

1 OCNMS Manuscript: What I did with my summer vacations before covid  
2 ruined everything

3 Tolimieri, N.

4 Liu, O.

5 Sullaway, Gsul.

6 Samhouri, J.

7 Harvey, C..

8           Shelton, A.

9 Andrews, K.

10 Williams, G.

11 Lonhart, S.

12 Feisty B.

13 Frick, K.

14 Jenny?

15       Whoever else.. no particular order above; subject to change

16 Abstract

17 TBW

18

19    **Introduction**

20    Jamealian intro on climate and changing environment? 1 Para max or just a few sentences.

21    Kelp forests occur in nearshore, marine habitats throughout temperate waters (Dayton 1985,  
22    Steneck et al. 2002, Smale 2020). These communities are highly productive (Mann 1973) with kelp  
23    supporting nearshore food webs (Carr and Reed 2016, Yorke et al. 2019, Smale 2020, Chittaro et al.  
24    in preparation), and providing physical structure for array of vertebrate and invertebrate species  
25    (REF, Carr, Anderson, etc), especially juvenile rockfishes *Sebastodes* spp (REF). Other ecosystem effects  
26    include influencing sedimentation dynamics (Connell 2005), reducing wave energy (Pinsky et al.  
27    2013), and providing carbon storage (Wilmers et al. 2012).

28    A range of abiotic and biotic factors influence the dynamics of kelp forest communities. Cool,  
29    nutrient rich waters promote high kelp cover, while warm, nutrient poor waters, and high wave  
30    energy can reduce kelp coverage (Pfister et al. 2018, Pinsky et al. 2019), sometimes dramatically  
31    (Rogers-Bennett and Catton 2019). At the same time, predators impose top-down forcing on  
32    herbivores and reducing herbivory and allowing kelp forests to persist. Along the west coast of  
33    North America, otters *Enhydra lutris*, urchins, and kelp form a well-studied and iconic trophic  
34    cascade (Estes et al. 2004, Watson and Estes 2011, Shelton et al. 2018). However, within this  
35    cascade, there is also a redundancy of predators. Large asteroids, especially *Pycnopodia*  
36    *helianthoides* are important urchin predators (Burt et al. 2018), as are California sheepshead  
37    *Semicossyphus pulcher* and spiny lobsters *Panulirus interruptus* in waters off of southern California

38    (Beas-Luna et al. 2020, Eisaguirre et al. 2020). When these cascades are disrupted by climatic  
39    events or changes in predator or urchin density, the kelp forests can shift to an alternate stable  
40    state of urchin barrens, which may revert back to kelp forests with the reestablishment of

**Deleted:** In New Zealand predation by snapper (*Pagrus auratus*) reduces the density of sea urchins *Evechinus chloroticus* and herbivory on the kelp *Ecklonia radiata* and the fucoid *Carpophyllum maschalocarpum* (Shears and Babcock 2003)

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**Deleted:** This disruption can come in many forms including loss of top predators (otters), loss of kelp canopy due to climatic impacts and related changes in urchin foraging behavior, and large urchin recruitment events evade top-down control, potentially due to loss predator redundancy (Dunn and Hovel 2019). Conversely, reestablishment of the top predators and/or decreases in herbivore densities due to mortality events can result in a shift back to kelp forests

56 [predators or die offs of herbivores](#), (Watson and Estes 2011, Shelton et al. 2018, Rogers-Bennett and  
57 Catton 2019, Williams et al. 2021).▼

**Deleted:**

**Deleted:** Both states have associated socio-ecological costs and benefits (Gregor et al. 2020).

58 Kelp forest communities along the west coast of North America have experienced at least two  
59 major perturbations in the last decade. Starting in 2013 sea star wasting disease (SSWD) decimated  
60 asteroid populations of at least 20 species from California to Alaska leading to extensive reductions  
61 in population density, and in some cases, apparent local extinctions (Hewson et al. 2014,  
62 Montecino-Latorre et al. 2016, Hewson et al. 2018). As many of the hardest hit sea stars (*P.*  
63 *helianthoides* and *Pisaster* spp.) are urchin predators, the die off likely resulted in a reduction in top  
64 down pressure on urchins.

65 Concurrently, the eastern Pacific experienced a marine heat wave (MHW) from 2014-2016  
66 (Bond et al. 2015, Jacox et al. 2018), which had profound effects on West Coast ecosystems  
67 including substantial losses of kelp cover in some regions. There were subsequent decreases red  
68 abalone *Haliotis rufescens* and red sea urchins *Mesocentrotus franciscanus* due to starvation, while  
69 purple urchin *Strongylocentrotus purpuratus* populations increased and their behavior shifted to  
70 active herbivory (Cavanaugh et al. 2019, Rogers-Bennett and Catton 2019, Smith et al. 2021). The  
71 MHW may have also exacerbated sea star die off (Harvell et al. 2019). Additionally, seabird mass  
72 mortality events (Piatt et al. 2020) and increases in whale entanglements in fishing gear due to  
73 habitat compression (Santora et al. 2020) were also associated with the MHW. This same period  
74 also saw changes in the ichthyoplankton (Nielsen et al. 2021), especially large increases in pelagic  
75 rockfish (*Sebastodes* spp) juveniles off the U.S. West Coast (Field et al. in press).

**Commented [NT1]:** This section a bit long? Drop the general MHW stuff and just focus on the 2014-2016 info?

**Deleted:** In addition to the direct effects of temperature on kelp cover (Pfister et al. 2018, Pinsky et al. 2019), warmer temperatures can lead to increases in grazing pressure (Smale 2020), and alter competitive interactions (Filbee-Dexter and Wernberg 2018). MHWs may also produce changes in nutrient availability (Carr and Kearns 2003, Kearns and Carr 2003) and may result in biodiversity loss (Smale 2020). The 2014-2016 MHW

76 However, community responses to the combination of the sea star die-off and the MHW varied  
77 regionally (Cavanaugh et al. 2019, Beas-Luna et al. 2020). For example, kelp loss in northern  
78 California was substantial, likely due to the combined effects of high water temperatures, low otter

90 densities, and a decrease in predatory sea stars (Rogers-Bennett and Catton 2019, Beas-Luna et al.  
91 2020, McPherson et al. 2021). Central and southern Californian kelp forests were more resilient,  
92 possibly due to greater predator redundancy (Beas-Luna et al. 2020), while in Baja California  
93 reductions in kelp cover likely due to species being at the range margins (**Meh**). Similar variation in  
94 the dynamics of kelp forests occur at smaller scales as well (Eisaguirre et al. 2020).

95 Here, we examine responses of fish and integrate communities to the sea star die off and the  
96 recent marine heat wave at five kelp forest sites along the coast of Washington, U.S.A. from 2016-  
97 2019. We start by examining assemblage structure and relationships with habitat for fish and  
98 macroinvertebrates to better understand the importance of habitat, and spatial and temporal  
99 variation in these communities. We then highlight three vignettes related to the SSWD and MHW  
100 and kelp forest communities. First, we ask whether sea stars have shown any recovery from SSWD  
101 and examine relationships between sea star density and prey density. Second, we examine trends in  
102 urchin density and the relationship between urchins and kelp to determine whether the sea star die  
103 off lead to or allowed increases in urchin densities and subsequent reductions in kelp cover. Finally,  
104 we determine whether the high numbers of pelagic rockfish juveniles seen during the heat wave  
105 translated to higher recruitment in 2016, examine spatial patterns in recruitment, and distinguish  
106 whether different species complexes vary in their spatial and temporal patterns. As our data are  
107 limited to 2016-2019 we highlight changes (potentially recovery) in these communities following  
108 these events, but cannot measure direct impacts of the events themselves.

**Commented [NT2]:** Language probably overly causal.

**Commented [NT3]:** The rockfish recruits feel a little orphaned and out of place here. We could delete. However, the connection would be recruitment to kelp and the high number of recruits seen in pelagic surveys during the blob.

109    **Materials and Methods**

110    *Study sites*

111    We conducted dive surveys at five sites in late July or early August of 2016-2019 within the  
112    Olympic Coast National Marine Sanctuary (OCNMS, designated in 1994) along the coast of  
113    Washington, U.S.A. (Fig. 1). These sites span much of the OCNMS from Destruction Island in the  
114    south to Neah Bay in the north. Four sites were on the outer coast, while Neah Bay is within the  
115    Strait of Juan de Fuca and just outside of the OCNMS. All sites were relatively protected from wave  
116    action and had subtidal rocky reefs and supported kelp stands consisting of *Macrocystis pyrifera*  
117    and/or *Nerocystis luekana* as well as understory algae such as *Pterygophora californica* (Shelton et  
118    al. 2018).

119    *Survey design*

120    At each site, we conducted visual surveys on scuba on 30 x 2 m transects to quantify: 1) fish  
121    abundance, 2) macroinvertebrate abundance, 3) kelp abundance, 4) other biotic habitat, and 5)  
122    substratum type (abiotic habitat, e.g., cobble, pavement, etc) (modified from Pondella et al. (2019)).  
123    At each site, we sample two locations, separated by 100+ m and marked by separate down lines,  
124    and two depths at each location (5 m and 10 m). One pair of divers sampled fish and quantified  
125    biotic habitat. The second pair of divers sampled macroinvertebrates and kelp and quantified  
126    substratum type. The lead diver laid down the transect tape and counted fish or  
127    macroinvertebrates and kelp. The second diver followed recording biotic habitat or substratum  
128    characteristics respectively. Both biotic habitat and substratum type were quantified using uniform  
129    point contact (UPC) methods by recording the organism or substratum directly under every meter  
130    mark along the transect for 30 data points per transect. Each pair of divers began transects from the

131 same drop point marked by the down-line and followed the same overall heading. However, pairs  
132 did not necessarily cover the exact same ground, so one cannot directly match fish counts to  
133 substratum characteristics at the transect level, for example. Therefore, we often summarize data  
134 by year x site x depth for some analyses.

Commented [NT4]: # of transects in general.

135 We counted and estimated the size (total length) of all fishes we observed within 2 m of the  
136 bottom and greater than 5 cm total length. The exception was rockfishes *Sebastodes* spp, for which we  
137 estimated sizes for all individuals since we were interested in monitoring rockfish recruitment.  
138 Divers estimated visibility on each transect by determining the distance at which the lead diver  
139 could see the fingers their buddy. Transects with visibility less than 2.0 m were excluded from the  
140 analyses including fishes.

141 For biotic habitat, the diver recorded the organism directly under the transect every meter  
142 mark (universal point contact, UPC). Biotic habitat included the following functional groups: brown  
143 algae, red algae, green algae, encrusting species, diatom layer, eelgrass/surfgrass, non-mobile  
144 invertebrates, or non-living substratum (rock/sand).

145 Large mobile invertebrates were enumerated for individuals greater than 2.5 cm in diameter or  
146 width, with the exception of sea stars where we measured radius. We counted individuals under  
147 prostrate algae and within bottom topography and on algae up to a height of 1 m above the  
148 substrate. This category included species of sea urchins, sea star, sea cucumbers, crabs, bivalves,  
149 nudibranchs, etc. We included only species that were easily identifiable to avoid concerns about the  
150 detection of cryptic species. For abundant species the transect was broken into 10-m segments, and  
151 the distance at which 30 individuals were counted per segment was noted, to be used in expansion  
152 calculations. We also recorded sea urchin test diameter, sea star radius, and crab carapace width.

153        We counted canopy-forming kelp species within on the same transect as macroinvertebrates.  
154      For *M. pyrifera* the stipes were counted when greater than 1 m in height. *N. luetkeana* and  
155      *Pterygophora californica* plants with stipes greater than 30 cm in height were included, along with  
156      other brown algae species greater than 30 cm in overall length. We again used the segment  
157      subsampling for abundant species described for invertebrate species.

158        We classified abiotic habitat (substratum) based on a simplified version of a system used  
159      extensively on the U.S. West Coast (Pearcy et al. 1989, Hixon et al. 1991, Stein et al. 1992, Greene et  
160      al. 1999, Tolimieri et al. 2008): sand, cobble, boulder, or bedrock; these features were recorded  
161      every meter (UPC). Additionally, we included an estimate of the slope every 10 m by estimating the  
162      drop in elevation across the 2-m width of the transect as: 0-10 cm, 10-100 cm, 1-2 m, or >2 m.

163      *Rockfish recruits*

164      **How we id them**

165      *Sea stars and prey*

166        We calculated separate sea star and prey indices by first examining sea star diets. For sea stars,  
167      we lumped all species but excluded *Henricia* spp because they eat primarily sponges and bacteria.  
168      Based on the sea star diets we lumped bivalves, shelled mollusks, shelled gastropods, and the three  
169      urchins to produce a prey index. We then plotted prey abundance against total sea start abundance.

170      *Urchins and Kelp*

171      **Expansion info?**

172    **Results**

173    ***Abiotic habitat***

174    Sites varied in their abiotic substratum characteristics, and these differences were largely  
175    consistent across depth (Fig. S 1). The substratum at Destruction Island and Tatoosh Island  
176    comprised primarily bedrock; these sites also had high relief (Fig. S 2) relative to other sites with  
177    greater than 25% of the bottom having changes in elevation of >2 m across the width of the  
178    transects . The bottom at Neah Bay was also primarily bedrock, but the relief was much lower being  
179    primarily in the 10-cm to 1-m bin. At Cape Johnson and Cape Alava, boulder made up the most  
180    common substratum type and relief was generally low in the 10-cm to 1-m bin.

181    ***Fish and invertebrate community structure***

182    *We recorded 23 (non-cryptic) fish taxa on the transects (Table S 1Supplement table*

183

184    Table S 1). Ten of these (Fig. S 5) were encountered frequently enough to be included in the  
185    ordination analyses. Fish assemblages differed among sites, depths, and years (dRDA,  $p < 0.001$ , Fig.  
186    2). While there was variation among years for all sites, Cape Johnson ordinated separately from  
187    Cape Alava. Neah Bay and Tatoosh Island were intermediate between the previous two while  
188    Destruction Island assemblages were highly variable through time. Tubesnout (AUFL) were  
189    abundant at a subset of sites in 2016 and to a lesser extent in 2019. Greenlings (HEXA), copper  
190    rockfish (SECA), China rockfish (SENE), lingcod (OPEL), and cabezon (SCMA) characterized Cape  
191    Alava and Neah Bay, with the exception of 2016. Surfperch (EMBI) were also common at Cape  
192    Alava and at Cape Johnson, but only in 2017 and 2018 for the latter. Neah Bay, Tatoosh Island, and

**Commented [NT5]:** These subheadings are not necessarily meant to be permanent. At present they help with navigating the document. Probably drop them for the final draft.

**Commented [NT6]:** Note = these are the larger fish that we regularly recorded not the smaller ones like little sculpins. These are also the fish included in the ordinations.

193 Cape Johnson did not show any temporal trends in the ordination with 2016 being much like 2019  
194 (Fig. 2 and Fig. S 6). However, Cape Alava and Destruction Island showed some slight trends with  
195 2019 having more rockfish, especially black rockfish (SEME) in 2019 than earlier. See  
196 Supplementary Material for more detail.

197 We grouped macroinvertebrates into 29 taxa and species (Fig. S 8, Fig. S 9, Fig. S 10, Fig. S 11).

**Commented [NT7]:** Correct format in final

198 Community structure differed among sites (dRDA,  $p < 0.001$ , Fig. 3), and these differences were  
199 partly related to habitat characteristics (Fig. S 13). However, relationships between the  
200 invertebrate fauna and habitat largely driven by the three urchins and their relationship with  
201 macroalgae, with little pattern among the other macroinvertebrate species. All three urchin species  
202 showed positive associations with brown understory algae, *N. leptkana*, *P. californica*, and other  
203 macroalgae and areas with boulder habitat (Fig. S 13). See Supplementary Material for more detail.  
204 Invertebrate assemblages showed little variation among years with year centroids for individual  
205 site clustering together and 2016 similar to 2019 (Fig. 3 and Fig. S 12). However, Destruction Island  
206 did show a slight temporal trend likely associated with a decrease in sea star density (Fig. 3 and Fig.  
207 S 12).

#### 208 Sea stars

209 Sea star abundance was highest at Destruction Island but generally low across other sites (Fig. 4).  
210 At Destruction Island, leather stars *Dermasterias imbricata*, ochre stars *Pisaster ochraceous*, and large  
211 sea stars all declined from 2016 – 2019, while brood sea stars *Leptasterias* spp increased at  
212 Destruction Island and Cape Johnson. *P. ochraceous* may have increased slightly at Tatoosh Island  
213 and Cape Alava from largely absent to present at very low density. Blood star *Henricia* spp densities  
214 remained fairly stable from 2016-2019. We did note a pulse of sea star recruitment in 2017, which  
215 was strongest in the south at Destruction Island and decreased with increasing latitude. Given the

**Commented [NT8]:** Listed in the data set. Are we sure these were ochraceous and not brevispinus? Isn't ochraceous intertidal?

**Commented [NT9]:** Kinsey needs to define her groupings in the Methods.

216 change in brood star densities, especially at Destruction Island and Cape Johnson, these were likely  
217 brood star recruits.

218 Among sites, prey abundance was declined at high sea star density at the transect level (GAM, p  
219 < 0.05, Fig. 5). Much of this relationship was due to differences among sites, especially Tatoosh and  
220 Destruction Islands. Prey items were most abundant but also highly variable (large variation along  
221 the y-axis in Fig. 5) at Tatoosh Island, where sea stars were less abundant. Sea stars were most  
222 abundant and also highly variable at Destruction Island and to a lesser extent Cape Alava, where  
223 prey was less abundant. Both sea stars and invertebrate prey were comparatively uncommon at  
224 Cape Johnson and Neah Bay.

**Commented [NT10]:** Not super happy with these stats.  
Visually the patterns seem obvious, but there are so many  
points in the lower left that the stats are NS in most cases.

#### 225 *Macro-algae*

226 There were three primary macroalgae found at the study sites: *M. pyrifera*, *N. leptophylla*, *P.*  
227 *californica*. We grouped the remaining macroalgae into an 'other' category due to rarity (Fig. 6). *M.*  
228 *pyrifera* was found on the 5-m transects at Cape Johnson and Neah Bay but was absent or less  
229 abundant in other areas. *N. leptophylla* was also more abundant at 5-m depths but was also found on  
230 10-m transects at Tatoosh Island and Neah Bay. *N. leptophylla* was less common at Cape Johnson and  
231 Neah Bay than at other sites. *P. californica*, and under-story kelp, occurred at sites at 5-m in similar  
232 abundance, although densities were slightly higher at Tatoosh Island and Neah Bay than other  
233 areas. *P. californica* was also found at 10-m at Tatoosh and Neah Bay.

#### 234 *Urchins and kelp*

235 Green, red, and purple urchins all showed increase in abundance from 2016 to 2017 at Tatoosh  
236 Island (Fig. S 8). Following this initial increase, both green and red urchins declined through 2019,  
237 while purple urchins remained abundant. Purple urchins also showed low densities but minor

238 increases at Destruction Island from 2017-2019 (Fig. S 8). Qualitative observations and urchin test  
239 size distributions (measured in 2018 and 2019, Fig. S 15) suggest a recruitment pulse occurred  
240 sometime in 2017 or possibly early 2018.

241 Relationships between urchins and kelp differed among and within sites. Among sites urchins  
242 were negatively associated with *M. pyrifera* but positively associated with *N. luekana* as is evident  
243 from the first canonical axis in the invertebrate-habitat ordination (Fig. S 13). Sites with high  
244 abundance of *M. pyrifera* had few urchins (Fig. 7). However, this effect was largely due to the  
245 absence of *M. pyrifera* at Tatoosh Island, so the effect may geographical and not due to ecological  
246 interactions within the site.

247 The positive association between urchins and *N. luekana* among sites (Fig. S 13) stemmed from  
248 their both being found at Tatoosh Island (Fig. 7). However, within Tatoosh, the abundance of *N.*  
249 *luekana* was negatively correlated with the abundance of purple urchins ( $p = 0.015$ ,  $r = -0.53$ , Fig. 7).  
250 Thus, as the densities of purple urchins increased at Tatoosh Island, kelp density decreased (Fig. 6).  
251 Interestingly, variability in the density of *P. californica* seemed to decrease with urchin density for  
252 both purple and red urchins (Fig. 7). The same was true for *N. luekana* and red urchins. For red  
253 urchins, the relationships may be partially spurious; red urchins increased then declined all while  
254 *N. pyrifera* declined likely due to grazing by purple urchins.

#### 255 Rockfish recruitment

256 Recruitment of rockfishes was temporally episodic (Fig. 8). While the intensity of recruitment  
257 varied among sites within a year, most species showed strong recruitment at multiple sites within a  
258 specific year. However, species had successful recruitment in different years. Black and yellow tail  
259 rockfishes showed strong recruitment at most sites in 2016 and to a lesser extent in 2019. This  
260 strong recruitment at especially Destruction Island and Cape Alava appears to have resulted in an

**Commented [NT11]:**

I'm not sure about this. Might be BS. Could just delete and ignore size stuff.

We need to clarify:

1. Size of recruitment and growth for the urchins
2. SST during the relevant condition in 2017 and 2018
3. Currents around Tatoosh Island.

261 increase in adult numbers at those sites seen both in the ordinations (Fig. 2 and Fig. S 6) and  
262 univariate plots (Fig. S 5). In contrast, copper rockfish (including unidentified recruits, which were  
263 most likely copper or quillback) had high recruitment at most sites in 2019. Canary recruitment  
264 pulses occurred in 2016 and 2018.

265 **Discussion**

266 *Assemblage structure and habitat*

267 Assemblage structure for fish and invertebrates differed among sites but was not strongly  
268 associated with habitat, apart from the association of urchins with *N. leuckana* at Tatoosh. The sites  
269 were originally chosen as a suite of relatively similar, rocky-reef, kelp habitats with some shelter  
270 (Kvitek et al. 1989, Kvitek et al. 1998, Shelton et al. 2018), so the sites may not differ substantially  
271 in their habitat characteristics from the point of view of the fauna; they are all kelp forests. Instead,  
272 differences in assemblage structure may be related to other local processes like larval supply and  
273 interspecific interactions within sites leading to a diversity of assemblage structures. Interestingly,  
274 invertebrate assemblages showed little temporal variation in assemblage structure with individual  
275 sites having stable assemblage structure across years. Invertebrate densities declined substantially  
276 from the late 1980s to 2015, likely due to recolonization of these areas by sea otters (Shelton et al.  
277 2018). Only Destruction Island showed evidence of any temporal trend due to the continued decline  
278 in sea star densities. Therefore, lack of substantial changes following the marine heatwave and sea  
279 star die off may be due to relatively low invertebrate densities limiting reproductive output and the  
280 potential for population growth.

**Commented [NT12]:** These headings in the discussion are mostly for navigation at the moment. We could keep them, but I do not expect to have sections.

281 *Sea stars and their prey*

282 Sea star wasting disease caused substantial die-offs of asteroids from Mexico to Alaska between  
283 2013-2015, including marked declines in abundance for most species on the Washington coast  
284 (Hewson et al. 2014, Menge et al. 2016, Montecino-Latorre et al. 2016, Hewson et al. 2018). Within  
285 the Salish Sea and on the Washington coast, there were concurrent increases in sea star prey like  
286 red and green urchin (Montecino-Latorre et al. 2016). Our data are largely post-die-off and show  
287 little evidence of recovery of sea star populations as of 2019. In fact, *P. ochraceous*, *D. imbricata*, and  
288 large sea stars continued to decline at Destruction Island and remained at low density at other sites.  
289 However, *Henricia* spp. densities were stable across years, and *Leptasterias* spp actually increased  
290 at the southern two sites, Cape Johnson and Destruction Island, likely due to recruitment at the site  
291 in 2017. However, large sea star densities tracked urchin densities at Tatoosh Island, increasing in  
292 2017 and then dropping again in 2018 and 2019. The abundance of large sea stars also increased  
293 slightly from absent at Cape Johnson and Cape in 2016 to less than 0.05 individuals per 30x2 m

294 ~~transect~~ in 2019.↓

295 Sea stars are important benthic predators in intertidal and subtidal communities, and we  
296 might expect their rapid decline to have impacts on community structure and the abundance of  
297 prey species (Lubchenco and Menge 1978, Menge et al. 1994, Menge et al. 2016, Montecino-Latorre  
298 et al. 2016). Here, we saw a negative relationship between sea star density and the density of prey  
299 species, primarily urchins. At the larger scale, among sites, this relationship was driven largely by  
300 Tatoosh and Destruction Islands. Prey density was highest at Tatoosh Island where there were few  
301 sea stars (and few otters (Shelton et al. 2018)). Sea star densities were highest, and variable, at  
302 Destruction Island. Within Destruction Island, prey densities increased and became more variable  
303 as sea star densities decreased from 2016 to 2019, suggesting a release from top-down control.  
304 Thus both among and within sites, absence of sea stars appears to allow for increases in prey

**Commented [NT13]:** Need to check metrics all around. I think;

1. Urchins are m-2
2. Stars are transect (60m-2)

**Deleted:** Given that many sea stars were almost completely extirpated, lack of recovery is likely due to recruitment failure due to aleo effects (Allee and Bowen 1932) and oceanographic conditions.

309 species, suggesting top-down pressure from the stars, but does not guarantee and increase in prey  
310 species. Among sites variability in recruitment due to climate and oceanic drivers almost certainly  
311 plays a large role.

312 *Urchins and kelp*

313 We saw dramatic increases in all three urchins at Tatoosh Island from 2016 to 2017. Purple  
314 urchins increased almost four-fold from approximately  $0.5 \text{ m}^{-2}$  to almost  $2.0 \text{ m}^{-2}$ , red urchins five-  
315 fold from circa  $0.2 \text{ m}^{-2}$  to  $1.0 \text{ m}^{-2}$ , and green urchins doubled from approximately  $0.4 \text{ m}^{-2}$  to  $0.8 \text{ m}^{-2}$ .  
316 Red and green urchins then declined, while purple urchin densities remained high. These increases  
317 were likely due to a recruitment pulse in 2017 given urchin sizes in 2018 and the changes in size  
318 from 2018-2019 (Tegner and Dayton 1981, Pearse and Hines 1987), but we do not have  
319 recruitment data for these species. Recruitment of purple urchins in northern California is  
320 associated with warmer SST conditions (Okamoto et al. 2020), so the marine heat wave in 2014-  
321 2016 may have contributed to a strong recruitment leading to the observed increases in 2017.  
322 Likewise, while the marine heat wave dissipated in 2017, some warm water remained off the US  
323 West Coast, including in the vicinity of Tatoosh Island (Harvey et al. 2018), potentially also leading  
324 to higher recruitment in 2017. Additionally, meso-scale habitat features like capes can create  
325 oceanographic features that may entrain and concentrate larvae leading to higher recruitment  
326 around promontories like Tatoosh Island/Cape Flattery (Danilowicz et al. 2001).

327 For purple urchins, recruitment pulses can lead to rapid increases in density (Pearse and Hines  
328 1987, Pearse 2006), which can be short-lived and followed by rapid declines (50% within 1-yr) due  
329 to predation (Pearse and Hines 1987). Here, purple urchin numbers declined slightly in 2019  
330 remained approximately twice that of 2017. Otters have not been common at Tatoosh Island in  
331 recent years (Shelton et al. 2018). We did see an increase in large sea stars at Tatoosh in 2017, but

**Commented [NT15]:** Right now, there is a fair bit of narrative detail/results in the Discussion to highlight specific trends, etc. We might consider removing much of it. Open for discussion.

**Commented [NT16]:** I'm not really sure about the size stuff. Could delete this part but leave the MHW stuff below.

332 densities were still very low ( $\sim 0.015 \text{ m}^{-2}$ ). The lack of otters combined with the die off of predatory  
333 sea stars (Hewson et al. 2014, Montecino-Latorre et al. 2016) suggests that there were few  
334 predators at Tatoosh able to control urchin populations, which may have contributed to the  
335 persistent increase in purple urchin densities (Dunn and Hovel 2019, Eisaguirre et al. 2020). Red  
336 and green urchin density decreased rapidly after 2017 suggesting that other processes might have  
337 affected these species. Purple urchins do compete with red urchins (Tegner 2000, Pearse 2006),  
338 and it is possible the few large sea stars that were present in 2017 fed preferentially on red and  
339 green urchins releasing purple urchins from competition.

**Commented [NT17]:** Check the metric m-2 or # per transect? Etc  
Here and elsewhere

340 At large scale, there was a negative relationship between *M. pyrifera* and urchin densities for  
341 both purple and red urchins. This relationship is hard to interpret as *M. pyrifera* forest can be  
342 resilient to loss of sea otters and urchin grazing (Foster and Schiel 1988), and because the  
343 relationship it is driven primarily by the low *M. pyrifera* density and high urchin density at one site,  
344 Tatoosh Island. Nevertheless, high purple urchin density can lead to barrens, while die-offs have  
345 resulted in rapid re-forestation within six months in some areas (Williams et al. 2021). Conversely,  
346 at the large scale urchin abundance was highest at sites with *N. leptolepis* and *P. californica*, specific  
347 ally Tatoosh Island and Destruction Island in 2018 and 2019.

**Commented [NT18]:** My arms hurt from all the waving.  
I may have strained something.

348 At Tatoosh Island, the increase in urchin densities coincided with a decrease in *N. leptolepis* on  
349 transects. Strong recruitment events can lead to intense grazing that would result in loss of kelp  
350 canopy (Watanabe and Harrold 1991). However, the dynamics can be more complex. In healthy  
351 kelp forests, urchins tend to move less, have higher gonadal-somatic index (GSI), and feed on drift  
352 kelp – acting as passive detritivores (Pearse 2006, Kriegisch et al. 2019, Smith et al. 2021) and  
353 functioning to transfer kelp detritus to other benthic consumers (Yorke et al. 2019). If kelp  
354 densities decrease, urchins switch to active herbivory, move more, have lower GSI, and are less  
355 appealing to otters as prey. Kelp canopy did decrease substantially along the Washington Coast in

356 2013-2015 (Shelton et al. 2018), likely due to the marine heat wave as warm temperatures tend to  
357 lead to loss of kelp (Pfister et al. 2018, Fewings and Brown 2019, Rogers-Bennett and Catton 2019).  
358 Thus it is possible that a change in urchin grazing behavior combined with a pulse of recruitment  
359 and few urchin predators lead to more, less cryptic urchins and active herbivory on *N. leptostoma*  
360 further precipitating the decline kelp at the transect level within Tatoosh. Interestingly, *P.*  
361 *californica* density increased at Tatoosh over the same suggesting that a decrease in canopy kelp  
362 may have allowed more light penetration and better growing conditions for the understory  
363 macroalgae.

364 ***Rockfish recruits***

365 The processes governing rockfish (*Sebastodes* spp) recruitment appear to operate at large spatial  
366 scales with many locations showing recruitment pulses in the same year. However, there is spatial  
367 variability in intensity within years, and the patterns differ among species with different life  
368 histories. For example, Field et al. (in press) found considerable spatial coherence in the relative  
369 abundance pelagic young-of-year (pre-recruits) of winter-spawning rockfishes associated with the shelf  
370 break in mid-water trawls along the West Coast of the US. In our data, recruitment was episodic and  
371 spatially variable, but individual taxon had recruitment pulses at most sites in a given year. Black  
372 rockfish and yellowtail rockfish had recruitment pulses at most sites in 2016, copper rockfish in  
373 2019, and canary rockfish in 2016 and 2018. The intensity varied among sites within a year, with  
374 copper rockfish showing a latitudinal trend in recruitment in 2019. Density of copper recruits was  
375 highest at Destruction Island in the south and decreased as one moved north to Neah Bay (Fig. 8,  
376 panel SECAY). For black and yellowtail rockfishes, there was variability among sites, but no obvious  
377 latitude trend. In 2016, recruitment was high at Destruction Island in the south and at Neah Bay to  
378 the north (Fig. 8, panel SEBYTy).

**Commented [NT19]:** This section feels somewhat orphaned and un-related to the previous two. Should we just delete it? It IS related to MHW and recruitment stuff but not really to the sea star – urchins – algae relationships, which could just be the focus of the paper.

**Commented [NT20R19]:**

**Commented [NT21]:** Why?

379       The differences among taxa in their temporal patterns of recruitment appear related to the life-  
380       history of the species. Nearshore rockfishes follow two general life-histories: benthic-solitary  
381       species versus mid-water-aggregating species (Hyde and Vetter 2007, Markel and Shurin 2020).  
382       For solitary benthic species, good recruitment typically corresponds with warmer water and weak  
383       upwelling, which allows faster growth and onshore transport. The mid-water species have higher  
384       recruitment in cold water years with strong upwelling (Lenarz et al. 1995, Carr and Syms 2006).  
385       Copper rockfish fall in the CQB complex (copper, quillback, and brown rockfishes) of solitary,  
386       benthic species. Black and yellowtail rockfishes are aggregating mid-water species. Thus the peaks  
387       in recruitment in different years for we observed for these complexes is consistent with their life-  
388       history and previous observations. Off of Vancouver Island, Canada, the CQB complex had good  
389       recruitment in 2005, while black rockfishes had strong recruitment in 2006 (Markel and Shurin  
390       2020). Consistent with previous observations (Lenarz et al. 1995, Carr and Syms 2006), these  
391       groups also responded differently to oceanographic conditions. High CQB recruitment in 2005  
392       occurred during a period with prolonged downwelling and warm water temperature, and settlers  
393       had late parturition dates, fast presettlement growth, short pelagic durations, and small size at  
394       settlement. Strong upwelling and cool ocean temperatures were associated with the high black  
395       rockfish recruitment in 2006, when fish had slow pre-settlement growth and long pelagic durations  
396       (Markel and Shurin 2020).

397       The timing of settlement also differs among these groups, which likely affects their larval  
398       dynamics and interaction with oceanography. Yellow tail and black rockfish tend to settle between  
399       May and June, while fishes in the CQB complex settle later in July-October (Johansson et al. 2018,  
400       Ottmann et al. 2018). Interestingly, we did not see strong recruitment of copper rockfish in 2016,  
401       which was a warm year, but we did see high recruitment of black and yellowtail and rockfishes.  
402       However, in Oregon, there was strong recruitment of CQB fishes but much later in the year

403 (September) than normal (Ottmann et al. 2018); our surveys would have missed this recruitment  
404 pulse. Source water is an important driver of rockfish recruitment (Schroeder et al. 2019), and  
405 anomalous oceanographic conditions may have upset more typical relationship. For example,  
406 overall, winter spawners showed high abundance during the years of the marine heat wave (Field  
407 et al. in press), which differs from what one might expect based on their normal association with  
408 colder, upwelling conditions.

409 *Bringing it all back home...*

410 Overall, our data show a combination of large-scale temporal coherence for some processes but  
411 also important site-level variation. Dynamics related to oceanic scale processes and likely  
412 influenced by climate showed the temporal coherence. For example, sea stars had high recruitment  
413 at most sites in 2017, and rockfish showed high recruitment across sites within a given year,  
414 although the specific year differed among complexes. These results are consistent with other  
415 observations like the impact of the MHW on the abundance of rockfish pre-recruits (pelagic  
416 juveniles) (Field et al. in press) and the loss of canopy cover in kelp forests (Cavanaugh et al. 2019,  
417 Rogers-Bennett and Catton 2019, Beas-Luna et al. 2020), as well as the effects of water temperature  
418 on urchin recruitment (Okamoto et al. 2020).

419 Within this broad-scale temporal coherence is important site level variation. It is no surprise  
420 that recruitment was spatially variable within years; however, we saw two general patterns.  
421 Recruitment for sea stars and the copper-quillback-brown rockfish complex decreased from south  
422 to north, while the yellow tail-black rockfish complex did not demonstrate any latitudinal trend.  
423 Furthermore, there was site-level variation in other dynamics: urchins increased (and kelp  
424 declined) at Tatoosh Island, sea stars continued to decline in abundance at Destruction Island, and

425 black rockfish showed substantial increases at Destruction Island (likely due to the observed  
426 recruitment).

427 Fish and invertebrate assemblages differed among sites, providing an array of somewhat  
428 different kelp forest communities along the Washington coast. We also saw different dynamics  
429 among sites with increased in urchins at Tatoosh Island with concurrent declines in kelp. While at  
430 Destruction Island, sea stars continued to decline in abundance. This portfolio effect (Schindler et  
431 al. 2015) may be important to both the overall ecology of the system and to the effective  
432 conservation and management of these marine resources by allowing for a range of responses to  
433 various perturbations. For example, while urchin barrens are generally considered a negative  
434 outcome (Eisaguirre et al. 2020, Williams et al. 2021), urchins are important food items for sea  
435 otters and *Pycnopodia* (as well as for spiny lobster and sheepshead in southern California), and they  
436 are important in the detrital food chain (Yorke et al. 2019). Urchin densities were generally low  
437 among our sites, but increased rapidly in 2017 at Tatoosh Island likely due to a combination of  
438 climate and oceanic influencing larval supply and to local-scale benthic biotic interactions. These  
439 urchins may serve as seed populations and provide propagules to other locations along the coast  
440 with low urchin densities. Thus when attempting to understand both the ecology of the system, and  
441 implementing conservation and management systems, ecologists and managers may need to take a  
442 portfolio approach to understanding the system and planning for the future. |

**Commented [NT22]:** I fully admit that this final paragraph, and especially this final sentence, are lame...

443

#### 444 Acknowledgments

445 We thank XX anonymous reviewers and XX, XX, and XX for comments on the manuscript. More here:  
446 boat crew, coast guard at Neah Bay, etc.

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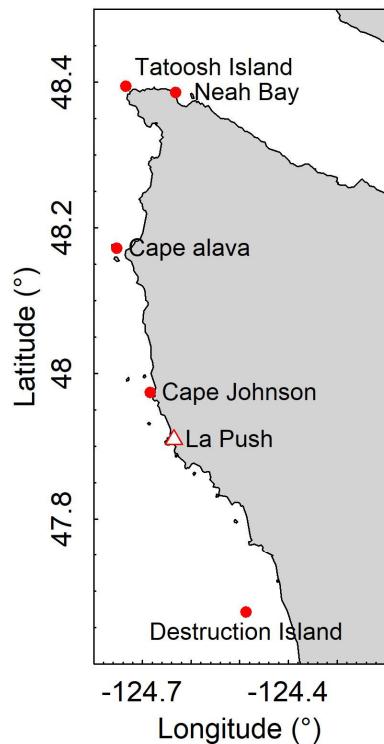
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613

614 **Figures**

615

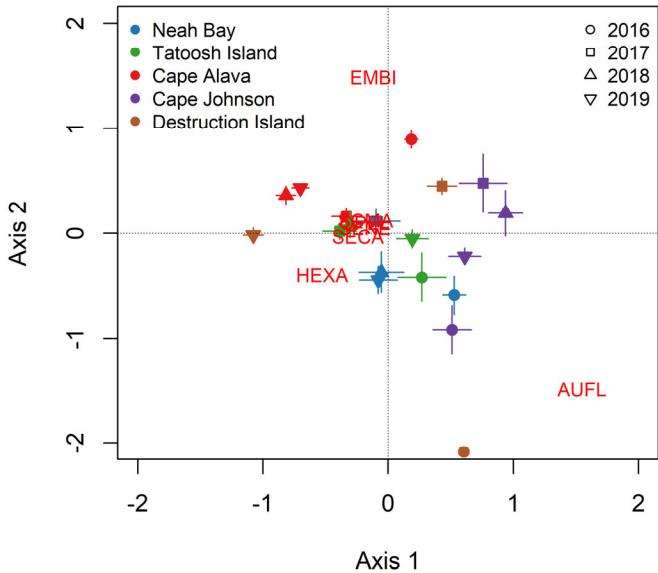


616

617 Fig. 1 Location of study sites. The town of La Push is included for reference, but is not a  
618 sampling site.

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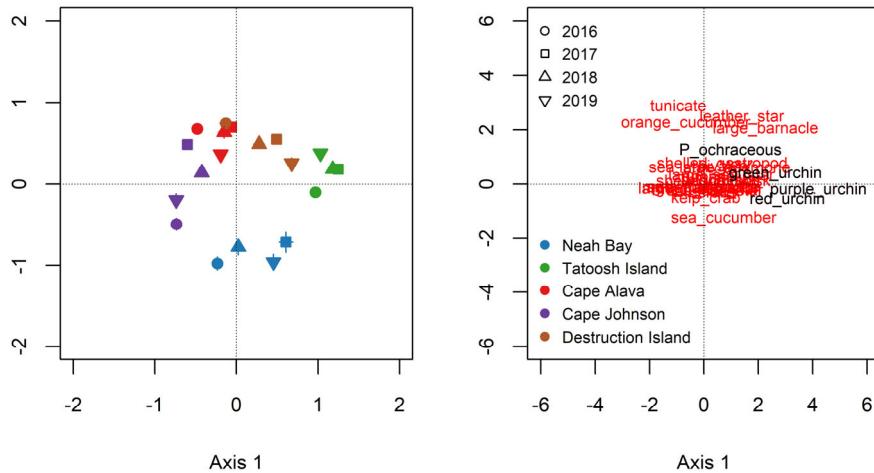


621

622 Fig. 2 Ordination of sites based on the fish taxa present on 30 x 2 m transects from a  
 623 distanced-based redundancy analysis. The analysis used individual transects, but the axes  
 624 were averaged by site and year for clarity in the presentation. Error bars indicate  $\pm 1.0$  s.e.  
 625 Red text shows the loadings for fish taxa. The overlapping taxa just left of the center are:  
 626 SCMA, SENE, SECA, OPEL. See XX for taxa designations.

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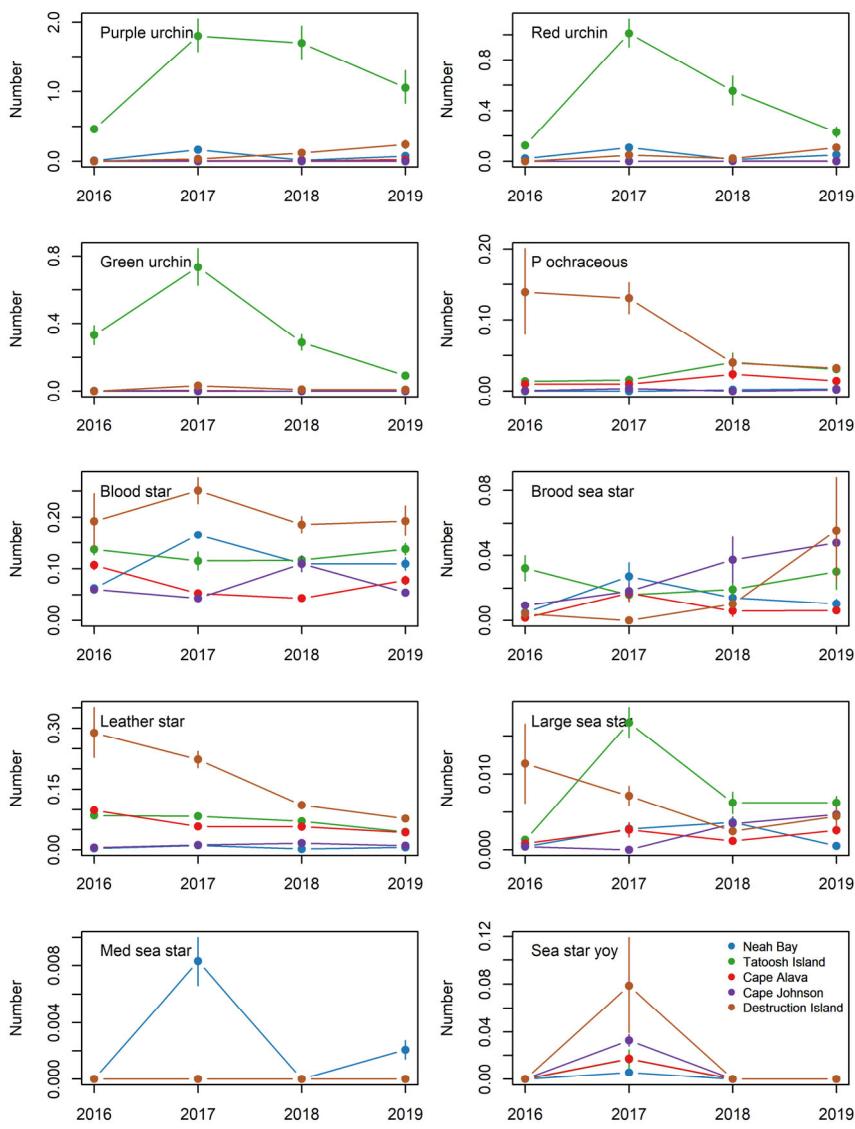


629

630 Fig. 3 Ordination of sites based on the invertebrate taxa present on 30 x 2 m transects from  
 631 a distance-based redundancy analysis. The analysis used individual transects, but the axes  
 632 were averaged by site and year for clarity in the presentation. Error bars indicate  $\pm 1.0$  s.e.  
 633 In most cases, error bars are smaller than the points. The results are presented in two  
 634 panes with the species loadings plotted on the second pane for readability. Species colors  
 635 on the loadings pane are for readability and used to emphasize particular species.

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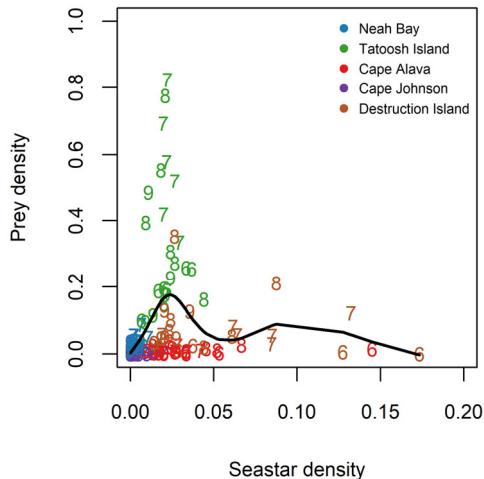
639 Fig. 4 Abundance (number per  $m^2$ ) of individual urchin and sea star species through time.

**Commented [NT23]:**

What is the measure here? Must be  $m^2$  given the the numbers. Couldn't be # per  $30 \times 2$  m transect. Too low.

Double check: do large sea stars, and medium sea stars include other listed species here? Delete?

640



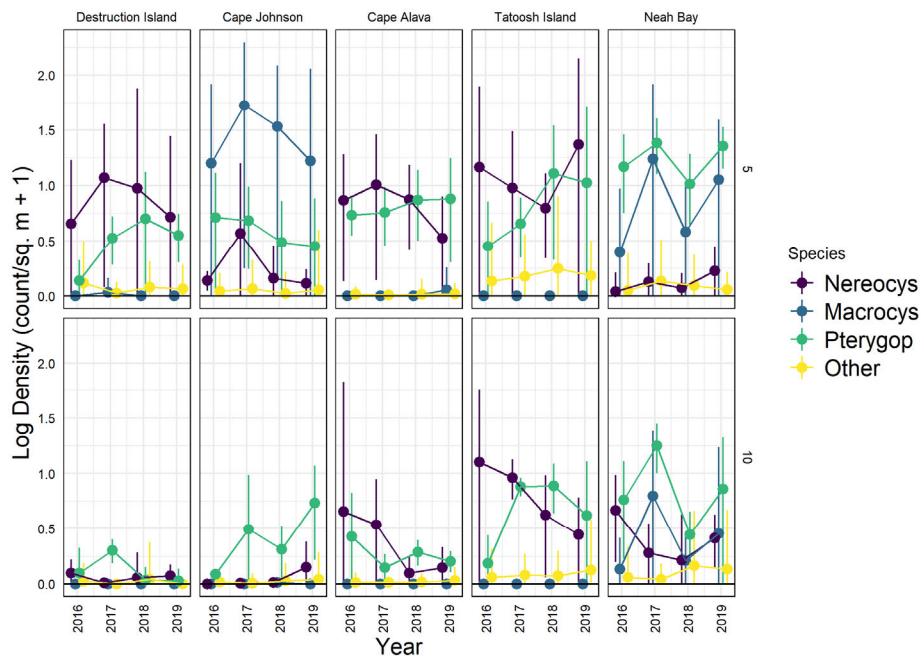
641

642 Fig. 5 Relationship between sea stars and their prey on 30x2m transects at five sites.  
643 *Henricia* spp. were excluded because they eat sponges and bacteria. Numbers in the top  
644 figure are the year of the survey (ie, 9 = 2019).

645

**Commented [NT24]:** Black line is from a GAM. Do we need it or should we just do a visual test? Open to other stats too. Negative exponential growth is NS because of the large number of points in the lower left.

646



647

648 Fig. 6 Abundance of macroalgae on 60 x 2 m transects at each sites and at two depths (5  
649 and 10 m). Values are the log(stipes m<sup>-2</sup> + 1). **MORE**

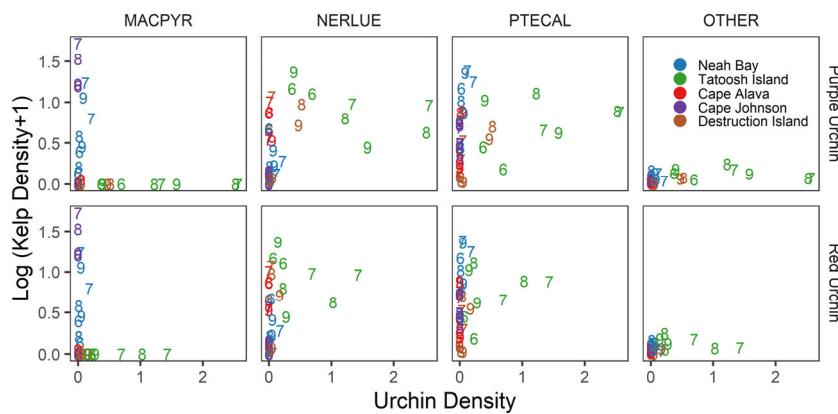
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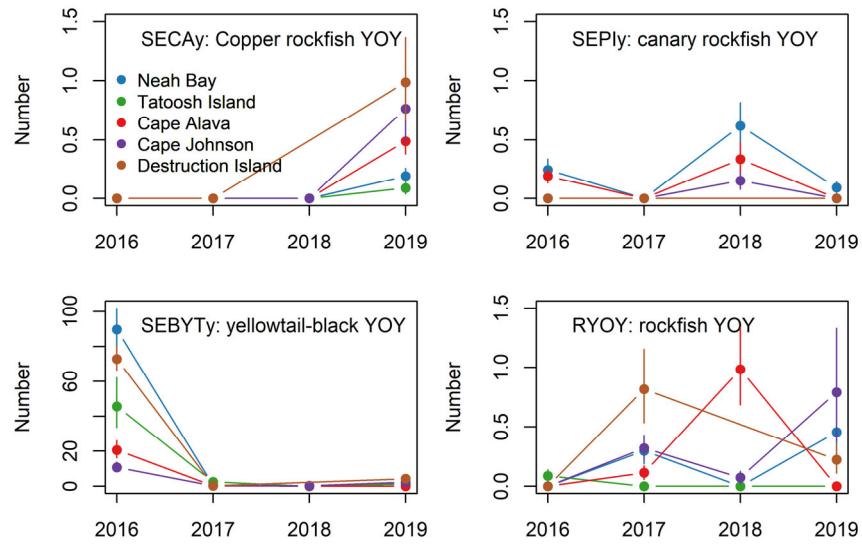
656 Fig. 7 Relationships between the density of canopy and understory kelps and the  
657 abundance of purple and red urchins. MACPYR = *Macrocystis pyrifera*, NERLUE = *Nerocystis*  
658 *luekana*, PTECAL = *Pterygophora californica*, and OTHER = other macroalgae. Numbers  
659 indicate the year of survey (e.g., 9 = 2019).

660

661

662

663



664

665 Fig. 8 Abundance of rockfish recruits (young-of-year, YOY) by site and year. Data are the  
666 back-calculated site x year means ( $\log x+1$ ) and s.e. for number of recruits per 30x2-m  
667 transect.

668

669

670    **Supplement**

671    *Multivariate ordinations*

672    We used distance-based redundancy analysis (dRDA, implemented via the 'capscale' function in  
673    R 4.0.2; Legendre and Anderson 1999, R Core Team 2020) to ordinate multivariate patterns and  
674    understand relationships between fish or invertebrate community structure and habitat predictor  
675    variables (kelp, UPC, and substratum). First, we ordinated transects (fish or invertebrates) among  
676    sites to determine whether assemblage structure varied among sites (where site x depth x years  
677    were the constraining variables). We then also conducted a second set of ordinations using habitat  
678    variables to constrain the ordination. For this second set, we used site x year x depth averages  
679    because habitat variables did not map directly to fish or invert transects. In all cases, we square-  
680    root transformed the data prior to analysis to reduce the effect of highly abundant (Clarke and  
681    Warwick 2001) species and used Bray-Curtis distance. Note, rockfish young-of-year (YOY) were  
682    excluded from the analyses due to their ephemeral and highly variable occurrence.

683    The habitat variables matrix included kelp density, biotic habitat, and substratum  
684    characteristics. For kelp density, we included the stipe counts for four taxa *M. pyrifera*, *N. luekana*,  
685    *P. californica*, and 'other' macroalgae. For the biotic habitat and the substratum data, we first  
686    conducted separate principal components analyses (PCA) to reduce the number of variables  
687    entering into dRDA above and to understand variation among sites and depths. We used the first  
688    two PCA axes from each analysis in the above dRDAs after averaging each by site x year x depth.

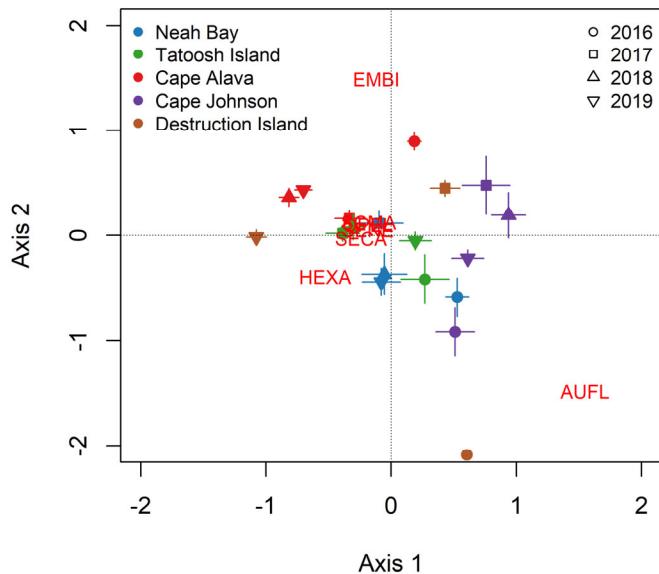
689    *Multivariate results*

690    For the PCA of biotic benthic habitat, the first PC separated transects with red versus brown  
691    algae (Fig. S 3). The second PC distinguished among transects with encrusting species and non-

692 mobile invertebrates from those with more red or brown algae. Thus PC2 gives an indication of  
693 understory algal coverage. There was no clear separation of sites within this ordination, however.

694 The PCA of abiotic substratum characteristics (Fig. S 4) separated transects of primarily  
695 bedrock from those with boulder structure along the first PC. Destruction Island and Tatoosh Island  
696 had more bedrock than other sites, while Cape Johnson and Cape Alava had more boulder or cobble  
697 habitat. The second PC explained differences among transects in slope (0-10 cm vs 10 cm – 1 m  
698 drop over the 2-m width of the transect). This second PC did not appear strongly associated with  
699 sites or depths.

700 Fish assemblages (Fig. S 5) differed among sites, depths, and years (dRDA,  $p < 0.001$ , Fig. 2



701

702 Fig. 2). While there was variation among years for all sites, Cape Johnson ordinated separately  
703 from Cape Alava. Neah Bay and Tatoosh Island were intermediate between the previous two while  
704 Destruction Island assemblages were highly variable through time. Some species like black rockfish  
705 (SEME) were found at all sites (Fig. S 5) and did not distinguish among sites in the ordination.  
706 Others like tubesnout (AUFL) were abundant at a subset of sites in 2016 and to a lesser extent in  
707 2019. Greenlings (HEXA), copper rockfish (SECA), China rockfish (SENE), lingcod (OPEL), and  
708 cabezon (SCMA) characterized Cape Alava and Neah Bay, with the exception of 2016. Surfperch  
709 (EMBI) were also common at Cape Alava and at Cape Johnson, but only in 2017 and 2018 for the  
710 latter.

711 The fish assemblage did not show strong correlation with the combined kelp-biotic-substrate  
712 habitat matrix (dRDA ,  $p > 0.05$ , Fig. S 7). This is not entirely surprising given Cape Alava and Cape  
713 Johnson, which had dissimilar fish assemblages (Fig. 2), had similar biotic benthic habitats (Fig. S  
714 4). Moreover, given that all transects were done in somewhat sheltered kelp forests, the habitat  
715 may not have varied significantly among sites from the point of view of a fish. Large scale factors  
716 (circulation, settlement, etc) may have been more important in driving differences in fish  
717 assemblages among sites.

718 The invertebrate assemblages (Fig. S 8, Fig. S 9, Fig. S 10, Fig. S 11) showed a clear separation of  
719 sites, especially when factors were averaged by site and year (dRDA,  $p < 0.001$ , Fig. 3). While there  
720 was some variation among years, it was much less than the spread among sites. Tatoosh Island was  
721 notable for having more urchins (Axis 1) than other sites. Urchins also characterized Destruction  
722 Island and Neah Bay relative to other sites but were much less common at these two sites than at  
723 Tatoosh Island. Tunicates, leather stars, large barnacles and orange cucumbers were more common  
724 at Tatoosh Island, Destruction Island, and Cape Alava than at Neah Bay, and at Cape Johnson in 2017  
725 and 2018 than in 2016 and 2019.

726        Associations between macroinvertebrates and habitat features were largely driven by urchins  
727        and Tatoosh Island (Fig. S 13). All three urchin species loaded positively on the first axis indicating  
728        positive associations with brown understory algae, *N. leukana*, *P. californica*, and other macroalgae  
729        and areas with boulder habitat.

730

731 *Supplement table*

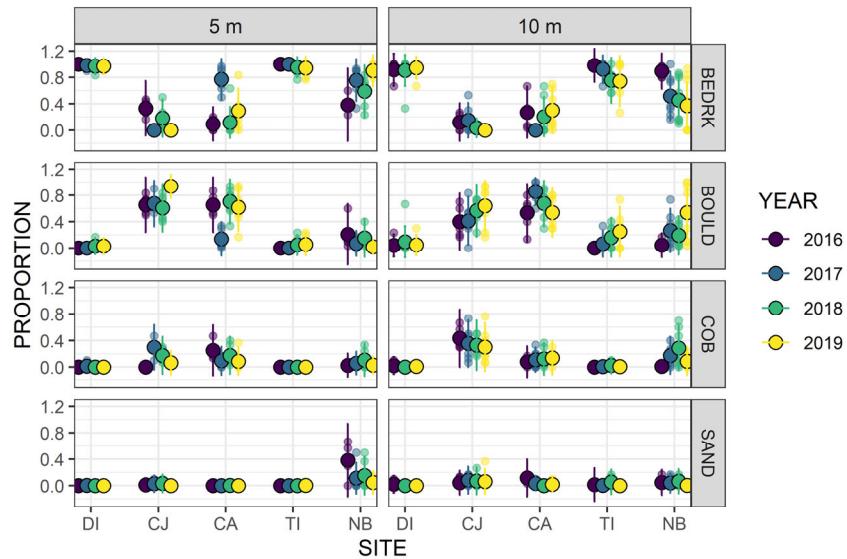
732

733 Table S 1. List of fish species observed on visual surveys. Taxa were lumped into Group for  
734 statistical analyses. Note, rockfish young-of-year (YOY) were excluded from the ordinations  
735 due to their ephemeral nature.

Species	Common name	Group
<i>Aulorhynchus flavidus</i>	tubesnout	AUFL
bait-sardines-anchovy	bait	BAIT
<i>Brachyistius frenatus</i>	kelp surfperch	EMBI
Clupeidae	herring	BAIT
<i>Cymatogaster aggregata</i>	shiner surfperch	EMBI
<i>Embiotoca lateralis</i>	striped surfperch	EMBI
Embiotocidae	surfperches	EMBI
<i>Engraulis mordax</i>	northern anchovy	BAIT
<i>Hemilepidotus hemilepidotus</i>	red irish lord	HEXA
<i>Hexagrammos spp</i>	greenlings	HEXA
<i>Hexagrammos decagrammus</i>	kelp greenling	HEXA
<i>Hexagrammos lagocephalus</i>	rock greenling	HEXA
<i>Hexagrammos stelleri</i>	whitespotted greenling	HEXA
<i>Ophiodon elongatus</i>	lingcod	OPEL
<i>Oxylebius pictus</i>	painted greenling	HEXA
<i>Rhacochilus vacca</i>	pile perch	EMBI
<i>Sardinops sagax</i>	Pacific sardine	BAIT
<i>Scorpaenichthys marmoratus</i>	cabezon	SCMA
<i>Sebastodes caurinus</i>	copper rockfish	SECA
<i>Sebastodes caurinus</i> YOY	copper rockfish yoy	SECAy
<i>Sebastodes melanops/flavvidus</i> YOY	yellowtail-black yoy	SEBYTy
<i>Sebastodes melanops</i>	black rockfish	SEME
<i>Sebastodes melanops</i> YOY	black rockfish yoy	SEMEy
<i>Sebastodes mystinus</i>	blue rockfish	SEMY
<i>Sebastodes nebulosus</i>	China rockfish	SENE
<i>Sebastodes pinniger</i> YOY	canary rockfish yoy	SEPIy
<i>Sebastodes</i> YOY	rockfish yoy	RYOY

736

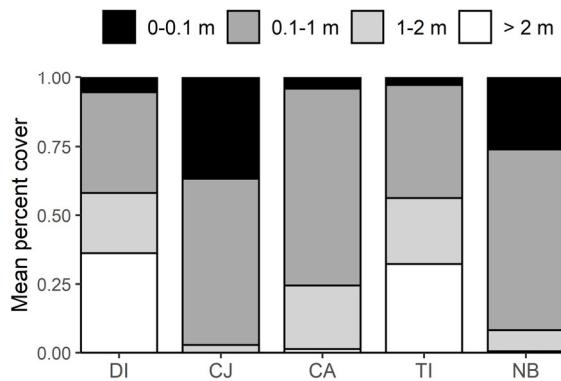
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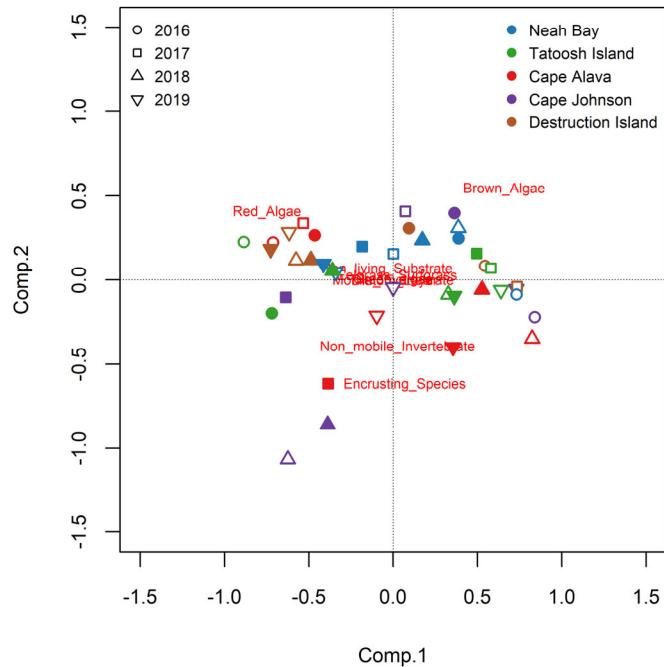
740 Fig. S 1 Substratum characteristics by site year and depth. BEDRK = bedrock, BOULD =  
741 boulder, COB = cobble, SAND = sand.

742



743

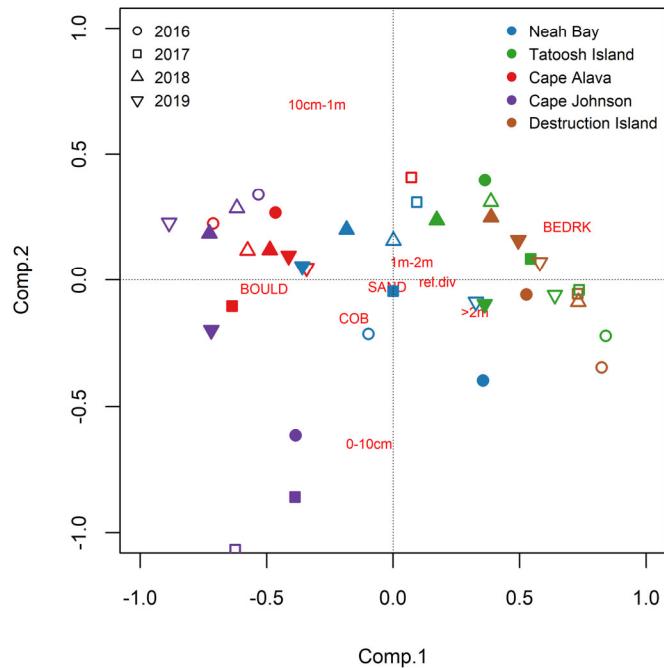
744 Fig. S 2 Estimate of slope sites, summarized across depths and years. Ranges are the drop in  
745 elevation across the width of a 2-m transect. Data are the average of XX measurements per 30-m  
746 transect.



747

748 Fig. S 3 Results of a principal components analysis ordinating biotic benthic habitat by site  
 749 x year x depth. Open and closed symbols indicate 5-m and 10-m transects, respectively.

750

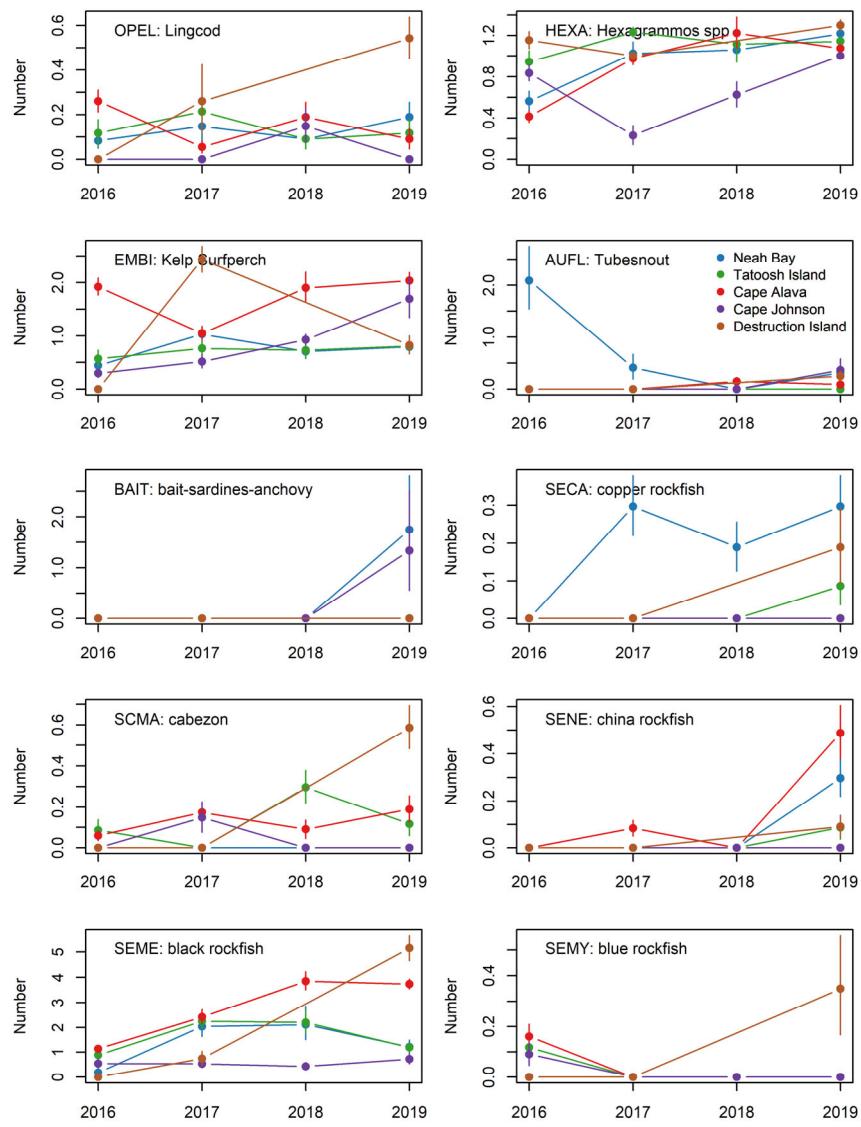


751

752 Fig. S 4 Principal components analysis of abiotic substratum characteristics by site x year x  
753 depth. Open and closed symbols indicate 5-m and 10-m transects, respectively. BEDRK =  
754 bedrock, COB = cobble, BOULD = boulder, SAND = sand; distance ranges (e.g., 1 m - 2 m)  
755 indicate the high mean high difference across the 2-m width of the transect – a measure of  
756 slope.

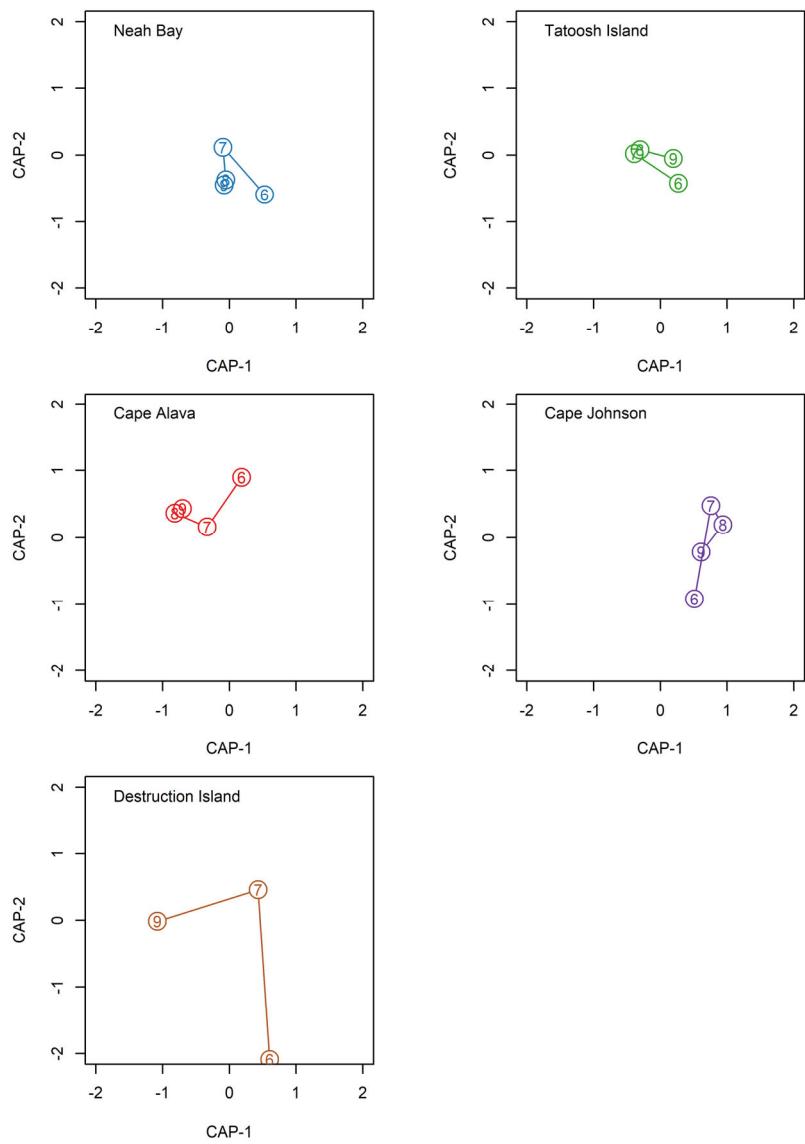
757

758



760 Fig. S 5 Abundance of the primary fish species seen on at five sites from 2016-2019. Data  
761 are the back-calculated site x year means ( $\log x+1$ ) and s.e.

762



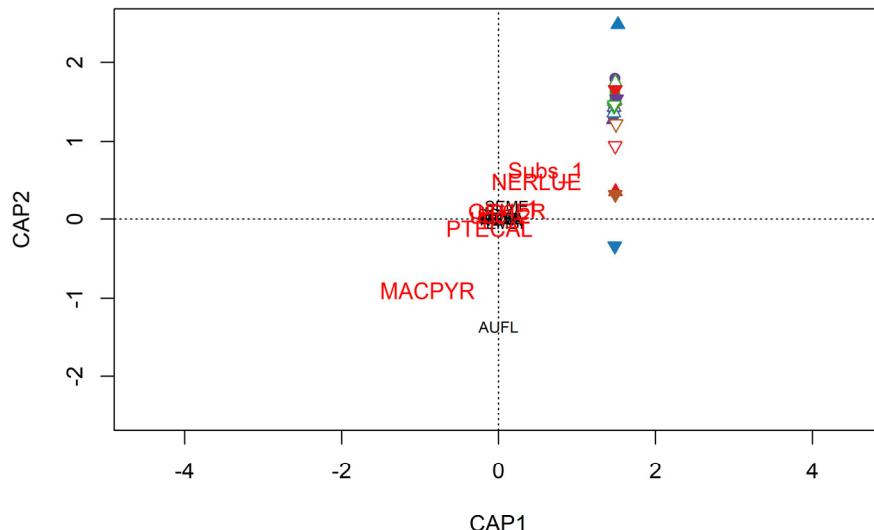
763

764 Fig. S 6 Ordination of sites based on the fish taxa present on 30 x 2 m transects from a  
765 distanced-based redundancy analysis. The analysis used individual transects, but the axes

766 were averaged by site and year for clarity in the presentation. Numbers are the years (9 =  
767 2019) for sampling.

768

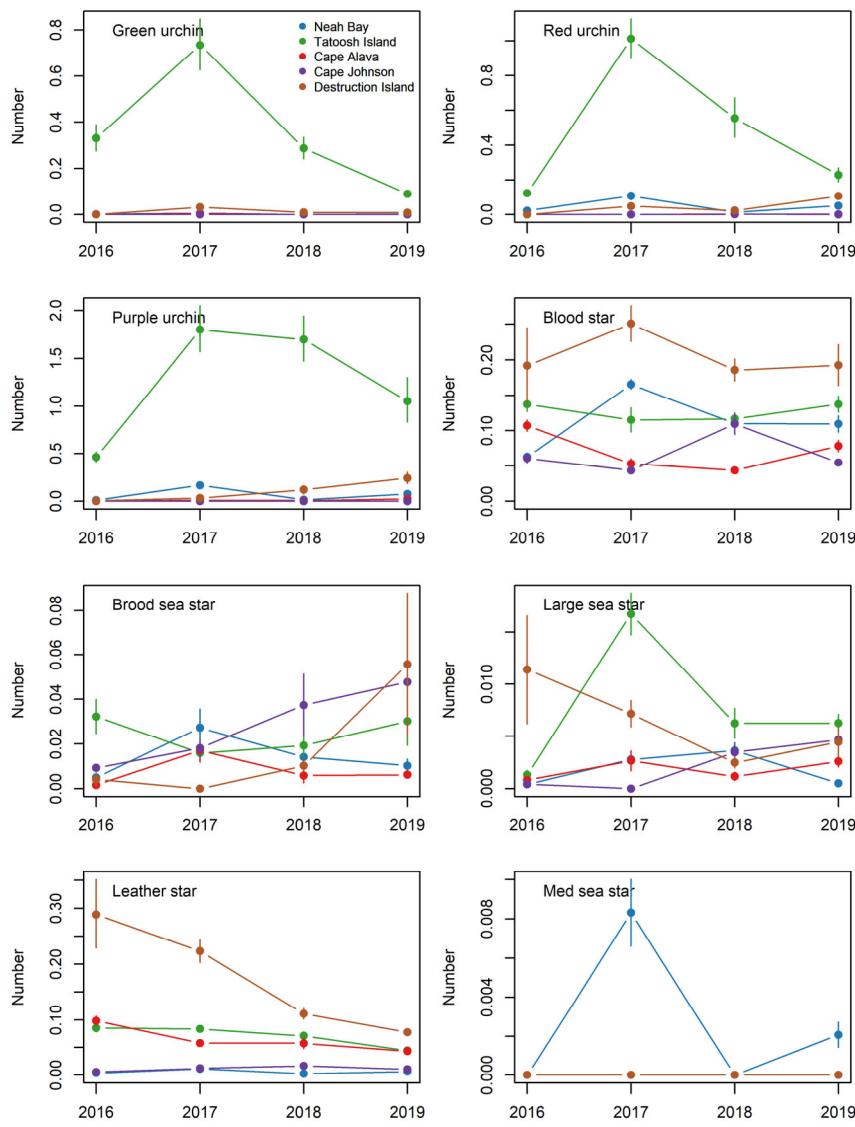
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770

771 Fig. S 7 Results of distance-based redundancy analysis with fish species assemblages  
772 constrained by kelp, bioitic benthic habitat, and substratum variables. The ordination was  
773 non-significant ( $p > 0.05$ ).

774



775

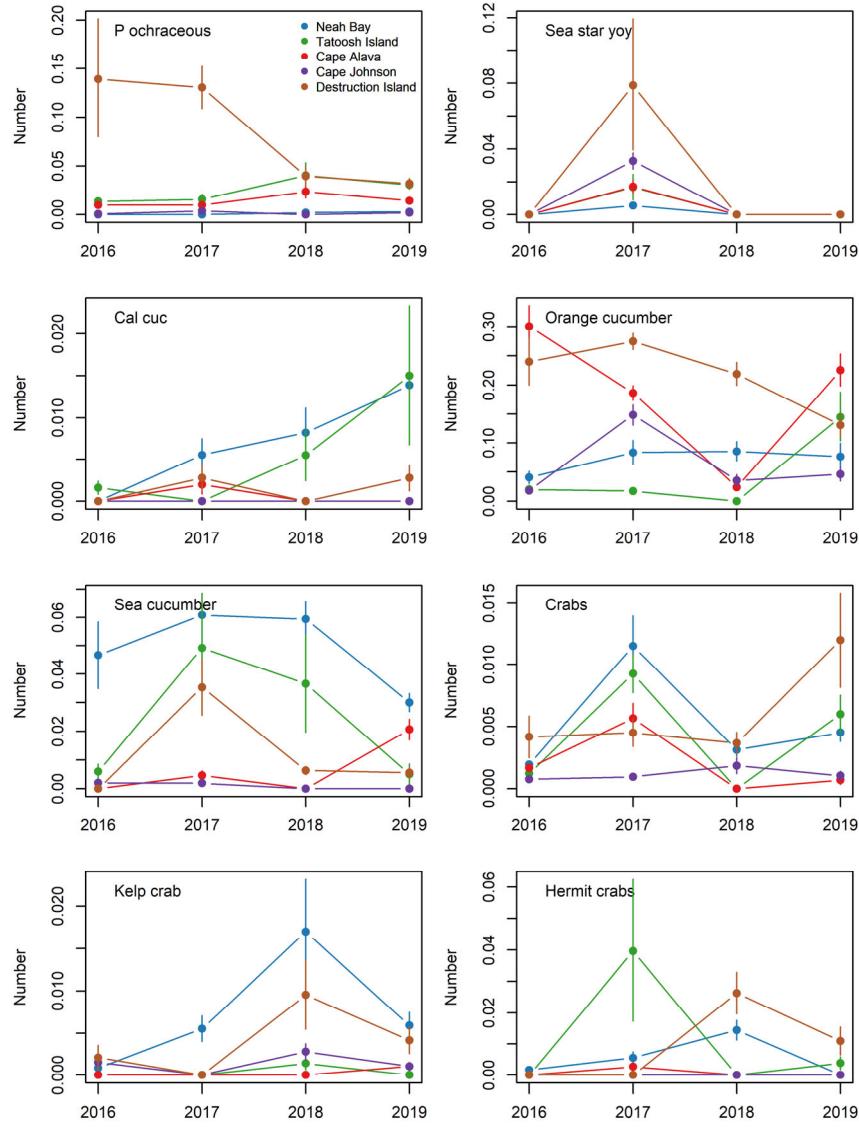
776 Fig. S 8 Abundance of the primary invertebrate species seen on at five sites from 2016-  
777 2019. Data are the back-calculated site x year means ( $\log x+1$ ) and s.e. Large sea stars

778 include: *Easterias troschelii* (99), *Orthasterias koehleri* (62), *Pisaster brevispinus* (7),  
779 *Pisaster giganteus* (1), *Pycnopodia helianthoides* (8), and *Solaster stimpsoni* (14). Medium  
780 sea stars include: *Crossaster papposus* (1), *Mediaster aequalis* (7), and *Patiria miniata* (135).  
781 Numbers in parentheses are the total observed from 2016-2019.

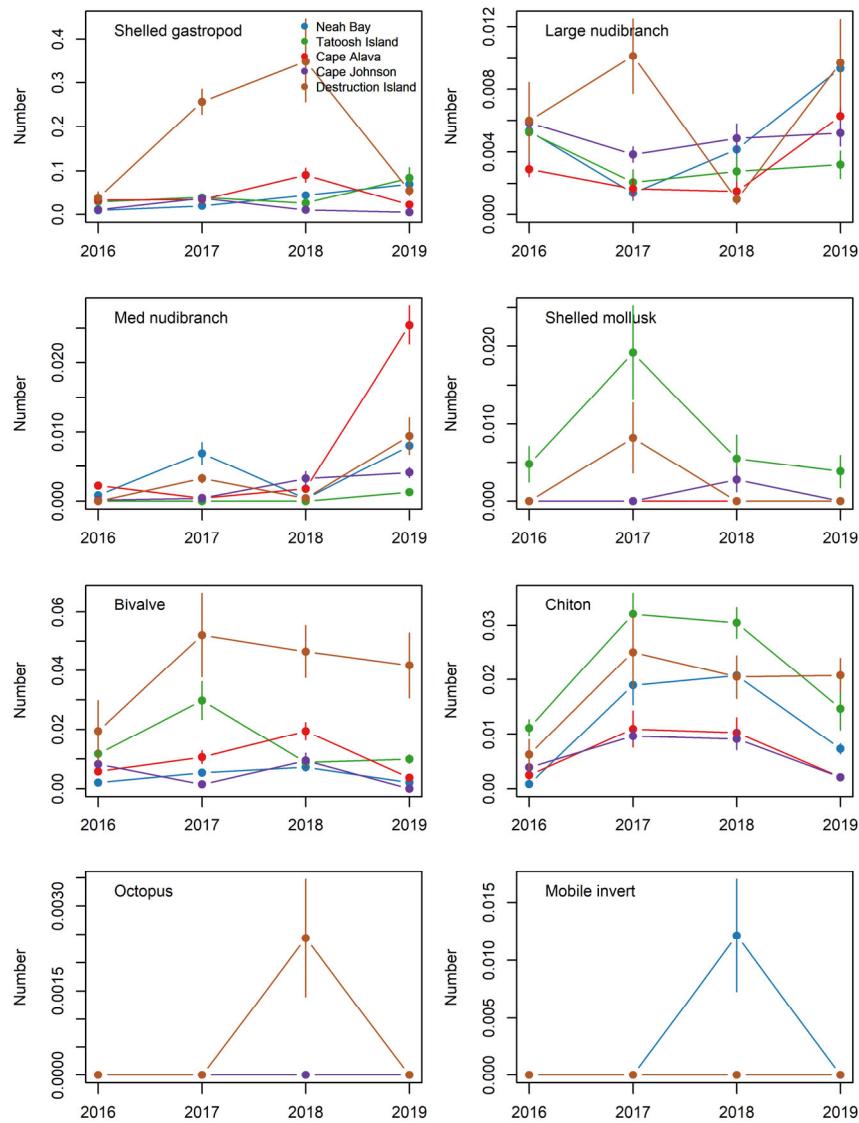
782

**Commented [NT25]:** Check numbers. Make sure these values do not include 2015.

Why lump Easterias and Orthasterias...saw lots. Add to Methods.

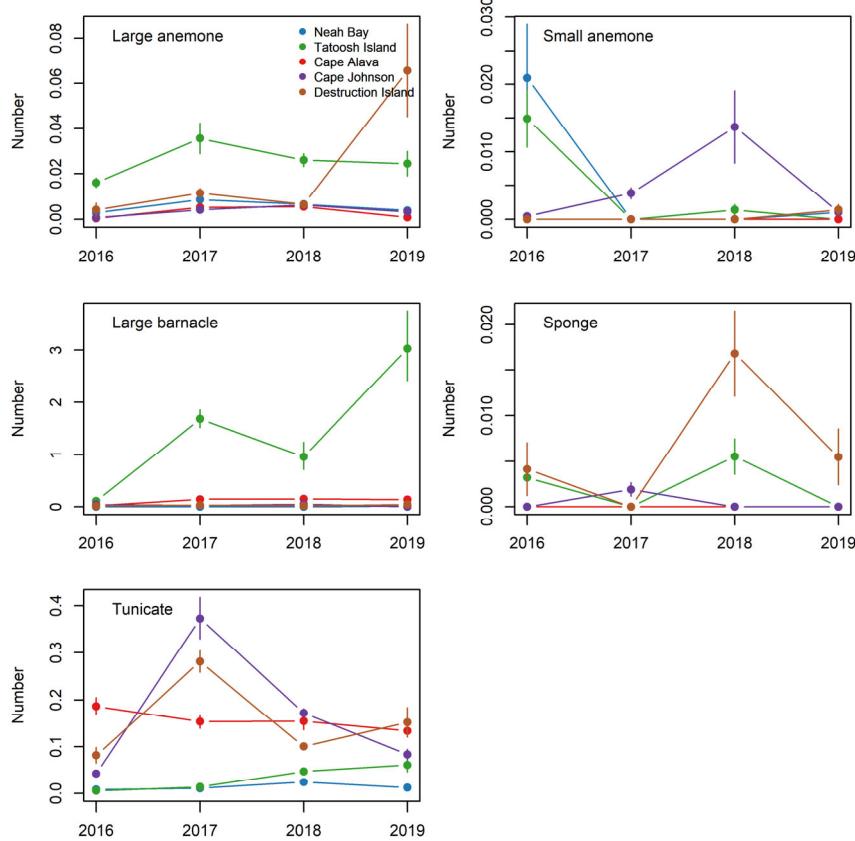


784 Fig. S 9 Abundance of the primary invertebrate species seen on at five sites from 2016-  
785 2019. Data are the back-calculated site x year means ( $\log x+1$ ) and s.e. Note, the for seastar  
786 YOY the value for Cape Alava overlaps that of Tatoosh Island in 2017.



787

788 Fig. S 10 Abundance of the primary invertebrate species seen on at five sites from 2016-  
789 2019. Data are the back-calculated site x year means (log x+1) and s.e.

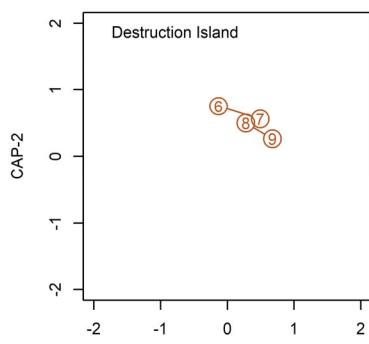
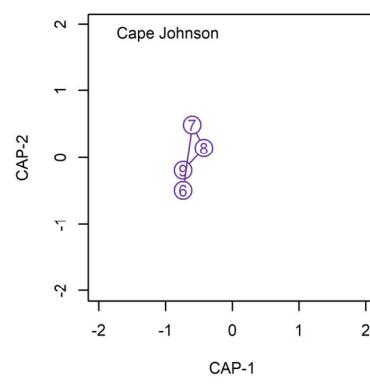
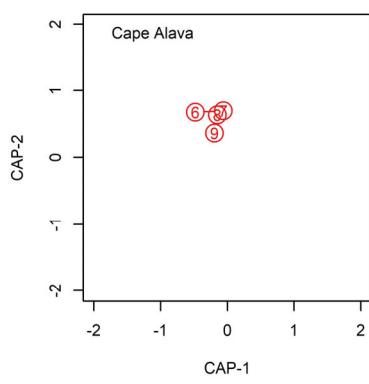
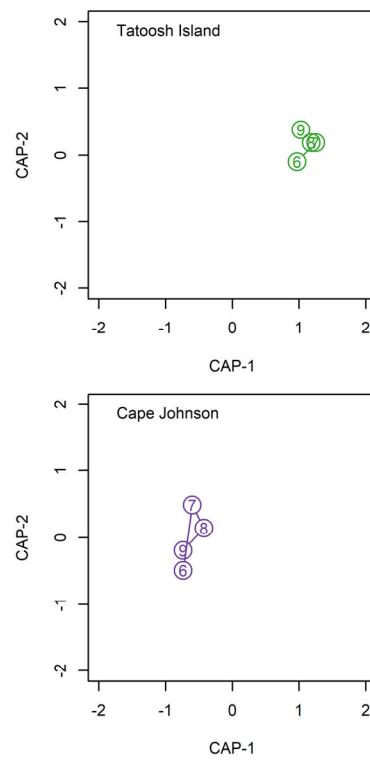
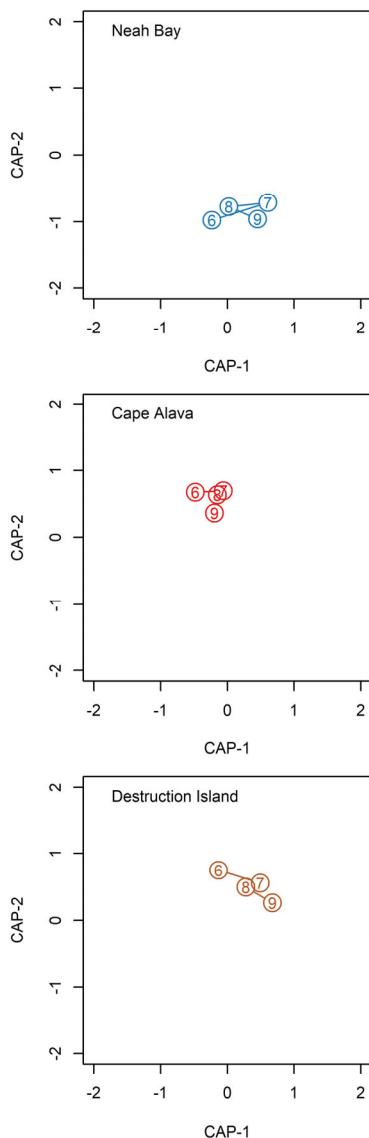


790

791 Fig. S 11 Abundance of the primary invertebrate species seen on at five sites from 2016-  
792 2019. Data are the back-calculated site x year means ( $\log x+1$ ) and s.e.

793

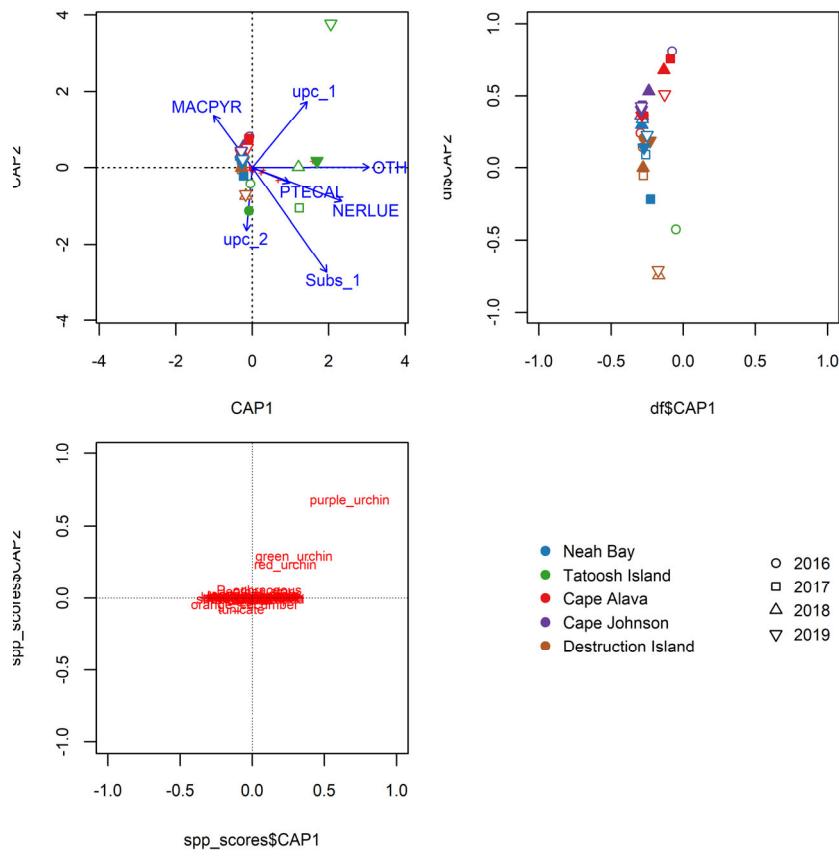
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795

796 Fig. S 12

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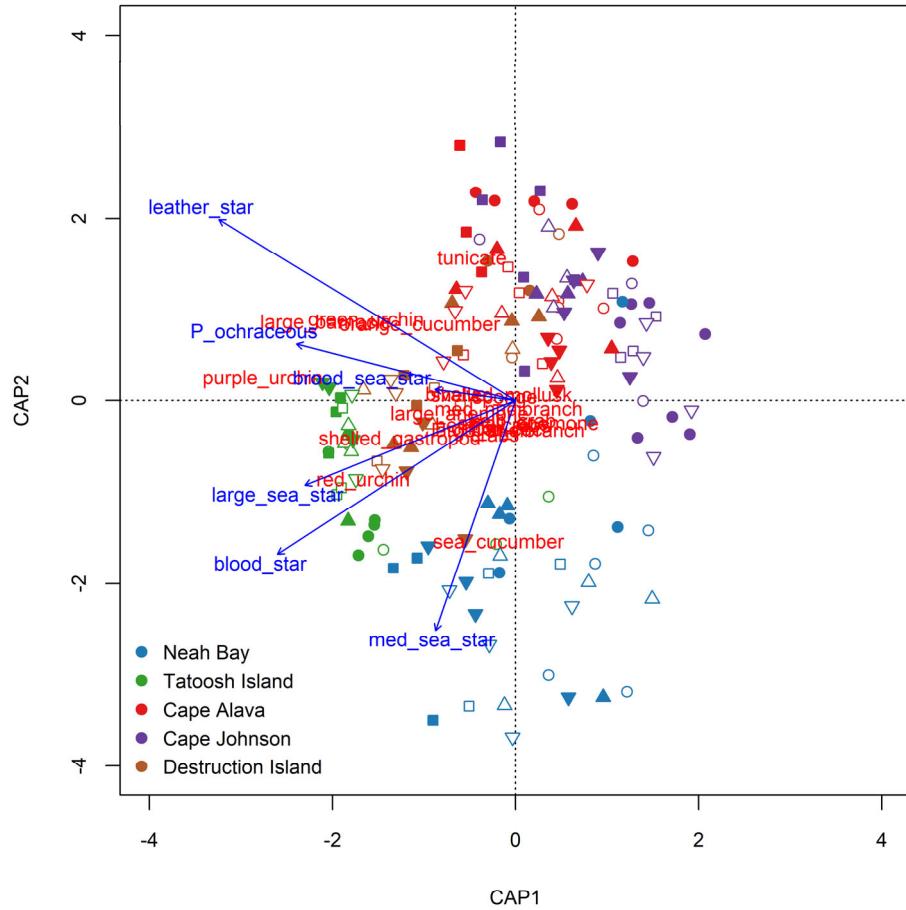


797

spp\_scores\$CAP1

798 Fig. S 13 Inverts vs habitat CAP MACPYR = *Macrocystis pyrifera*, NERLUE = *Nerocystis*  
 799 *luekana*, PTECAL = *Pterygophora californica*. **Update after updating names in figure FIX axis**  
 800 **labels.**

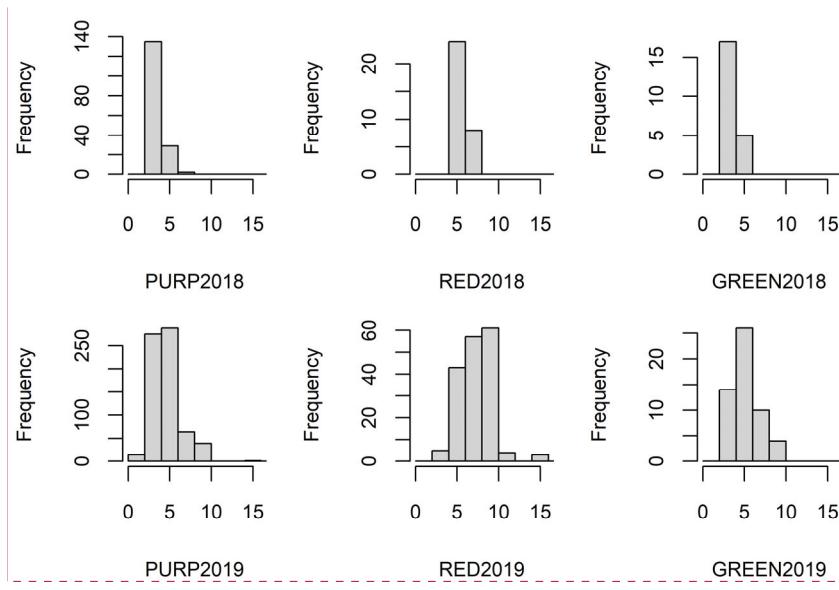
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802

803 Fig. S 14 Ordination (dRDA) of sea stars versus their potential prey items.

804



Commented [NT26]:

805

806 Fig. S 15 Urchin test diameters (mm) for 2018-2019 at Tatoosh Island, WA. Note that the y-  
807 axes vary.

808

809

810