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**Title:** Marine deforestation leads to widespread loss of ecosystem function

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42

43 **Abstract:**

44 Trophic interactions can result in changes to the abundance and distribution of habitat-forming  
45 species that dramatically reduce ecosystem health and functioning. Nowhere may this be as  
46 dramatic as in the coastal zone of the Aleutian Archipelago, where overgrazing by herbivorous  
47 sea urchins that began in the 1980s resulted in widespread deforestation of the region's kelp  
48 forests. Here we show that this deforestation resulted in decreased macroalgal and invertebrate  
49 abundance and diversity, increased benthic irradiances, and reduced rates of gross primary  
50 production and respiration by the ecosystem. These opposing metabolic processes remain in  
51 balance, however, which resulted in little-to-no changes to net ecosystem production. These  
52 patterns were consistent across nine islands spanning more than 1000 kilometers of the  
53 archipelago. In light of the worldwide declines in kelp forests observed in recent decades, our  
54 findings suggest that marine deforestation profoundly affects the health of coastal ecosystems  
55 and how they function.

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58 **Significance statement:** Widespread marine deforestation results in reduced biodiversity and  
59 primary productivity throughout more than 1000 km of the Aleutian Archipelago.

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65 **Introduction:**

66 Predators fundamentally affect ecosystems through trophic interactions (1). These interactions  
67 are especially important if they result in changes to the abundance or distribution of ecosystem  
68 engineers, such as forest-forming trees, which can lead to changes in microclimates, biodiversity,  
69 primary production, nutrient cycling, and energy flow (2). For example, the reintroduction of  
70 gray wolves (*Canis lupus*) into Yellowstone National Park, USA in the 1990s resulted in  
71 increased predation on elk (*Cervus elaphus*) and subsequently reduced herbivory on canopy-  
72 forming trees such as aspens (*Populus tremuloides*), willows (*Salix* spp.), and cottonwoods  
73 (*Populus* spp.) (3). This ultimately led to changes in the morphology and hydrology of the  
74 region's river systems and its riparian plant communities (4, 5). Similarly, large marine algae,  
75 such as kelps, can form subtidal forests whose biogenic structures alter hydrodynamic, nutrient  
76 and light conditions, modify patterns of biodiversity, enhance primary production and carbon  
77 sequestration, and provide food and habitat for numerous other species (6-9). Consequently, the  
78 loss of these forest-forming kelps and the benthic macroalgae they support can have dramatic  
79 impacts to how nearshore ecosystems function, especially if they occur over large geographic  
80 areas. Indeed, kelp deforestation has occurred worldwide in recent decades due to a variety of  
81 forcing factors (10, 11), and the subtidal rocky reefs of the Aleutian Archipelago serve as a  
82 model system to investigate the broader impacts of such deforestation. Here, the collapse of sea  
83 otter (*Enhydra lutris*) populations led to large increases in their primary prey, herbivorous sea  
84 urchins (*Strongylocentrotus polyacanthus*), which subsequently resulted in overgrazing and  
85 widespread losses of the region's kelp forests (12). This collapse began in the late 1980s, likely  
86 in response to a dietary shift by killer whales toward sea otters, and by 2000 sea otter densities  
87 had declined throughout the archipelago to around 5-10% of their estimated equilibrium density

88 (13). Currently, most of the kelp forests have either disappeared from the archipelago or are in  
89 the process of disappearing, although some small forests remain in their ‘historical state’ at  
90 scattered locations on most of the islands (14, 15) (Fig. 1). These remnant forests provide an  
91 excellent benchmark against which we evaluated the effects of widespread deforestation on two  
92 important metrics of ecosystem health and function, namely biodiversity and primary  
93 productivity.

94  
95 Characterizing patterns of primary productivity is essential to fully understanding ecosystem  
96 health and function (16, 17). This includes three basic metrics: gross primary production (*GPP*),  
97 which describes all the CO<sub>2</sub> fixed by the autotrophs during photosynthesis, total ecosystem  
98 respiration (*Re*), which describes the release of CO<sub>2</sub> during the production of energy by  
99 autotrophs, heterotrophs, decomposers and microbes, and net ecosystem production (*NEP*),  
100 which is the difference between *GPP* and *Re* and describes net changes in the total amount of  
101 organic carbon in an ecosystem available for consumption, storage and export to adjacent  
102 ecosystems, or nonbiological oxidation to carbon dioxide (18-21). In general, ecosystems with  
103 high rates of *GPP* also exhibit high rates of *Re*, with the central tendency being that *GPP* and *Re*  
104 are in balance (i.e. similar in magnitude) and therefore have median *GPP* / *Re* ratios close to 1.0,  
105 and *NEP* values near zero (21, 22). Indeed, a review of five decades (1950 to 1990) of studies in  
106 aquatic ecosystems demonstrated that these two opposing processes are indeed generally in  
107 balance, although unproductive ecosystems tend towards net heterotrophy with *GPP* / *Re* < 1.0  
108 and *NEP* < 0, while productive ecosystems tend towards net autotrophy with *GPP* / *Re* > 1.0 and  
109 *NEP* > 0 (19-22). Further, the amount of *Re* associated with any given *GPP* in shallow coastal  
110 ecosystems tends to be greater when the complete benthic communities are considered (22). This

111 may be especially true if microbial metabolism, which is an important component of  $Re$ , is large  
112 compared to  $GPP$  (19-21). This is important for coastal kelp forests, which generally have higher  
113 microbial diversity relative to the adjacent ocean waters (23-25). Consequently, loss of these  
114 forests may lead to complex patterns of  $GPP$ ,  $Re$  and  $NEP$  within coastal ecosystems. On one  
115 hand, reductions in primary producer biomass should result in lowered  $GPP$  and thus reduced  
116  $NEP$ . Alternately, deforestation may result in reduced biodiversity and lowered abundances of  
117 macroalgae, invertebrates, fishes and microbes, which may lead to reduced  $Re$  and enhanced  
118  $NEP$ . At the same time, loss of the habitat-forming kelps also results in increased benthic  
119 irradiances (17) and thus potentially to increased compensatory production by any remaining  
120 fleshy macroalgae, encrusting coralline algae, and microalgae (26-28), which can result in  
121 enhanced  $NEP$ . Thus, understanding the balance between  $GPP$  and  $Re$  in addition to  $NEP$  can be  
122 instrumental in discerning the broader impacts of deforestation on ecosystem health and  
123 productivity. This may be especially relevant for the Aleutian Archipelago where widespread  
124 kelp deforestation has resulted in significant reductions in fishes, invertebrates and fleshy  
125 macroalgae, increases in encrusting coralline algae (12, 29), and elevated benthic irradiances  
126 (14).

127

## 128 **Results:**

129 We studied patterns of benthic macroalgal and invertebrate abundance and diversity, and rates of  
130  $NEP$ ,  $GPP$  and  $Re$  within remnant kelp forests, urchin barrens, and habitats that were in  
131 transition to becoming urchin barrens (Fig. 1) at nine islands spanning more than 1000  
132 kilometers of the Aleutian Archipelago (Fig. 2, Table 1). These kelp forest and urchin barrens  
133 occur as alternate stable states of one another, often with sharply delineated boundaries between

134 them (15). Our results show that the benthic communities within the remnant kelp forests have  
135 more than a 10-fold greater biomass of fleshy macroalgae than those in the urchin barrens  
136 (Permutation post hoc:  $p = 0.004$ ), while the urchin barrens have a nearly 3-fold greater biomass  
137 of urchins than the kelp forests (Fisher's LSD:  $p < 0.001$ , Fig. 3, Tables 2 & 3). The kelp forests  
138 also had greater diversity of macroalgae and encrusting invertebrates than either the urchin  
139 barrens or transition habitats (30), primarily due to the presence of large kelps within the kelp  
140 forests and abundant sea urchins within the barren grounds (Fig. 4). The transition habitats were  
141 similar to (i.e. did not differ from) the urchin barrens with high abundances of urchins ( $p =$   
142  $0.096$ ) and low abundance of fleshy macroalgae ( $p = 0.120$ ) on the benthos (Fig. 3), and are  
143 similar to the kelp forests in the mid-water and at the surface with many canopy-forming kelp  
144 (*Eualaria fistulosa*) still remaining (Fig. 1). All three habitats have high bottom covers of  
145 encrusting coralline algae that lie below the fleshy macroalgae and become exposed following  
146 deforestation (Fig. 1). Benthic irradiances (*PAR* – *photosynthetically active radiation*) vary  
147 among the three habitat types (ANOVA:  $F_{2,16} = 7.697$ ,  $p = 0.004$ ) and are greatest in the urchin  
148 barrens, lowest in the kelp forests, and intermediate in the transition habitats (Fig. 3, Tables 4 &  
149 5).

150

151 We examined how the differences in benthic communities and *PAR* influenced *NEP*, *GPP*, *Re*  
152 and the balance between *GPP* and *Re* by measuring changes in seawater oxygen concentrations  
153 within replicate ( $n = 3$ ) chambers (collapsible benthic incubation tents; hereafter cBITs) that  
154 were placed on the benthos over representative assemblages within each habitat type at each  
155 island. We predicted that *NEP* at the benthos would be reduced in the urchin barrens due to the  
156 loss of photosynthetic macroalgae. Instead, we found that *NEP* does not differ between any of

157 the habitat types, nor does it differ from zero (i.e.,  $GPP = Re$ ) in any of the habitat types (Figs. 3  
158 & 5; Tables 4 & 5). Benthic  $GPP$  in contrast, was 33% higher in the kelp forests than in the  
159 urchin barrens (Fisher's LSD:  $p = 0.067$ ), and 23% higher in the kelp forests than in the  
160 transition habitats ( $p = 0.225$ ), but it differs by only 7% between the transition habitats and  
161 urchin barrens ( $p = 0.532$ ) (Fig. 3, Table 2 & 3). This is presumably due to the higher abundance  
162 of benthic fleshy macroalgae in the kelp forests, but similar abundances of fleshy macroalgae in  
163 the urchin barrens and transition habitats (Fig. 4). Similarly, benthic  $Re$  is 35% higher in the kelp  
164 forests than it is in both the urchin barrens (Fisher's LSD:  $p = 0.011$ ) and the transition habitats  
165 ( $p = 0.035$ ), but it differs by less than 1% between the transition habitats and the urchin barrens  
166 ( $p = 0.621$ ) (Fig. 3, Table 4 & 5). This is presumably due to the higher biomass of fleshy  
167 macroalgae and invertebrates, lower irradiances, and greater diversity of kelp-associated  
168 microbes (23-25) in the kelp forests, while the urchin barrens and transition habitats have  
169 similarly high abundances of urchins and low biomasses of macroalgae. Lastly, the difference  
170 (i.e. range) between  $GPP$  and  $Re$ , which we believe to be a better measure of ecosystem function  
171 than  $NEP$ , is 34% greater in the kelp forests than in the urchin barrens (Fisher's LSD:  $p = 0.027$ ),  
172 and 29% greater in the kelp forests than in the transition habitats ( $p = 0.086$ ), but this range  
173 varies by less than 4% between the transition habitats and the urchin barrens ( $p = 0.603$ ) (Fig. 3,  
174 Table 4 & 5). Thus, while we expected  $NEP$  to scale positively with autotroph biomass by  
175 habitat, we found no differences in benthic  $NEP$  among the three habitat types. Instead, we found  
176 that kelp forests have the highest  $GPP$  and  $Re$ , and that the urchin barrens and the transition  
177 habitats do not differ with respect to these metrics. PAR did vary significantly among the three  
178 habitat types and was greater in the urchin barren grounds than in the kelp forests or the  
179 transition habitats (Fisher's LSD:  $p < 0.001$ ) (Tables 4 & 5). This indicted deforestation resulted

180 in widespread losses to primary production and respiration by the ecosystem, and increases in  
181 benthic irradiances.  
182  
183 Our study is in agreement with previous studies in aquatic ecosystems that have shown *GPP* and  
184 *Re* to generally be in balance and thus exhibit *GPP / Re* ratios near 1.0, and *NEP* values near  
185 zero (21, 22). Indeed, when we examine the relationships between *GPP* and *Re* in each of the  
186 cBITs in each habitat type separately, *GPP* and *Re* are consistently similar in magnitude, with no  
187 differences in *GPP / Re* ratios among habitat types (ANCOVA:  $F_{2,62} = 0.16$ ,  $p = 0.852$ ) (Fig. 5,  
188 Table 6). Further, the distribution of these ratios is symmetrical around 1.0 in each habitat (Fig.  
189 6). Interestingly, the highest individual values of *NEP* were not observed in the kelp forests but  
190 rather in the urchin barrens, which we believe was due to higher irradiances in the urchin barrens  
191 than the other two habitats (Fig. 3) combined with compensatory production by the encrusting  
192 coralline algae and benthic diatoms (28). However, those few observations aside, it is clear that  
193 all three benthic habitats remain in balance following deforestation, with  $GPP \approx Re$ ,  $GPP / Re$   
194 ratios  $\approx 1$ , and median *NEP* values  $\approx 0$ . Thus, although *NEP* may help differentiate between  
195 productive and unproductive ecosystems (22), it poorly describes changes in primary  
196 productivity following widespread kelp deforestation in the Aleutian Archipelago. Instead, it is  
197 clear that deforestation results in significant changes to the region's benthic communities, and  
198 these led to declines in both *GPP* and *Re*, which better reflect a reduction in ecosystem  
199 functioning (16, 17). Further, it appears that even partial deforestation, where the benthic  
200 macroalgae and invertebrates have been lost but the canopy-forming kelps remain, results in a  
201 decrease in *GPP* and *Re* at the benthos that is similar to trends found in urchin barrens.

202



203 **Discussion:**

204 Trophic interactions can lead to changes to the distribution and abundance of habitat-forming  
205 species, which can have profound impacts on ecosystem health and function (2, 31).

206 Deforestation, in particular, can result in changes to biodiversity and energy flow (2), altered  
207 regional and global climates (32), and even lead to species extinctions (33). Coastal kelps are an

208 excellent example of such ecosystem engineers in nearshore habitats that have suffered large-  
209 scale deforestation over the past few decades due to both biological and physical stressors (10,

210 11). Consequently, our study is relevant to other areas of the world where kelp forests have

211 exhibited local to broad scale declines, such as the northwest coast of the United States (34),

212 Nova Scotia (35), western Europe (36), southwestern Japan (37), the east coast of South Korea

213 (38), and along the southern coast of Australia (39). Indeed, recent estimates suggest that global

214 declines in kelp abundances may be as high as 2% per year (11), which can negatively impact

215 numerous other species that depend on them for food and habitat. Certainly, the kelp forests of

216 the Aleutian Archipelago are in critical condition in the face of widespread overgrazing by

217 urchins, and this has had profound effects on the region's benthic communities and on patterns of

218 gross primary production and ecosystem respiration. Whether these forests will recover and

219 return to prior ecosystem functioning regarding these metrics is unknown, but observations of

220 kelp forests from other areas of the world suggest it is possible. For example, *Laminaria*

221 *longicuris* forests recovered from overgrazing following localized disease outbreaks that

222 decimated sea urchin populations in Nova Scotia (40), while *L. hyperborea* forests recovered in

223 mid-Norway due to low sea urchin recruitment (41). *Ecklonia maxima* expanded its range

224 eastward in South Africa, coincident with cooling of the local ocean waters (42). Likewise,

225 *Macrocystis pyrifera* recovered along a ~100 km stretch of the Pacific coast of Baja California,

226 Mexico following nearly two decades of absence after the strong 1997-98 El Niño Southern  
227 Oscillation (43). Recovery of the *Eualaria fistulosa* forests throughout the Aleutian Archipelago,  
228 however, would likely require widespread mortality in the urchin populations, which today  
229 seems unlikely. Until then, benthic biodiversity, *GPP* and *Re* will likely remain lower in areas of  
230 kelp forest loss because the high abundance of urchins limits regrowth of macroalgae and  
231 maintains the urchin barrens (15). Thus, we present a benchmark against which we can evaluate  
232 this recovery, and understand the effects of further deforestation in this ecosystem.

233  
234 Although we have learned much about the effects of the otter-urchin-kelp trophic cascade in the  
235 Aleutian Archipelago, this study offers new insights into the consequences of such widespread  
236 deforestation on the region's benthic primary productivity. Certainly, benthic *GPP*, *Re* and the  
237 difference between them are all greatest in the kelp forests where macroalgae, fish, invertebrate,  
238 and presumably microbial, communities are all most abundant. Deforestation then resulted in  
239 reductions in these metrics, identifying loss of ecosystem health and function regarding  
240 biodiversity, macroalgal abundances, and primary productivity. In contrast, benthic biodiversity,  
241 macroalgal abundances, *GPP*, *Re* and the difference between them are all similar in the urchin  
242 barrens and transition habitats, suggesting that the transition habitats have already suffered  
243 reduced ecosystem function following losses of their benthic communities. This, of course,  
244 reflects productivity at the benthos and not in the mid-water or at the surface where the canopy-  
245 forming *Eualaria fistulosa* remains in the transition habitats. It is likely that these canopy-  
246 forming macroalgae would increase *GPP* and perhaps result in positive values of *NEP* in the  
247 mid-water and at the surface in both the kelp forests and transition habitats. However, at the  
248 benthos, *GPP* and *Re* remain in balance following deforestation, leading to similar, near-zero

249 *NEP* in all three habitats. We believe this reflects balance between the autotrophic and  
250 heterotrophic components of the ecosystem. Specifically, the macroalgae exhibit positive *GPP* as  
251 they photosynthesize, grow and increase in abundance, but this results in a concomitant increase  
252 in heterotrophic metabolism, which increases *Re*. In the face of deforestation, both *GPP* and *Re*  
253 decrease, resulting in little to no changes in *NEP*. Thus, we propose that *GPP* and *Re* are better  
254 measures of changes to primary productivity than *NEP*. Combining these with estimates of  
255 macroalgal and invertebrate diversity and abundance revealed that the Aleutian Archipelago  
256 suffered substantial losses to ecosystem function following widespread deforestation.

257

## 258 **Materials and Methods:**

259 While many past experiments examining primary production by autotrophic communities have  
260 relied on laboratory experiments that do not incorporate natural fluctuations in abiotic  
261 conditions, recent studies have identified techniques that measure primary production *in situ*,  
262 thereby increasing the ecological realism of their experiments (44-46). For example, *in situ*  
263 chamber designs have been developed for estimating primary production by individual species  
264 (45, 46) and whole benthic communities (27, 46). In general, estimates of net ecosystem  
265 production (*NEP*) on the benthos can be made by measuring changes in dissolved oxygen within  
266 benthic chambers that are placed *in situ* over of macroalgae and invertebrate communities. In this  
267 study, we deployed collapsible benthic isolation tents (cBITs) modelled after those described by  
268 Haas et al. (47) and Calhoun et al. (48) that directly measured *in situ* benthic oxygen production  
269 and allowed us to estimate gross primary production (*GPP*), ecosystem respiration (*Re*) and net  
270 ecosystem production *NEP* by the benthic communities (27, 28, 45). By linking temporal  
271 changes in oxygen concentrations within the cBITs to incident irradiance conditions and

272 organism abundances, we can relate variation in *GPP*, *Re*, and *NEP* to primary producer and  
273 invertebrate biomass (27, 49). Further, because our cBITs encompassed whole benthic  
274 communities, species interactions (e.g., shading), and invertebrate and microbial respiration were  
275 incorporated into production measurements. These interactions are often not captured in  
276 laboratory experiments but are pertinent to understanding *GPP*, *Re*, and *NEP* (50).

277

### 278 Experimental Design

279 Our cBITs were made from 0.106 cm polycarbonate plastic triangle sheets glued to fiberglass-  
280 reinforced vinyl panels (Fig. 7). The frames were reinforced using stainless steel tubes with  
281 stainless steel cable to facilitate handling and to ensure they held their pyramidal shape with an  
282 internal volume of 192 L and a basal area of (0.64 m<sup>2</sup>). The cBITs each had 26” skirts around the  
283 perimeter, upon which chain was laid to hold them to the benthos and prevent water exchange  
284 with the surrounding environment. The polycarbonate walls were thin and flexible to allow  
285 hydrodynamic energy transfer into the cBITs, thereby reducing boundary layer formation around  
286 the macroalgal thalli. We verified this energy transfer using dissolving plaster blocks placed  
287 within cBITs and by using video analysis of internal seaweed movements. Sensor arrays that  
288 included a Photosynthetic Active Radiation (*PAR*) sensor (Odyssey Dataflow Systems Ltd), and  
289 a Dissolved Oxygen (DO mg/L) and Temperature (°C) sensor (MiniDOT Logger, PME) were  
290 placed at the center of each cBIT (Fig 8).

291

292 During two cruises aboard the *RV Oceanus* in 2016 and 2017, we deployed three cBITs in each  
293 of the three habitats (kelp forest, urchin barrens, transition habitats) on each of nine islands (Figs  
294 2, 8) for 24-36 hour periods to measure both day and night patterns of *NEP* and *Re*. However,

295 occasionally, replicates were lost due to logistical difficulties associated with the chamber-  
296 benthos seals (Table 1). For each deployment, the cBITs were placed over haphazardly-selected  
297 targeted assemblages in the field. The water within each cBIT was replaced once per day by  
298 opening the side of the chamber and completely replacing the water with new ambient seawater  
299 to reduce “chamber effects” (i.e. the build-up of oxygen and depletion of inorganic carbon and  
300 nutrients). After each deployment, the chambers and sensors were retrieved. At six of the islands  
301 (Table 1), all organisms within each of the chambers’ benthic footprints were collected, brought  
302 back to the ship, enumerated and weighed. We measured *NEP* over the whole diurnal cycle, *Re*  
303 during the nighttime hours, and calculated *GPP* during the day for each cBIT during each  
304 incubation period separately according to Olivé et al. (46). Specifically, measurements made  
305 during the night (the dark) were used to infer rates of *Re*, which were then combined with  
306 measurements of *NEP* to estimate *GPP* by the autotrophs (19-21).

307

### 308 Statistical Analyses

309 All analyses were done in either Systat ver. 12, Primer ver 6. Prior to analyses, all data were  
310 evaluated for normality by graphical examination of the residuals, which suggested they were  
311 slightly non-normal. Data were then square-root transformed and re-graphed, which suggested  
312 the problems were corrected, with the exception of macroalgal biomass, which could not be fixed  
313 by transformation. The transformed data were then examined for equality of variances using  
314 Bartlette’s tests, which indicated they were homoscedastic. We then evaluated if urchin biomass,  
315 PAR, *GPP*, *Re*, *NEP* and the range between *GPP* and *Re* varied among the three habitats (kelp  
316 forests, urchin barrens, and transition habitats), and among islands using separate two-way  
317 Model III ANOVAs, with habitat type as a fixed factor, and island as a random factor.

318 Regardless of ANOVA outcomes, we then used Fisher's LSD tests to evaluate *a priori*  
319 hypotheses about how these metrics differed between pairs of habitat types. We examined if  
320 macroalgal biomass varied among the three habitat types using Euclidean distance based  
321 PERMANOVA. Regardless of PERMNOVA outcome, we used permutation post hoc tests to  
322 evaluate *a priori* hypotheses about how biomass differed among the three habitat types. We  
323 evaluated if the relationship between *GPP* and *Re* varied among habitats using ANCOVA, with  
324 *Re* as the response variable, *GPP* as the covariate, and habitat type as the categorical independent  
325 variable. We evaluated if the ratios in any of the habitats differed from 1.0 (i.e.  $GPP = Re$ ) by  
326 assessing if 1.0 occurred within the 95% confidence intervals around their average values.

327

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336 **Competing Interests:** No authors have competing interests. **Data and materials availability:**

337 Data are available on our NSF bco-dmo data page at <https://www.bco-dmo.org/dataset/755658>

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497 **Figure legends:**

498 **Fig. 1.** Photographs of each habitat type showing (A) high abundance of benthic macroalgae and  
499 canopy-forming kelps in the kelp forests, (B) lack of benthic macroalgae but remaining canopy-  
500 forming kelps and high abundances of sea urchins in the transition habitats, and (C) lack of  
501 benthic macroalgae and canopy-forming kelps, but high abundances of sea urchins in the urchin  
502 barrens.

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504 **Fig. 2.** Map of the Aleutian Archipelago showing locations of the nine islands (denoted by red  
505 circles) where ecosystem productivity (*NEP*, *GPP* and *Re*) was measured in the cBITs.

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507 **Fig. 3.** Box plots showing (A) Macroalgae (gray bars) and invertebrate (white bars) biomass, (B)  
508 Irradiance (*PAR*), (C) Net Ecosystem Production (*NEP*), (D) Gross Primary Production (*GPP*),  
509 and (E) Ecosystem Respiration (*Re*), as measured in the cBITs deployed within each habitat type  
510 (kelp forests, transition habitats, and urchin barrens). Macroalgae and invertebrate diversity and  
511 biomass were measured at six islands, and *PAR*, *GPP*, *Re*, and *NEP* were measured at nine  
512 islands (Fig 2, Table 1). Red diamonds represent mean values, and horizontal lines represent  
513 median values. Boxes within each graph that do not share letters represent significant differences  
514 between habitat pairs.

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517 **Fig. 4.** Mean biomass ( $\pm$  SE) of (A) all kelps, and red, brown and green macroalgae, and (B) the  
518 most abundant taxonomic groups of invertebrates collected within the cBITs within each habitat  
519 type at six of the islands where the cBITs were deployed (Table 1).

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521 **Fig 5** Relationship between gross primary production (*GPP*) and ecosystem respiration (*Re*) for  
522 each habitat type across all nine islands where cBITs were deployed (Table S1). Each point  
523 represents measurements from a single cBIT. Gray shading denoted 95% confidence intervals.

524

525 **Fig 6.** Frequency distribution of *GPP / Re* ratios within each habitat type across all nine islands  
526 where cBITs were deployed (Table S1). Each data point represents measurements from a single  
527 cBIT. Note the urchin barrens have the highest ratios observed, and the kelp forests have the  
528 largest number of low values. The vertical dashed line represents the 1:1 ratio.

529

530 **Fig. 7.** Photograph of cBIT before deployment showing 26” skirt around perimeter, flexible  
531 polycarbonate walls, steel framing, anchor chain used to hold skirt and cBIT to the benthos.

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533 **Fig 8.** Photograph of cBIT deployed in kelp forest showing *PAR* and oxygen sensors

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544 **Tables**

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**Table 1.** List of the nine islands in the Aleutian Archipelago where we deployed cBITs to measure *NEP*, *GPP* and *Re*, and the six islands where we collected all macroalgae and invertebrates from within the cBITs to estimate their biomass. The number of cBITs deployed, and whether macroalgae and invertebrates were collected from within them are noted.

<u>Island</u>	<u>No. cBITs deployed</u>			<u>Collections made?</u>
	Kelp forests	Transition habitats	Urchin barrens	
Adak	3	2	3	No
Amchitka	3	2	3	Yes
Atka	3	3	2	Yes
Attu	3	3	1	Yes
Chuginadak	2	2	3	Yes
Kiska	3	3	2	Yes
Nizki	3	3	2	Yes
Tanaga	2	1	2	No
Yunaska	3	3	3	No

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**Table 2.** Results of A) a two-way Model III Permutation Analysis of Variance testing differences in Algae biomass, and B) a two-way Model III Analyses of Variance testing differences in Urchin biomass, among the nine islands and three habitat types (kelp forests, transition habitats, and urchin barrens). For each analysis, island was considered a random factor and habitat was considered a fixed factor.

**A) Algae biomass**

Source	Type III SS	df	MS	Pseudo-F	p-value
Island	5	4.533	0.907	6.146	0.001
Habitat	2	32.126	16.063	24.525	0.002
Hab*Isl	10	6.550	0.655	4.440	0.002
Error	36	5.310	0.148		

**B) Urchin biomass**

Source	Type III SS	df	MS	F-ratio	p-value
Island	0.837	5	0.167	3.523	0.011
Habitat	4.185	2	2.092	10.676	0.003
Hab*Isl	1.962	10	0.196	4.131	0.001
Error	1.71	36	0.047		

**Table 3.** Results of A) permutation post hoc comparisons testing for differences in macroalgal biomass, and B) Fisher's LSD pairwise comparisons testing for differences in urchin biomass, among habitat type pairs. These tests were done as *a priori* hypotheses and thus done regardless of PERMANOVA or ANOVA outcomes (see Table 2).

**A) Macroalgae**

Habitat 1	Habitat 2	t	P(perm)	perms
Barren	Kelp	12.266	0.004	960
Barren	Transition	1.811	0.120	974
Kelp	Transition	3.991	0.020	974

**B) Urchins**

Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	0.643	<0.001	0.495	0.79
Barren	Transition	0.124	0.096	-0.023	0.272
Kelp	Transition	-0.518	<0.001	-0.666	-0.371

**Table 4.** Results of separate two-way Model III Analyses of Variance testing for differences in A) net ecosystem production (*NEP*), B) gross primary production (*GPP*), C) respiration (*Re*), D) the range (difference) between *GPP* and *Re*, and E) *PAR* among the nine islands and three habitats (kelp forests, transition habitats, and urchin barrens). For each analysis, island was considered a random factor and habitat was considered a fixed factor.

<b>A) <i>NPP</i></b>					
Source	Type III SS	df	MS	F-ratio	p-value
Island	7.98E+02	8	99.783	4.623	0.001
Habitat	93.089648	2	46.545	0.502	0.314
Hab*Isl	1.48E+03	16	92.561	4.289	0.001
Error	8.85E+02	41	21.583		
<b>B) <i>GPP</i></b>					
Source	Type III SS	df	MS	F-ratio	p-value
Island	4.57E+03	8	5.71E+02	8.077	0.001
Habitat	2.65E+02	2	1.33E+02	0.788	0.471
Hab*Isl	2.69E+03	16	1.68E+02	2.378	0.013
Error	2.90E+03	41	7.07E+01		
<b>C) <i>Re</i></b>					
Source	Type III SS	df	MS	F-ratio	p-value
Island	4.58E+03	8	5.73E+02	9.766	0.001
Habitat	4.94E+02	2	2.47E+02	1.246	0.314
Hab*Isl	3.17E+03	16	1.98E+02	3.375	0.001
Error	2.41E+03	41	58.684		
<b>D) Range</b>					
Source	Type III SS	df	MS	F-ratio	p-value
Island	8.77E+03	8	1.10E+03	8.857	0.001
Habitat	7.36E+02	2	3.68E+02	1.077	0.363
Hab*Isl	5.46E+03	16	3.41E+02	2.758	0.005
Error	5.07E+03	41	1.24E+02		
<b>E) <i>PAR</i></b>					
Source	Type III SS	df	MS	Pseudo-F	p-value
Island	11.856	2	5.928	7.964	0.004
Habitat	6.074	8	0.759	1.020	<0.001
Hab*Isl	11.909	16	0.744	6.554	<0.001
Error	3.748	33	0.114		

**Table 5.** Results of Fisher's LSD pairwise comparisons testing for differences in A) *NEP*, B) *GPP*, C) *Re*, D) the range (difference) between *GPP* and *Re*, and E) *PAR* among habitat type pairs. These tests were carried out as *a priori* hypotheses, and thus done regardless of ANOVA outcomes (see Table 4).

<b>A) <i>NEP</i></b>					
Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	1.289	0.642	-2.055	4.633
Barren	Transition	-1.647	0.523	-5.093	1.800
Kelp	Transition	-2.936	0.107	-6.238	0.367

<b>B) <i>GPP</i></b>					
Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	-4.871	0.067	-9.898	0.155
Barren	Transition	-1.719	0.532	-6.899	3.462
Kelp	Transition	3.153	0.225	-1.811	8.117

<b>C) <i>Re</i></b>					
Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	-6.311	0.011	-10.890	-1.731
Barren	Transition	-1.235	0.621	-5.955	3.485
Kelp	Transition	5.076	0.035	0.553	9.598

<b>D) RANGE</b>					
Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	-7.838	0.027	-14.487	-1.188
Barren	Transition	-1.887	0.603	-8.740	4.966
Kelp	Transition	5.951	0.086	-0.616	12.517

<b>E) <i>PAR</i></b>					
Habitat 1	Habitat 2	Difference	p-value	95.0% Confidence Intervals	
				Lower	Upper
Barren	Kelp	1.090	<0.001	0.876	1.304
Barren	Transition	0.456	<0.001	0.239	0.673
Kelp	Transition	-0.634	<0.001	-0.854	-0.415

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**Table 6.** Analysis of covariance testing the effect of *GPP* and habitat on *Re*. Note the non-significant Habitat\**GPP* interaction hat shows no differences in the slopes (i.e. relationships) between *GPP* and *Re* among the three habitat types. See Fig 5 for graphical representation.

Source	Type III SS	df	MS	F-ratio	p-value
<i>GPP</i>	8.46E+03	1	8.5E+03	3.2E+02	0.001
HABITAT	20.791443	2	1.0E+01	3.9E-01	0.680
HABITAT* <i>GPP</i>	8.6140845	2	4.3E+00	1.6E-01	0.852
Error	1.66E+03	62	2.7E+01		

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Figure 1



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Figure 2

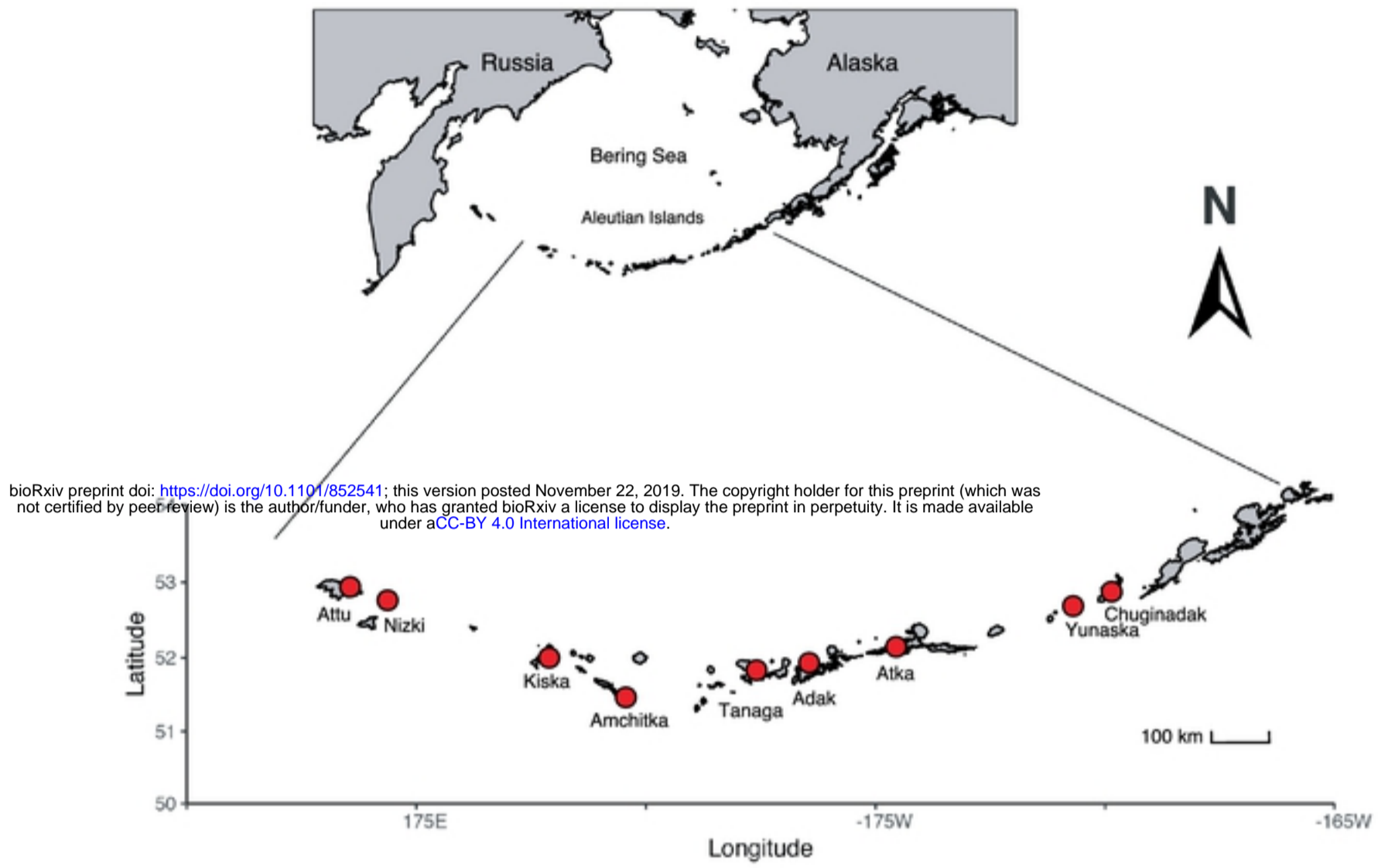
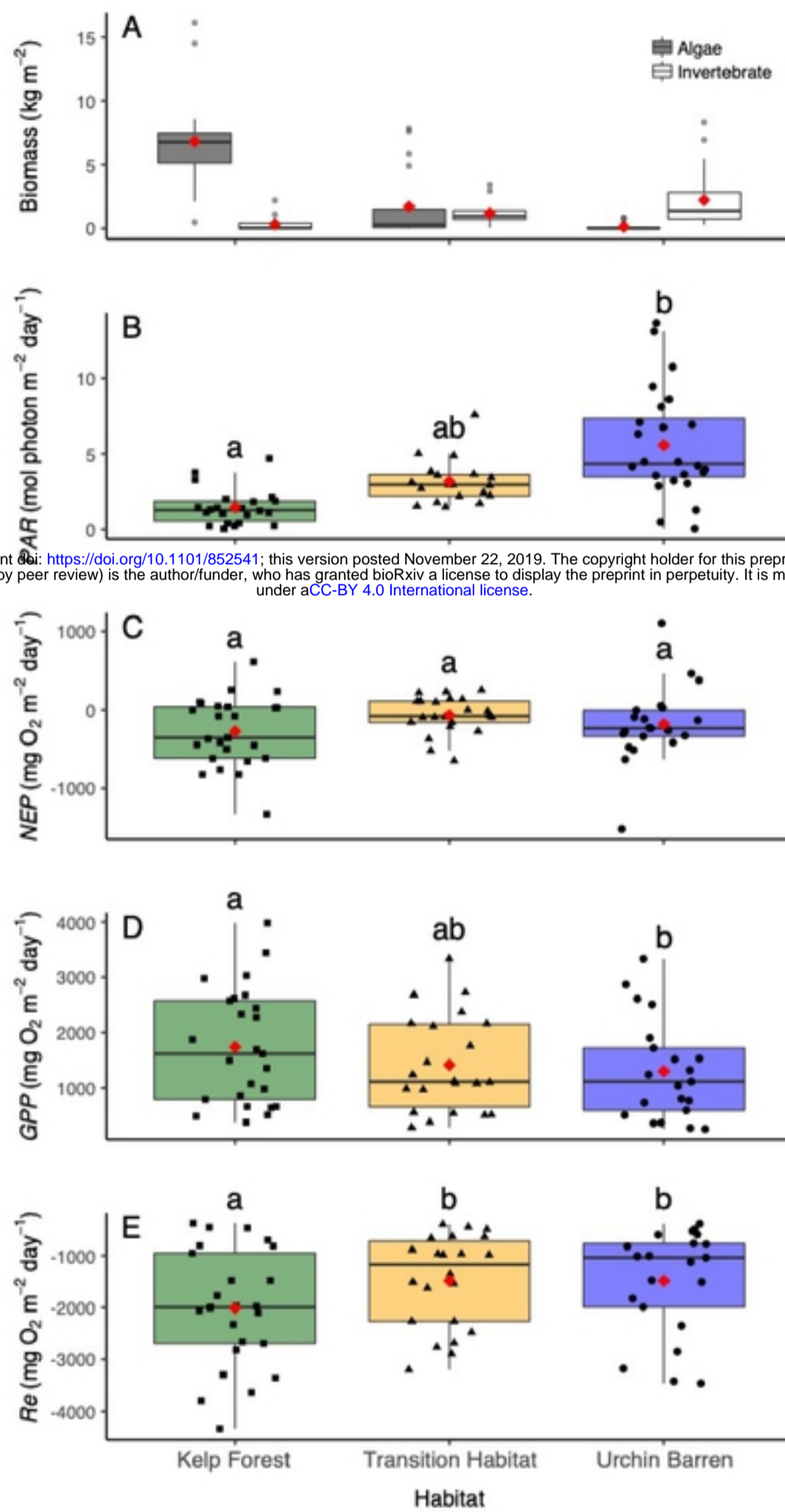
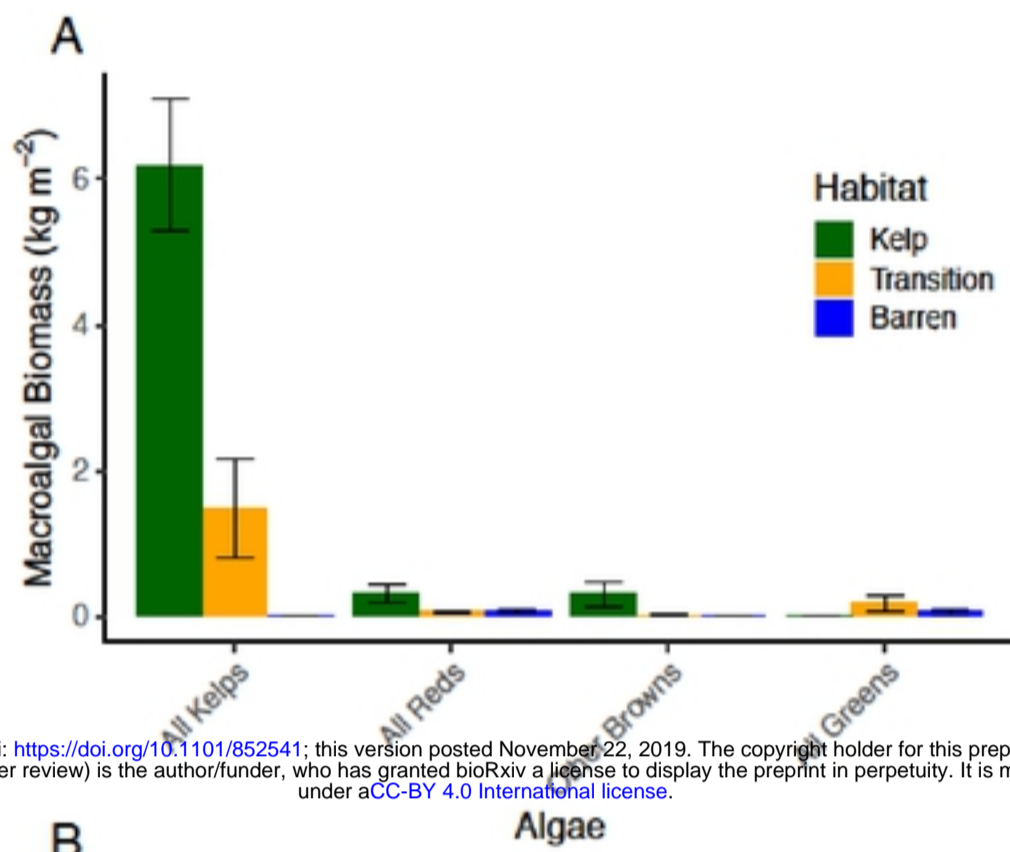


Figure 3



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Figure 4



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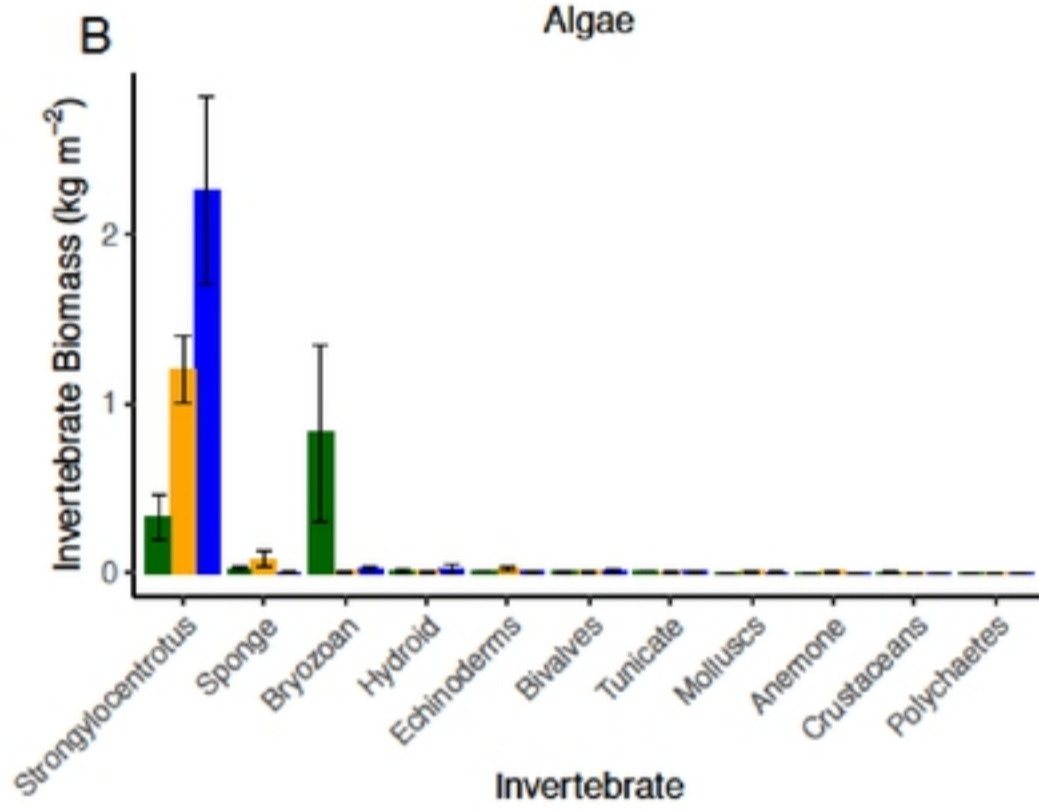
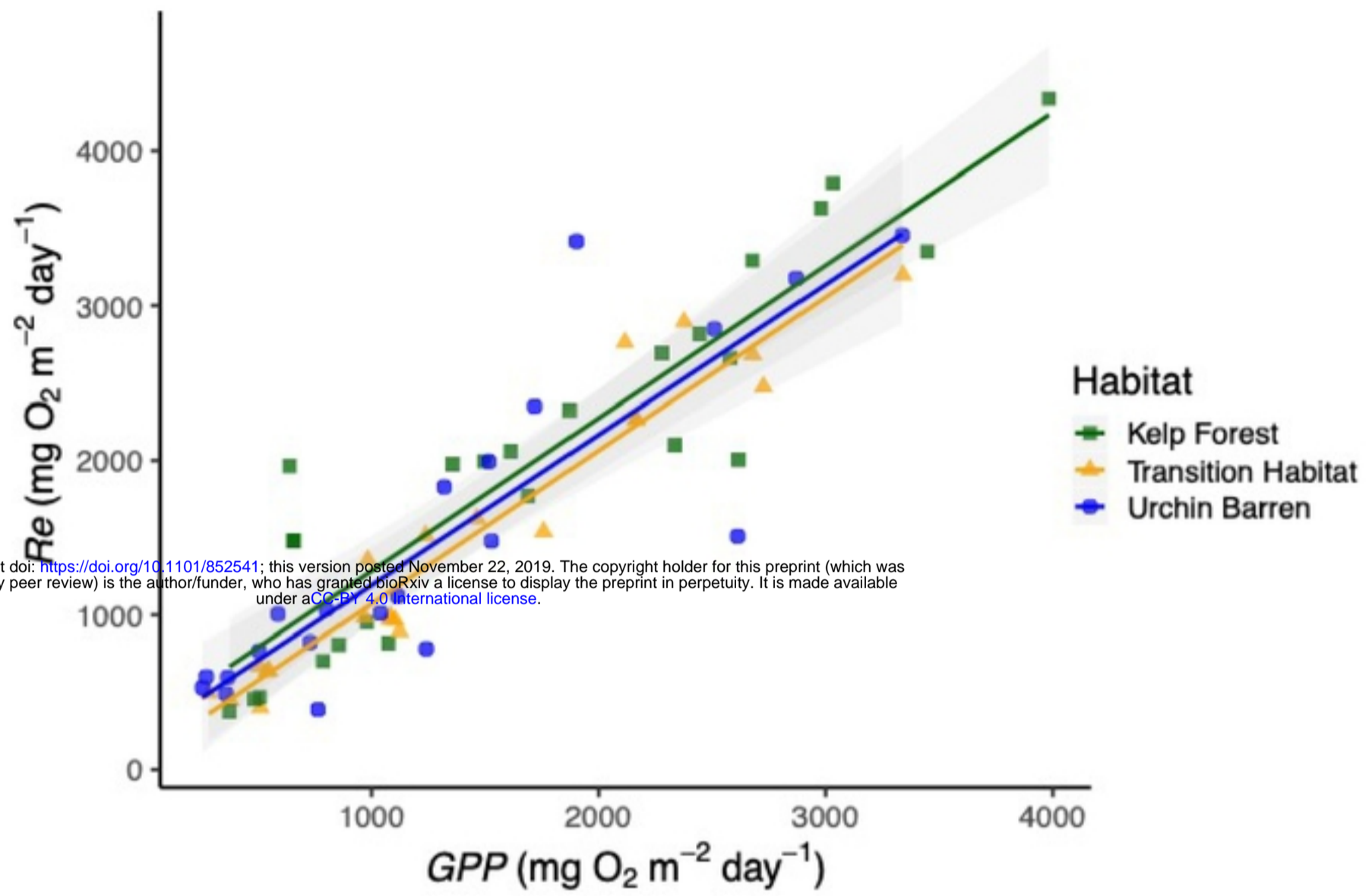


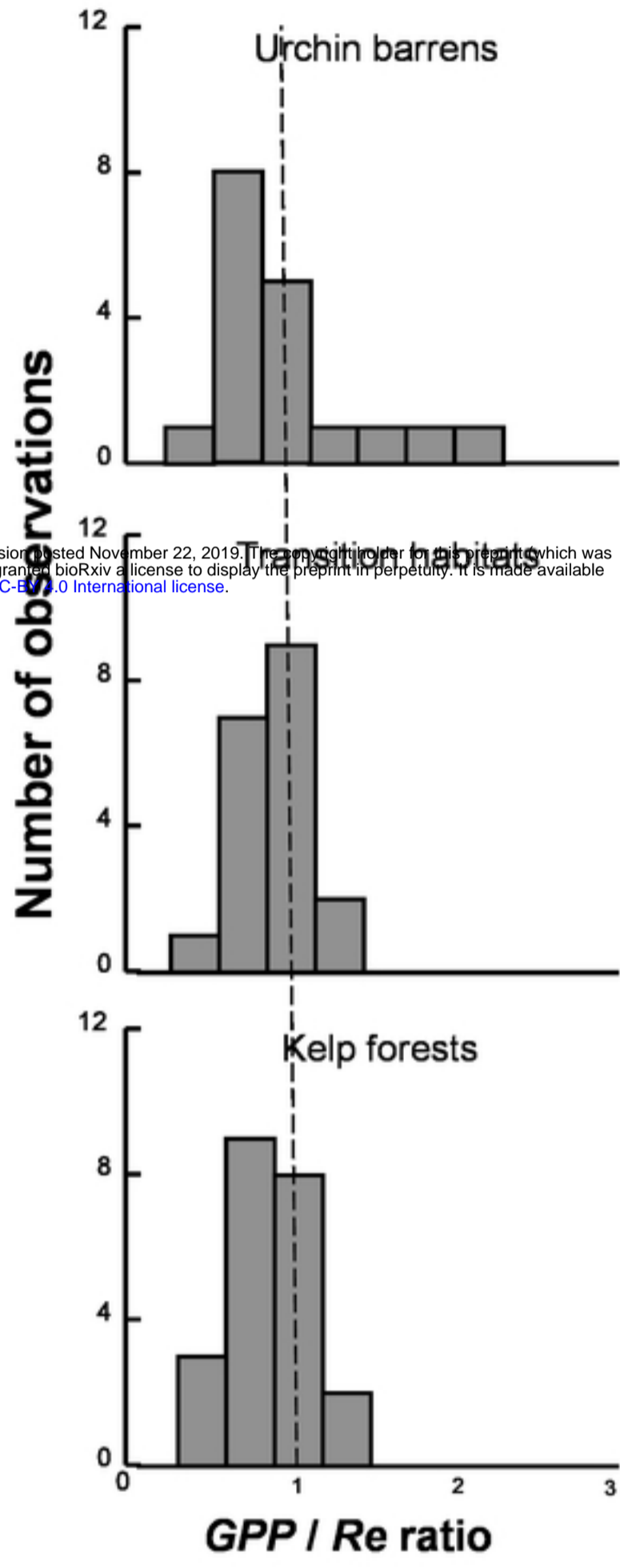
Figure 4



Figure 5



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2 **Figure 6**



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Figure 7



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Figure 8



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