

1 **Assessing commercial fishery bait in Dungeness crab (*Cancer magister*) feeding ecology:**
2 **$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope and gut content analysis**

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40 Abstract

41 Dungeness crabs support Oregon's largest fishery, which inputs millions of pounds of
42 bait, including squid, razor clams, and sardines into the coastal ocean every year. This paper
43 assesses evidence for seasonal consumption of commercial Dungeness crab (*Cancer magister*)
44 fishery bait off the Oregon coast by that target species using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope and gut
45 content analysis. Fishing effort and associated bait inputs are typically concentrated in the winter
46 between December and February. Using Dungeness crab samples collected on Oregon's inner to
47 mid-continental shelf, variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are assessed according to sex, size class,
48 region, and season using nested analysis of variance (ANOVA), Euclidean vector statistics, and
49 Bayesian standard ellipse areas (SEAc) in R (Version 4.0.4). Trophic ecologists commonly use
50 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope ratios in consumer tissues to assess prey provenance and trophic level. The
51 isotopic signatures of sampled crabs show statistically significant variation by sex, region, and
52 season; the differences in the isotopic niches of large male versus female crabs (carapace width \geq
53 159mm) are especially pronounced. $\delta^{15}\text{N}$ in female crabs peak in spring and decline to fall with
54 similar mean $\delta^{13}\text{C}$, which could be indicative of higher trophic level bait consumption in the
55 winter, while $\delta^{13}\text{C}$ vary seasonally in males with similar mean $\delta^{15}\text{N}$. The approximated trophic
56 niches (using SEAc) of both male and female crabs were greatest in fall, suggesting broader
57 foraging in the absence of bait inputs. This work provides a step towards understanding the
58 ecological role of fishery activities on one of the most economically valuable species on the west
59 coast of the United States.

60

61 1. Introduction

62 Oregon's commercial Dungeness crab fishery inputs millions of pounds of bait into the
63 coastal ocean each year (Davis et al. 2017, Harbison 2021), especially during the wintertime
64 when fishing effort peaks (Deweese et al. 2004). In this paper, we seek to discern if $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$
65 stable isotope signatures and gut contents within Dungeness crabs provide evidence for
66 spatiotemporally variable consumption of fishery bait by that target species. Exploring
67 relationships between bait subsidies and commercially targeted crustaceans is not without
68 precedent. Several authors have hypothesized that fisheries discards increase the abundance of
69 benthic scavengers (Furness et al. 1988, Berghahn 1990, Wassenberg & Hill 1990, Kaiser &
70 Spencer 1996, Ramsay et al. 1997). Research on trap-based commercial lobster fisheries in
71 Maine and Western Australia found that bait subsidies have altered the trophodynamics of
72 lobsters in those regions (Saila et al. 2002, Grabowski et al. 2009, Waddington & Meeuwig
73 2009). Grabowski et al. (2009) asserted that herring bait "augmented lobster populations" at a
74 heavily fished site in the Gulf of Maine. On a global scale, fisheries discards increase the
75 availability of organic material to benthic communities (Britton & Morton 1994). These food
76 subsidies impact ecosystem functioning in numerous ways, including increasing secondary
77 productivity (Ramsay et al 1997, Groenewold & Fonds 2000), reducing consumption of natural
78 prey species (Waddington & Meeuwig 2009), and transporting biomass from pelagic to coastal
79 systems (Grabowski et al. 2009).

80 Understanding Dungeness crab trophodynamics has tremendous economic implications.
81 Oregon's commercial Dungeness crab (*Cancer magister*) ocean fishery is typically the largest
82 and most profitable fishery in the state. During the 2019-2020 season, 320 active crabbing permit
83 holders landed 19.9 million pounds of crab, generating \$72.7 million in ex-vessel value (Oregon

84 Department of Fish and Wildlife (ODFW) 2020). Oregon manages the fishery under the “3S”
85 system: sex, size, and season, with limited vessel entry and pot limits of 200, 300, or 500 per
86 commercial permit. Male crabs over 159 mm carapace width (CW) can be commercially
87 harvested during the season, which generally runs between December 1st and August 14th for the
88 ocean fishery. Oregon also supports a smaller scale bay fishery that is open through fall, but that
89 fishery represents just 0.2% of the total Dungeness crab harvest (ODFW 2021a). Current
90 exploitation rates indicate that 80-90% of the legal sized males are harvested each year, and yet
91 the population maintains high reproductive success (Hankin et al. 1997, Dunn & Shanks 2012).
92 While numerous species around the world have been overfished and depleted, evidence suggests
93 that the *Cancer magister* fishery off the Oregon coast has not caused an overall reduction in the
94 resource.

95 The Dungeness crab population is not subject to formal stock assessments; rather,
96 commercial catch is considered a sufficient proxy for legal sized male abundance (Richerson et
97 al. 2020). Historically, catch has fluctuated in roughly decadal cycles, although this cyclical
98 trend has broken down over the last several decades (Botsford et al. 1982; Botsford and
99 Lawrence 2002), when average landings have increased (Richerson et al. 2020). Crabbers landed
100 the largest recorded annual catch during the 2004-2005 season, at 33.7 million pounds (ODFW
101 2021b). Researchers have presented various hypotheses to explain population fluctuations
102 (Johnson et al. 1986, Shanks and Roegner 2007, Armstrong et al. 2010, Shanks et al. 2010,
103 Rasmuson 2013, Shanks 2013), generally citing environmental and oceanographic rather than
104 fishery related drivers. One pertinent theory is that density-dependent prevalence of cannibalism
105 may also contribute to population fluctuations (Higgins et al. 1997, Fernandez 1999, Shanks
106 2013).

107 Crabbers use a wide variety of baits, including squid, clams, sardines, mackerel, mink,
108 tuna, rockfishes, chicken, herring, anchovy, black cod, hake, halibut, and salmon (Bostrom et al.
109 2018, ODFW 2020, Harbison 2021), although specific species of the above listed baits are
110 generally not reported. Fishermen use a variety of baiting equipment inside their pots, including
111 bait jars, chew bags, and bait pins. Bait jars have holes that allow the scent to escape but are not
112 large enough for captured crabs to access the bait. Chew bags made of large mesh and bait pins,
113 on the other hand, allow the crabs consume bait while in the pots. After pulling the pots, crabbers
114 toss used bait overboard. Each crabber uses approximately $35,000 \pm 12,432$ pounds of bait per
115 season (Harbison 2021) resulting in an estimated 11.2 million pounds of bait input to the coastal
116 ocean during the 2019-2020 season by Oregon's 320 permit holders. The most intense fishing
117 effort and associated bait inputs occur within the first six weeks of the open season (Deweese
118 2004); fishermen caught 86% of total harvest within the first two months of the 2019-2020
119 season (ODFW 2020).

120 Stable isotope analysis (SIA) and gut content analysis complement each other, and
121 combined, constitute a powerful tool for inferring diet composition. $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ SIA provides
122 information regarding dietary preferences over weeks to months. Studies show that isotopic
123 ratios of consumers reflect those of their prey. Traditionally, $\delta^{15}\text{N}$ values have been used to
124 evaluate trophic position, while $\delta^{13}\text{C}$ help determine the ecological provenance of food sources,
125 such as terrestrial, estuarine, benthic, or pelagic. Ecologists frequently use trophic discrimination
126 factors (TDFs) to estimate the trophic position of consumers as well as the degree to which they
127 assimilate their food into their tissues. Although TDFs vary widely across organisms, $\delta^{13}\text{C}$ in
128 animals usually remains within around 0-1‰ of their diet and $\delta^{15}\text{N}$ generally increases by around
129 3-3.5‰ per trophic level (Deniro & Epstein 1978, Michener & Schell 1994, Post 2002, Viozzi et

130 al. 2021). One key factor to consider when reading SIA results is that tissue turnover rates
131 determine the amount of time it takes for the isotopic composition of consumer tissues to reflect
132 changes in that consumer's diet. These tissue turnover rates differ across and within species,
133 depending on several factors including the type of tissue analyzed (Tieszen et al. 1983).

134 Although tissue turnover rates have not been assessed for Dungeness crab, this study used
135 Dungeness crab leg muscle tissue to assess seasonal change in the species' diet composition
136 based on tissue turnover rates approximated in other decapod species. A study on two decapod
137 species, *Episesarma singaporense* and *E. versicolor*, showed that $\delta^{15}\text{N}$ of muscle tissue shifted
138 significantly after a change in diet after between 50 and 70 days (Herbon & Nordhaus 2013).
139 Additionally, Bui & Lee (2014) suggested that tissue turnover results in isotopic equilibrium
140 within the muscle tissues of the crab *Parasesarma erythodactyla* within 56 days. Møller et al.
141 (2008) used a tissue turnover rate of ≥ 63 days in an experimental study on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$
142 isotope ratios in the blue swimmer crab *Portunus pelagicus* but cautioned that tissues may not
143 have reached complete isotopic equilibrium during that period.

144 While SIA can be used to estimate prey provenance and trophic level, it cannot identify
145 specific prey species, thus, differentiating relative consumption of food items with similar
146 isotopic compositions can be challenging. This limitation of SIA is particularly relevant to this
147 study because some Dungeness crab prey species, such as small bivalves and decapods, are
148 isotopically similar to commercial bait species, like razor clams. Gut content analysis partially
149 offsets this limitation. Prey items can theoretically be identified within guts down to the species
150 level, although crustaceans heavily masticate their prey, making identification a difficult task
151 (Waterman 1960, Stevens et al. 1982). Gut contents provide information about an organism's
152 feeding preferences hours to days prior to capture. Several authors hypothesize that gut content

153 analysis tends to underestimate the importance of food items that lack hard structures, because
154 they are digested more quickly (Stevens et al. 1982). However, a consumer's isotopic
155 composition reflects soft food sources even if they leave few remnants in their guts.

156 We conducted SIA on crabs as well as natural prey and bait species to compare the
157 isotopic ratios of the consumers to the potential sources. In accordance with approximated tissue
158 turnover rates of between 50-70 days in other crab species (Møller et al. 2008, Herbon &
159 Nordhaus 2013, Bui & Lee 2014), we assumed that stable isotope ratios in the tissues of crabs
160 collected in each season would reflect food consumption from the previous season. Gut contents,
161 on the other hand, were assumed to reflect consumption days to hours before sample collection.
162 Given that fishing effort generally peaks between December and February (Deweese 2004) in the
163 ocean fishery, SIA values and gut contents were hypothesized to reflect peak bait consumption
164 during that period, characterized by comparatively higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ from the consumption
165 of some higher trophic level and/or pelagic bait species, including rockfish and mackerel, that are
166 unlikely to be prevalent in wild Dungeness crab diets. In the spring, juvenile Dungeness crab
167 settle in estuaries and the nearshore (Gunderson et al. 1990), and authors report cannibalism
168 between (MacKay 1942, Butler 1954, Gotshall 1977) and within age class (Jacoby 1983, Karpov
169 1983, Fernandez et al. 1993a, b, 1994). Accordingly, guts collected in the spring and summer
170 were hypothesized to contain *Cancer magister* fragments. Both juvenile settlement and
171 commercial Dungeness crab harvest in the ocean fishery cease almost entirely by early fall,
172 therefore, we hypothesized that crabs collected in October and December would reflect peak
173 consumption of benthic invertebrate food sources such as bivalves, gastropods, polychaetes, and
174 small teleost flatfish (Bernard 1979, Feder & Paul 1980, Stevens et al. 1982) characterized by the
175 lowest relative $\delta^{15}\text{N}$ ratios. Additionally, we hypothesized that female and sub-legal male (<159

176 mm carapace width (CW)) crabs would show stronger bait signatures than legal-sized males
177 (≥ 159 mm CW) because they have the opportunity to feed on bait in multiple pots and be
178 returned to the ocean, while legal males are harvested upon capture.

179

180 2. Methods

181 2.1 Study Area

182 Dungeness crabs were collected across three geographic regions of the Oregon coast
183 (North, Central, and South) during four seasons (December 2019, March/April 2020, June/July
184 2020, and October 2020) at 20-50 m depth on the shelf outside bays and estuaries. Regions were
185 determined by splitting the Oregon coastline into three latitudinal sections; the Oregon/California
186 border (41.99°N) to Reedsport, OR (43.72°N) was considered “South,” north of Reedsport to
187 Lincoln City, OR (44.96°N) was considered “Central,” and north of Lincoln City to the
188 Oregon/Washington (46.26°N) border was considered “North” (*Figure 1*). All three regions lie
189 within the California Current system on a relatively narrow continental shelf and are subject to
190 variably timed summer upwelling and winter downwelling regimes accompanied by strong storm
191 surge (Kaiser et al. 2001). The “South” region (Cape Arago, Langlois, and Port Orford study
192 sites) encompasses a major north-south shift in oceanographic conditions and invertebrate
193 recruitment patterns that occurs in the Cape Arago and Cape Blanco region (Broitman et al.
194 2008). The collection areas lay within commercial fishing grounds, which are generally
195 characterized by low relief and structural complexity (Marine Stewardship Council 2010) and
196 predominantly silt and/or sand covered bottoms (Pacific Fisheries Management Council 1978).

197

198 *2.2 Sample Collection*

199 Whenever possible, 10 legal-sized males (CW \geq 159mm), 10 sub-legal males (CW <
200 159mm), and 10 female crabs were collected during each sampling session, except in December
201 2019 when only males were obtained through ODFW's meat fullness sampling. Samples were
202 collected by commercial fishermen at the Garibaldi (North) and Pacific City (North) sites in
203 Spring 2020 and Port Orford (South) in Spring 2021 using varying baiting methods. COVID-19
204 travel restrictions prevented sampling of crabs in the South region in Spring 2020. Crabbers
205 recorded the geographic location and depth of each collection site. Collected crabs were stored
206 on deck after capture, rather than in holding tanks. All other samples were collected by the
207 authors using closed bait pitchers to prevent crabs from consuming bait inside the pot and
208 contaminating their stomach contents. Pots were baited with chicken, salmon, halibut, and/or
209 rockfish. A total of 358 individual Dungeness crabs were collected; their CWs ranged from 108-
210 198mm (*Table 1*). None of the adult Dungeness crab samples were collected in the vicinity of
211 fish processing plant dumping grounds.

212 Fishery bait species were selected based on ODFW fishery logbook data from 2013-
213 2017. Squid, mackerel, razor clams, and sardines were acquired from Pacific Seafood, Inc., in
214 Newport, OR, during December 2020. Rockfish carcasses were sourced from a recreational
215 charter vessel in Garibaldi, OR, in July 2020. Dungeness crab food sources identified from
216 literature, including macroalgae, bivalves, and eelgrass were collected from the Yaquina Bay
217 mudflats near Newport, OR, in April 2021 along with cockle clams, which are used as bait in the
218 commercial fishery. All other putative prey based on literature, including *Callianax* sp., *Crangon*
219 sp., juvenile *Cancer magister*, cumaceans, *Citharichthys sordidus*, and small bivalves were
220 sorted from beam trawl samples collected off Newport, OR, by Henkel between 2011 and 2016.

221

222 *2.3 Gut Content Analysis*

223 Complete digestive tracts were removed from collected crabs after they were euthanized
224 according to Institutional Animal Care and Use Committee regulations (except in December
225 2019 when samples had been frozen by ODFW prior to acquisition) and stored in 70% ethanol.
226 Stomachs were dissected using a straightedge blade and tweezers and inspected under a
227 dissecting microscope. Similar items were sorted into piles and photographed with a Leica
228 camera connected to the scope for later identification. Gut contents were identified to the lowest
229 taxa possible but then grouped at coarser taxonomic levels for analysis as contents could not be
230 identified from all crabs with equal resolution. The presence or absence of each prey category,
231 soft tissue, and sand were recorded for each stomach. The frequency of occurrence (FO) of each
232 category was calculated as the percentage of stomachs that contained a given item or were empty
233 within each sample site, region, and season. FO across sex and size classes and within and across
234 sites and seasons were compared.

235

236 *2.4 Stable Isotope Analysis*

237 All the legs from each sampled crab were frozen at 20°C at the time of collection. After
238 the samples were partially thawed, the muscle tissue was extracted from the shells and dried at
239 60°C for ≥ 48 hours. Leg tissue was the only type of tissue extracted from the adult Dungeness
240 crab samples to avoid the possible confounding factor of varying tissue turnover rates across
241 multiple tissue types. All inorganic carbon structures were excluded from the samples. Studies
242 indicate that lipid extraction from crustacean tissues does not have a significant effect on $\delta^{13}\text{C}$

243 nor $\delta^{15}\text{N}$ (Bodin et al. 2007). Therefore, lipids were not removed during processing and no
244 mathematical lipid corrections were applied.

245 The bait and prey collected in April 2020 from the Yaquina Bay mudflats were dried
246 fresh at 60°C for ≥ 48 hours without being frozen because we were able to process them quickly
247 immediately after collection. All other bait and prey samples were frozen upon collection and
248 partially thawed prior to drying at 60°C for ≥ 48 hours. In processing the bait and prey, inorganic
249 carbon structures were excluded in all species except crustacean prey, which were processed
250 whole without acid washing. All dried samples were ground manually to a fine powder using a
251 mortar and pestle. The mortar and pestle were cleaned with water and acetone between each
252 sample. The powdered samples were stored in airtight 1.5-2mL glass vials. 1 mg (± 0.1 mg) of
253 each powdered sample was weighed, transferred into tin capsules (EA Consumables–Part
254 #D1002), and placed in 96 well plates (VWR–Part #10062-902).

255 Samples were analyzed at the NOAA Alaska Fisheries Science Center in Auke Bay, AK,
256 or at the College of Earth, Ocean, and Atmospheric Science (CEOAS) Stable Isotope Lab at
257 Oregon State University (OSU) in Corvallis, OR. Samples of adult Dungeness crab collected
258 from Langlois, Port Orford, and Cape Arago on 12/16/2019 and Port Orford on 5/18/2021 as
259 well as small bivalve prey ($<20\text{mm}$), eelgrass (*Zostera marina*), and cockle clams (*Clinocardium*
260 *nuttallii*) were processed at the OSU lab (total $n = 144$). All other adult Dungeness crab, bait, and
261 prey samples were processed at the NOAA lab (total $n = 514$) (See Tables 3 & 4). In the OSU
262 lab, the carbon and nitrogen isotopic composition were analyzed by continuous-flow isotope
263 ratio mass spectrometry using a Carlo Erba elemental analyzer (EA) connected to a Thermo
264 DeltaPlus isotope ratio mass spectrometer (IRMS). The international standard glutamic acid
265 (United States Geological Survey (USGS)-40) and Stable Isotope Laboratory (SIL) sucrose were

266 used as standards for $\delta^{13}\text{C}$, measured relative to Vienna Pee Dee Belemnite (V-PDB) while
 267 glutamic acid (USGS-40) and International Atomic Energy Agency (IAEA) N-2 ammonium
 268 sulfate were used as standards for $\delta^{15}\text{N}$, measured relative to atmospheric N_2 . Long-term records
 269 of internal standards yield an analytical precision (standard deviation) of 0.19 ‰ and 0.27 ‰ for
 270 $\delta^{13}\text{C}$ and for $\delta^{15}\text{N}$, respectively. IAEA-600 caffeine was also used to calibrate each SI run.

271 At the NOAA lab, tissue samples were analyzed using a Thermo FlashSmart elemental
 272 analyzer in line with a Thermo DeltaPlus XP continuous-flow isotope ratio mass spectrometer
 273 (CF-IRMS; Thermo Scientific, Bremen, Germany). Measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values obtained
 274 from crab tissue sample analysis were scale calibrated based on contemporaneously analyzed
 275 isotopic reference materials of accepted δ values relative to the appropriate reference scale acting
 276 as scale anchors. The isotopic reference materials used were supplied by the IAEA (IAEA-N-1,
 277 $\delta^{15}\text{N} = 0.4 \pm 0.2$ ‰; IAEA-CH-7, $\delta^{13}\text{C} = -32.151 \pm 0.050$ ‰; IAEA-CH-3, $\delta^{13}\text{C} = -24.724 \pm 0.041$
 278 ‰) and the USGS (USGS25, $\delta^{13}\text{C} = -34.58 \pm 0.06$ ‰, $\delta^{15}\text{N} = -0.94 \pm 0.16$ ‰; USGS40, $\delta^{13}\text{C} = -$
 279 26.389 ± 0.042 ‰, $\delta^{15}\text{N} = -4.5 \pm 0.1$ ‰; USGS41, $\delta^{13}\text{C} = +37.626 \pm 0.049$ ‰, $\delta^{15}\text{N} = 47.6 \pm 0.2$
 280 ‰). Internal laboratory standards were included with all samples as quality controls (all error
 281 data are SD for purified methionine, Alfa Aesar, $\delta^{13}\text{C} = -34.58 \pm 0.06$ ‰, $\delta^{15}\text{N} = -0.94 \pm 0.16$ ‰;
 282 homogenized Chinook salmon muscle, NOAA Fisheries, $\delta^{13}\text{C} = -19.27 \pm 0.05$ ‰, $\delta^{15}\text{N}$
 283 $= 15.56 \pm 0.13$ ‰). Long-term records of internal standards yield an analytical precision (standard
 284 deviation) of 0.11 ‰ and 0.12 ‰ for $\delta^{13}\text{C}$ and for $\delta^{15}\text{N}$, respectively. Relative SI abundance
 285 values from both labs are reported in δ notation and are given as per mil values (‰) according to
 286 the following equation (1):

$$287 \quad \delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] (1000) \quad (1)$$

288 where X represents ^{13}C or ^{15}N and R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ ratio, respectively.

289 The linear lipid correction model presented by Post et al. (2007) was used to correct $\delta^{13}\text{C}$
 290 for lipids present in teleost bait and prey samples. That model uses the following equation

$$291 \quad \delta^{13}\text{C}_{corr} = \delta^{13}\text{C}_{bulk} + a \times C:N_{bulk} + b \quad (2)$$

292 where $\delta^{13}\text{C}_{corr}$ is the lipid corrected value of $\delta^{13}\text{C}_{bulk}$, a and b are parameters obtained from a
 293 linear relationship between $C:N_{bulk}$ and tissue lipid content. In this study, we used the values of
 294 a and b proposed by Post et al. 2007 for aquatic animals, which are 0.99 and -3.32, respectively.

295

296 *2.5 Data Analysis*

297 The SIBER (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) package was
 298 used to assess relative variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios and isotopic niche area across sex and
 299 size classes (sub-legal males (<159mm), legal males (>159mm), small females (<159mm), and
 300 large females (>159mm)) and across seasons (winter, spring, summer, and fall). Isotopic niche
 301 was estimated by calculating SEAc (Standard Ellipse Area, corrected for sample size), a metric
 302 that reports the area of an ellipse drawn around the centroid, containing 40% of the sample points
 303 first for each of the sex-size classes (with winter samples excluded because no female samples
 304 were collected during the winter). The directionality and magnitude of the differences between
 305 each class were approximated by calculating the pairwise polar vectors among all groups. These
 306 vectors were visualized using polar histograms. Next, the polar coordinates were converted into
 307 cartesian space using the following function:

$$308 \quad f(r, \theta) = (r \cos\theta, r \sin\theta)$$

309 The median angle and median length of each class-wise comparison in cartesian space were then
 310 reported following Jackson (2021). Based on the results of the class-wise comparisons, the same
 311 SEAc procedure was repeated comparing all male crabs across four seasons and all female crabs

312 across three seasons. Sexes were not subdivided into size classes due to limited sample size when
313 considering individual seasons.

314 The SI signature for each sample area in each region was summarized according to mean
315 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios ± 1 standard deviation. The mean ± 1 standard deviation was then calculated
316 for each sex within each region. Regional means ± 1 standard deviation were calculated for all
317 samples within each region (*Table 1*).

318 Analyses of variance (ANOVAs) for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of all crab samples were
319 performed for males ($n = 250$) and females ($n = 98$) separately with region and season as main
320 factors and site nested within region. For males, we also considered size ($</\geq 159$ mm) as a
321 factor. Normality was tested by plotting model residuals and equal variance was tested using
322 Levene's Test for Homogeneity of Variance. *Post hoc* Tukey tests were performed on the
323 ANOVA outputs to further explore difference among levels of significant factors. A one-way
324 ANOVA was also used to assess if, on average, bait and prey differed significantly in $\delta^{13}\text{C}$ or
325 $\delta^{15}\text{N}$. The significance level, α , was set at 0.05 for all analyses. All data analyses were conducted
326 in R Version 4.0.4 in RStudio.

327 Although Dungeness crab tissue turnover rates are unknown, studies on other decapod
328 species suggest that their muscle tissues turnover after between 50-70 days (Møller et al. 2008,
329 Herbon & Nordhaus 2013, Bui & Lee 2014). In the present study, Dungeness crab samples were
330 collected ~58-98 days apart. Therefore, we approximate tissue samples collected in any given
331 season to be representative of feeding habits in the previous season.

332

333 3. Results

334 3.1 Gut Content Analysis

335 The most frequently occurring gut items overall from greatest to least were teleost,
336 bivalve, unidentified soft tissue, decapod, and gastropod. Less frequently occurring items
337 consisted of macroalgae, sand, bryozoans, echinoderms, wood debris, and seagrass (*Table 2*). 4%
338 of guts were completely empty. On average, the frequency of occurrence of teleost parts and soft
339 tissue (ST) was consistent across seasons; however, there was a great deal of variability in these
340 items among sites especially for teleost parts (*Figure 2; Table 2*). The frequency of occurrence of
341 the other items and empty guts varied seasonally (spring, summer, and fall guts only) and across
342 sites within each season.

343 In the spring, an average of 24% of guts contained teleost parts including scales, bones,
344 and fin rays (*Figure 2*), but only 3% of stomachs collected from Garibaldi contained teleost
345 fragments while 43% of those from Pacific City did (*Table 2*). The Pacific City samples also
346 contained the highest FO of soft tissue (23%), compared to the other spring sites (Garibaldi =
347 10%; Newport = 13%). The FO of gastropods was higher Newport (33%) than at the other two
348 sites (Garibaldi = 7%; Pacific City = 3%). An average of 35% of spring guts were completely
349 empty, which is over four times greater than the mean percent of empty stomachs in the other
350 two seasons (summer = 8%; fall = 0%).

351 Summer had the highest proportion of soft tissue (24%), decapods (30%), macroalgae
352 (10%), bryozoans (12%), echinoderms (4%), wood (3%), and seagrass (6%) relative to other
353 seasons (*Figure 2*). June Newport guts contained the highest frequency of soft tissue (37%), July
354 Garibaldi guts contained the highest frequency of decapods (63%), and July Reedsport guts
355 contained the highest frequency of microalgae (28%), seagrass (17%), bryozoans (12%), and

356 wood (7%) (*Table 2*). In fact, macroalgae was over four times more frequent at Reedsport than
357 any other site in any season. 67% of the summer Garibaldi sample contained teleost parts, up
358 from 3% at the same site in the spring and over twice as frequently as any other site in the
359 summer (Newport = 10%; Cape Perpetua = 7%; Reedsport = 24%). The FO of sand at all the
360 summer sites was $\geq 3\%$, whereas some of the sites in other seasons were devoid of sand.

361 Fall guts contained the highest mean proportion of teleost (28%), bivalve (31%), and
362 gastropod (28%), and sand (10%) compared to spring and summer (*Figure 2*). The October Port
363 Orford samples contained the highest frequency of teleost fragments (77%), bivalves (37%), and
364 sand (33%) compared to any other site in any season (*Table 2*). All four fall sites had a FO of
365 gastropods between 20-37%, whereas the FO of gastropods in the other two seasons had wider
366 ranges and lower means (spring = 3-33%, 14%; summer = 3-17%, 10%). The most frequently
367 found gastropod part within the fall samples was the operculum, which unfortunately could not
368 be used to identify the prey type down to the species level. Sand was over four times more
369 frequent within October Port Orford samples than any other site in any season.

370

371 3.2 Stable Isotope Analysis

372 3.2.1 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of Fishery Bait and Benthic Prey

373 While there was a great deal of overlap in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the expected bait and prey species
374 (*Figure 3*), on average, the bait species were higher in $\delta^{15}\text{N}$ and more depleted in $\delta^{13}\text{C}$ (*Table 3*).
375 The difference in average isotopic ratio was marginally statistically significant for $\delta^{15}\text{N}$ ($F_{1,13} =$
376 4.70, $p = 0.049$) while not statistically significant for $\delta^{13}\text{C}$ ($F_{1,13} = 2.60$, $p = 0.131$). Commonly
377 used bait species Black rockfish (*Sebastes melanops*), Pacific mackerel (*Scomber japonicus*), and
378 Pacific sardines (*Sardinops sagax caerulea*) had the highest relative mean $\delta^{15}\text{N}$ values. The squid

379 *Illex* sp. was low in $\delta^{15}\text{N}$, indistinguishable from many of the common invertebrate benthic prey
380 species, but more depleted in $\delta^{13}\text{C}$ as expected for pelagic species as were mackerel (*Scomber*
381 *japonicus*) and the one salmon sample. In terms of $\delta^{13}\text{C}$, the frequent bait species cockle clam
382 (*Clinocardium nuttallii*) and razor clam (*Siliqua patula*) were nearly identical to the composite of
383 small offshore bivalve species analyzed. Juvenile *Cancer magister* under 25mm CW, which were
384 included due to the reported frequency of cannibalism within the Dungeness crab population, had
385 the highest mean $\delta^{13}\text{C}$ (-15.74, similar in value to the adults sampled) compared to all other bait
386 and prey sampled, except for eelgrass, at -11.04. Notably, the *C. magister* under 25mm CW had
387 much lower $\delta^{15}\text{N}$ (10.22) than the sampled adults.

388

389 3.2.2 Dungeness Crab Isotopic Niche

390 The isotopic niches of each Dungeness crab sex and size class varied from each other,
391 although the magnitude and directionality of those variations differed between the two sexes.
392 The Standard Ellipse encompassing 40% of the samples around the centroid of the legal male
393 ellipse showed to greatest degree of overlap with the sub-legal male ellipse and the least overlap
394 with the large females (*Figure 4a*). Across sizes and sexes the tissue of legal males contained the
395 highest mean $\delta^{13}\text{C}$ values (-15.69 ± 0.49) and the lowest mean $\delta^{15}\text{N}$ values (13.22 ± 0.52)
396 (*Figure 4a*) while the large females contained the lowest mean $\delta^{13}\text{C}$ values (-16.35 ± 0.60) and
397 the highest mean $\delta^{15}\text{N}$ values (13.75 ± 0.60) (*Table 4*) with a median vector distance of 0.924
398 and a median vector angle of 2.20 between LM and LF (*Figure 4b*). The mean $\delta^{13}\text{C}$ value of sub-
399 legal males (-16.01 ± 0.58) was lower than legal males, while $\delta^{15}\text{N}$ was similar at 13.32 ± 0.48 .
400 The small female group showed still lower $\delta^{13}\text{C}$ (-16.35 ± 0.59 ; like large females) and similar
401 $\delta^{15}\text{N}$ (13.34 ± 0.50) compared to sub-legal males. In descending order by median vector distance

402 followed by median vector angle, the remaining pair-wise outputs were LM vs. SF (0.76; -1.41),
403 LM vs. SM (0.57; 2.47), LF vs. SF (0.46; 1.21), LF vs. SM (0.45; -1.36), and lastly SF vs. SM
404 (0.35; 1.64). SEAc values were slightly larger for females (LF = 0.94; SF = 0.94) than males
405 with legal-sized males having the smallest ellipse area (LM = 0.83; SM = 0.89).

406 The ellipses comparing $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of all females across three seasons show
407 mean $\delta^{15}\text{N}$ decreased from a high of 13.98 ± 0.58 in the spring through summer to a low of 13.07
408 ± 0.53 in the fall, while $\delta^{13}\text{C}$ remained similar (*Figure 5a*), particularly in the north and at least
409 between summer and fall in the south (*Figure 6*). Median pairwise vector distances were greatest
410 between spring and summer (0.96), followed by spring and fall (0.61), and summer and fall
411 (0.49). SEAc, which approximates the relative size of a consumer's trophic niche, was largest in
412 the fall (1.19), followed by the spring (0.67) and the summer (0.51) (*Table 4*).

413 ANOVA of average isotopic values of female crabs confirmed season to be highly
414 statistically significant for $\delta^{15}\text{N}$ ($F_{2,88} = 33.03$, $p < 0.001$) with significant differences in each
415 pairwise comparison of seasons (Tukey HSD all $p < 0.001$). There was no effect of region alone
416 ($F_{2,88} = 2.07$, $p = 0.123$) while there was a significant interaction between region and season
417 ($F_{3,88} = 6.07$, $p < 0.001$) likely due to the apparent lack of seasonal variability in the Central
418 region (*Figure 6*). There was some variability of site within region for $\delta^{15}\text{N}$ ($F_{2,88} = 4.33$, $p =$
419 0.016). In contrast, there was no effect of season on $\delta^{13}\text{C}$ ($F_{2,88} = 1.72$, $p = 0.185$) while there
420 were strong regional differences ($F_{2,88} = 18.83$, $p < 0.001$) due to females from the southern
421 region having much lower $\delta^{13}\text{C}$ values (*Figure 6*). There was no interaction of region and season
422 for $\delta^{13}\text{C}$ in females ($F_{3,88} = 4.33$, $p = 0.464$) and only marginal influence of site within region
423 ($F_{2,88} = 4.33$, $p = 0.055$).

424 Trophic variation of all males across four seasons showed the highest relative mean $\delta^{13}\text{C}$
425 ratios (-15.40 ± 0.41) in the spring with the rest of the seasons having high overlap and the
426 lowest relative mean $\delta^{15}\text{N}$ ratios in the fall (13.06 ± 0.65) with the rest of the seasons having high
427 overlap (*Figure 5b; Table 4*). Median pairwise vector distance was greatest between spring and
428 fall (0.67), followed by spring vs. summer (0.56), spring vs. winter (0.51), summer vs. fall
429 (0.34), fall vs. winter (0.29), and summer vs. winter (0.24). SEAc was greatest for fall (1.06),
430 followed by summer (0.74), winter (0.68), and spring (0.48) (*Table 4*).

431 ANOVA of average isotopic values of male crabs confirmed season to be statistically
432 significant for $\delta^{13}\text{C}$ ($F_{3,235} = 15.91$, $p < 0.001$), with spring higher overall than other seasons and
433 the other seasons being statistically indistinguishable. There also were regional differences in
434 $\delta^{13}\text{C}$ for male crabs ($F_{2,235} = 39.93$, $p < 0.001$) with each of the regions significantly different
435 from one another (with the south having the lowest $\delta^{13}\text{C}$ as in females) and no significant effect
436 of site within region ($F_{4,235} = 1.99$, $p = 0.096$). There was a significant interaction between region
437 and season ($F_{6,235} = 2.92$, $p = 0.009$) likely again due to the apparent lack of seasonal variability
438 in the Central region and with winter higher than spring in the southern region (*Figure 6*). $\delta^{13}\text{C}$
439 also differed between legal and sublegal sized male crabs ($F_{1,235} = 16.10$, $p < 0.001$) with the
440 sublegal males generally more depleted in $\delta^{13}\text{C}$.

441 $\delta^{15}\text{N}$ varied significantly among seasons ($F_{3,235} = 5.01$, $p = 0.003$; Tukey HSD indicates
442 summer different from fall) and regions ($F_{2,235} = 50.25$, $p < 0.001$) for males; however, the
443 interaction of season and region was highly significant ($F_{6,235} = 4.48$, $p < 0.001$), due to seasonal
444 variability in $\delta^{15}\text{N}$ being only apparent in the South (*Figure 6*). There was no significant effect of
445 site within region ($F_{4,235} = 0.45$, $p = 0.776$). $\delta^{15}\text{N}$ also differed between legal and sublegal sized
446 male crabs ($F_{1,235} = 16.10$, $p = 0.023$) with the sublegal males generally more enriched in $\delta^{15}\text{N}$.

447

448 4. Discussion

449 Three aspects of the results provided the strongest evidence for seasonal consumption of
450 commercial fishery bait by Dungeness crab. First, sampled females showed high springtime $\delta^{15}\text{N}$
451 values declining through the fall. This trend could be indicative of overall higher trophic level
452 bait consumption during the peak commercial fishing season, followed by feeding on lower
453 trophic level wild prey in the fall. Second, a high proportion of empty guts were observed in the
454 spring compared to the summer and fall. Empty guts could reflect consumption of soft tissue bait
455 that doesn't leave as many hard structures behind compared to wild prey. Third, both male and
456 female crabs showed the largest approximated trophic niches in the fall compared to the other
457 seasons, which could be indicative of broader foraging for wild prey in the absence of
458 abundantly available bait.

459 However, non-fisheries dependent factors also undoubtedly influence seasonal variation
460 in the feeding ecology of Dungeness crab, given the dynamic nature of benthic food webs at the
461 marine-terrestrial interface. A better understanding of the species' feeding strategy would aid in
462 clarifying the influence of anthropogenic organic matter subsidies on the *Cancer magister*
463 population. This study contributes to that understanding by suggesting an underestimation of
464 both lower trophic level and carbon-enriched food sources in previous Dungeness crab feeding
465 studies and demonstrating strong regional variations in the crabs' $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values.

466 We hypothesized that the strongest isotopic bait signature would be evident in the spring,
467 following the wintertime peak in fishing effort, characterized by relatively high $\delta^{15}\text{N}$ and
468 depleted $\delta^{13}\text{C}$ due to the use of higher trophic level, pelagic species such as herring, mackerel, and
469 sardines. The seasonal variation in $\delta^{15}\text{N}$ of sampled female crabs supported this hypothesis, with

470 the highest mean values in the spring, declining through summer and fall. However, average $\delta^{13}\text{C}$
471 values varied little across seasons for females, suggesting either consistent food source
472 provenance or shifting sources creating a similar cumulative signature over time. In males, mean
473 $\delta^{15}\text{N}$ did not vary seasonally and $\delta^{13}\text{C}$ was relatively enriched in the springtime compared to all
474 other seasons, which contradicts the hypothesis of depleted $\delta^{13}\text{C}$ through pelagic bait
475 consumption.

476 Commercial fishery baiting practices could explain the differences in seasonal isotopic
477 variation between males and females. The Oregon Department of Fish and Wildlife (ODFW)
478 only permits harvest of male crabs over 159 mm CW; however, females also enter the pots.
479 Fishermen return captured females to the ocean where they can eat discarded bait, reenter pots,
480 and consume more bait. Repeated consumption of higher trophic level bait species would lead to
481 $\delta^{15}\text{N}$ enrichment in females compared to legal males. However, sub-legal males (<159 mm CW)
482 are also caught and returned to the ocean. If repeated capture and bait consumption does increase
483 $\delta^{15}\text{N}$, this impact would be evident in both sublegal males and females.

484 In this study, we did not see seasonal nitrogen enrichment in sublegal males, however,
485 spring sublegal males ($n = 9$) were only sampled at the Newport site (Central), which showed the
486 lowest overall seasonal variation of any site in the study. The small sample size for spring
487 sublegal males means that the average values for all spring males combined are weighted
488 towards legal males ($n = 60$). On the other hand, sub-legal males did have overall higher nitrogen
489 than legal males, supporting the hypothesis of enhancement due to repeated bait access as
490 compared to legal-sized males. Further study would be required to discern possible nitrogen
491 enrichment of sublegal males in the spring.

492 Although our ANOVAS on $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of bait vs. prey did show significantly higher
493 $\delta^{15}\text{N}$ in prey than bait, the isotopic composition of bait inputs likely varies dynamically given the
494 wide variety of baits used by the commercial Dungeness crab fishery and the temporal variation
495 in fishing effort. According to Bostrom et al. (2018), the three most used bait types are squid,
496 clams, and sardines, all of which occupy distinct ecological niches and trophic positions. Some
497 feeding on bait could be difficult to discern from wild prey consumption using consumer isotope
498 ratios. For instance, a Dungeness crab consuming only razor clams from commercial crab pots
499 would be difficult to differentiate from a Dungeness crab feeding only on small, naturally
500 occurring bivalves. Information on the types, amounts, and spatiotemporal distribution of
501 commercial bait use would help to develop a more dynamic and accurate representation of
502 variable bait inputs.

503 Non-fishery related factors, including site fidelity and reproductive strategy, could also
504 contribute to the highly statistically significant ($p < 0.001$) differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of male
505 versus female Dungeness crabs observed in this study. Some evidence suggests that female crabs
506 inhabit smaller ranges than males, which could lead to less variation in $\delta^{13}\text{C}$ among females
507 compared to males. Stone & O'Clair (2001) found that female Dungeness crabs in Fritz Cove,
508 Southeast Alaska typically only ranged ~1.5 km outside the cove while their male counterparts
509 ranged ~7.2 km. Cerdal & Wolff (1993) hypothesized that observed heterogeneous diets of male
510 and female *Cancer polyodon*, a closely related species to *Cancer magister*, were the result of
511 relatively mobile male crabs protecting a "harem" of sedentary female crabs (Orensanz &
512 Galucci 1988, Wolff & Soto 1992). The mobile males would be more likely to graze on broader
513 suite of available epibenthic sources, while the females would be more likely to exhibit predatory
514 behavior within a reduced range. Although mate guarding has not been observed in *Cancer*

515 *magister*, some authors hypothesize that it likely occurs (Christy 1987, Smith et al. 1994). Higher
516 rates of predatory behavior among females could lead the enriched $\delta^{15}\text{N}$ if their prey occupy
517 higher trophic positions than the epibenthic foods males consume. Furthermore, females form
518 dense brooding aggregations (Diamond & Hankin 1985, Armstrong et al. 1987, O'Clair et al.
519 1996, Scheduling et al. 2001), burying themselves in sediment and reducing feeding and foraging.
520 Stone & O'Clair (2002) documented female Dungeness in Southeast Alaska entering a period of
521 relative inactivity during the winter and early spring at around 16 m depth, especially if they
522 were carrying eggs. These periods of starvation would likely result in distinct isotopic signatures
523 within the tissues of female vs. male crabs, although further study would be required to
524 determine the magnitude and directionality of this variation.

525 Seasonal variation in both the percentage of empty guts and SEAc also provide evidence
526 for feeding on commercial fishery bait. In both sexes, the SEAc values approximating trophic
527 niche were the largest among crabs collected in the fall, which is consistent with broad foraging
528 due to bait scarcity in the summer. By far the greatest proportion of empty crab guts were
529 sampled in the spring, while none of the fall guts were empty. This difference could be the result
530 of feeding on soft baits (like squid, fish, and razor clam flesh) during the fishery season, which
531 can be digested and extruded relatively quickly versus food sources with hard parts (like small
532 invertebrate prey) in the fall. The high proportion of empty guts in the spring was surprising
533 given our hypothesis that cannibalism would contribute heavily to crab diets during that season.
534 In fact, we did not find any evidence of cannibalism within the guts. This result could be
535 explained by the observation that cannibalism occurs most frequently among small crabs with
536 $\text{CW} < 60\text{mm}$ (Stevens et al. 1982).

537 If Dungeness crab feed seasonally on higher trophic level bait inputs, this feeding could
538 impact their growth rates and/or reproduction, which could have profound implications for the
539 productivity of the commercial fishery. Based on the estimated amount of herring bait consumed
540 by American lobster (*Homarus americanus*) in the Gulf of Maine and the calculated growth rates
541 of that species, Saila et al. (2002) approximated that secondary productivity resulting from
542 commercial bait consumption accounted for up to one third of in-shore landings within that
543 fishery. Additionally, Kennish (1997) found that seasonal variation in food availability impacted
544 the reproductive output and body condition of an herbivorous crab, *Grapsus albolineatus*, off
545 Hong Kong. If fishery bait inputs contribute to Dungeness crab productivity, reducing fishing
546 effort could cause declines in that productivity by reducing caloric availability on the seafloor.

547 In recent years, domoic acid outbreaks and concerns regarding whale entanglement have
548 caused commercial Dungeness crab fishery closures. A naturally occurring algae, *Pseudo-*
549 *nitzschia australis*, produces the neurotoxin domoic acid, which causes amnesic shellfish
550 poisoning (ASP). This toxin accumulates in crab tissue, rendering it temporarily unsuitable for
551 human consumption. Evidence suggests that climactic-scale marine heat waves off the west coast
552 correlate to increased domoic acid production (McKibben 2016) that could become more
553 frequent as ocean temperatures rise. Regulatory bodies close Dungeness crab fisheries during
554 domoic acid outbreaks, a fact that had particularly catastrophic effects on the 2015-2016 fishery
555 season, when domoic acid levels were unusually high. If there is less bait input, crabs might eat
556 more benthic algae, resulting in even higher toxin loads.

557 Whale entanglement in crabbing gear, which has been on the rise since 2014, shortened
558 the 2018-2019 season. Prior to 2014, an average of fewer than 10 west coast whale
559 entanglements were reported each year; between 2015 and 2018 that number has increased to an

560 average of 44 confirmed entanglements per year (NOAA 201). This increased threat to protected
561 marine mammals has caused the California, Oregon, and Washington Departments of Fish and
562 Wildlife to shorten commercial Dungeness crab seasons and in some cases reduce the amount of
563 allowable gear in the water (ODFW 2019), which would again reduce bait inputs and could
564 affect productivity.

565 Although springtime $\delta^{15}\text{N}$ enrichment in female crabs, empty gut percentages, and the
566 SEAc values all support the idea that bait subsidies influence variation in Dungeness crab
567 feeding ecology, non-fishery influences likely play an even greater role in spatiotemporal
568 isotopic variation. Physical mixing in estuaries and primary production in coastal waters drives
569 fluctuations in the sources of organic materials (Hughes et al. 2000, Luís Antonio et al. 2012)
570 available for benthic organisms to eat. The high degree of isotopic variability within Dungeness
571 crabs and their food sources observed in this study agrees well with previous studies of
572 macroinvertebrate scavengers at this fluctuating land-sea interface. An analysis of seasonal
573 variation in the trophic niches of three decapod species, *Upogebia africana*, *Callichirus kraussi*,
574 and *Palaeomon peringueyi*, in the Kowie River Estuary of South Africa indicated that their diets
575 shifted temporally according to changes in food availability (Antonio & Richoux 2014).
576 Cannicci et al. (2007) found that in the Mediterranean, the intertidal crab *Pachygrapsus*
577 *marmoratus* shifts seasonally between carnivory and herbivory, taking advantage of shifting
578 marine and terrestrial inputs as food sources. All these examples relate to species that spend most
579 of their lives within estuaries and/or the intertidal zone. Researchers have focused less research
580 on seasonal variation in the feeding behaviors of species, like *Cancer magister*, that primarily
581 inhabit estuaries as juveniles but then travel back and forth into the ocean as adults.

582 Gaining a better understanding of overall Dungeness crab feeding strategies would allow
583 organic matter subsidies from the commercial fishery to be more discernable. This study
584 advances our understanding of Dungeness crab diets by suggesting a previous underestimation of
585 both lower trophic level and carbon-enriched food. Additionally, the strong regional variations in
586 the crabs' $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values demonstrate the complexity of the isotopic landscape and the
587 importance of avoiding broad generalizations about the isotopic compositions of consumer
588 species from different geographic areas.

589 Many of the crab guts contained lower trophic level food sources, especially at the
590 summer Reedsport (South) site, which stood out from all other sample sites across regions and
591 seasons with the highest mean proportion of their guts contained macroalgae (28%), seagrass
592 (*Zostera marina*) (17%), and wood (7%) with 8% containing sand. Numerous authors have
593 suggested that lower trophic level food sources, such as benthic microalgae, are often
594 underrepresented in Dungeness crab feeding studies due to the difficulty of identifying food
595 sources that lack hard structures. Jensen & Asplen (1998) hypothesized that filamentous diatoms,
596 eelgrass epiphytes, and algae could provide food during periods of prey scarcity or intense
597 competition between densely recruited juveniles. They observed early instar crabs feeding on
598 eelgrass epiphytes in Puget Sound. In British Columbia, MacKay (1942) reported algae as the
599 fourth most important food source for Dungeness crabs behind crustaceans, bivalves, and
600 polychaetes. Cerdal & Wolff (1993) observed at least five macroalgae species in *Cancer*
601 *polyodon* guts in a Chilean bay, including *Gracilaria* sp., *Polysiphonia* sp., *Ulva* sp, an
602 unidentified Phaeophyta, and an unidentified Rhodophyta. According to Luís Antonio et al.
603 (2012), coastal benthic macroinvertebrates, including crabs, utilized microalgae, terrestrial leaf
604 litter, and riverine particulate organic matter as food sources in shallow waters of the Tango Sea

605 off Japan. Additionally, several researchers have cautioned against ignoring sand in gut contents,
606 suggesting that crabs could eat it on purpose to capture calories from epibenthic microalgae
607 (Jensen & Asplen 1998, Haefner 1990).

608 In addition to dynamic seasonal variation, the stable isotope values also showed
609 statistically significant regional variation within and across seasons. This regionality suggests
610 that caution should be used when making assumptions about Dungeness crab isotopic values and
611 the magnitude and directionality of seasonal changes in those values within a given region based
612 on data from a different geographic area. For instance, the $\delta^{15}\text{N}$ values of male crabs in the South
613 region during the fall were significantly lower than any other region or season; indeed, mean
614 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were consistently the lowest in the South. The distinctively low $\delta^{15}\text{N}$ and
615 $\delta^{13}\text{C}$ values observed at the Port Orford site (*Table 4*) are likely linked to a shift in the north-
616 south shift in oceanographic conditions and invertebrate recruitment patterns in the Cape Arago-
617 Cape Blanco region (Broitman et al. 2008). If we had only sampled in the South region, our
618 estimates of mean isotopic values of Dungeness crabs would also have been significantly lower.
619 Similarly, Boecklen et al. (2011) urge that ecologists should avoid relying on literature for key
620 model parameters, consider “multiple sources of variation in isotopic signatures” beyond those
621 being tested, be sure not to make over-generalized inferences about diverse systems.

622 In assessing these results, several potential confounding factors must be carefully
623 considered. First, given the dynamic nature of coastal food webs, adult Dungeness crab and wild
624 prey samples would ideally have been collected in the same locations and time periods.
625 However, COVID-19 travel restrictions and partially fisheries-dependent sample collection made
626 that procedure impossible. As a result, prey samples within this study provide a general
627 understanding of their isotopic composition compared to fishery bait, rather than a precise

628 snapshot of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios at any given place and point in time. If adult Dungeness crab
629 and prey samples could be collected at the same place and time, Bayesian stable isotope mixing
630 models could potentially be used to gain more precise information about Dungeness crab dietary
631 composition and trophic position.

632 Another factor to consider is that the presence of inorganic carbon and lipids in stable
633 isotope samples sometimes confounds the interpretation of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios in food web
634 studies; acid washing of inorganic carbon and lipid extraction or quantitative correct are often
635 used to reduce these potential impacts. However, literature indicates that lipid extraction does not
636 have a significant effect on $\delta^{15}\text{N}$ nor $\delta^{13}\text{C}$ in crustacean muscle tissues (Bodin et al. 2007),
637 therefore neither lipid extraction nor arithmetic lipid correction was used for the adult Dungeness
638 crab samples. Additionally, all inorganic carbon structures in the adult Dungeness crab samples
639 were carefully excluded by hand, and therefore are unlikely to impact the results.

640 As for the bait and prey samples, inorganic carbon structures were excluded except in the
641 crustaceans prey (*Crangon* sp., cumaceans (Diastylidae), hermit crabs (Paguroidea), and juvenile
642 *Cancer magister* (CW<25mm)). These prey species were not acid washed, which could
643 confound the interpretation of their $\delta^{13}\text{C}$ ratios. However, Bunn et al. 1995 found that acid
644 washing one species of shrimp did not affect mean $\delta^{13}\text{C}$ ratios in that species but did affect mean
645 $\delta^{15}\text{N}$. For crustacean prey, as with adult Dungeness crab, lipid extraction has been shown to have
646 no significant impact on $\delta^{15}\text{N}$ nor $\delta^{13}\text{C}$ (Bodin et al. 2007), and therefore neither lipid extractions
647 nor arithmetic corrections were applied to crustacean prey samples. Marine invertebrates,
648 including crustaceans and bivalves, tend to store carbon as glycogen rather than lipids, which
649 potentially reduces the need for lipid extraction (Patterson & Carmichael 2016). Lipids in teleost
650 fish, on the other hand, are widely known to alter the $\delta^{13}\text{C}$ ratios compared to results derived

651 from pure protein samples; therefore, we applied a linear correction model from Post et al. 2007
652 on all teleost bait and prey samples.

653 This analysis highlighted the inherent complexity of coastal marine and estuarine
654 ecosystems, which create dynamic contexts in which to interpret evidence for seasonal
655 fluctuations in the consumption of commercial fishery bait by Dungeness crabs. Despite and
656 perhaps because of this complexity, the results contribute to the pre-existing body of knowledge
657 about Dungeness crab feeding ecology, especially by characterizing differences between the
658 isotopic niches of sampled male and female crabs, demonstrating strong seasonal and regional
659 variations in isotopic tissue composition, and indicating that previous Dungeness crab feeding
660 studies may have underestimated the importance of lower trophic level food sources.
661 Additionally, this study revealed numerous opportunities to advance our understanding of
662 benthic food webs at the estuarine-marine gradient and the influence of anthropogenic organic
663 matter subsidies on Dungeness crabs within those systems. The isotopic composition of female
664 Dungeness crabs as they exit their brooding period, possible nitrogen enrichment of sublegal male
665 crabs through repeated capture, and the identification of micro and macroalgal species within
666 crab stomachs are all topics that warrant further investigation.

667

668 5. Conclusion

669 Despite the economic and ecological importance of *Cancer magister* off the Oregon coast
670 and on the west coast of the United States in general, this was the first study to look for evidence
671 of an impact of commercial Dungeness crab fishery bait on the feeding ecology of that species. It
672 was also the first study to investigate variation in the isotopic niches of male and female
673 Dungeness crabs. The results demonstrate the ecological complexity of feeding pathways across

674 the estuarine-coastal zone, with substantial variation in isotopic composition in crab tissues and
675 gut contents across regions, seasons, sexes, and size classes. Female crabs in the North region
676 showed the strongest evidence for trophic enrichment through bait consumption in the spring.
677 The gut contents added support to a growing body of literature suggesting that lower trophic
678 level sources must be included in future Dungeness crab diet studies to gain a more complete
679 understanding of their feeding strategies. Laboratory studies to determine stable isotope trophic
680 discrimination values and tissue turnover rates would help to further advance such dietary
681 analyses. Additionally, more specific information about spatiotemporal variation in commercial
682 fishery bait inputs and the relative caloric values of wild prey and bait would advance our
683 understanding of the role of bait in Dungeness crab diets. The further progression of this work
684 would have implications for both our knowledge of benthic trophodynamics and Oregon's
685 coastal economy.

686

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694

695

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- 930

931 *Table 1: Dungeness crab collected sample sizes by sex, carapace width, and season.*

	Legal Males (>159 mm)	Sub-Legal Males (<159 mm)	Large Females (>159 mm)	Small Females (<159 mm)	Total
<i>Winter</i>	50	3	0	0	53
<i>Spring</i>	50	9	18	10	934
<i>Summer</i>	31	44	10	33	935
<i>Fall</i>	38	25	11	16	90
TOTAL	169	81	39	59	937

938 *Table 2: Frequency of occurrence (FO) of identified gut content items and empty guts within adult Dungeness crabs sampled across*
 939 *three seasons (spring, summer, and fall 2020) within three regions of the Oregon coast. FO is calculated by dividing the number of*
 940 *crab guts that contained a particular item (or was empty) at each sample site and date divided by the total number of crabs collected*
 941 *at that sample site and date.*

Date	Region	n	Location	Teleost	Bivalvia	Soft Tissue	Decapoda	Gastro-poda	Macro-algae	Sand	Bryozoa	Echino-derm	Wood	Seagrass	Empty
Spring															
3/12/2020	North	30	Garibaldi	0.03	0.17	0.1	0.1	0.07	0.03	0	0.07	0	0.03	0.03	0.43
3/25/2020	North	30	Pacific City	0.43	0.13	0.23	0.07	0.03	0.03	0.03	0	0	0	0	0.23
4/3/2020	Central	30	Newport	0.27	0.17	0.13	0.07	0.33	0	0	0	0	0	0	0.4
			Average	0.24	0.16	0.16	0.08	0.14	0.02	0.01	0.02	0	0.01	0.01	0.35
Summer															
6/10/2020	Central	30	Newport	0.1	0.2	0.37	0.13	0.17	0.07	0.07	0	0.07	0	0.03	0.2
7/1/2020	North	30	Garibaldi	0.67	0.27	0.2	0.63	0.03	0.03	0.1	0.07	0.07	0	0	0
7/9/2020	Central	30	C. Perpetua	0.07	0.33	0.1	0.30	0.07	0.03	0.03	0	0.03	0.07	0.03	0.13
7/10/2020	South	25	Reedsport	0.24	0.24	0.28	0.12	0.12	0.28	0.08	0.12	0	0.07	0.17	0.12
			Average	0.27	0.26	0.24	0.30	0.1	0.1	0.07	0.05	0.04	0.03	0.06	0.08
Fall															
10/15/2020	North	30	Garibaldi	0.3	0.33	0.07	0.2	0.37	0.1	0.07	0.07	0	0	0	0
10/17/2020	Central	15	C. Perpetua	0	0.2	0.13	0.13	0.20	0.2	0	0	0.07	0	0	0
10/17/2020	Central	30	Newport	0.03	0.33	0.17	0.13	0.27	0	0	0	0	0	0	0
10/30/2020	South	30	Port Orford	0.77	0.37	0.5	0.13	0.30	0.07	0.33	0	0	0	0	0
			Average	0.28	0.31	0.22	0.15	0.28	0.09	0.1	0.02	0.02	0	0	0

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945 *Table 2: Sample size (n), mean, and standard deviation (σ) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in sampled*
 946 *commercial Dungeness crab fishery bait and prey species. Wherever possible, inorganic carbon*
 947 *structures were excluded from the samples. Crustacean prey was processed whole, which could*
 948 *confound the interpretation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. $\delta^{13}\text{C}$ in teleost bait and prey and mink were*
 949 *arithmetically lipid corrected according to Post et al. (2007) and are marked with an apostrophe*
 950 *after the value below. The presence of lipids in marine invertebrates has no significant impact on*
 951 *$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (Bodin et al. 2007), and therefore lipid corrections were not applied to those*
 952 *samples. The rows in gray contain samples that were processed at the Oregon State University*
 953 *(OSU) stable isotope lab, whereas the rows in white contain samples that were processed at*
 954 *NOAA's Alaska Fisheries Science Center. "n.d." indicates no data.*

Source	n	$\delta^{13}\text{C}$	σ	$\delta^{15}\text{N}$	σ
Prey					
Bivalve (<20mm)	10	-17.00	0.83	9.71	0.16
Shrimp (<i>Crangon</i> sp.)	17	-16.58	1.33	11.66	0.65
Cumacean (Diastylidae)	15	-16.91	0.74	8.07	0.67
Eelgrass (<i>Zostera marina</i>)	4	-11.04	1.11	7.07	0.46
Hermit Crab (Paguroidea)	10	-16.54	1.31	9.42	0.50
<i>C. magister</i> (CW<25mm)	15	-15.74	1.13	10.22	0.71
Olive Snail (<i>Callinax</i> sp.)	16	-17.80	0.33	9.86	0.59
Pacific Sanddab (<i>Citharichthys sordidus</i>)	5	-21.07'	0.70'	11.43	0.35
Bait					
Cockle (<i>Clinocardium nuttallii</i>)	7	-16.84	0.15	9.20	0.19
Herring (<i>Clupea pallasii</i>)	10	-14.71'	1.74'	9.42	0.50
Pacific Razor Clam (<i>Siliqua patula</i>)	10	-17.00	0.22	9.26	0.22
Squid (<i>Illex</i> sp.)	11	-19.00'	1.61'	11.36'	0.77'
Mackerel (<i>Scomber japonicus</i>)	11	-19.17'	0.97'	14.75	0.32
Mink (<i>Neovison vison</i>)	10	-17.16'	0.65'	9.75	0.41
Black Rockfish (<i>Sebastes melanops</i>)	7	-18.09'	0.21'	14.95	0.58
Salmon (<i>Oncorhynchus</i> sp.)	1	-21.51'	n.d.	11.25	n.d.
Sardine (<i>Sardinops sagax caerulea</i>)	11	-17.38'	0.29'	13.75	0.19

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960 *Table 3: Contains the sample size (n), mean, and sample standard deviation (σ) of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$*
 961 *ratios for sampled adult Dungeness crabs, divided by sex, across four seasons (December 2019-*
 962 *May 2021) and three regions of the Oregon coast. It also includes Standard Ellipse Area*
 963 *corrected by sample size for all crabs collected at each site and date, divided by sex, region, and*
 964 *season. Inorganic carbon structures were excluded from the samples; only leg tissue was*
 965 *included for all samples. Gray rows contain samples run at the OSU stable isotope lab, while all*
 966 *other samples were analyzed at the NOAA's Alaska Fisheries Science Center. "n.d." indicates*
 967 *no data.*

Date	Region	Area	$\delta^{13}\text{C}$ v. V-PDB \pm							
			n		σ		$\delta^{15}\text{N}$ v. Air $\pm \sigma$		SEAc	
			M	F	M	F	M	F	M	F
Spring										
3/12/2020	North	Garibaldi	21	9	-15.45 ± 0.35	-16.17 ± 0.40	13.44 ± 0.38	13.87 \pm 0.49	0.54	0.62
3/25/2020	North	Pacific City	20	10	-15.36 ± 0.30	-16.42 ± 0.49	13.39 ± 0.33	14.42 \pm 0.38	0.79	0.45
4/3/2020	Central	Newport	18	9	-15.36 ± 0.56	-16.14 ± 0.43	13.16 ± 0.40	13.58 \pm 0.55	0.90	0.68
5/18/2021	South	Port Orford	10	n.d.	-16.13 ± 0.25	n.d.	12.65 ± 0.42	n.d.	0.26	n.d.
Summer										
7/1/2020	North	Garibaldi	20	10	-16.66 ± 1.22	-16.45 ± 0.19	13.62 ± 0.34	13.54 \pm 0.23	0.97	0.16
6/10/2020	Central	Newport	20	10	-15.44 ± 0.26	-15.99 ± 0.62	13.25 ± 0.57	13.40 \pm 0.45	0.80	0.96
7/9/2020	Central	Cape Perpetua	22	11	-15.90 ± 0.54	-16.43 ± 0.31	13.27 ± 0.43	13.49 \pm 0.27	0.57	0.29
7/10/2020	South	Reedsport	13	12	-16.34 ± 0.47	-16.87 ± 0.45	13.24 ± 0.45	13.45 \pm 0.27	0.52	0.42
Fall										
10/15/2020	North	Garibaldi	20	10	-16.04 ± 0.55	-16.07 ± 0.83	13.48 ± 0.52	13.00 \pm 0.54	1.16	1.15
10/17/2020	Central	Newport	23	7	-15.58 ± 0.33	-15.90 ± 0.16	13.29 ± 0.38	13.50 \pm 0.32	0.37	0.17
10/30/2020	South	Port Orford	20	10	-16.38 ± 0.30	-16.91 ± 0.27	12.41 ± 0.52	12.85 \pm 0.51	0.49	0.42
Winter										
12/16/2019	North	Astoria	10	n.d.	-15.95 ± 0.56	n.d.	13.76 ± 0.32	n.d.	0.61	n.d.
12/16/2019	Central	Newport	7	n.d.	-15.47 ± 0.40	n.d.	13.12 ± 0.34	n.d.	0.38	n.d.
12/16/2019	Central	Cape Perpetua	10	n.d.	-15.54 ± 0.38	n.d.	13.28 ± 0.31	n.d.	0.42	n.d.
12/16/2019	South	Langlois	10	n.d.	-15.94 ± 0.31	n.d.	13.17 ± 0.48	n.d.	0.14	n.d.
12/16/2019	South	Cape Arago	9	n.d.	-15.95 ± 0.47	n.d.	13.06 ± 0.48	n.d.	0.64	n.d.
12/16/2019	South	Port Orford	7	n.d.	-16.31 ± 0.30	n.d.	12.93 ± 0.52	n.d.	0.65	n.d.

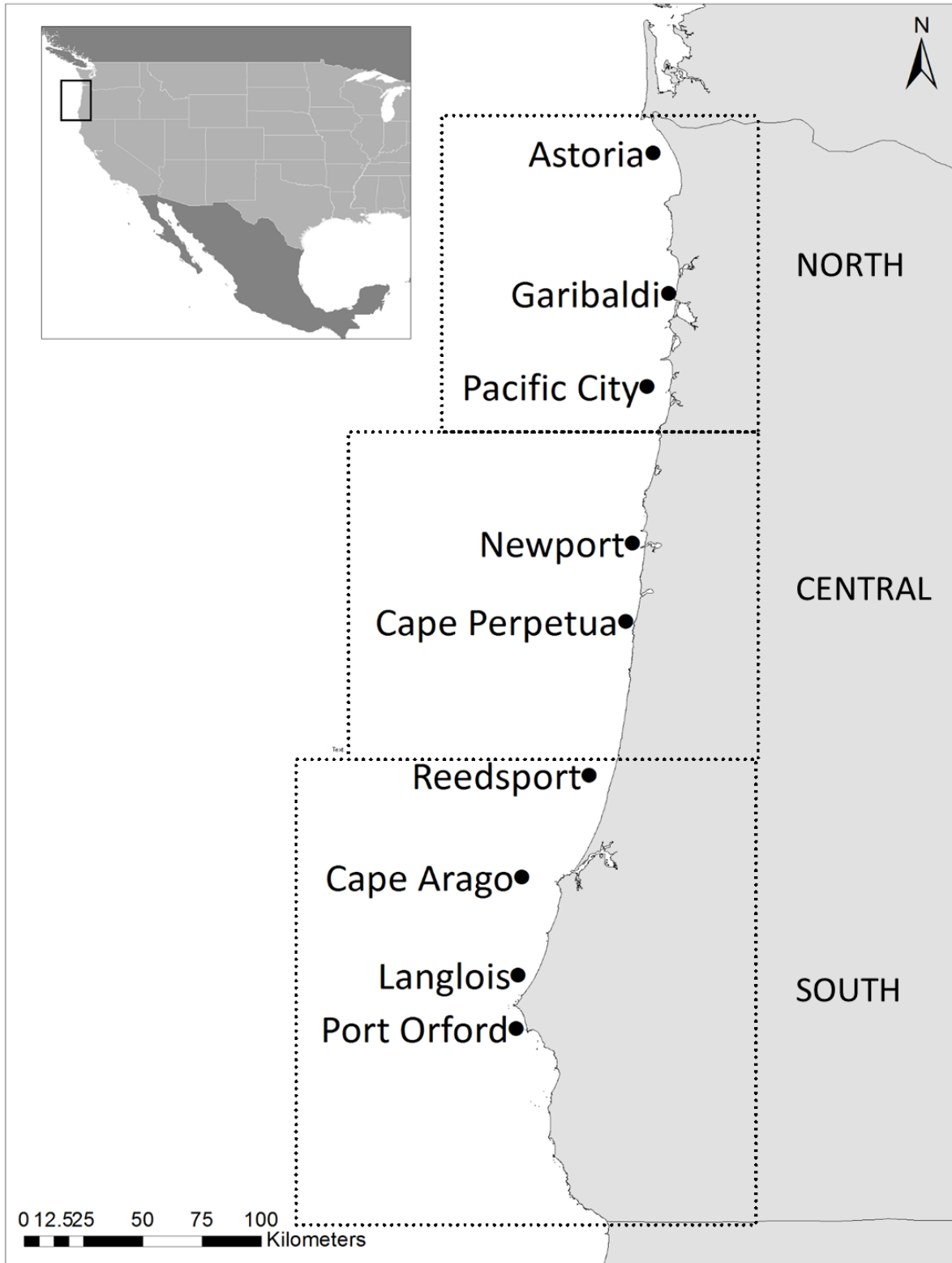
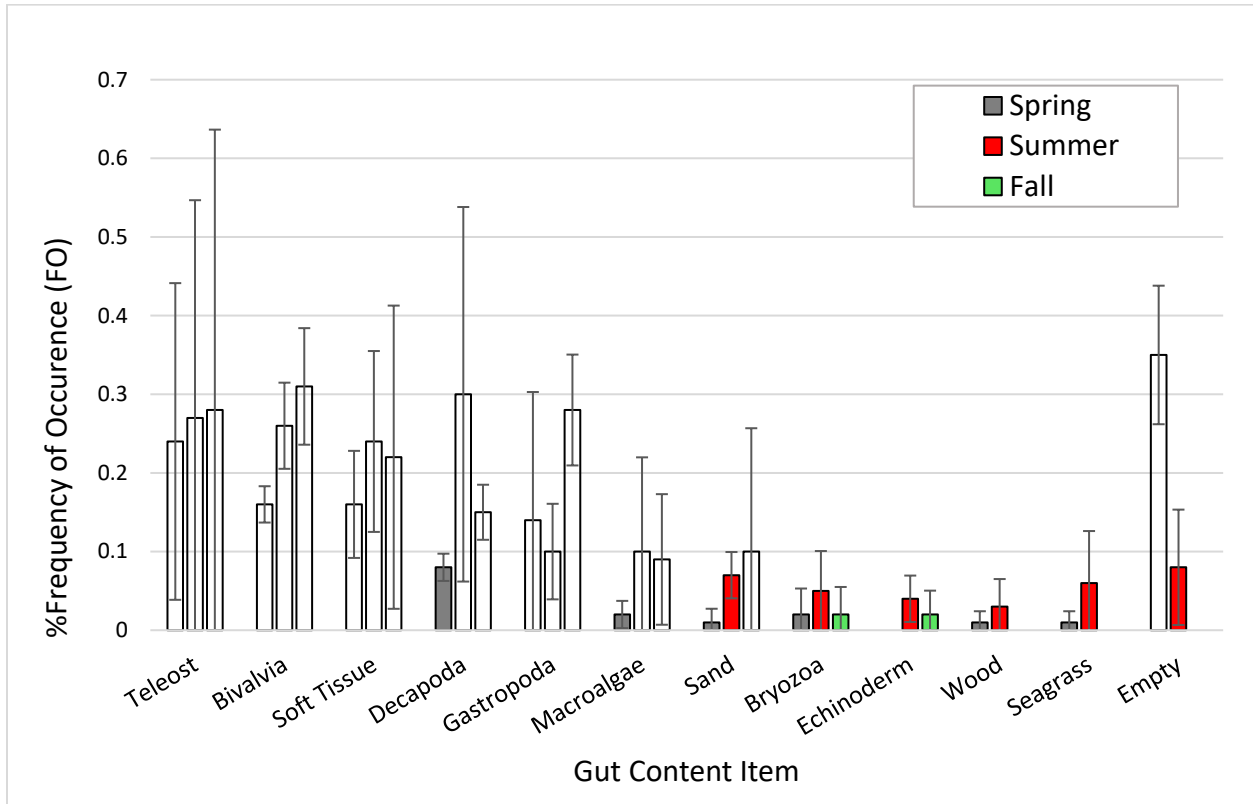


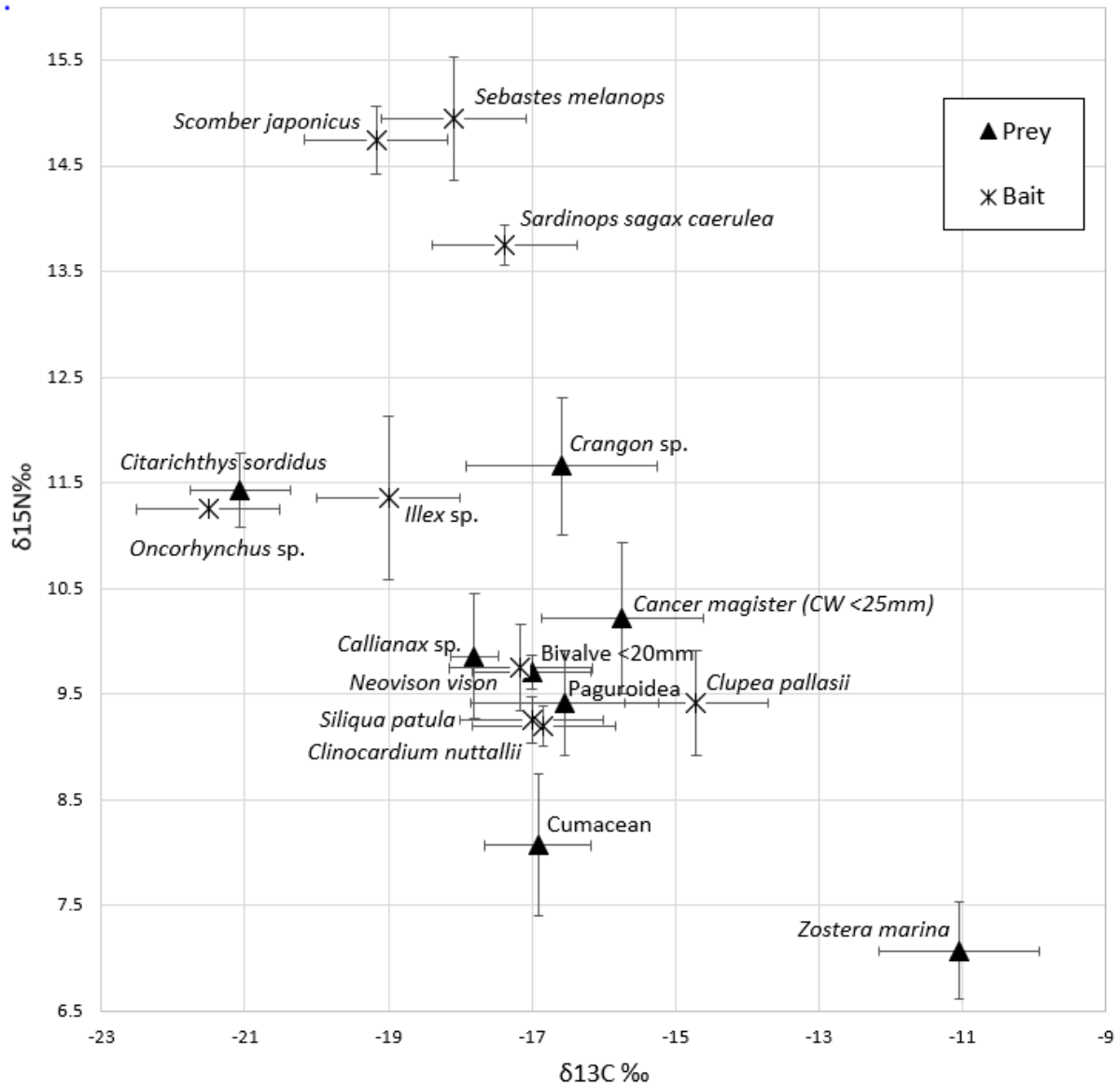
Figure 1: A map of the sample collection sites off the Oregon coast. Sample sites were divided into "North," "Central," and "South" regions. The dashed boxes represent the extent of each region. The map projection is State Plan NAD 1983 (Meters), and the base map data source is ESRI 2010.

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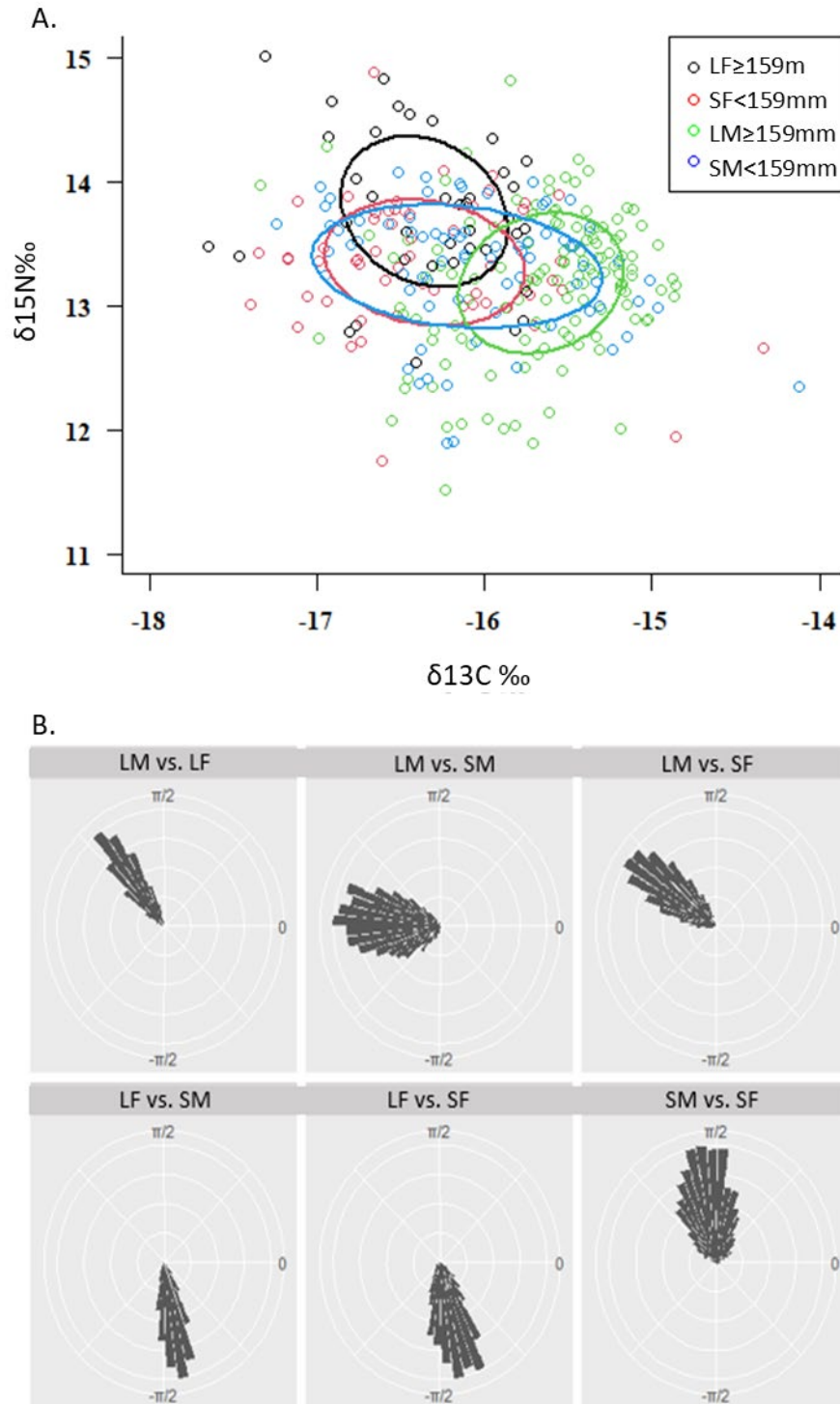
970

971 *Figure 2: Mean frequency of occurrence (FO) of gut content items and empty stomachs for all*
 972 *sampled stomachs across regions, separated by season. The error bars depict standard deviation*
 973 *of frequency of each item type within each season. Item types or empty guts that lack bars for a*
 974 *particular season indicate that none of that item type was found in guts during that season, or*
 975 *that no guts were empty during that season. Notice that mean FO of items in the category*
 976 *Decapoda was over twice as high as in the summer compared to the other seasons. Similarly,*
 977 *items in the category Gastropoda occurred over twice as frequently in the fall compared to*
 978 *summer and spring. Also, a mean of 35% of stomachs were empty in the spring, whereas 0%*
 979 *were empty in the fall.*



980

Figure 3: This figure depicts a source tracer biplot by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for Dungeness crab bait and prey species. The triangles indicate prey species, while the X represent bait. The error bars associated with both symbols show sample standard deviation for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. $\delta^{13}\text{C}$ for teleost bait and prey species are arithmetically lipid corrected according to the linear model from Post et al. 2007. Only muscle tissue was used for fishes, shells were removed from molluscs, crustacean prey (*Crangon sp.*, cumaceans (*Diastylidae*), hermit crabs (*Paguroidea*), and juvenile *Cancer magister (CW <25mm)* were ground and processed whole.

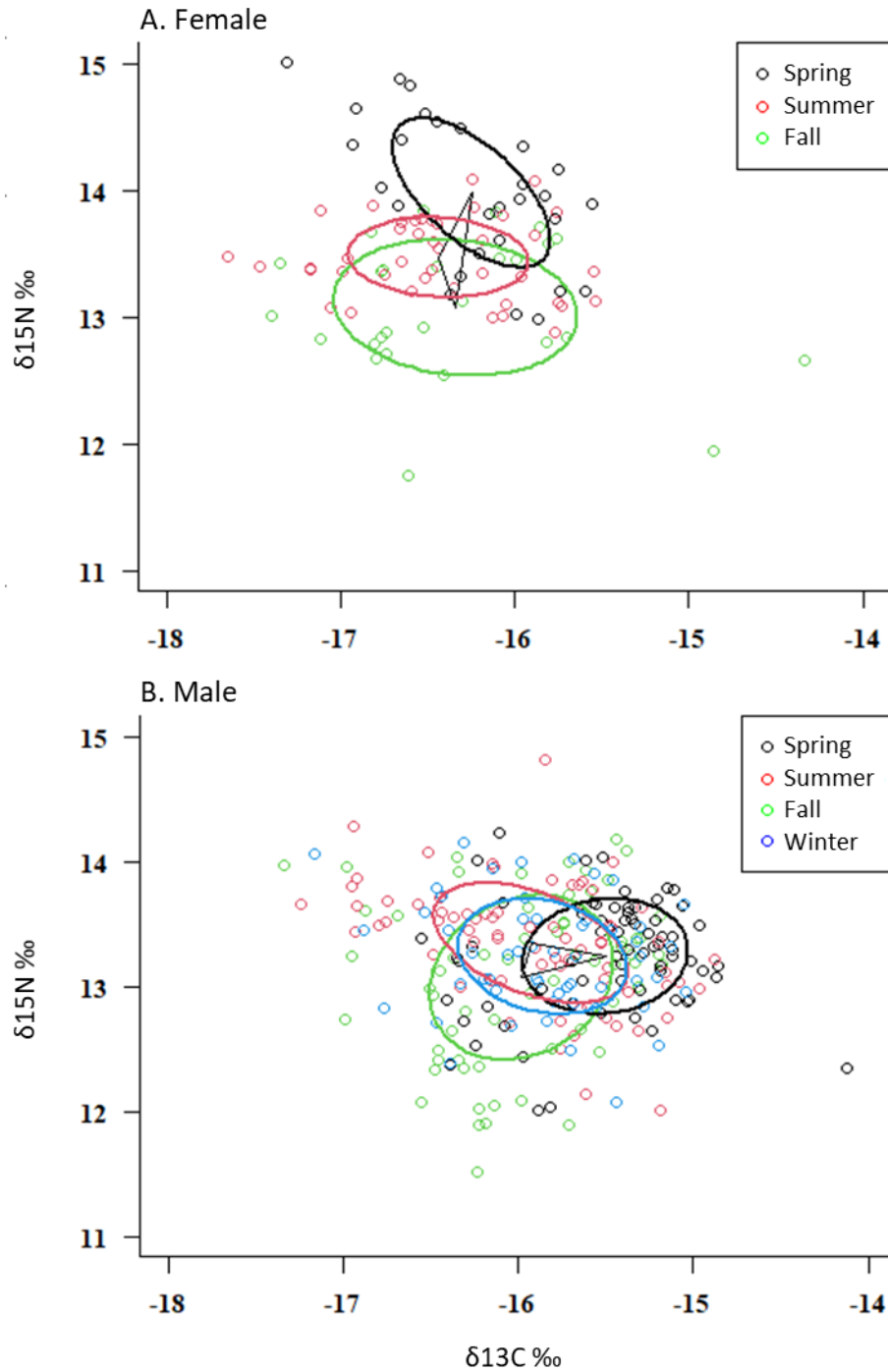


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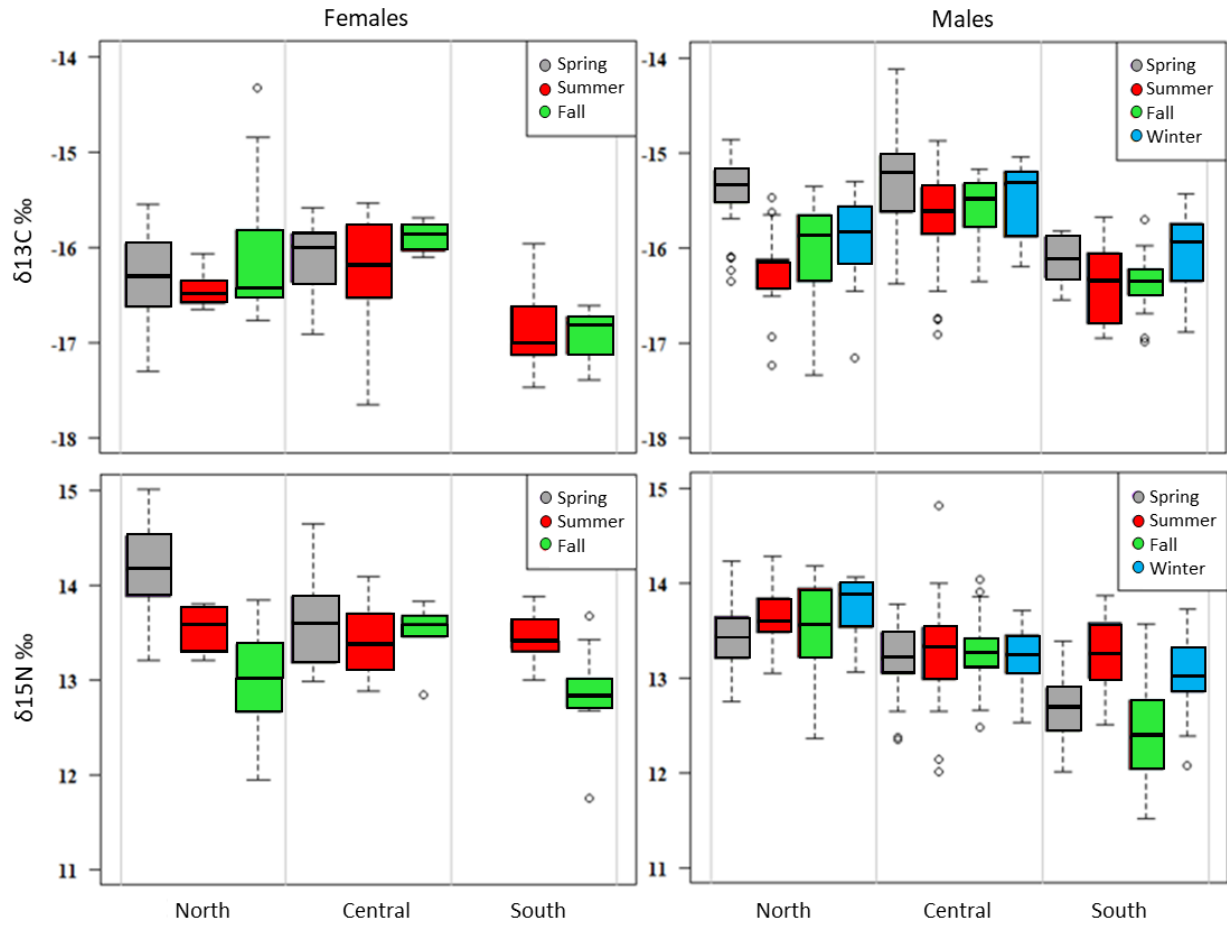
983

Figure 4: A. The SI position of each sampled crab (smaller hollow circles) and Standard Ellipse Areas (larger ellipses) corrected by sample size (SEAc) for legal-sized males (LM; $CW \geq 159\text{mm}$), sub-legal males (SM; $CW < 159\text{mm}$), large females (LF; $CW \geq 159\text{mm}$), and small females (SM; $CW < 159\text{mm}$). SEAc encompasses 40% of the sample points from each group around their centroid, plotted with $\delta^{13}\text{C}$ on the x-axis and $\delta^{15}\text{N}$ on the y-axis. B. Polar histograms indicating the direction of paired difference vectors between all points in each group (listed above). Data include all spring, summer, and fall samples. Winter samples were excluded from these plots because no female samples were collected during the winter.



984

Figure 5: Seasonal variation in Standard Ellipses Areas corrected by sample size (SEAc) to approximate trophic niche for female (A) and male (B) crabs. Each ellipse encompasses 40% of all the sample points (depicted as small hollow circles) around the centroid separated by season. The lines within the ellipses connect the centroids of each ellipse. Plot A does not contain wintertime samples because female crabs were not sampled during the winter.



985

986 *Figure 6: Seasonal and regional variation in $\delta^{13}\text{C}$ (top panels) and $\delta^{15}\text{N}$ (bottom panels) ratios*
 987 *of sampled female (left panels) and male (right panels) Dungeness crabs. The center bar in the*
 988 *box represents the median value, while the upper and lower bounds of the box show the first and*
 989 *third quartiles. The whiskers extend from the minimum to maximum values, excluding outliers,*
 990 *which are depicted as open circles. No females crabs were collected during the spring season in*
 991 *the south region.*