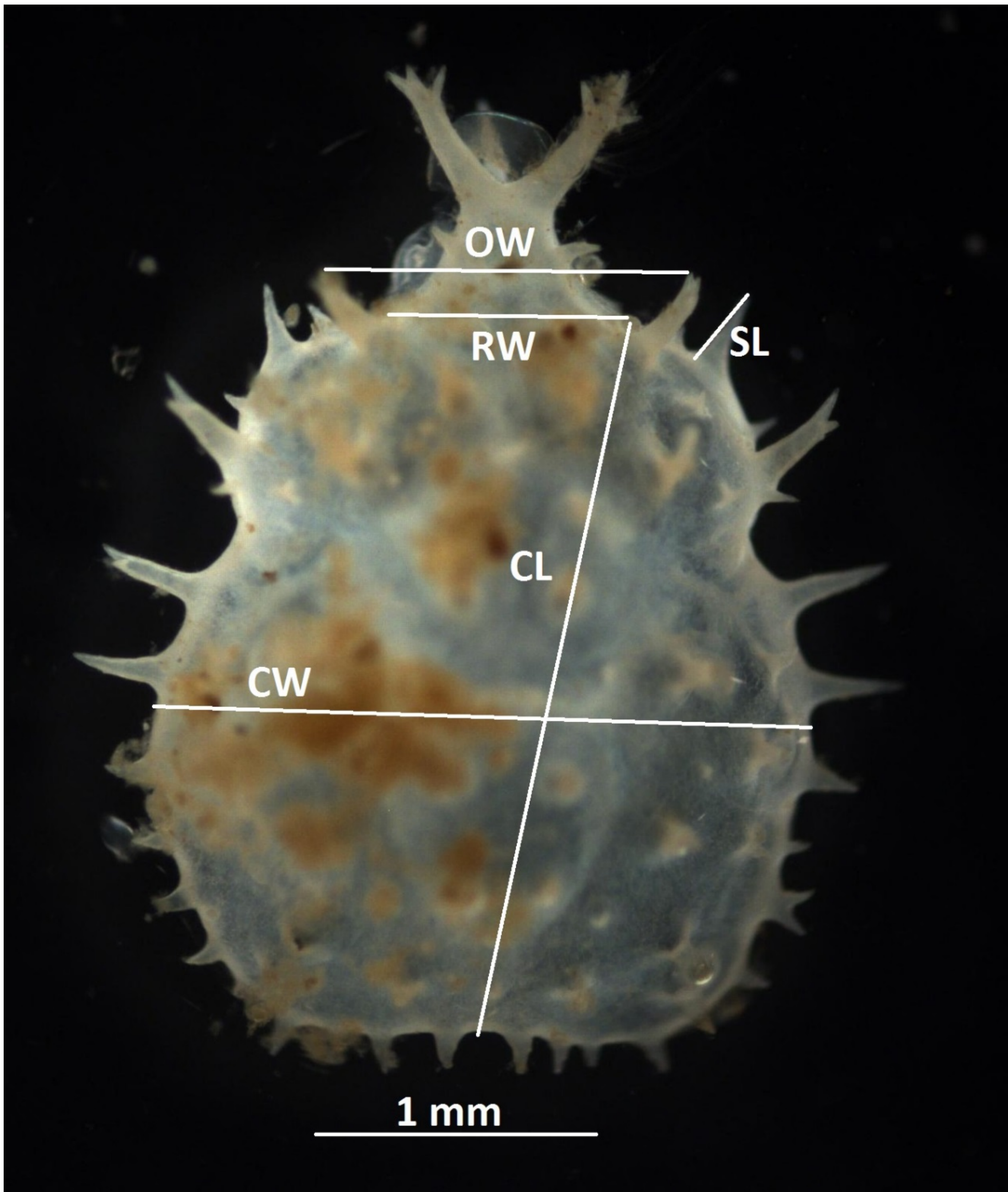

Figure 1. Young-of-the-year golden king crab morphometric measurements: carapace width (CW), carapace length (CL), rostrum base width (RW), orbital spine width (OW), and the first spine length (SL).

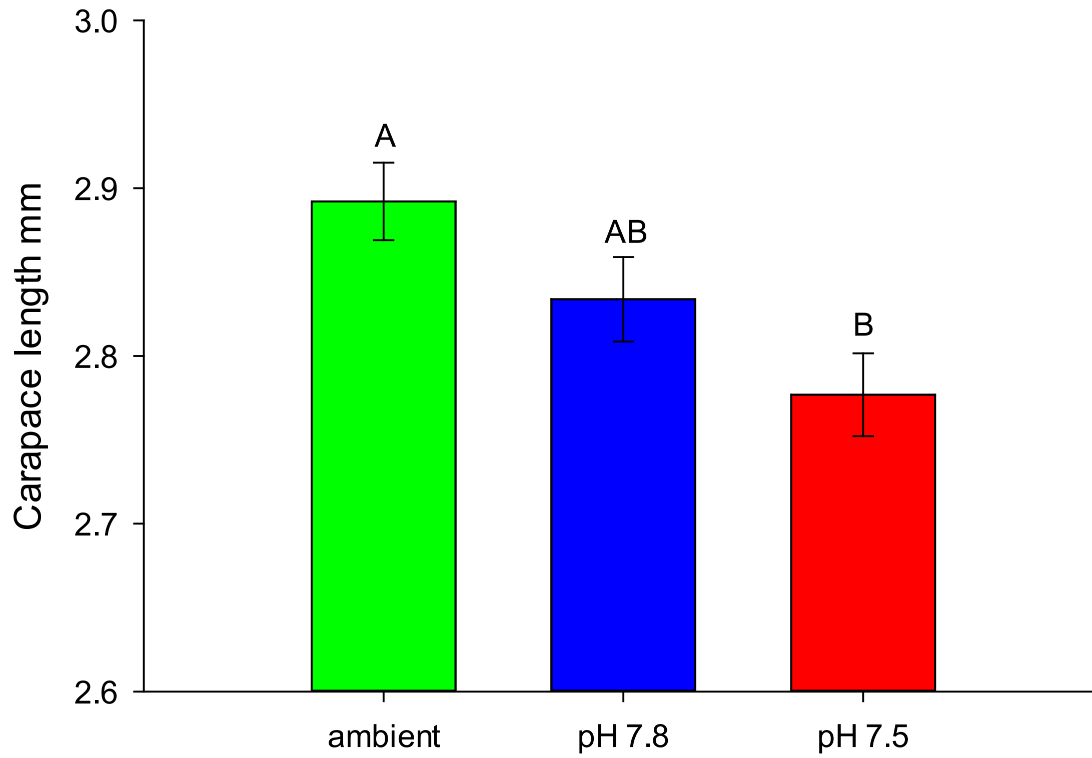

Figure 2. Comparison of young-of-the-year golden king crab carapace length (mm) after molting by pH treatment. Bars are means with standard error. Bars with different letters above them differ significantly.

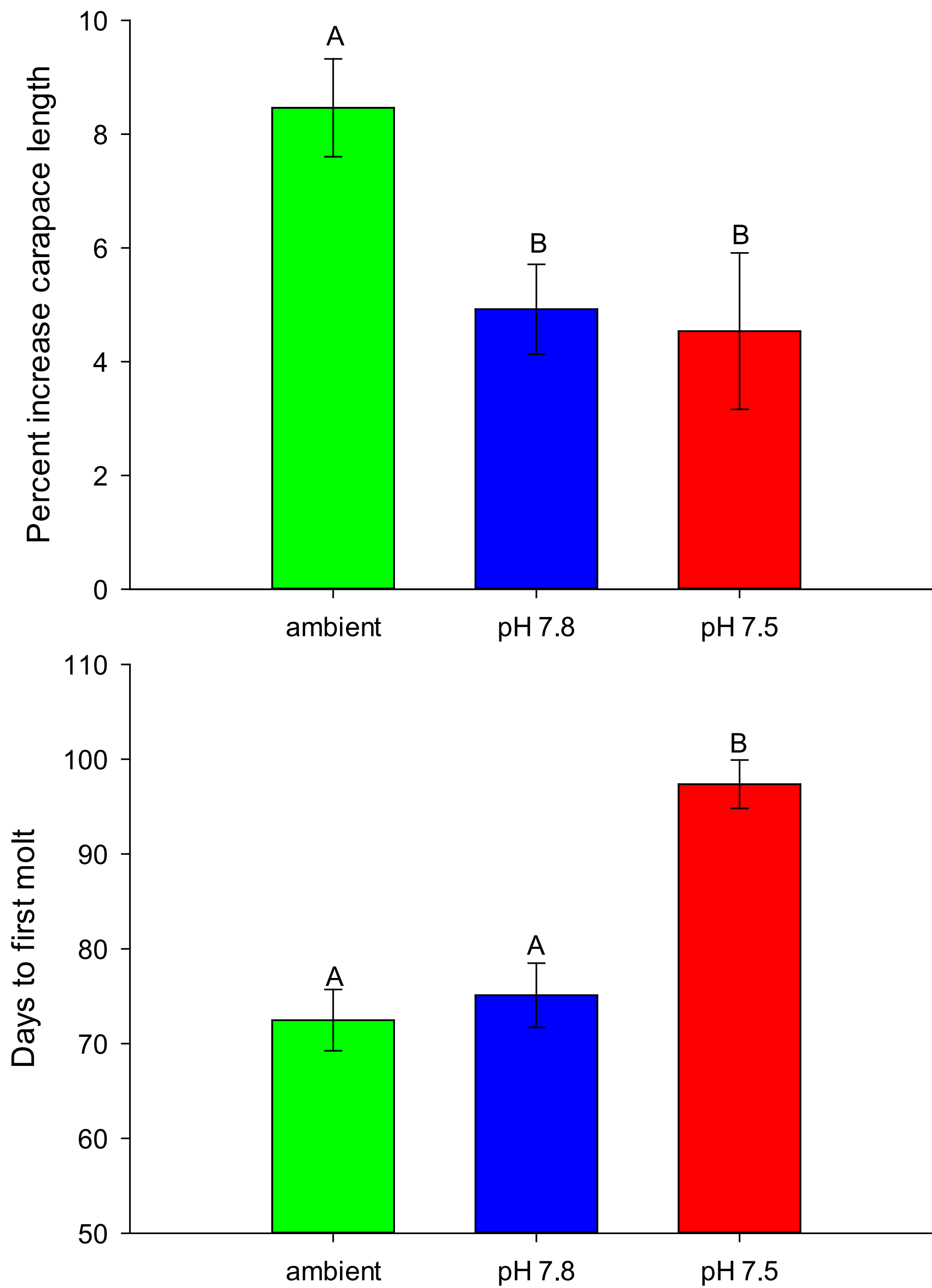

Figure 3. a) Percentage increase in young-of-the-year golden king crab carapace length between initial size and after molting and b) the time in to molt by treatment. Bars are means with standard error. Bars with different letters above them differ significantly.

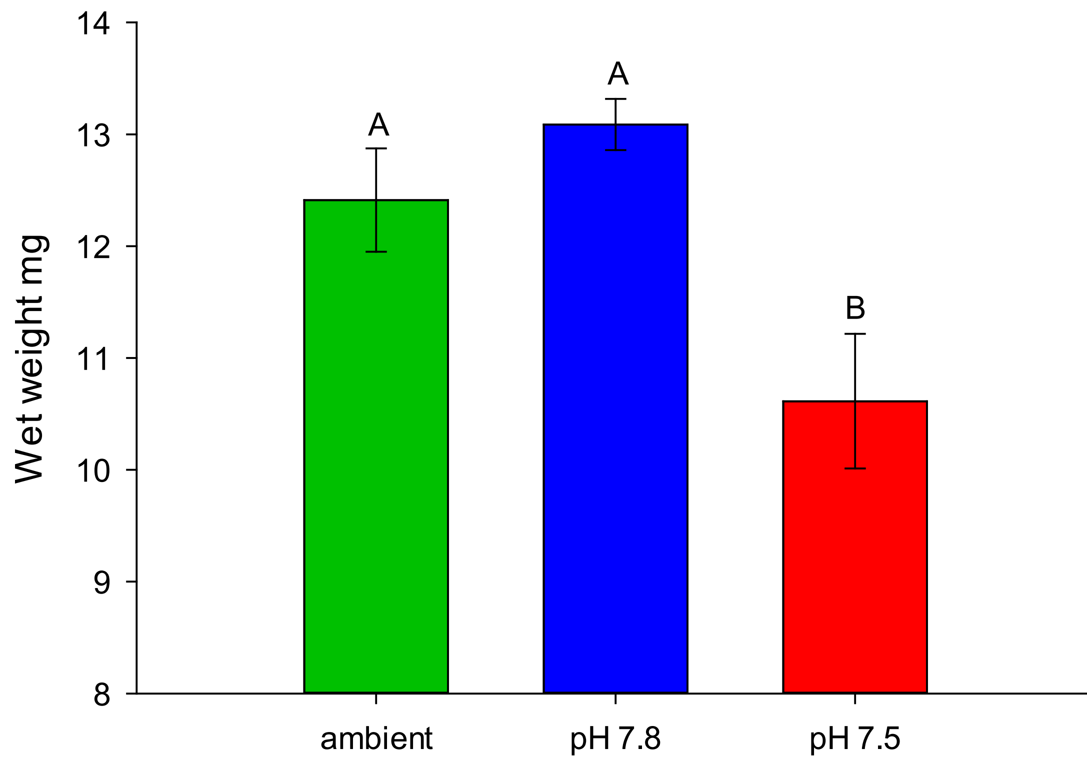

Figure 4. Young-of-the-year golden king crab wet weight at the end of the experiment. Bars are means with standard error. Bars with different letters above them differ significantly.

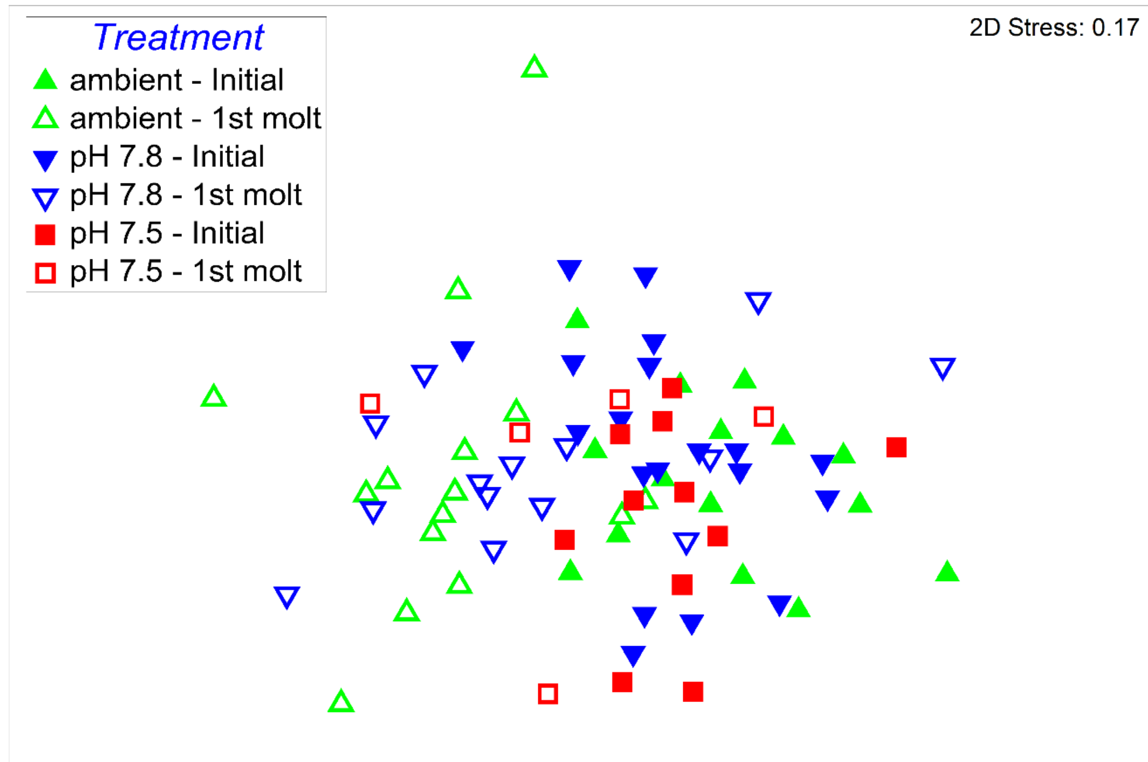

Figure 5: Non-metric multidimensional scaling plot of juvenile golden king crab morphometric measurements (see Fig. 1) for crabs held in three pH treatments. "Initial" represents the crabs when first placed into the treatments and "1st molt" represents measurements made after the first molt.

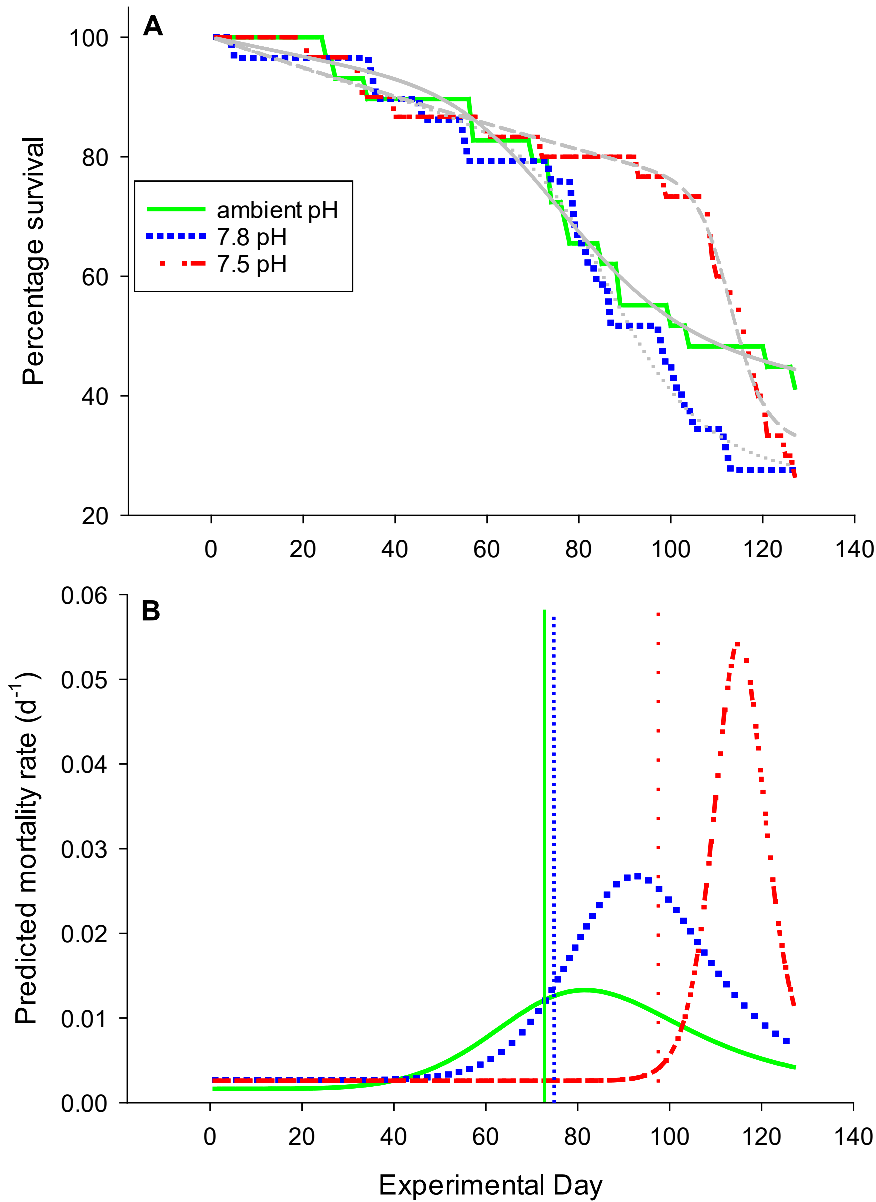

Figure 6. A) Percent of initial number young-of-the-year golden king crab surviving on each day by pH treatment and best-fit model (model m(T), mmolt(T), Table 2). Stepwise lines represent observed survival and smoothed lines predicted survival. B) Daily mortality rates predicted by the best-fit model for each pH treatment. Horizontal lines represent the average days to molt for each of the pH treatments.

Supplement 1: The data from this project that and the associated metadata are included in a single zip folder with separate files for the metadata and each data table.