

1 TITLE: Mature and developing kelp bed community composition in a glacial estuary

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4 AUTHORS:

5 Sarah Beth Traiger^a, corresponding author, sbtraiger@alaska.edu, (323) 369-5488

6 Brenda Konar^a, bhkonar@alaska.edu

7 a. University of Alaska Fairbanks, PO Box 757220, Fairbanks, AK 99709 United States

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9 ABSTRACT:

10 The assembly and maintenance of biological communities is influenced by environmental
11 factors, which are predicted to shift with climate change. Glaciers are melting at increasing rates,
12 delivering sediment and fresh water to coastal habitats. We hypothesized that environmental
13 factors related to glacial discharge would be correlated to the initial recruitment and colonization
14 of sessile communities in kelp beds, and to the abundance of mobile epibenthic invertebrates and
15 adult kelp. To test these hypotheses, cleared rocks were placed at six sites at 10-m depth across a
16 gradient of glacial-influence in Kachemak Bay, Alaska and the percent cover of the initial
17 recruitment and the subsequent progression of the sessile community was monitored over 18
18 months. Small mobile invertebrates (such as limpets and chitons) were also monitored on these
19 rocks for 18 months. Lastly, larger invertebrates (such as sea stars) and adult kelp were surveyed
20 over the same time period along transects in the immediate vicinity of the cleared rocks.
21 Environmental factors (sedimentation rates, salinity, temperature, irradiance, and nutrient
22 concentration) were concurrently monitored at each site. Recruitment and subsequent
23 colonization varied along the glacial gradient. At sites with higher sedimentation rates,

24 recruitment and the subsequent developing community was dominated by barnacles with little or
25 no kelp recruits and other macroalgae and high temporal variation in availability of bare space.
26 At more oceanic sites, these communities were characterized by a slow increase in cover of
27 encrusting and upright macroalgae, also with high variability among sites. Mobile invertebrates
28 and adult kelp were more abundant at oceanic sites than the glacial sites. Using distance-based
29 linear models, inorganic sedimentation rate was correlated to patterns of kelp bed recruitment
30 and colonization and to the abundance of mobile invertebrates and adult kelps in the surrounding
31 area. Changes in inorganic sedimentation with climate change may alter how kelp beds are
32 distributed and structured in glacial estuaries.

33

34 **KEYWORDS:** glacial melt, kelp, mobile invertebrates, recruitment, succession, sedimentation

35

36 1. Introduction

37

38 Kelp beds are important ecosystems around the world. Kelp beds support a wide range of
39 commercial, recreational and subsistence fish and invertebrate species (Efrid and Konar, 2014;
40 Hamilton and Konar, 2007; Markel and Shurin, 2015). The primary productivity in kelp beds is
41 large, and as such, kelp beds feed nearshore and offshore communities via detritus and through
42 kelp drift (Abdullah et al., 2017; Duggins et al., 2016; Yorke et al., 2013). Kelp is harvested for
43 subsistence and commercial use, as well as for herring roe, which use kelp blades for substrate
44 (Holen et al., 2012; van Tamelen and Woodby, 2001; Vásquez et al., 2012). Hence kelp beds are
45 important to nearshore and offshore ecosystems and to human communities.

46

47 Kelp beds naturally experience environmental and biological disturbances that result in space
48 being cleared for recruitment. Recruitment can be affected by larval or propagule supply,
49 environmental conditions, and biotic interactions. Hydrodynamic factors such as upwelling
50 variability and current direction can affect propagule supply and the pool of species that can
51 recruit to an area (Billot et al., 2003; Menge, 2000). Environmental conditions such as high
52 sedimentation may also prevent certain organisms from establishing (Balata et al., 2007). Kelp
53 microscopic stage growth, survival, and subsequent recruitment may be inhibited by high
54 temperature, low nutrient conditions (Ladah and Zeruche-Gonzalez, 2007; Mabin et al., 2013;
55 Nielsen et al., 2014) and interactions between temperature and salinity (Fredersdorf et al., 2009).
56 The effects of eutrophication and disturbance on kelp recruitment can vary by species, resulting
57 in compositional changes to kelp beds (Carnell and Keough, 2014). The study of initial
58 recruitment and early colonization can give clues to ecological processes such as propagule
59 supply, competition, and disturbance (Benes and Carpenter, 2015; Gagnon et al., 2005; Konar
60 and Iken, 2005; Maggi et al., 2012). Recruitment is critical for sustaining populations, so
61 understanding the effects of multiple stressors on recruitment is needed to assess population and
62 community stability (Perkol-Finkel and Airoldi, 2010).

63
64 Contrasts between communities in recently disturbed patches and more established communities
65 can indicate environmental factors that affect adult populations. The community that persists to
66 reproduce may be very different than the community that initially recruits. Localized mortality of
67 macroalgae and invertebrates sometimes follows influxes of sediment or fresh water (Branch et
68 al., 1990; Karsten, 2007). Kelp responses to warming can vary among co-existing species,
69 potentially leading to changes in kelp bed species composition with future temperature increases

70 (Hargrave et al., 2017). Kelp beds may be replaced by filamentous turf communities under
71 persistent high sedimentation rates and elevated temperature (Bogen, 2009). Sea star movement
72 and feeding can be inhibited by low salinity conditions (Agüera et al., 2015; Held and Harley,
73 2009). Variation in epibenthic invertebrate assemblages has been attributed to organic
74 sedimentation, sediment type, and wave exposure (Eddy and Roman, 2016). Persistent changes
75 in environmental conditions, such as increasing temperature at an ocean warming hotspot, can
76 result in large scale changes in kelp biomass and species composition of kelp communities
77 (Filbee-Dexter et al., 2016).

78
79 Glaciers are important features in high latitudes with direct connections to the nearshore
80 environment (tidewater glaciers) or indirect connections through rivers fed by glaciers. Glaciers
81 are melting at accelerating rates (Neal et al., 2010), resulting in increased glacial discharge that
82 reduce water temperatures and salinities, increase sedimentation rates, reduce light availability
83 (Wiencke et al., 2007), and degrade substrate quality (Spurkland and Iken, 2011). These
84 environmental changes have been observed to diminish benthic biodiversity and macroalgal
85 abundance (Spurkland and Iken, 2011; Wlodarska-Kowalczyk and Weslawski, 2001); however,
86 it is not yet understood whether these declines are due to differences in survival of initial recruits
87 or drivers impacting subsequent colonization. This study investigated the role of environmental
88 factors in a glacial estuary in structuring several components of kelp bed communities including
89 1) the recruitment and subsequent colonization of the sessile community on bare rocks over a
90 time period of 18 months, and 2) mobile epibenthic invertebrate and adult kelp abundance.
91 Identifying potential drivers of kelp beds among the environmental factors affected by glacial

92 melt will aid in selecting variables for further study. This study also contributes to the discussion
93 of how environmental drivers structure kelp bed communities in glacial estuaries.

94

95 2. Material and methods

96

97 2.1. Study Site

98

99 Kachemak Bay, Alaska, is a high latitude estuary whose kelp beds are exposed to an
100 environmental gradient influenced by glaciers. It is divided into an inner and outer bay at the
101 Homer spit, which extends several kilometers into the bay (Figure 1). Oceanic water from the
102 Alaska Coastal Current enters the outer bay along the southern shore and flows counter-
103 clockwise to then exit along the northern shore (Schoch and Chenelot, 2004). The outer, southern
104 bay is free of glacial sediments while the inner bay has a sedimentation gradient along the coast
105 with lower light and salinity and greater inorganic sedimentation at the head of the bay
106 (Abookire et al., 2000; Spurkland and Iken, 2011). The counter-clockwise circulation carries
107 some glacial fresh water and sediment westward along the bay's north shore toward the mouth
108 (Gatto, 1982). Six sites at 10-m water depth were established to encompass the range of glacial
109 exposure in Kachemak Bay (Figure 1). Three sites were in the more oceanic outer bay (O1, O2,
110 and O3) and three were in the glacially fed inner bay (I1, I2, and I3). These sites were chosen to
111 visually have similar bottom slope and substrate composition. At each site, several components
112 of the biological community and various environmental factors associated with glacial melt were
113 sampled.

114

115
116 2.2. Sampling of recruitment of the sessile community and of mobile invertebrates and adult kelp
117 over time

118
119 Six bare slate rocks were placed at each site to estimate recruitment of the sessile community
120 (invertebrates and macroalgae) and the presence of mobile invertebrates over time. For this, 72
121 rocks were collected from two intertidal sites located mid-bay (Kasitsna Bay and Jakolof Bay).
122 The rocks were scraped clean with a wire brush, placed in the sun for 48 hours to eliminate any
123 spore bank, and individually tagged with white-out paint. All rocks were approximately 5 cm
124 thick, 25 cm wide and 35 cm long with two flat surfaces, one facing down to ensure that the rock
125 did not roll and one facing up for settlement. Six rocks were randomly assigned to each site.
126 Rocks were haphazardly placed along a 10-m permanent transect along the 10-m isobath at mean
127 lower-low water marked with a plastic-coated steel cable.

128
129 Percent cover was visually estimated for all recruiting sessile invertebrates and macroalgae.
130 Individual kelp were also counted and pictures were taken of the rocks so that rock area could be
131 calculated using Image J (Schneider et al., 2012). Counts were standardized to rock surface area
132 by dividing the raw count by the surface area. The first set of rocks was deployed in March 2013.
133 A subsequent set was deployed in April 2014 to examine temporal variability in recruitment and
134 colonization. After deployment, all rocks were surveyed in April of both years, and biweekly
135 from May to September in 2013 and 2014 using SCUBA. No surveys were conducted from
136 October to March due to inclement weather. Initial recruitment and colonization were examined

137 over the first 1 – 6 months for rocks deployed in 2013 and 2014 and from 12 – 18 months for the
138 rocks deployed in March 2013.

139

140 At each site, the density of small mobile invertebrates (such as limpets and chitons) was
141 monitored by counting all individuals present on each experimentally cleared rock. These small
142 invertebrates were identified to the lowest taxonomic level possible in the field (usually to class
143 or lower). Counts were standardized to rock surface area by dividing the raw count by the
144 surface area and expressed as density per m².

145

146 Larger invertebrates (e.g., sea stars such as *Asterias amurensis*) and adult kelp were counted
147 along two haphazardly-placed replicate 2 x 10-m transects at each site. Transects started 1 m
148 from each end of the permanent transect where cleared rocks were placed and the direction of
149 each transect was chosen haphazardly. All invertebrates and kelp along these transects were
150 identified to the lowest taxonomic level possible. Fish were not surveyed because of the
151 logistical challenges of visual surveys in low visibility conditions.

152

153 2.3. Environmental factors

154

155 At each site, environmental factors directly related to glacial discharge were monitored,
156 including sedimentation rate, bottom water temperature, irradiance, salinity, and nutrient
157 concentrations [nitrate (NO₃⁺), ammonium (NH₄⁺), phosphate (PO₄³⁻), and silicate (SiO₄²⁻)].
158 Sediment traps were used to determine sedimentation rates at each site from March to September
159 2013 and April to September 2014. These traps consisted of three polyvinyl chloride pipes with a

160 height: diameter ratio of 5:1 to prevent resuspension (Hargrave and Burns, 1979) and were
161 placed with the mouth of the trap approximately 0.7 m above the bottom. Once per month, traps
162 were retrieved and replaced with new ones. Particulate mass flux was quantified by filtering the
163 trap samples onto pre-weighed Whatman GF/F glass microfiber filters (0.7 μm). Filters were
164 dried for 24 h at 60°C to obtain dry weight. Filters were then burned for 6 h at 500°C and re-
165 weighed to determine organic content as the ash-free dry weight. Inorganic content was
166 estimated as the remaining content after the organic content was burned off.

167

168 Bottom temperature and irradiance (photon intensity per area) were recorded hourly at each site
169 using Honest Observer by Onset (HOBO) Pendant data loggers (Onset Computers, Bourne,
170 Massachusetts) fixed to cinderblocks on the sea floor. Two-week averages of temperature and
171 irradiance were calculated from daily averages of the hourly data. For irradiance, data points
172 between sunset and sunrise were excluded. The maximum and minimum temperature and
173 maximum irradiance value within each two-week period were also included as variables in our
174 analysis. Minimum irradiance was not used because the minimum irradiance was always zero.
175 Due to loss of data loggers, no data are available for some of the outer sites (O1 in 2013 and O2
176 and O3 from July to September 2013).

177

178 Bottom salinity was measured with a hand-held multi-parameter instrument (Yellow Springs
179 Instruments ProPlus, Yellow Springs Instrument Company, Yellow Springs, Ohio) at each site
180 and each sampling event in 2013. In 2014, salinity was monitored hourly with HOBO
181 conductivity U24 data loggers (Onset Computers, Bourne, Massachusetts) fixed to cinderblocks
182 next to the light and temperature loggers at each site. Two-week averages of the daily average

183 salinity data from 2014 were used in the analysis. Maximum and minimum salinity in each two
184 week period was compared to long-term colonization (2014 data). Only mean salinity was
185 compared to 1 – 6 month colonization because maximum and minimum salinities were not
186 available; only one salinity measurement was taken at each site and each sampling event in 2013.

187
188 For nutrient analysis, water samples were collected from less than one meter above the bottom at
189 each site on each visit. Water samples were filtered with Nalgene syringe filters (0.45 μm) within
190 one hour of collection and transported back to the lab in a cooler with ice. Water samples were
191 then frozen for up to five months until nutrient analysis. Nutrient samples were analyzed
192 approximately one month after the last sample was taken, so samples collected earlier in the
193 summer were frozen for longer than those collected at the end of the summer. Nitrate,
194 ammonium, phosphate, and silicate were measured with a Technicon AutoAnalyzer II (SEAL
195 Analytical Inc., Mequon, Wisconsin).

196

197 2.5. Data Analysis

198

199 Multivariate analyses were carried out in PRIMER, a multivariate statistical software package
200 (v7, Plymouth Marine Laboratories). Before statistical analyses, all variables in each data set
201 were examined for univariate correlations using draftsman plots (Clarke et al., 2014). Abundance
202 of the sea star *Leptasterias hexactis* was deleted because of high correlations with other variables
203 ($r > 0.95$, Clarke et al., 2014). Biological data were 4th-root transformed to prevent the most
204 abundant organisms from dominating the analysis (McCune et al., 2002). Percent cover data
205 were analyzed separately from kelp recruitment density data, so no standardization was needed.

206 Environmental data (sedimentation rates, minimum and maximum temperature, mean and
207 maximum light, salinity, nitrate, ammonium, phosphate, and silicate) were normalized by
208 subtracting the mean and dividing by the standard deviation for each variable (Clarke et al.,
209 2014).

210
211 PERMANOVA and SIMPER analyses were used to describe spatial differences in the biological
212 community. Separate analyses were conducted on the sessile community that recruited onto the
213 cleared rocks, the mobile invertebrate data sets, and the adult kelp transect data. Separate Bray-
214 Curtis similarity matrices were generated from the multivariate percent-cover data from rocks
215 deployed in March 2013 (except for site O2 where rocks were deployed in May) through
216 September 2014, the mobile invertebrate density, and the adult kelp transect density. Percent
217 cover data among replicate rocks were averaged at each site for each sampling event. Adult kelp
218 transect data were averaged for the two replicate transects at each site and sampling event. The
219 PERMANOVA design included Region (fixed, 2 levels: Outer Bay, Inner Bay), Site (random,
220 nested in Region, 6 levels: O1, O2, O3, I1, I2, I3), Month (random, 6 levels: April, May, June,
221 July, August, September), and Year (random, 2 levels: 2013, 2014). To account for the repeated
222 measures aspect of the study design for the percent cover recruitment data, the number of months
223 rocks were deployed was included as a covariate and designated as “Age.” SIMPER analysis was
224 used to determine species that contributed to similarity within each site and constructed time
225 series plots to visualize changes in percent cover over time for the most important species.
226 PERMANOVA analysis based on Euclidean distance and Principal Component Analysis (PCA)
227 were used to describe spatial and temporal variation in environmental data.
228

229 Distance-based linear models (DistLM) were used to determine the importance of environmental
230 factors for affecting each biological community data set. “Age” was included as an ordinal
231 variable available for the model to select for the analysis with cleared rocks. Step-wise selection
232 procedure and adjusted R² selection criteria were used.

233

234 3. Results

235

236 3.1. Patterns of sessile community colonization, mobile invertebrates and adult kelp abundance 237 over time

238

239 There were clear differences in initial recruitment and early colonization over the first six months
240 between the inner bay and outer bay regions (Figures 2AB, 3). The two regions differed in the
241 composition of early colonizers (Table 1). Species that contributed to similarity within the outer
242 bay included spirorbid worms, encrusting brown and red algae, and filamentous brown algae
243 (Table 2A). Bare space was abundant at outer bay sites for the first six months after rocks were
244 deployed, while percent cover of encrusting brown and red algae and filamentous brown algae
245 gradually increased in the early summer (SI Table 1). In the inner bay, barnacles quickly
246 colonized rocks, resulting in a decline in availability of bare space (SI Table 1). Barnacles and
247 hydroids contributed to similarity within the inner bay (Table 2B), while these were largely
248 absent from the outer bay. Kelp recruits appeared at site O1 in June and O2 in July, while no
249 kelp recruits appeared at O3 (SI Table 2). Kelp recruits appeared in July at I1, in May at I2, and
250 no kelp recruits appeared at I3 (SI Table 2). Juvenile *Saccharina latissima* occurred at O1, O2,
251 and I1. Juvenile *Agarum clathratum* occurred at O1 and O2. Juvenile *Laminaria yezoensis*

252 occurred at O1. Even after variability due to “Age” was partitioned, there were still significant
253 effects of region (Table 1, $P = 0.003$), and site nested within region (Table 1, $P = 0.005$).
254 Colonization over time differed between regions and among sites, as indicated by the significant
255 interaction between “Age” and these factors (Table 1).

256
257 In the second summer of colonization (12 – 18 months after rocks were deployed) differences in
258 community structure among sites became more apparent with less distinction between regions
259 (Figure 2B). This can be seen from the tight clustering of data points by site on the MDS (Figure
260 2B) and the larger *Pseudo-F* value associated with site (region) than region (Table 3). During
261 this time period, there was no longer a significant effect of the “Age” covariate (Table 3).
262 However, some sites were more variable over time than others, which is reflected by the spread
263 of points within sites in Figure 2B and the significant interaction of “Age” and sites (region)
264 (Table 3). The number of species contributing to similarity was higher in both regions over the
265 12 – 18 month time period than the 1 – 6 month period. In the outer bay, encrusting brown algae
266 and spirorbid worms were again among the most important contributors to similarity (Table 4A).
267 Percent cover of these groups remained similar through this time in the outer bay (SI Table 3).
268 O3 in the outer bay, located on the northern side of Kachemak Bay, varied from the other two
269 outer bay sites in the high availability space during this period. This can be seen by the
270 placement of the O3 data points near the top of the plot where the vector for bare space indicates
271 high availability of bare space (Figure 2B). As in the 1 – 6 month period, barnacles and hydroids
272 were among the most important contributors to similarity within the inner bay (Table 4B). I1 in
273 the inner bay had lower cover of barnacles, and this can be seen in Figure 2B by the placement of
274 these data points closer to the outer bay sites where barnacles were absent or very rare (Figure

275 2B). Kelp was more abundant at the outer bay than inner bay (SI Table 4). *Saccharina latissima*
276 and *A. clathratum* grew to adult size at sites where they occurred. In contrast to sites O1 and O2,
277 only one kelp recruit occurred at O3, which became identifiable as a juvenile *A. clathratum* in
278 late summer. Only two *Nereocystis luetkeana* appeared at site O1 and these only survived for one
279 month.

280

281 Abundance of both smaller and larger mobile invertebrates differed between the outer and inner
282 bay (Figure 2C, SI Table 5). Unidentified limpets contributed 40% to similarity within the outer
283 bay and were the most abundant herbivores (Figure 2C, SI Table 6). Other mobile invertebrates
284 including the chiton *Tonicella* spp., and the green sea urchin *Strongylocentrotus droebachiensis*
285 were also more abundant in the outer bay region. The sea star *Asterias amurensis* only occurred
286 at inner bay sites.

287

288 The adult kelp assemblage surveyed in transects differed between the outer bay and the glacially-
289 influenced inner bay region (Figure 2D, SI Table 7). Abundance of kelp was generally higher in
290 the outer bay (SI Table 8). The understory kelps, *A. clathratum* and *S. latissima* contributed to
291 similarity within both regions and were more abundant in the outer bay (SI Table 8). The
292 canopy-forming kelps, *N. luetkeana* and *Eualaria fistulosa* were never observed in the inner bay
293 or at site O3.

294

295 3.2. Environmental factors

296

297 Glacially influenced environmental factors were significantly different among months (SI Table
298 9). The PCA reflects the PERMANOVA by showing clear separation of data points among
299 months (Figure 4A). Maximum temperature and mean salinity showed seasonal changes in both
300 regions (SI Table 10). Maximum temperature increased from May to September and salinity
301 declined in late summer (Figure 4A). There was high variability in inorganic and organic
302 sedimentation rates, though rates were highest in late summer for the inner bay region (SI Table
303 10). Phosphate concentration increased slightly at the end of the summer at both regions (SI
304 Table 10, Figure 4A).

305
306 In contrast, regions were not clearly distinguished by environmental factors (SI Table 9, Figure
307 4B) although there were significant differences in environmental factors among some sites (SI
308 Table 11). There were significant differences in environmental conditions between the most
309 upstream site, site O1, and all inner bay sites (SI Table 11B). Site O2, on the southern side of the
310 outer bay was only significantly different from site I3, a downstream site (SI Table 11B).

311 Although overall environmental conditions were not significantly different between the outer and
312 inner bay regions, some differences in variables were apparent between regions over time.

313 Inorganic sedimentation rates were almost always higher at the inner bay sites, (Figure 5). The
314 exceptions to this pattern are in May 2013, where inorganic sedimentation rates at O1 were
315 unusually high and for site O3, which occasionally had high rates of inorganic sedimentation
316 (Figure 5). Correspondingly, irradiance was almost always lower at the inner bay region than the
317 outer bay region (SI Table 10). Concentration of silicate tended to be higher in the outer bay
318 earlier in the summer, while ammonium concentration tended to be higher in the inner bay later
319 in the summer (SI Table 10).

320

321 3.3. Biological correlations with environmental factors

322

323 Colonization in the first summer that rocks were deployed (1-6 months) was most strongly
324 correlated to maximum temperature, followed by inorganic sedimentation rate, and mean
325 temperature. These three variables together explained 46.3% of the variation in the recruited rock
326 communities (Table 5B). Organic sedimentation also explained 4.1% of the variation (Table 5A).
327 The “Age” factor also explained a small amount of the variation (Table 5A). Correlations with
328 temperature and rock “Age” is likely related to the seasonal increase in overall percent cover of
329 organisms on the rocks. Variation in rock colonization in the second summer (12-18 months)
330 was related to inorganic sedimentation explaining 29.5% of variation (Table 5B).

331

332 DistLM analysis was additionally performed with kelp recruit density (including unidentified
333 recruits < 2 cm in length) in the first summer (1-6 months). Variation in kelp recruit density was
334 related to maximum irradiance ($Pseudo-F = 7.6674$, $P = 0.011$, variation explained = 16.1%).

335 DistLM analysis was also conducted on density of kelp that occurred on cleared rocks during the
336 12 – 18 month period. This included unidentified kelp recruits (< 2 cm in length), *S. latissima*, *A.*
337 *clathratum*, *L. yezoensis*, *Cymathære triplicata*, and *N. luetkeana*. Variation in kelp density on
338 rocks was best correlated to maximum irradiance ($Pseudo-F = 11.129$, $P = 0.001$, variation
339 explained 30.8%), “Age” ($Pseudo-F = 3.157$, $P = 0.027$, variation explained = 8.0%), mean
340 temperature ($Pseudo-F = 5.126$, $P = 0.001$, variation explained = 11.1%), and inorganic
341 sedimentation rate ($Pseudo-F = 3.126$, $P = 0.033$, variation explained = 6.2%).

342

343 Inorganic sedimentation rate was the variable most strongly correlated to mobile invertebrate and
344 adult kelp distribution (Table 5CD). Inorganic sedimentation explained 14.0% of variation in the
345 mobile invertebrate assemblage, followed by silicate concentration (8.7%) and ammonium
346 concentration (7.2%, Table 5C). Inorganic sedimentation explained 25.6% of variation in adult
347 kelp abundance, followed by silicate concentration which explained 6.9% (Table 5D).

348

349

350 4. Discussion

351

352 Monitoring initial recruitment and colonization by sessile communities can help to form
353 hypotheses about successional processes in kelp beds. Kelp bed community recruitment and
354 development in the glacially influenced estuary examined in this study differed between the
355 oceanic-influenced outer region and the glacially-influenced inner region. The most abundant
356 members of the recruiting communities were spirorbid worms and macroalgae in the outer bay
357 and barnacles in the inner bay. This is similar to patterns of macroalgal abundance in relation to
358 sedimentation in Ireland (Maughan, 2001), the Mediterranean (Balata et al., 2007), and Norway
359 (Bogen, 2009). Our observations of higher cover of hydroids in the inner bay agrees with an
360 experimental study finding that sessile organisms with upright growth forms, including hydroids
361 were unaffected by sedimentation (Houle, 2015). Similar to high sediment coastal lagoons in
362 south Texas, we observed high barnacle recruitment despite the presence of sediment (Gray,
363 2014). Shifts between algal and invertebrate-dominated communities have also been observed in
364 Antarctica when changes in sea ice affected sedimentation and light conditions (Clark et al,
365 2017).

366

367 Similar to other high-latitude studies, in this study bare space was colonized slowly (Barnes and
368 Conlan, 2007; Konar, 2007). Although most kelp and red macroalgal species are reproductive
369 during early summer in Kachemak Bay (personal observation), kelp recruitment was slow and
370 not observed until two to three months after rocks were deployed (SI Table 1). This may be
371 because kelp gametophytes can delay reproduction and production of macroscopic sporophytes
372 until they are triggered by changing environmental factors such as light or nutrients (Carney and
373 Edwards, 2006). Slow substrate colonization in high latitude systems compared to temperate
374 systems has been reported previously (Barnes and Conlan, 2007). For example, in an Arctic
375 boulder field, experimentally cleared boulders still had over 90% bare space after 3 years (Konar,
376 2007). In contrast, recovery of kelp cover over several weeks has been observed in experimental
377 and natural clearings at lower latitudes (Barradas et al., 2011; Dayton et al., 1992). In many
378 systems, following a disturbance, typical succession process includes early opportunists followed
379 by later slower growing species. In rocky temperate intertidal systems, early opportunists can
380 include *Ulva* spp. and filamentous algae, which may be later replaced by slower growing red
381 macroalgae (Aquilino and Stachowicz, 2012; Kraufvelin et al., 2007). In our system, the early
382 opportunists were spirorbid worms and barnacles. Spirorbid worms are also abundant early
383 colonizers in highly disturbed subtidal habitats in Antarctica (Barnes and Conlan, 2007).

384

385 Competitive interactions among early recruits to bare space may be stronger in the inner bay
386 region with high barnacle recruitment than at the outer bay. Recruitment rates varied among our
387 sites with barnacles quickly colonizing bare space in the inner bay and with recruitment
388 occurring much more slowly by spirorbid worms and macroalgae in the outer bay. Competition

389 for space may not have been important in the early stages of colonization in the outer bay where
390 bare space was abundant during the first summer of the study. Preemptive competition among
391 macroalgae has been shown to be an important structuring mechanism of communities in other
392 systems. For example, in littoral rock pools in Italy, turf forming algae and *Cystoseira* spp. have
393 non-hierarchical competitive interactions where whichever group is present in higher density can
394 exclude recruitment of the other group; however, when turf algae and *Cystoseira* spp. recruit at
395 the same time, they can coexist (Benedetti-Cecchi and Cinelli, 1996). This type of competition
396 between *Cystoseira* spp. and turf algae can be more important in shaping communities than
397 storm disturbance (Maggi et al., 2012). Similarly, in subtidal kelp beds in Australia, dense mats
398 of filamentous algae can preempt kelp recruitment (Connell and Russell, 2010). Hence, the
399 availability of bare space and the availability of propagules can be crucial to the coexistence of
400 species. Encrusting algae can inhibit kelp recruitment; however, kelp canopies can persist despite
401 high cover of encrusting algae because kelp produce very high numbers of spores, which can
402 settle in minute bare patches or on top of encrusting algae (Okamoto et al., 2013). Although there
403 is strong evidence that space is limiting in many sessile communities (Benes and Carpenter,
404 2015; Gorman and Connell, 2009; Maggi et al., 2012), we should be cautious in our
405 interpretation of high availability of bare space as an indication of low competition, as members
406 of the sessile community may be competing for other limiting resources such as planktonic food
407 (Svensson and Marshall, 2015).

408

409 Some glacially-influenced environmental factors were significantly correlated to patterns of
410 recruitment and colonization. While many environmental factors were similar among sites,
411 inorganic sedimentation differed with the highest rates at sites downstream of glacial discharge

412 point sources. In addition, colonization in the first summer (1-6 months) was primarily driven by
413 temperature and inorganic sedimentation while colonization in the second summer (12-18
414 months) was only correlated with inorganic sedimentation (Table 5AB). Irradiance was
415 correlated to kelp recruitment in the first and second summers. Our results agree with previous
416 studies finding that sedimentation and irradiance are important factors structuring macroalgal
417 communities (Bogen, 2009; Clark et al., 2017; Desmond et al., 2015). Low salinity can cause
418 osmotic stress in recruiting barnacles, causing latent effects on growth and survival (Nasrolahi et
419 al., 2013; Qiu and Qian, 1999). Sedimentation inhibits recruitment of spirorbid polychaetes
420 (Connell, 2003). Kelp recruitment is negatively correlated to sedimentation rates (Spurkland and
421 Iken, 2011; Valentine and Johnson, 2005) and sedimentation and low salinity decrease the
422 success of *Nereocystis luetkeana* spore settlement and attachment (Deiman et al., 2012), and
423 gametophyte survival and growth (Lind and Konar, 2017). Sediments can kill early macroalgal
424 and invertebrate life stages through burial or smothering, scour, and changes in substrate stability
425 (Airoldi, 2003). In southeastern Tasmania, kelp recruits transplanted to urchin barrens, where
426 thick sediment layers accumulate, experienced high mortality, even when urchins were excluded
427 (Valentine and Johnson, 2005). Irradiance was correlated to kelp abundance on rocks in this
428 study. In some cases sedimentation can cause light limiting conditions for kelp (Desmond et al.,
429 2015) but sediment can also protect kelp from high light (Roleda and Dethleff, 2011).

430

431 Similar to recruitment and colonization, the composition and abundance of mobile invertebrates
432 and adult kelp differed between these two regions. Mobile invertebrates and adult kelp in the
433 established community were more abundant in the oceanic-influenced outer bay. Some glacially-
434 influenced environmental factors were significantly correlated to the surrounding community.

435 For example, inorganic sedimentation was significantly correlated to mobile invertebrates and
436 adult kelp. The identification of inorganic sedimentation as a potential driver of kelp and mobile
437 invertebrate assemblage structure is supported by similar observations of differences in
438 abundance in relation to sedimentation (Airoldi and Virgilio, 1998; Bogen, 2009) and
439 experimental studies indicating that sedimentation can cause mortality of kelp and invertebrates
440 (Deiman et al., 2012; Geange et al., 2014; Kawamata et al., 2012; Walker, 2007). Sediment has
441 been shown to directly affect the spatial distribution, survival, and grazing of limpets (Airoldi
442 and Hawkins, 2007; Branch et al., 1990). Observed low mobile invertebrate abundances were
443 associated with high rates of inorganic sedimentation at the glacially-influenced, inner bay sites.
444 Mobile invertebrates may be more abundant upstream of glacial discharge due to lower
445 sedimentation rates (Airoldi and Hawkins, 2007), or due to the higher abundance of kelp in the
446 surrounding community that many mobile invertebrates feed on (Bustamante et al., 1995).
447 *Tonicella* spp. also graze benthic diatoms (Latyshev et al., 2004), which may be more abundant
448 at sites with low glacial influence.

449
450 The environmental conditions observed in this study were more spatially homogeneous than
451 expected, which indicates that currents are important in spreading glacially-influenced
452 water throughout Kachemak Bay. Our findings contrast previous work in Kachemak Bay,
453 which found large differences in surface salinity, water column salinity stratification,
454 temperature, irradiance, and nitrate concentrations between sites upstream and
455 downstream of glacial discharge (Abookire et al., 2000; Spurkland and Iken, 2011).
456 Conductivity temperature depth (CTD) profiles conducted at Halibut Cove, downstream
457 of our site I1, showed that there is a halocline at 4-m depth, below which salinities are

458 similar to those found in the outer bay (Schoch and Chenelot, 2004). In Kachemak Bay,
459 Spurkland and Iken (2011) observed differences in salinity and irradiance at 5-m depth,
460 but in this study, sites were at 10-m depth, so the low salinity, low temperature, low
461 nitrate, high sediment water from glacial discharge, though present, may have reached the
462 loggers or experimental rocks at the deeper depth only occasionally. Stratification may
463 therefore partially protect subtidal kelp beds from glacial meltwater-related effects.
464 Similarly, flooding of the Orange River in Africa caused high mortality of algae and
465 invertebrates in the intertidal zone while the subtidal zone was not affected (Branch et al.,
466 1990). Rates of inorganic sedimentation did follow spatial patterns similar to previous
467 findings in this and other systems (Spurkland and Iken, 2011; Svendsen et al., 2002).
468 Similar to the Kongsfjorden glacial fjord system in Svalbard, we observed a gradient in
469 inorganic sedimentation with rates declining toward the mouth of the bay (Svendsen et
470 al., 2002). Some of our sites (site I1 & O3) may be located at regions representing
471 transitions between the outer bay oceanic conditions and the inner bay glacially-
472 influenced conditions. Circulation patterns may help homogenize conditions around the
473 bay by spreading glacial fresh water and sediment to the north shore of the outer bay. The
474 incoming current from Cook Inlet on the southern side of the inner bay may mix with the
475 fresher and more turbid waters of the inner bay, decreasing the glacial influence along the
476 southern side of inner Kachemak Bay (i.e., site I1, Figure 1). As glacial discharge
477 increases with warming temperatures in the future, our expectations about locations to be
478 affected by changing water conditions will be based on the extent of glacial influence,
479 including sedimentation, possibly reaching tens of kilometers past point sources of glacial
480 discharge (Svendsen et al., 2002; this study).

481
482 In addition to glacial melt, other factors are also likely important to the observed patterns in the
483 biological community. We expected to see some similarities in early colonizers between
484 upstream and downstream sites due to the common water mass that passes through the study area
485 (Figure 1), possibly resulting in a somewhat similar propagule pool reaching multiple sites;
486 however, there were few early colonizers in common between sites upstream and downstream of
487 glacial discharge. Spirorbid polychaetes were among the earliest colonizers at sites upstream of
488 discharge while barnacles were early colonizers downstream of glacial discharge. Several
489 processes could be responsible for this pattern. A hydrodynamic front located at the boundary of
490 the inner and outer bay at Homer spit may concentrate larvae, leading to higher transport into the
491 inner bay, as was observed for the decorator crab, *Oregonia gracilis* (Murphy and Iken, 2014).
492 Concentration and net transport into the inner bay may explain the much higher abundance of
493 species with longer larval duration such as barnacles in the inner bay than was observed in the
494 outer bay. Spirorbid worms, which were common upstream but not downstream of glacial
495 discharge, brood their larvae (Knight-Jones et al., 1991), and presumably have shorter dispersal
496 distance than many other marine invertebrates such as barnacles. Encrusting algae such as
497 crustose corallines also have short dispersal distances (Opazo and Otaiza, 2007), so populations
498 upstream of glacial discharge may not supply propagules to glacially-influenced sites. The
499 abundance of adult kelp at each site also likely affected propagule supply to our experimental
500 rocks and may have contributed to the observed differences in kelp recruitment between the
501 inner and outer bay regions. Kelp have short dispersal distances (Gaylord et al., 2004) and
502 experimentally increasing adult density or reproductive material can increase local recruitment
503 (Fejtek et al., 2011; Hernandez-Carmona et al., 2000).

504

505 4.1. Implications

506

507 Glacial melt may have significant effects on kelp communities through impacts on recruitment,
508 survival, and interactions among species. As glacial melt dynamics are altered by climate
509 change, the influence of glacially-influenced environmental factors is likely to change. This
510 study contributes to the body of evidence indicating that kelp are negatively affected by
511 sedimentation and could be threatened by increased glacial melt with climate change (Spurkland
512 and Iken, 2011; Zacher et al., 2016). Increased sedimentation rates have already been associated
513 with decreased diversity and dominance of a few opportunistic species (Balata et al., 2007;
514 Connell, 2007; Pratt et al., 2014). In Alaska and other high latitude systems, we can expect kelp
515 beds to be negatively impacted by the spread or increase of glacial sediment (Zacher et al.,
516 2016). Climate change may also cause the peak in glacial discharge to shift from late summer
517 and early fall to earlier in the summer. A better understanding of how environmental variables
518 impact recruitment and colonization may help predict the effects of changes in glacial melt
519 dynamics on kelp bed communities. Globally, kelp beds naturally experience environmental
520 disturbances and can be highly resilient. In California, kelp beds can be greatly thinned or
521 eliminated by El Niño conditions of high temperature and low nutrients, but kelp can quickly
522 recover when conditions return to normal (Dayton et al., 1992). Other environmental
523 disturbances may result in phase shifts with more permanent effects. In Australia, coastal
524 development led to reduced water quality (eutrophic and high sedimentation), causing a phase
525 shift from kelp to turf algal dominated (Connell and Irving, 2008). It is critical to understand the

526 impacts of changing environmental conditions on existing and developing kelp beds, as they
527 provide important ecosystem services.

528

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530

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543

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761 TABLES:

762

763 Table 1. Results of a PERMANOVA comparing community structure over 1-6 months between
 764 regions (fixed, two levels), among sites nested within regions (random, six levels), months
 765 (random, five levels: May, June, July, August, and September), and years (random, two levels:
 766 2013 and 2014). "Age" was included as a covariate. Significant *P*-values are in boldface. High
 767 values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	25156	25156	14.405	0.0021
Region	1	35464	35464	3.9234	0.0027
Month	5	7675.7	1535.1	1.3829	0.2047
Year	1	3878.2	3878.2	2.294	0.0861
Site(Region)	4	18596	4649	3.372	0.0048
Age x Region	1	6899.8	6899.8	6.4239	0.0119
Age x Site(Region)	4	4057.3	1014.3	3.1206	0.0021
Region x Month	5	4403.5	880.7	1.0115	0.4915
Region x Year	1	1720.9	1720.9	1.458	0.2532
Site(Region) x Year	4	1944.2	486.05	1.8956	0.0747
Res	26	5246.7	201.8		
Total	117	0.00001			

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770 Table 2. Percent contribution (Contrib.) of discriminating species for community structure over
 771 1-6 months in each region using SIMPER analysis. Average percent cover (\pm SD) and
 772 cumulative percent contribution to similarity (Cum.).
 773

	Average % Cover \pm SD	Contrib.	Cum.
Outer Bay			
Bare space	92.7 \pm 9.5	72.96	72.96
Spirorbid	3.2 \pm 4.6	8.80	81.76
Encrusting brown algae	1.4 \pm 2.7	4.43	86.19
Encrusting red algae	0.3 \pm 0.6	2.38	88.57
Filamentous brown algae	0.9 \pm 2.7	2.04	90.60
Inner Bay			
Bare space	61.5 \pm 31.0	60.00	60.00
Barnacle	31.9 \pm 32.2	24.11	84.11
Hydroid	2.0 \pm 2.3	8.90	93.01

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781 Table 3. Results of a PERMANOVA comparing community structure over 12-18 months
 782 between regions (fixed, two levels), among sites nested within regions (random, six levels), and
 783 months (random, five levels: May, June, July, August, and September). "Age" was included as a
 784 covariate. Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude
 785 of variance explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	6200.6	6200.6	2.9578	0.1912
Region	1	34233	34233	3.4634	0.0059
Month	5	9703	1940.6	1.006	0.4769
Site(Region)	4	31697	7924.3	23.247	0.0001
Age x Region	1	483.7	483.7	4.1022	0.0962
Age x Site(Region)	4	3026.9	756.72	2.595	0.0291
Region x Month	5	493.81	98.763	0.29901	0.978
Total	63	93448			

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794 Table 4. Percent contribution (Contrib.) of discriminating species for community structure over
 795 12-18 months in each region using SIMPER analysis. Average percent cover (\pm SD) and
 796 cumulative percent contribution to similarity (Cum.).
 797

	Average % Cover \pm SD	Contrib.	Cum.
Outer Bay			
Bare space	60.7 \pm 19.3	27.08	27.08
Encrusting brown algae	9.5 \pm 4.9	15.38	42.46
Spirorbid	9.5 \pm 9.7	12.09	54.55
Crustose Coralline	6.3 \pm 11.8	9.61	64.16
Unidentified Polychaetes	1.3 \pm 1.2	9.01	73.17
<i>Saccharina latissima</i>	1.9 \pm 2.2	4.31	77.48
Kelp Recruits	2.0 \pm 4.1	3.62	81.10
Unidentified Sand-tube Polychaete	1.3 \pm 1.4	3.54	84.64
Encrusting red algae	1.4 \pm 2.7	2.32	86.97
<i>Agarum clathratum</i>	0.4 \pm 0.6	2.29	89.25
Filamentous red algae	1.6 \pm 3.5	1.30	90.55
Inner Bay			
Bare space	76.1 \pm 15.3	39.49	39.49
Barnacle	11.7 \pm 11.4	13.43	52.92
Hydroid	4.8 \pm 6.9	9.77	62.70
Filamentous red algae	1.3 \pm 1.5	7.28	69.98
<i>Saccharina latissima</i>	0.9 \pm 0.8	6.21	76.19
Kelp Recruits	0.3 \pm 0.3	4.63	80.81
Filamentous brown algae	1.2 \pm 2.2	3.08	83.89
<i>Metridium</i> spp	0.6 \pm 0.9	2.65	86.54
Brown tube polychaete	1.0 \pm 2.4	1.74	88.27
Peach bryozoan	0.3 \pm 0.4	1.50	89.77
Red blades	0.2 \pm 0.3	1.47	91.24

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812 Table 5. Results of sequential DistLM tests on A) first year (1-6 months) of community
 813 structure, B) second year (12-18 months) of community structure, C) adult kelp from transects,
 814 and D) mobile invertebrates showing significant variables, their contribution to explained
 815 variation (Contrib.), the cumulative contribution of the explained variation (Cum.) and *P*-values.
 816

817 A) First year (1-6 months) of community structure

	<i>Pseudo-F</i>	Contrib.	Cum.	<i>P</i> -value
A) First year community structure				
Max. temperature	9.428	19.1	19.1	0.001
Inorganic sedimentation	6.997	12.3	31.4	0.001
Mean temperature	10.525	14.9	46.3	0.001
Organic sedimentation	3.4714	4.1	55.0	0.012
Age	3.303	2.2	57.1	0.017
B) Second year community structure				
Inorganic sedimentation	10.457	29.5	29.5	<0.001
C) Mobile invertebrates				
Inorganic sedimentation	6.515	14.0	14.0	<0.001
SiO ₄	4.365	8.7	22.7	0.001
NH ₄	3.888	7.2	29.8	0.002
D) Adult kelp from transects				
Inorganic sedimentation	13.751	25.6	25.6	<0.001
SiO ₄	3.976	6.9	32.5	0.017

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839 SUPPLEMENTAL INFORMATION:

840

841 SI Table 1. Average \pm standard deviation percent cover of selected species that contributed to
842 similarity within the A) outer bay, and B) inner bay on cleared rocks up to six months.

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	April	May	June	July	Aug	Sept
Outer Bay						
Bare space	99.9 \pm 0.1	99.3 \pm 0.7	97.8 \pm 1.9	93.3 \pm 5.1	86.5 \pm 8.5	82.8 \pm 13.9
Encrusting brown algae	0 \pm 0	0.1 \pm 0.2	0.1 \pm 0.2	0.6 \pm 0.8	3.4 \pm 3.5	4.1 \pm 4.0
Encrusting red algae	0 \pm 0	0.05 \pm 0.1	0.1 \pm 0.2	0.5 \pm 1.0	0.3 \pm 0.5	0.5 \pm 0.4
Filamentous brown algae	0 \pm 0	0.05 \pm 0.2	0.3 \pm 0.9	1.0 \pm 1.8	0.8 \pm 1.2	2.6 \pm 5.7
Inner Bay						
Bare space	100 \pm 0	87.4 \pm 22.5	55.4 \pm 36.4	40.9 \pm 25.6	64.3 \pm 24.1	55.3 \pm 21.9
Hydroids	0 \pm 0	0.1 \pm 0.3	1.2 \pm 1.7	2.6 \pm 2.6	2.4 \pm 1.8	4.0 \pm 1.9
Barnacles	0 \pm 0	12.4 \pm 22.6	39.5 \pm 39.5	49.6 \pm 32.9	26.5 \pm 28.6	31.4 \pm 23.0

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846 SI Table 2. Average density (x/ 900 cm²) +/- standard deviation of kelp recruits in each month in
847 the first summer rocks were deployed at each site. Surface area of rocks was approximately 900
848 cm².

Month	O1	O2	O3	I1	I2	I3
April	0 \pm 0	No data	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
May	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.1 \pm 0.1	0 \pm 0
June	2.4 \pm 2.9	0 \pm 0	0 \pm 0	0 \pm 0	0.03 \pm 0.07	0 \pm 0
July	3.5 \pm 3.5	1.3 \pm 2.2	0 \pm 0	2.9 \pm 4.1	0.3 \pm 0.3	0 \pm 0
August	1.5 \pm 2.3	4.5 \pm 7.8	0 \pm 0	2.0 \pm 2.7	0 \pm 0	0 \pm 0
September	1.2 \pm 1.4	13.9 \pm 9.5	0 \pm 0	1.2 \pm 1.1	0.1 \pm 0.2	0 \pm 0

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 861 SI Table 3. Average percent cover \pm standard deviation of selected species that contributed to
 862 similarity within the A) outer bay, and B) inner bay on cleared rocks from 12 to 18 months.

863 A) Outer Bay

	April	May	June	July	Aug	Sept
Outer Bay						
Bare space	66.8 \pm 26.7	60.7 \pm 27.1	66.4 \pm 18.1	63.4 \pm 17.9	56.6 \pm 15.1	52.7 \pm 16.9
Encrusting brown algae	6.8 \pm 4.3	7.5 \pm 4.7	8.5 \pm 5.5	9.8 \pm 5.5	11.9 \pm 3.9	11.4 \pm 5.0
Spirorbids	8.4 \pm 8.4	10.3 \pm 9.4	9.4 \pm 9.6	9.3 \pm 11.2	11.3 \pm 12.9	8.2 \pm 10.7
Inner Bay						
Bare space	71.6 \pm 26.9	70.1 \pm 25.8	75.2 \pm 12.2	78.5 \pm 7.9	76.4 \pm 14.7	81.5 \pm 10.2
Hydroids	4.6 \pm 7.9	10.1 \pm 13.8	5.6 \pm 6.4	4.0 \pm 4.1	2.1 \pm 2.3	3.3 \pm 3.4
Barnacles	14.6 \pm 17.0	13.4 \pm 14.5	5.3 \pm 9.5	8.6 \pm 8.6	15.2 \pm 15.3	11.8 \pm 8.8

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867 SI Table 4. Average density (x/ 900 cm²) \pm standard deviation of kelp on rocks at A) outer bay
 868 and B) inner bay over 12-18 months.

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	April	May	June	July	Aug	Sept
Outer Bay						
<i>S. latissima</i>	0.8 \pm 0.9	0.9 \pm 0.9	2.5 \pm 3.7	1.6 \pm 2.0	2.9 \pm 2.7	1.4 \pm 1.8
<i>A. clathratum</i>	0.6 \pm 1.0	0.6 \pm 1.0	0.8 \pm 1.3	0.8 \pm 1.4	1.2 \pm 1.3	0.9 \pm 1.2
Kelp Recruits	54.6 \pm 94.5	46.5 \pm 74.1	44.3 \pm 68.5	44.3 \pm 69.2	25.0 \pm 36.4	13.9 \pm 23.1
Inner Bay						
<i>S. latissima</i>	0.6 \pm 0.7	0.7 \pm 0.7	0.8 \pm 0.7	0.5 \pm 0.7	0.9 \pm 0.9	1.1 \pm 1.1
<i>A. clathratum</i>	0 \pm 0	0 \pm 0	0 \pm 0	0.03 \pm 0.08	0 \pm 0	0 \pm 0
Kelp Recruits	1.1 \pm 0.8	0.6 \pm 0.6	2.2 \pm 2.4	0.1 \pm 0.1	0.1 \pm 0.2	0.1 \pm 0.1

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877 SI Table 5. Results of a PERMANOVA comparing mobile invertebrates between regions (fixed,
 878 two levels), among sites nested within regions (random, six levels), months (random, five levels:
 879 May, June, July, August, and September), and years (random, two levels: 2013 and 2014).
 880 Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance
 881 explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Region	1	26837	26837	2.805	<0.001
Month	5	8484.2	1696.8	1.502	0.048
Year	1	1288.7	1288.7	0.98597	0.480
Site(Region)	4	32308	8076.9	5.2141	<0.001
Region x Month	5	4164.5	832.9	0.88352	0.693
Region x Year	1	1899.5	1899.5	1.2362	0.262
Month x Year	4	3485.8	871.45	1.2508	0.235
Site(Region) x Month	20	15265	763.26	1.0967	0.342
Site(Region) x Year	4	4717.6	1179.4	1.6923	0.060
Region x Month x Year	4	3920.7	980.17	1.4069	0.154
Site(Regions) x Month x Year	14	9766.8	697.63	1.0385	0.398
Res	50	33589	671.78		
Total	113	0.00002			

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885 SI Table 6. Percent contribution (Contrib.) of discriminating species for mobile invertebrates in
 886 A) outer bay and B) inner bay using SIMPER analysis.

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	Average density (individuals m ⁻²) ± SD	Contrib.	Cum.
Outer Bay			
Unidentified limpets	15.6 ± 12.5	40.11	40.11
<i>Tonicella</i> spp	0.7 ± 0.5	18.76	58.87
<i>Pagurus</i> spp	0.7 ± 1.4	10.26	69.13
<i>Calliostoma</i> spp	1.4 ± 2.4	7.89	77.03
<i>Pycnopodia</i> <i>helianthoides</i>	0.4 ± 1.2	7.18	84.21
<i>Strongylocentrotus</i> <i>droebachiensis</i>	2.2 ± 5.8	3.34	87.55
<i>Acmaea mitra</i>	0.1 ± 0.2	3.03	90.58
Inner Bay			
<i>Pycnopodia</i> <i>helianthoides</i>	0.4 ± 1.2	38.58	38.58
<i>Pagurus</i> spp	0.2 ± 0.3	22.45	61.03
Unidentified limpets	0.7 ± 1.3	15.26	76.29
<i>Tonicella</i> spp	0.1 ± 0.2	6.39	82.68
<i>Asterias amurensis</i>	0.5 ± 1.6	4.83	87.51
Unidentified gastropods	0.1 ± 0.1	4.33	91.84

888

889 SI Table 7. Results of a PERMANOVA comparing adult kelp counted in transects between
 890 regions (fixed, two levels), among sites nested within regions (random, six levels), months
 891 (random, five levels: May, June, July, August, and September), and years (random, two levels:
 892 2013 and 2014). Significant p values are in boldface. High values of pseudo-F indicate the
 893 magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P(perm)</i>
Region	1	11741	11741	2.640	0.005
Month	5	4782.7	956.5	0.887	0.644
Year	1	1727	1727	1.510	1.955
Site(Region)	4	17133	4283.2	13.193	<0.001
Region x Month	5	1914.2	382.85	2.101	0.015
Region x Year	1	82.5	82.5	1.219	0.312
Month x Year	4	48.17	1204.2	4.659	<0.001
Site(Region) x Month	20	4332.9	216.6	0.840	0.704
Site(Region) x Year	7	715.1	178.8	0.691	0.733
Region x Month x Year	4	366.3	91.6	0.354	0.958
Site(Regions) x Month x Year	14	3613.2	259.4	1.101	0.339
Res	50	11776	235.5		
Total	113	79278			

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898 SI Table 8. Percent contribution of discriminating species for adult kelp counted in transects in
 899 each region using SIMPER analysis.

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	Average density (individuals m ⁻²) ± SD	% Contribution	Cumulative
Outer Bay			
<i>Agarum clathratum</i>	10.2 ± 10.3	53.38	54.3
<i>Saccharina latissima</i>	11.6 ± 16.0	31.28	84.66
<i>Nereocystis luetkeana</i>	0.5 ± 0.8	5.01	89.67
<i>Eualaria fistulosa</i>	1.7 ± 4.9	3.76	93.43
Inner Bay			
<i>Saccharina latissima</i>	4.0 ± 3.9	65.77	65.77
<i>Agarum clathratum</i>	1.4 ± 2.0	34.02	99.79

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910 SI Table 9. Results of a three-way PERMANOVA comparing environmental variables among
 911 regions (fixed, two levels), months (random, five levels), years (random, two levels), and site
 912 nested in region (random, six levels). Significant p values are in boldface. High values of
 913 pseudo-F indicate the magnitude of variance explained by that factor. * Indicates that the term
 914 has one or more empty cells.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P</i> (perm)
Region	1	18.069	18.069	1.3631	0.158
Month	4	97.319	24.33	2.5457	0.003
Year	1	12.027	12.027	2.4677	0.0873
Site(Region)	4	45.475	11.369	1.4503	0.100
Region x Month	4	34.796	8.6991	1.4974	0.2093
Region x Year	1	4.0198	4.0198	1.0964	0.434
Month x Year*	3	15.559	5.1862	3.0548	0.006
Site(Region) x Month*	15	63.863	4.2576	2.5078	0.005
Site(Region) x Year*	3	12.509	4.1698	2.4561	0.019
Region x Month x Year*	1	2.3826	2.3826	1.4034	0.2464
Res	4	6.7908	1.6977		
Total	41	492			

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917 SI Table 10. Monthly means \pm SD of inorganic sedimentation, bottom salinity, mean
 918 temperature, mean irradiance, silicate, ammonium, and phosphate in the outer bay and inner bay.

	May	June	July	August	September
Inorganic sedimentation (mg cm ⁻² d ⁻¹)					
Outer Bay	1.7 \pm 1.7	2.9 \pm 3.6	1.0 \pm 0.007	2.0 \pm 1.4	3.8 \pm 3.2
Inner Bay	3.2 \pm 2.0	4.0 \pm 1.8	5.3 \pm 3.5	6.9 \pm 3.3	7.6 \pm 2.0
Bottom Salinity					
Outer Bay	31.4 \pm 0.3	31.1 \pm 0.2	30.5 \pm 0.4	29.8 \pm 0.2	30.4 \pm 0.5
Inner Bay	31.3 \pm 0.6	31.4 \pm 0.4	31.1 \pm 0.3	30.4 \pm 0.3	30.7 \pm 0.3
Mean Temperature (°C)					
Outer Bay	6.0 \pm 1.0	7.7 \pm 0.8	10.2 \pm 0.5	12.1 \pm 0.2	11.4 \pm 0.1
Inner Bay	6.0 \pm 1.1	7.2 \pm 0.6	8.6 \pm 1.5	10.7 \pm 1.5	11.7 \pm 0.1
Mean Irradiance (μ mol m ⁻² s ⁻¹)					
Outer Bay	16.0 \pm 13.1	12.3 \pm 10.7	26.1 \pm 10.3	21.7 \pm 16.4	33.4 \pm 25.5
Inner Bay	11.6 \pm 8.6	14.1 \pm 5.8	11.9 \pm 8.2	8.0 \pm 4.7	6.0 \pm 6.0
Silicate (μ M)					
Outer Bay	10.8 \pm 5.7	6.1 \pm 4.9	9.7 \pm 5.5	5.9 \pm 0.9	14.1 \pm 0.7
Inner Bay	2.4 \pm 1.3	4.9 \pm 3.2	6.5 \pm 1.9	8.3 \pm 2.5	15.7 \pm 1.8
Ammonium (μ M)					
Outer Bay	2.1 \pm 0.8	1.2 \pm 0.5	0.8 \pm 0.6	1.6 \pm 0.6	1.7 \pm 0.6
Inner Bay	1.8 \pm 1.2	2.2 \pm 1.2	3.2 \pm 0.9	3.3 \pm 1.3	3.5 \pm 0.3
Phosphate (μ M)					
Outer Bay	0.5 \pm 0.2	0.3 \pm 0.1	0.9 \pm 0.3	0.7 \pm 0.1	1.7 \pm 0.4
Inner Bay	0.4 \pm 0.2	0.3 \pm 0.3	1.0 \pm 0.1	0.9 \pm 0.1	1.7 \pm 0.2

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 920 SI Table 11. Results of a one-way PERMANOVA comparing environmental variables among
 921 sites (random, six levels). Significant p values are in boldface.

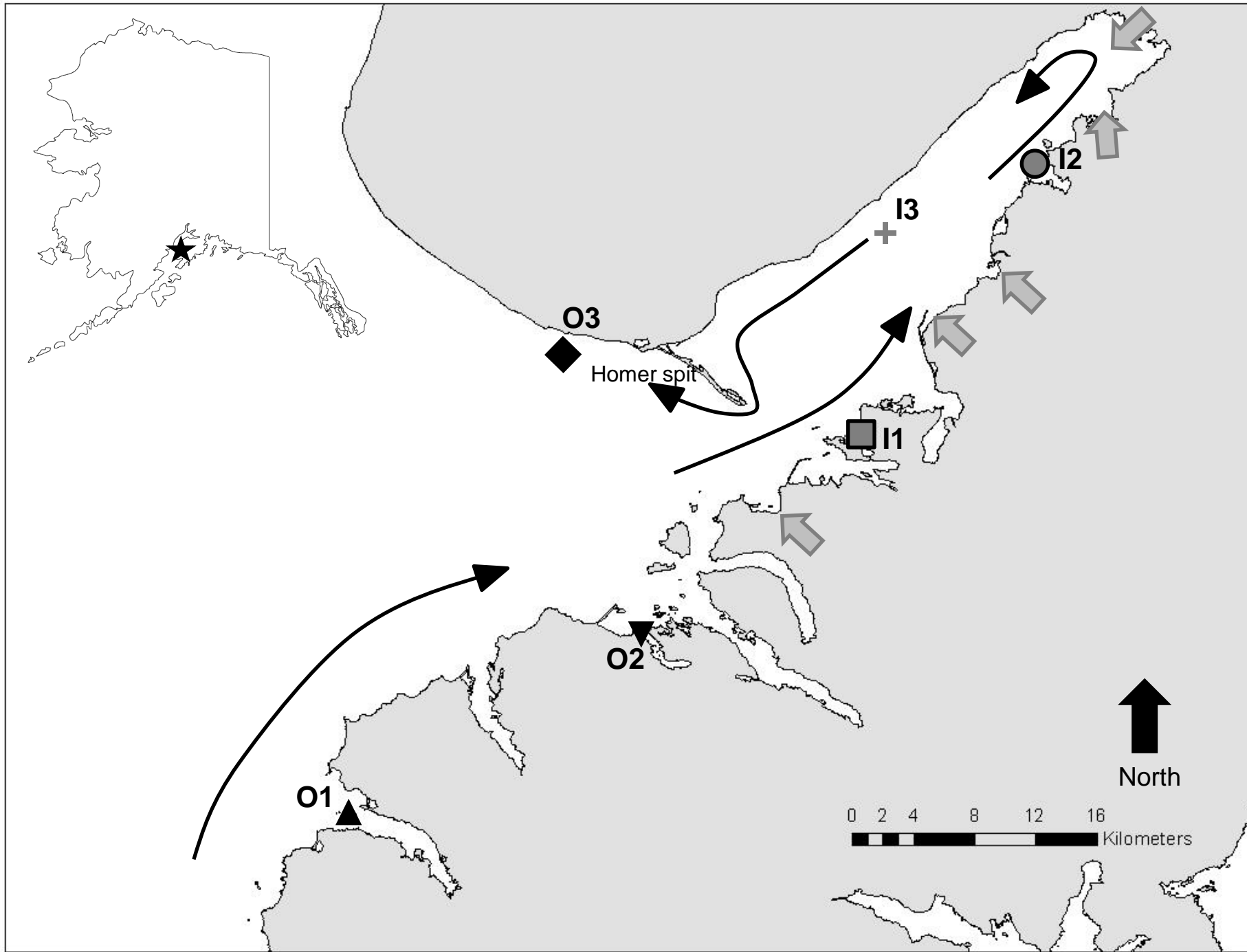
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 923 A) Main test

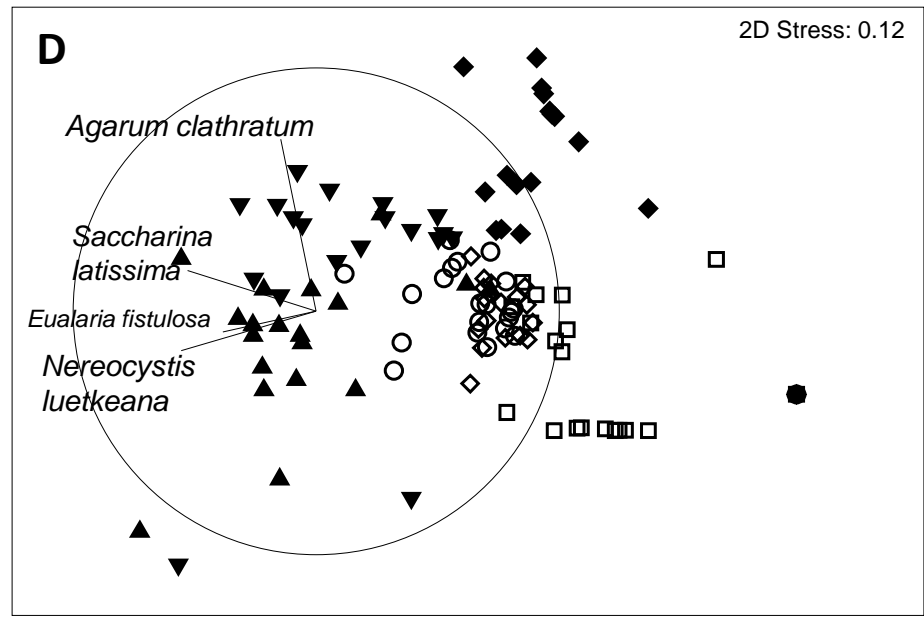
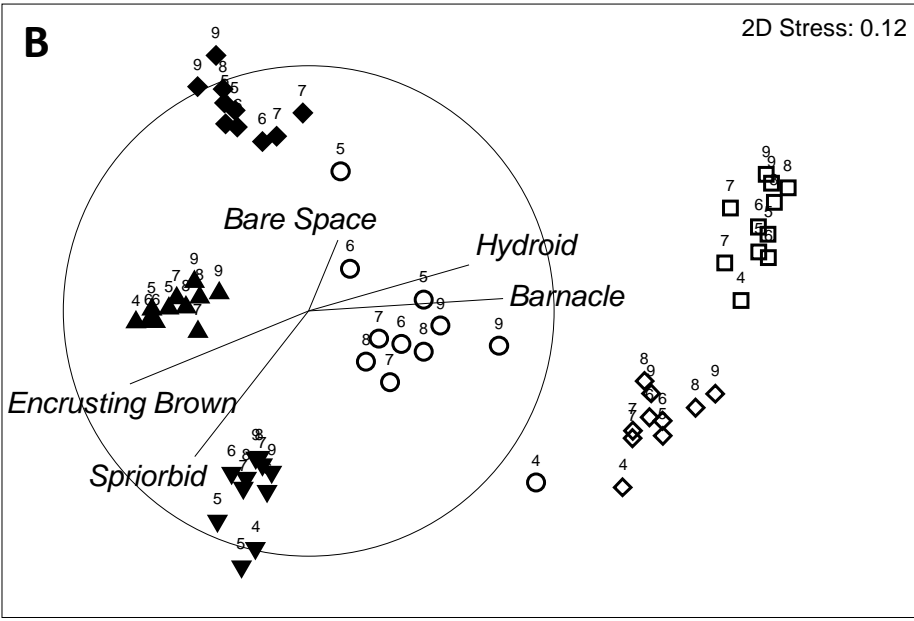
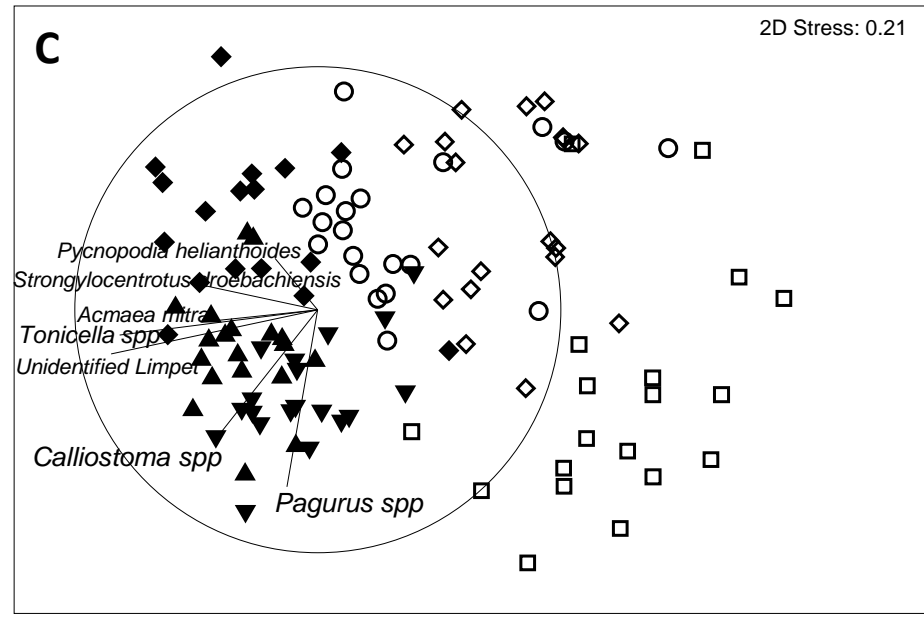
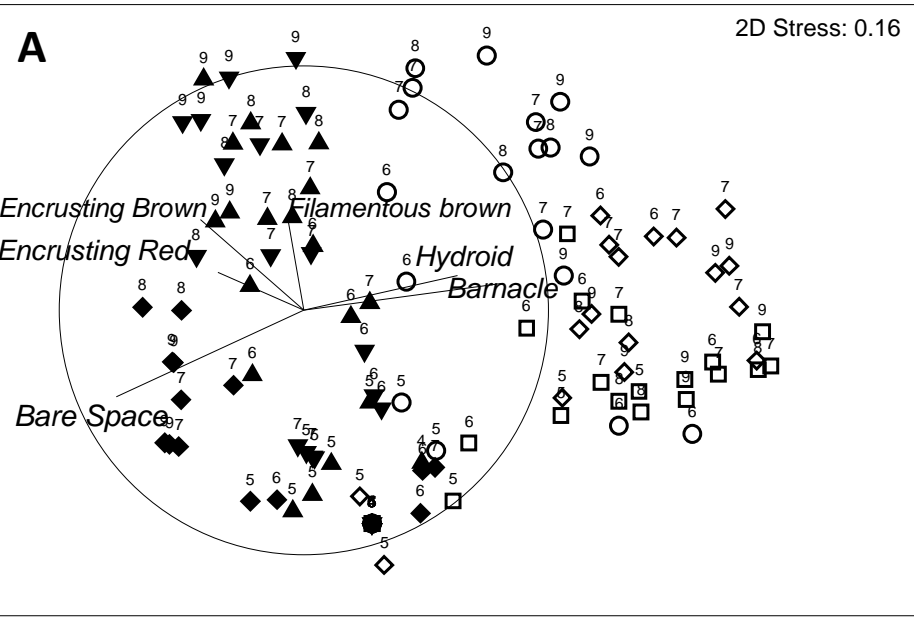
Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P-value</i>
Site	5	99.693	19.939	1.8297	0.010
Res	36	392.31	10.897		
Total	41	492			

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 925 B) Pairwise PERMANOVA comparison of environmental variables among sites. Significant *P*-
 926 values are in boldface.

		Outer			Inner		
		O1	O2	O3	I1	I2	I3
Outer	O1						
	O2	0.430					
	O3	0.200	0.205				
Inner	I1	0.045	0.176	0.194			
	I2	0.021	0.318	0.537	0.527		
	I3	0.001	0.002	0.400	0.096	0.1169	

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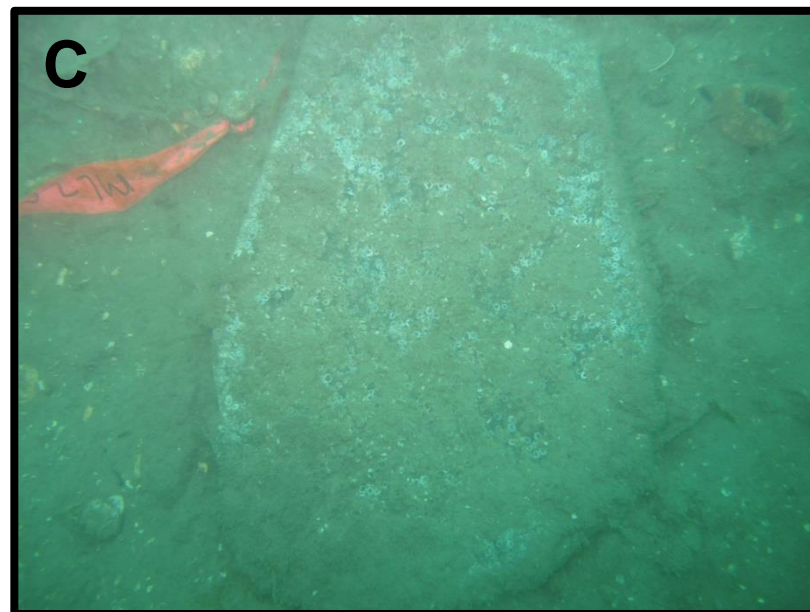




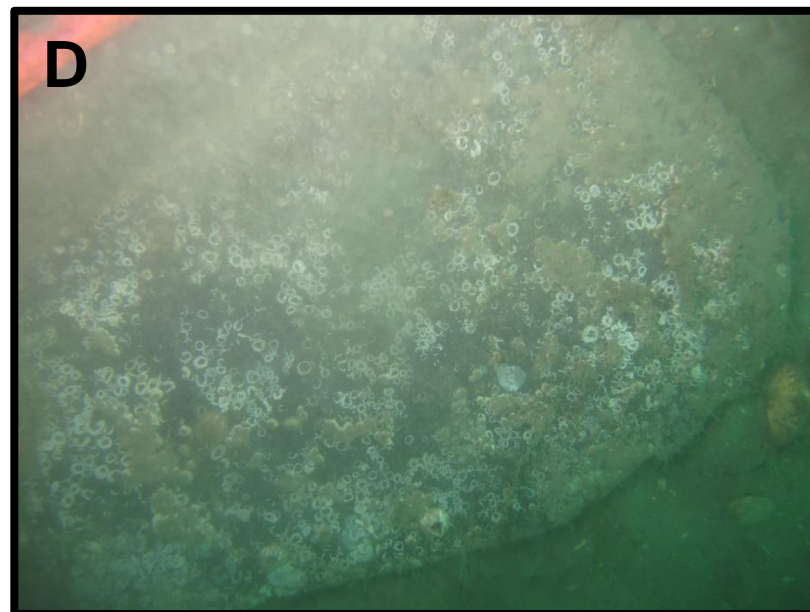
Site #: O1 O2 O3 I1 I2 I3
 ▲ ▼ ◆ ○ ◇ □

Outer Bay

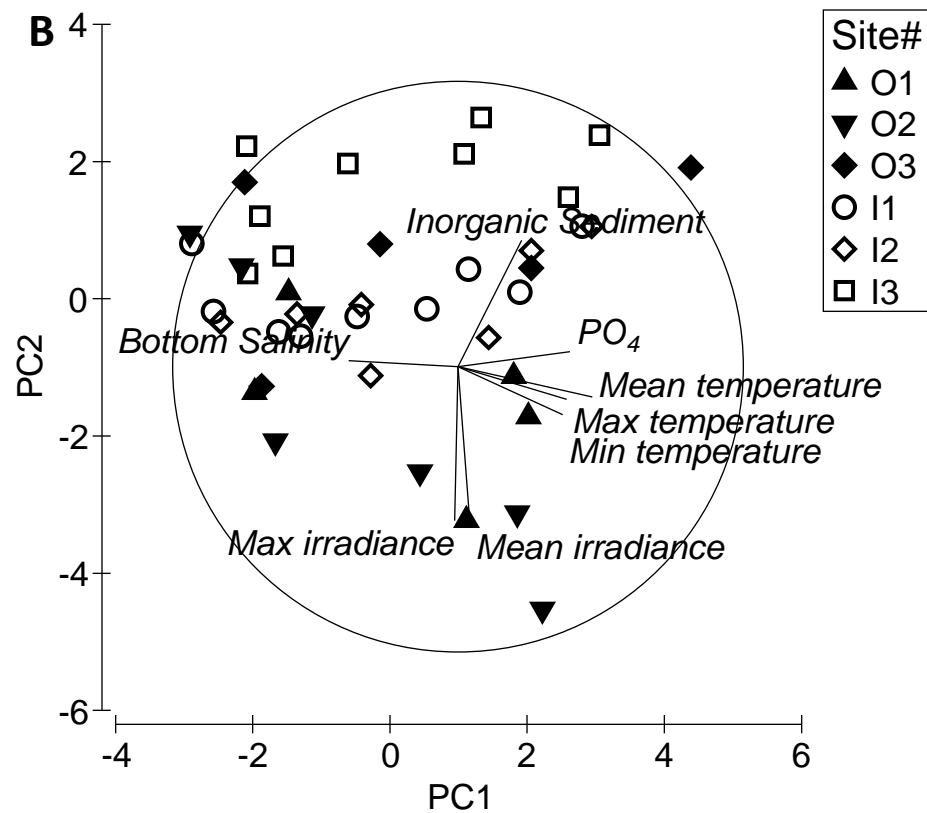
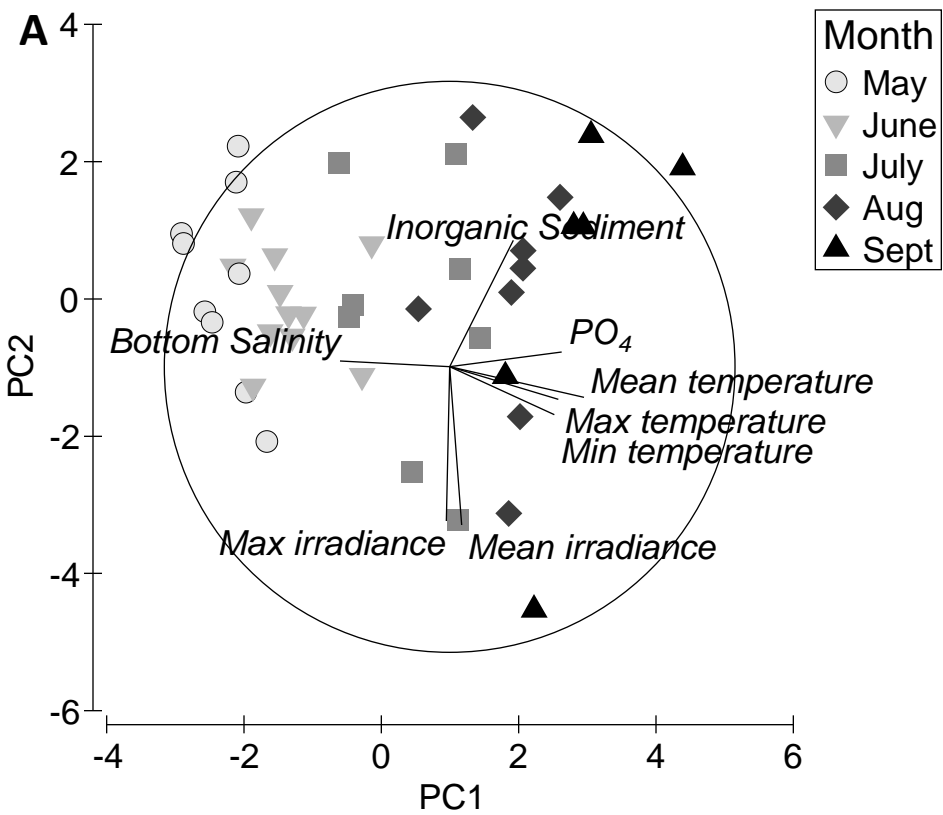
Inner Bay



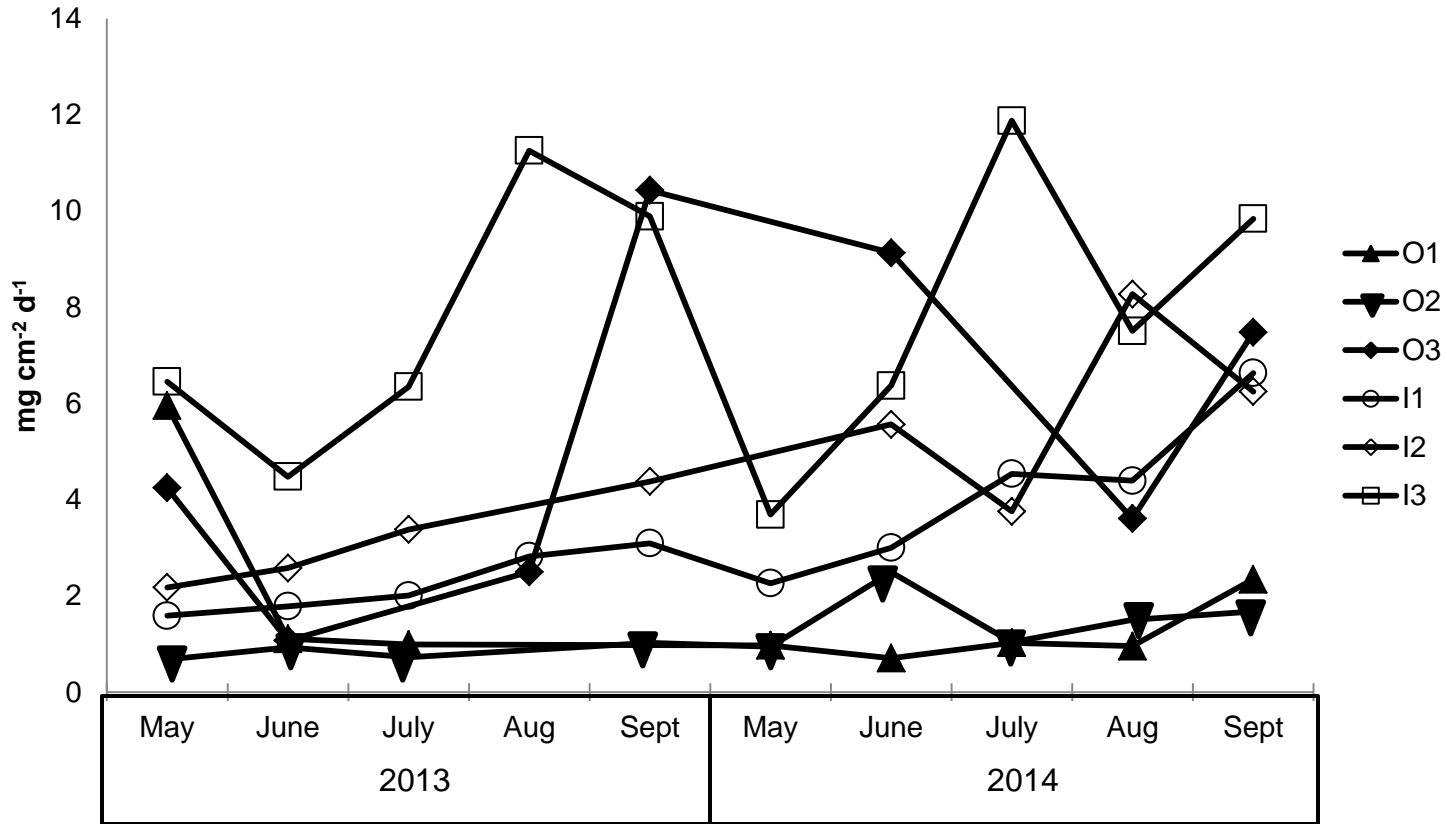
6 months



18 months



Inorganic Sedimentation



TABLES:

Table 1. Results of a PERMANOVA comparing community structure over 1-6 months between regions (fixed, two levels), among sites nested within regions (random, six levels), months (random, five levels: May, June, July, August, and September), and years (random, two levels: 2013 and 2014). “Age” was included as a covariate. Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	25156	25156	14.405	0.0021
Region	1	35464	35464	3.9234	0.0027
Month	5	7675.7	1535.1	1.3829	0.2047
Year	1	3878.2	3878.2	2.294	0.0861
Site(Region)	4	18596	4649	3.372	0.0048
Age x Region	1	6899.8	6899.8	6.4239	0.0119
Age x Site(Region)	4	4057.3	1014.3	3.1206	0.0021
Region x Month	5	4403.5	880.7	1.0115	0.4915
Region x Year	1	1720.9	1720.9	1.458	0.2532
Site(Region) x Year	4	1944.2	486.05	1.8956	0.0747
Res	26	5246.7	201.8		
Total	117	0.00001			

Table 2. Percent contribution (Contrib.) of discriminating species for community structure over 1-6 months in each region using SIMPER analysis. Average percent cover (\pm SD) and cumulative percent contribution to similarity (Cum.).

	Average % Cover \pm SD	Contrib.	Cum.
Outer Bay			
Bare space	92.7 \pm 9.5	72.96	72.96
Spirorbid	3.2 \pm 4.6	8.80	81.76
Encrusting brown algae	1.4 \pm 2.7	4.43	86.19
Encrusting red algae	0.3 \pm 0.6	2.38	88.57
Filamentous brown algae	0.9 \pm 2.7	2.04	90.60
Inner Bay			
Bare space	61.5 \pm 31.0	60.00	60.00
Barnacle	31.9 \pm 32.2	24.11	84.11
Hydroid	2.0 \pm 2.3	8.90	93.01

Table 3. Results of a PERMANOVA comparing community structure over 12-18 months between regions (fixed, two levels), among sites nested within regions (random, six levels), and months (random, five levels: May, June, July, August, and September). "Age" was included as a covariate. Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Age	1	6200.6	6200.6	2.9578	0.1912
Region	1	34233	34233	3.4634	0.0059
Month	5	9703	1940.6	1.006	0.4769
Site(Region)	4	31697	7924.3	23.247	0.0001
Age x Region	1	483.7	483.7	4.1022	0.0962
Age x Site(Region)	4	3026.9	756.72	2.595	0.0291
Region x Month	5	493.81	98.763	0.29901	0.978
Total	63	93448			

Table 4. Percent contribution (Contrib.) of discriminating species for community structure over 12-18 months in each region using SIMPER analysis. Average percent cover (\pm SD) and cumulative percent contribution to similarity (Cum.).

	Average % Cover \pm SD	Contrib.	Cum.
Outer Bay			
Bare space	60.7 \pm 19.3	27.08	27.08
Encrusting brown algae	9.5 \pm 4.9	15.38	42.46
Spirorbid	9.5 \pm 9.7	12.09	54.55
Crustose Coralline	6.3 \pm 11.8	9.61	64.16
Unidentified Polychaetes	1.3 \pm 1.2	9.01	73.17
<i>Saccharina latissima</i>	1.9 \pm 2.2	4.31	77.48
Kelp Recruits	2.0 \pm 4.1	3.62	81.10
Unidentified Sand-tube Polychaete	1.3 \pm 1.4	3.54	84.64
Encrusting red algae	1.4 \pm 2.7	2.32	86.97
<i>Agarum clathratum</i>	0.4 \pm 0.6	2.29	89.25
Filamentous red algae	1.6 \pm 3.5	1.30	90.55
Inner Bay			
Bare space	76.1 \pm 15.3	39.49	39.49
Barnacle	11.7 \pm 11.4	13.43	52.92
Hydroid	4.8 \pm 6.9	9.77	62.70
Filamentous red algae	1.3 \pm 1.5	7.28	69.98
<i>Saccharina latissima</i>	0.9 \pm 0.8	6.21	76.19
Kelp Recruits	0.3 \pm 0.3	4.63	80.81
Filamentous brown algae	1.2 \pm 2.2	3.08	83.89
<i>Metridium</i> spp	0.6 \pm 0.9	2.65	86.54
Brown tube polychaete	1.0 \pm 2.4	1.74	88.27
Peach bryozoan	0.3 \pm 0.4	1.50	89.77
Red blades	0.2 \pm 0.3	1.47	91.24

Table 5. Results of sequential DistLM tests on A) first year (1-6 months) of community structure, B) second year (12-18 months) of community structure, C) adult kelp from transects, and D) mobile invertebrates showing significant variables, their contribution to explained variation (Contrib.), the cumulative contribution of the explained variation (Cum.) and *P*-values.

A) First year (1-6 months) of community structure				
	<i>Pseudo-F</i>	Contrib.	Cum.	<i>P</i> -value
A) First year community structure				
Max. temperature	9.428	19.1	19.1	0.001
Inorganic sedimentation	6.997	12.3	31.4	0.001
Mean temperature	10.525	14.9	46.3	0.001
Organic sedimentation	3.4714	4.1	55.0	0.012
Age	3.303	2.2	57.1	0.017
B) Second year community structure				
Inorganic sedimentation	10.457	29.5	29.5	<0.001
C) Mobile invertebrates				
Inorganic sedimentation	6.515	14.0	14.0	<0.001
SiO ₄	4.365	8.7	22.7	0.001
NH ₄	3.888	7.2	29.8	0.002
D) Adult kelp from transects				
Inorganic sedimentation	13.751	25.6	25.6	<0.001
SiO ₄	3.976	6.9	32.5	0.017

SUPPLEMENTAL INFORMATION:

SI Table 1. Average \pm standard deviation percent cover of selected species that contributed to similarity within the A) outer bay, and B) inner bay on cleared rocks up to six months.

	April	May	June	July	Aug	Sept
Outer Bay						
Bare space	99.9 \pm 0.1	99.3 \pm 0.7	97.8 \pm 1.9	93.3 \pm 5.1	86.5 \pm 8.5	82.8 \pm 13.9
Encrusting brown algae	0 \pm 0	0.1 \pm 0.2	0.1 \pm 0.2	0.6 \pm 0.8	3.4 \pm 3.5	4.1 \pm 4.0
Encrusting red algae	0 \pm 0	0.05 \pm 0.1	0.1 \pm 0.2	0.5 \pm 1.0	0.3 \pm 0.5	0.5 \pm 0.4
Filamentous brown algae	0 \pm 0	0.05 \pm 0.2	0.3 \pm 0.9	1.0 \pm 1.8	0.8 \pm 1.2	2.6 \pm 5.7
Inner Bay						
Bare space	100 \pm 0	87.4 \pm 22.5	55.4 \pm 36.4	40.9 \pm 25.6	64.3 \pm 24.1	55.3 \pm 21.9
Hydroids	0 \pm 0	0.1 \pm 0.3	1.2 \pm 1.7	2.6 \pm 2.6	2.4 \pm 1.8	4.0 \pm 1.9
Barnacles	0 \pm 0	12.4 \pm 22.6	39.5 \pm 39.5	49.6 \pm 32.9	26.5 \pm 28.6	31.4 \pm 23.0

SI Table 2. Average density (x/ 900 cm²) \pm standard deviation of kelp recruits in each month in the first summer rocks were deployed at each site. Surface area of rocks was approximately 900 cm².

Month	O1	O2	O3	I1	I2	I3
April	0 \pm 0	No data	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0
May	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0.1 \pm 0.1	0 \pm 0
June	2.4 \pm 2.9	0 \pm 0	0 \pm 0	0 \pm 0	0.03 \pm 0.07	0 \pm 0
July	3.5 \pm 3.5	1.3 \pm 2.2	0 \pm 0	2.9 \pm 4.1	0.3 \pm 0.3	0 \pm 0
August	1.5 \pm 2.3	4.5 \pm 7.8	0 \pm 0	2.0 \pm 2.7	0 \pm 0	0 \pm 0
September	1.2 \pm 1.4	13.9 \pm 9.5	0 \pm 0	1.2 \pm 1.1	0.1 \pm 0.2	0 \pm 0

SI Table 3. Average percent cover \pm standard deviation of selected species that contributed to similarity within the A) outer bay, and B) inner bay on cleared rocks from 12 to 18 months.

A) Outer Bay	April	May	June	July	Aug	Sept
Outer Bay						
Bare space	66.8 \pm 26.7	60.7 \pm 27.1	66.4 \pm 18.1	63.4 \pm 17.9	56.6 \pm 15.1	52.7 \pm 16.9
Encrusting brown algae	6.8 \pm 4.3	7.5 \pm 4.7	8.5 \pm 5.5	9.8 \pm 5.5	11.9 \pm 3.9	11.4 \pm 5.0
Spirorbids	8.4 \pm 8.4	10.3 \pm 9.4	9.4 \pm 9.6	9.3 \pm 11.2	11.3 \pm 12.9	8.2 \pm 10.7
Inner Bay						
Bare space	71.6 \pm 26.9	70.1 \pm 25.8	75.2 \pm 12.2	78.5 \pm 7.9	76.4 \pm 14.7	81.5 \pm 10.2
Hydroids	4.6 \pm 7.9	10.1 \pm 13.8	5.6 \pm 6.4	4.0 \pm 4.1	2.1 \pm 2.3	3.3 \pm 3.4
Barnacles	14.6 \pm 17.0	13.4 \pm 14.5	5.3 \pm 9.5	8.6 \pm 8.6	15.2 \pm 15.3	11.8 \pm 8.8

SI Table 4. Average density (x/ 900 cm²) \pm standard deviation of kelp on rocks at A) outer bay and B) inner bay over 12-18 months.

	April	May	June	July	Aug	Sept
Outer Bay						
<i>S. latissima</i>	0.8 \pm 0.9	0.9 \pm 0.9	2.5 \pm 3.7	1.6 \pm 2.0	2.9 \pm 2.7	1.4 \pm 1.8
<i>A. clathratum</i>	0.6 \pm 1.0	0.6 \pm 1.0	0.8 \pm 1.3	0.8 \pm 1.4	1.2 \pm 1.3	0.9 \pm 1.2
Kelp Recruits	54.6 \pm 94.5	46.5 \pm 74.1	44.3 \pm 68.5	44.3 \pm 69.2	25.0 \pm 36.4	13.9 \pm 23.1
Inner Bay						
<i>S. latissima</i>	0.6 \pm 0.7	0.7 \pm 0.7	0.8 \pm 0.7	0.5 \pm 0.7	0.9 \pm 0.9	1.1 \pm 1.1
<i>A. clathratum</i>	0 \pm 0	0 \pm 0	0 \pm 0	0.03 \pm 0.08	0 \pm 0	0 \pm 0
Kelp Recruits	1.1 \pm 0.8	0.6 \pm 0.6	2.2 \pm 2.4	0.1 \pm 0.1	0.1 \pm 0.2	0.1 \pm 0.1

SI Table 5. Results of a PERMANOVA comparing mobile invertebrates between regions (fixed, two levels), among sites nested within regions (random, six levels), months (random, five levels: May, June, July, August, and September), and years (random, two levels: 2013 and 2014). Significant *P*-values are in boldface. High values of *Pseudo-F* indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P</i> -value
Region	1	26837	26837	2.805	<0.001
Month	5	8484.2	1696.8	1.502	0.048
Year	1	1288.7	1288.7	0.98597	0.480
Site(Region)	4	32308	8076.9	5.2141	<0.001
Region x Month	5	4164.5	832.9	0.88352	0.693
Region x Year	1	1899.5	1899.5	1.2362	0.262
Month x Year	4	3485.8	871.45	1.2508	0.235
Site(Region) x Month	20	15265	763.26	1.0967	0.342
Site(Region) x Year	4	4717.6	1179.4	1.6923	0.060
Region x Month x Year	4	3920.7	980.17	1.4069	0.154
Site(Regions) x Month x Year	14	9766.8	697.63	1.0385	0.398
Res	50	33589	671.78		
Total	113	0.00002			

SI Table 6. Percent contribution (Contrib.) of discriminating species for mobile invertebrates in A) outer bay and B) inner bay using SIMPER analysis.

	Average density (individuals m ⁻²) ± SD	Contrib.	Cum.
Outer Bay			
Unidentified limpets	15.6 ± 12.5	40.11	40.11
<i>Tonicella</i> spp	0.7 ± 0.5	18.76	58.87
<i>Pagurus</i> spp	0.7 ± 1.4	10.26	69.13
<i>Calliostoma</i> spp	1.4 ± 2.4	7.89	77.03
<i>Pycnopodia</i> <i>helianthoides</i>	0.4 ± 1.2	7.18	84.21
<i>Strongylocentrotus</i> <i>droebachiensis</i>	2.2 ± 5.8	3.34	87.55
<i>Acmaea mitra</i>	0.1 ± 0.2	3.03	90.58
Inner Bay			
<i>Pycnopodia</i> <i>helianthoides</i>	0.4 ± 1.2	38.58	38.58
<i>Pagurus</i> spp	0.2 ± 0.3	22.45	61.03
Unidentified limpets	0.7 ± 1.3	15.26	76.29
<i>Tonicella</i> spp	0.1 ± 0.2	6.39	82.68
<i>Asterias amurensis</i>	0.5 ± 1.6	4.83	87.51
Unidentified gastropods	0.1 ± 0.1	4.33	91.84

SI Table 7. Results of a PERMANOVA comparing adult kelp counted in transects between regions (fixed, two levels), among sites nested within regions (random, six levels), months (random, five levels: May, June, July, August, and September), and years (random, two levels: 2013 and 2014). Significant p values are in boldface. High values of pseudo-F indicate the magnitude of variance explained by that factor.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P(perm)</i>
Region	1	11741	11741	2.640	0.005
Month	5	4782.7	956.5	0.887	0.644
Year	1	1727	1727	1.510	1.955
Site(Region)	4	17133	4283.2	13.193	<0.001
Region x Month	5	1914.2	382.85	2.101	0.015
Region x Year	1	82.5	82.5	1.219	0.312
Month x Year	4	48.17	1204.2	4.659	<0.001
Site(Region) x Month	20	4332.9	216.6	0.840	0.704
Site(Region) x Year	7	715.1	178.8	0.691	0.733
Region x Month x Year	4	366.3	91.6	0.354	0.958
Site(Regions) x Month x Year	14	3613.2	259.4	1.101	0.339
Res	50	11776	235.5		
Total	113	79278			

SI Table 8. Percent contribution of discriminating species for adult kelp counted in transects in each region using SIMPER analysis.

	Average density (individuals m ⁻²) ± SD	% Contribution	Cumulative
Outer Bay			
<i>Agarum clathratum</i>	10.2 ± 10.3	53.38	54.3
<i>Saccharina latissima</i>	11.6 ± 16.0	31.28	84.66
<i>Nereocystis luetkeana</i>	0.5 ± 0.8	5.01	89.67
<i>Eualaria fistulosa</i>	1.7 ± 4.9	3.76	93.43
Inner Bay			
<i>Saccharina latissima</i>	4.0 ± 3.9	65.77	65.77
<i>Agarum clathratum</i>	1.4 ± 2.0	34.02	99.79

SI Table 9. Results of a three-way PERMANOVA comparing environmental variables among regions (fixed, two levels), months (random, five levels), years (random, two levels), and site nested in region (random, six levels). Significant p values are in boldface. High values of pseudo-F indicate the magnitude of variance explained by that factor. * Indicates that the term has one or more empty cells.

Source	<i>df</i>	SS	MS	Pseudo-F	<i>P</i> (perm)
Region	1	18.069	18.069	1.3631	0.158
Month	4	97.319	24.33	2.5457	0.003
Year	1	12.027	12.027	2.4677	0.0873
Site(Region)	4	45.475	11.369	1.4503	0.100
Region x Month	4	34.796	8.6991	1.4974	0.2093
Region x Year	1	4.0198	4.0198	1.0964	0.434
Month x Year*	3	15.559	5.1862	3.0548	0.006
Site(Region) x Month*	15	63.863	4.2576	2.5078	0.005
Site(Region) x Year*	3	12.509	4.1698	2.4561	0.019
Region x Month x Year*	1	2.3826	2.3826	1.4034	0.2464
Res	4	6.7908	1.6977		
Total	41	492			

SI Table 10. Monthly means \pm SD of inorganic sedimentation, bottom salinity, mean temperature, mean irradiance, silicate, ammonium, and phosphate in the outer bay and inner bay.

	May	June	July	August	September
Inorganic sedimentation (mg cm ⁻² d ⁻¹)					
Outer Bay	1.7 \pm 1.7	2.9 \pm 3.6	1.0 \pm 0.007	2.0 \pm 1.4	3.8 \pm 3.2
Inner Bay	3.2 \pm 2.0	4.0 \pm 1.8	5.3 \pm 3.5	6.9 \pm 3.3	7.6 \pm 2.0
Bottom Salinity					
Outer Bay	31.4 \pm 0.3	31.1 \pm 0.2	30.5 \pm 0.4	29.8 \pm 0.2	30.4 \pm 0.5
Inner Bay	31.3 \pm 0.6	31.4 \pm 0.4	31.1 \pm 0.3	30.4 \pm 0.3	30.7 \pm 0.3
Mean Temperature (°C)					
Outer Bay	6.0 \pm 1.0	7.7 \pm 0.8	10.2 \pm 0.5	12.1 \pm 0.2	11.4 \pm 0.1
Inner Bay	6.0 \pm 1.1	7.2 \pm 0.6	8.6 \pm 1.5	10.7 \pm 1.5	11.7 \pm 0.1
Mean Irradiance (μ mol m ⁻² s ⁻¹)					
Outer Bay	16.0 \pm 13.1	12.3 \pm 10.7	26.1 \pm 10.3	21.7 \pm 16.4	33.4 \pm 25.5
Inner Bay	11.6 \pm 8.6	14.1 \pm 5.8	11.9 \pm 8.2	8.0 \pm 4.7	6.0 \pm 6.0
Silicate (μ M)					
Outer Bay	10.8 \pm 5.7	6.1 \pm 4.9	9.7 \pm 5.5	5.9 \pm 0.9	14.1 \pm 0.7
Inner Bay	2.4 \pm 1.3	4.9 \pm 3.2	6.5 \pm 1.9	8.3 \pm 2.5	15.7 \pm 1.8
Ammonium (μ M)					
Outer Bay	2.1 \pm 0.8	1.2 \pm 0.5	0.8 \pm 0.6	1.6 \pm 0.6	1.7 \pm 0.6
Inner Bay	1.8 \pm 1.2	2.2 \pm 1.2	3.2 \pm 0.9	3.3 \pm 1.3	3.5 \pm 0.3
Phosphate (μ M)					
Outer Bay	0.5 \pm 0.2	0.3 \pm 0.1	0.9 \pm 0.3	0.7 \pm 0.1	1.7 \pm 0.4
Inner Bay	0.4 \pm 0.2	0.3 \pm 0.3	1.0 \pm 0.1	0.9 \pm 0.1	1.7 \pm 0.2

SI Table 11. Results of a one-way PERMANOVA comparing environmental variables among sites (random, six levels). Significant p values are in boldface.

A) Main test

Source	<i>df</i>	SS	MS	<i>Pseudo-F</i>	<i>P-value</i>
Site	5	99.693	19.939	1.8297	0.010
Res	36	392.31	10.897		
Total	41	492			

B) Pairwise PERMANOVA comparison of environmental variables among sites. Significant *P*-values are in boldface.

		Outer			Inner		
		O1	O2	O3	I1	I2	I3
Outer	O1						
	O2	0.430					
	O3	0.200	0.205				
Inner	I1	0.045	0.176	0.194			
	I2	0.021	0.318	0.537	0.527		
	I3	0.001	0.002	0.400	0.096	0.1169	