1 Changes in kelp forest communities along the coast of

2 Washington, USA during and after the 2014-2016 marine

3 heatwave and sea star wasting syndrome

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Abstract

Canopy-forming kelps are foundation species in many coastal ecosystems, but kelp-forest communities are subject to abrupt state changes caused by environmental drivers and trophic dynamics. We examined changes in kelp communities at five sites along the Olympic Coast of Washington State, USA during and following the recent perturbations of anomalous warm-water events and sea star wasting syndrome (SSWS). Anomalously warm water in 2013 and 2014 corresponded with a loss of approximately 50% of *Macrocystis pyrifera* and *Nereocystis luetkeana* canopy. However, the canopy quickly recovered, and stipe density increased after 2015. Purple sea urchins *Strongylocentrotus purpuratus* increased in density 164-fold, largely at one site, but this increase was first observed in 2017 and peaked in 2019, after the warm period. Sea stars did not show recovery from SSWS, with several species including *Pycnopodia helianthoides* continuing to decline. The majority of variation in assemblage structure occurred at the site level for kelps, macroinvertebrates, and fishes, while year explained most of the variability for juvenile rockfishes (*Sebastes* spp.). We did not see strong top-down effects of urchins on kelp, suggesting that top-down impacts were not dominant regionally during this period. In contrast, we found evidence for a bottom-up influence of kelp habitat on juvenile rockfishes, as rockfish recruits occurred with higher probability where kelp stipe density was higher. Our analyses highlight the importance of spatial variation in structuring changes in kelp forest communities associated with disturbance and suggest that it is essential to ensure the protection of a diversity of kelp forests.

Key Words: kelp, marine heat wave, sea star wasting syndrome, urchins, rockfish recruitment, microhabitat

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1. Introduction

Kelps forests are iconic nearshore habitats found in temperate and subpolar waters along approximately a quarter of the world's shorelines (Smale 2020). As foundation species (Teagle et al. 2017, Wernberg et al. 2019), these large brown algae (primarily order Laminariales) provide biogenic habitat for many species and form the basis of highly productive, diverse and complex nearshore food webs (Duggins 1988, Duggins et al. 1989, Gabara et al. 2021, Smith & Fox 2022). Kelps influence nearshore sedimentation dynamics (Connell 2005), provide coastal protection from wave energy (Pinsky et al. 2013), and increase carbon sequestration and buffering against ocean acidification (Wilmers et al. 2012, Weigel & Pfister 2021, but see Gallagher et al. 2022). By fueling nearshore production and providing extensive juvenile and adult fish habitat, kelp forests support diverse ecological communities (Graham 2004, Schiel & Foster 2015, Teagle et al. 2017) and important commercial, recreational and subsistence fisheries for both fish and invertebrate species (Rogers-Bennett & Catton 2019). As many ecosystem-level perturbations are anticipated to intensify under scenarios of climate and ocean change (IPCC 2022), maintaining services from kelp forests requires regional, mechanistic studies to understand dynamic community responses.

Kelp forests are susceptible to state changes from kelp-dominated (i.e., kelp forests) to sea urchin-dominated (urchin barrens) habitat (Ling et al. 2015, Beas-Luna et al. 2020), which poses a risk to the wide range of the valuable ecosystem functions provided by kelp forests (Smith et al. 2021, Smith & Fox 2022). These state changes can be precipitated by climate and oceanographic variability (Pearse & Hines 1987, Pfister et al. 2018, Smale 2020), or by trophic dynamics triggered by shifts in populations and behaviors of key consumers (Ling et al. 2009,

128 Watson & Estes 2011, Feehan & Scheibling 2014, Ling et al. 2015, Shelton et al. 2018, Dunn et

129 al. 2021). The distribution of kelps is strongly related to ocean temperature (Breeman 1990,

130 Smale 2020) making them vulnerable to both long-term ocean warming and the more temporally

131 discrete effects of marine heatwaves (MHW, prolonged but defined periods of anomalously

132 warm water; Hobday et al. 2016). For example, decadal scale warming in Japan, the Iberian

133 Peninsula, and the Northwest Atlantic has led to canopy loss, range shifts, and loss of species in

134 these regions (Smale 2020). Rapid loss of kelp cover in response to MHWs (Straub et al. 2019)

135 has been documented in New Zealand (Thomsen et al. 2019), Western Australia (Smale &

136 Wernberg 2013, Wernberg et al. 2016), the North Atlantic (Filbee-Dexter et al. 2020) and some

137 but not all regions of the northeast Pacific (Beas-Luna et al. 2020). High SST is often associated

138 with low nutrient conditions, which can contribute to low kelp growth or die-offs (e.g.,

139 Cavanaugh et al. 2011, Wernberg et al. 2016, Pfister et al. 2018, Smale 2020), while some

140 studies suggest that elevated temperatures have independent physiological impacts (Muth et al.

141 2019, Hamilton et al. 2020). Wave action can have different impacts based on location and

142 species life history—both impacting kelps directly and by influencing herbivore behavior

143 (Dayton & Tegner 1984, Siddon & Witman 2003, Reed et al. 2011, Hamilton et al. 2020).

144   Intense herbivory by sea urchins when at high density can also drive shifts from kelp-

145 dominated to urchin-dominated system states (Ling et al. 2015). However, kelp forests can be

146 maintained or promoted by trophic cascades in which urchin predators depress urchin abundance

147 thereby facilitating dense kelp stands—the iconic example being the otter-urchin-kelp trophic

148 cascade described for the northeast Pacific (Watson & Estes 2011, Shelton et al. 2018), although

149 fishes and invertebrates (Ling et al. 2009, Eurich et al. 2014, Selden et al. 2017, Eisaguirre et al.

150 2020) are important in some areas regionally and around the globe. However, these trophic

Deleted: While sea surface temperature (SST) is the primary parameter used to identify MHWs (Hobday et al. 2016), multiple drivers significantly influence the occurrence and nature of MHWs, and temperature extremes co-occur with changes in many interacting environmental conditions, especially the availability of nutrients which are difficult to disentangle (Straub et al. 2019). Specific to kelp research, High SST is often associated with low nutrient conditions, which can contribute to low kelp growth or die-offs has been used as a proxy for nutrient conditions based on experimentally derived relationships(Wernberg et al. 2013, Wernberg et al. 2016) (e.g., Cavanaugh et al. 2011, Wernberg et al. 2016, Pfister et al. 2018, Smale 2020), while othersome studies suggest that elevated temperatures have independent physiological impacts (Muth et al. 2019, Hamilton et al. 2020).

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183 relationships can be more complex than the simple trophic cascade story as predator redundancy,

184 urchin behavior, and habitat complexity all impact the dynamics (Pearse 2006, Eurich et al.

185 2014, Ling et al. 2015, Burt et al. 2018, Kriegisch et al. 2019, Randell et al. 2022).

186   Kelp forests along the west coast of North America have experienced several major

187 perturbations in the last decade. The northeast Pacific Ocean (Baja California to Alaska)

188 experienced a massive and prolonged MHW, which developed in the southeast Gulf of Alaska in

189 the boreal winter of 2013/2014, began to impact the nearshore in 2014 (hence our use of 2014

190 throughout as the start date), and persisted until 2016 (Bond et al. 2015, Cheung et al. 2016,

191 Jacox et al. 2018, Scannell et al. 2020). This MHW had profound effects on both the offshore

192 and nearshore ecosystems (Cavole et al. 2016, Lonhart et al. 2019, Morgan et al. 2019, Sanford

193 et al. 2019, Cheung & Frölicher 2020), including substantial loss of kelp in some areas (Beas-

194 Luna et al. 2020). The timing and intensity of the 2014-2016 MHW impacts on the nearshore

195 environment varied with latitude, and subsequent MHWs followed in 2019, 2020, and 2021

196 (Bond et al. 2015, Scannell et al. 2020, Harvey et al. 2022).

197   Additionally, beginning in late 2013, sea star wasting syndrome (SSWS) impacted

198 populations of at least 20 species of sea stars from California to Alaska, including the Salish Sea

199 (Hewson et al. 2014, Montecino-Latorre et al. 2016, Hewson et al. 2018, Hamilton et al. 2021),

200 rapidly reducing many populations by 2014 and leading to local extinctions for some species. On

201 the outer coast of Washington, *Pycnopodia helianthoides* (hereafter *Pycnopodia)* declined by

202 75% prior to 2018 and had lost 99.6% of its population by 2020 (Hamilton et al. 2021). Some

203 areas, particularly in northern California, experienced large increases in purple urchins

204 *Strongylocentrotus purpuratus* (Rogers-Bennett & Catton 2019). As some of the hardest hit sea

205 stars (e.g., *Pycnopodia*) consume urchins, the die-off may have reduced top-down predation

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Comments / margin annotations:

Moved up [1]: including habitat provisioning and enhanced productivity of nearshore food webs (Duggins et al. 1989, Smith & Fox 2022b), support for highly diverse and complex food webs (Gabara et al. 2021), influence on sedimentation dynamics (Connell 2005), coastal protection from wave energy (Pinsky et al. 2013), and carbon sequestration and buffering against ocean acidification (Wilmers et al. 2012, Weigel & Pfister 2021, but see Gallagher et al. 2022). By fueling nearshore production and providing extensive adult and juvenile fish habitat, kelp forests also support diverse ecological communities (Graham 2004, Schiel & Foster 2015) and important commercial, recreational and subsistence fisheries for both fish and invertebrate species (Rogers-Bennett & Catton 2019). As many ecosystem-level perturbations are anticipated to intensify under scenarios of climate and ocean change (IPCC 2022), maintaining services from kelp forests requires regional mechanistic studies to understand dynamic community responses.

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231 pressure on sea urchins. However, urchins follow well-documented boom-bust reproductive

232 cycles (Pearse & Hines 1987, Uthicke et al. 2009, Ebert 2010), and the dramatic increase of

233 purple urchin populations in the early 2010s, which was temporally and spatially disjunct along

234 the northeastern Pacific, may have been due to a combination of a reduction in a minor predator

235 (sea stars, especially *Pycnopodia*; Hamilton et al. 2021), a change in foraging behavior due to a

236 SST-driven decrease in available drift kelp (Kriegisch et al. 2019), and a numeric increase due to

237 successful recruitment.

238   There were large regional differences in the response of kelp forests to these events. Kelp

239 cover in Oregon was either stable or increased during and following the 2014-2016 MHW

240 (Hamilton et al. 2020), while Northern California saw substantial and persistent loss of kelp

241 canopy and a shift to urchin barrens (Rogers-Bennett & Catton 2019, McPherson et al. 2021).

242 Responses in Central California and the Southern California Bight were more muted, as kelp

243 cover declined only slightly even though there were large increases in urchins in Central

244 California (Beas-Luna et al. 2020). In Baja California, both kelp and sea urchins decreased

245 sharply (Cavanaugh et al. 2019, Beas-Luna et al. 2020). The regionally distinctive responses of

246 kelp forest communities are likely due to both spatial variation in climate dynamics and

247 associated bottom-up environmental drivers (especially in relation to species' tolerances and

248 range margins), and to regional differences in food web structure, in particular, top-down

249 pressure (Reed et al. 2016, Beas-Luna et al. 2020). For example, ocean temperatures did not get

250 as warm in Oregon as in Northern California, and Hamilton et al. (2020) did not observe loss of

251 kelp canopy in Oregon. Additionally, the presence of sea otters *Enhydra lutria* in Central

252 California (Gregr et al. 2020) and the combination of sheepshead *Archosargus probatocephalus*

253 and spiny lobsters *Panulirus interruptus* in Southern California (Tegner & Levin 1983, Selden et

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266   al. 2017, Eisaguirre et al. 2020) may have provided enough top-down pressure to limit urchin

267   densities and affect urchin feeding behavior sufficiently to prevent a shift to urchin-dominated

268   habitats in these regions. However, in Northern California, where there was substantial warming

269   and little predator redundancy, the die-off of *Pycnopodia* may have released urchins from top-

270   down control, allowing their outbreak (Beas-Luna et al. 2020)

271   Kelp forests in California have been monitored regularly for decades, including the

272   periods before and after the recent marine heatwaves, sea star die-off, and localized changes in

273   kelp-urchin dynamics (Rogers-Bennett & Catton 2019, Beas-Luna et al. 2020). However, kelp

274   forests along the outer coast of Washington, USA (Fig. 1), have received only sporadic attention.

275   Past studies have documented recovery of kelp and declines in invertebrate abundance following

276   the restoration of sea otters, a keystone predator, to the Washington coast with otter populations

277   initially reintroduced in 1969-1979 and then increasing rapidly between the 1980s and 2010s

278   (Kvitek et al. 1989, Kvitek et al. 1998, Shelton et al. 2018). Less is known about interannual

279   dynamics, including how kelp forest sites in Washington have changed following recent major

280   perturbations. Moreover, little is known about the ecology of fish communities in these kelp

281   stands, despite the important role of kelp habitat in the life history of multiple commercially

282   important species in the region. For example, many Northeast Pacific rockfishes (genus

283   *Sebastes*) settle in kelp habitats as juveniles (Ammann 2004); some species, like black rockfish

284   *S. melanops*, remain in kelp throughout their lives, while others move to deeper areas as they

285   mature, promoting teleconnections between nearshore and offshore environments (Love et al.

286   2002). Washington kelp forests are occupied by juveniles of two highly valuable commercial

287   species, yellowtail rockfish *S. flavidus*, and canary rockfish *S. pinniger*, and by both juvenile and

288   adult black rockfish, which are among the most highly valued recreational fishes in the state. In

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291 other regions, habitat complexity is known to affect the recruitment of juvenile rockfishes

292 (Johnson 2006), and the vertical structure and canopy of kelps in particular can be especially

293 important (Holbrook et al. 1990, Carr 1991, Markel & Shurin 2020).

294   Here, we examine recent kelp community dynamics at five sites along the Olympic Coast

295 of Washington, USA, using diver surveys (2015-2021), kelp canopy cover information from

296 overflight surveys, and SST data. We assess spatiotemporal trends and community composition

297 patterns for the major species of macroalgae (giant kelp *Macrocystis pyrifera*, bull kelp

298 *Nereocystis luetkeana*, stalked kelp *Pterygophora californica,* and other stipitate kelps), sea

299 urchins, sea stars, and fishes, including juvenile rockfishes. Our main objectives were to

300 examine: (1) the prevalence, timing, and severity of MHWs and elevated SST in general along

301 the Washington Coast, (2) if and how kelp forest communities changed in the periods during and

302 following the 2014-2016 MHW and other warm SST anomalies, and SSWS; (3) whether

303 community composition of kelps, invertebrates, and fishes was structured more by spatial

304 differences or shared temporal variation; and (4) whether we can detect interactions involving

305 multiple guilds, which are hypothesized to structure kelp forest communities. Specifically we

306 investigate the relationship between kelp and sea urchin densities at multiple spatial scales, and

307 assess the link between the abundance of kelp and juvenile rockfishes. We predict fewer strong

308 impacts from the 2014-2016 MHW and SSWS on Washington kelp forests compared to those in

309 California because both *Macrosystis* and *Nereocystis* are in the central portion of their range in

310 Washington (Smale 2020) and absolute temperature extremes are less likely to exceed species

311 tolerances at these latitudes (Hamilton et al. 2020). Moreover, top-down pressure from sea otters

312 may help to prevent a shift to urchin barren habitats in the event of substantial, initial kelp loss.

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2. Materials & Methods

2.1 Study sites

We conducted dive surveys at five sites in late July or early August of 2015-2021 (but excluding 2020 due to COVID-19 restrictions) within or adjacent to Olympic Coast National Marine Sanctuary (OCNMS, designated in 1994) along the coast of Washington, USA (Fig. 1). These sites range from Destruction Island in the south to Neah Bay in the north. All sites were relatively protected from wave action, primarily subtidal rocky reefs (Fig. S1; Shelton et al. 2018), and supported the surface-canopy forming kelp species *Macrocystis pyrifera* (hereafter *Macrocystis*) and/or *Nereocystis luetkeana* (hereafter *Nereocystis*), as well as the mid-water (~ 1.0 m off the bottom) stipitate kelp *Pterygophora californica* (hereafter *Pterygophora*), and various understory kelps (Shelton et al. 2018). Previous work suggests that wave exposure was not important in explaining variability in kelp cover among these sites (Shelton et al. 2018), likely because these sites were initially selected to be somewhat protected from wave action to allow for dive surveys (Kvitek et al. 1989).

2.2 Survey design

Our survey provides estimates of species-level abundance for four guilds in kelp forest ecosystems: (1) major macrophytes (*Macrocystis, Nereocystis*, *Pterygophora,* and 'Other', the sum of other stipitate macrophytes), (2) major benthic invertebrates (e.g., urchins, sea stars), (3) fishes; and (4) juvenile rockfishes *Sebastes* spp., defined here as individuals less than 10 cm total length. Divers on SCUBA conducted *in situ* surveys to count targeted species at each site along

343   benthic belt transects (30 m by 2 m) following slightly modified procedures described in Malone

344   et al. (2022). At each of the five sites (Fig. 1), we sampled two locations, separated by >100 m,

345   and two depths within each location (5 and 10 m; in 2015 we only sampled at 5 m). Our goal was

346   to complete six replicate transects at each year-site-depth combination, but actual sampling effort

347   varied (Table S1).

348   For algae and invertebrates, we surveyed a 30-m long by 2-m wide swath centered on

349   each transect (60 m^2 total area), and for fishes we surveyed a 30-m long by 2-m wide by 2-m tall

350   volume (120 m^3 total volume). We recorded all invertebrates larger than 2.5 cm in size

351   (maximum dimension) and all kelp stipes greater than 30 cm in height, except for *Macrocystis*

352   where we counted stipes > 1.0 m. In some instances we found high densities of kelp or

353   invertebrates and subsampled these species. In each of three 10-m segments along a transect, we

354   recorded the distance at which we observed 30 individuals and then converted these data to a

355   total estimate of density for the 60 m^2 transect. We counted and estimated the size (total length to

356   nearest cm) of all fishes greater than 5 cm total length; the exception was rockfishes *Sebastes*

357   spp., for which we estimated sizes of all individuals. Rockfishes ≤10 cm were considered

358   juveniles. Divers also estimated horizontal visibility on each transect by determining the distance

359   at which the lead diver could distinguish their buddy's extended fingers. Transects with visibility

360   less than 2.0 m were excluded from the analyses including fishes, since species identification

361   becomes imprecise.

362   Because it is difficult to distinguish visually many rockfish species when they are small,

363   we categorized juvenile rockfishes into five groups established in the literature (Johansson et al

364   2018, Markel & Shurin 2020). Yellowtail and black (YTB) included both yellowtail *S. flavidus*

365   and black *S. melanops* rockfishes. The copper/quillback/brown (CQB) group included copper *S.*

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367   *caurinus*, quillback *S. maliger*, and brown *S. auriculatus* rockfishes. We were able to identify

368   canary *S. pinniger* and blue rockfish *S. mystinus* to species. Unidentified individuals were

369   categorized as juvenile rockfishes.

2.3 Sea surface temperature (SST)

371   To evaluate SST trends at our sites, we obtained daily mean sea surface temperature

372   (SST) data from the NOAA Optimum Interpolation (OI) SST V2.1 High Resolution Dataset

373   (Reynolds et al. 2007, Huang et al. 2021) for 1992-2021 for each of the five sites

374   (https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.highres.html). These data are available daily

375   in a 0.25-degree latitude x 0.25-degree longitude global grid. The Neah Bay and Tatoosh sites

376   fall within the same OISST grid cell, so their values are identical.

377   We quantify maximum monthly mean SST at our sites for each year because prior work

378   has identified this metric as a predictor of kelp cover dynamics in other areas along the West

379   Coast (Cavanaugh et al. 2019, Beas-Luna et al. 2020, Hamilton et al. 2020), and because

380   absolute temperature has been a better predictor than temperature anomalies for the 2014-2016

381   MHW (Cavanaugh et al. 2019, Hamilton et al. 2020). We also calculated the number of days

382   above 15°C for each site by year because there is some evidence that growth of both *Macrocystis*

383   and *Nereocystis* tends to decline above 15°C in conjunction with changes in nutrient availability

384   (Zimmerman & Kremer 1984, Camus & Buschmann 2017, Supratya et al. 2020). While

385   *Nereocystis* may be unable to produce sporophytes in 18°C water (Muth et al. 2019),

386   *Macrocystis* sporophyte production may be more tolerant to higher temperatures (Deysher &

387   Dean 1986a, Deysher & Dean 1986b).

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401   To provide a more formal analysis of MHW prevalence at our sites, we also calculated

402 MHW statistics following Hobday et al. (2016) and using the 'heatwaveR' package (Schlegel &

403 Smit 2018) in R 4.2.0 (R Core Team 2022). We evaluated the number of discrete events that met

404 MHW criteria (Hobday et al. 2016), as well as the length of these events, and the number of

405 individual days above the 90% percentile of SST by year and site.

2.4 Area of canopy kelps

407   We augmented our kelp stipe counts with data from aerial overflight surveys of kelp

408 surface-canopy cover to provide a broader temporal context of how kelp canopy species varied

409 prior to our initiating benthic surveys in 2015. Prior analyses of the aerial survey data have

410 revealed the influence of bottom-up environmental processes and top-down forcing through

411 trophic cascades on kelp abundance over the past 30 years (Pfister et al. 2018, Shelton et al.

412 2018). The Washington Department of Natural Resources (WDNR) conducts these surveys

413 annually in late July or early August during peak kelp canopy coverage. Data were available for

414 1989-2020, excluding 1993, with area data derived from the analysis of aerial photographs (Van

415 Wagenen 2015, WDNR 2017, Shelton et al. 2018). The survey distinguishes between

416 *Macrocystis* and *Nereocystis*. Canopy area is defined as the spatial extent of kelp blades, bulbs

417 and stipes floating on the water surface (Van Wagenen 2015).

2.5 Data analysis

419   To understand changes in kelp forest communities since 2015, we created regionally

420 aggregated time series (2015-2021) for each of the focal taxa within the four guilds of our

421 SCUBA surveys (kelps, invertebrates, fishes, juvenile rockfishes); in some cases, rare species

422 were combined into a larger taxon (Tables S2-S5, Fig. 2). We first averaged densities by Site and

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Deleted: We examined the WDNR kelp data to estimate the response of canopy cover to the SST conditions at our sites, especially anomalously warm SST. These data have revealed the influence of bottom-up environmental processes and top-down forcing through trophic cascades on kelp abundance over the past 30 years (Pfister et al. 2018, Shelton et al. 2018). Here we qualitatively examined the short-term response of canopy cover from area on the outer coast of Washington and the western Strait of Juan de Fuca to Neah Bay in the years during and following the MHW to better understand changes during our study period in the context of the longer-term kelp dynamics. ¶

437 Year and then took the yearly mean of Site averages to obtain a region-wide mean for each taxon

438 to identify any strong temporal trends at the scale of the full study region (Fig. 1). As we have

439 only six years of data, we limited our evaluation to qualitative analysis of trends in these data.

440   While aggregate time series are useful for understanding generalized trajectories of each

441 species, we expect different members of the kelp forest community to have distinct spatial and

442 temporal patterns in abundance due to differences in recruitment, other life-history

443 characteristics, and food-web interactions. Furthermore, identifying shared spatial and temporal

444 patterns of abundance can reveal factors important in structuring kelp forest communities. We

445 focused on understanding the patterns of variation in each of four guilds—kelp, benthic

446 invertebrates, large fishes, and juvenile rockfishes—and then compared factors explaining

447 variation in abundance among guilds. We applied permutation-based, multivariate analyses to

448 understand how each guild (see Tables S2-S5 for species included in the analyses and higher-

449 level taxon groupings of uncommon species) was structured with respect to the three

450 independent variables appropriate to our survey structure: Depth, Site, and Year, plus all two-

451 way interactions with transects as replicates. Each independent variable was coded as a factor.

452 We ordinated sites using canonical analysis of principal coordinates (CAP, implemented in R

453 using 'CAPdiscrim'; Anderson & Willis 2003) to visualize abundance variation. We used

454 permutation-based multivariate analysis of variance R 4.2.0 (PerMANOVA, implemented via

455 'adonis' in R; Anderson 2001, Okamoto et al. 2020, R Core Team 2022) to determine the

456 variance explained by each independent variable (Depth, Site, and Year, plus all two-way

457 interactions). Here we present the r^2 values with the terms treated as fixed effects, not variance

458 components from random effects. We applied a square-root transform to the data and used a

459 Bray-Curtis distance matrix with 999 permutations for both the CAP and PerMANOVA analyses

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460 (Anderson 2001). We summarized results for the ordinations at the Site x Year level for

461 presentation. We then compared results among the guilds to assess if the four guilds are

462 structured in a similar manner that would suggest shared, cross-guild drivers.

463   In addition to focusing on broad taxonomic guilds, we examine two interactions

464 involving multiple taxa that have been identified as particularly important components of kelp

465 forest communities. First, we investigated the relationship between sea urchins and kelp as this

466 interaction plays a disproportionate role in determining kelp forest community structure

467 including mediating between kelp-dominated and urchin barren states (Estes et al. 2004, Watson

468 & Estes 2011). Second, we assessed the role kelp forests play in providing vital juvenile

469 settlement habitat for supporting fish communities and fisheries by assessing the relationship

470 between juvenile rockfish density and kelp abundance (Holbrook et al. 1990, Carr 1991).

471   We assessed the relationship between total sea urchin density (summed across the three

472 observed species, purple urchins, green urchins *S. droebachiensis,* and red urchins

473 *Mesocentrotus franciscanus*) and kelp stipe density using correlation and regression analyses. As

474 sea urchins are major herbivores in this system, we expected negative relationships between

475 urchin and kelp abundance. For the analyses, we included three kelps species and one combined

476 taxon: each the two major surface-canopy kelps *Macrocystis* and *Nereocystis*, the mid-water

477 canopy kelp *Pterygophora*, and the sum of other stipitate species which are mostly understory

478 species (Table S2), at three scales: the region-scale (using the mean of the five sites in each

479 year), the site-scale (average densities within a site in each year), and the within-site scale

480 (average densities within a depth-zone and site in each year). Such comparisons at multiple

481 scales allow us to consider the range of relationships that can be generated at different spatial

482 scales and enable closer comparisons between our focal communities and those in other regions.

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Deleted: We used correlations and linear regression to examine the relationship between urchins and kelp at multiple spatial scales.

Deleted: We assessed the relationship between total sea urchin density (summed across the three observed species, *Strongylocentrotus purpuratus*, *S. droebachiensis,* and *Mesocentrotus franciscanus*) and kelp stipe density.

492 For Tatoosh Island, the only site with substantial numbers of and variability in urchins, we also

493 fit a random-effects-within-between model (REWB, Bell et al. 2019, Scharkow et al. 2020) to

494 account for differing relationships between urchin density and kelp density within and between

495 depths, areas, and years. Because transects were not uniquely identifiable across years, the model

496 focuses on depth x area x year:

$$y_{daty} = \mu + \beta_d + \beta_a + \beta_y + \gamma_1(\bar{x}_{d,a,y} - \bar{x}_{d,a}) + \gamma_2 x_{d,a} + \gamma_3(x_{d,a,t,y} - \bar{x}_{d,a,y}) + \varepsilon_{d,a,y,t,0}.$$

499 where y is kelp density, x is urchin density, and d is depth, a is area, y is year and t is transect.

500 Models for *Nereocystis* and *Pterygophora* were fit using the lme4 package in R (Bates et al.

501 2015). *Macrocystis* densities were too low at Tatoosh Island to conduct a parallel analysis of this

502 canopy species. The differenced terms ($\gamma_{d,a}$ and $\gamma_{d,a,y}$) represent random effects. We exclude the

503 $\gamma_4 \bar{x}_{d,a,y}$ term because $\bar{x}_{d,a,y}$ is used in the calculation of both within-effects terms and its

504 inclusion results in a rank deficient model.

505   Finally, we tested whether the density kelp stipes (from our SCUBA surveys) explained

506 the occurrence and abundance of juvenile rockfishes to better understand the downstream effects

507 of any changes in kelp abundance on rockfish recruitment. We fit a hurdle model (Maunder &

508 Punt 2004, Potts & Elith 2006) to our data because of the large number of observed zero juvenile

509 rockfish counts in the data set. Hurdle models separate the analysis into two models: a

510 presence/absence model and an abundance (here mean density) model, which uses only the

511 positive observations. Predictions from the two models are then combined. Because juvenile

512 rockfishes and kelp density were quantified on similarly located but not identical transects (see

513 Supplementary Materials), we averaged both the densities of kelps and juvenile rockfishes by

514   Site x Year x Depth x Location bins (hereafter, "strata"). For the occurrence portion of the hurdle

515   model, we fit the presence/absence data with a binomial distribution and logit-link (using the

516   'glmer' package R). We considered a range of covariates as independent predictors (see next

517   paragraph) and used weights to adjust for variation in the total volume sampled among strata (the

518   weight for a given stratum was the total volume of fish transects of each stratum divided by the

519   maximum value for all strata). For the abundance portion of the hurdle model, we fit

520   complementary models using $\log_e$ (mean density) of juvenile rockfish per stratum (positive

521   observations only) using an identity link and normal distribution ('lmer' package in R). As

522   above, we included transect volume per stratum as a weighting factor to account for differences

523   in sampling effort.

524   We compared four model structures involving multiple kelp covariates to test whether

525   rockfish density was related to kelp stipe abundance: (1) the sum of the all stipitate kelps, (2) the

526   sum of the surface-canopy kelps (*Macrocystis* and *Nereocystis*) with and without *Pterygophora*

527   and 'other' kelp (sum of the remaining stipitate kelps) included as separate variables, and (3)

528   *Macrocystis, Nereocystis, Pterygophora,* and other kelp as individual, independent variables,

529   including models with one to four taxa. In all models, Site and Year were included as random

530   factors to account for spatial and temporal variation in the intensity of recruitment unrelated to

531   kelp density. We evaluated each array of models and selected the best fit model using AICc

532   (Burnham & Anderson 1998).

533 # 3. Results

534 ## 3.1 Sea surface temperature

535   The warmest recent mean monthly SST at our sites (between 2000 and 2021) occurred in

536 2013 (Fig. 1a) with warm temperatures in both July and September (Figs. S2 & S3), before the

537 development of the MHW in the boreal winter of 2013-2014 (Bond et al 2014). In 2013 the mean

538 SST of the warmest month peaked at 15.1°C (± 1.32 s.d.), after which SST declined each year

539 through 2017 before spiking again in 2019 to 14.9°C (± 1.11 s.d.). The warm SST in 2019 aligns

540 with a 2019 MHW (Harvey et al. 2022). There were also warm periods in both 2020 and 2021,

541 but these periods were short enough that they did not register as high when averaged by month

542 (Fig. S3). SST was warmest at Destruction Island and coolest at Tatoosh/Neah Bay (Fig. 1a).

543 While 2013 and 2019 mark the highest recent SST, temperatures were actually higher in 1994

544 and 1997 (Fig. S2), approaching and exceeding 16°C in these El Nino years.

545   Tatoosh Island and Neah Bay, as well as Cape Alava, had very few days above 15°C

546 from 2014-2016 (two and six days respectively, Table S6). Cape Johnson had 6-15 days per year

547 above 15°C (29 total) from 2014-2016, while Destruction Island (the site farthest from the coast)

548 was the warmest with 101 days (27-39 days per year) above 15°C. Sites tended to be warmer in

549 2013 with 25 or more days above 15°C, except for Tatoosh Island and Neah Bay, which had only

550 five days above 15°C (Table S6).

551   The 2014-2016 years stand out for all sites in terms of increased MHW statistics with

552 more events and longer durations for all sites compared to most other years since 1992, with the

553 exception of 1994 and 1997 (Fig. S4, Table S6). However, many of the MHW events during the

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563 2014-2016 period (defined in terms of anomalies) occurred in early summer or autumn when

564 temperatures were lower (Fig. S32 & S4), and thus, these MHWs may have not exceeded the

565 kelp temperature thresholds locally. While 2013 had fewer MHW days and events, these

566 anomalously warm events occurred at the warmest time of year (Fig. S3 & S4) resulting in a

567 warmer overall year in terms of maximum monthly mean SST and the number of days that

568 exceeded 15°C (Table S6).

569 ## 3.2 Region-wide temporal trends

570 The lowest kelp surface-canopy cover in the past 20 years occurred in 2013 and 2014,

571 coincident with the anomalously warm SST in 2013 and 2014 (Fig. 1b). Surface-canopy area for

572 both *Macrocystis* and *Nereocystis* throughout the study area dropped to 337 ha in 2014, which

573 was 47% of the mean canopy area of the previous decade prior to high SST in 2013 (mean 2003-

574 2012: 720 ha ± 116 s.d.). Canopy cover along the Washington coast quickly recovered to earlier

575 levels (Fig. 1b, Fig. S5), averaging 645 ha (± 185 s.d.) for 2015-2020—or about 90% of that of

576 the previous decade (2003-2012) prior to the warming in 2013-2014. For both *Macrocystis* and

577 *Nereocystis*, canopy area increased from 2015 through 2020 with the annual species *Nereocystis*

578 showing greater magnitude of year-to-year variability (Figs. 1b, S5).

579 At the scale of our survey region, stipe density (from SCUBA surveys) for each of the

580 three major kelp species largely followed the broad-scale patterns derived from aerial imagery.

581 Stipe density for all three major kelp species increased two- to four-fold from 2015-2017 (Fig.

582 2a). *Macrocystis* and *Nereocystis* decreased in 2018, after which *Macrocystis* stipe density

583 remained at more than twice its 2015 level. *Nereocystis* stipe density dropped in 2021 to levels

584 similar to 2015 (Figs. 2a, S6). *Pterygophora* continued to nominally increase through 2019, but

18

585 densities were largely similar for 2017-2021. At our specific dive sites, *Macrocystis* stipe density

586 was high at Neah Bay and Cape Johnson, while *Nereocystis* was prevalent at Tatoosh Island,

587 Destruction Island, and Cape Alava (Fig. S6). There are some differences between the canopy

588 and stipe density data (Figs. S5 & S6), but these are likely scale issues as the aerial canopy

589 survey covers a broader area than our stipe counts.

590 Density of all three urchins increased in 2017 (Fig. 2b, S7), well after the short-lived drop

591 in kelp abundance and warm SST in 2013 and 2014. Purple urchins showed the largest increases

592 from 0.011 urchins m^{-2} in 2015 to 1.8 m^{-2} in 2019, a 164-fold increase across the five sites. In

593 2021 density dropped to 0.72 m^{-2}, which was still 65 times that of 2015. This trend was largely

594 driven by Tatoosh Island where the density of purple urchins increased from near zero to 4.4 m^{-2}

595 in the 5-m depth zone in 2021. In the 10-m depth zone, urchins increased to 9.5 m^{-2} in 2019

596 before dropping to 2.2 m^{-2} in 2021 (Fig. S7). Increases for red and green urchins were much

597 lower and densities of these two species declined again after 2017 (Fig. 2b, S7). As we searched

598 extensively for small, hidden urchins in all years of the study, it is unlikely that the low densities

599 from early in the study period were due to a failure to count large numbers of hidden urchins.

600 We saw little evidence for recovery of sea stars following the declines from SSWS

601 described by Hamilton et al. (2021). Blood stars (*Henricia* spp.) and leather stars (*Dermasterias*

602 *imbricata*) were relatively common in our surveys, but other species were not (Fig 2c). Leather

603 stars decreased by about fifty percent from 2015 to 2021, and we saw a total of eight

604 *Pycnopodia*, mesopredators that consume urchins (Moitoza & Phillips 1979, Duggins 1983),

605 over the entire six years of surveys: four in 2016, three in 2018, one in 2019, and none in 2021.

606 Blood stars were variable but remained more or less common, while the only stars to show any

607 evidence of recovery were brooding stars (*Leptasterias* spp.).

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618   We did not see strong temporal trends for most of the larger fishes (>10 cm) with the

619   exception of black rockfish, which increased in abundance through 2019 (Fig. 2d, Fig. S8). This

620   increase may have been the result of strong recruitment of YTB rockfishes to most sites in 2016

621   (Fig. 2e). While much less abundant, other rockfish species also showed annual variation in

622   juvenile density, but often in different years. Canary rockfish had minor peaks in 2016, 2018,

623   and 2021, while CQB rockfishes were more abundant in 2019 and 2021 (Fig. S9).

3.3 Multivariate analyses of kelp forest community guilds

625   The factors Site, Depth, and Year and all two-way interactions explained approximately a

626   third to half of the total variability in each of the four guilds (range r^2 = 0.32 - 0.59). The

627   composition of the kelp, invertebrate, and fish guilds was largely driven by among-site

628   differences as shown in the first three ordinations (CAP, Fig. 3a-f) and PerMANOVA (Fig. 4,

629   Tables S7-S10). For the full fish assemblage, Site explained the largest proportion of variance (r^2

630   =0.12) but this was substantially less than the explained variance by site for kelp (r^2 =0.26) or

631   invertebrates (r^2 = 0.41), which is evident in Figure 3, where there is considerably less overlap

632   among sites for kelp and invertebrates than fish. In contrast, juvenile rockfishes were driven by

633   year-to-year variation, and Site was not important, suggesting a strong shared temporal driver of

634   juvenile rockfishes among sites (Fig. 3g, Fig. 4).

635   Beyond the broad patterns in the amount of variance explained, it is valuable to

636   understand the specific causes of variation within guilds. For kelp, Sites ordinated based on the

637   prevalence of the mid-water canopy species *Pterygophora* (on the first axis) and also on

638   *Macrocystis* and *Nereocystis,* the two surface-canopy kelps, which loaded in opposite directions

639   on second axis (Fig. 3a,b). In the context of our data, this result makes sense as three sites are

640 *Nereocystis* dominated (Tatoosh Island, Destruction Island, and Cape Alava) while the others are

641 *Macrocystis* dominated (Neah Bay, Cape Johnson). The kelp guild also showed substantial

642 variance explained by the depth and depth-by-site interaction (r^2 = 0.10 and 0.12, respectively;

643 Fig. 4, Table S7), which would be expected as a function of light limitation for autotrophs

644 (Dayton et al. 1984). We found very little evidence of shared temporal effects for kelp (Year

645 effect, r^2 = 0.02), and only minor indication of site-specific year effects (Site x Year effect, r^2 =

646 0.05), suggesting limited effects of large scale environmental drivers on the kelp community

647 over the survey span (2015-2021), and that differences among sites in terms of which algae were

648 present, remained consistent.

649   For invertebrates virtually all of the explained variance was in the Site term (Fig. 4) with

650 sites showing clear separation in the ordination (Fig. 3c,d). Tatoosh Island clustered separately

651 from the other sites and was distinguished by the abundance of the three urchin species (axis 1,

652 Fig. 3c). The ordination also tracked increases in urchin densities at Destruction Island and Neah

653 Bay from 2018 as these years ordinated negatively on the first axis, which is consistent with the

654 significant Site x Year effect ($p < 0.05$, r^2 = 0.07) in the PerMANOVA (Table S8). Leather stars,

655 *Pisaster* spp., tunicates, and sea cucumbers were prevalent at Destruction Island and Cape Alava

656 (positive loading on axis 2), while brood stars were more abundant at Neah Bay and Cape

657 Johnson (negative loading on axis 2, notably the two lowest relief sites in Fig. S1). Depth or Site

658 x Depth explained very little of the variance for invertebrates (r^2 for both < 0.04) and only minor

659 Year (r^2 = 0.03) and Site x Year (r^2 = 0.07) effects.

660   Variability in the fish guild was the least well explained by Site, Year, and Depth (Fig.

661 3e,f, Fig. 4). While Site explained the greatest proportion of the variation (r^2 = 0.12) not in the

662 residual term, there was less separation among sites in the ordinations (Fig. 3e). Neah Bay and

663 Cape Johnson showed some separation from the other locations, whereas Tatoosh Island, Cape

664 Alava, and Destruction Island all overlapped. Similar to the invertebrates, a minimal amount of

665 variance was explained by Depth ($r^2 = 0.03$) or Site x Depth ($r^2 = 0.05$), and only slightly more

666 was explained by Year ($r^2 = 0.04$) or Site x Year ($r^2 = 0.06$) (Table S9).

667 For juvenile rockfishes, the ordination showed little clustering of sites (Fig. 3g,h), and

668 most of the explained variance was in the Year term in the PerMANOVA ($r^2 = 0.29$, Fig. 4,

669 Table S10) with a smaller contribution from the Site x Year term ($r^2 = 0.07$). Specifically, 2016

670 was a year of shared high recruitment of yellowtail and black (YTB) rockfish region-wide (Fig.

671 2e) and largely drives the ordination and associated loadings. This pattern shows that recruitment

672 was temporally variable and site difference played a reduced role in terms of the intensity or

673 assemblage of arriving recruits.

674 ## 3.4 Urchins and kelp

675 We did not see strong, negative correlations between urchins and kelp across years at the

676 coastwide scale that would suggest top-down pressure by urchins on kelp throughout our study

677 region. Neither *Macrocystis* nor *Nereocystis* stipe densities were correlated with urchin density

678 when averaged across the sites within a year (p > 0.05 for both, Fig. 5a), and unexpectedly we

679 found a positive relationship between *Pterygophora* stipe density and total urchin density (Fig.

680 5a, $r^2 = 0.78$, p = 0.02). Both *Pterygophora* and total urchin density increased through 2019 but

681 then dropped in 2021 (Fig. 2b,c).

682 Consideration of site- and year-specific variation revealed an apparent, negative

683 exponential relationship between *Macrocystis* stipe densities and urchins (Fig. 5b), but this

684 relationship was driven by one site (Tatoosh Island) where *Macrocystis* was largely absent and

685 urchins were abundant and by other sites where *Macrocystis* was present but urchin densities

686 were near zero (Figs. S6 & S7). Consequently, it is hard to come to firm conclusions regarding

687 this relationship. *Nereocystis* showed no obvious relationship to urchin density across sites and

688 years (Fig. 5c). Overall, *Pterygophora* was not correlated with urchin density, but at Tatoosh

689 Island urchins and *Pterygophora* were positively associated across years ($r^2 = 0.82$, p= 0.03, Fig.

690 5d) and thus Tatoosh Island is largely responsible for the urchin-kelp relationship at the region-

691 scale (Fig. 5a). Other kelps did not show correlations at the site scale across years (Fig. 5e).

692 However, the scale of the axes in Figures 5b and 5d obscures positive relationships between

693 urchin density and both *Macrocystis* and *Pterygophora* at Neah Bay (Fig. 5f), although the range

694 of urchin density is quite small.

695   At Tatoosh Island where urchin densities changed the most, the REWB models did not

696 find evidence for an impact of urchins on either *Nereocystis* or *Pterygophora* with the 95%

697 confidence limits coefficients for the fixed effects all overlapping zero with the exception of the

698 Year term (Tables S11 & S12, Fig. S10). However, at the transect level (ignoring other factors),

699 linear regression did find a negative relationship between urchin density and $\log_e$(*Nereocystis*

700 stipe density) ($r^2 = 0.16$, p = 0.002, Fig. 5g), suggesting that at this small scale, urchin herbivory

701 may have led to patchy reductions in *Nereocystis* density, although the effect appears

702 confounded with time. Divers did notice active grazing, and loss of stipitate kelps, along with the

703 remaining *Pterygophora* showing heavy signs of grazing in many areas on Tatoosh. However,

704 *Pterygophora* showed no relationship to urchins at the transect level (Fig. 5f), unlike at the site

705 level across years.

Deleted: Because urchin densities changed the most at Tatoosh Island, w

Deleted: e examined small-scale (transect-level) relationships between urchins and the kelps present there to determine whether increased urchin densities resulted in localized kelp loss.

3.5 Kelp density and rockfish recruitment

The probability of occurrence of juvenile rockfishes was positively correlated with the stipe density of surface-canopy kelps. The best-fit model included summed surface-canopy stipe density as a predictor (Fig. 6a, Table S13). The next best models (ΔAICc=1.39) included the sum of all kelp stipes and surface canopy plus *Pterygophora* (ΔAICc=1.74), which is qualitatively similar to the best-fit model in terms of the inclusion of most kelp. The two models including *Macrocystis* and *Nereocystis* as individual predictors (ΔAIC = 2.27) was just outside the cut off of ΔAIC = 2.0, supporting summed surface-canopy stipe density as a predictor, at least for the presence/absence model. The relationships were similar, with the summed surface-canopy or individual surface-canopy kelps all having coefficients of approximately 2.5 (Table S13 & S14). For the random effects (Table S14), Year had higher variance (5.33 ± 2.31) than did Site (3.25 ± 1.80) for the summed canopy model and similar amounts when *Macrocystis* and *Nereocystis* were included as individual predictors (5.31 ± 2.30 and 3.28 ± 1.81, respectively). For the abundance portion of the hurdle model, the model Year and Site had the lowest AICc value with the next best model 2.17 points higher (Table S15). Figure 6b shows the combined hurdle model including *Macrocystis* and *Nereocystis* for the occurrence model and Site and Year abundance model.

4. Discussion

Ocean temperature, wave exposure, nutrient and light availability, grazing, predator-prey dynamics, and a host of anthropogenic factors produce geographic variability and changes over time in the composition of kelp forest communities. In the northeastern Pacific Ocean, the 2014-

733 2016 marine heatwave (MHW) had strong effects on kelp forests and associated invertebrate and

734 fish species in some regions but not others (Arafeh-Dalmau et al. 2019, Cavanaugh et al. 2019,

735 Rogers-Bennett & Catton 2019, Beas-Luna et al. 2020, Hamilton et al. 2020, McPherson et al.

736 2021). We provide evidence from a relatively understudied region, along the Washington coast,

737 that spatial differences among sites were consistent across time for kelps, invertebrates, and

738 fishes, resulting in a relatively stable community structure during and following the 2014-2016

739 MHW. These findings stand in contrast to other areas, like Northern California that suffered

740 large, persistent losses in kelp canopy and increases in sea urchin densities (Rogers-Bennett &

741 Catton 2019, Beas-Luna et al. 2020). However, we also found similarities between patterns in

742 Washington and those observed elsewhere in the Northeast Pacific during this time period.

743 Specifically, the composition of the juvenile rockfish community in Washington kelp forests

744 showed clear year-to-year variation that was consistent with the idea that oceanographic forces

745 influence larval stages of many species (Schroeder et al. 2019, Field et al. 2021) and that these

746 offshore influences can be moderated by characteristics of nearshore habitats and kelp densities

747 in particular (Schmitt & Holbrook 1990, Carr 1991, Markel & Shurin 2020). Filling in the gap in

748 our knowledge along the Washington coast provides a more complete picture for kelp forest

749 communities in the eastern Pacific and California Current ecosystem in particular and suggests

750 paths forward for conservation and management of these important habitats and the valuable

751 fisheries species they contain.

752 In our study, the assemblage structure of kelps, invertebrates, and fishes exhibited

753 consistent differences among sites during the 2015-2021 period, and we did not see a shift to

754 urchin-dominated habitat. This pattern is initially surprising given the strong perturbation

755 introduced by the 2014-2016 MHW in other regions, which could have reverberated community-

756 wide and led to a cascade of recovery dynamics (Beas-Luna et al. 2020). However, while we did

757 observe an increase in MHW prevalence in the 2014-2016 period (Table S6), the 2014-2016

758 MHW was not the dominant SST feature in nearshore waters along the Washington coast.

759 Maximum monthly mean SST peaked in 2013 prior to the 2014-2016 MHW, and this peak was

760 coincident with a short-lived drop of about 50% canopy cover (compared to the previous decade)

761 in 2013-2014. Our study region is far from the range margins for *Macrocystis* and *Nereocystis*

762 (Smale 2020), so we might expect them to be well within their thermal thresholds at our sites

763 (Burrows et al. 2020) resulting in a somewhat ephemeral changes following warm water in 2013

764 and during the MHW. In fact maximum SST in Washington and Oregon were lower than in

765 Northern California (Hamilton et al. 2020), which may explain persistence of kelp-dominated

766 habitat in Washington compared to the 90% loss in Northern California. At our sites, maximum

767 monthly mean temperature reached 15.1°C in 2013 and 14.5°C in 2014—approximately 1.0 -

768 1.5°C lower than in Northern California but comparable to or slightly warmer than Oregon

769 (Hamilton et al. 2020). Growth for both species appears to decline slightly around 15°C

770 (Zimmerman & Kremer 1984, Camus & Buschmann 2017, Supratya et al. 2020), so maximum

771 SST in our study region only approached species tolerances in 2013. Moreover, while MHW

772 activity was higher during the 2014-2016 period, most of the anomalous events occurred during

773 the early summer or autumn, not during the summer peak in SST. Thus, although we might have

774 expected the communities associated with kelps–which are foundation species (Lamy et al.

775 2020)–to track such SST perturbations, they did not probably due to the relatively moderate and

776 short-term decrease in kelp cover at our sites.

777   We did not detect large-scale spatial differences in community structure in Washington

778 that would suggest that sea urchins drove kelp density trends through herbivory, supporting the

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Deleted: In factThe SST extremes in Washington (and Oregon; Hamilton et al. 2020) and Oregon were lower than in Northern California (Hamilton et al. 2020), which may explain persistence of kelp-dominated habitat in Washington compared to the 90% loss in Northern California. At our sites, maximum monthly temperature reached 15.1 °C in 2013 and 14.5 °C in 2014—approximately 1.0 -1.5 °C lower than in Northern California but comparable to or slightly warmer than Oregon (Hamilton et al. 2020). (Deysher & Dean 1986a, Deysher & Dean 1986b, Camus & Buschmann 2017)

MHW, SSWS, and Washington Kelp Forests

791 primary role of environmental drivers in determining kelp abundance along the Washington

792 coast in recent decades (Pfister et al. 2018). Urchins were rare at most of our sites, likely due in

793 part to otter predation (Shelton et al. 2018), and overall density was lower than that associated

794 with a shift to urchin-dominated habitat in Northern California. Prior to 2014, purple urchin

795 densities in Northern California were 0.0 - 1.7 urchins m^{-2}, spiking to 8.2 - 12.9 urchins m^{-2} in

796 2015 and 9.2 - 24.1 urchins m^{-2} by 2018 (Rogers-Bennett & Catton 2019). Across our sites in

797 Washington, mean urchin densities increased from 0.012 m^{-2} in 2015 to 1.8 m^{-2} at their

798 maximum in 2019, which is comparable to the period prior to the shift to urchin-dominated

799 habitat in Northern California. Moreover, the increase in urchin density on the Washington coast

800 was most evident in 2017 and peaked in 2019, well after the 2013-2014 nadir in kelp density

801 (during the 2003-2020 period). The availability of drift kelp appears to mediate a switch in

802 foraging behavior by urchins from passive detritivory to active herbivory (Pearse 2006,

803 Kriegisch et al. 2019). The latter behavior may promote a shift to urchin-dominated habitats.

804 Here when urchins were abundant, there may have been sufficient drift kelp (and potentially

805 threat of predation by otters), to lead urchins to remain largely passive feeders.

806   At Tatoosh Island there was a substantial increase in purple urchins with densities rising

807 to 5-10 purple urchins m^{-2} (Fig. S7). Otters have been less abundant at Tatoosh than at Olympic

808 Coast sites farther south (Shelton et al. 2018), which may have allowed this large increase in

809 urchin abundance. At Tatoosh, we did see a negative relationship between purple urchins and

810 *Nereocystis* stipe density at the transect-level that does suggest patchy, local top-down herbivory

811 impacts. However, this effect also appears potentially confounded by time with the REWB

812 model suggesting an effect of Year but providing no evidence for an impact of urchins on

813 *Nereocystis* stipe density (coefficients were negative but s.e. overlapped zero). The persistence of

27

818 kelp in the face of this large increase in urchins may have been related to habitat complexity,

819 which may also cause the transect-level variability (Randell et al. 2022). Diver observations at

820 Tatoosh suggest that shallower areas with ridges and more complex habitat contained fewer

821 urchins and more kelp (consistent with the depth distribution of both taxa), while other more

822 bowl-like and flatter areas contained large numbers of urchins and less *Nereocystis.* The steeper

823 and more complex habitat in the shallower areas of the Tatoosh site (Fig. S1) may have retained

824 drift kelp and allowed urchins to feed as passive detritivores, while less retained drift kelp in the

825 deeper areas may have caused a shift to active herbivory leading to the patchy but negative

826 correlation between urchin density and *Nereocystis* stipe density (Pearse 2006, Kriegisch et al.

827 2019, Randell et al. 2022). Interestingly, maximum monthly SST was lowest at Tatoosh Island

828 where increases in purple urchin density were strongest. Purple urchins do show latitudinal

829 variation in recruitment success related to SST in California, although previously observed

830 patterns would have predicted higher recruitment with warmer water in more northern latitudes

831 (Okamoto et al. 2020). In southern California, gonadal indices for purple urchins tend to peak in

832 October and November following summer feeding, so warm waters in the fall might impact

833 gamete production (Basch & Tegner 2007). However, temperatures in Washington did not

834 approach 17°C where gamete storage appears to be reduced (Basch & Tegner 2007).

835   We did not see shared temporal variation in the invertebrate assemblages (i.e., the

836 multivariate results) in conjunction with the die-off of sea stars–important predators within kelp

837 forests–due to SSWS (Burt et al. 2018). Invertebrate densities have been low at these sites since

838 recolonization of the area by sea otters, and otter predation likely explains the low density

839 (Shelton et al. 2018) and lack of temporal variation. Additionally, with the exception of blood

840 and leather stars, sea stars were uncommon, so they may have exhibited little top-down pressure.

850 We also lack recent pre-SSWS data for these sites. The sea star die-off began in 2013 in

851 Southern California, with the first declines evident on the Washington coast and Puget Sound in

852 2014 (Montecino-Latorre et al. 2016, Hamilton et al. 2021). Species like *Pycnopodia* did not

853 fully crash until late 2017 (declined to 75% occurrence as defined by Hamilton et al. 2021).

854 Thus, our surveys from 2015 and 2016 provide some information during the decline, but sea star

855 densities were already low at this point. We also did not detect signs of sea star recovery from

856 SSWS after 2017. For example, *Pycnopodia* had been common at these sites in the late 1980s,

857 reaching densities of 0.22-0.28 m^{-2} (Kvitek et al. 1988), but we saw only eight *Pycnopodia* over

858 all surveys from 2015-2021, declining from four in 2016 to zero in 2021. The lack of any

859 recovery of *Pycnopodia* and other sea star populations (as well as many of the other

860 invertebrates) may be due to Allee effects leading to failed reproduction. However, especially for

861 *Pycnopodia,* disease persistence may also be preventing the recovery of sea star populations

862 (Hamilton et al. 2021).

863   In nearby Puget Sound, where *Nereocystis* is the sole canopy forming kelp, the effects of

864 the MHW on kelp are somewhat hard to assess. Waters from the 2014-2016 MHW did penetrate

865 Puget Sound leading to a 2.3°C increase in water temperatures (Khangaonkar et al. 2021).

866 However, in the eastern Strait of St. Juan de Fuca, *Nereocystis* declined from 2007 onwards and

867 did not show obvious MHW impacts, such as an abrupt change in canopy cover (Pfister et al.

868 2018). In South Puget Sound there have been long-term declines (Berry et al. 2021), but

869 *Nereocystis* cover was lower in 2017 and 2018 than in 2013 (Berry et al. 2019). Purple and green

870 urchins to increase in various basins within Puget Sound, potentially due to a lack of top-down

871 control by predators as the predatory sea stars *Pisaster brevispinnus* and *Pycnopodia* both began

872 to decline in 2014.(Montecino-Latorre et al. 2016). *Pycnopodia* was highly abundant in Puget

29

Deleted: The sea star die-off began in 2013 before our data collection commenced (Montecino-Latorre et al. 2016, Hamilton et al. 2021), but off the Washington coast populations of species like *Pycnopodia* did not fully crash until late 2017 (declined to 75% occurrence as defined by Hamilton et al. 2021).

Deleted: With the exception of blood and leather stars, sea stars were uncommon; in fact, we saw only eight *Pycnopodia* over all surveys from 2015-2021 declining from four in 2016 to zero in 2021. *Pynopodia* had been common at these sites in the late 1980's reaching densities of 0.22-0.28 m^{-2} (Kvitek et al. 1988), although recolonization of the Olympic Coast by sea otters had large impacts on the benthic environment (Shelton et al. 2018).

887 Sound and the Salish Sea in general prior to SSWS (Montecino-Latorre et al. 2016), and may be

888 the only major urchin predator in the area (Duggins 1983, Schultz et al. 2016); otters are not

889 present as they are on the coast (Gregr et al. 2020).

890 The lack of strong temporal variation in the assemblage structure of the analyzed fish

891 community corresponds well with the long life spans of many of the species and the relatively

892 moderate, and short-term, impact of ocean warming on kelps in Washington. It does stand in

893 contrast to other regions, such as Baja California, where persistent and pervasive loss of

894 *Macrocystis* and exceptionally warm SST led to the disappearance of as many as half of the kelp-

895 associated fish and invertebrate species and an increase in the abundance of warmer water

896 species (Arafeh-Dalmau et al. 2019). While the full fish community at our study sites in

897 Washington was relatively stable temporally, we found that most of the variation in the

898 assemblage structure of juvenile rockfishes was temporal. Interestingly, the 2016 pulse in our

899 SCUBA surveys coincided with high abundance of winter-spawned pelagic rockfish juveniles

900 observed by Field et al. (2021) in the northernmost portion of their survey in 2016 (Figs. 4 & 8 in

901 Field et al. 2021) indicating the importance of large-scale oceanic processes, especially source

902 water (Schroeder et al. 2019). Additionally, the abundance of larger (> 10 cm) black rockfish

903 increased in from 2016-2019 following high recruitment of YTB rockfishes in 2016. Von

904 Bertalanffy growth curves (Wallace et al. 1999) indicate age-1 males and females would be 24

905 cm and 18.4 cm, respectively (thus larger than our 10 cm cut off), suggesting that our SCUBA

906 surveys may act as a leading indicator of changes in population size for this recreationally and

907 commercially important species, although a longer time series is certainly necessary to be more

908 confident in this conclusion.

Deleted: For the other invertebrates, which have been characterized by low densities since recolonization of the area by sea otters (Shelton et al. 2018), otter predation likely explains the low density and lack of temporal variation, although Allee effects may also play a part. ¶

Moved up [2]: invertebrates, which have been characterized by low densities since recolonization of the area by sea otters (Shelton et al. 2018), otter predation likely explains the low density and lack of temporal variation, although Allee effects may also play a part.

919   While interannual variability explained most of the changes in the species composition of

920   juvenile rockfishes associated with Washington kelp forests, the occurrence of juvenile rockfish,

921   regardless of species, was positively associated with kelp densities. In our analyses (Fig. 6,

922   Tables S13-15), juvenile rockfish presence exhibited a positive correlation with the abundance of

923   canopy kelps (no matter which combination of kelps we considered), reinforcing the role of kelp

924   forests as critical or essential fish habitat (NMFS 2014, PFMC 2020) for these commercially and

925   recreationally valuable species. In other regions, there are strong relationships between juvenile

926   rockfish and aquatic vegetation as well (Holbrook et al. 1990, Carr 1991, Markel & Shurin

927   2020). The vertical structure and canopy of kelps can be especially important for recruitment of

928   larvae into nearshore areas, where it serves as shelter from predators and provides ample

929   opportunities for foraging for prey species during a critical life stage (Carr 1991, Andrews &

930   Anderson 2004).

931   Overall, this study adds insights from a relatively understudied region to a growing body

932   of information about kelp forest communities in the Northeastern Pacific. We suggest that in

933   Washington the combination of lower thermal stress, lower magnitude kelp canopy declines, and

934   lower total urchin densities may have precluded a transition to a urchin barrens as in Northern

935   California. Trophic dynamics involving the almost complete extirpation of sea stars due to

936   SSWS may have been offset by redundancy of other important consumers, such as sea otters

937   (Shelton et al. 2018), and affected the patterns we observed relative to those seen in other regions

938   (Eurich et al. 2014, Beas-Luna et al. 2020, Gregr et al. 2020). Consequently, our analyses point

939   toward the importance of spatial variation in structuring the responses of kelp forest communities

940   to disturbance, across a range of spatial scales. From a habitat conservation perspective, this

941   insight leads to consideration of spatial portfolio effects (Schindler et al. 2015, Thorson et al.

31

942   2018) for kelp forests, in which different locations are characterized by a diversity of community

943   types, each of which can afford resilience to different types of stressors (McNaughton 1977,

944   Carpenter et al. 2009). This finding is consistent with recent work suggesting that kelps

945   themselves benefit from spatial portfolio diversification in the face of wave exposure-induced

946   disturbance-recovery dynamics (Walter et al. 2022). From a fisheries management perspective,

947   protection of a spatial portfolio of kelp forest locations may ensure the preservation of essential

948   fish habitat for critical life stages of managed species (Castorani et al. 2015). For instance,

949   increasing the probability that kelp densities remain high at multiple locations may enhance the

950   probability of juvenile rockfishes joining these nearshore communities in years when offshore

951   oceanographic conditions are favorable for larvae. In order to maintain sustainable fisheries,

952   then, what is essential is not to pick and choose a small subset of kelp forests for protection, but

953   rather to protect a diversity of kelp forests, each of which harbors habitats that can exhibit unique

954   responses to ecological surprises yet to come.

955

Acknowledgements

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Figures
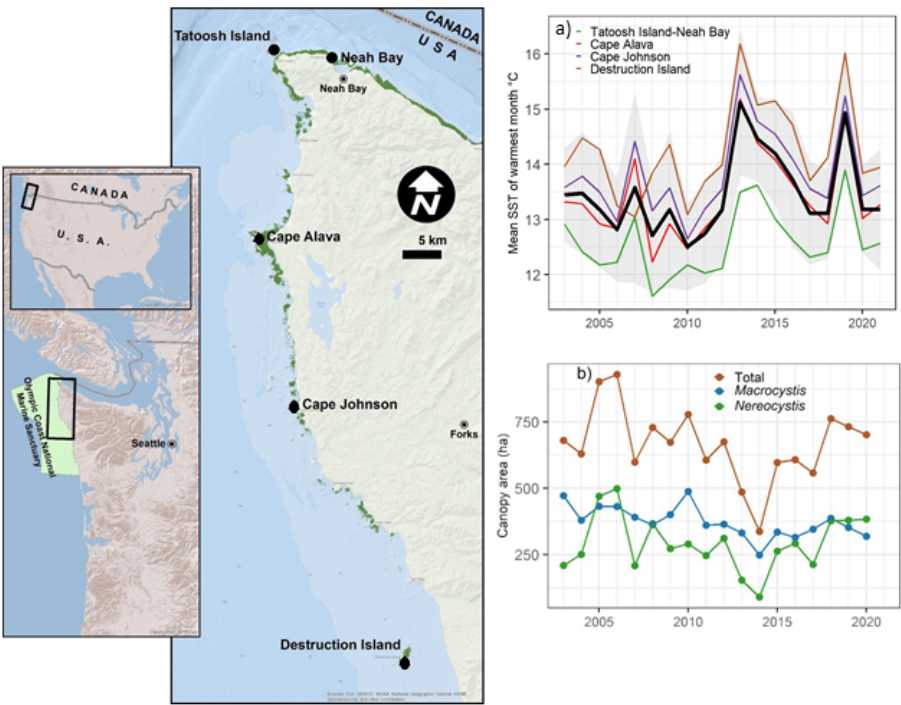
Figure 1. Location of the five study sites with distribution of floating kelp shown in green. Plots on right (2003-2021) are: a) Mean SST of the warmest month averaged across the five sites (black line), and b) total area of kelp canopies floating on the surface within the Olympic Coast National Marine Sanctuary (the outer coast of Washington and the western Strait to Neah Bay). Black line in (a) is the mean across sites; colored lines are mean SST of the warmest month by site; gray envelope is +/- 1.0 s.d.
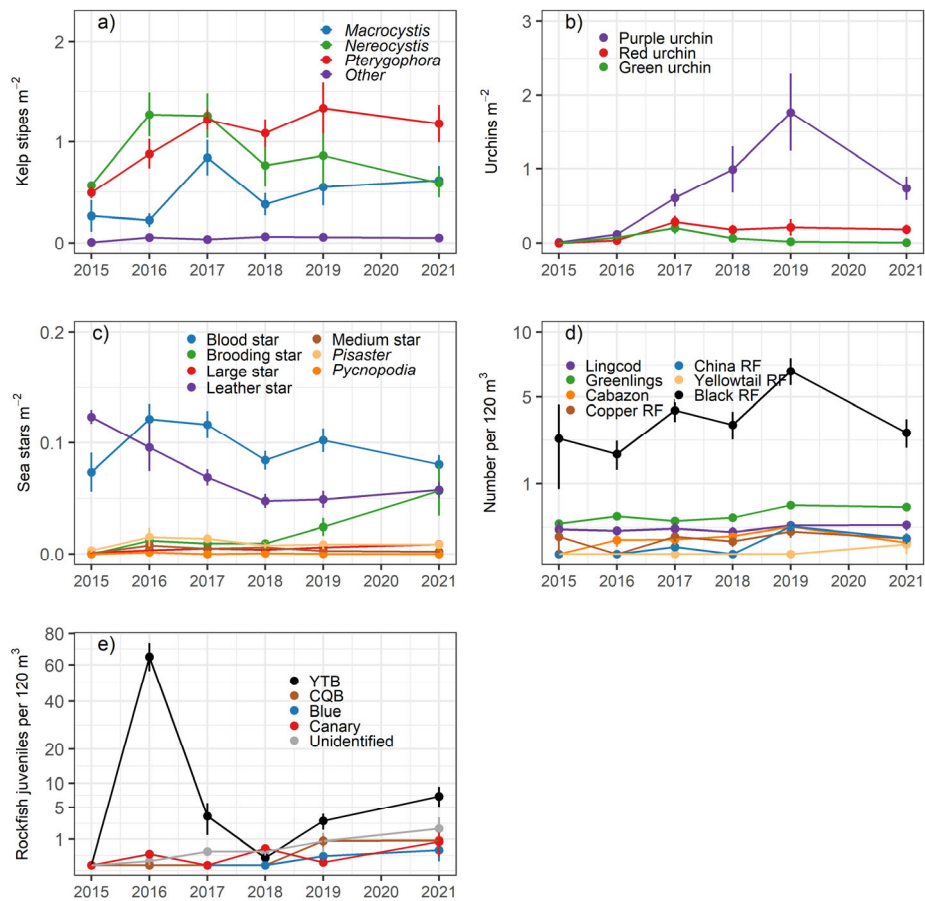
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Figure 2. Time series of the focal groups coastwide from dive surveys from 2015-2021. a) density of kelp
stipes, b) urchin density, c) sea star density, d) fish abundance, and e) abundance of juvenile rockfishes.
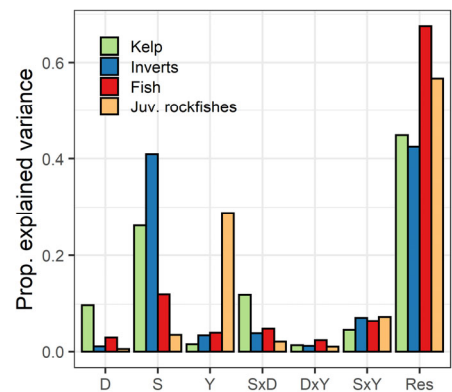For sea stars see Table S4 for species included in the medium and large sea star categories.

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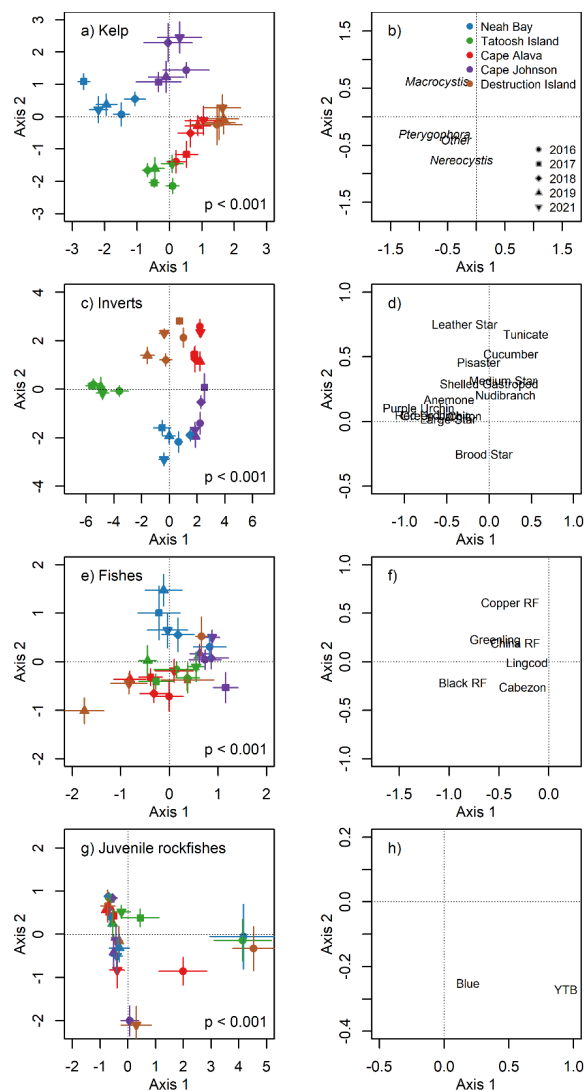
Figure 3. Results of canonical analysis of principal coordinates (CAP) of the assemblage structure of four guilds: kelps, invertebrates, fishes, and juvenile rockfishes. Left panes (a,c,e,g) show the ordination of Site x Year averages and p-values for the CAP analysis. Right panes (b,d,f,h) show the loadings for each taxon. RF = rockfish, YTB = yellowtail and black rockfishes.
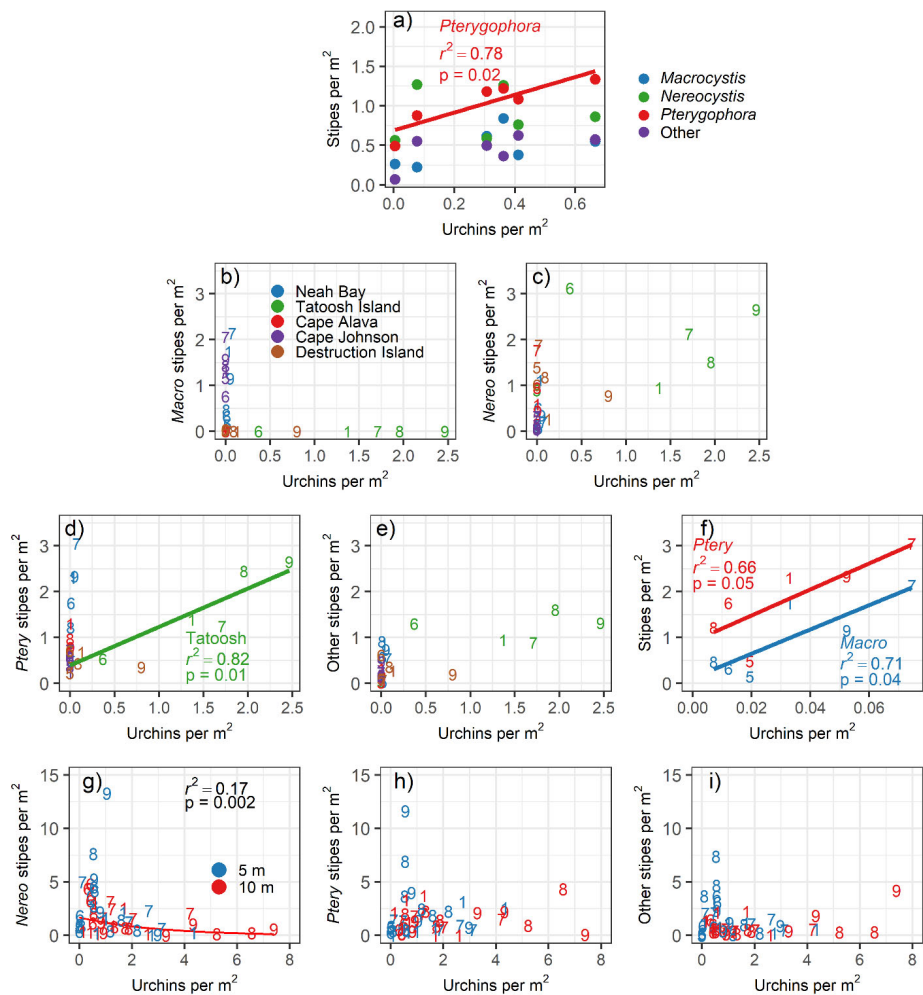
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Figure 4. Explained variation from permutation-based multivariate analysis of variance (PerMANOVA)
for four guilds: kelp, invertebrates, fish, and juvenile rockfishes. All terms are fixed effects and results are
the r^2 values. D = depth, S = site, Y = year, Res = Residual.

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Figure 5. Relationship between the density of kelp stipes and total urchin density at different spatial scales: a) coastwide across years; Site by Year means for b) *Macrocystis*, c) *Nereocystis,* d) *Pterygophora,*, e) other stipitate kelps, and f) for *Macrocystis* and *Pterygophora* at Neah Bay to show pattern obscured by the scale in other panes; and at the transect level at Tatoosh Island for g) *Nereocystis,* h) *Pterygophora*, and ii) other stipitate kelps. For panel f the regression was for $\log_e$(Nereo stipes) = Urchin density. In panels b-i, numbered points refer to the year of data collection: 5 = 2015; 6 = 2016; 7 =2017; 8 = 2018; 9 =2019; 1=2021.
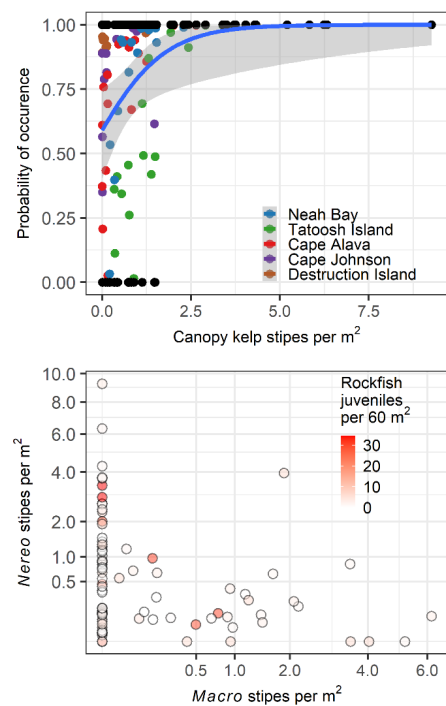
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Figure 6. Relationship between kelp density and the abundance of juvenile rockfishes from the hurdle model. (a) Probability of occurrence of juvenile rockfishes in relation to the total stipe density of the canopy kelps *Macrocystis and Nereocystis*. Blue line shows the result of the binomial presence/absence model. Black points are the actual observations (present =1, absent = 0). Colored points are predicted probability of occurrence. (b) Results of the combined presence/absence model and abundance model. Larger circles have a higher probability of occurrence. Data were summarized by Site x Depth x Location x Year strata prior to analysis.