

1 **Comparative predator-mediated habitat use in early juvenile southern Tanner crab (*Chionoecetes***
2 ***bairdi*), snow crab (*Chionoecetes opilio*), and red king crab (*Paralithodes camtschaticus*)**

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11 Abstract

12 Despite declining populations, southern Tanner crab (*Chionoecetes bairdi*), snow crab
13 (*Chionoecetes opilio*) and red king crab (*Paralithodes camtschaticus*) support economically important
14 fisheries in the Gulf of Alaska and the southeastern Bering Sea. In the southeastern Bering Sea these
15 crab species have distinct although overlapping habitats. Juvenile snow crab, a stenothermic arctic
16 species, are concentrated in waters below 2 °C, in contrast distributions of Tanner crab and red king crab
17 which occupy much wider thermal ranges. Other aspects of the habitat associations of early benthic
18 stages of *Chionoecetes* spp. have not been extensively studied. We describe habitat selection and
19 predation avoidance strategies of early benthic stages (C1-C4) of Tanner crab, snow crab, and red king
20 crab with experiments examining (1) sediment grain size distributions, (2) burial behavior and (3) use of
21 emergent benthic habitat structure (artificial worm tubes) in response to a predator presence, and (4)
22 effect of worm tube density on the survival of age-0 Tanner crabs in the presence of predatory juvenile
23 Pacific cod (*Gadus macrocephalus*) and age-1 Tanner crab. Tanner crabs were the only species that
24 exhibited a clear sediment association, selecting silty muds to fine sand rather than larger sands and
25 pebbles. Tanner and snow crabs buried deeper in sandy mud than in fine sand and both species
26 significantly increased burial behavior in response to introduction of a cod predator. Conversely, red
27 king crabs did not exhibit burial behavior even in the presence of a predator. Early juvenile Tanner and
28 red king crabs displayed strong affinity for emergent structure, while snow crabs were evenly distributed
29 between emergent structure and bare sand habitats. Contrary to expectations, crab selection of
30 emergent structure was not significantly influenced by a cod predator presence. In trials with actively
31 foraging predators, survival of juvenile Tanner crabs was higher in worm tube habitat. Our results
32 demonstrate that early juvenile Tanner and snow crabs use burial behavior as the first line of
33 avoidance/defense, while red king crabs rely upon occupancy of structurally complex habitat. Tanner
34 crab affinity for worm tube structure may facilitate foraging in addition to serving as a refuge. Snow

35 crabs settle on organically rich, fine sediments with little to no emergent structure in the eastern Bering
36 Sea and may benefit from reduced predation pressure in cold waters, suggesting the importance of low
37 temperature as a critical habitat feature for this species.

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39 Keywords: habitat selection, predation, eastern Bering Sea

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41 **1. Introduction**

42 Since the 1970s, stocks of southern Tanner crab (*Chionoecetes bairdi*, hereafter “Tanner crab”),
43 snow crab (*Chionoecetes opilio*), and red king crab (*Paralithodes camtschaticus*) have declined
44 dramatically in the eastern Bering Sea. Overexploitation, environmental regime shifts, and predation
45 affecting juvenile recruitment success appear to have contributed to decreasing population levels
46 (Orensanz et al., 1998; Orensanz et al., 2004; Lang et al., 2018). Despite these declines, commercial crab
47 catches have continued to support an important fishery in Alaska with annual revenues of over \$200
48 million (Garber-Yonts and Lee, 2021). While the geographic ranges of these species vary, adult
49 populations support overlapping fisheries in the southeastern Bering Sea (SEBS). The SEBS represents
50 the southernmost range of snow crab, a stenothermic, arctic species that primarily inhabits deep, cold
51 waters (-1.5 to 5 °C). In contrast, the SEBS is the northernmost range of congeneric Tanner crab, a
52 subarctic species, which also occurs in the Gulf of Alaska (GOA) and extends as far south as Puget Sound,
53 WA with temperature tolerances of 2 to 12 °C (Ryer et al., 2016; Murphy, 2020). Red king crab, an
54 anomuran crab, is found in the Bering Sea and the GOA south to British Columbia, Canada

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57 From a fisheries perspective, it is important to understand the ecological drivers that influence
58 cohort strength and the role of juvenile nursery habitats in population productivity (Ernst et al., 2012).

59 Warming of the SEBS is resulting in community level changes including northward shifts of arctic and
60 subarctic species (Mueter and Litzow, 2008) including snow crab (Fedewa et al., 2020; Szuwalski et al.,
61 2021). Another such species, Pacific cod, is expanding northward with warmer bottom temperatures
62 resulting in increasing spatial overlap with snow crab (Orensanz et al., 2004; Zheng and Kruse, 2006;
63 Fedewa et al., 2020). Pacific cod are primary consumers of juvenile Tanner crab and prey heavily on
64 juvenile snow crab in this region (Livingston, 1989). Pacific cod predation, in conjunction with increasing
65 bottom seawater temperatures, is believed to be contributing to the northward shift of snow crab
66 distribution and limiting their recovery (Orensanz et al., 2004). Understanding nursery habitat
67 requirements of these crab species is critical to predicting species abundances and distributions in the
68 face of shifting thermal and biological conditions.

69

70 *Chionoecetes* spp. is limited. In the Bering Sea, early benthic stages of Tanner crabs are found on the
71 outer shelf at depths > 100 m where temperatures are generally > 2 °C and sediments are dominated by
72 sand mixed with gravel (Smith and McConnaughey, 1999; McConnaughey and Smith, 2000; Ryer et al.
73 2016). Annual melting of sea ice on the Bering Sea results in the formation of the “cold pool” (near
74 bottom temperatures < 2 °C) over the shelf at depths of 50-100 m (Orensanz et al., 2004) where early
75 juvenile snow crabs are most abundant (Zheng et al., 2001; Copeman et al., 2021). In addition, seasonal
76 stratification and high productivity of the surface waters over the middle shelf result in organically rich
77 sand and mud substrates (Smith and McConnaughey, 1999; McConnaughey and Smith, 2000). Juvenile
78 red king crab use the shallowest habitats of the three species, commonly found at depths of 20-60 m in
79 the GOA and SEBS. In coastal waters of the GOA, Tanner crabs have been associated with biogenic
80 benthic structure (Ryer et al. 2016) and red king crabs are often associated with rocks, shell hash or a
81 variety of biological covers (Loher and Armstrong, 2000). The availability and distribution of these
82 emergent benthic features is not well characterized on the Bering Sea shelf and the affinity of juvenile

83 snow crab for such habitat features is not known. As such the potential importance of benthic habitat
84 structures to juvenile crab nursery areas in the Bering Sea remains largely unknown.

85 Marine benthic organisms employ a variety of related anti-predation strategies for survival
86 including behavioral (e.g., habitat selection and sheltering) and morphological defenses (e.g., claw, shell,
87 and spines). Many benthic crustaceans avoid predation by associating with structurally complex habitats
88 that serve as refuges. Juvenile spiny lobster (*Panulirus argus*; Herrnkind and Butler, 1986), Dungeness
89 crab (*Cancer magister*; Fernández et al., 1993), and blue crab (*Callinectes sapidus*; van Montfrans et al.,
90 2003) actively select complex habitats, providing shelter from predators. Similarly, juvenile red king crab
91 are known to prefer structurally complex habitats such as highly branched macroalgae, bryozoans, and
92 hydroids as a refuge from predators, relying on immobility and crypsis to further reduce predation risk
93 (Babcock et al., 1988; Stoner, 2009; Pirtle et al., 2012). In the GOA, where early juvenile Tanner crabs
94 inhabit worm tube habitats, it is unknown whether the crabs select this habitat to mediate predator-
95 prey interactions or if the crabs and tube-forming *Sabellides sibirica* have shared preferences for other
96 aspects of habitat (i.e., depth and substrate; Ryer et al., 2015).

97 In addition to inhabiting structurally complex habitats, benthic crustaceans can also use burial to
98 mediate predator-prey interactions (Davis et al., 2004). Since both Tanner and snow crab lack dermal
99 spines, they may have a tendency to bury as the first line of defense. Older Tanner crabs are known to
100 bury in muddy and sandy substrates and both species may settle in nursery habitats consisting of
101 organically rich fine sediments (Stevens et al., 1994; Rosenkranz et al., 1998; Moles and Stone, 2002).
102 The literature for early juvenile snow crab habitat associations is mainly from the Gulf of Saint Lawrence
103 and emphasizes the importance of temperature in mediating predation risk (Brethes et al., 1987; Conan
104 et al., 1996; Dionne et al., 2003).

105 In the present study, we examined the behavior and habitat selection of early benthic stages (C1
106 – C4) of Tanner crab, snow crab, and red king crab in a series of laboratory experiments. Specifically, we

107 examined sediment grain size associations, burial behavior (in two sediments), and selection of worm
108 tube habitat (using an artificial worm tube mimic). In addition, we examined the effect of predator
109 presence (juvenile cod) on burial behavior and use of worm tube habitat. Finally, we examined the
110 effect of artificial worm tube presence and density on the survival of age-0 Tanner crabs in the presence
111 of predatory juvenile Pacific cod and age-1 Tanner crab. Based on observed distributions in the field, we
112 hypothesized that Tanner and snow crabs would select finer sediments (mud-sand) and that red king
113 crab would select larger grain sizes. We also hypothesized that Tanner and snow crabs would exhibit
114 burial as an anti-predator behavioral response and that red king crab would exhibit an association with
115 artificial worm tube structures. Finally, we predicted that the presence and density of worm tubes would
116 affect crab survival in the face of both piscine and crustacean predators.

117

118 **2. Methods**

119 **2.1. Experimental Animals**

120 All laboratory trials were conducted at the Alaska Fisheries Science Center (AFSC) laboratory at
121 Hatfield Marine Science Center (HMSC) in Newport, OR. All behavioral experiments were conducted
122 between 2010 and 2016 based on the availability of each species. Experiments for each species used
123 identical procedures and were conducted in the same experimental apparatus. All crabs used in habitat
124 and behavior trials were post-metamorphic juveniles, with stages referring to the number molts
125 completed in the juvenile stage (including the transition from megalopa to juvenile); that is, C2 refers to
126 a crab that completed one molt following the juvenile transition. Stage C2 Tanner crabs were collected
127 from depths of 10-30 m near Kodiak Island, Alaska, using an epibenthic sled (Ryer et al., 2015). Tanner
128 crabs were shipped in seawater in insulated containers (4-8 °C) to HMSC within 24 hours. Following
129 shipment, crabs were reared in 0.75-m square polyethylene tanks with 0.5 cm of sand on the bottom
130 and supplied with 8 °C filtered seawater. Tanner crabs were fed daily for the first 2 weeks, after which

131 feeding was reduced to 3×/week; crabs were fed a combination of finely chopped capelin, squid and
132 krill.

133 Age-0 snow crabs were cultured from the egg stage at HMSC due to the inability to collect early
134 juvenile crabs from the field. Ovigerous females were collected in the vicinity of the Pribilof Islands
135 during AFSC's annual groundfish assessment survey. They were transported to HMSC in coolers layered
136 with burlap and frozen ice packs. Adult snow crabs (50.47-60.52 mm CW) were held in a 3-m diameter
137 insulated fiberglass tank supplied with 5 °C filtered seawater and fed chopped capelin and clam
138 2×/week. Embryonic development was examined once a month to determine initial larval release. As
139 embryonic development neared the final stage, adult snow crabs were isolated in 11.7-L clear,
140 rectangular enclosures. After hatching, zoea were siphoned from the enclosures, acclimated to 9 °C, and
141 transferred to 1-L containers for larval culture. Larval culture was modeled after Yamamoto et al. (2014)
142 with stocking densities of 20-40 zoea/L and daily water exchanges with filtered (< 1 µm) 9 °C seawater.
143 Larvae were fed daily with *Artemia* nauplii enriched with Selco S.presso (INEV Aquaculture, Inc., Salt
144 Lake City, UT). Dihydrostreptomycin sulfate at 20 mg/L was added to each beaker at the time of *Artemia*
145 feeding to prevent bacterial growth. When crab larvae molted to C1 stage (2.50-3.25 mm carapace
146 width, CW), they were transferred to 1-m diameter grow-out tanks at 5 °C and fed a diet of finely
147 chopped clam, capelin, and krill 3×/week.

148 Red king crabs were supplied by the Alutiiq Pride Shellfish Hatchery in Seward, Alaska (see
149 Stoner et al., 2010 for details on larval culture). C1 crabs (1.92-2.11 mm CW), ~4 days post-settlement,
150 were shipped in seawater in insulated containers (4-5 °C) to HMSC. Upon arrival they were acclimated
151 and transferred to 80-L rectangular polyethylene tanks supplied with 8 °C filtered seawater. Crabs were
152 held in groups of ~200 and fed daily with frozen copepods (Cyclop-Eeze, Argent Chemical Laboratories,
153 Redmond, WA) and high-protein dry pellets (Otohime, Marubeni Nisshin Feed Co., Tokyo, Japan).

154 Known predators of these juvenile crab species include Pacific cod, Arctic cod (*Boreogadus*
155 *saida*), and older crabs (Livingston, 1989; Lønne and Gulliksen, 1989). Age-1 Pacific cod and Arctic cod
156 were used as predators in experiments. Juvenile Pacific cod and Arctic cod were collected near Kodiak
157 Island and Prudhoe Bay, respectively, and shipped and reared according to Laurel et al. (2016). In
158 addition, some age-0 Tanner crabs were reared for 1 year for use as predators in the predator
159 consumption experiments (at sizes of 21.5–32.4 mm CW).

160 **2.2. Sediment Association Experiment**

161 Juvenile crabs were tested for sediment associations under static seawater conditions in a
162 temperature-controlled room at 9 °C in circular 19-L (25 cm D) tanks with seven equal wedges of
163 different sediment types 20 mm deep. Consistent with Stoner and Ottmar (2003), sediment
164 classifications were pebbles (mean grain size of ~10 mm), granules (2-4 mm), coarse sand (1 mm),
165 medium sand (0.5 mm), fine sand (0.2 mm), muddy sand (~0.1 mm), and sandy mud (~0.04 mm).
166 Pebbles and granules were sorted river gravel; coarse, medium and fine sands were silica sand #16, #30,
167 and #70, respectively. Fine sand was mixed with diatomaceous earth to create muddy sand (7:3) and
168 sandy mud (3:7). All sediment materials were obtained from local suppliers, washed, and presumed to
169 have little to no organic content. Sediment types were arranged haphazardly in the experimental tanks.
170 Fluorescent lighting directly above experimental tanks provided light levels of $2-3 \times 10^{-1} \mu\text{mol m}^{-2} \text{s}^{-1}$ from
171 0600 to 2200 h.

172 Sediment association experimental protocols generally followed those of Stoner and Ottmar
173 (2003). Crabs to be tested were fed in the holding tank ~ 5 h prior to transfer to an experimental tank at
174 1300-1500 h. An individual crab was released at the center of the tank (where all sediments are in close
175 proximity). The following day, observations of crab location were made at 0800, 1000, and 1200 h. After
176 the observations, each crab was captured and photographed under a dissecting microscope to confirm
177 molt stage. Carapace width was measured from the photograph with the Image-Pro Plus v. 7.0 software

178 program (Media Cybernetics, Inc., Rockville, Maryland, USA). See Table 1 for molt stages, sizes, and
179 number of replicate trials conducted for each experiment and species. We used a log-likelihood test (G-
180 test) to determine the effects of molt stage on sediment occupancy within each species and to compare
181 sediment associations between species. The observed frequency distribution of sediment occupancy
182 was tested against the null hypothesis of an even distribution for each species with an extrinsic
183 hypothesis G-test.

184 **2.3. Burial Behavior Experiment**

185 A separate set of experiments examined the burial behavior of juvenile crabs and the influence
186 of predator presence on burial (Table 1). Due to availability of appropriately sized fish in the laboratory
187 at the time of experiments, age-1 Pacific cod (135-167 mm total length TL) were used as predators in
188 Tanner crab and red king crab trials and age-1 Arctic cod (133-160 mm TL) were used in snow crab trials.
189 Trials were conducted in 1-m diameter tanks supplied with 8 °C filtered seawater. Test tanks had a 20-
190 mm deep layer of fine sand or sandy mud (as defined above) and the two sediment types were
191 interspersed among four replicate tanks used in the trials.

192 The day before each trial, crabs were fed in the morning in the holding tanks. At ~ 1500 h, 10
193 individuals were captured and introduced to the center of each experimental tank and allowed to
194 acclimate and redistribute throughout the tank overnight. The following day, predators were fed to
195 satiation in their holding tanks at 0900 h to prevent predation of crabs during the trials (only 2 of 680
196 crabs were not recovered). Crab burial in the absence of predators was scored at 1000, 1020, and 1040
197 h. Predators were introduced at 1100 h and crab burial was scored again at 1120, 1140, and 1200 h.
198 Burial was scored for each crab at each time interval. Body burial index was scored on a scale of 1 to 4
199 with the rankings of 1: crab on top of the sediment, 2: carapace partly recessed in a depression or the
200 posterior end nestled in the sediment, 3: top of the carapace flush with the sediment surface and 4: >
201 1/3 of carapace covered with sediment. After the last observation, the predator was removed and crabs

202 were recovered. The smallest and largest crabs from each replicate trial were measured (CW) with
203 digital calipers. Red king crabs were often observed clinging to the walls of the tank above the sediment
204 surface; this was rarely observed in snow crabs and not observed with Tanner crabs. These were
205 excluded from the statistical analyses of burial behavior. Replicate trials were conducted on each
206 sediment type with each stage of Tanner crabs and snow crabs and pooled stages of red king crabs
207 (Table 1). The mean burial index at each observation point in each trial was used as the observation in
208 statistical analyses. The effects of sediment type, stage, and period (and their interactions) on Tanner
209 crab burial behavior were tested using a repeated measures ANOVA and post-hoc Tukey's multiple
210 comparisons (Sokal and Rohlf, 1969). Snow crab burial data did not meet assumptions of normality and
211 homoscedasticity. Therefore, Friedman's test was applied in tests with all 1-6 burial observation periods.
212 Log-transformed values were used in ANOVA tests with data from observation periods 4-6. Statistical
213 analyses were not performed on red king crab data due to a lack of burial behavior throughout the
214 experiment.

215 **2.4. Worm Tube Structure Association Experiment**

216 A third set of experiments was conducted to examine the association of juvenile crabs with
217 structured habitat and the influence of predation risk. These trials were performed in the same manner
218 as the burial behavior experiment except for the inclusion of artificial worm tube habitat on one half of
219 the tank area. The artificial worm tube structure was designed to closely mimic natural worm tubes
220 found in Tanner crab habitats in the Gulf of Alaska (Stoner et al. 2007; Ryer et al. 2015). The artificial
221 worm tubes were constructed from black, 2-mm diameter surgical tubing attached to a flat rubber mat
222 at a density of 60 tubes/m². The rubber mat was buried under the sand such that each tube extended 8
223 cm above the sediment surface. The sand depth allowed for the crab to bury completely.

224 At each observation interval, crab location ("bare" sand vs. worm tube habitat) and burial index
225 were recorded. The statistical analyses of the observed frequency distribution in sand versus worm tube

226 habitat included observations of crabs clinging to the tank wall, but these were excluded from the burial
227 behavior analyses. For crabs in the worm tube habitat, we recorded the precise position of the crab
228 relative to the worm tube structure (on sediment surface between worm tubes; on the sediment surface
229 in contact with worm tube structure; on the worm tube structure). Tanner crab and red king crab molt
230 stages were combined in each trial; snow crabs were tested separately at C2 and C3 molt stages (Table
231 1). The observed frequency distribution in sand versus worm tube habitat within each species was
232 tested with an extrinsic hypothesis G-test. As above, time period and stage effects on habitat occupancy
233 were tested with a log-likelihood test (G-test); burial scores were tested for normality and
234 homoscedasticity and main effects tested with ANOVA or a Friedman's test. Again, statistical analyses
235 were not performed on red king crab burial data due to a lack of burial behavior throughout the
236 experiment.

237 **2.5. Predation Vulnerability Experiments**

238 In a final set of experiments, we tested effects of habitat structure on the survival of juvenile
239 Tanner crabs in the presence of age-1 Pacific cod and Tanner crab predators. Experiments were
240 conducted with 4 different habitat treatments in 1-m diameter tanks. Habitat treatments were bare
241 tank bottom, a 20-mm layer of fine sand, sparse worm tubes (60 tubes/m²), and dense worm tubes (870
242 tubes/m²). The artificial worm tube structures were as described above. When present, worm tubes
243 covered the entire area of the tank and were embedded in a 20-mm layer of fine sand.

244 The day prior to predation trials with Pacific cod predators, a clear, acrylic ring (72-cm diameter
245 with 5-mm holes in the sides for seawater circulation) was placed in the center of the tank. Twenty C3
246 Tanner crabs were transferred inside the ring and two age-1 cod were placed outside (separating the
247 predators from the prey) in total darkness at approximately 1600 h. To standardize predator hunger
248 levels, the cod were deprived of food for 48 h prior to trials and pairs of cod were utilized to elicit social
249 facilitation in foraging behavior (Ryer et al., 2004). On the day of the trial, the lights turned on at 0800 h.

250 After a 2-h acclimation period the acrylic ring was gently removed and the predators allowed to forage
251 on the crabs. After 4 h the predators were removed from the tanks and all surviving crabs were captured
252 and enumerated. Six replicate trials were conducted with each of the four habitat treatments (Table 1).
253 Following the above described times for each trial, we ran two trials each day, with randomly selected
254 substrates. Due to limited numbers of crabs, 8 of 24 trials included surviving individuals from earlier
255 trials. Preliminary analysis showed no overall difference within each habitat treatment in predation of
256 naïve crab prey vs surviving crab from an earlier trial. A total of 16 Pacific cod were used as predators
257 across the trials. Because data did not meet parametric assumptions, effect of habitat on the survival of
258 Tanner crabs was tested with a Kruskal-Wallis ANOVA and significant effects analyzed with a multiple
259 range test (Conover, 1971).

260 The day prior to predation trials with age-1 Tanner crab predators, twenty C2 to C4 Tanner crabs
261 were transferred to the experimental tanks at approximately 16:00 h. The following morning at 10:00 h,
262 two age-1 Tanner crabs were introduced to the center of tanks and immediately allowed to forage.
263 Predators were removed and surviving prey enumerated at 8:00 h the next day for a 22 h foraging
264 period. Illumination was on an 8-h light and 16-h dark cycle. Four replicate trials were conducted for
265 each of the habitat treatments (Table 1). Four trials were performed per day with habitat types
266 randomly selected. Due to limited availability of juvenile Tanner crabs for these experiments, the last
267 two trials of each habitat treatment contained a combination of naïve crabs and surviving individuals
268 from earlier trials; preliminary analysis confirmed that there was no difference in predation rates
269 between trials using naïve and "experienced" crab prey. The number of consumed prey between the
270 habitats was analyzed using ANOVA and Tukey's multiple comparisons (Sokal and Rohlf, 1969).

271

272 **3. Results**

273 **3.1. Sediment Association Experiment**

274 The distribution of crabs across sediments differed between species ($G = 47.52$, $df = 12$, $P <$
275 0.001), with only juvenile Tanner crabs exhibiting a clear sediment association. Tanner crabs were
276 concentrated on the three finest sediments (extrinsic $G = 56.19$, $df = 6$, $P < 0.001$) and infrequently
277 occupied the coarser sediment types (8% of observations; Fig. 1). There was a significant difference in
278 distribution between C3 and C4 Tanner crabs ($G = 13.33$, $df = 6$, $P = 0.038$), with C3 crabs most
279 commonly observed on fine sand (48% of observations) and C4 crabs most commonly found on sandy
280 mud (45% of observations; stage effect not shown, stages pooled in Fig. 1).

281 Conversely, early juvenile snow crabs and red king crabs did not exhibit a significant association
282 with any particular sediment type in these trials (snow crab: extrinsic $G = 3.35$, $df = 6$, $P = 0.764$; red king
283 crab: extrinsic $G = 4.68$, $df = 6$, $P = 0.585$) despite a trend toward occupancy of finer sediments by snow
284 crabs and larger sediments by red king crabs. In addition, there was no significant effect of stage on crab
285 distribution across sediment types in juvenile snow crabs (C2 vs. C3; $G = 11.80$, $df = 6$, $P = 0.067$) or red
286 king crabs (C1 vs. C2; $G = 7.30$, $df = 6$, $P = 0.294$).

287 **3.2. Burial Behavior Experiment**

288 **3.2.1. Tanner Crab**

289 Tanner crabs exhibited more burial behavior than the other species and their degree of burial
290 was affected by molt stage, sediment type, and predator presence (Fig. 2A). C2 crabs buried deeper than
291 C3 crabs (molt stage effect: ANOVA, $F_{(1,20)} = 29.85$, $P < 0.001$) and this difference was more pronounced
292 in sandy mud than in fine sand (molt stage \times substrate interaction: ANOVA, $F_{(1,20)} = 4.59$, $P = 0.045$). Post-
293 hoc tests revealed that highest burial scores of C2 crabs on sandy mud were significantly higher than the
294 other stage and substrate combinations (Tukey, $P > 0.05$; C3 on fine sand were the least buried).
295 Predator presence led to an increase in burial among C3 crabs, but did not change burial status of C2
296 crabs (molt stage \times period interaction, ANOVA, $F_{[5,100]} = 31.76$, $P < 0.001$). C3 crabs responded almost
297 immediately to the predator by burying further into the sediment, as demonstrated by increased burial

298 between periods 3 and 4 (Tukey, $P < 0.05$). There was further modest increase in burial from period 4
299 through 6 (Tukey, $P < 0.05$).

300 **3.2.2. Snow Crab**

301 Across all conditions burial indices for snow crabs were lower than those observed in Tanner
302 crabs (Fig. 2B). In the absence of predators, neither stage of snow crabs exhibited burial behavior on
303 either sediment type (multiple comparisons, $P > 0.05$). Snow crabs, regardless of molt stage or sediment
304 type, responded to predation risk by exhibiting burial behavior (Friedman ANOVA, $P < 0.05$ for each).
305 When exposed to the predators, C3 snow crabs increased burial more than C2 crabs (molt stage effect:
306 ANOVA, $F_{(1,28)} = 41.19$, $P < 0.001$) and snow crabs buried more deeply in sandy mud than in fine sand
307 (substrate effect: ANOVA, $F_{(1,28)} = 4.76$, $P = 0.038$). There was no significant interaction between molt
308 stage and substrate (ANOVA, $F_{(1,28)} = 3.09$, $P = 0.090$) or between substrate and period ($F_{(2,56)} = 1.51$, $P =$
309 0.229) on snow crab burial.

310 **3.2.3. Red King Crab**

311 Unlike Tanner and snow crabs, red king crabs rarely displayed any burial behavior and burial was
312 not affected by sediment type or predator presence (Fig. 2C).

313 **3.3. Worm Tube Structure Association Experiment**

314 **3.3.1 Tanner Crab**

315 When given a choice between artificial worm tube habitat and bare sand, early juvenile Tanner
316 crabs exhibited a strong association with the worm tube habitat (Fig. 3A; extrinsic $G = 118.59$, $df = 1$, $P <$
317 0.001). This association with worm tubes was not influenced by predator presence ($G = 0.46$, $df = 5$, $P =$
318 0.9935). Interestingly, although Tanner crabs were found within the worm tube habitat, they remained
319 on the sediment surface. Only 2 of 79 crabs actually climbed up worm tubes. The majority of the Tanner
320 crabs (73%) in the worm tube habitat were positioned with the posterior margin of their carapace in
321 contact with the base of a worm tube. Tanner crabs in worm tube habitats and those remaining in the

322 sand habitat increased their degree of burial in response to the introduction of the predator (repeated
323 measures ANOVA, $F_{[5,70]} = 14.31$, $P < 0.001$) but there was no interaction between habitat type and
324 predator presence on burial index (ANOVA, $F_{[5,70]} = 0.93$, $P = 0.4669$).

325 **3.3.2. Snow Crab**

326 Unlike Tanner crabs, snow crabs were evenly distributed between artificial worm tube habitat
327 and the bare sand habitat (pooled molt stage and periods, extrinsic $G = 1.95$, $df = 1$, $P = 0.163$). Although
328 C2 crabs showed a tendency to associate with the worm tubes (extrinsic $G = 4.07$, $df = 1$, $P = 0.044$),
329 while C3 crabs did not, this difference between stages was not significant (Fig. 4A and B; $G = 2.11$, $df = 1$,
330 $P = 0.146$). Neither stage of snow crabs shifted their habitat association following introduction of the
331 predator ($G = 1.88$, $df = 5$, $P = 0.865$). Among the snow crabs located in the worm tube habitat, all were
332 associated with the sediment and did not climb onto the worm tube structures. C2 crabs (59%) showed
333 a tendency to be in physical contact with the base of the worm tubes, whereas the majority of C3 (63%)
334 were positioned between but not in physical contact with the base of the worm tubes. Across molt
335 stages in both habitats, snow crabs responded to a predator by burying more deeply between periods 3
336 and 4 (Fig. 4B and 5B; Friedman ANOVA, $P < 0.05$; multiple comparisons, $P < 0.05$).

337 **3.3.3. Red King Crab**

338 As observed in Tanner crabs, red king crabs exhibited a strong association with the worm tube
339 habitat over the bare sand habitat (Fig. 5A; extrinsic $G = 116.97$, $df = 1$, $P < 0.001$). Predator presence
340 reinforced this association, increasing occupancy of worm tube habitat by ~10% (Fig. 5A), although this
341 effect was not significant ($G = 3.25$, $df = 5$, $P = 0.6615$). Unlike Tanner and snow crabs, most juvenile red
342 king crabs in the worm tube habitat climbed up on the worm tube structures: 71% of red king crabs in
343 the worm tube habitat were not in contact with the sediment. Red king crabs that remained on the
344 sediment surface (not on worm tubes) did not bury, and burial index was not affected by the presence
345 of the predator (Fig. 5B).

346 **3.4. Predation Vulnerability Experiments**

347 Predation mortality of early juvenile Tanner crabs was modulated by worm tube density (Fig. 6).
348 In trials with Pacific cod, survival of crabs increased with increasing density of worm tubes (Kruskal-
349 Wallis, $P = 0.002$) with Tanner crab in the dense worm tube habitat suffering no predation mortality.
350 Predation mortality in the sparse worm tubes was 23% lower than that observed in the bare tank and
351 sand treatments, but this difference was not significant (multiple range test, $P > 0.05$). The presence of
352 sand alone reduced mortality by only 5% from that observed with the bare tank bottom (multiple range
353 test, $P > 0.05$). The effect of the worm tubes on crab mortality appeared at least in part due to an effect
354 of the habitat structure on the behavior of the Pacific cod predators. In trials with no habitat (bare tank
355 bottom), bare sand, and sparse worm tubes, Pacific cod swam close to the tank bottom and periodically
356 rested on the bottom. In trials with dense worm tubes, Pacific cod tended to swim above the worm tube
357 structures and their ability to approach the bottom was obstructed by the dense worm tube habitat.

358 Worm tube structure also reduced predation mortality of juvenile Tanner crab by older, age-1
359 Tanner crab (ANOVA, $F_{[3,12]} = 12.9$, $P = 0.0005$). Mortality in the high-density worm tube habitat was
360 significantly (74.5%) lower than in the bare tank bottom and bare sand habitats (Tukey, $P < 0.05$).
361 Mortality in the low-density worm tube habitat was 43% lower than in the sand and bare habitats, but
362 this difference was not significant (Tukey, $P > 0.05$). As seen above, the presence of sand did not reduce
363 predation rates compared to the bare tank bottom (Tukey, $P > 0.05$). As observed, with the Pacific cod
364 predators, the worm tube habitat affected the mobility and presumed access of the age-1 Tanner crab
365 predators to the smaller juvenile crab prey. In the dense worm tube treatment, age-1 Tanner crabs were
366 suspended on the worm tube structure canopy at vertical angles with only one side of walking legs in
367 contact with the sediment.

368

369 **4. Discussion**

370 Tanner crab, snow crab and red king crab display differing sediment grain size association,
371 degree of burial in sediment, and association with emergent structural habitat features. These
372 behavioral traits, which influence vulnerability to predators, likely reflect differences in the dominant
373 habitat features in their overlapping but distinct distributions in the Gulf of Alaska and Bering Sea. These
374 regions vary from substrates with structurally complex geologic and biogenic features (common to
375 coastal areas in the GOA and inner Bristol Bay) to areas characterized by fine-grained sediment, lacking
376 such emergent structure (offshore in the central and northern Bering Sea). Red king crab and snow crab
377 would appear to occupy the extremes of this association spectrum, with red king crab residing in
378 structurally complex habitats and snow crab associating exclusively with unstructured, fine-sediment
379 benthic habitats. Tanner crab appear to employ a mixed strategy, exhibiting an association with fine
380 sediments but also a willingness to utilize emergent structural features, such as polychaete tube
381 structures, to mitigate predation risk.

382 Field studies have found early juvenile red king crab residing in complex relief/habitats with
383 rocks, shell hash, and biogenic structures such as branched macroalgae, bryozoans, and hydroids
384 (McMurray et al., 1984; Loher and Armstrong, 2000). Structurally complex habitats appear critical for the
385 survival of early benthic red king crab, since they rely on crypsis and reduced activity to avoid predation
386 (Stoner, 2009; Pirtle et al., 2012). Our results are consistent with previous findings confirming attraction
387 of early juvenile stages of red king crab to emergent structures with complex vertical relief (Stevens,
388 2003; Stevens and Swiney, 2005; Pirtle and Stoner, 2010). They also extend the range of body sizes
389 examined for sediment grain size preference in post-settlement red king crab. Interestingly, the small
390 red king crab tested here (1.9 – 2.3 mm CW) showed little association with large grain sizes, but this is
391 consistent with the work of Stoner and Pirtle (2010) who observed weaker associations in small (2 – 4
392 mm CW) than larger (7.5 – 9 mm CW) crabs. Combined, these results suggest the vertical relief aspect as
393 a key feature of habitat complexity for early post-settlement red king crabs.

394 In addition to differences in behavioral habitat selection, red king crab also differ
395 morphologically from *Chionoecetes* spp. which plays a role in their anti-predation strategies. Whereas
396 the *Chionoecetes* spp. have smooth shells, red king crab have spiny armoring of the carapace and
397 appendages, which is common in species in the Lithodidae family. While effective at interfering with
398 consumption by predators (Pirtle et al., 2012), this armoring results in a larger body surface area that
399 may inhibit effective burial.

400 **Habitat associations of *Chionoecetes* spp.**

401 Compared to red king crab, little is known about habitat associations of early benthic
402 *Chionoecetes* spp.; however, adult and larger juvenile (> C5 stage) Tanner crabs are known to associate
403 with fine rather than coarse sediments, and burial of Tanner crabs has been observed in finer substrates
404 (Stevens et al., 1994; Zhou and Shirley, 1997). Consistent with previous studies and hypotheses
405 (Rosenkranz et al., 1998; Moles and Stone, 2002), early juvenile Tanner crabs selected finer sediments.
406 We suspect that Tanner crabs are attracted to sediment types that allow them to bury to avoid
407 predation. We found that C4 stage Tanner crabs occupied finer sediments more frequently than C3
408 stage crabs. This strategy may reflect an ontogenetic change related to sediment-depth relationships in
409 regions where sediment grain sizes are larger inshore than offshore. In the GOA, Tanner crabs settle in
410 shallow water nursery grounds and as they increase in size, they move offshore to finer sediment
411 habitats. In the eastern Bering Sea (EBS), wind-driven advection transport delivers Tanner crab to
412 offshore nursery grounds where fine sediments are the dominant habitat for all demersal life stages
413 (Rosenkranz et al., 1998).

414 Juvenile snow crabs have been shown to associate with muddy sediments in laboratory and field
415 studies in the Gulf of Saint Lawrence (Brethes et al., 1987; Lovrich et al., 1995; Dionne et al., 2003).
416 Consistent with those studies, we observed a tendency for early juvenile snow crabs to occupy sandy
417 mud and muddy sand. In laboratory studies Dionne et al. (2003) concluded that temperature preference

418 overrides sediment preferences in determining C3 stage snow crab distribution, with crabs selecting
419 temperatures of 0 to 1.5 °C. In our experiments, conducted at higher temperatures, the snow crabs'
420 higher activity levels may have resulted in use of a wider array of sediment types.

421 **Burial Behavior**

422 The burial behavior exhibited by juvenile crabs is widely presumed to serve as a mechanism to
423 reduce predation risk (Bellwood, 2002) and has been demonstrated in experiments with lady crabs
424 subject to predation by blue crabs (*Callinectes sapidus*) (Barshaw and Able, 1990). Consistent with this,
425 both Tanner and snow crabs increased their burial depth in response to introduction of a predator. In
426 our experiments however, there was no difference in survival of juvenile Tanner crab when exposed to
427 actively foraging predators in sediment-free tanks (no burial opportunity) and sand-filled tanks (offering
428 a burial opportunity). While this result may suggest questioning the anti-predator value of burial, we
429 believe that this outcome is due to the confined spatial scale of the experiment and forced proximity of
430 the predator and prey. Because of this constraint, the crab prey did not benefit from decreased
431 encounter rates with mobile predators that would be associated with burial in natural settings. Our
432 observations suggest that the benefits of burial behavior in early juvenile *Chionoecetes* spp. are
433 associated with reduced detection and predator encounter rates rather than surviving a predator attack
434 once detected.

435 *Chionoecetes* spp. bury by entering the sediment backwards using the last pair of pereopods to
436 excavate the sediment and pull the body backwards into the sediment, a common mechanical form of
437 burial for brachyurans (M. Ottmar, pers. observ.; Bellwood, 2002). The degree of burial behavior
438 exhibited by crabs is frequently a function of both body size and sediment characteristics. As observed
439 here for Tanner and snow crabs, other smaller bodied crab species have been shown to bury more
440 readily in fine than in coarse sediments (Dugan et al., 2000; Bellwood, 2002; but see Barshaw and Able,
441 1990). Species-specific habitat use has also been linked to specific substrates that allow for burial

442 behavior (McGaw, 2005; Lipcius et al., 2007). The EBS shelf is dominated by soft sediments with mud
443 and sand in the primary habitats of snow crab on the middle shelf and more sand and gravel on the
444 outer shelf where Tanner crab have higher occurrences (Zheng and Kruse, 2006; Copeman et al., 2021).

445 **Emergent Benthic Structure**

446 A variety of juvenile crustaceans are known to preferentially associate with a range of emergent
447 benthic structures. These structures may provide an opportunity for foraging in addition to serving as a
448 refuge from predation. In our study, early juvenile Tanner crab and red king crab, exhibited an affinity
449 for emergent polychaete tube structures. This finding is consistent with field observations in the GOA
450 where Tanner crab distribution coincided with worm tubes of *Sabellides sibirica* (Ryer et al., 2015).
451 Because Tanner crabs are known to feed on polychaetes (Jewett and Feder, 1983), the association with
452 worm tube structures may reduce the costs of potential trade-offs between protection and feeding.
453 Active habitat selection for protection and foraging is observed in other crab species (Iribarne et al.,
454 1995; Perkins-Visser et al., 1996).

455 Burial appears to be the first line of defense for *Chionoecetes* spp. and may be the best strategy
456 for crabs with few other defense mechanisms. However, occupancy of structurally complex habitat also
457 plays a role in reducing predation vulnerability by interfering with a predator's activity and ability to
458 locate, encounter and attack prey (Bartholomew et al., 2000; Ryer et al., 2004; Stoner, 2009). In our
459 laboratory trials, high densities of artificial worm tubes significantly reduced the predation vulnerability
460 of Tanner crabs to both piscine and crustacean predators. This effect was due in part to the habitat
461 structure disrupting the ability of the predator to access the sediment surface to capture benthic crabs,
462 even if they could be located. Similar effects of benthic habitat structure interfering with prey searching
463 behavior have been observed in interactions between juvenile fishes and piscivores (Ryer et al., 2004).

464 Prey may also exhibit specific anti-predator behavioral tactics associated with complex habitats
465 (Main, 1987; Ryer et al., 2004). Whereas red king crabs left the sediment surface, climbing the structure

466 of worm tubes, Tanner crabs partially buried themselves with the posterior margin of their carapace
467 against the base of an individual worm tube. If detected by a predator, this positioning would restrict
468 predators to striking from the anterior and in the event of an attack allow the crab to utilize their chelae
469 to defend themselves. Such habitat-specific behavioral tactics have been described for other species
470 (Main, 1987; Sandt and Stoner, 1993; Weiss et al., 2008), including Caridean shrimp (*Tozeuma*
471 *carolinense*) which shift from swimming between seagrass blades to clinging vertically to seagrass blades
472 to avoid predation. Such shifts in prey behavior in complex habitats may be important contributions to
473 the refuge value by compromising predators' ability to capture prey.

474 **Thermal predation refuges**

475 The lack of attraction to worm tube structure among early juvenile snow crabs was an
476 unexpected outcome of these experiments and may be related to a general lack of such structure in
477 their primary Bering Sea nursery habitats. In the field, early settled snow crabs may not frequently
478 encounter structure in the middle domain of the EBS. Structures such as rhizoid mats and hard
479 substrates are rare in the middle domain at depths of 50-100 m (R. McConnaughey, AFSC, pers. comm.;
480 Haflinger, 1981). However, it has been hypothesized that early benthic snow crabs hide in rafts of
481 macroalgal debris in the EBS (Kruse et al., 2007). Selection of emergent structure and burial by early
482 settled snow crab may be complicated by other habitat characteristics such as temperature dominating
483 their selections (Lovrich et al., 1995; Dionne et al., 2003).

484 Rather than relying upon biogenic benthic structures, post-settlement juvenile snow crab may
485 benefit from the low temperatures of their habitats to mitigate predation risk (Dionne et al., 2003). Early
486 benthic snow crabs are adapted to colder temperatures, unlike congeneric Tanner crabs (Somerton,
487 1981). Snow crab are found in the EBS on the middle shelf at depths of 50-100 m where near-bottom
488 temperatures are below 2 °C (Zheng et al. 2001; Orensanz et al. 2004; Kruse et al. 2007). Juvenile snow
489 crab are preyed upon by a variety of groundfishes including Alaska plaice (*Pleuronectes*

490 *quadrituberculatus*), arrowtooth flounder (*Atheresthes stomias*), and northern rock sole (*Lepidopsetta*
491 *polyxystra*), but Pacific cod appear to be the dominant consumers of juvenile *Chionoecetes* spp. (Zheng
492 and Kruse, 2006). However, these species are concentrated in warmer areas of the EBS and generally
493 avoid the “cold pool” with temperatures of < 2 °C (Zheng and Kruse, 2006; Kotwicky and Lauth, 2013;
494 Stevenson and Lauth, 2019).

495 **Conclusions**

496 Our laboratory results show that *Chionoecetes* and *Paralithodes* spp., with overlapping
497 distributions in the GOA and EBS, exhibited distinct suites of habitat selection and behaviors which are
498 important in mediating predator–prey interactions. Their life histories and survival strategies reflect the
499 patterns of variation in substrate, structure, depth, and temperature in their primary settlement
500 habitats. Early juvenile red king crab occupy structurally complex habitat to reduce predation risk and
501 did not bury, even in the presence of predators. Tanner crab and snow crab employed similar strategies,
502 with burial as their first line of defense against predation. Tanner crab also exhibited a strong
503 association with fine sediments and emergent structure. Despite the demonstrated impact of emergent
504 structures reducing the vulnerability of *Chionoecetes* sp. to predation by both piscine and crustacean
505 predators, snow crab did not strongly associate with these structures. Rather, snow crabs appear to rely
506 on the reduced abundance and consumption rates of predators in near freezing environments. The suite
507 of strategies exhibited by these species suggest that the survival of these populations depend upon the
508 spatial coincidence of particular combinations of habitat characteristics (i.e., substrate, structure,
509 temperature, and depth) (Rosenkranz et al., 2001; Dionne et al., 2003). Future studies should examine
510 how shifting climate conditions may result in shifting distributions of structure-forming invertebrates as
511 well as benthic predators, and the impacts of those shifts on the habitat use and recruitment potential
512 of Alaska commercial crab species.

513

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538 **References**

- 539
- 540 Babcock, M.B., Brodersen, C.C., Rounds, P.A., 1988. Habitat preference in juvenile red king crabs
541 (*Paralithodes camtshatica*). Am. Zool. 28(4):27A.
- 542 Barshaw, D., Able, K., 1990. Deep burial as a refuge for lady crabs *Ovalipes ocellatus*: Comparisons with
543 blue crabs *Callinectes sapidus*. Mar. Ecol. Prog. Ser. 66, 75–79.
544 <https://doi.org/10.3354/meps066075>.
- 545 Bartholomew, A., Diaz, R.J., Cicchetti, G., 2000. New dimensionless indices of structural habitat
546 complexity: Predicted and actual effects on a predator's foraging success. Mar. Ecol. Prog. Ser. 206,
547 45–58. <https://doi.org/10.3354/meps206045>.
- 548 Bellwood, O., 2002. The occurrence, mechanics and significance of burying behaviour in crabs
549 (Crustacea: Brachyura). J. Natl. Hist. 36, 1223–1238. <https://doi.org/10.1080/00222930110048891>.
- 550 Brethes, J.-C.F., Coulombe, F., Lafleur, P.-E., Bouchard, R., 1987. Habitat and spatial distribution of early
551 benthic stages of the snow crab *Chionoecetes opilio* O. Fabricius off the North Shore of the Gulf of
552 St. Lawrence. J. Crustacean Biol. 7, 667. <https://doi.org/10.2307/1548650>.
- 553 Conan, G.Y., Starr, M., Comeau, M., Therriault, J.C., Robichand, G., Hernández, F.X.M., 1996. Life history
554 strategies, recruitment fluctuations, and management of the Bonne Bay Fjord Atlantic snow crab
555 (*Chionoecetes opilio*), p. 59-97. In: Proceedings of the International Symposium on Biology,
556 Management and Economics of Crabs from High Latitude Habitats, October 1995, Anchorage,
557 Alaska. Lowell Wakefield Fish Symposium Series, Alaska Sea Grant College Program Report No. 96-
558 02, University of Alaska Fairbanks, Fairbanks, AK.
- 559
- 560 Conover, W.J., 1971. Practical Nonparametric Statistics. John Wiley & Sons, Inc., New York.
- 561 Copeman, L.A., Ryer, C.H., Eisner, L.B., Nielsen, J.M., Spencer, M.L., Iseri, P.J., Ottmar, M.L., 2021.
562 Decreased lipid storage in juvenile Bering Sea crabs (*Chionoecetes* spp.) in a warm (2014)
563 compared to a cold (2012) year on the southeastern Bering Sea. Polar Biol. 44, 1883–1901.
564 <https://doi.org/10.1007/s00300-021-02926-0>.
- 565 Davis, J.L.D., Young-Williams, A.C., Aguilar, R., Carswell, B.L., Goodison, M.R., Hines, A.H., Kramer, M.A.,
566 Zohar, Y., Zmora, O., 2004. Differences between hatchery-raised and wild blue crabs: Implications
567 for stock enhancement potential. Trans. Am. Fish. Soc. 133, 1–14. <https://doi.org/10.1577/t03-004>.
- 568 Dionne, M., Sainte-Marie, B., Bourget, E., Gilbert, D., 2003. Distribution and habitat selection of early
569 benthic stages of snow crab *Chionoecetes opilio*. Mar. Ecol. Prog. Ser. 259, 117–128.
570 <https://doi.org/10.3354/meps259117>.
- 571 Dugan, J.E., Hubbard, D.M., Lastra, M., 2000. Burrowing abilities and swash behavior of three crabs,
572 *Emerita analoga* Stimpson, *Blepharipoda occidentalis* Randall, and *Lepidopa californica* Efford

- 573 (Anomura, Hippoidea), of exposed sandy beaches. *J. Exp. Mar. Biol. Ecol.* 255, 229–245.
574 [https://doi.org/10.1016/S0022-0981\(00\)00294-X](https://doi.org/10.1016/S0022-0981(00)00294-X).
- 575 Ernst, B., Armstrong, D.A., Burgos, J., Orensanz, J.M., 2012. Life history schedule and periodic
576 recruitment of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Can. J. Fish.*
577 *Aquat. Sci.* 69, 532–550. <https://doi.org/10.1139/F2011-173>.
- 578 Fedewa, E.J., Jackson, T.M., Richar, J.I., Gardner, J.L., Litzow, M.A., 2020. Recent shifts in northern Bering
579 Sea snow crab (*Chionoecetes opilio*) size structure and the potential role of climate-mediated range
580 contraction. *Deep. Sea Res. Pt. II Top. Stud. Oceanogr.* 181–182, 104878.
581 <https://doi.org/10.1016/j.dsr2.2020.104878>.
- 582 Fernandez, M., Iribarne, O., Armstrong, D., 1993. Habitat selection by young-of-the-year Dungeness crab
583 *Cancer magister* and predation risk in intertidal habitats. *Mar. Ecol. Prog. Ser.* 92, 171–177.
584 <https://doi.org/10.3354/meps092171>.
- 585 Garber-Yonts, B., Lee, J., 2021. Stock assessment and fishery evaluation report for the king and Tanner
586 crab fisheries of the Gulf of Alaska and Bering Sea/Aleutian Islands area: Economic status of the
587 BSAI king and Tanner crab fisheries off Alaska, 2019, 202 p. Alaska Fish. Sci. Cent., Natl. Mar. Fish.
588 Serv., Seattle, WA. Available from <https://www.npfmc.org/>.
- 589 Haflinger, K., 1981. A survey of benthic infaunal communities of the southeastern Bering Sea shelf. In:
590 Hood, D.W., Calder, J.A. (Eds.), *The Eastern Bering Sea Oceanography and Resources*. Office of
591 Marine Pollution Assessment, NOAA, University of Washington Press, Seattle, pp. 1091–1103.
- 592 Herrnkind, W., Butler, M., 1986. Factors regulating postlarval settlement and juvenile microhabitat use
593 by spiny lobsters *Panulirus argus*. *Mar. Ecol. Prog. Ser.* 34, 23–30.
594 <https://doi.org/10.3354/meps034023>.
- 595 Iribarne, O., Armstrong, D., Fernández, M., 1995. Environmental impact of intertidal juvenile Dungeness
596 crab habitat enhancement: Effects on bivalves and crab foraging rate. *J. Exp. Mar. Biol. Ecol.* 192,
597 173–194. [https://doi.org/10.1016/0022-0981\(95\)00060-5](https://doi.org/10.1016/0022-0981(95)00060-5).
- 598 Jewett, S.C., Feder, H.M., 1983. Food of the Tanner crab *Chionoecetes bairdi* near Kodiak Island, Alaska.
599 *J. Crustacean Biol.* 3(2), 196-207.
- 600 Kotwicki, S., Lauth, R.R., 2013. Detecting temporal trends and environmentally-driven changes in the
601 spatial distribution of bottom fishes and crabs on the eastern Bering Sea shelf. *Deep Sea Res. Pt. II*
602 *Top. Stud. Oceanogr.* 94, 231–243. <https://doi.org/10.1016/j.dsr2.2013.03.017>.
- 603 Kruse, G.H., Tyler, A. V., Sainte-Marie, B., Pengilly, D., 2007. A workshop on mechanisms affecting year-
604 class strength formation in snow crabs *Chionoecetes opilio* in the eastern Bering Sea. *Alaska Fish.*
605 *Res. Bull.* 12, 278–291.
- 606 Lang, C.A., Richar, J.I., Foy, R.J., 2018. The 2017 eastern Bering Sea continental shelf and northern Bering
607 Sea bottom trawl surveys: Results for commercial crab species. U.S. Dep. Commer., NOAA Tech.
608 Memo. NMFS-AFSC-233.

- 609 Laurel, B.J., Spencer, M., Iseri, P., Copeman, L.A., 2016. Temperature-dependent growth and behavior of
610 juvenile Arctic cod (*Boreogadus saida*) and co-occurring North Pacific gadids. *Polar Biol.* 39, 1127–
611 1135. <https://doi.org/10.1007/s00300-015-1761-5>.
- 612 Lipcius, R.N., D.B. Eggleston, K.L. Heck, Jr., R.D. Seitz, and J. van Montfrans. 2007. Post-settlement
613 abundance, survival, and growth of postlarvae and young juvenile blue crabs in nursery habitats.
614 Chapter 13, pp. 535-565 *In* Kennedy, V.S., L.E. Cronin (Eds.), *Biology and Management of the Blue*
615 *Crab*. University of Maryland Press, 800 pp.
- 616 Livingston, P.A., 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three
617 commercially important crab species in the eastern Bering Sea. *Fish. Bull.*, U.S. 87, 807–827.
- 618 Loher, T., Armstrong, D.A., 2000. Effects of habitat complexity and relative larval supply on the
619 establishment of early benthic phase red king crab (*Paralithodes camtschaticus* Tilesius, 1815)
620 populations in Auke Bay, Alaska. *J. Exp. Mar. Biol. Ecol.* 245, 83–109.
621 [https://doi.org/10.1016/S0022-0981\(99\)00157-4](https://doi.org/10.1016/S0022-0981(99)00157-4).
- 622 Long, W.C., Daly, B., 2017. Upper thermal tolerance in red and blue king crab: sublethal and lethal
623 effects. *Mar. Biol.* 164(8), 1-10. <https://doi.org/10.1007/s00227-017-3190-1>.
- 624 Lønne, O.J., Gulliksen, B., 1989. Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice
625 covered waters. *Polar Biol.* 9, 187–191. <https://doi.org/10.1007/BF00297174>.
- 626 Lovrich, G.A., Sainte-Marie, B., Smith, B.D., 1995. Depth distribution and seasonal movements of
627 *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. *Can. J.*
628 *Zool.* 73, 1712–1726. <https://doi.org/10.1139/z95-203>.
- 629 Main, K.L., 1987. Predator avoidance in seagrass meadows : Prey behavior, microhabitat selection, and
630 cryptic coloration. *Ecology* 68(1), 170–180.
- 631 McConnaughey, R.A., Smith, K.R., 2000. Associations between flatfish abundance and surficial sediments
632 in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* 57, 2410-2419.
- 633 McGaw, I.J., 2005. Burying behaviour of two sympatric crab species: *Cancer magister* and *Cancer*
634 *productus*. *Sci. Mar.* 69, 375–381. <https://doi.org/10.3989/scimar.2005.69n3375>.
- 635 McMurray, G., Vogel, A.H., Fishman, P.A., Armstrong, D.A., Jewett, S.C, 1984. Distribution of larval and
636 juvenile red king crabs (*Paralithodes camtschatica*) in Bristol Bay. *OCSEAP Final Rep.* 53:267-477.
- 637 Moles, A., Stone, R.P., 2002. Habitat preferences of juvenile Tanner and red king crabs: Substrate and
638 crude oil p. 631–644. *In*: Paul AJ, Dawe EG, Elnor R, Jamieson GS, Kruse GH, Otto RS, Sainte-Marie
639 B, Shirley TC, Woodby D (eds.), *Crabs in cold water regions: Biology, management, and economics*,
640 Vol. 19. Lowell Wakefield Fisheries Symposia Series, Fairbanks, Alaska.
- 641 Mueter, F.J., Litzow, M.A., 2008. Sea ice retreat alters the biogeography of the Bering Sea continental
642 shelf. *Ecol. Appl.* 18, 309–320. <https://doi.org/10.1890/07-0564.1>.

- 643 Murphy, J.T., 2020. Climate change, interspecific competition, and poleward vs. depth distribution shifts:
644 Spatial analyses of the eastern Bering Sea snow and Tanner crab (*Chionoecetes opilio* and *C. bairdi*).
645 Fish. Res. 223, 105417. <https://doi.org/10.1016/j.fishres.2019.105417>.
- 646 Orensanz, J.M., Armstrong, J., Armstrong, D., Hilborn, R., 1998. Crustacean resources are vulnerable to
647 serial depletion - The multifaceted decline of crab and shrimp fisheries in the Greater Gulf of
648 Alaska. Rev. Fish Biol. Fish. 8, 117–176. <https://doi.org/10.1023/A:1008891412756>.
- 649 Orensanz, J.L., Ernst, B., Armstrong, D.A., Stabeno, P.J., Livingston, P., 2004. Contraction of the
650 geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an
651 Environmental Ratchet? CalCOFI Rep. 45, 65–79.
- 652 Perkins-Visser, E., Wolcott, T.G., Wolcott, D.L., 1996. Nursery role of seagrass beds: Enhanced growth of
653 juvenile blue crabs (*Callinectes sapidus* Rathbun). J. Exp. Mar. Biol. Ecol. 198, 155–173.
654 [https://doi.org/10.1016/0022-0981\(96\)00014-7](https://doi.org/10.1016/0022-0981(96)00014-7).
- 655 Pirtle, J.L., Eckert, G.L., Stoner, A.W., 2012. Habitat structure influences the survival and predator-prey
656 interactions of early juvenile red king crab *Paralithodes camtschaticus*. Mar. Ecol. Prog. Ser. 465,
657 169–184. <https://doi.org/10.3354/meps09883>.
- 658 Pirtle, J.L., Stoner, A.W., 2010. Red king crab (*Paralithodes camtschaticus*) early post-settlement habitat
659 choice: Structure, food, and ontogeny. J. Exp. Mar. Biol. Ecol. 393, 130–137.
660 <https://doi.org/10.1016/j.jembe.2010.07.012>.
- 661 Rodin, V.E., 1989. Population biology of the king crab *Paralithodes camtschatica* Tilesius in the North
662 Pacific Ocean. In Proceedings of the International Symposium on King and Tanner Crabs,
663 Anchorage, Alaska, pp. 133-144. Alaska Sea Grant College Publication AK-SG-90-04.
- 664 Rosenkranz, G.E., Tyler, A. V., Kruse, G.H., 2001. Effects of water temperature and wind on year-class
665 success of Tanner crabs in Bristol Bay, Alaska. Fish. Oceanogr. 10, 1–12.
666 <https://doi.org/10.1046/j.1365-2419.2001.00153.x>.
- 667 Rosenkranz, G.E., Tyler, A. V., Kruse, G.H., Niebauer, H.J.C.N.-A. 05. 1. 01.-024, 1998. Relationship
668 between wind and year class strength of Tanner crabs in the southeastern Bering Sea. Alaska Fish.
669 Res. Bull. 5, 18–24.
- 670 Ryer, C.H., Long, W.C., Spencer, M.L., Iseri, P., 2015. Depth distribution, habitat associations, and
671 differential growth of newly settled southern Tanner crab (*Chionoecetes bairdi*) in embayments
672 around Kodiak Island, Alaska. Fish Bull., U.S. 113, 256-269.
- 673 Ryer, C.H., Ottmar, M., Spencer, M., Anderson, J.D., Cooper, D., 2016. Temperature-dependent growth
674 of early juvenile southern Tanner crab *Chionoecetes bairdi*: Implications for cold pool effects and
675 climate change in the southeastern Bering Sea. J. Shellfish Res. 35, 259–267.
676 <https://doi.org/10.2983/035.035.0128>.

- 677 Ryer, C.H., Stoner, A.W., Titgen, R.H., 2004. Behavioral mechanisms underlying the refuge value of
678 benthic habitat structure for two flatfishes with differing anti-predator strategies. *Mar. Ecol. Prog.*
679 *Ser.* 268, 231–243. <https://doi.org/10.3354/meps268231>.
- 680 Sandt, V.J., Stoner A.W, 1993. Ontogenetic shift in habitat by early juvenile queen conch, *Strombus*
681 *gigas*—patterns and potential mechanisms. *Fish. Bull. Fish. Wildl. Serv. US*, 91, 516–525.
682
- 683 Smith, K.R., McConnaughey, R.A., 1999. Surficial sediments of the eastern Bering Sea continental shelf:
684 EBSSED database documentation. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-104.
685
- 686 Sokal, R.R., Rohlf, F.J., 1969. *Biometry: the Principles and Practice of Statistics in Biological Research.*
687 W.H. Freeman and Company, San Francisco.
- 688 Somerton, D.A., 1981. Regional variation in the size of maturity of two species of Tanner crab
689 (*Chionoecetes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management
690 subareas. *Can. J. Fish. Aquat. Sci.* 38, 163–174. <https://doi.org/10.1139/f81-022>.
- 691 Stevens, B.G., 2003. Settlement, substratum preference, and survival of red king crab *Paralithodes*
692 *camtschaticus* (Tilesius, 1815) glaucothoe on natural substrata in the laboratory. *J. Exp. Mar. Biol.*
693 *Ecol.* 283, 63-78. [https://doi.org/10.1016/S0022-0981\(02\)00471-9](https://doi.org/10.1016/S0022-0981(02)00471-9).
- 694 Stevens, B.G., Haaga, J.A., Donaldson, W.E., 1994. Aggregative mating of Tanner crabs, *Chionoecetes*
695 *bairdi*. *Can. J. Fish. Aquat. Sci.* 51, 1273–1280. <https://doi.org/10.1139/f94-127>.
- 696 Stevens, B.G., Swiney, K.M., 2005. Post-settlement effects of habitat type and predator size on
697 cannibalism of glaucothoe and juveniles of red king crab *Paralithodes camtschaticus*. *J. Exp. Mar.*
698 *Biol. Ecol.* 321, 1-11. <https://doi.org/10.1016/j.jembe.2004.12.026>.
- 699 Stevenson, D.E., Lauth, R.R., 2019. Bottom trawl surveys in the northern Bering Sea indicate recent shifts
700 in the distribution of marine species. *Polar Biol.* 42, 407–421. [https://doi.org/10.1007/s00300-018-](https://doi.org/10.1007/s00300-018-2431-1)
701 [2431-1](https://doi.org/10.1007/s00300-018-2431-1).
- 702 Stoner, A.W., 2009. Habitat-mediated survival of newly settled red king crab in the presence of a
703 predatory fish: Role of habitat complexity and heterogeneity. *J. Exp. Mar. Biol. Ecol.* 382, 54–60.
704 <https://doi.org/10.1016/j.jembe.2009.10.003>.
- 705 Stoner, A.W., Ottmar, M.L., 2003. Relationships between size-specific sediment preferences and burial
706 capabilities in juveniles of two Alaska flatfishes. *J. Exp. Mar. Biol. Ecol.* 282, 85–101.
707 [https://doi.org/10.1016/S0022-0981\(02\)00447-1](https://doi.org/10.1016/S0022-0981(02)00447-1).
- 708 Stoner, A.W., Ottmar, M.L., Haines, S.A., 2010. Temperature and habitat complexity mediate
709 cannibalism in red king crab: Observations on activity, feeding, and prey defense mechanisms. *J.*
710 *Shellfish Res.* 29, 1005–1012. <https://doi.org/10.2983/035.029.0401>.
- 711 Stoner, A.W., Spencer, M.L., Ryer, C.H., 2007. Flatfish-habitat associations in Alaska nursery grounds:
712 Use of continuous video records for multi-scale spatial analysis. *J. Sea Res.* 57, 137–150.
713 <https://doi.org/10.1016/j.seares.2006.08.005>.

- 714 Szuwalski, C., Cheng, W., Foy, R., Hermann, A.J., Hollowed, A., Holsman, K., Lee, J., Stockhausen, W.,
715 Zheng, J., 2021. Climate change and the future productivity and distribution of crab in the Bering
716 Sea. ICES J. Mar. Sci. 78, 502–515. <https://doi.org/10.1093/icesjms/fsaa140>.
- 717 van Montfrans, J., Ryer, C.H., Orth, R.J., 2003. Substrate selection by blue crab *Callinectes sapidus*
718 megalopae and first juvenile instars. Mar. Ecol. Prog. Ser. 260, 209–217.
719 <https://doi.org/10.3354/meps260209>.
- 720 Weiss, H.M., Lozano-Álvarez, E., Briones-Fourzán, P., 2008. Circadian shelter occupancy patterns and
721 predator-prey interactions of juvenile Caribbean spiny lobsters in a reef lagoon. Mar. Biol. 153,
722 953–963. <https://doi.org/10.1007/s00227-007-0867-x>.
- 723 Yamamoto, T., Yamada, T., Fujimoto, H., Hamasaki, K., 2014. Effects of temperature on snow crab
724 (*Chionoecetes opilio*) larval survival and development under laboratory conditions. J. Shellfish Res.
725 33, 19–24. <https://doi.org/10.2983/035.033.0103>.
- 726 Zheng, J., Kruse, G.H., 2006. Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-
727 down effects? Prog. Oceanogr. 68, 184–204. <https://doi.org/10.1016/j.pocean.2006.02.002>.
- 728 Zheng, J., Kruse, G.H., Ackley, D.R., 2001. Spatial distribution and recruitment patterns of snow crabs in
729 the eastern Bering Sea, p. 233-255. *In* Spatial Processes and Management of Marine Populations.
730 Alaska Sea Grant College Program AK-SG-01-02.
- 731 Zhou, S., Shirley, T.C., 1997. Distribution of red king crabs and Tanner crabs in the summer by habitat
732 and depth in an Alaskan fjord. Invest. Mar. 25, 59–67. [https://doi.org/10.4067/s0717-](https://doi.org/10.4067/s0717-71781997002500005)
733 [71781997002500005](https://doi.org/10.4067/s0717-71781997002500005).
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746 **Figure Captions:**

747 Fig. 1. Observed frequencies for individual Tanner crab (pooled molt stages C3 and C4), snow crab
748 (pooled molt stages C2 and C3), and red king crab (pooled molt stages C1 and C2) located on a sediment
749 type. Results of the extrinsic hypothesis G-test for distribution among the seven sediment types are
750 indicated for each species. Sediment classifications are from finest to coarsest grains: sM = sandy mud,
751 mudS = muddy sand, fS = fine sand, mS = medium sand, cS = coarse sand, G = granules, P = pebbles.

752 Fig. 2. Mean body burial depth (\pm SE) of (A) Tanner crabs, (B) snow crabs and (C) red king crabs in sandy
753 mud versus fine sand sediment types in the absence (periods 1-3) and presence (periods 4-6) of a
754 perceived predation risk. Body burial index values are defined as: 1 = crab on top of the sediment, 2 =
755 carapace partly recessed in a depression or the posterior end nestled in the sediment, 3 = top of the
756 carapace flush with the sediment surface and 4 = $> 1/3$ of carapace covered with sediment.

757 Fig. 3. Habitat associations of Tanner crab, molt stage C2 and C3, in artificial worm tube and bare sand
758 habitat in the absence (periods 1-3) and presence (periods 4-6) of a perceived predation risk. (A) Counts
759 and (B) body burial index presented as means \pm SE.

760 Fig. 4. Habitat associations of snow crab, molt stages C2 and C3, in artificial worm tube and bare sand
761 habitat in the absence (periods 1-3) and presence (periods 4-6) of a perceived predation risk. (A and B)
762 Counts and (C and D) body burial index presented as means \pm SE.

763 Fig. 5. Habitat associations of red king crab, molt stage C2, C3, and C4 in artificial worm tube and bare
764 sand habitat in the absence (periods 1-3) and presence (periods 4-6) of a perceived predation risk. (A)
765 Counts and (B) body burial index presented as means \pm SE.

766 Fig. 6. Age-0 Tanner crabs eaten by both age-1 Pacific cod and age-1 Tanner crab predators in 4 different
767 habitat treatments: (B) bare bottom tank, (S) fine sand at a depth of 20 mm, (Sparse WT) artificial sparse
768 worm tube structure with density of 18 tubes per 0.3048 m² in 20 mm sand, and (Dense WT) artificial
769 dense worm tube structure of 265 tubes per 0.3048 m² in 20 mm sand. Values presented as means \pm SE.

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781 **Table 1**

782 Table 1. Species, molt stages, sizes, and replicates with total number of crabs for four different
 783 experiments.

Experiment	Species	Molt Stages	Size range (mm CW)	Replicates (total # of crab)
Sediment Association	Tanner Crab	C3	5.08 – 6.93	11 (n = 11)
		C4	7.11 – 7.56	7 (n = 7)
	Snow Crab	C2	4.25 – 4.90	18 (n = 18)
		C3	5.00 – 7.13	18 (n = 18)
	Red King Crab	C1	1.92 – 2.11	13 (n = 13)
		C2	2.13 – 2.30	5 (n = 5)
Burial Behavior	Tanner Crab	C2	3.13 - 4.27	6 per sediment type (n = 120)
		C3	4.49 - 5.51	6 per sediment type (n = 120)
	Snow Crab	C2	3.54 - 4.97	8 per sediment type (n = 160)
		C3	5.28 - 7.14	8 per sediment type (n = 160)
	Red King Crab *	C2, C3	2.21 - 3.40	6 per sediment type (n = 120)
Worm Tube Structure Association	Tanner Crab *	C2, C3	3.76 - 5.50	8 (n = 80)
	Snow Crab	C2	4.10 - 4.80	4 (n = 40)
		C3	5.53 - 6.86	4 (n = 40)
	Red King Crab *	C2, C3, C4	2.27 - 4.17	8 (n = 80)
Predation Vulnerability				
Predators				
Age-1 Pacific Cod	Tanner Crab	C3	4.76 - 5.49	6 per habitat type (total n = 480)
Age-1 Tanner Crab	Tanner Crab*	C2, C3, C4	4.29 - 7.68	4 per habitat type (total n = 320)

784 * Indicates pooled molt stages in the experimental trials.

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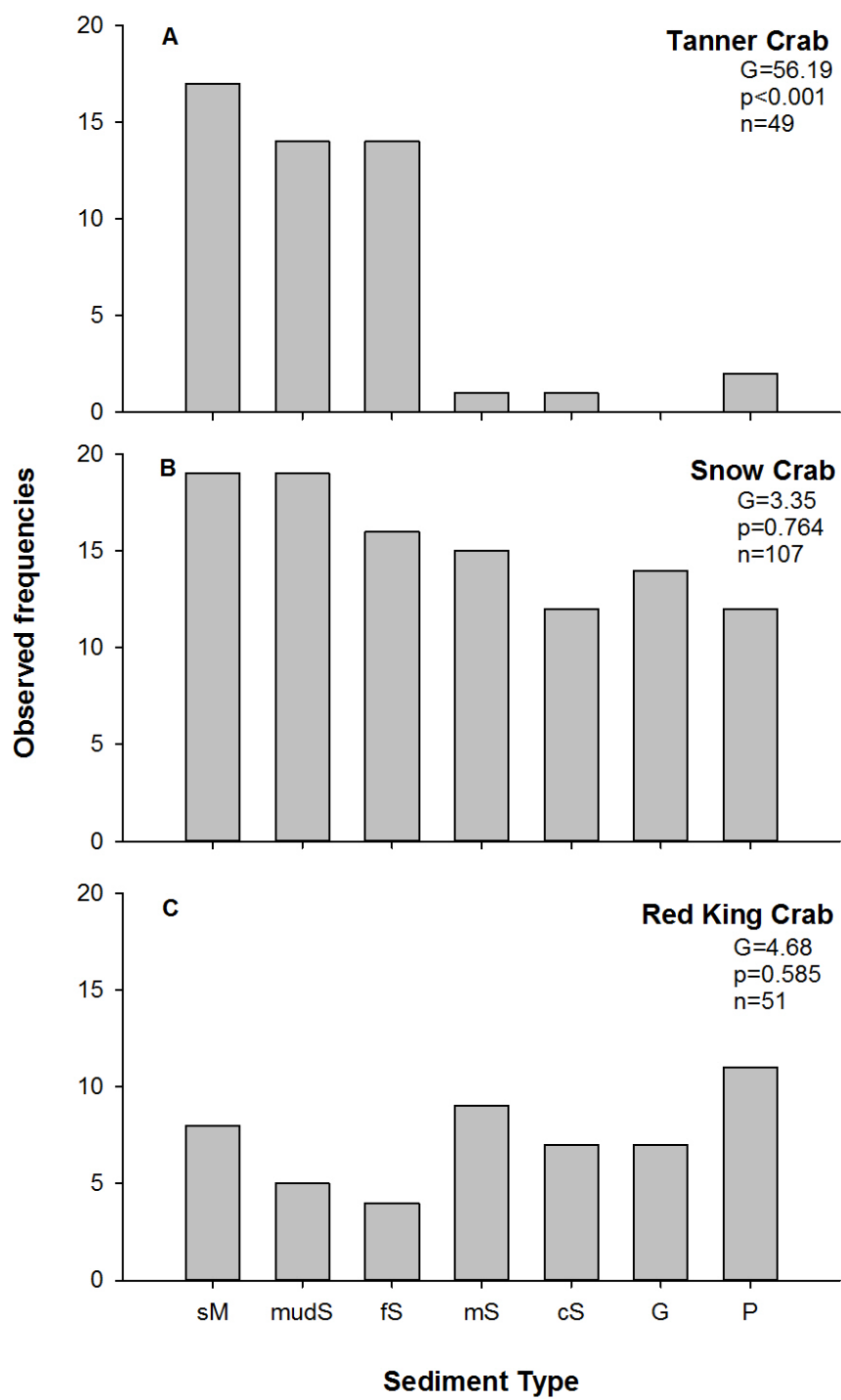
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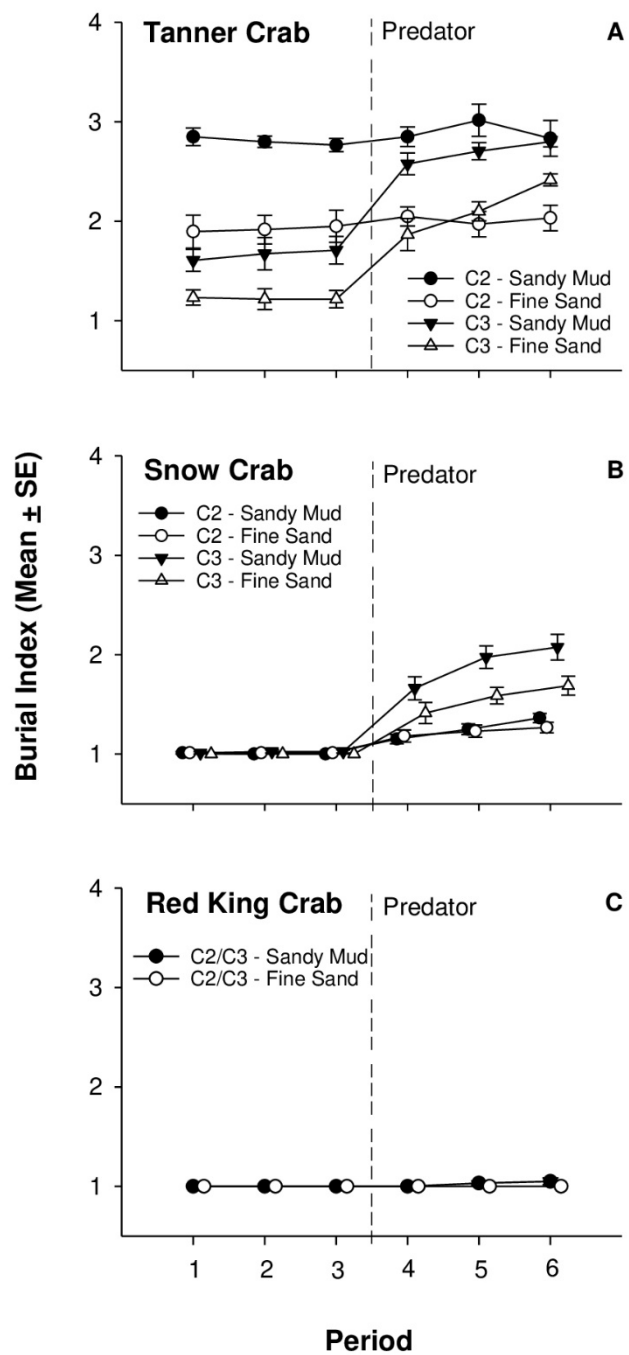
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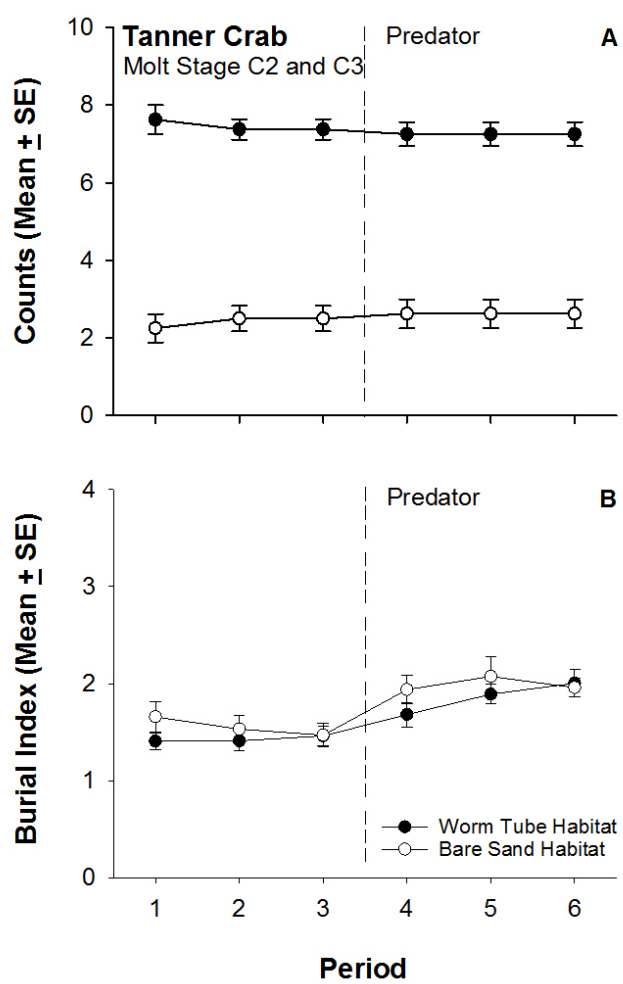
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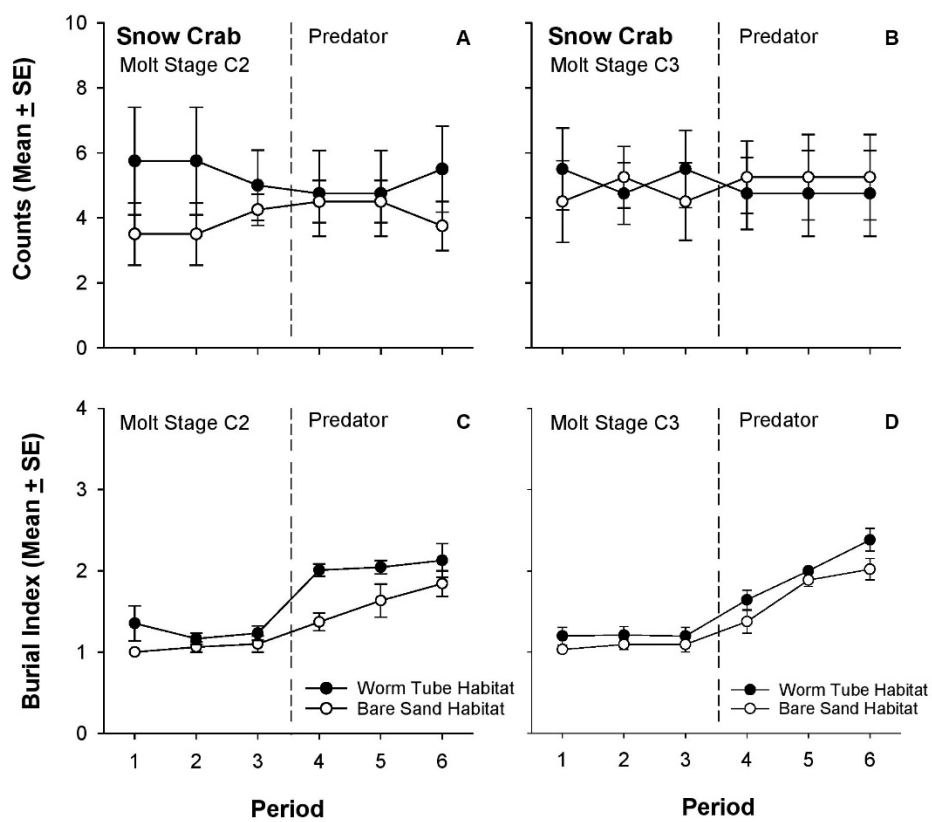
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792 **Figure 1**

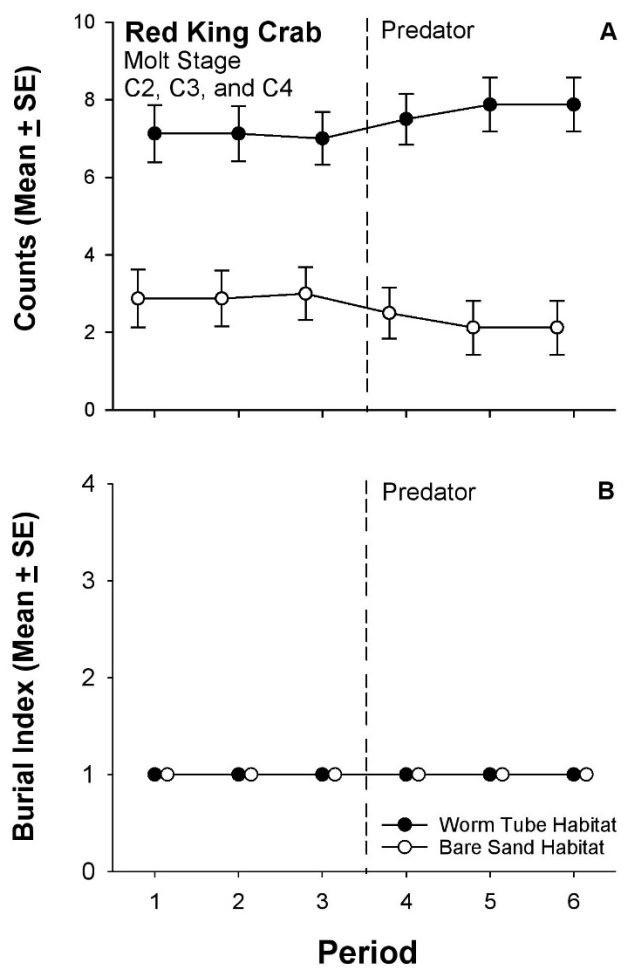
794 **Figure 2**



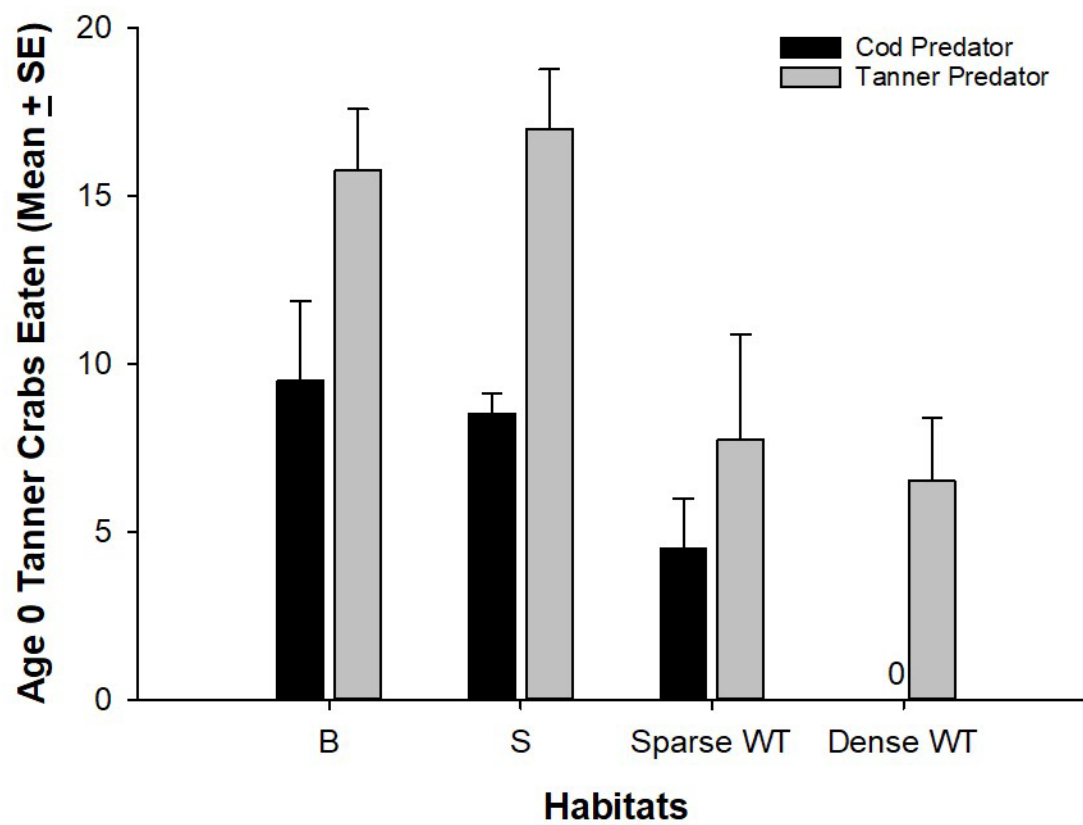
796 **Figure 3**

798 **Figure 4**

800 Figure 5



802 Figure 6



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