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The dynamics of Kelp Forests in the Northeast Pacific Ocean and the relationship with

environmental drivers

Running head: long-term kelp forest dynamics

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ABSTRACT

1. The dynamics of foundation species in ecosystems are key to the fate of many species. Kelp forests are foundation species in temperate ocean ecosystems and contribute to carbon storage, macronutrient dynamics, primary production, and biodiversity of myriad associated species. Downward trends in their abundance globally have been of concern.

2. We analyzed 26 years of aerial censuses (1989-2015) of 2 canopy kelp species in Washington State (USA) waters. We compared these modern censuses with censuses in 1911 and 1912 to determine the persistence of kelp cover over the past century. Using Auto-regressive Integrated Moving Average (ARIMA) models, we compared kelp dynamics with likely environmental drivers, including local environmental variables and ocean indices for this region.

3. Kelp remains at historic levels in many areas, though some eastern populations in proximity to greater human populations are the exception to this pattern. Over the last 26 years, kelp abundance showed high spatial autocorrelation in western areas of Straits of Juan de Fuca, with more variable populations in the annual species and eastward toward Puget Sound. Both species covaried positively in their abundance throughout most of the study area, suggesting environmental factors rather than competition, drove their dynamics. The population dynamics of these kelp species showed that the abundance one year previous was an important predictor, and cyclic dynamics were not indicated using Auto-regressive Integrated Moving Average (ARIMA) models. Kelp abundance correlated inversely with the Pacific Decadal Oscillation and the Oceanic Nino Index, and positively with the North Pacific Gyre Oscillation, indicating that large-scale processes associated with colder seawater temperatures were associated with greater relative abundance of kelp.

4. *Synthesis*. Kelp beds in the northern California Current Large Marine Ecosystem have mostly remained persistent over the past century and over many km, but some areas may have decreased in abundance. The sensitivity of these populations to indices of ocean climate, our demonstration that a historic 93-year SST record (Race Rocks, Canada) showed a 0.72^{o}C increase, and the classification of some areas as high variability-low abundance, suggest that the viability of these foundational species remain a concern into the future.

INTRODUCTION

Foundational species provide habitat and food resources and alter the physical environment. It is imperative that we understand their dynamics and links to environmental variables. In coastal marine systems, many foundational species provide essential ecosystem services (Barbier *et al.*, 2011), yet are affected by the stressors that are associated with increasing human populations near coasts (Small and Nichols 2003, Lotze et al. 2006). Canopy kelp species are foundation species that provide an important natural feature in temperate oceans globally. Their primary productivity is unsurpassed (Mann 1973), and their tissues enhance productivity *in situ* and in adjacent ecosystems ((Dayton *et al.*, 1998) (Krumhansl & Scheibling, 2012) (Hansell, 2013). Kelp provide habitat and food for myriad invertebrates and fishes (Bodkin 1986, Duggins et al. 1989, Teagle *et al.*, 2017); their biogenic structure means that any changes in their abundance will have cascading effects (Sunday *et al.*, 2016). Their abundance is determined by sea surface temperature, salinity and nutrient provisioning, possibly generated by large-scale climate drivers (Wernberg et al. 2013, 2016). Local interactions that include herbivory (Graham, 2002)(Sala & Graham, 2002)(Vergés *et al.*, 2016) (Pfister & Betcher, in press), and microbial interactions (Michelou et al. 2013) are also important. Compilations of kelp populations globally

showed a diversity of trends in kelp species abundances, with some populations and species increasing, while others are decreasing (Steneck *et al.*, 2002) (Krumhansl et al. 2016). Understanding these foundation species requires an analysis of local versus regional factors on kelp dynamics.

A key challenge for predicting the fate of ocean primary producers is linking current and past dynamics to large-scale climate factors. Globally, we know that warming sea surface temperatures (SSTs) can be associated with changes to marine phototrophs, either free-living (Wernberg *et al.*, 2010, Dijkstra *et al.*, 2017) or symbiotic ((Baker, 2001)). Increased urban runoff, pollution, and excess nitrogen also alters the abundance of diverse types of coastal algae and plants (Antrim *et al.*, 1995)(Deegan *et al.*, 2012).

Among kelp species, abundance is positively related to colder SSTs and upwelling regimes where nitrate is supplied to surface waters (Dayton, 1999)(Edwards, 2004)(Pfister & Wang, 2005)(Parnell, 2010)(Cavanaugh *et al.*, 2011) (Schiel & Foster, 2015)). Because cold SSTs are often associated with increased nitrate, the separate effect of each is difficult to determine, although experimental evidence in southern California suggests the negative effects of warm SST can be offset with nitrate additions ((North & Zimmerman, 1984). Kelp growth may also benefit from increased carbon dioxide inputs to the surface ocean (Sunday *et al.*, 2016), though some stages of the kelp life cycle are sensitive to ocean acidification (Gaitán-Espitia *et al.*, 2014). In addition to large-scale climate drivers, local scale factors and their interaction with large-scale factors may be important. Changes to food web structure negatively affect kelp if they result in increased grazing pressure (Vergés *et al.*, 2016), as in the iconic example of sea urchin increases following sea otter extirpation (Estes & Palmisano, 1974). Local disturbance, including pollutants, also negatively affect kelp (Antrim *et al.*, 1995)(Schiel & Foster, 2015).

A recurrent theme in the study of kelp forest communities is the dynamic nature of abundance and thus the need for long-term data to interpret temporal pattern. In the northern California Current Large Marine Ecosystem (CCLME), there are 2 species of floating canopy forming kelp: the annual bull kelp, *Nereocysis luetkeana* (Mertens) Postels *et* Ruprecht, and the perennial giant kelp *Macrocystis pyrifera* (Linnaeus) C. Agardh. While we understand some of the factors important to *Macrocystis* in the southern CCLME, *Nereocystis* is absent south of Point Conception, and relatively little is known about either *Macrocystis* or *Nereocystis* in the northern region. *Macrocystis* in the southern California region shows a relationship with SST, with demonstrated positive responses to lower sea surface temperatures (SST) (Parnell, 2010) (Wernberg *et al.*, 2016). Cavanaugh *et al.* (2011) found that annual *Macrocystis* biomass was inversely related to SST and waves. While we recognize that low SST is correlated with high nutrient concentrations, warm SSTs caused by a power plant outfall was associated with the virtual disappearance of *Nereocystis* and replacement by *Macrocystis* over an 18 year period (Schiel *et al.*, 2004). However, the response of *Macrocystis* to a recent warming event in southern California was modest enough that investigators suggested this species is not a 'sentinel' species for warming effects (Reed *et al.*, 2016).

The identification of climate cycles such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO) provide motivation to determine whether these climate patterns are reflected in biological data. The PDO is a decadal or greater pattern of sea surface temperature variation in the north Pacific related to the strength of the Aleutian low-pressure cell (Mantua *et al.*, 1997)(Hare & Mantua, 2000). Sea surface temperatures are warmer and productivity is reduced throughout the California Current Large Marine Ecosystem (CCLME) during a positive PDO, while the opposite occurs during a negative phase of the PDO. The

NPGO index has roughly the opposite features, and is thought to be associated with sea level pressure changes in the region (Di Lorenzo *et al.*, 2008). Both the PDO and the NPGO are often characterized as long-term events lasting 10-20 years. Further, variability in upwelling and the association of episodic events such as ENSO, where upwelling and nutrient supply are dampened (quantified with the Oceanic Niño Index (ONI)), can negatively affect kelp abundance (Dayton, 1999). The cyclic and episodic nature of these climate events provide further value for querying biological data with the greatest length possible.

Here, we use a 26 year span of annual aerial survey data from 1989-2015 for the two co-occurring canopy kelp species *Macrocystis* and *Nereocystis* in coastal Washington state to test whether these species show a trend in abundance through time, linkages to climate indicators, and spatial coherence in response over the 455 km of coastline that we censused. We tested whether both species responded similarly or distinctly to environmental variables in light of their divergent life histories. Specifically, we tested 1) whether the 70-116 year time span of environmental variables show pattern, 2) whether there were trends in kelp abundance and correlates with environmental variables, 3) whether there is coherence in outer coast populations with populations in the western versus eastern portions of the Strait of Juan de Fuca, and 4) whether the 66 areas differ in how correlated their abundance is through time.

We complement this 26 year pattern of abundance with a census of these same kelp populations in 1911 and 1912 (Cameron & United States., 1915). Comparison of 1989 to 2015 to these historic 1911-1912 surveys suggested local extirpation of kelp beds in some areas, with high variability in the abundance of some kelp beds in particular locales.

STUDY SYSTEM & METHODS

Nereocystis luetkeana occurs from the Aleutian Islands to Point Conception, CA, while *Macrocystis pyrifera* extends further south to Baja California, Mexico (Druehl, 1970). *Nereocystis* is primarily an annual, with a long stipe and a terminal bulb with blades that proliferate on the surface. Individual *Macrocystis* can live for 2-3 years and have similar-sized alternating fronds along 1 or more stipes. Both species occur singly and together, with *Macrocystis* often slightly closer to shore than *Nereocystis*. Since 1989, the aerial cover of both kelp species (*Macrocystis* and *Nereocystis)* has been estimated from low-flying aircraft every August when canopy cover is near a maximum, allowing both the canopy area and estimates of discrete kelp beds to be measured. The Washington Department of Natural Resources has led these efforts and data are archived (http://www.dnr.wa.gov/programs-and-services/aquatics/aquatic-science/kelp-monitoring).

Aerial photography and satellite imaging are established tools for aquatic and terrestrial vegetation research, due to their ability to distinguish photosynthetic pigments spectrally and to census large areas efficiently (Xie et al., 2008). Color infrared (CIR) photography specifically was used in this study due to the strong contrast between kelp reflectance and seawater in the near infrared spectrum (Jensen et al. 1980, Foreman 1984). Water absorbs infrared flux, while *Macrocystis* reflects 60-70% of the flux, leading to high contrast between kelp and seawater (Jensen et al. 1980). Indeed CIR photography was used to ground truth satellite data analyses in California kelp forests (Cavanaugh et al. 2010). In regions where imaging windows are limited to brief periods when low tides, calm seas and low cloud cover coincide, aircraft can be deployed rapidly during ideal conditions whereas satellite imagery collection times cannot be adjusted (Jensen et al. 1980, Stekoll et al. 2006). Figure S1 shows an example of the visibility of the kelp

bed via natural color and CIR imagery. In the few instances where kelp beds have been harvested, the biomass estimates are proportional to aerial estimates (Foreman 1984, Tegner et al. 1996), although the relationship was less variable when CIR photography was used. No biomass estimates are used in this study to avoid destructive sampling of the kelp forest and because other studies suggest that biomass estimates at the spatial scale of this study would be prohibitively expensive and low in precision (Foreman 1975, Stekoll et al. 2006).

To further optimize visualizing kelp, flights were made at late season low tide (between MLLW and +0.9 m) when the kelp canopy was maximally concentrated. The distinct morphological traits of each species make them distinguishable from the air. Additional low altitude aerial flights (600 m altitude) were conducted to photograph and quantify species composition within individual beds. Through 2008, color-infrared film was used; following that, digital images were used. In 2008, both methods were used to standardize the methodology. Aircraft altitude was maintained at approximately 2300 m with a photographic scale of 1:30,000 and a base mapping scale of 1:12,000 over the 177 km from Port Townsend to Destruction Island, WA. The digital files were high-resolution 12-bit files of 15.4 MB each. Throughout the 26-year censusing period, biases were minimized because: 1. image collection and processing techniques were unchanged, including quantification by the same individual, and 2. imagery was collected when environmental conditions maximized kelp visibility, including low, tide, minimal cloud/fog cover, surface winds less than 10 knots, and sea swell less than 1.5 m. Tides and currents can affect estimated bed size from aerial photography (Britton Simmons et al. 2008), so the timing of the photos during low, slack tides reduced this effect. Thus, although aerial imaging with CIR undoubtedly had some local error, the resulting spatial and temporal extent of the data allowed for larger scale analysis.

To test whether canopy kelp population dynamics showed pattern through time, we used an Auto Regressive Integrated Moving Average (ARIMA) modelling framework (Jassby & Powell, 1990) (Legendre & Legendre, 2012)(Ives *et al.*, 2010), to test whether the previous abundance values determined the abundance at time *t* (auto-regressive), suggesting autocorrelation. We further tested whether variability in the data at each time t was caused by species interactions, the environment, or measurement error (moving average). Thus, the auto-regressive term can reveal longer cycles due to density dependence, while the moving average term could suggest another biological or physical correlate of abundance (e.g. a predator or weather). Each data point can also be a difference of two observations to reduce variance (termed 'differencing' or an 'integrated' form of the data); we thus analyzed whether differences in census data through time revealed statistical pattern in abundance. The advantage of ARIMA models for these kelp populations is there are few parameters needed and it provides a robust method for inferring internal dynamics and possible species interactions (Ives *et al.*, 2010) (Ziebarth *et al.*, 2010). Comparing ARIMA models for environmental data to the kelp data allowed us to see if there was similar underlying pattern between environmental variables and the abundance of kelp. Although specific interactions cannot be inferred from ARIMA, significant AR and MA terms give an indication that biotic interactions may be important. To aid in ARIMA model selection, we first tested the degree of autocorrelation through time in each species abundance, followed by a partial autocorrelation analysis to assess the autoregressive component of an ARIMA model and any possible MA term (Crawley, 2007)(Ives *et al.*, 2010). We then used this estimate as a starting point to systematically test a number of ARIMA models with the form (p, d, q), where p is the AR term, d is the differencing, and q is the MA term. All models were compared with an AIC. All analyses were done with R 3.3.0, and modules 'Forecast' for the ARIMA modeling.

To determine whether there are environmental or climate drivers that correlate with kelp abundance, we also examined the patterns in these variables. We focused our analyses on measures directly related to SST and nutrient supply, including the PDO, the NPGO, and the Upwelling Index (UI). We used annual means based on monthly averages. The UI is a metric based on wind shear values, and we used values for 48°N (https://www.pfeg.noaa.gov/). Although long-term nutrient data are unavailable in many sites in the CCLME, data from Tatoosh Island show a positive relationship between UI (characterized by colder SST) and nitrate concentrations ((Pfister *et al.*, 2007), a relationship characteristic of upwelling shorelines (Capone & Hutchins, 2013). Remotely measured SST was sparse in the coastal areas of Washington state until the establishment of the Neah Bay Buoy (#46087) in 2004. Race Rocks, Canada, in the eastern Strait of Juan de Fuca (48.299 N, 123.531 W, www.pac.dfo-mpo.gc.ca, Figure 1), has a 93-year record initiated in 1921, and mean monthly sea surface temperature at Race Rocks correlates strongly with the Neah Bay Buoy between 2004-2015 when the 2 buoys have simultaneously recording ($r=0.903$, $df=118$, $p<0.001$). We thus used Race Rocks sea surface temperature data to look for temperature correlates with kelp forest abundance. The PDO and NPGO extend much further back in time compared with the kelp species data; the PDO is from 1900 and the NPGO from 1950. The UI began in 1946. The Race Rocks SST record has a hiatus for months in 1940 and 1941, requiring us to use data after 1941 for analysis of cycles. We used ARIMA and spectral analyses on monthly means to reveal any inherent cycles. By comparing the dynamics of environmental data with the dynamics of kelp forests, we tested whether dynamic components of environmental data correlate to patterns in kelp abundance. We performed all the above analyses on the conspicuous sporophyte stage of both species, though we recognize that both species have a microscopic gametophyte stage for which little is known.

The documentation that sea surface temperature has increased at other coastal locales (Wernberg *et al.*, 2011) (Lima & Wethey, 2012)(Tanaka *et al.*, 2012) prompted us to test whether the extensive Race Rocks record showed a long-term temperature increase. To decompose the seasonal pattern from the annual data, we used the post-1942 data portion of the time series that had no missing data to extract the annual means after we accounted for a seasonal cycle. We further used a linear regression on annual means for 93 years to test for a significant slope through time. We used "STL" (Seasonal and Trend Analysis using Loess in the 'stats' module in R).

Spatial Patterns of Abundance

We analyzed the kelp forest data at two spatial scales. We first grouped the kelp forests on the outer coast and Strait of Juan de Fuca into 3 broad spatial areas and asked whether abundance was correlated across these 3 areas (Figure 1). The populations on the outer coastal areas of Washington State that are exposed to open ocean conditions are 'outer coast' and extend from the northeast corner of the state at Cape Flattery to the southern extent at Destruction Island. We excluded the southern outer coast from Destruction Island south to the Columbia River from further analysis because floating kelp was never recorded along these shorelines in the historical or modern dataset. Populations on the western end of the Strait of Juan de Fuca extended from the westernmost Cape Flattery to Crescent Bay in the east, an area over which open ocean influence diminishes. The third area continued eastward from Crescent Bay to Port Townsend, at the entrance of Admiralty Inlet and the more protected areas of Puget Sound. Shoreline length within the 3 areas ranged from 113 to 203 km.

The second scale of spatial analysis further divided the kelp forest into 66 spatial regions that were bounded by geomorphological features, such as headlands, and encompassing on average 8 km of shoreline per unit (Figure 1). Using these 66 areas and all t years of data, we estimated 1-year autocorrelations in abundance for each species in each of these areas from 1989-2015; thus, a correlation of t versus $t+1$ for all t, excepting the missing 1993 data. We interpreted a high autocorrelation estimate to indicate relatively high predictability in abundance through time, whereas a low autocorrelation indicated that abundance fluctuated independently in year t+1 compared to year t.

A Century-scale Comparison

The potential to harvest kelp for fertilizer and potash resulted in an ambitious sampling of kelp populations from Alaska south to California in 1911-1912 (Cameron 1915). Washington State coastal areas were censused in 1911 and 1912 from a fifty-foot vessel with a 40 hp motor. The areal cover of both canopy kelp species combined was drawn on bathymetric nautical maps that were digitized to estimate the extent in area of kelp beds. The mapping, the depth contours that the kelp beds follow, and the descriptions in accompanying reports seem especially carefully done by G. B. Rigg (then a Professor of Botany at the University of Washington) for the regions of Puget Sound and the Strait of Juan de Fuca, with extensive documented survey effort (Rigg 1912, Cameron 1915). Although the (Cameron & United States., 1915) study recognized the two species, they were combined for areal analyses and we thus combined both canopy species in the modern estimates in our comparisons.

We compared these 1911 and 1912 estimates of area in the Strait of Juan de Fuca to all aerial estimates from 1989-2015. We also noted any populations that existed in 1911-1912 that are no

longer present. We recognize that the censuses in 1911-1912 could be incomplete, resulting in a bias such that kelp beds might have been present, but were not recorded by Rigg if conditions prevented their modest boat operations from maneuvering in an area. We thus did not assume kelp present in 1989-2015 but absent in 1911-1912 were new beds. If, however, an area was identified as containing a kelp bed in 1911-1912, we were able to test whether a kelp bed was still present and compare it with the range of modern areas. If Rigg and colleagues identified a bed in 1911-1912 that had no record of occupancy since 1989, we concluded local extirpation. On the outer coast of Washington in the Cape Alava region, W. C. Crandall, not G.B. Rigg continued the survey, and these seemed less reliable, indicating kelp beds extending into depths that could be unrealistic (Figure S5). There was also less field survey documentation and effort compared with areas in the Strait, perhaps reflecting the challenging nature of surveying these outer coast areas. We have thus excluded a quantitative analysis of these outer coast areas from our analysis. Because Rigg and colleagues were estimating area from a boat, their definition of area might have included extending the entire area into one 'bed'. We used an analogous metric by including a 25 m buffer around any isolated kelp, and tested whether this had any effect on our comparison of mode and historical bed size.

RESULTS

Patterns of Kelp Abundance over the Past 26 years

Kelp abundance varied by almost a factor of 3.6 along Washington State's Strait of Juan de Fuca and outer coast, with a low of 722 hectares to a high of 2574. Maximum extent was measured in the middle of the time series (2000), while low values were measured early (1989, 1997) and late (2014) in the time series. Since 1989, *Macrocystis* and *Nereocystis* contributed

equally on average (Figure 2), with *Macrocystis* varying from 439 to 1042 hectares, while *Nereocystis* showed more extreme variation from 198 to 1532 hectares, although there were distinct geographic differences. The abundance of these two species was significantly correlated through time ($r=0.845$, $p<0.001$, $df=23$) and there were no lag terms that had greater significance than the contemporaneous term. Thus, where they co-occur *Macrocystis* at time *t* is most correlated with *Nereocystis* at time *t* (Table 1). The abundance of canopy kelp increased through the study if 1989 was included ($p=0.030$), but the linear trend was not significant if 1989 was excluded ($p= 0.076$). In either analysis, the r^2 value was small ($r^2=0.147$ and 0.093) and 2014 was a year of relatively low kelp, suggesting any increasing linear trend was slight.

The autocorrelation function for both species showed a gradual decay expected if an AR component equals 1.0 (Figure S2). The partial autocorrelation function showed relatively weak terms beyond $t=1$. Because the kelp species show little evidence of stationarity, we also fit difference terms of 1 or 2. The ARIMA models that best described the dynamics of each species separately or together were similar, with an autoregressive and moving average term of 1 time step with a difference of 2 time steps. Thus, even though *Macrocystis* can live a year or two longer than *Nereocystis*, their dynamics were similar and density-dependent effects were suggested for one time step only. Although the partial autocorrelation function for *Nereocystis* had a suggestion of a positive two-year lag and a negative lag at year 3, the 1-year lag dominated and ARIMA models with an AR term of 1 were consistently the best fit to the data (Table 2), indicating that *Nereocystis* abundance at time *t* was best predicted by the previous time step and longer lags were unimportant. We ignored any correlations at t>6 to follow the general recommendation that we do not extend tests of lags more than approximately one-fourth of our data series (Jassby & Powell, 1990). We fit ARIMA models with varying differencing terms as

well as different moving average values. Both species separately or together showed the best model fit was a differencing of 1 or 2 years with a moving average for only a single time step (Table 2). In all cases, residuals were independent and normally distributed. Consistent with the ARIMA modeling, neither kelp species showed a long-term trend through time when we plotted abundance with a number of moving averages from 1 to 6 time intervals. A spectral analysis (R, 'spec.pgram') of abundance for each also did not indicate the presence of cycles over the current range of the data. (Figure S3)

Environmental data

Environmental data for the region, including the large-scale ocean climate variables (PDO, NPGO, UI, and ONI) and local sea surface temperatures all showed variability over the time span where kelp were censused (Figure 2). All environmental data also showed a similar autocorrelation function to both canopy kelp species with autocorrelation terms steadily declining after 1 year (Figure S2). In ARIMA models, an autoregressive term of 1 was always the best fit, while the best fit for the moving average term was 2 for the ONI, 4 for the NPGO and 1 (as with both kelp species) for the SST, PDO and UI (Table 2). The yearly mean PDO, SST at Race Rocks, and the Upwelling Index at 48 degrees North latitude all show a similar partial autocorrelation function to the kelp: a lag of only 1 time step was the most significant outcome, although a partial autocorrelation term >1 was suggested for the PDO and the ONI, with a lag of 4 for the NPGO (Figure S2).

Because the environmental data occur over a much larger time span than the kelp data, we asked if there was any evidence of periodicity in the environmental data that may not yet be detectable in the kelp data. A spectral analysis ('spec.pgram' in the stats module of R) of multiple environmental variables suggested some periodicity (Figure S3). The time series for the

mean annual PDO and NPGO suggested a 10-year cycle. The indices for upwelling as well as the ONI were similar and both indicated short cycles of ~3-4 years and long cycles of ~10-11 years. No long-term cycles were suggested in the Race Rocks SST data.

The ARIMA model that best fit the environmental variables was similar to that of the kelp. An autoregressive term of 1 was always the best fit. Either zero or one differencing and either no moving average or a single order term had the lowest AIC (Table 2). When we increased the autoregressive term, it did not improve model fit, even though we had a much longer time series in environmental data over which to test a greater range of parameter combinations.

A decomposition of the Race Rocks SST data indicated a long-term increasing trend since 1942, though it was slight (Figure S4). Linear regression on annual mean SST revealed a $0.0076^{o}C$ (0.0015 SE) increase per year since 1921, an increase of ~$0.72^{o}C$ between 1921-2015 (r^2=0.0209, p<0.001). If the temperature is divided into the upwelling season from April to August versus the winter months of September to March, the trends are different, with a coefficient that indicated decreasing temperature through time (-0.00456, r^2=0.067, p=0.007) in the summer versus increasing in the winter (0.00855, r^2=0.270, p<0.001). Thus, the overall temperature increase that is being recorded at Race Rocks seems to be due to an increase during the winter period, when upwelling is weakest. During the Apr to Aug period of seasonal upwelling, and the greatest kelp growth, the temperature decrease may indicate a slight strengthening of upwelling through time, bringing down summer water temperature.

When we tested whether environmental variables could be predictors of total kelp canopy area, cross-correlation analyses indicated that the PDO and the ONI correlated negatively with total kelp canopy area within the same year, with positive values of the PDO and the ONI indicating lower abundance of kelp (Table 3). While the ONI, the PDO, and especially the

NPGO showed significant correlations as leading variables one or more years previously, the SST and UI showed little correlation, except that values of the UI two to three years previous was correlated with *Macrocystis* abundance. While Table 3 reports correlations with the annual mean of an environmental variable, the results were similar when we used Apr to Aug values only. Overall, the NPGO and PDO explained the most variance in kelp abundance, accounting for 10-57% of the variance in kelp abundance.

Spatial Patterns of Abundance

When the kelp distribution was divided into three broad areas, *Macrocystis* correlated positively with *Nereocystis* within the outer coast and Western Juan de Fuca regions (Table 1), while they were uncorrelated in the Eastern area where *Macrocystis* is rare (Table 1, Figure 2). *Nereocystis* abundance was strongly correlated across all 3 broad regions, and *Macrocystis* was strongly correlated in the two regions (outer coast and Western Juan de Fuca) where it is common (Table 1). For every comparison between regions, the correlation between the spatially disjunct regions (East-Coast) was lower than between adjacent areas (East-West and West-Coast).

When we analyzed the 66 regions individually, there were distinct patterns of abundance and temporal variation in the kelp forest. Some areas were consistently low abundance and highly variable, particularly at either end of the study area near Destruction Island and areas around Protection Island (Figure 1), while the Western Strait showed relatively high areal abundance and persistence through time. Only one area (Cape Flattery) showed generally high abundance in *Nereocystis* with high variability. Overall, *Macrocystis* showed generally lower variability than

Nereocystis as indicated by low autocorrelation estimates; the CV in abundance for *Macrocystis* also was approximately half of that of *Nereocystis* (39.8 versus 81.6).

Kelp beds in the Strait of Juan de Fuca have been persistent features for at least 100 years, though there is evidence of decreased abundance in the most easterly regions (Figure 3). Most of the beds recorded in the Straits by G.B. Rigg (Cameron & United States., 1915) are still present today, with some notable exceptions (Figure S5). The location of the Neah Bay kelp bed (index area 15.4) currently differs from 1911-12, likely following the construction of the breakwater during WWII. Protection Island (index area 2.5) had abundant kelp in 1911, then Cameron (1915) reported that "only scattering plants were found" in 1912. When we examined the range of sizes of kelp beds in each area from 1989-2015, most of the 1911-12 censuses fall within those ranges, excepting five kelp beds eastward in the Strait of Juan de Fuca in the vicinity of Port Angeles and Port Townsend that appear to have decreased in size, including sites at Port Townsend (index area 1.1), Gray's Marsh (index area 3.2), and Sequim (index area 4.1). In the central and western Straits, Freshwater Bay (index area 7.3), Crescent Bay (index area 8.3) and 1 of the 3 areas at Cape Flattery (index area 16.3) also have not had a kelp bed with the aerial extent of those identified by Rigg in 1911-1912 (Figure 3), though their populations have been persistent (Figure 1). Our conclusions are unchanged based on whether we included a 25 m buffer area around sparse kelp cover in the modern surveys (analogous to Cameron (1915)).

DISCUSSION

Negatively correlated dynamics among species are associated with competition (Rees *et al.*, 1996), and can increase stability in multispecies models (Ives, 1999). Instead, our study indicated that both kelp forest species appeared to covary positively through time, despite somewhat

different life histories and longevities, suggesting that conditions favorable to one species were also favorable to the other. Although there is evidence of ecological differences between the two species (Schiel *et al.*, 2004) (Watson & Estes, 2011), the similarity of response to environmental variables in this study suggests that both species occupy a similar niche and have similar resource requirements. Studies of a number of terrestrial plant assemblages have similarly found that positive covariance was common among foundational plant species (Houlahan *et al.*, 2007), suggesting that species respond primarily to environmental variability and that competitive interactions may be absent or difficult to detect from survey data. The positive covariance in the abundance of these two canopy forming species revealed that kelp forests in the Northern CCLME potentially have no complementarity in their abundance; a poor year for one species is a poor year for both and low canopy cover results. Thus, environmental forcing, not competition, is suggested to be the primary driver of species dynamics in these kelp forests. Spatially, both species also showed positive covariation with outer coast and Strait of Juan de Fuca regions showing similar trends. The only exception to this was *Macrocystis* in east Strait of Juan de Fuca, likely due to its virtual absence in this area.

Positive covariance in abundance, rather than negative relationships that can result in compensatory dynamics, could lead to fluctuations in productivity when the environment varies (Hallett *et al.*, 2004). If true, this could result in vulnerability of kelp forest species and productivity if environmental variation increases in the future. Certainly, the spatial coherence in the overall dynamics of canopy kelp, including positive covariance in *Macrocystis* and *Nereocystis* abundance and a positive correlation in Outer Coast and Western Strait areas, suggest that large-scale environmental drivers are important. Indeed, our tests of environmental data for the region showed similar dynamics to kelp. Specifically, the PDO, the UI, and SST all

had an autoregressive term of 1 in ARIMA models, as did kelp, suggesting spatial coherence. Not only do these relationships have implications for kelp in particular, but the fitness and fate of myriad invertebrates and fishes that use this habitat (Bodkin, 1988)(Duggins *et al.*, 1989)(Teagle *et al.*, 2017) are similarly connected to the temporal and spatial coherence in canopy kelp dynamics

Although the PDO and UI additionally had evidence of 10-year cycles in a spectral analysis (Figure S4), detecting that signal in kelp is not yet possible given the length of the data. Thus, the kelp data through 2015 indicate that kelp abundance in the previous year has the greatest explanatory power for abundance in year t. Kelp abundance was also negatively correlated with the PDO and ONI, with the PDO and UI being leading indicators of kelp abundance (Table 3). The correlation between kelp abundance and temperature was not significant within the same year (Table 3). It may be that indices such as the PDO, NPGO, ONI, and UI, though averaged over large scales, are a better correlate of kelp abundance throughout the region compared with a temperature in a single locale.

Previous studies with kelp suggest sensitivity to increased temperature, decreased nitrate, and decreased salinity. *Nereocystis* in British Columbia, Canada showed warmer SST at time t is associated with lower kelp abundance in that same year (Foreman 1984). An 18-year study by Schiel et al. (2004) concluded that increased temperature was associated with a decrease in *Nereocystis* abundance and an increase in *Macrocystis* abundance. *Macrocystis* distribution was also negatively affected by increased temperature, which also corresponds with decreased salinity in British Columbia; transplant studies suggested low salinity during summer may limit its distribution (Druehl, 1978). However, Reed et al. (2016) argued that canopy kelp were poor sentinel species for sea surface warming, and did not show a dramatic negative response during a

2014-2015 warm water event in Southern California. Although the 'sentinel species' label (sensu Reed *et al.*, 2016) may not apply, canopy kelp abundance repeatedly shows an inverse relationship to temperature in the Northern and the Southern Hemispheres, and in the Pacific and Atlantic Oceans (Foreman, 1984), Tegner et al. 1996, (Wernberg *et al.*, 2012) (Wernberg *et al.*, 2016)(Filbee-Dexter *et al.*, 2016)(Cavanaugh *et al*, 2011). Despite the slight SST increase shown in Race Rocks over 93 years (Figure S3), there were only 9 days when the SST was 14.0^{o}C or higher, a value used as a benchmark in the Southern CCLME for compromised kelp performance (Tegner & Dayton, 1987). Whether decreased kelp with positive PDO and negative NPGO indices is a direct result of temperature is unknown. Higher SSTs can be associated with lower salinity and nutrients, both of which are associated with decreased kelp fitness (Druehl, 1967)(Druehl, 1978)(Schiel & Foster, 2015). While Race Rocks provides regional information in an area with complex circulation (e.g. Newton *et al.*, 2003), its placement away from the shore means that it will not record the temperature fluctuations of sites immediately at the shore and may not indicate the temperature events important to kelp. Long-term temperature records in close proximity to Washington kelp forests is thus lacking and prevents a rigorous test of the direct effect of temperature.

   As with other studies of kelp ((Dayton, 1999)(Edwards, 2004)), we also found relationships between climate indices and kelp performance. This study found a significant cross correlation between total Washington kelp canopy and PDO (0-2 year lag), NPGO (0-3 year lag), and ONI (0,1 year lag). Additionally, the UI was a leading indicator for *Macrocystis* abundance at 2 and 3 years (Table 3). Although *Macrocystis* in Southern California was not correlated with the PDO at 0 to 6 year lags, the NPGO and SST were significant explanatory variables (Cavanaugh *et al.*, 2011). Thus, despite the close anti-correlated relationship between the PDO and NPGO, they

have slightly different relationships with kelp populations in the different parts of the CCLME. The correspondence between kelp abundance and climate indices suggest that climate effects are not mediated through grazers, as is the case for the understory kelp *Pleurophycus gardneri* in this region (Pfister & Betcher, 2017).

Populations that are highly variable at a local scale can be persistent if their population sizes are large or if they are connected to other populations (Reddingius & den Boer, 1970). Our analysis of the 66 map indices showed that high variability in kelp abundance at the scale of approximately 8 km of shoreline, (range 0.9 – 25.0), while the 2 kelp species were persistent over an entire scale of 455 km of shoreline (Figure 1). Some areas showed continual abundance of either *Macrocystis* or *Nereocystis* thorough time (a high autocorrelation), while others were characterized by high variability. An area of *Nereocystis* west of Neah Bay (index area 16.2) was typically highly abundant, while variable in abundance through time (Figure 1, Figure S4). Those populations that are variable and low abundance are at particular risk of extinction (Lande *et al.*, 2003), and these tended to be concentrated in the eastern areas of the Strait of Juan de Fuca where only *Nereocystis* occurs and the southern areas of the outer coast, especially for *Macrocystis*. The eastern areas lay at one end of a strong gradient in environmental conditions along the Strait of Juan de Fuca due to natural (i.e. wave energy) and anthropogenic (i.e. development) causes. The southern areas of the outer coast are at a habitat transition from predominantly rocky shorelines to sandy ones where kelp attachment is prevented. While, it is unknown whether these patches of kelp have autonomy or are linked genetically, these factors will be key to determining whether the entire population is stabilized through migration among variable patches. Any future risk of extirpation depends upon the connectedness within the existing population (Wootton & Pfister, 2013). Why populations are variable from one time to

the next is unknown and may be related to localized effects. Although aerial censusing allowed us to analyze a large area, future analysis of demography and genetics *in situ* is needed to understand small, variable populations.

Kelp populations are known to be negatively affected by increasing seawater temperatures (Wernberg *et al.*, 2011; Krumhansl *et al.*, 2016; Wernberg *et al.*, 2016) and there is evidence of sea surface temperatures increasing globally (Lima & Wethey, 2012). We show an increasing trend in seawater temperature at the Race Rocks locale in the Strait of Juan de Fuca, but recognize that the overall change since 1921 is small ($+0.72^{o}$C) (Figure S4). This SST increase using daily values was less than that of the Rogers-Bennett *et al.* (2011) estimate of 1°C annually based on yearly data from 1969-2006, perhaps reflecting both our use of the entire time series and the elimination of any seasonal cycles. Because this is a region dominated by upwelling, the documentation of a warming trend is unexpected and potentially significant. When we divided the year into the upwelling season versus the winter months of downwelling, the downwelling period is the one that showed increasing temperature. Thus, the downwelling winter period, when the intrusion of deeper cold water is less pronounced, may be an interval when surface temperature changes are best detected, although its importance relative to spring/summer values is unknown. Although currently a small increase in an annual mean, increasing changes could have important effects in these coastal ecosystems. Kelp distributions are generally associated with higher latitudes and colder water (Steneck *et al.*, 2002). There is evidence of episodes of increased sea surface temperatures in the California Current in recent years (Di Lorenzo & Mantua, 2016), (Reed *et al.*, 2016), and analysis of the Race Rocks data suggested an ongoing trend (Figure S4, Rogers-Bennett *et al.*, 2011), that is seasonally divergent (Figure S3).

Coherence between large-scale environmental drivers and the fitness of primary producers breaks down when local-scale factors are important. One notable pattern in kelp abundance is a striking threefold increase followed by a decrease that occurs in the middle of the time series and creates two periods of relative stability, separated by rapid change. Although we cannot explain this pattern, we recognize that a number of local factors have been shown to be important to kelp bed abundance in North Pacific Ocean kelp beds. Trophic cascades via sea otter consumption of sea urchins (Estes & Palmisano, 1974), have been shown to be a key driver. Sea otter predation on sea urchins following their reintroduction in 1969 and 1970 (Kvitek *et al.*, 1989)(Laidre & Jameson, 2006), as well as an extensive sea urchin fishery that started in the 1980s (Pfister & Bradbury, 1996), has likely resulted in low sea urchin populations and thus reduced herbivory on kelp. This suggests that the area has generally been in an algal-dominated, rather than urchin-dominated, phase state (Watson & Estes, 2011). In some subareas during the study period, changes in urchin abundance may be associated with observed changes in kelp abundance. On the outer coast, sea otters expanded their numbers and range to the north and south between 1987 and 1995, and then farther to the north in 1999, and urchin abundance decreased rapidly in the newly occupied territories (Kvitek *et al.*, 1998) (Laidre & Jameson, 2006). Along the Strait of Juan de Fuca, intensive harvest in the early 1990s substantially decreased urchin abundance throughout the Strait of Juan de Fuca. While red urchin population densities were higher during the end of the study period (2013-2014) along the Strait of Juan de Fuca relative to levels in the early 2000s, they remain generally low with many areas containing a fraction of an urchin per m^2 with a high of only 1.4 urchins per m^2 (WDFW unpublished data). The historic Rigg study in 1911 and 1912, however, occurred during a period of likely relatively increased sea urchin abundance due to local sea otter extirpation and no subtidal urchin harvest. Yet, this era did not

differ greatly from the modern era in the western Strait where urchin harvest has increased. Thus, the extent to which variation in sea urchin density has controlled kelp forest abundance in this study is unclear.

The kelp beds that were censused over a century ago provide insight into kelp dynamics in the northeast Pacific, demonstrating overall persistence of kelp beds over much of the study area (Figure 4, Figure S5). The persistence of these kelp forests over the past century contrasts with other foundation species that show declines, including salt marshes (O'Donnell & Schalles, 2016), seagrass beds (Waycott *et al.*, 2009), and mangroves (Polidoro *et al.*, 2010). Declines in foundational plant species in other regions have been attributed to increasing drought frequency (O'Donnell & Schalles, 2016), changes in herbivory (Verges *et al.*, 2014; O'Donnell & Schalles, 2016; Vergés *et al.*, 2016) and disease outbreaks (Waycott *et al.*, 2009). There are strong correlations between human population density and direct human activities and the decline of foundational species, with factors such as pollution and harvesting implicated (Ellison *et al.*, 2005; Waycott *et al.*, 2009). The kelp beds in our study that show a reduced abundance relative to 1911-12 are those eastward toward Puget Sound and include sites between Dungeness and Port Townsend. Modern censuses indicate these are beds have low and variable cover. This pattern of reduced kelp abundance eastward is coupled with the loss of some populations further eastward into Puget Sound that were recorded in Cameron (1915), but have been absent for more than a decade (e.g. Bainbridge Island, WDNR unpublished data). The possible reasons for declines in these two kelp species in the eastern Strait of Juan de Fuca and Puget Sound locales could be varied and include increased turbidity (Schiel & Foster, 2015), increased point source pollution, and numerous other anthropogenic stressors associated with increasing human population size over the last century. Compared with outer coast kelp beds and those in the

western areas of the Strait, these beds in proximity to urban centers in the east show possible declines in abundance. Assuming all three regions experience the same ocean climate drivers, the declines in the eastern region suggest that climate may play a secondary role where direct anthropogenic effects are enhanced due to a human population size that exceeds 4 million surrounding Puget Sound (e.g. Shelton *et al.*, 2016). The important role that foundation species play, and the repeated demonstration of their demise over multiple ecosystems (Ellison *et al.*, 2005), suggest that the interaction between human activities and kelp forests deserves greater attention.

The differences in the trends seen in Washington kelp beds may mirror the diversity of trends reported globally in kelp species, with some populations and species increasing, while others are decreasing (Krumhansl *et al.*, 2016), likely due to a difference in the factors that drive kelp populations depending upon their proximity to concentrated anthropogenic effects. Throughout the range of the study, we find that kelp beds are relatively persistent throughout the Strait of Juan de Fuca and exposed coast of Washington state, while still showing connections to climate. At smaller spatial scales, there can be high variability. However, we did document areas of high variability and low abundance, and areas of extirpation. Coupled with the documented connections of Washington kelp beds to climate, and the estimation that local SST is increasing, we suggest that kelp forest viability remains an area of active investigation.

AUTHOR CONTRIBUTIONS

CAP: Wrote the manuscript, analyzed the data; HB: contributed to writing the manuscript, collecting and analyzing the data; TM contributed to collecting the data and editing the manuscript.

DATA ACCESSIBILITY

Data will be made accessible via Dryad. Archival maps are now accessible via the The University of Chicago Library.

Table 1. The relationships in abundance of *Macrocystis* and *Nereocystis* among years. The blue diagonal represents the correlation coefficients between the 2 species across the entire study area. Above the diagonal are the spatial correlations for *Macrocystis* abundance alone; below the diagonal are the spatial correlations for *Nereocystis* alone. All bold values are statistically significant at p<0.001.

		Macrocystis		
	locale	Eastern Strait	Western Strait	Outer Coast
Nereocystis	Eastern Strait	0.192	0.159	0.123
	Western Strait	**0.864**	**0.842**	**0.786**
	Outer Coast	**0.576**	**0.629**	**0.689**

Table 2. The AIC values for ARIMA models fit to the kelp and environmental data. The model is designated as: (auto regressive term, difference, moving average term). The best fitting model has bold, italic text. Not all model combinations are shown. The best-fitting ARIMA model for *Nereocystis* and *Macrocystis* showed an AR coefficient of -.398, -.358 and MA coefficient of -1.00 and -.912, respectively.

ARIMA Model	*Macrocystis*	*Nereocystis*	Total canopy	Race Rocks SST	PDO	UI	ONI	NPGO
(1,0,0)	314.90	359.35	389.46	52.70	146.00	568.58	120.62	183.60
(1,0,1)	315.83	360.39	389.86	53.24	*145.60*	569.52	118.52	185.35
(1,1,1)	300.11	346.75	373.81	*48.26*	145.92	*565.47*	123.83	184.68
(1,2,0)	300.66	343.56	369.90	101.94	188.17	613.60	193.25	222.59
(1,2,1)	*294.19*	*337.62*	*364.24*	63.97	157.87	572.35	154.61	198.40
(1,0,2)	317.08	359.95	389.16	50.61	146.61	569.55	*112.15*	187.35
(1,0,4)	319.45	365.27	393.17	56.02	151.73	541.36	117.77	*182.33*
(2,0,0)	315.44	359.64	388.95	54.24	146.26	567.69	114.99	185.32
(5,0,0)	320.82	364.27	393.63	53.08	149.94	571.39	120.64	186.88
(10,0,0)	---	---		62.06	155.15	572.68	122.29	193.02

Table 3. The cross correlation between the total kelp canopy cover and environmental variables with the same year and 1, 2 and 3 years previous. Bold values are significant at p<0.05.

Environmental Variable	Canopy Species	time 0	1 year previous	2 years previous	3 years previous
PDO	*Macrocystis*	**-0.321**	**-0.477**	**-0.319**	-0.143
	Nereocystis	**-0.440**	**-0.517**	**-0.258**	-0.140
	Total Canopy	**-0.376**	**-0.467**	**-0.263**	-0.209
ONI	*Macrocystis*	**-0.326**	**-0.330**	-0.002	-0.012
	Nereocystis	**-0.384**	**-0.312**	0.004	0.043
	Total Canopy	**-0.305**	**-0.329**	-0.062	-0.058
UI	*Macrocystis*	-0.054	0.063	**0.265**	**0.405**
	Nereocystis	0.089	0.124	0.116	0.229
	Total Canopy	-0.008	-0.009	0.162	0.251
Race Rocks SST	*Macrocystis*	-0.095	-0.126	-0.091	-0.126
	Nereocystis	-0.088	-0.199	-0.114	-0.082
	Total Canopy	-0.014	-0.205	-0.079	-0.124
NPGO	*Macrocystis*	**0.753**	**0.746**	**0.551**	**0.363**
	Nereocystis	**0.650**	**0.797**	**0.503**	**0.287**
	Total Canopy	**0.651**	**0.760**	**0.624**	**0.371**

Figure 1. The abundance of each species of canopy kelp is shown by the size of the circle (*Nereocystis*) and diamond (*Macrocystis*), while the color indicates the autocorrelation through time for each locale from 1989 to 2015; increased consistency in abundance through time leads to a greater autocorrelation. Each coastal polygon delineates an 'index area'. Detailed maps of kelp abundance and index area boundaries are shown in Figure S5.
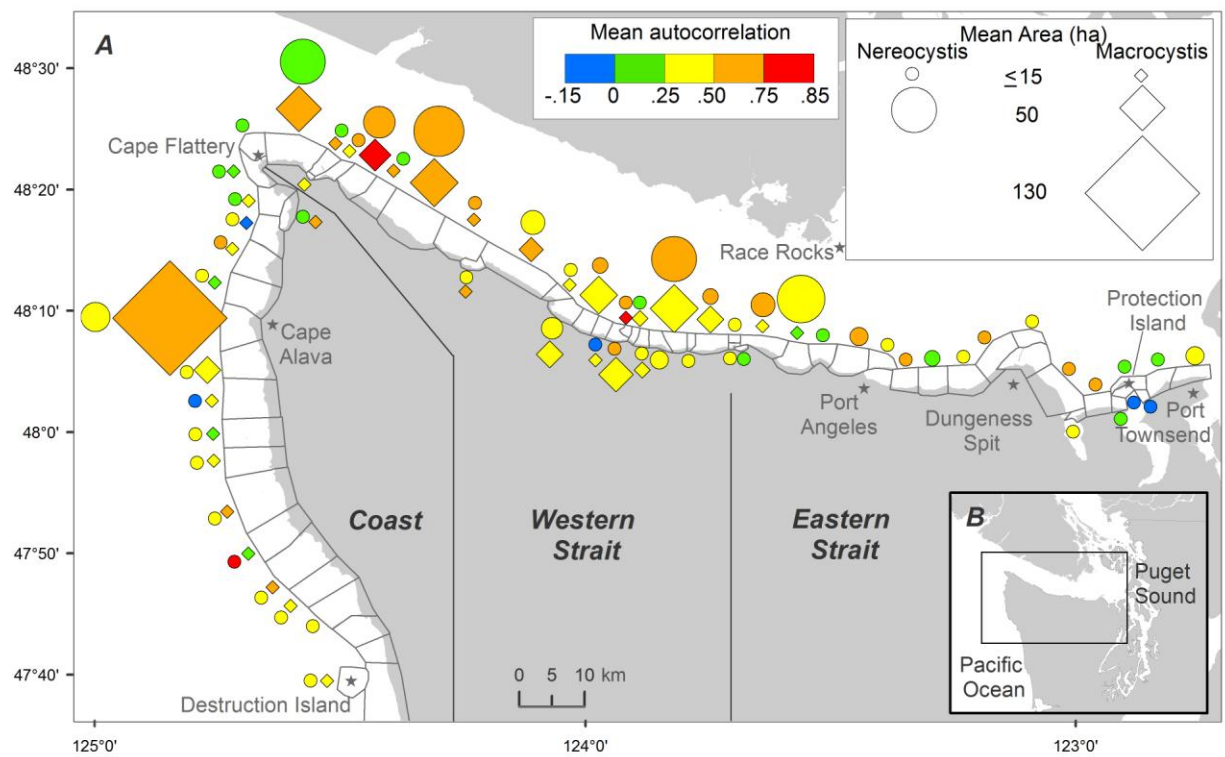
Figure 2. The relative abundance (in hectares) of the total canopy, *Nereocystis* and *Macrocystis* from 1989-2015 based on aerial surveys in the A. outer Coast region, B. Western Strait, and C. Eastern Strait. There was no census in 1993. The environmental variables over the same time period for the region include D. the PDO and the NPGO and E. the UI and ONI. Correlations between kelp abundance and environmental variables are shown in Table 3. Figure S5 shows the temporal and spatial variability in kelp abundance.

D. PDO and NPGO
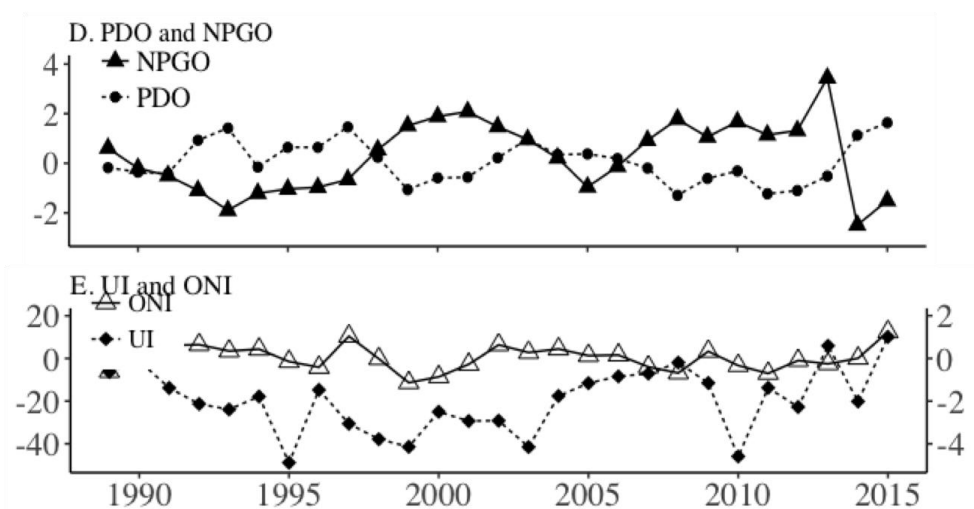▲ NPGO
● PDO

E. UI and ONI
△ ONI
◆ UI
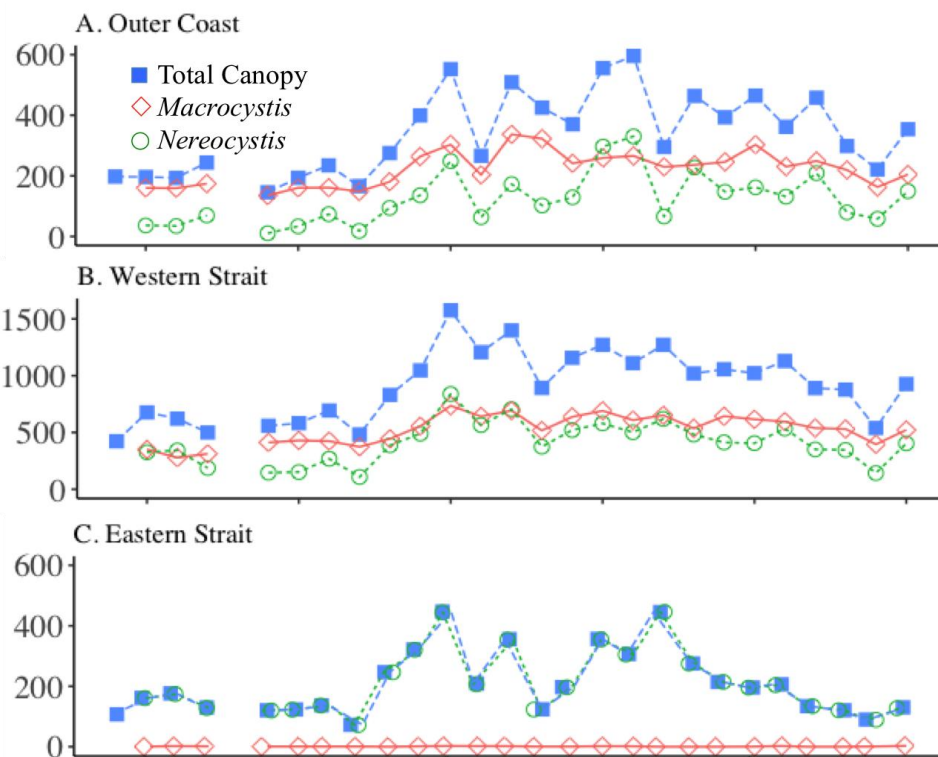
Figure 3. The kelp bed area in hectares in 1911-1912 (black circles) compared with annual

surveys from 1989 to 2015 (red circles), from areas along the Strait of Juan de Fuca where Rigg

(Cameron 1915) identified kelp beds. Here, the modern surveys include a 25 m buffer area to

include the possibility that 1911-1912 surveys extended the bed size. Yellow highlighting

indicates the modern Index Areas where kelp beds were noted in 1911-1912. Detailed maps of

historical and modern kelp abundance are presented in Figure S5.
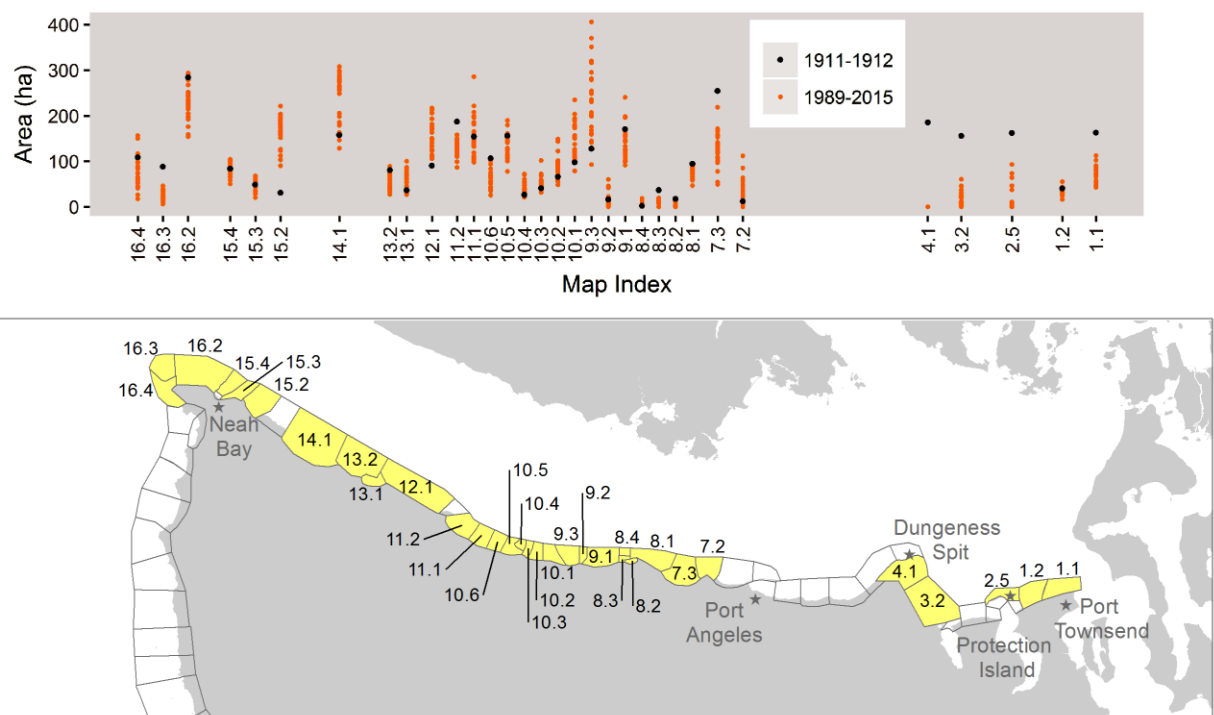
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