

1 Title: Optimizing release strategies for red king crab stock enhancement: effects of release timing

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20 **Abstract**

21 Red king crab, *Paralithodes camtschaticus*, was commercially important around Kodiak, Alaska, USA, in
22 the 1960s and 1970s; however, the stock crashed in the late 1970s and has remained closed since 1983.
23 The lack of recovery inspired consideration of stock enhancement through the release of hatchery-
24 reared juveniles as a means to bolster the wild population. We examined the effects of release timing
25 on *in situ* survival of hatchery-reared red king crab by releasing juveniles in June, August, and September
26 2015 in Trident Basin, Kodiak. We monitored densities inside and outside of release plots for six months
27 using quadrat counts to determine loss and emigration rates. Relative predation risk was determined
28 using tethering experiments performed after each release, and predator densities were quantified using
29 quadrat counts and predator transect counts. Initial mortality over the first 24 h was approximately
30 53%, and subsequent mortality rates decreased with month-of-release, likely due to a combination of
31 larger size-at-release and seasonal changes in predation. Although predator density was consistent over
32 time, relative predation risk of tethered crabs decreased with season, suggesting later releases may be
33 beneficial. However, the extended hatchery rearing period needed for later releases presents other
34 challenges, including cannibalism, and the potential for developing maladaptive traits. Stock
35 enhancement programs must balance these trade-offs to maximize overall success. Early releases of
36 small juveniles immediately after settlement may be optimal if large-scale hatchery communal rearing
37 results in significant juvenile production loss and/or hatchery conditioning is impractical.

38 Keywords: Red king crab, *Paralithodes camtschaticus*, stock enhancement, release strategy, hatchery,
39 size-at-release, mortality, tethering

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42 1. Introduction

43 Red king crab, *Paralithodes camtschaticus*, represented a major fishery species in Kodiak, Alaska,
44 USA, during the 1960s and 70s, but the population crashed in the early 1980s (Bechtol and Kruse, 2010).
45 The commercial fishery was closed in 1983 but the population has since failed to recover. The cause of
46 the population crash is not fully understood, but it likely was due to a combination of climactic shifts,
47 changes in the food web structure, recruitment failure, and overfishing (Bechtol and Kruse, 2009; Blau,
48 1986; Orensanz et al., 1998; Zheng and Kruse, 2000). The population crash and lack of a subsequent
49 recovery, have spurred interest in using stock enhancement to supplement wild populations, with the
50 hope of rebuilding local stocks to the point that sports or commercial fisheries would be viable again
51 (Kron, 1992; Stevens, 2006; Stevens et al., 2014). Although large-scale hatchery production techniques
52 have been developed for rearing red king crab from the larval to juvenile stages (Swingle et al., 2013)
53 release strategies must be further developed to maximize post-release survival.

54 Red king crab are a long-lived crustacean with a complex life history (Fig. 1). Mature female red
55 king crab brood between about 10,000 and 450,000 eggs annually before hatching in the spring (Stevens
56 and Swiney, 2007; Swiney and Long, 2015; Swiney et al., 2012). Larvae pass through 4 zoeal stages prior
57 to molting to the glaucothoe, or settling, stage; total larval duration is temperature-dependent,
58 approximately 450 degree-day, which generally takes about 2-3 months *in situ* (Long, 2016; Shirley and
59 Shirley, 1989). Glaucothoe seek complex habitats for settlement, and once they have found it, molt to
60 the first crab stage (Stevens, 2003). Juvenile crab are highly cryptic (Daly and Long, 2014) and rely on
61 complex habitat, such as hydroids, shell-hash, or rocky substrates (Loher and Armstrong, 2000;
62 Sundberg and Clausen, 1979), to reduce predation (Long et al., 2012b; Long and Whitefleet-Smith, 2013;
63 Stoner, 2009) for about the first 2 years of life. After the second year, when crab have become too large
64 to effectively use crypsis to avoid predation, they undergo an ontogenetic behavioral shift, forming

65 groups of crabs called pods (Powell and Nickerson, 1965), which forage at night, and form piles during
66 the day, likely as a predator-avoidance strategy as they grow to maturity (Dew, 1990). Crabs reach
67 sexual maturity at about 6 years of age (Stevens and Munk, 1989). Although hatchery techniques have
68 developed for large scale rearing of juveniles, embryo and female biology do not offer much scope for
69 varying the time of hatching more than a few months. The easiest way to achieve this is to vary holding
70 temperatures during embryo development; however, red king crab embryos are primed to hatch in the
71 spring and although holding temperature can alter hatch date to a small extent, by 2-3 months, lower
72 temperatures lead to hatch failure and higher temperatures to hatched, but inviable larvae (Shirley et
73 al., 1989).

74 Red king crab is likely a good candidate for stock enhancement. In addition to being a high-
75 value species, mortality during the larval phase is believed to be high in the wild, with perhaps 1%
76 survival from hatching to the glaucothoe stage (Shirley and Shirley, 1989), likely due to a combination of
77 environmental factors such as high rates of predation, starvation, and failure to reach suitable
78 settlement habitat, amongst others. *In situ* survival to the first crab stage is nearly impossible to
79 estimate but is also likely low due to several factors. First, metamorphosis to the first crab stage is
80 associated with high mortality even in the laboratory or hatchery (Persselin and Daly, 2010; Swingle et
81 al., 2013). In addition, successful recruitment requires the glaucothoe to find suitable habitat to settle in,
82 and it is unknown what proportion of them are able to do so. The development of large-scale hatchery
83 rearing techniques has overcome these bottlenecks: survival to the first juvenile stage can exceed 60%
84 (Persselin and Daly, 2010; Swingle et al., 2013), several orders of magnitude higher than *in situ* survival.
85 The Kodiak area appears to be recruitment limited; a recent study in Trident Basin which was historically
86 a nursery habitat for red king crab (Dew, 1991), found no evidence of wild recruitment (Long et al.,
87 2018).

88 Post-release survival of hatchery-reared individuals can vary widely with a number of factors.
89 Survival of hatchery-reared blue crab, *Callinectes sapidus*, decreases with release density (Hines et al.,
90 2008), likely because the predator functional response of the major predator of juvenile blue crab, larger
91 blue crab (Hines and Ruiz, 1995), is a type III response, indicating a low-density refuge from predation
92 (Long et al., 2012a). Size-at-release and release season can affect post-release survival as predation
93 rates generally decrease with prey size (Johnson et al., 2008; Lebata et al., 2009) and predator densities
94 (or predation rates) vary throughout the year (Johnson et al., 2008; van der Meeren, 2000). Because
95 predator densities vary in space, release location is also an important consideration. In Chesapeake Bay
96 both lower bay (near the mouth) and upper bay sites are under carrying capacity for juvenile blue crab;
97 however, mortality rates are much higher in the lower bay, which is generally attributed to higher
98 predator densities (Hines et al., 2008; Seitz et al., 2008). In systems where predator activity varies
99 between night and day, the time of day of release may also be an important determinant of post-release
100 mortality (Poh et al., 2018).

101 In this study, we released red king crab at three different times (release timing) to determine
102 the optimal release strategy. This builds on previous research that demonstrated that release density
103 (between 25 and 75 crab/m²) of hatchery-reared red king crab did not affect post-release survival (Long
104 et al., 2018). Because there is currently no way to control red king crab broodstock hatch timing (and
105 thus the timing of hatchery rearing), later releases consisted of older, larger crabs. As such, we could not
106 unambiguously distinguish between the effects of release date and size-at-release. However, our intent
107 was to determine optimal release strategies for this species in realistic future enhancement scenarios.
108 Throughout this manuscript, we will refer to our treatments as release timing or the time of release
109 (relative to hatchery production) to differentiate it from the release date (the calendar day of release)
110 and the size-at-release.

111

112 **2. Methods**

113 This study was designed to build on previous work on red king crab stock enhancement (Long et
114 al., 2018). Except insofar as the two studies were designed to address different aspects of release
115 strategies, all other pertinent aspects, including broodstock source, crab transportation and holding,
116 hatchery procedures, release and monitoring locations and protocols, and modeling were the same
117 between the two studies. This was done to maximize our ability to quantitatively compare the results
118 from these two studies.

119 *2.1. Ethic approval and data availability*

120 Animal care followed all applicable federal and institutional guidelines. Research was permitted
121 through the Alaska Department of Fish and Game (Fish Resource Permit P-15-013 and Fish Transport
122 Permit 15A-0034). Data generated or analyzed during this study will be publicly available through
123 figshare upon publication of this manuscript (Long et al., 2024).

124 *2.2. Crab rearing*

125 Thirty ovigerous female red king crab were captured in crab pots in November, 2014 in Alitak
126 Bay, Kodiak, Alaska, USA, and transported to the Alutiiq Pride Shellfish Hatchery in Seward, Alaska, by air
127 where they were held in flowing seawater and fed to excess a diet of chopped frozen herring and squid
128 until larval hatching. Larvae were reared according to Swingle et al. (2013). In brief, they were stocked
129 at 50 larvae l⁻¹ and reared in conical tanks in flowing seawater at 12 °C, and fed a diet of *Artemia*
130 enriched with DC DHA Selco (INVE Aquaculture, UT, USA). Resulting first crab stage juveniles were
131 transported to Kodiak in two shipments of about 12,000 crabs each on June 5 and 17, 2015 in 4 L
132 containers with chilled seawater and gill netting packed inside a larger cooler with ice blocks. Shipments

133 were completed in a single day and no mortality of animals was noted. Until experimental release,
134 juveniles were held in tanks with gill nets in flowing, unfiltered seawater at local ambient salinity ($31.6 \pm$
135 0.3 , mean \pm SD) and temperature, which ranged from 8.7°C in early June to a maximum of 13.0°C at the
136 end of September before decreasing to 5.3 in late December). Because the experimental release and the
137 water intake for the laboratory are both in Trident Basin, Kodiak, these conditions are also reflective of
138 those at the release site. Crabs were fed a diet of frozen bloodworms and *Artemia* (Brine Shrimp Direct,
139 Ogden, Utah, USA), frozen Cyclop-eeze and Cyclop-eeze flakes (Argent Laboratories, Redmond,
140 Washington, USA), and Gelly Bely mixed with Cyclop-eeze powder, walleye pollock bone powder (U.S.
141 Department of Agriculture, Agricultural Research Service, Kodiak, Alaska, USA), and astaxanthin (Daly et
142 al., 2012b) three times a week to excess.

143 *2.3. Enhancement site and release design*

144 Experiments were performed in Trident Basin, Kodiak, along a continuous stretch of shoreline at
145 a depth of 8-10 m. Methods used were identical to those in a previous study on the effect of density on
146 red king crab stock enhancement success (Long et al., 2018). Twelve 5×5 m release plots separated by
147 a distance of 10 m from each other were established along a transect that ran parallel to the shoreline
148 ($57^{\circ}46'56.6''\text{N}$ $152^{\circ}23'36.4''\text{W}$ to $57^{\circ}46'51.9''\text{N}$ $152^{\circ}23'41.4''\text{W}$). Each plot was assigned to one of four
149 treatments: 1) Control (no crabs released), 2) June release (crabs at approximately the second instar
150 stage, C2), 3) August release (crabs at approximately the third instar stage, C4), and 4) September (crabs
151 at approximately the fifth instar stage, C5). Three replicate plots were assigned to each treatment.
152 Substrate in each plot was quantified once by estimating the percent cover of rock, gravel, shell, sand,
153 and mud in three 50×50 cm quadrats during diver monitoring of crab densities (below). Substrate was
154 analyzed with an analysis of similarity (ANOSIM) on a Euclidian distance difference matrix, with
155 treatment and plot (nested within treatment) as factors. All multivariate data analyses were performed

156 in Primer (v. 7.0.13, Primer-e, Plymouth, UK). The substrate was primarily a mixture of complex
157 habitats: rock, shells, and gravel (Fig. 2) and did not differ among treatments (Global R = -0.102, p =
158 0.80). Plots were also covered with macroalgae (primarily *Saccharina latissima*); average percent cover
159 (estimated in quadrats) was about 40%.

160 Releases were separated by approximately 6 weeks. Crab were counted by hand into containers
161 and were released immediately by SCUBA divers; a maximum of 2 h elapsed between beginning
162 counting out the crabs and release. Plots were sub-divided into 4 equal parts, and crabs were counted
163 and released into each quarter separately to ensure that crabs were evenly spread within each plot.
164 During the June and August releases, crabs were released at densities of 75 m⁻². The same density was
165 planned for September; however, mortality, primarily from cannibalism, in the holding tanks reduced
166 the total available for release, constraining this release to a density of 13.1 m⁻². The releases occurred
167 on June 23, August 4, and September 21, 2015. At each release, the carapace widths (including spines)
168 of a subset of crabs were measured to the nearest 0.01 with digital calipers. Average size at release ± SD
169 was 2.02 ± 0.18 mm in June, 3.29 ± 0.44 mm in August, and 5.10 ± 1.04 mm in September and size at
170 release differed among the release months (ANOVA, $F_{2,142} = 249.711$, $p < 0.0005$).

171 2.4. Release Monitoring

172 Crab densities were sampled by divers using 50 × 50 cm quadrats. Densities were sampled the
173 day after release (day 1), days 2, 3, 4, then twice a week for the following 2 weeks, followed by once a
174 week for the following 3 weeks, then every 2 weeks for the next 2 months, and then finally, monthly. All
175 sampling ceased in December when densities had dropped to a level not reliably detectable; this was
176 182, 142, and 81 days post-release for the June, August, and September releases, respectively. Three
177 haphazardly placed quadrats were sampled inside each plot during each sampling event. Additionally,
178 three more were placed outside each plot along the edge to quantify emigration from the plots. Control

179 plots were only sampled inside, as no emigration can occur in the absence of crabs and on the same
 180 schedule as the earliest release treatment (June). Each quadrat was carefully searched, and all red king
 181 crab were counted. Measuring densities outside the plots allowed us to estimate the number of crabs
 182 present outside the sites and, assuming that mortality rates are the same inside and outside the sites,
 183 distinguish between losses due to mortality and those due to emigration. In addition, all predators were
 184 identified to the lowest taxonomic level possible and were counted in each quadrat.

185 No red king crab were found in any control plot during the experiment, so the density of wild crabs is
 186 assumed to be below detectable limits, and the control plots were not included in any of our analyses of
 187 crab density. Further, given this, we assume that all red king crab encountered during monitoring were
 188 of hatchery origin. Red king crab densities both inside and outside of experimental plots were modeled
 189 using the model described in (Long et al., 2018). In short, the average density of crabs in the absence of
 190 mortality, C , was modeled as a function of t , time from release; C_0 , the density at $t = 0$; D , the diffusion
 191 parameter assuming a random walk model; and r , the distance from the center of the initial distribution
 192 (allowing for differentiation between counts performed inside and outside the plots):

$$193 \quad C = f(t, C_0, D, r).$$

194 The expected number of crabs in a quadrat, λ , was modeled assuming a Poisson distribution:

$$195 \quad \lambda = Ac_e S(t)C,$$

196 where A is the area searched, c_e is the counting efficiency, and $S(t)$ is expected survival as a function of
 197 time. Survival was modeled in several ways. In the first, the mortality rate was kept constant such that

$$198 \quad S(t) = (1 - m_i)e^{-mt},$$

199 where m_i is the initial mortality right after release and m is the instantaneous mortality rate. In addition,
 200 using a difference model, we allowed mortality to vary with time from release such that

201
$$S_t = (1 - m_i)(1 - m_a e^{m_b t})S_{t-1} ,$$

202 where m_a and m_b are parameters describing how the mortality rate changes over time. See Long et al.
 203 (2018) for a full model description and development. A was set to 0.75 m^2 , and to avoid
 204 pseudoreplication, we used the sum of the crabs counted in the three quadrates for each day a plot was
 205 sampled both inside and outside the plots. We set c_e to 0.74, the counting efficiency previously
 206 determined for juvenile red king crab in this habitat (Long et al., 2018). We fit the data to a series of
 207 models in which we allowed the diffusion coefficient, D , and the parameters describing mortality, m or
 208 m_a and m_b , to vary among the treatments (treated as a discrete factor) using maximum likelihood in R
 209 v.3.6.1 (Vienna, Austria). We estimated m_i as the average proportional decrease in density over the
 210 plots in the first day. When mortality (m or m_a and m_b) was modeled as the same across all treatments,
 211 we used the average m_i over all the plots: 0.525. When mortality was allowed to differ among
 212 treatments, we used the average m_i within each treatment: June- 0.415 ± 0.270 , August- 0.663 ± 0.134 ,
 213 and September- 0.496 ± 0.079 (mean \pm SD). The Akaike Information Criterion corrected for small sample
 214 size (AIC_c) was calculated for each model, and the best model selected; models whose AIC_c s differed by
 215 <2 were considered to explain the data equally well (Burnham and Anderson, 2002).

216 *2.5. Tethering Experiments*

217 Relative predation risk was assessed through tethering experiments (Hines and Ruiz 1995). The
 218 crab tethered were from the same cohort as those released and were held in the laboratory specifically
 219 for this purpose. Tethers consisted of 15 cm length of 1 kg test monofilament line and were attached to
 220 individual crabs on the dorsal side of the carapace with cyanoacrylate glue. Crabs were held in
 221 individual containers overnight to ensure that the tethers were securely attached and that crabs did not
 222 display obvious effects from the tether attachment process (e.g., limb immobility from incidental glue
 223 application). At approximately 0900 h, three crabs were tethered at a haphazard location at each plot,

224 separated by at least 2 m, and marked with a marker flag. Crabs were checked after 8 and 24 hours
225 (roughly day and night). When an intact carapace was found on the line, the crab was assumed to have
226 molted and was excluded from analysis. The experiments were performed during the week after each
227 release on July 9, August 13, and October 1; only control plots and plots into which crab had already
228 been released were used. Immediately prior to each tethering deployment, diver transects were
229 conducted to quantify larger or more mobile predators not well accounted for in the quadrat counts;
230 this included piscine predators (ronquils, rockfish, greenlings, sculpins, and shanneys; see results for full
231 species identifications), and two large invertebrate predators (giant Pacific octopus and *Telmessus*
232 *cheiragonus*); note that there was overlap between the species included in the two predator data sets.
233 In each transect, divers swam along the 5 m lines on opposite sides of each plot and counted all
234 potential predators to the lowest taxonomic level possible within 1 m on either side.

235 Predation rates were modeled as per (Long et al., 2018), assuming a constant rate of predation
236 such that $N_t = N_0 e^{-pt}$, where N_t is the number remaining alive on a plot at time t , N_0 is the initial
237 number, and p is the predation rate. We fit a series of models in which p was allowed to vary with
238 calendar month (July, August, October), release treatment, and time of day (day/night), all treated as
239 discrete factors, assuming a binomial distribution, in R v3.6.1. The AIC_c was calculated, and the best-fit
240 model was selected (as above). Predator counts from both the transects and the plot counts were
241 visualized using non-metric multidimensional scaling plots based on a Bray-Curtis similarity matrix and
242 analyzed using an analysis of similarity, with release treatment and calendar month of the experiment
243 (July, August, October) as factors. Predator assemblages were compared using non-metric
244 multidimensional scaling (nMDS), and analyses of similarity (ANOSIM). Predators in quadrat counts were
245 analyzed with ANOSIM, with sampling month crossed with treatment and plot nested within treatment
246 as factors. Larger predators from transects were analyzed with an ANOSIM, with release treatment
247 crossed with sampling month as factors.

248 3. Results

249 Red king crab juveniles demonstrated highly cryptic behavior shortly after release: crabs were
250 almost exclusively found under rocks or shells, or within kelp holdfasts. The best-fit model of movement
251 and mortality was the most complex model fit, and none of the other models had any support
252 whatsoever (Table 1). Both the diffusion term and mortality differed among the treatments, and
253 mortality also decreased with time from release (Table 1, Fig. 3). Emigration (diffusion) rates were
254 lowest in the June release and highest in September (Table 2, Fig. 3). Mortality followed the opposite
255 trend being generally highest in the June release, and lowest in September (Table 2; Figs. 3, 4). Densities
256 inside plots dropped rapidly after release for all treatments, but the decrease slowed over time.
257 Densities outside plots were nearly undetectable after the June release; however, in the August and
258 September releases, they were detected outside plots almost immediately after release and peaked
259 about 20-40 days post-release. Given the estimated mortality rates (Table 2), predicted survival 90 days
260 post-release for crab that survived the first day was 3.8%, 6.4%, and 10.0% for the June, August, and
261 September releases, respectively.

262 In the best-fit model, predation on tethered crabs varied with month and time of day but not
263 release treatment (Table 3). *Post hoc*, we noted that the predation rates in the July and August
264 tethering experiments were almost the same, so we fit an additional model where they were the same
265 but differed from the October experiment. This model had an AIC_c value that was more than 2 lower
266 than the full model, showing that there was no support for including the dropped parameter (Burnham
267 and Anderson, 2002), and as such, this reduced model was selected due to parsimony. Predation was
268 higher in July and August than in September and was higher during the day than at night (Fig. 4).

269 Predators observed in and around the experimental plots included piscine predators such as
270 greenlings (*Hexagrammidae* spp.), rockfish (mostly *Sebastes ciliatus* (Tilesius, 1813)), Arctic shanny

271 (*Stichaeus punctatus* (Fabricius, 1780)), crescent gunnels (*Pholis laeta* (Cope, 1873)), Alaskan ronquils
272 (*Bathymaster caeruleofasciatus* (Gilbert and Burke, 1912)), and sculpins (*Cottoidea* spp.). Invertebrate
273 predators included hermit crabs (mostly *Elassochirus gilli* (J. E. Benedict, 1892) and *E. tenuimanus* (Dana,
274 1851)), and dock shrimp (*Pandalus danae* (Stimpson, 1857)). Predator assemblages of smaller, less
275 mobile species, in quadrats did not vary among release treatments (Global R = 0.025, p = 0.348, Fig. 5) or
276 sampling months (Global R = -0.016, p = 0.623). Similarly, in transects conducted during the tethering
277 experiments, the assemblages of larger, more mobile predators did not vary among release treatments
278 (Global R = 0.078, p = 0.260, Fig. 5) or sampling months (Global R = 0.151, p = 0.074).

279

280 4. Discussion

281 When extended hatchery-rearing and post-release mortality are considered, releasing crabs
282 soon after molting to the first crab stage is likely the best strategy for this species. We demonstrated
283 that juvenile post-release survival increased from the June to the September releases. This is
284 unsurprising, as later release dates corresponded with a larger release size, which likely decreased
285 predation risk. We also found that crab migration rates were higher at later releases, also likely due to
286 increased release size as larger crabs tend to be more active. Relative predation rate decreased with
287 increasing calendar date, further substantiating these conclusions. However, although later release
288 dates were associated with better survival post-release, the difference was small and would likely not
289 offset the high rates of cannibalism in extended hatchery communal holding conditions (Daly et al.
290 2009), production cost, or the possibility of developing maladapted traits (Daly et al. 2020). Rearing
291 individual crabs in isolation improves survival but it is labor intensive on a large scale, affects growth
292 (Swiney et al. 2013), and could impede brain development (Sandeman and Sandeman, 2000).

293 The greatest difficulty in the interpretation of these release results is that the densities in the
294 September release were markedly lower than those in the other two releases. We cannot say for
295 certain whether the differences between this treatment and the other two are due to the later release
296 (larger body size and/or reduced predation), the density at release, or a combination of the two. In a
297 previous experiment, performed with the same methods in the same areas and designed to test the
298 effects of release density on release success, we found no density-dependent effects on either mortality
299 or migration (Long et al., 2018). This provides fairly strong evidence that the differences observed in this
300 experiment were due primarily to differences in release timing and not density. In addition, the effects,
301 increasing migration rate and decreasing mortality rate, are both continuations of the trend apparent in
302 the June and August releases and are consistent with likely mechanisms (see discussion below). Also, if
303 density were to effect migration, one would expect that it would be positively correlated with density
304 (Hines et al., 2008), not negatively correlated, as observed here. Although we acknowledge that the
305 results could be affected by density, we believe that the differences observed between the September
306 release and the other two are primarily driven by release timing.

307 Post-release survival varied with release timing. Initial mortality (within the first 24 h) was high
308 in all treatments and it was highest in August and lowest in June, yet the high variability in our estimates
309 makes any interpretation of this pattern questionable. Subsequent mortality, however, followed two
310 clear patterns: decreasing with time-of-release (release timing), and decreasing with time after release.
311 Several non-exclusive mechanisms could be contributing to the decreasing mortality with month of
312 release. The first is that predation rates on released red king crab decrease with size (Pirtle et al., 2012).
313 Larger crabs exclude predation from a greater proportion of gape-limited predators and they may also
314 be better able to defend themselves or flee from all predators. Blue crabs, similarly, suffer heavy
315 predatory mortality at smaller sizes, which decreases with size (Hines and Ruiz, 1995; Johnson et al.,
316 2008; Pile et al., 1996), and survival of mud crabs, *Scylla* spp., increases with size-at-release (Lebata et

317 al., 2009). It is worth noting that this trend holds despite the red king crab in our study (2-5 mm CW)
318 being much smaller than the sizes of the blue crab (20 – 70 mm CW) or the mud crabs (20-30 mm) in
319 these other studies (Johnson et al., 2008; Lebata et al., 2009). Second, there may be seasonal
320 differences in predation risk. In both this study and the previous one (Long et al., 2018), predation risk
321 on tethered crabs decreased after August. In neither did we see a change in the predator guild;
322 however, as temperatures decrease into the fall months, predation rates by ectothermic predators are
323 likely to decrease. It is likely that both of these are factors in this case. A similar effect of release season
324 on stock enhancement success occurs for other species. In blue crab (Johnson et al., 2008) and
325 European lobster (van der Meeren, 2000), seasonal differences in release success are likely driven by
326 changes in predator abundance. Differences in predator activity, rather than abundance, likely drive
327 differences in mortality of released individuals for both the queen conch, *Strombus gigas* (Stoner and
328 Glazer, 1998) and hard clams, *Mercenaria mercenaria* (Peterson et al., 1995). On the other hand, there
329 is a strong effect of season on the survival of hatchery-reared striped mullet, *Mugil cephalus*, likely
330 driven by the ability of hatchery fish to integrate into the anti-predator schooling behavior of similarly-
331 sized wild fish (Leber et al., 1997). This last effect is likely not a significant factor at the early benthic
332 stage for red king crab; however, given that red king crab transition to podding behavior at around the
333 end of their second year (Dew, 1990), the availability of other crabs to pod with could become a
334 significant factor at this later stage.

335 In the tethering experiments, predation was higher during the day than at night. Superficially,
336 this is the opposite pattern observed in our previous tethering experiment (Long et al., 2018). However,
337 in both experiments, the period directly after placement of the tethered crabs had the highest mortality,
338 suggesting that the period of highest predation risk is in the first few hours after release. The difference
339 between day and night was more than 50% greater in this study than in the previous experiment (Long
340 et al. 2018), which supports the hypothesis of lower predation rates at night and it is consistent with a

341 similar study in southeast Alaska, where tethered crabs were more likely to be attacked and consumed
342 during daylight hours (Daly et al., 2013). The importance of visual detection of prey likely varies by
343 predator species; however, if predation rates are generally higher in daylight hours, this could, in part,
344 explain higher survival later in the season when periods of daylight are relatively shorter (Kodiak
345 daylight ~18 h in June and ~10 h in October).

346 In this study and our previous study (Long et al., 2018), there was a clear pattern of high
347 mortality soon after release which decreased with time and approached a low limit. The decline was
348 steepest in the first 2-3 weeks post-release. Notably, in the August and September releases, the
349 mortality rate during these first 2-3 weeks was higher than the estimated rate for the June release at the
350 same time (that is, the calendar date, not the time from release as shown in Fig. 5), suggesting that post-
351 release mortality in hatchery-reared red king crab occurs in three general phases. First, there is high
352 (~50-70%) mortality in the first 24 h after release, likely caused by the disorientation of being
353 transferred from the hatchery environment to the natural environment. Hatchery-reared European
354 lobsters, another species that relies on crypsis to avoid predators, will freeze or even swim toward the
355 surface when released leading to high predation rates (van der Meeren, 1991; van der Meeren, 2000).
356 Although red king crab cannot swim, we observed individuals motionless and failing to proactively seek
357 structural refugia shortly after release. Second, there is a phase that lasts 2-3 weeks during which the
358 mortality rate rapidly declines. During this phase, we propose that crabs exhibiting less adaptive
359 behaviors, such as a low degree of crypsis, a high degree of activity, or maladaptive feeding behaviors,
360 are more likely to die. This could be due to innate differences in behavioral characteristics among
361 individuals, or to a learning curve, or to a combination, though the latter is the most likely. Red king
362 crab juveniles that have not been exposed to predators are less cryptic than those that have (Long et al.,
363 2015), and this behavior makes them more vulnerable to predation (Daly et al., 2012a). In the same
364 way, hatchery-reared mud crabs have a lower survival rate than their wild counterparts, suggesting

365 similar mechanisms (Lebata et al., 2009). Finally, after 2-3 weeks, mortality rates level off at a low level
366 which is, presumably, close to what wild crabs would experience in the same environment. The same
367 pattern occurred in our previous release experiment, but because all the releases were simultaneous, it
368 was impossible to determine if the decline during the second phase was due to environmental changes
369 or gradual acclimation of released crabs.

370 Movement (diffusion) rates increased with the time of release. This is almost certainly primarily
371 due to the size of the crabs being released. Larger crabs are expected to be able to move faster and
372 likely show a lower degree of crypsis and more movement due to a lower risk of predation (Pirtle et al.,
373 2012). For this ectothermic species, a positive correlation between temperature and activity level would
374 be expected (Hill, 1980). The highest migration rates occurred after the September release when
375 temperatures were close to their seasonal maximum so temperature could be an important factor too.
376 Overall, the migration rates were very low, which is not surprising given juvenile red king crab reliance
377 on crypsis. There are few studies to compare this to; however, hatchery-reared blue crab also show
378 slow migration after release (Davis et al., 2005), and the movement rates differ between hatchery-
379 reared and wild crab (Davis et al., 2004).

380 When considering optimal release timings for red king crab, it is important to consider all
381 sources of mortality, including both holding and post-release mortality. Red king crab are highly
382 cannibalistic, and mortality rates of communally held crabs are high with average survival over 6-7
383 weeks around 30-80% depending on holding conditions (Daly et al., 2009; Daly et al., 2012c). In
384 contrast, survival of individually held crabs can be much higher (Swiney et al., 2013), but it is impractical
385 at a large scale because it is labor-intensive, requires large amounts of space/cost, and introduces the
386 possibility of developing maladaptive traits (Daly et al., 2021). To provide an estimate of overall survival,
387 we used estimates for holding mortality from Daly et al. (2009), who found an average survival of 52.9%

388 when holding crabs from C1 to C3 over 42 days (approximately the same time as between our June and
389 August releases), and an average survival of 38.0% from C3 to C6 over 44 days (approximately the same
390 time as between our August and September treatments). We then used our initial and post-release
391 mortality estimates from this experiment to estimate cumulative survival for all 3 treatments at 90 days
392 after a September release (Table 4). When all sources of mortality are included, overall survival was
393 highest in the June release, which was about twice as high as the September release, and three times as
394 high as the August release (Table 4). This leads us to the conclusion that the best release strategy for
395 red king crab is to release them as soon as possible after they are reared to the C1 stage. Fortuitously,
396 this strategy is also the most economic, as it avoids the costs inherent to holding crabs in a hatchery
397 after they reach the C1 stage.

398 There are few estimates of mortality or movement rates for juvenile red king crab. Compared
399 with our previous study, overall mortality rates were much higher in this experiment; for our August
400 release, the same month of release as our previous study, the estimated 6-month survival of crabs that
401 survived the first day after release was only 2.4%, compared with 47% (Long et al., 2018), and the
402 maximum estimated 6-month survival in this study was 8.8% for the September release. In the only
403 other study from which an estimate of mortality of wild red king crab juveniles can be calculated, wild
404 red king crab survival was estimated at 27% over a 6-month period (Loher and Armstrong, 2000). In
405 addition, the movement (diffusion) rate of crabs in this study was far lower than that of our previous
406 study by about an order of magnitude (Long et al., 2018). What is causing these differences is unclear,
407 but it is apparent that there is wide variation in survival rates of juvenile king crabs. In comparing this
408 study to our previous study (Long et al., 2018), predation rates on tethered crabs were more than 25%
409 higher in September and more than 100% higher in October in this study. This suggests that predation
410 may have played a large role in determining the higher overall mortality rate in this study. However, the
411 difference in movement rates suggests that there may have also been behavioral differences between

412 the crabs in the 2 years, which could also contribute. Whether this is due to differences in rearing,
413 genetic differences, or environmental factors is not clear. Although the estimates of survival for year-0
414 red king crab vary considerably, this occurs in other crabs as well. For example, survival of hatchery-
415 reared blue crab varies extensively both within and among years as well as spatially (Hines et al., 2008;
416 Johnson et al., 2011). Despite this variance, the survival rates of hatchery and wild blue crabs do not
417 differ in the field (Johnson et al., 2011). Given this, and since our estimates of red king crab mortality
418 are both much higher, and much lower than our only estimate for wild mortality, we suggest that the
419 mortality rates observed on hatchery-reared crabs are likely similar to those that wild crabs would
420 experience.

421 This study demonstrates that releasing hatchery-reared red king crab as early as possible after
422 transition to the first benthic juvenile stage is the best strategy to both maximize survival for the first 6
423 months and to minimize rearing costs. Future work should focus on methods to increase post-release
424 survival, particularly during the first 24 hours, but also during the first 2-3 weeks. Providing partial
425 protection to the juveniles by releasing them under screens or inside cages to provide protection while
426 the crabs adapt to the field environment (Beal et al., 2002), and from which they can move into the
427 surrounding substrate, should be attempted. Alternatively, releasing at night, when predation is lower
428 (Daly et al., 2013), may reduce predation in the first few hours or days, as it does for the prawn
429 *Metapenaeus dalli* (Poh et al., 2018). In addition, it may be worth considering techniques to condition
430 hatchery-reared crabs (Daly et al., 2021; Hinchcliffe et al., 2022). There is evidence that exposure to
431 predators prior to release can induce a greater degree of cryptic behavior in red king crab, which might
432 decrease predation rates soon after release (Daly et al., 2012a). Results in other hatchery-reared
433 crustaceans are mixed; conditioning blue crab (Davis et al., 2004; Young et al., 2008) and New Zealand
434 rock lobster (Oliver et al., 2006, 2008) is effective in increasing anti-predator behaviors but it does not
435 decrease mortality in the field, whereas conditioning European lobsters is effective in both increasing

436 shelter use behavior (van der Meeren, 2001) and in decreasing predation after release (Agnalt et al.,
437 2017; Aspaas et al., 2016). How such conditioning could be performed at scale and whether it would
438 reduce post-release mortality in red king crab have yet to be determined. Alternatively, it would be
439 worth comparing releasing glaucothoe to releasing crab stage juveniles. Laboratory-reared glaucothoe
440 are attracted to complex habitats (Stevens, 2003; Stevens and Kittaka, 1998) thus releases in targeted
441 habitats may be an effective strategy. Releases of glaucothoe or recently-settled first-stage juveniles
442 would reduce production costs substantially, allow for more production cycles in a given season in a
443 given hatchery, minimize cannibalism associated with communal holding, and preclude the need for
444 conditioning. Finally, the experimental releases conducted to date have been performed only on a
445 small-scale, both spatially and temporally. To what degree these estimates will apply if release areas are
446 scaled up from 10s to 1,000s of m² is unknown. Further, the time that crabs in these small-scale
447 experiments can be effectively tracked is short, as migration out of small plots and mortality quickly
448 reduces densities below detectable limits. Future work should focus on performing large-scale releases
449 and tracking crabs for at least the first two years of life, after which monitoring becomes more difficult
450 because of the shift to podding behavior (Dew, 1990). This will allow for more accurate estimates of
451 survival, which would better inform estimates of the economic feasibility of red king crab enhancement.
452 Finally, it is clear that post-release mortality can vary by more than an order of magnitude, and the
453 factors that contribute to that variance, such as genetic variability, temperature, predator densities,
454 habitat, or other biological or environmental factors should be further investigated (e.g., Hines and Ruiz,
455 1995; Long et al., 2011).

456

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464

465 **Literature Cited**

466 Agnalt, A.-L., Grefsrud, E.S., Farestveit, E., Jørstad, K.E., 2017. Training camp—A way to improve survival
467 in European lobster juveniles? *Fisheries Research* 186, 531-537.

468 Aspaas, S., Grefsrud, E.S., Fernö, A., Jensen, K.H., Trengereid, H., Agnalt, A.-L., 2016. An enriched
469 environment promotes shelter-seeking behaviour and survival of hatchery-produced juvenile
470 European lobster (*Homarus gammarus*). *PLoS One* 11(8), e0159807.

471 Beal, B.F., Mercer, J.P., O'Conghaile, A., 2002. Survival and growth of hatchery-reared individuals of the
472 European lobster, *Homarus gammarus* (L.), in field-based nursery cages on the Irish west coast.
473 *Aquaculture* 210(1), 137-157.

474 Bechtol, W., Kruse, G., 2009. Reconstruction of historical abundance and recruitment of red king crab
475 during 1960–2004 around Kodiak, Alaska. *Fisheries Research* 100(1), 86-98.

476 Bechtol, W.R., Kruse, G.H., 2010. Factors affecting historical red king crab recruitment around Kodiak
477 Island, Alaska, in: Kruse, G.H., Eckert, G.L., Foy, R.J., Lipcius, R.N., Sainte-Marie, B., Stram, D.L.,
478 Woodby, D. (Eds.), *Biology and Management of Exploited Crab Populations under Climate*
479 *Change*, 25th ed. Alaska Sea Grant College Program, University of Alaska Fairbanks, Anchorage,
480 AK, pp. 413-442.

- 481 Blau, S.F., 1986. Recent declines of red king crab (*Paralithodes camtschatica*) populations and
482 reproductive conditions around the Kodiak Archipelago, Alaska, in: Jamieson, G.S., Bourne, N.
483 (Eds.), North Pacific Workshop on Stock Assessment and Management of Invertebrates.
484 Canadian Special Publication of Fisheries and Aquatic Sciences, p. 360.
- 485 Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: A practical
486 information-theoretic approach, 2nd ed. Springer Science + Business Media, New York.
- 487 Daly, B., Eckert, G.L., White, T.D., 2013. Predation of hatchery-cultured juvenile red king crabs
488 (*Paralithodes camtschaticus*) in the wild. Can. J. Fish. Aquat. Sci. 70(3), 358-366.
489 <https://doi.org/10.1139/cjfas-2012-0377>
- 490 Daly, B., Long, W.C., 2014. Intra-guild predation among early benthic phase red and blue king crabs:
491 Evidence for a habitat-mediated competitive advantage. J. Exp. Mar. Biol. Ecol. 451, 98-104.
- 492 Daly, B., Stoner, A.W., Eckert, G.L., 2012a. Predator-induced behavioral plasticity of juvenile red king
493 crabs (*Paralithodes camtschaticus*). J. Exp. Mar. Biol. Ecol. 429, 47-54.
- 494 Daly, B., Swingle, J.S., Eckert, G.L., 2009. Effects of diet, stocking density, and substrate on survival and
495 growth of hatchery-cultured red king crab (*Paralithodes camtschaticus*) juveniles in Alaska, USA.
496 Aquaculture 293(1-2), 68-73. <https://doi.org/10.1016/j.aquaculture.2009.04.010>
- 497 Daly, B., Swingle, J.S., Eckert, G.L., 2012b. Dietary astaxanthin supplementation for hatchery-cultured
498 red king crab, *Paralithodes camtschaticus*, juveniles. Aquacult. Nutr. 19(3), 312-320.
499 <https://doi.org/10.1111/j.1365-2095.2012.00963.x>
- 500 Daly, B., Swingle, J.S., Eckert, G.L., 2012c. Increasing hatchery production of juvenile red king crabs
501 (*Paralithodes camtschaticus*) through size grading. Aquaculture 364–365(0), 206-211.
502 <https://doi.org/10.1016/j.aquaculture.2012.08.034>

- 503 Daly, B.J., Eckert, G.L., Long, W.C., 2021. Moulding the ideal crab: implications of phenotypic plasticity
504 for crustacean stock enhancement. ICES J. Mar. Sci. 78(1), 421-434.
505 <https://doi.org/10.1093/icesjms/fsaa043>
- 506 Davis, J.L., Young-Williams, A.C., Hines, A.H., Yonathan, Z., 2005. Assessing the potential for stock
507 enhancement in the case of the Chesapeake Bay blue crab (*Callinectes sapidus*). Can. J. Fish.
508 Aquat. Sci. 62(1), 109-122.
- 509 Davis, J.L.D., Young-Williams, A.C., Aguilar, R., Carswell, B.L., Goodison, M.R., Hines, A.H., Kramer, M.A.,
510 Zohar, Y., Zmora, O., 2004. Differences between hatchery-raised and wild blue crabs:
511 implications for stock enhancement potential. Trans. Am. Fish. Soc. 133(1), 1-14.
- 512 Dew, C.B., 1990. Behavioral ecology of podding red king crab, *Paralithodes camtschatica*. Can. J. Fish.
513 Aquat. Sci. 47(10), 1944-1958.
- 514 Dew, C.B., 1991. Characterization of preferred habitat for juvenile red king crab in three Kodiak bays.
515 Final report to the Kodiak Island Borough, Kodiak, Alaska Contract Number 89-226, 1-90.
- 516 Hill, B., 1980. Effects of temperature on feeding and activity in the crab *Scylla serrata*. Mar. Biol. 59(3),
517 189-192.
- 518 Hinchcliffe, J., Agnalt, A.L., Daniels, C.L., Drengstig, A.r., Lund, I., McMinn, J., Powell, A., 2022. European
519 lobster *Homarus gammarus* aquaculture: Technical developments, opportunities and
520 requirements. Rev. Aquac. 14(2), 919-937.
- 521 Hines, A., Ruiz, G., 1995. Temporal variation in juvenile blue crab mortality: nearshore shallows and
522 cannibalism in Chesapeake Bay. Bull. Mar. Sci. 57(3), 884-901.
- 523 Hines, A.H., Johnson, E.G., Young, A.C., Aguilar, R., Kramer, M.A., Goodison, M., Zmora, O., Zohar, Y.,
524 2008. Release strategies for estuarine species with complex migratory life cycles: Stock
525 enhancement of Chesapeake blue crabs (*Callinectes sapidus*). Rev. Fish. Sci. 16(1), 175-185.

- 526 Johnson, E.G., Hines, A.H., Kramer, M.A., Young, A.C., 2008. Importance of season and size of release to
527 stocking success for the blue crab in Chesapeake Bay. *Rev. Fish. Sci.* 16(1), 243-253.
- 528 Johnson, E.G., Young, A.C., Hines, A.H., Kramer, M.A., Bademan, M., Goodison, M.R., Aguilar, R., 2011.
529 Field comparison of survival and growth of hatchery-reared versus wild blue crabs, *Callinectes*
530 *sapidus* Rathbun. *J. Exp. Mar. Biol. Ecol.* 402(1-2), 35-42.
- 531 Kron, T., 1992. Keynote address, in: White, L.E., Nielsen, C. (Eds.), *Proceedings of the International Crab*
532 *Rehabilitation and Enhancement Symposium*. Alaska Department of Fish and Game , Fisheries
533 Rehabilitation, Enhancement and Development Division, Kodiak, Alaska, pp. 2-4.
- 534 Leбата, M.J.H.L., Le Vay, L., Walton, M.E., Biñas, J.B., Qunitio, E.T., Rodriguez, E.M., Primavera, J.H.,
535 2009. Evaluation of hatchery-based enhancement of the mud crab, *Scylla* spp., fisheries in
536 mangroves: comparison of species and release strategies. *Marine and Freshwater Research*
537 60(1), 58-69.
- 538 Leber, K.M., Blankenship, H., Arce, S.M., Brennan, N., 1997. Influence of release season on size-
539 dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary. *Fish. Bull.*,
540 U.S. 95(2), 267-279.
- 541 Loher, T., Armstrong, D.A., 2000. Effects of habitat complexity and relative larval supply on the
542 establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815)
543 populations in Auke Bay, Alaska. *J. Exp. Mar. Biol. Ecol.* 245(1), 83-109.
- 544 Long, W.C., 2016. A new quantitative model of multiple transitions between discrete stages, applied to
545 the development of crustacean larvae. *Fish. Bull.*, U.S. 114(1), 58-66.
546 <https://doi.org/10.7755/FB.114.1.5>
- 547 Long, W.C., Cummiskey, P., Munk, J.E., 2018. How does stocking density affect enhancement success for
548 hatchery-reared red king crab? *Can. J. Fish. Aquat. Sci.* 75(11), 1940-1948.
549 <https://doi.org/10.1139/cjfas-2017-0330>

- 550 [dataset] Long, W.C., Daly, B., Cummiskey, P., 2024. Data from: Optimizing release strategies for red king
551 crab stock enhancement: effects of release timing. figshare.
552 <https://doi.org/https://doi.org/10.6084/m9.figshare.25174760>
- 553 Long, W.C., Grow, J.N., Majoris, J.E., Hines, A.H., 2011. Effects of anthropogenic shoreline hardening and
554 invasion by *Phragmites australis* on habitat quality for juvenile blue crabs (*Callinectes sapidus*). J.
555 Exp. Mar. Biol. Ecol. 409(1-2), 215-222. <https://doi.org/10.1016/j.jembe.2011.08.024>
- 556 Long, W.C., Johnson, E.G., Gamelin, E.F., Hines, A.H., 2012a. Density dependent indirect effects:
557 apparent mutualism and apparent competition coexist in a two-prey system. Mar. Ecol. Prog.
558 Ser. 456, 139-148. <https://doi.org/10.3354/meps09702>
- 559 Long, W.C., Popp, J., Swiney, K.M., Van Sant, S.B., 2012b. Cannibalism in red king crab, *Paralithodes*
560 *camtschaticus* (Tilesius, 1815): Effects of habitat type and predator density on predator
561 functional response. J. Exp. Mar. Biol. Ecol. 422-423, 101-106.
562 <https://doi.org/10.1016/j.jembe.2012.04.019>
- 563 Long, W.C., Van Sant, S.B., Haaga, J.A., 2015. Habitat, predation, growth, and coexistence: Could
564 interactions between juvenile red and blue king crabs limit blue king crab productivity? J. Exp.
565 Mar. Biol. Ecol. 464, 58-67. <https://doi.org/10.1016/j.jembe.2014.12.011>
- 566 Long, W.C., Whitefleet-Smith, L., 2013. Cannibalism in red king crab: Habitat, ontogeny, and the
567 predator functional response. J. Exp. Mar. Biol. Ecol. 449, 142-148.
568 <https://doi.org/10.1016/j.jembe.2013.09.004>
- 569 Oliver, M.D., MacDiarmid, A.B., Stewart, R.A., Gardner, C., 2006. Spiny lobster population enhancement:
570 moderation of emergence behaviour of juvenile *Jasus edwardsii* reared in captivity. N. Z. J. Mar.
571 Freshwat. Res. 40(4), 605-613.
- 572 Oliver, M.D., Macdiarmid, A.B., Stewart, R.A., Gardner, C., 2008. Anti-predator behavior of captive-
573 reared and wild juvenile spiny lobster (*Jasus edwardsii*). Rev. Fish. Sci. 16(1-3), 186-194.

- 574 Orensanz, J., Armstrong, J., Armstrong, D., Hilborn, R., 1998. Crustacean resources are vulnerable to
575 serial depletion—the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of
576 Alaska. *Rev. Fish Biol. Fish.* 8(2), 117-176.
- 577 Persselin, S., Daly, B., 2010. Diet and water source effects on larval red king crab cultivation, in: Kruse,
578 G.H., Eckert, G.L., Foy, R.J., Lipcius, R.N., Sainte-Marie, B., Stram, D.L., Woodby, D. (Eds.), *Biology
579 and Management of Exploited Crab Populations under Climate Change*, 25th ed. Alaska Sea
580 Grant College Program, University of Alaska Fairbanks, Anchorage, AK, pp. 479-494.
- 581 Peterson, C.H., Summerson, H.C., Huber, J., 1995. Replenishment of hard clam stocks using hatchery
582 seed: combined importance of bottom type, seed size, planting season, and density. *J. Shellfish
583 Res.* 14(2), 293-300.
- 584 Pile, A.J., Lipcius, R.N., Montfrans, J.v., Orth, R.J., 1996. Density-dependent settler-recruit-juvenile
585 relationships in blue crabs. *Ecol. Monogr.* 66(3), 277-300.
- 586 Pirtle, J.L., Eckert, G.L., Stoner, A.W., 2012. Habitat structure influences the survival and predator-prey
587 interactions of early juvenile red king crab *Paralithodes camtschaticus*. *Mar. Ecol. Prog. Ser.* 465,
588 169-184. <https://doi.org/10.3354/meps09883>
- 589 Poh, B., Tweedley, J.R., Chaplin, J.A., Trayler, K.M., Loneragan, N.R., 2018. Estimating predation rates of
590 restocked individuals: The influence of timing-of-release on metapenaeid survival. *Fisheries
591 Research* 198, 165-179.
- 592 Powell, G.C., Nickerson, R.B., 1965. Aggregations among juvenile king crabs (*Paralithodes camtschatica*,
593 Tilesius) Kodiak, Alaska. *Anim. Behav.* 13(2-3), 374-380.
- 594 Sandeman, R., Sandeman, D., 2000. “Impoverished” and “enriched” living conditions influence the
595 proliferation and survival of neurons in crayfish brain. *J. Neurobiol.* 45(4), 215-226.

- 596 Seitz, R.D., Lipcius, R.N., Knick, K.E., Seebo, M.S., Long, W.C., Brylawski, B.J., Smith, A., 2008. Stock
597 enhancement and carrying capacity of blue crab nursery habitats in Chesapeake Bay. *Rev. Fish.*
598 *Sci.* 16(1-3), 329-337. <https://doi.org/10.1080/10641260701696985>
- 599 Shirley, S.M., Shirley, T.C., 1989. Interannual variability in density, timing and survival of Alaskan red king
600 crab *Paralithodes camtschatica* larvae. *Mar. Ecol. Prog. Ser.* 54(1-2), 51-59.
- 601 Shirley, T.C., Shirley, S.M., Korn, S., 1989. Incubation period, molting and growth of female red king
602 crabs: effects of temperature, in: Melteff, B. (Ed.), *Proceedings of the International Symposium*
603 *on king and Tanner crabs. Lowell Wakefield Symposia. Alaska Sea Grant Report 90-04*, pp. 51-63.
- 604 Stevens, B., 2006. Alaska crab stock enhancement and rehabilitation: an introduction, in: Stevens, B.
605 (Ed.) *Alaska Crab Stock Enhancement and Rehabilitation: Workshop Proceedings. Alaska Sea*
606 *Grant College Program AKSG-06-04*, pp. 5-8.
- 607 Stevens, B.G., 2003. Settlement, substratum preference, and survival of red king crab *Paralithodes*
608 *camtschaticus* (Tilesius, 1815) glaucothoe on natural substrata in the laboratory. *J. Exp. Mar.*
609 *Biol. Ecol.* 283(1-2), 63-78.
- 610 Stevens, B.G., Dunham, A., Kittaka, J., Kovatcheva, N.P., Persselin, S., van der Meeren, G.I., 2014.
611 *Aquaculture and stock enhancement of king crabs*, in: Stevens, B.G. (Ed.), *King Crabs of the*
612 *World: Biology and Fisheries Management. CRC Press, Boca Raton, FL*, pp. 403-448.
- 613 Stevens, B.G., Kittaka, J., 1998. Postlarval settling behavior, substrate preference, and time to
614 metamorphosis for red king crab *Paralithodes camtschaticus*. *Mar. Ecol. Prog. Ser.* 167, 197-206.
- 615 Stevens, B.G., Munk, J.E., 1989. A temperature-dependent growth model for juvenile red king crab,
616 *Paralithodes camtschatica*, in Kodiak, Alaska in: Davis, S.K., Kruse, G.H., Otto, R.S., Shirley, T.C.
617 (Eds.), *Proceedings of the International Symposium on King and Tanner Crabs*, 8th ed. Alaska Sea
618 Grant College Program, University of Alaska Fairbanks, Anchorage, AK, pp. 293-304.

- 619 Stevens, B.G., Swiney, K.M., 2007. Hatch timing, incubation period, and reproductive cycle for captive
620 primiparous and multiparous red king crab, *Paralithodes camtschaticus*. J. Crust. Biol. 27(1), 37-
621 48.
- 622 Stoner, A.W., 2009. Habitat-mediated survival of newly settled red king crab in the presence of a
623 predatory fish: role of habitat complexity and heterogeneity. J. Exp. Mar. Biol. Ecol. 382(1), 54-
624 60.
- 625 Stoner, A.W., Glazer, R.A., 1998. Variation in natural mortality: implications for queen conch stock
626 enhancement. Bull. Mar. Sci. 62(2), 427-442.
- 627 Sundberg, K.A., Clausen, D., 1979. Post-larval king crab (*Paralithodes camtschatica*) distribution and
628 abundance in Kachemak Bay Lower Cook Inlet, Alaska, 1976, in: Melteff, B.R. (Ed.) Alaska
629 Fisheries: 200 Years and 200 Miles of Change: Proceedings of the 29th Alaska Science
630 Conference. University of Alaska Sea Grant Program, pp. 747-766.
- 631 Swiney, K.M., Long, W.C., 2015. Primiparous red king crab, *Paralithodes camtschaticus*, are less fecund
632 than multiparous crab. J. Shellfish Res. 34(2), 493-498. <https://doi.org/10.2983/035.034.0233>
- 633 Swiney, K.M., Long, W.C., Eckert, G.L., Kruse, G.H., 2012. Red king crab, *Paralithodes camtschaticus*, size-
634 fecundity relationship, and inter-annual and seasonal variability in fecundity. J. Shellfish Res.
635 31(4), 925-933.
- 636 Swiney, K.M., Long, W.C., Persselin, S.L., 2013. The effects of holding space on juvenile red king crab
637 (*Paralithodes camtschaticus*) growth and survival. Aquacult. Res. 44, 1007–1016.
638 <https://doi.org/10.1111/j.1365-2109.2012.03105.x>
- 639 Swingle, J.S., Daly, B., Hetrick, J., 2013. Temperature effects on larval survival, larval period, and health
640 of hatchery-reared red king crab, *Paralithodes camtschaticus*. Aquaculture 384–387(0), 13-18.
641 <https://doi.org/10.1016/j.aquaculture.2012.12.015>

- 642 van der Meeren, G., 1991. Out-of-water transportation effects on behaviour in newly released juvenile
643 Atlantic lobsters *Homarus gammarus*. *Aquacult. Eng.* 10, 55-64.
- 644 van der Meeren, G.I., 2000. Predation on hatchery-reared lobsters released in the wild. *Can. J. Fish.*
645 *Aquat. Sci.* 57(9), 1794-1803.
- 646 van der Meeren, G.I., 2001. Effects of experience with shelter in hatchery-reared juvenile European
647 lobsters *Homarus gammarus*. *Marine and Freshwater Research* 52(8), 1487-1493.
- 648 Young, A.C., Johnson, E.G., Davis, J.L.D., Hines, A.H., Zmora, O., Zohar, Y., 2008. Do hatchery-reared blue
649 crabs differ from wild crabs, and does it matter? *Rev. Fish. Sci.* 16(1), 254-261.
- 650 Zheng, J., Kruse, G., 2000. Recruitment patterns of Alaskan crabs in relation to decadal shifts in climate
651 and physical oceanography. *ICES J. Mar. Sci.* 57(2), 438.

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Table 1: Ranking of models describing morality and emigration of juvenile red king crab in experimental plots using Akaike's Information Criterion corrected for small sample size (AIC_c). Models contained parameters for diffusion (D) and mortality (m). Where T is included parenthetically, the parameter was modeled as a linear function of release treatment (release timing). Where t is included parenthetically, it indicates mortality varied with time from release. See methods for full model descriptions. K represents the number of parameters.

Model	K	AIC_c	ΔAIC_c	Likelihood	AIC_c Weight
<i>D,m</i>	2	869.40	80.89	0.00	0.00
<i>D(T),m</i>	4	871.00	82.50	0.00	0.00
<i>D,m(T)</i>	4	868.94	80.44	0.00	0.00
<i>D(T),m(T)</i>	6	861.58	73.08	0.00	0.00
<i>D,m(t)</i>	3	807.24	18.73	0.00	0.00
<i>D(T),m(t,T)</i>	9	788.50	0.00	1.00	1.00

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688 Table 2: Parameter estimates for the best-fit model of red king crab emigration out of experimental
 689 plots and mortality as plotted in Fig 2. See text for model description.

Treatment	D (m² day⁻¹)	m_a	m_b (day⁻¹)
June	0.000022 ± 0.000007	0.134 ± 0.016	-0.041 ± 0.007
August	0.000581 ± 0.000002	0.0494 ± 0.0077	-0.012 ± 0.0058
September	0.00178 ± 0.0000005	0.077 ± 0.035	-0.032 ± 0.029

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704 Table 3: Models of predation rates, p , on tethered, hatchery-reared red king crab ranked by Akaike's
 705 Information Criterion corrected for small sample size (AIC_c). Parenthetical factors indicate that p was
 706 modeled as a linear function of the indicated factors. Factors included T : release treatment (June,
 707 August, or September), M : calendar month of the tethering experiment (July, August, or October), and t :
 708 time of day (day or night). An x indicates inclusion of an interactive effect. An $*$ indicates a *post hoc*
 709 model where the predation rates in June and July did not differ. See text for full model details.

Model	K	AIC_c	ΔAIC_c	Likelihood	AIC_c Weight
p	1	114.68	16.47	0.00	0.00
$p(T)$	4	116.58	18.37	0.00	0.00
$p(t)$	2	110.18	11.97	0.00	0.00
$P(M)$	3	103.01	4.80	0.09	0.06
$p(M,t)$	4	100.50	2.29	0.32	0.20
$p(M^*,t)$	3	98.21	0.00	1.00	0.63
$p(M,t,M \times t)$	6	104.34	6.13	0.05	0.03
$p(T,M)$	6	104.07	5.87	0.05	0.03
$p(T,t)$	5	110.28	12.07	0.00	0.00
$p(T,M,t)$	7	103.28	5.07	0.08	0.05

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712 Table 4: Estimated sources of mortality and cumulative mortality for releasing crabs at different times.
 713 Holding mortality is estimated from (Daly et al., 2009) for each of two holding periods. Initial release
 714 mortality and post-release mortality are estimated from this study. Days post-release indicates the
 715 number of days included in the estimate of post-release mortality. Total is estimated percent mortality
 716 over the same 180-day period for each treatment.

	June	August	September
Holding mortality (C1-C3, 42 days)	-	47.1%	47.1%
Holding mortality (C3-C6, 48 days)	-	-	62.0%
Initial release mortality	41.5%	66.3%	49.6%
Days post-release	180	132	90
Post-release mortality	96.5%	96.3%	90.0%
Total survival	2.0%	0.7%	1.0%

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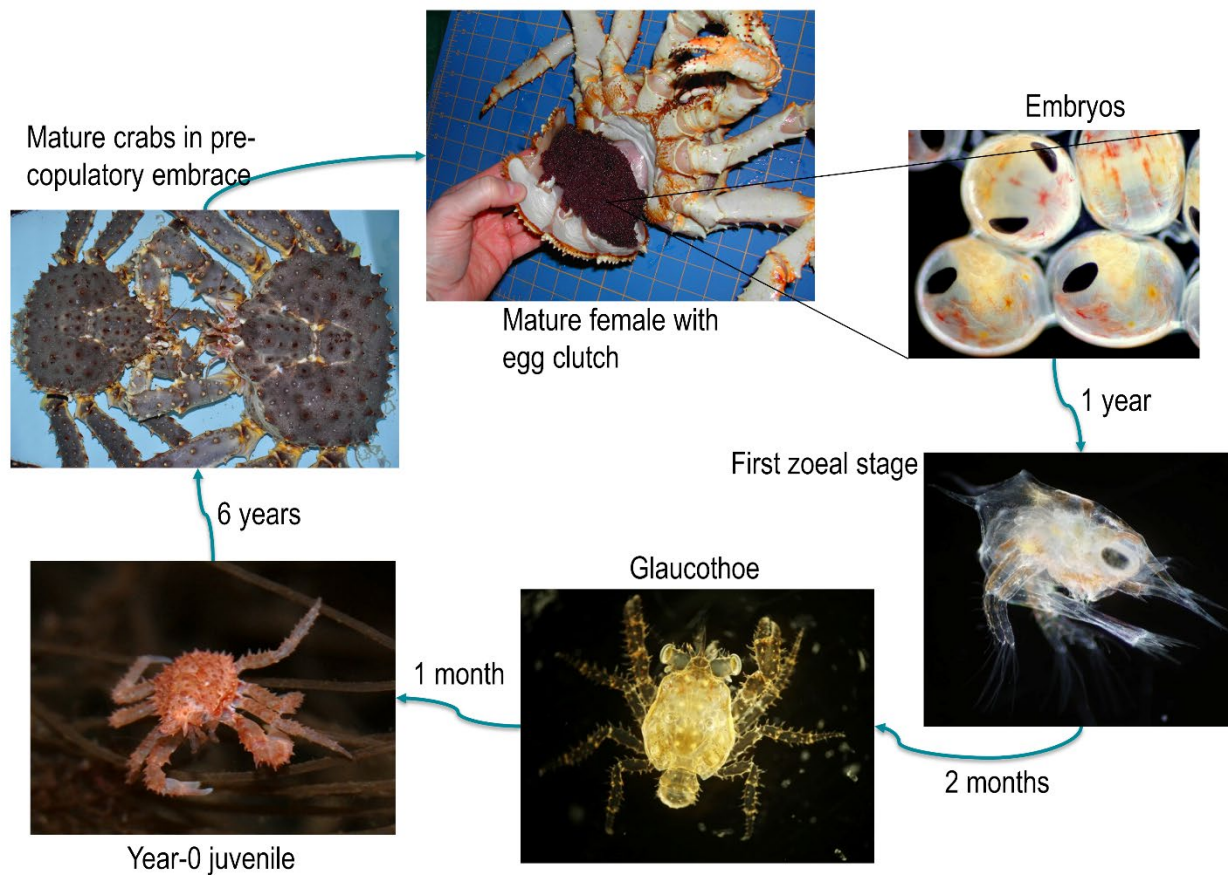
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729 Figure 1: Red king crab life history. Each life history stage is labeled and the approximate time between
 730 stages is indicated. Year-0 crab is approximately the size of the crabs used in this study. (Image credit:
 731 Mature female and glaucothoe- S. VanSant, NOAA Fisheries; remaining images- WCL)

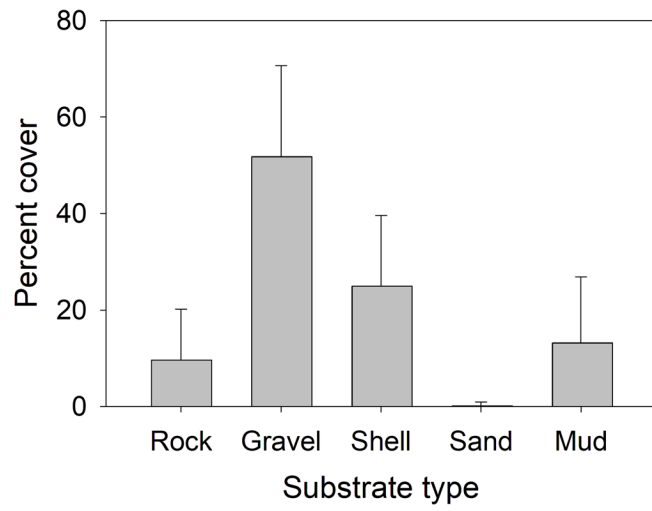
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738 Figure 2: Average percent cover of substrate categories in experimental plots. Bars represent the mean
739 and the error bars one standard deviation.

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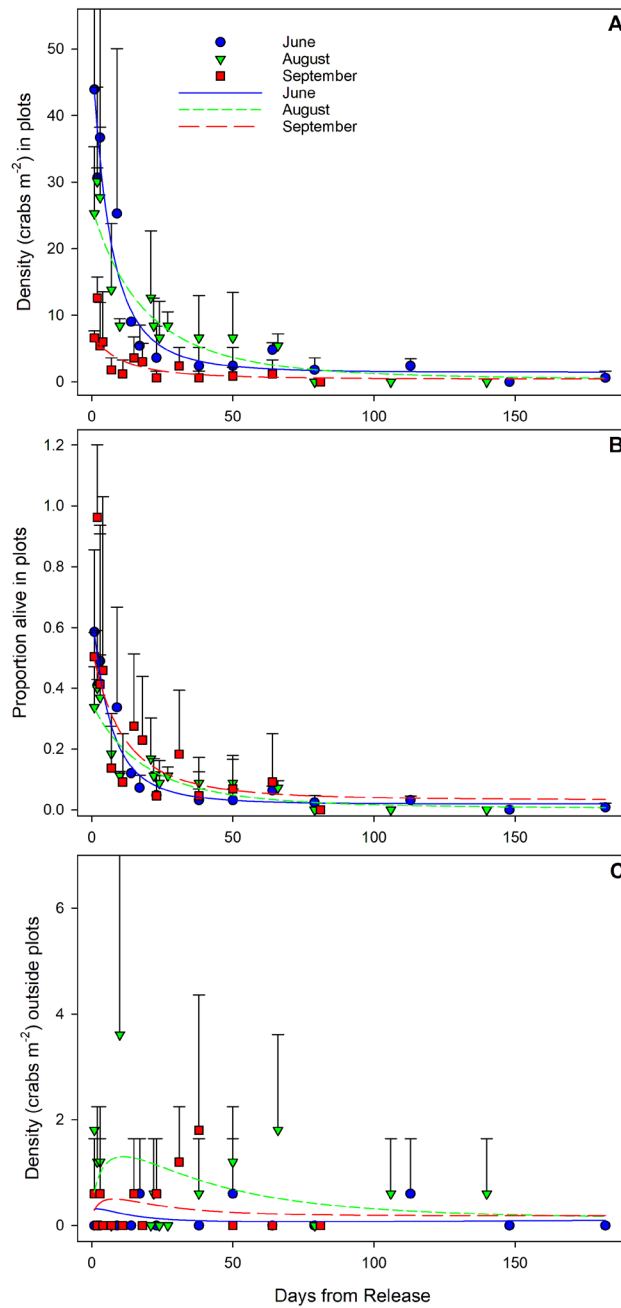
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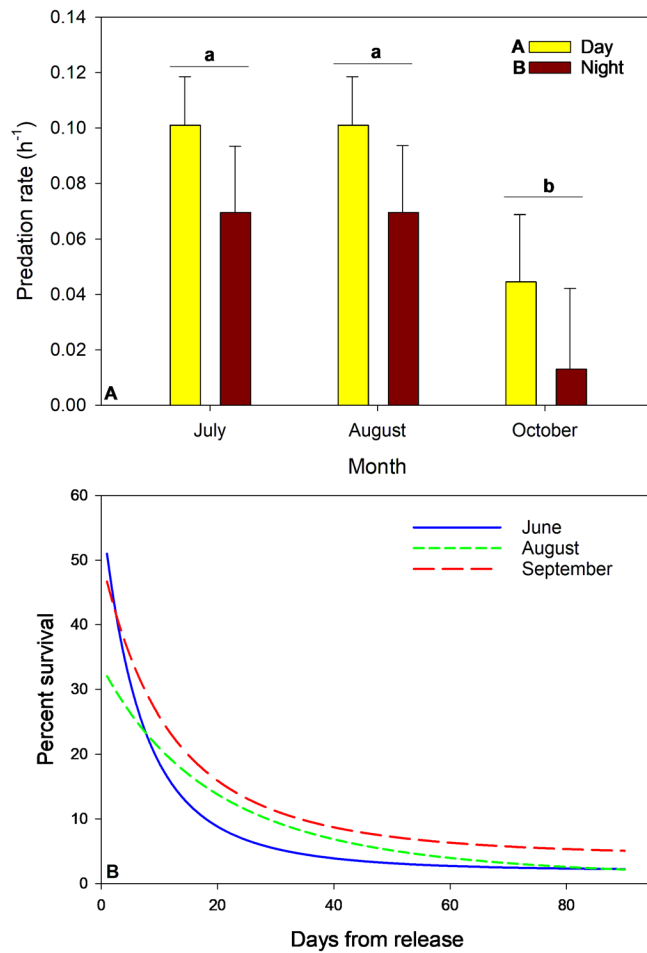
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751 Figure 3: Change over time in density (A) and proportion of initial release (B) and density outside plots

752 (C) of red king crab juveniles released into experimental plots at three different times. Points show the

753 mean counts and error bars are plus one standard deviation. Lines represent the best-fit models (see

754 text for description). Parameter estimates are given in Table 2.



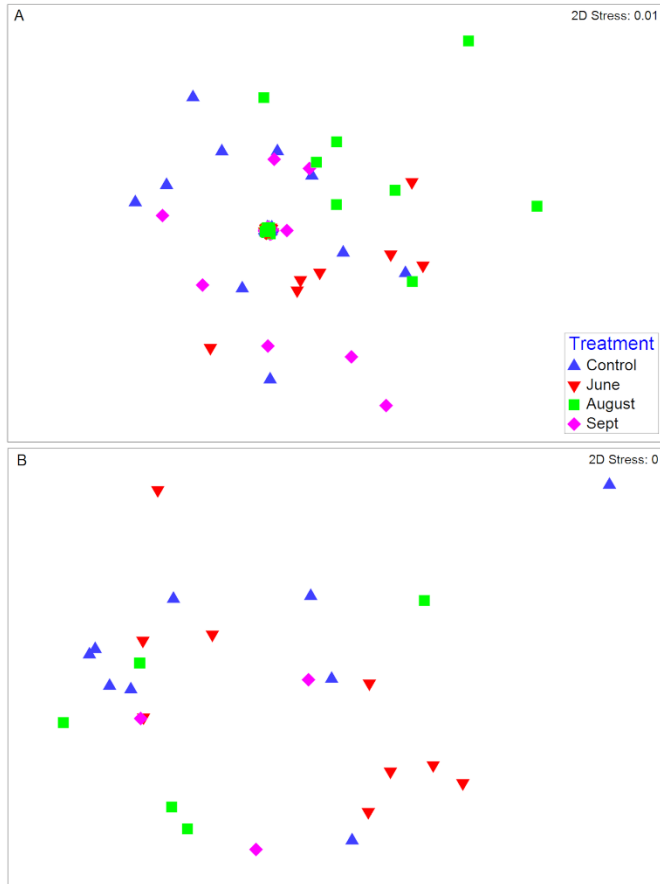
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756 Figure 4: A) Predation rates on tethered, hatchery-reared red king crab juveniles. Bars are mean plus
 757 one standard error. Month represents calendar month the crabs were tethered (not the release month
 758 treatment). Light bars represent predation rate during the day, and dark bars the predation rate during
 759 the night. Factors that differed in the best-fit model (Table 3) are indicated with different letters. B)

760 Overall survival of crabs in each of the three release periods, including the observed initial mortality and
 761 mortality predicted by the best-fit model (see Table 2 for parameter estimates).

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765 Figure 5: Non-metric, multidimensional scaling plots of predator assemblages on and around
766 experimental release plots in juvenile red king crab enhancement experiments. Assemblages included
767 A) Smaller, less mobile predators in quadrat counts and B) larger, more mobile predators in transect
768 counts. Different symbols represent different release treatments.