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From the predictable to the unexpected: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion
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Abstract:	The recovery of predators has the potential to restore ecosystems and fundamentally alter the services they provide. One of the iconic examples of this is keystone predation by sea otters in the Northeast Pacific. Here we combine spatial time-series of sea otter abundance, canopy kelp area, and benthic invertebrate abundance from Washington State, USA, to examine the shifting consequences of sea otter introduction for kelp and kelp forest communities. We leverage the spatial variation in timing and speed of sea otter recovery to understand connections between sea otters and the kelp forest community. Sea otter increases created a pronounced decline in sea otter prey - particularly kelp-grazing sea urchins - and led to an expansion of canopy kelps from the late 1980s until roughly 2000. However, while sea otter and kelp population growth rates were positively correlated prior to 2000, this association disappeared over the last two decades. This disconnect occurred despite surveys showing sea otter prey have continued to decline. Kelp area trends appear to be decoupled from both sea otter and benthic invertebrate abundance at current densities. Variability in kelp

abundance has declined in the most recent 15 years of the time series. Together this suggest that initial nearshore community responses to sea otter population expansion follow predictably from trophic cascade theory, but now other factors may be as or more important in influencing community dynamics. Thus, the utility of sea otter predation in ecosystem restoration must be considered within the context of complex and shifting environmental conditions.

3/19/2018

Dear Editorial Board.

This letter accompanies the manuscript, "From the predictable to the unexpected: kelp forest and benthic invertebrate community dynamics following decades of sea otter expansion" which we wish to submit for consideration as an article to Oecologia.

Understanding species interactions and their consequences for the dynamics, stability, and resilience of ecological communities are a fundamental aim of ecology. Both historically and today, studies of strongly interacting species play an outsized role in our understanding of how ecological communities function. In this manuscript, we combine data for three trophic levels of a classic trophic cascade community – sea otters, benthic invertebrates, and kelp – at 10 sites spanning 100 km and nearly thirty years to understand the multi-scale consequences of both direct effects of sea otters on their prey and their indirect connection with kelp forests. Our analyses bring a new spatial and temporal perspective to this classic and well-studied trophic interaction. We leverage the spatial time-series to show how inference about interactions at the coast-wide scale differ strongly from site level patterns. Furthermore, we show that the inferred interaction between sea otters and kelp shift from being tightly coupled during the first half of the time-series to statistically unrelated in the second half. We also document both immediate and gradual consequences of sea otter invasion for different components of the benthic invertebrate community. We believe our work can serve to reconcile distinct perspectives about the role of bottom-up vs. top-down forces in kelp forest communities and has implications for spatial management of resources when component species strongly interact.

Thank you for your consideration.

Sincerely,
A.O. Shelton

1   **From the predictable to the unexpected: kelp forest and benthic invertebrate community**

2   **dynamics following decades of sea otter expansion**

3

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Abstract

The recovery of predators has the potential to restore ecosystems and fundamentally alter the services they provide. One of the iconic examples of this is keystone predation by sea otters in the Northeast Pacific. Here we combine spatial time-series of sea otter abundance, canopy kelp area, and benthic invertebrate abundance from Washington State, USA, to examine the shifting consequences of sea otter introduction for kelp and kelp forest communities. We leverage the spatial variation in timing and speed of sea otter recovery to understand connections between sea otters and the kelp forest community. Sea otter increases created a pronounced decline in sea otter prey - particularly kelp-grazing sea urchins – and led to an expansion of canopy kelps from the late 1980s until roughly 2000. However, while sea otter and kelp population growth rates were positively correlated prior to 2000, this association disappeared over the last two decades. This disconnect occurred despite surveys showing sea otter prey have continued to decline. Kelp area trends appear to be decoupled from both sea otter and benthic invertebrate abundance at current densities. Variability in kelp abundance has declined in the most recent 15 years of the time series. Together this suggest that initial nearshore community responses to sea otter population expansion follow predictably from trophic cascade theory, but now other factors may be as or more important in influencing community dynamics. Thus, the utility of sea otter predation in ecosystem restoration must be considered within the context of complex and shifting environmental conditions.

Introduction

Sustainable management and conservation of marine ecosystems hinges on understanding natural and anthropogenic pressures and structural forces that act on system stability (Knowlton 2004). While marine resources and ecosystem services in coastal zones are affected by climate and environmental variability as well as human activities like fishing, nutrient loading and habitat alteration (e.g., Sherman and Duda 1999), species interactions also play an important and more nuanced role in marine ecosystem dynamics. For example, "keystone" species affect marine community structure and function to an extent that is disproportionate to their biomass (Paine 1969; Power et al. 1996). A classic example is the sea otter, *Enhydra lutris,* in coastal waters of the North Pacific Ocean from Alaska to California. Sea otter predation can severely reduce local densities of benthic grazing invertebrates such as sea urchins, thereby allowing kelp canopies to develop and expand (Estes and Palmisano 1974; Estes and Duggins 1995; Steneck et al. 2002; Watson and Estes 2011). The indirect effect of sea otters on kelp is important, given kelp forests are among the most productive ecosystems on Earth (Mann 1973), support distinct fish, invertebrate, and understory algal communities (Duggins 1988; Ebeling and Laur 1988, Reisewitz et al. 2006; Markel and Shurin 2015) and perform ecosystem roles such as wave energy attenuation (Pinsky et al. 2013) and carbon storage (Wilmers et al. 2012). Similar community- and ecosystem-level consequences of sea otters have been noted in other coastal habitats as well (e.g. seagrass communities; Hughes et al. 2013).

Sea otters are native to the coast of the Olympic Peninsula of Washington state, USA (Fig. 1), but were hunted to extirpation by the early 1900s (Lance et al. 2004). Reestablishment efforts began in 1969-1970, with 59 sea otters translocated to Washington from Amchitka Island, Alaska (Jameson et al. 1982). Despite high mortality in the early 1970s, the population

67 eventually expanded (Fig. 1), surpassing 200 individuals by 1989 (Jameson 1993) and 600 by the

68 late 1990s (Jameson and Jeffries 1999; Fig. 1). SCUBA surveys at multiple sites in 1987

69 indicated that otter densities were correlated with increased coverage of foliose and canopy-

70 forming kelps, and reduced abundance and size of benthic invertebrates, including kelp-grazing

71 sea urchins in the genera *Mesocentrotus* and *Strongylocentrotus* (Kvitek et al. 1989). Subsequent

72 surveys in 1995 and 1999 showed further declines in invertebrate communities along the

73 OCNMS (Kvitek et al. 1989, 1998, 2000). Kelp canopy area peaked at the scale of the Olympic

74 Coast around 2000 (Fig. 1; WADNR 2017; Pfister et al. 2018).

75   Since the subtidal community surveys in 1999, the Olympic Coast sea otter population has

76 more than doubled (Fig. 1; Jeffries and Jameson 2014). We expect that increased top down

77 predation by sea otters might have further suppressed benthic macroinvertebrates and increased

78 kelp canopy cover; however, the total kelp canopy area has declined from a peak abundance in

79 roughly 2005 (Fig. 1). The apparent decoupling of sea otter and kelp changes warrants renewed

80 research to understand patterns of nearshore community change at the regional and landscape

81 scales.

82   While sea otters are generally assumed to play a strong top-down role in shifting North

83 Pacific coastal ecosystems from herbivore-dominated to algae-dominated (Estes and Duggins

84 1995), this generality has been both affirmed and challenged over the past 40 years (Watson and

85 Estes 2011). There are numerous examples of Pacific coastal systems that are not herbivore-

86 dominated in the absence of sea otters (Foster 1990; Lafferty 2004; Carter et al. 2007; Reed et al.

87 2011). For example, Reed et al. (2011) found that wave disturbance overwhelmed the effect of

88 herbivory and nutrient availability in determining kelp forest dynamics in central and southern

89 California. This example highlights the importance of other physical and biological interactions

90 for structuring coastal habitats and encourages an explicit consideration of the spatiotemporal

91 heterogeneity of coastal kelp systems. Such a landscape perspective on the drivers of

92 heterogeneity and complexity has been used to improve understanding of kelp forest dynamics in

93 California (Bell et al. 2015).

94   Here we combine a 30-year time series of sea otter, kelp, and benthic invertebrate data along

95 the Olympic Coast in order to better understand nearshore marine community dynamics at

96 regional and landscape scales. We conduct spatio-temporal analyses on sea otter and kelp data

97 from publicly available surveys and conduct new field sampling to extend previous kelp forest

98 invertebrate surveys conducted at focal sites by Kvitek et al. (1989, 1998, 2000). Our ability to

99 understand the interactions between habitat, predators, and prey is essential for proper

100 management and conservation of coastal species, habitats, ecosystems and services, particularly

101 in this area where maintaining high native biodiversity and keystone species populations are

102 explicit management objectives (Office of National Marine Sanctuaries 2008).

103 **Materials and Methods**

104 *Study locations*

105   Our study sites fall within the Olympic Coast National Marine Sanctuary (OCNMS,

106 designated in 1994). We conduct analyses at landscape- (sea otter abundance and kelp coverage

107 for the entire OCNMS region) and local-scales (sea otter, kelp, and invertebrate abundance by

108 site). For the landscape-scale analysis, we use long-term monitoring surveys for sea otters and

109 kelp canopy surface coverage. Below we describe these data sources and detail how we connect

110 these OCNMS-wide surveys to provide sea otter and kelp abundance at our sites.

111   For local-scale analyses, we focus on ten kelp forest sites located within the range of

112 OCNMS surveys for sea otters and kelp canopies (Fig. 1). Eight sites are on the outer coast, and

two, Chibahdehl Rocks and Neah Bay, are inside the Strait of Juan de Fuca (Fig 1). All sites

feature subtidal rocky reef habitat with dense stands of canopy kelp (*Nereocystis luetkeana*

and/or *Macrocystis pyrifera)* and understory red, brown, and green algae. Canopy forming kelp

forests generally occupy depths shallower than 10 m in OCNMS. SCUBA divers surveyed each

site for benthic invertebrates in at least two of the three years (1987, 1995, and 1999) by Kvitek

and colleagues (1989, 1998, 2000) and 2015 (see below). Six sites (Teahwhit Head, Rock 305,

Cape Johnson, Cape Alava, Anderson Point, Neah Bay; Fig. 1) were surveyed in all four years

(1989, 1995, 1999, and 2015). In addition, a winter sea urchin fishery occurred between the early

1980s and 1997 in the area including two of the sites, Chibadehl Rocks and Neah Bay (WDFW

District 5; Laidre and Jameson 2006). Sea urchin fisheries never occurred at the remaining sites.

Spatially explicit sea urchin harvest information are not available within the harvest area.

For regional comparisons, we divided the ten sites into three geographic groups: northern

(Neah Bay, Chibahdehl Rocks, Tatoosh Island), central (Anderson Point, Point of the Arches,

Cape Alava) and southern (Cape Johnson, Rock 305, Teahwhit Head, Destruction Island). These

groupings are similar to the areas used to describe sea otter trends within OCNMS historically

(Lance et al. 2004) and reflect distinct geographic patterns in kelp and sea otter trends (see

Results). We also use these groupings to account for pseudo-replication in statistical analyses

and to test for regional differences in biological relationships. Finally, we calculated an exposure

metric for each site, which was a composite of potential wind driven wave energy, to use as an

explanatory variable in statistical models (Supplement; Fig. S1).

Sea otter abundance and distribution

We extracted sea otter location and abundance information from research reports (e.g., Lance

et al. 2004; Jeffries and Jameson 2014) to examine shifts in otter abundance and distribution over

136 the past several decades. Sea otter surveys along OCNMS have been conducted by a mix of

137 aerial surveys and land-based observations since 1977. Surveys were approximately biennial

138 through the 1980s and annual from 1989-2015 (but no surveys in 2009 or 2014). Sea otter

139 surveys were conducted in summer and thus reflect summer distribution and abundance (Laidre

140 et al. 2009). Available evidence does not suggest that summer and winter distributions of sea

141 otters are substantially different in this region (Laidre et al. 2009). However, sea otters are highly

142 mobile predators with substantial home ranges and seasonal patterns are uncertain.

143   To estimate trends in sea otter abundance at each focal site, we developed a kernel-smoothed

144 distribution of otters along the coast to incorporate uncertainty about how snapshot surveys

145 translate to effective numbers of otters present at a given site. First, we developed a one-

146 dimensional coastline for the Olympic Peninsula and identified the position of each WADNR

147 survey location along this coastline. We generated a smooth density of otters along the coastline

148 using kernel density estimates, which approximate the observed otter data using a mixture of

149 Gaussian (Normal) distributions. Specifically, we placed a Gaussian distribution centered at each

150 survey location with a standard deviation h (the bandwidth) that corresponds to the estimated sea

151 otter home-range size of 40 km for the Washington coast ($h = 10.2$; Laidre et al. 2009, their Fig.

152 3). After calculating the kernel probability density, we calculated the proportion of the total sea

153 otter population that was present within a radius of 10 km of each focal site by integrating the

154 probability density and multiplying by the total sea otter population. Due to uncertainty in the

155 effective home range size of sea otters, we used sensitivity analyses with a range of bandwidths

156 ($h = 5$ and 15). The qualitative pattern of results did not change with alternate bandwidths.

157   We estimated the temporal trend in sea otter abundance at each site and OCNMS-wide by

158 regressing the natural logarithm of sea otter abundance against time. We used the whole time-

159 series beginning with the first year of kelp canopy survey (1989, see below), and separately for

160 the two halves of the time-series (1989-2001 and 2002-2015) to assess if trends shifted over

161 time. As estimates of trends become progressively less precise with shorter time-series, we do

162 not further subdivide the time series. To facilitate comparison among sites that vary substantially

163 in sea otter abundance, we standardized the number of sea otters by dividing by the average

164 number of sea otters estimated at each site during the first three years of the kelp surveys (1989-

165 91; $N_{j,base}$) and calculated a natural logarithm of this ratio: $ln\left(\frac{N_{j,t}}{N_{j,base}}\right)$. Using this index allows

166 for sites across a large range of abundances to be visualized on the same axes and provides a

167 graphical interpretation of sea otter trend (linear trends are exponential changes in abundance).

168 We explored alternate years for dividing the time-series as well, setting the break variously at

169 1999 to 2003; these breaks made little qualitative change to the results.

Kelp canopy area

171 To describe kelp abundance at each site, we used publicly available data from aerial

172 overflight surveys of algae from the Washington Department of Natural Resources (Van

173 Wagenen 2015; WADNR 2017). Surveys were conducted annually between 1989 and 2015 (but

174 no survey in 1993) during peak kelp abundance for the region (late July or early August). Kelp

175 canopies in this region consist of a mix of *Macrocystis* and *Nereocystis*. While overflight surveys

176 differentiate between the two species, we are primarily interested in the total canopy habitat

177 provided, and thus we focus on the total surface coverage provided by the two species;

178 additionally, the two species' abundances are strongly positively correlated in this region

179 (Pearson's *r = 0.689;* Pfister et al. 2018). We examined kelp abundance at two scales. First, we

180 used kelp area within discrete area strata along the coast to provide estimates of local kelp

181 surface coverage, $K_{j,t}$, for the strata containing each of our ten sites, *j*, in each year, *t* (Fig. 1).

182   The strata (kelp index map regions) used by WADNR are substantially larger than the area

183   surveyed during invertebrate surveys. Unfortunately, these strata are the smallest spatial unit for

184   which it is appropriate to generate kelp area estimates (WADNR 2017). Second, we summed

185   kelp surface coverage in all strata between Neah Bay and Destruction Island to provide an

186   OCNMS-wide estimate of kelp area (Fig. 1).

187   We estimated the temporal trend in kelp canopy coverage at each site and OCNMS-wide by

188   regressing the natural logarithm of kelp area against time. We also calculated the standard

189   deviation (SD) and coefficient of variation (CV = SD / mean) of observations around each trend.

190   Thus, our measures of CV represent variability after accounting for the overall trend in area. We

191   performed this analysis on the entire time series (1989-2015), and separately for the two halves

192   of the time-series (1989-2001 and 2002-2015) in order to determine if trends shifted over time.

193   As with sea otter data, to facilitate comparison among sites that vary substantially in kelp area,

194   we constructed a log-index of kelp area; we standardized the area of kelp by dividing the average

195   kelp area observed during the first three years of the survey (1989-91)*,* $K_{j,base}$*,* for site *j* and

196   taking the natural logarithm of the ratio: $ln\left(\frac{K_{j,t}}{K_{j,base}}\right)$.

197   *Invertebrate SCUBA surveys*

198   We conducted SCUBA surveys between 3-7 August 2015 and gathered historical survey

199   information collected by Kvitek and colleagues in 1987, 1995, and 1999 (Kvitek et al. 1989,

200   1998, 2000). During 2015, SCUBA divers surveyed benthic communities in kelp beds at each

201   site (Fig. 1) at depths between 5-10 m, along visual transects (30 m x 2 m, *n* = 4 transects per

202   site). On each transect, divers counted large invertebrates (>5 cm diameter, sea urchins, sea stars,

203   sea cucumbers, crabs, bivalves, etc.).

204   For the 1987, 1995, and 1999 subtidal surveys, we extracted summary statistics on benthic

205   invertebrate densities from Kvitek and colleagues (1989, 1998, 2000). We include surveys that

206   occurred at the same sites and comparable depths (5-10m). All surveys use standard quadrat and

207   transect sampling methods, though the sample sizes vary among years (Table S1, S2). We

208   converted data from all subtidal surveys into units of counts·m^{-2}. Not all sites were sampled in

209   each year, and some taxonomic groups of interest were not identified in available reports (e.g.,

210   sea stars were reported for 1995). We used all available data for each site and year. When

211   necessary, we combined quadrat and transect data using a weighted average with weights

212   corresponding to the area surveyed by each type. We include only species that are large and

213   readily identifiable to avoid concertns about the detection of cryptic species (e.g., chitons; class

214   *Polyplacophora*). We present results for six species groups that are common members of the

215   Olympic coast invertebrate community: sea urchins (genera *Mesocentrotus* and

216   *Strongylocentrotus*), sea cucumbers (genera *Cucumaria* and *Parastichopus)*, crab (primarily

217   genera *Pugettia* and *Cancer)*, bivalves (primarily rock scallops, *Crassadoma gigantea*), and sea

218   stars (including genera *Pisaster, Orthasterias, Dermasterias, Henricia, Pycnopodia)*. Consistent

219   with previous research, we identified sea urchins as the dominant invertebrate grazer in this

220   system and contrast the trends in sea urchin abundance with the other invertebrate groups. Based

221   on published sea otter diet information, we classified these groups into broad categories of diet

222   preference (Estes et al. 2003; Laidre and Jameson 2006; Tinker et al. 2008; Walker et al. 2008).

223   Observed diet of sea otters vary with the available prey field and individual otter diet preference,

224   so we identified sea urchins and crabs as preferred prey, sea stars and sea cucumbers as frequent

225   prey, and rock scallops as rare prey. Other important prey for sea otters are not observed during

226   our surveys due to tidal range (e.g., intertidal mussels *Mytilus* spp.) or habitat requirement (e.g.,

227   soft sediment species like clams).

228   *Statistical Analyses*

229   To ask if local changes in sea otter abundance resulted in subsequent changes in kelp area

230   among the 10 focal sites, we regressed exponential trends in sea otter abundance against kelp

231   area. We performed this analysis for the entire time-series (1989-2015) and separately for each

232   half of the study period (1989-2001 and 2002-2015), using region and otter growth rate as fixed

233   effects. In the model with two time periods we allowed for a period × otter growth rate

234   interaction to ask if the relationship between sea otters and kelp shifted between periods. We also

235   included our measure of wave exposure as a potential covariate in all models.

236   To assess the effect of otter abundance on the variability of kelp cover, we used the

237   difference in CV of kelp area at each site between periods as the response variable with region,

238   wave exposure, difference in otter abundance between periods at each site, and CV of kelp area

239   in the 1989-2001 period as predictors. We explored only additive main effects due to a sample

240   size of 10 and selected among models using AIC corrected for small sample sizes (AICc).

241   To examine changes in the abundance of invertebrate groups over time, we used

242   permutation-based multivariate analysis of variance (PERMANOVA) to compare community

243   structure across three time periods (1987, 1999, 2015) or three regions (northern, central, and

244   southern) using the adonis function in R (R Core Team 2017). We exclude data from 1995

245   because sea star data were absent. The taxa-specific average densities (individuals m^{-2}) for each

246   site-year-region were used as the dependent variables, and converted to dissimilarity matrices

247   using Manhattan $\log(x + 1)$ distances. Manhattan dissimilarity treats joint absences of species as

248   informative and wanted to include that information; the more commonly used Bray-Curtis

249   dissimilarity excluded information about joint absences (Legendre et al. 2005; Anderson et al.

250   2006). We performed randomizations within strata based on regions or time periods. We also

251   tested whether community composition was more variable in among regions among time periods

252   by examining multivariate dispersion in community composition using the betadisper function in

253   R. To visualize differences among time periods or regions in invertebrate community structure,

254   we used non-metric multidimensional scaling (nMDS) based on the *nmds* function and related

255   variation individual taxa to community dissimilarity using the *envfit* function. All multivariate

256   analyses and visualizations were conducted in the R package vegan. We also calculated

257   proportional declines in mean abundance and used paired *t*-tests to evaluate their significance.

258   **Results**

259   *Spatiotemporal trends of sea otters and kelp*

260   Sea otter density trends have followed three spatially distinct patterns along the Olympic

261   Coast since the 1970s (Fig. 2a - c). Local trends in sea otters differ substantially from the

262   OCNMS-wide trend. Near the most northerly study sites, sea otter densities increased sharply

263   from the mid-1980s until the early 1990s before declining slightly and then remaining stable

264   from the mid-1990s to present (Fig. 2a). Sea otter densities in the central region including

265   experienced exponential growth from the late 1970s until the mid-1990s, but have remained

266   largely stable at approximately 1990 densities (Fig. 2b). This represents a longer period of

267   increasing otter densities than the northernmost region. The increase in sea otter density has been

268   strongest and most consistent in the southern region of the study area (Fig. 2c) with near

269   exponentially increases since the late 1970s; since roughly 2000, the rate of increase in the

270   Destruction Island area has outpaced rates near Teahwhit Head and Cape Johnson / Rock 305. At

271   present, the absolute abundance of sea otters is also greatest in the southern region; sea otter

272 abundances in the northern region are the lowest by at least an order of magnitude (estimated

273 2015 sea otter abundance of 18, 207, and 439 for Tatoosh Island (northern region), Cape Alava

274 (central), and Destruction Island (southern) respectively). Cape Johnson and Rock 305 have

275 essentially the same trend in Fig. 2c due to their proximity relative to the kernel bandwidth used

276 for home range estimation (Fig. 1; see Methods).

277 Further analysis of sea otter data shows that the distribution of the Olympic Coast population

278 has shifted over time (see also Jefferies and Jameson 2014). The population has had a bimodal or

279 multimodal distribution for much of the study period, with the most significant modes in the area

280 between Cape Alava and Cape Johnson, and another further south near Destruction Island (Fig.

281 3). The center of gravity of the population was in the vicinity of Teahwhit Head in the late 1970s,

282 but then shifted north to the area around Cape Alava for much of the 1980s and 1990s. Starting

283 in the late 1990s, the center of gravity shifted south to near Destruction Island, where it has

284 remained. In recent years sea otter observations are rare inside the Strait of Juan de Fuca (Fig. 3,

285 above dashed line) but common at most points to Point Grenville in the south (Fig. 3).

286 Canopy kelp area exhibited spatiotemporally distinct patterns in the three regions of the study

287 area from 1989-2015 (Fig. 2d-f). Kelp area showed substantial interannual variation both at the

288 individual sites and the OCNMS-wide scale (Fig. 1). While the area of kelp in absolute terms

289 varied substantially among sites within a region (Table 3; Pfister et al. 2018), kelp trends varied

290 predominantly by region within the Olympic Coast. At the furthest north sites, kelp area indices

291 showed no clear long-term trends but displayed notably higher interannual variability at Tatoosh

292 Island than Neah Bay and Chibahdehl Rocks inside the Strait of Juan de Fuca (Fig. 2d; note that

293 Neah Bay and Chibahdehl Rocks are in the same kelp stratum and thus share a single time series;

294 Fig. 1). The central region also showed within-region differences among sites (Fig. 2e). Canopy

295   area at Cape Alava increased from 1989 to 2000 before stabilizing and even declining in recent

296   years. Point of the Arches and Anderson Point decreased in the early 1990s before following a

297   qualitative pattern similar to Cape Alava. Canopy area at Cape Alava was far less variable than

298   the other two central sites. At the southern sites, canopy area generally increased until the early

299   2000s before stabilizing or declining slightly (Fig. 2f); as with the central region (Fig. 2e) there

300   were differences in short-term trends across the four southern sites early in the time series.

301   Interannual variability was fairly consistent among southern.

302   *Connections between sea otters, invertebrates, and kelp*

303   We detected differences in the kelp population growth rate between periods with a OCNMS-

304   wide average growth rate of 0.056 for 1989-2001 and of -0.037 for the 2002-2015 period

305   (difference between periods p =0.012; Fig. 4). While the temporal effect is intriguing, more

306   interesting is the interaction between sea otter population growth rate and time period. Sea otter

307   growth had a positive relationship with kelp during the earlier period (point estimate of slope =

308   0.285) but a negative effect of sea otters during the later period (point estimate of slope = -0.507;

309   interaction term p = 0.045). There was no support for regional variation in kelp population

310   growth after accounting for other factors (p = 0.128). The model considering only a single time

311   period found no effect of sea otters on kelp (p = 0.40) but did find differences in kelp population

312   growth rate among regions (p = 0.024). This result shows how the temporal context can

313   substantively alter the interpretation of mechanisms driving kelp population growth. Importantly,

314   our analyses should not be taken to suggest a discrete break in 2001 – using alternate breakpoints

315   in the time series between 1999 and 2003 yield qualitatively similar results. Rather, dividing the

316   time series is a way to summarize changes in a continuous time series (Fig. 2).

317   After accounting for kelp population growth rates, the variability in kelp area declined at

318   most sites between the two periods (Fig. S2). Specifically, bootstrapped estimates of CV showed

319   that variability at all sites but one (Tatoosh Island) declined, though the magnitude of decline

320   varied substantially by region. The three northern sites had virtually no change in CV (changes

321   of less than ±0.05 for all sites), the central region showed declines in CV but with variability

322   among sites (declines of 0.033, 0.343, and 0.351, for Cape Alava, Anderson Point, and Point of

323   the Arches, respectively), while the southern sites showed substantial declines in CV (declines of

324   0.175 to 0.694). For most sites, these are large and biologically significant changes in kelp

325   variability. Linear models showed that including kelp CV in 1989-2001 alone best predicted the

326   change in CV between periods ($\Delta AICc = 0$, *adj.* $R^2 = 0.54$). Sites with high CV in the first

327   period had reduced CV in the second. The only other model with a small amount of statistical

328   support included both kelp CV in 1989-2001 and the change in the number of otters ($\Delta AICc = 2$,

329   *adj.* $R^2 = 0.64$). In this model, the negative coefficient for the change in otters indicates

330   increased sea otter abundance was associated with reduced kelp CV (point estimates correspond

331   to an increase of approximately 13 otters leading to a decrease of 0.01 in CV). As we only have

332   10 sites for comparison, our statistical power and precision of these estimates is low. Estimates

333   of wave exposure were not a significant explanatory variable for any aspect of kelp CV.

334   As both primary sea otter prey and the major grazers of kelp, benthic invertebrates are the

335   mechanistic link between sea otters and kelp. While we lack continuous time series for

336   invertebrates at OCNMS, available information shows significant variation in the benthic

337   invertebrate community over years but not across regions (Fig. 5; Table 2). Not only was there a

338   shift in mean community composition between the first survey (1987) and later survey years

339   (1999, 2015), but community composition among sites became less variable after 1987 (Table 3).

340　The differences in community composition among years reflected substantial declines in all 5

341　major taxonomic groups from 1987-2015 (Fig. 6). Sea urchins declined precipitously with the

342　across-site mean density falling by more than 99% between 1987 to 2015 (from 3.7 m^{-2} to 0.01

343　m^{-2}). While the other five species groups did not decline as dramatically as urchins, they all

344　showed substantial declines from 1987 to 2015: bivalves (decline of 90%), sea cucumbers

345　(86%), crabs (84%), and sea stars (70%). All of these declines were significant (paired t-tests,

346　p<0.01 for all species groups). Only sea urchins showed a pattern in which the highest density

347　occurred in the three sites that Kvitek et al. (1989) defined as outside of the range of sea otters

348　(Neah Bay, Anderson Point, Point of the Arches; Fig. 6a). Despite the presence of substantial

349　commercial sea urchin fisheries before 1987 at Neah Bay, sea urchin density at this site fell

350　precipitously in response to sea otter increases in the early 1990s. Indeed, low sea urchin

351　densities due to sea otter predation is perceived as the main factor driving the closure the sea

352　urchin fishery around Neah Bay in 1997 (Laidre and Jameson 2006). For the four other species

353　groups, densities were not notably different between sites inside and outside of the otter range in

354　1987. This suggests that the dramatic and immediate effect of otters on invertebrates is limited to

355　a few species or species groups, even if over time there are substantial but gradual changes in

356　invertebrate communities. Beyond declines in mean densities, all five species also show notable

357　declines in the among-site variation in density; the among-site standard deviation fell by 75 to

358　99% for our six species groups. By all measures, the spatial variability in invertebrate densities

359　has declined over the past 30 years.

360　**Discussion**

361　　Sea otters are iconic keystone predators in coastal ecosystems of the northeastern Pacific, and

362　their presence radically affects invertebrate and algal communities (Estes and Duggins 1995;

363   Steneck et al. 2002; Watson and Estes 2011). Here we revisit historical invertebrate surveys and

364   complement these surveys with independent spatiotemporal data on kelp and sea otters in

365   Washington's OCNMS and new invertebrate surveys. Our analyses reveal a strong correlation

366   between sea otter and kelp population growth at the local scale during the rapid expansion of sea

367   otter populations. However, there is a temporal component to these associations: the relationship

368   between kelp and sea otter growth rates shifted from positive during the 1990s to neutral or

369   possibly slightly negative post-2000 (Fig. 4). Together our analyses demonstrate that OCNMS-

370   wide trends in sea otter, kelp, and benthic invertebrate abundance are not necessarily evident at a

371   finer spatial grain. They suggest that while a sea otter derived trophic cascade initially drove

372   changes in the nearshore community along the Washington coast, additional factors in more

373   recent years may account for fundamental shifts in invertebrate community dynamics. In

374   addition, contrary to predictions from trophic cascade theory (Estes et al. 2011), kelp and sea

375   otter abundance are statistically decoupled when viewed at an OCNMS-wide scale and over the

376   entirety of the 30-year period. The decoupling of otter and kelp abundance in more recent years,

377   and the disconnect between OCNMS-wide and local scale patterns, provides insight into

378   theoretical expectations for short- vs long-term dynamics following the reintroduction of

379   predators more generally (Sergio et al. 2014; Stier et al. 2016), and sparks intriguing hypotheses

380   about the influence of top-down versus bottom-up forcing in temperate coastal habitats.

381   Trophic cascade theory predicts that increased sea otter abundance should reduce the

382   abundance of their prey, including functionally important invertebrate grazers such as sea

383   urchins. In turn, reduced grazer abundance should release kelp and other algae from top-down

384   control and lead to increases in their abundance. Our results echo those of Kvitek et al. (1989,

385   1998, 2000) and demonstrate large, immediate, and persistent effects of sea otter expansion on

386 the main invertebrate kelp-grazer and a preferred prey, sea urchins. We also show that increases

387 in otter abundance were correlated with declines for a broad suite of invertebrate species and

388 multi-year increases in kelp area. These reductions in invertebrate abundances suggest that the

389 consequences of sea otter populations for kelp forest community composition are not exclusively

390 an immediate shift in state but can manifest gradually over the span of decades (Watson and

391 Estes 2011; Kenner et al. 2013). Furthermore, because invertebrate densities remain far below

392 historical levels and those associated with shifts to non-kelp dominated states (Filbee-Dexter and

393 Scheibling 2014), the observed declines in kelp population growth rates (Fig. 4) and total area

394 (Fig.1) in OCNMS since 2000 are unlikely to be caused by increased invertebrate grazing

395 pressure. Rather, these results suggest that forces unrelated to otter abundance drive kelp

396 abundance and community structure once kelp have equilibrated to the presence of sea otters.

397   One hypothesis for the decoupling of kelp and otter growth rates after 2001 is an increase in

398 the influence of abiotic factors. Oceanographic dynamics in the late 1990s and early 2000s in the

399 Northeast Pacific have been the subject of intense study because they were characterized by

400 major El Niño and La Niña events and shifts in productivity regimes (PDO; Mantua et al. 1997;

401 Mantua and Hare 2002). It is possible that at that time the vast majority of changes in

402 invertebrate grazer abundance due to otter predation had already occurred, and kelp dynamics

403 became more strongly influenced by sea surface temperature, upwelling, nutrient availability and

404 other bottom-up forces (Pfister et al. 2018). For kelp in particular, we expected that the

405 variability in kelp area would be strongly related to wave exposure at a given site (Reed et al.

406 2011; Bell et al. 2015). However, while kelp CV varied substantially among sites, it was

407 unrelated to calculated wave exposure values (Fig. S1). Surprisingly, Neah Bay, a site largely

408 protected from wave exposure, has had nearly equivalent kelp CVs since 2002 as five sites on

409   the outer coast, including Cape Alava and Destruction Island (Fig. S2; detrended CV of

410   approximately 0.2). We speculate that this may be driven predominantly by the fact that we only

411   have information about kelp area during the summer, when seasonal wave energy on the coast is

412   relatively low. An alternative prediction is that kelp CV in Neah Bay would decline if sea otters

413   invaded Neah Bay, as kelp CV appears to be related to the number of otters present at each site.

414   We cannot exclude the possibility of an effect of the sea urchin fishery and kelp variability at

415   Neah Bay, but the fishery has been closed since 1997 and cannot be considered a strong driver of

416   the ecosystem in recent years. While we cannot definitively identify what caused the decoupling

417   of otter and kelp dynamics in OCNMS, shifts in factors controlling alternate states within

418   ecological communities are not without precedent in other systems (Bellwood et al. 2006;

419   Petraitis et al. 2009). An additional possibility is that what were strong trophic interactions

420   historically may change in new climatic regimes (McCoy and Pfister 2014). Our study adds

421   richness and complexity to the classic trophic cascade explanation for the dynamics of kelp

422   forest communities.

423   Beyond the mean effects of sea otters on kelp and invertebrates, both kelp area and the

424   benthic invertebrate community showed reduced variability as sea otter abundance increased. We

425   know of no other study that has examined the interaction between otter abundance and kelp

426   variability but suggest this is a particularly interesting avenue of future research due to the

427   connection between canopy kelps, benthic community structure (Arkema et al. 2009), and

428   various ecosystem services (Wilmers et al. 2012; Pinsky and Fogarty 2012). Indeed,

429   incorporating the effects of keystone species and ecosystem engineers in marine planning seems

430   especially wise when ecological endpoints include conservation and restoration of biogenic

431   habitats such as kelp forests. For benthic invertebrates, both our multivariate and univariate

432   analyses show that invertebrate communities cluster by year rather than spatial region,

433   suggesting the primary driver of communities is a temporal rather than a spatial process (Fig. 5,

434   6). Thus, both kelp and invertebrates show evidence of homogenization in concert with the

435   expansion of sea otters, which aligns with previous suggestions that sea urchin-dominated

436   habitats may show more variability than sea otter controlled habitats (Watson and Estes 2011).

437   We acknowledge many potential consequences for other groups including understory algae

438   (Watson and Estes 2011) and fish (Markel and Shurin 2015) that we cannot explore here.

439   Our data do not allow us to examine year to year changes in the linkages between sea otters,

440   benthic invertebrates, and kelp, opening the possibility that invertebrate communities

441   substantially shifted during the years between surveys in a way that can explain kelp variation.

442   While there is ample evidence that other factors have affected the abundance of some

443   invertebrate groups (e.g. sea star wasting disease outbreak in 2013-4; Eisenlord et al. 2016),

444   personal observations of one authors (AOS) between 2004 and 2008 at two sites - Tatoosh Island

445   and Point of the Arches - do not support radical changes in invertebrate abundances during the

446   1999 to 2015 gap in our invertebrate time-series. We cannot exclude the possibility of variability

447   in invertebrate communities driving the patterns but we suggest that it is an unlikely cause.

448   Looking to the future, sea otter numbers appear to have stabilized in much of the northern

449   and central regions of the OCNMS (Fig. 2) and may be at or near carrying capacity in these

450   regions. Invertebrate densities in these regions are very low, which begs the question of how sea

451   otter populations are maintained with very low prey abundances. Rocky subtidal and kelp forest

452   habitats support higher densities of sea otters in Washington than either sandy bottom or

453   estuarine habitats (Laidre et al. 2001, 2002), suggesting that sea otters are not likely to simply be

454   foraging in nearby sandy habitats, but they may be capturing invertebrates in deeper or shallower

455   rocky habitats that were not included in our surveys or historical surveys. Furthermore, we note

456   that the abundance of sea otters in 2015 ($n > 1400$) is substantially above published estimates of

457   carrying capacity for equivalent region of the Washington outer coast (922 to 1189; Laidre et al.

458   2002), suggesting that either the carrying capacity of otters needs to be revisited or, if carrying

459   capacity estimates are correct, the population is predicted to decline in the coming years.

460   In conclusion, place-based management of resources and ecosystem services is of great

461   importance in coastal regions, and informed, holistic management requires accounting for the

462   dynamics of keystone species and major biogenic habitats. Along the Olympic Coast, place-

463   based management is a priority at both the state level—for example, the recently drafted

464   Washington state marine spatial plan (http://www.msp.wa.gov/wp-

465   content/uploads/2017/draft_MSP_and_appendices.pdf)—and the federal level, as practiced by

466   OCNMS (Office of National Marine Sanctuaries 2008) and the adjacent Olympic National Park

467   (National Park Service 2008). The reestablishment of a healthy sea otter population in this region

468   has already yielded considerable ecosystem change, through trophic cascade dynamics that have

469   enabled kelp canopy habitats to expand. However, our research shows that kelp canopy

470   dynamics are now being influenced predominantly by drivers other than otter abundance. This

471   apparent decoupling poses a challenge to spatial management of marine resources in the area

472   because the new prevalent mechanisms must be identified in order to anticipate further change

473   and understand how management actions interact with natural variation. A second challenge may

474   be in revising management objectives for sea otters, which have been prioritized as keystone

475   species that have major impacts on ecosystem structure and functioning, biodiversity, and other

476   attributes (Watson and Estes 2011; Wilmers et al. 2012). Our work suggests that their keystone

477   effect on kelp forests either diminished over time or is obscured by environmental factors. The

478 current ecological dynamics of sea otters at sites along the Olympic Coast need further study to

479 determine how their tremendous predatory demands are impacting other habitats and potentially

480 introducing new management tradeoffs in habitats beyond the shallow kelp forest studied here.

481 **Acknowledgments**

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612   Table 1. PERMANOVA partitioning of benthic invertebrate assemblages on the basis of

613   Manhattan log(x+1) dissimilarities in densities in response to (a) Year (fixed, 3 levels 1987,

614   1999, 2015) or (b) Region (fixed, 3 levels) using sequential sums of squares.

615   (a)

Source	df	MS	Pseudo-F	P
Year	2	0.887	6.927	0.001
Residuals	24	0.128		
Total	26			

616

617   (b)

Source	df	MS	Pseudo-F	P
Region	2	0.169	0.899	0.326
Residuals	24	0.188		
Total	26			

618

619   Table 2. Multivariate test of dispersion for benthic invertebrate assemblages on the basis of

620   Manhattan log(x+1) dissimilarities in densities in response to (a) Year (fixed, 3 levels 1987,

621   1999, 2015) or (b) Region (fixed, 3 levels).

622   (a)

Source	df	MS	Pseudo-F	P
Year	2	0.571	17.120	0.001
Residual	24	0.033		
Total	26			

623

624   (b)

Source	df	MS	Pseudo-F	P
Region	2	0.024	0.194	0.860
Residual	24	0.121		
Total	26			

625

626   **Figure 1:** Study area with survey site locations for invertebrate surveys (blue labeled dots).

627   Numbered areas along the coast indicate strata (kelp index map regions) within which WADNR

628   calculates kelp area. *Top right*: Time-series of sea otter abundance on the Washington coast.

629   *Bottom right*: Time-series of total kelp canopy area for kelp strata between 15.1 and 25.2

630

631   **Figure 2:** Time-series for sea otters (left column, *a, b, c*) kelp area (right column, *d, e, f*) at sites

632   divided into three regions (rows*)* in OCNMS. In all panels, points and dashed lines show log-

633   indices for sea otters and kelp area for individual sites. Both kelp area and sea otters are indexed

634   such that the average values for each site the 1989 to 1991 period are 0. Solid lines represent the

635   summed OCNMS-wide values for otters and kelp area, respectively, index to the average value
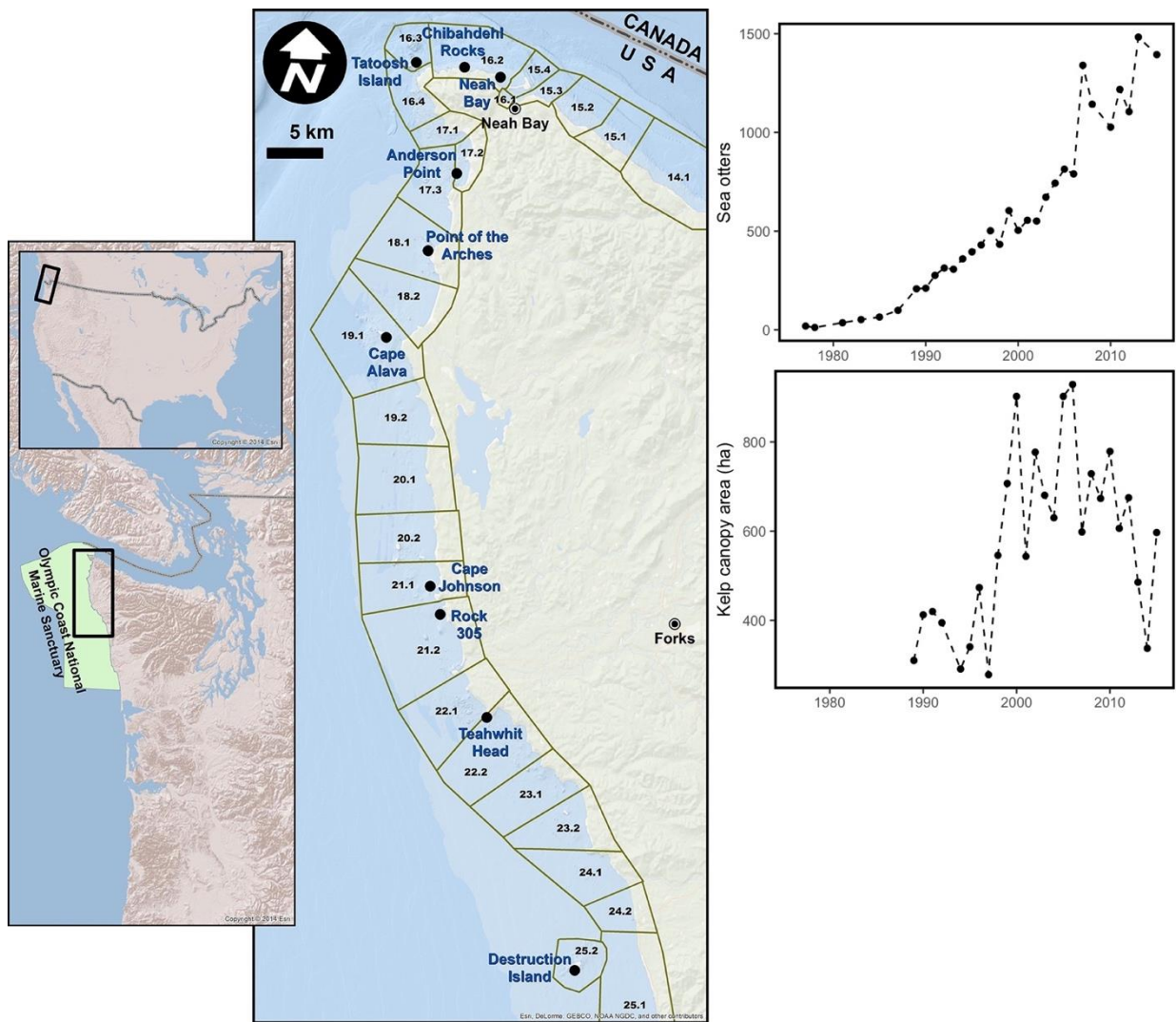
636   from 1989 to 1991.

637

638   **Figure 3.** Kernel smoothed sea otter distributions for sea otters on the Washington coast. Grey

639   densities show the probability distribution for each year, dots show the annual center of gravity

640   (median) of the distribution, and bold dashed line shows smoothed trend in the center of gravity

641   from a loess smoother. Prominent geographic points and invertebrate survey locations noted on

642   the y-axis. Dashed horizontal line indicates the entrance to the Strait of Juan de Fuca at Tatoosh

643   Island (see Fig. 1).

644

645   **Figure 4.** Sea otter and kelp area exponential growth rates at individual sites for two periods

646   (Mean ± SE; *a:* 1989-2001, *b:* 2002-2015). Shapes correspond to the three regions and shading

647   indicates the number of sea otters estimated to be at each site at the beginning of each time

648   period.

649   **Figure 5.** Non-metric multidimensional scaling results benthic invertebrate communities at

650   OCNMS sites grouped by year (*a*) or coastal region *(b).*

651

652   **Figure 6.** Time-series of densities of benthic invertebrates. Species are ordered roughly by otter

653   prey diet frequencey from common (top row) to rare (bottom row). Graphs show site means and

654   SE. Points have been jittered slightly along x-axis to reduce overlap. Red filled points show sites

655   designated by Kvitek et al. (1989) as outside the primary otter range in 1987. By 1995 all sites

656   were within the otter range. Note that data on seastars are not available for 1995
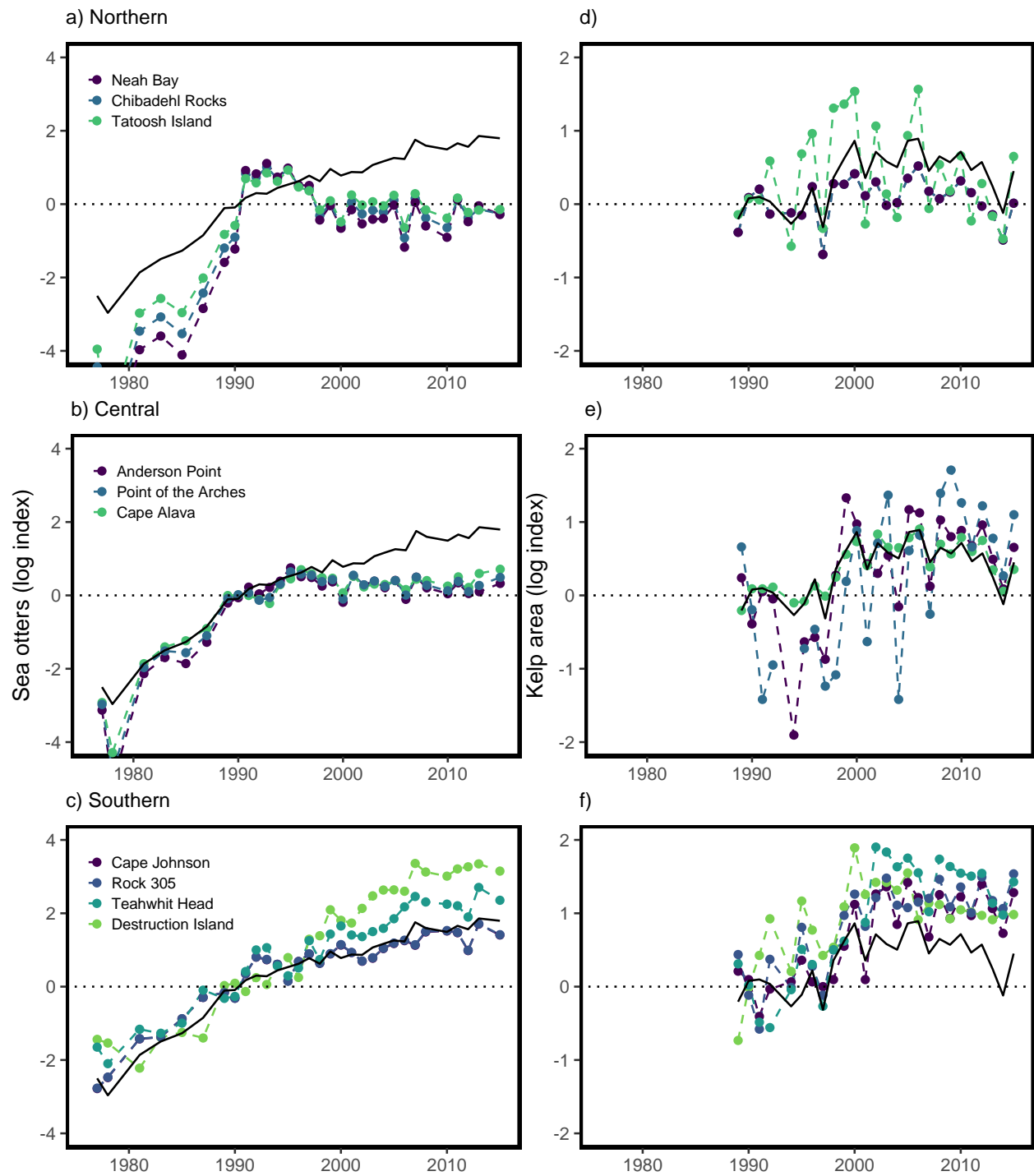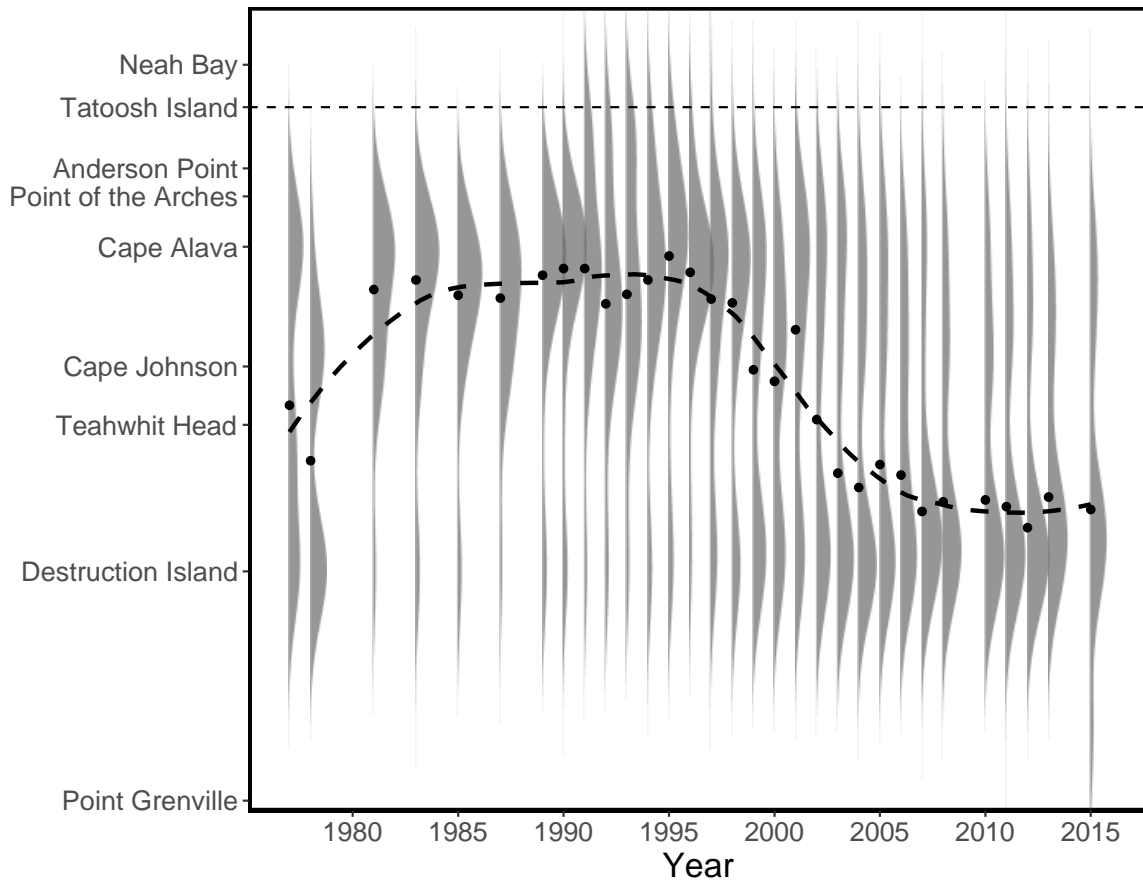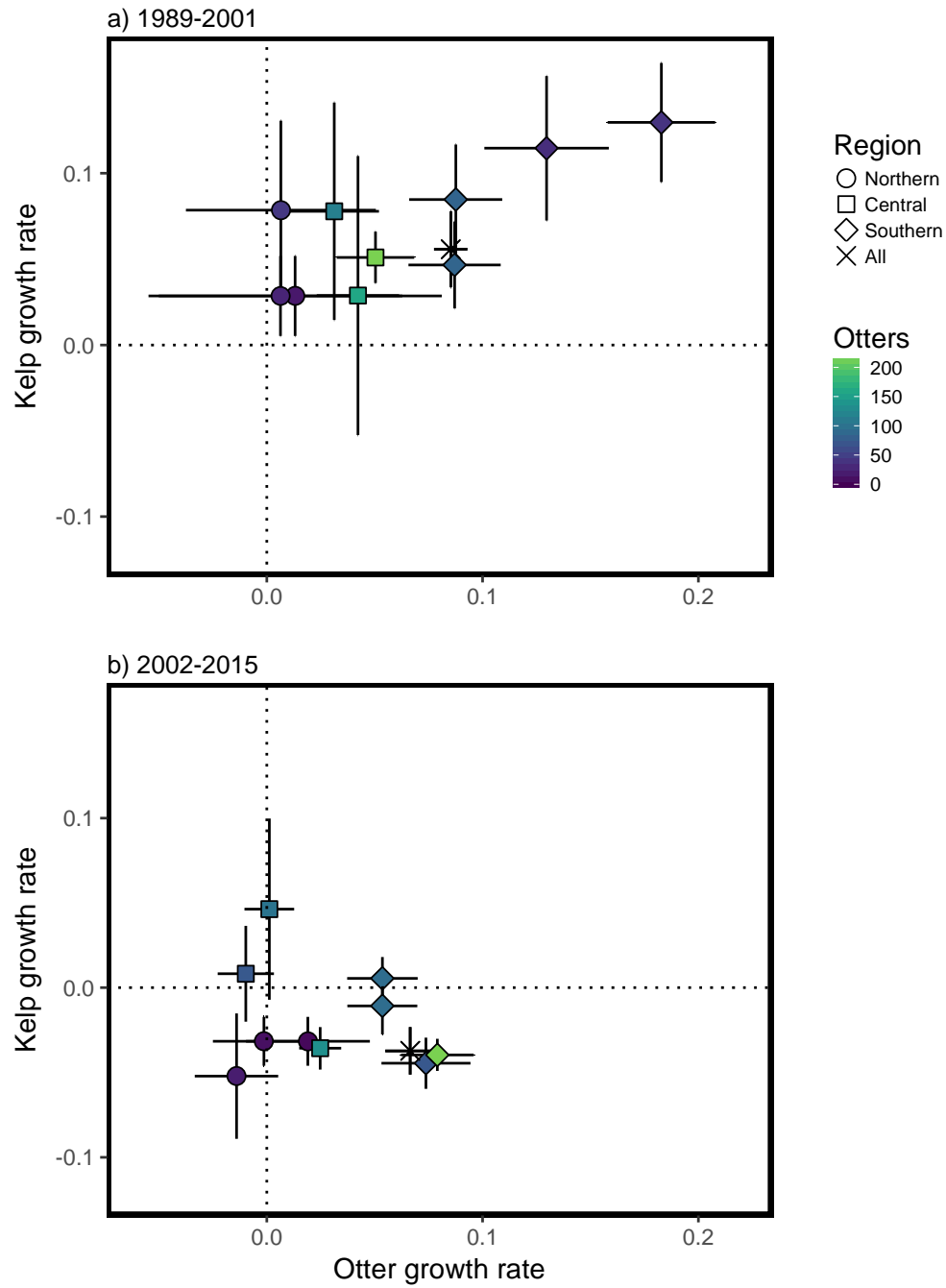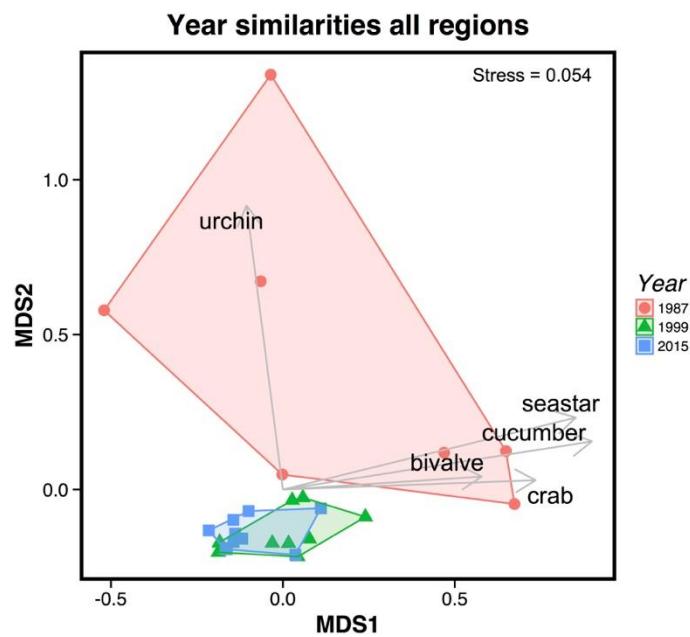
657

658   Figure 1

659

660   Figure 2

661

662

663   Figure 3

a) 1989-2001

b) 2002-2015

664

665   Figure 4

(a)

Year similarities all regions

Stress = 0.054

urchin

seastar
cucumber
bivalve
crab

Year
● 1987
▲ 1999
■ 2015

(b)

Regional similarities all years

Stress = 0.054

urchin

seastar
cucumber
bivalve
crab

Region
● Central
▲ Northern
■ Southern

666

667

668   Figure 5

36

a) Sea Urchins

b) Bivalves

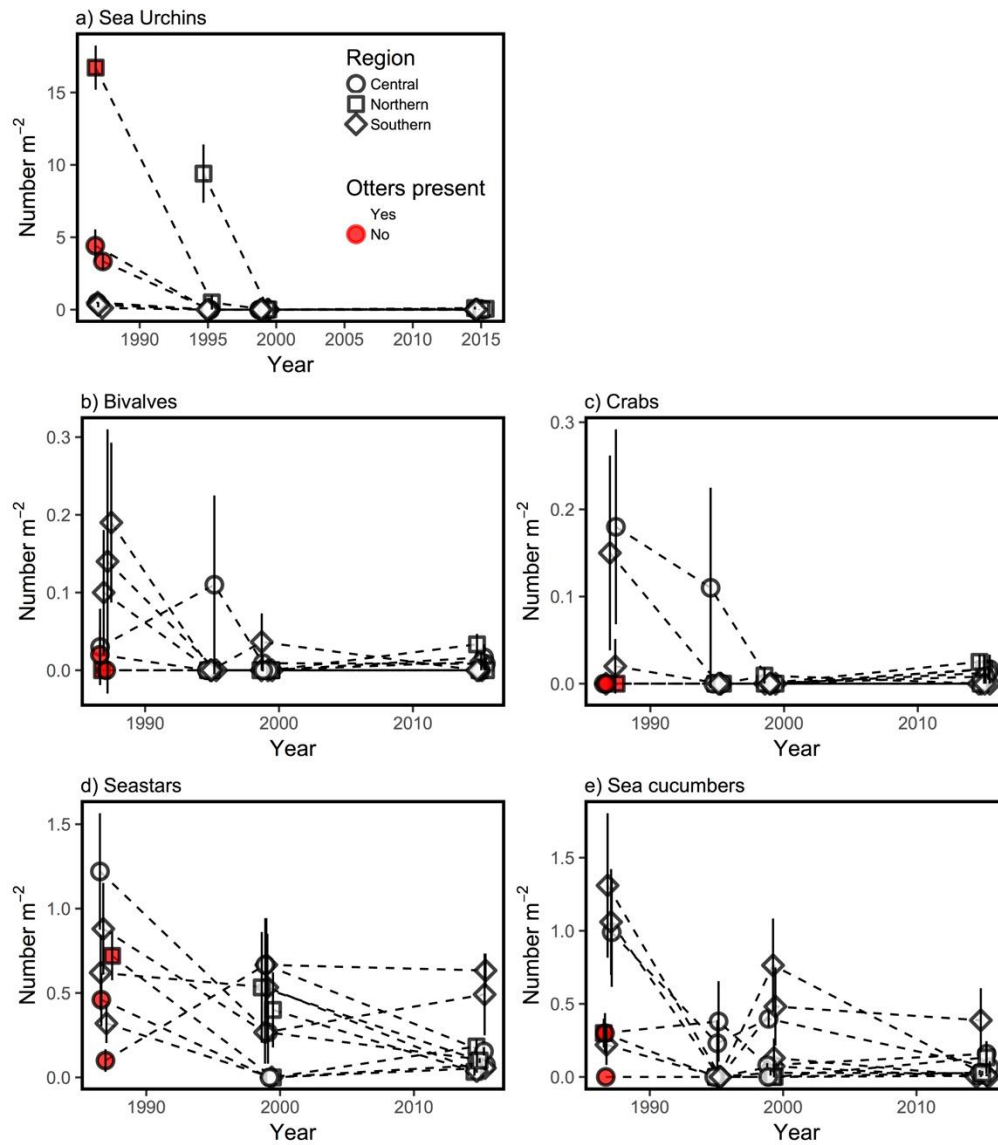c) Crabs

d) Seastars

e) Sea cucumbers

669
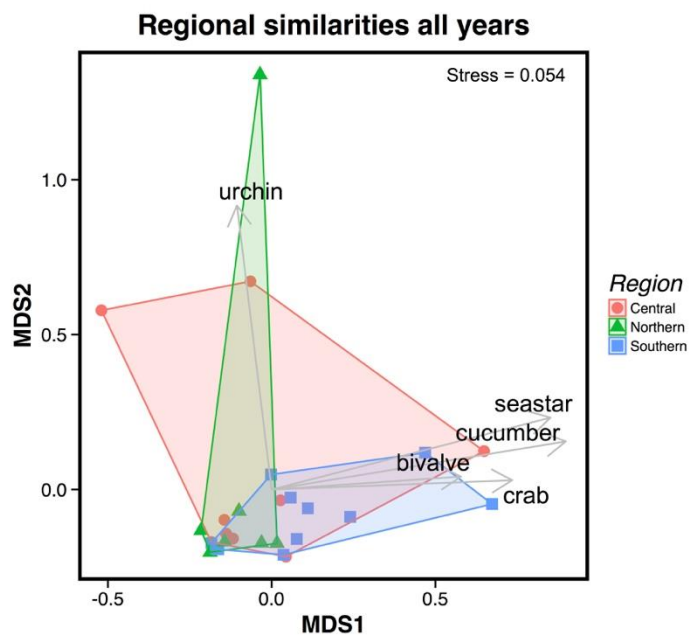
670   Figure 6

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