Remote sensing: generation of long-term kelp bed data sets for evaluation of impacts of climatic variation

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Abstract. A critical tool in assessing ecosystem change is the analysis of long-term data sets, yet such information is generally sparse and often unavailable for many habitats. Kelp forests are an example of rapidly changing ecosystems that are in most cases data poor. Because kelp forests are highly dynamic and have high intrinsic interannual variability, understanding how regional-scale drivers are driving kelp populations—and particularly how kelp populations are responding to climate change—requires long-term data sets. However, much of the work on kelp responses to climate change has focused on just a few, relatively long-lived, perennial, canopy-forming species. To understand how kelp populations with different life history traits are responding to climate-related variability, we leverage 35 yr of Landsat satellite imagery to track the population size of an annual, ruderal kelp, *Nereocystis luetkeana*, across Oregon. We found high levels of interannual variability in *Nereocystis* canopy area and varying population trajectories over the last 35 yr. Surprisingly, Oregon *Nereocystis* population sizes were unresponsive to a 2014 marine heat wave accompanied by increases in urchin densities that decimated northern California *Nereocystis* populations. Some Oregon *Nereocysti*s populations have even increased in area relative to pre-2014 levels. Analysis of environmental drivers found that *Nereocystis* population size was negatively correlated with estimated nitrate levels and positively correlated with winter wave height. This pattern is the inverse of the predicted relationship based on extensive prior work on the perennial kelp *Macrocystis pyrifera* and may be related to the annual life cycle of *Nereocystis*. This article demonstrates (1) the value of novel remote sensing tools to create long-term data sets that may challenge our understanding of nearshore marine species and (2) the need to incorporate life history traits into our theory of how climate change will shape the ocean of the future.

Key words: long-term ecological data; Macrocystis pyrifera; Nereocystis luetkeana; nutrients; Oregon; population dynamics; satellite imagery; waves.

INTRODUCTION

Earth's ecosystems are undergoing unprecedentedly rapid alteration as a consequence of climate change, challenging the ability of ecologists to keep pace with the rate of change and to document its outcomes. A critical tool in assessing ecosystem change is the analysis of long-term data sets, yet such information is generally sparse and often unavailable for many habitats. Thus, in such cases, many researchers have employed novel and creative ways to obtain long-term data. A prime example is the use of satellite-based remote sensing to quantify the abundance of vegetation, both on land and in the ocean. When combined with surface-based and other satellite sensors, these data enable researchers to investigate how long-term trends in vegetation vary in relation to potential environmental drivers in regions where lack of long-term data sets would otherwise make this impossible.

Kelp forests, which occupy mostly temperate to subpolar regions around the world, are an example of a rapidly changing ecosystem that is in most cases data poor. Furthermore, kelp are among the most prolific primary producers on earth (Mann 1973), support diverse and commercially important ecosystems (Smale et al. 2013), and provide a wealth of ecosystem services (Bennett et al. 2016). In one of the most comprehensive efforts to catalogue global time series of kelp abundance, Krumhansl et al. (2016) showed that, on average, Earth's kelp forests are decreasing in size, yet they were only able to obtain data from 34 of the 99 global ecoregions in which kelp is present. Furthermore, in many of the 34 regions where data were present, data sets were short term (<10 yr). This study also showed that global kelp populations have varied in their trajectories over

the last half century, from strong increases in regions such as the Iberian Peninsula to dramatic declines in the Aleutian Islands. However, it remains unclear whether regional-scale drivers are impacting kelps in variable ways or if kelp responses to regional drivers are similar, with the drivers varying among regions. Understanding kelp forest dynamics will depend on how environmental drivers vary and how kelp responses to these drivers vary at regional scales. Because kelp forests are highly dynamic and have high intrinsic interannual variability (Dayton et al. 1999), understanding how regional-scale drivers are impacting kelp populations—and particularly how kelp populations are responding to climate change—requires long-term data sets. Although some long-term data sets are available (e.g., the Santa Barbara LTER with 18 yr of data), long-term studies of kelp forests are unavailable for most of the world. In such cases, identifying population dynamics using remote sensing could exponentially increase data on long-term population dynamics for certain kelp species.

On the Pacific Coast of North America, scientists have employed remote sensing to gain insight into the population dynamics of giant kelp *Macrocystis pyrifera* (hereafter *Macrocystis*), providing valuable ecological insight into patch modularity, scales of spatial variability, and the influence of various environmental variables, such as the influence of nutrient limitations, wave height, and predation on kelp abundance (Cavanaugh et al. 2014, Bell et al. 2015, 2020, Young et al. 2016, Castorani et al. 2017). Remote-sensing studies have also begun to give us a better understanding of how *Macrocystis* populations are responding to climate change. For example, Cavanaugh et al. (2019) found that metrics of absolute temperature (e.g., maximum mean monthly temperature) were more successful than relative temperature (e.g., maximum mean temperature anomaly) in predicting resistance of a dozen *Macrocystis* populations to a marine heat wave (MHW) near its equatorward range limit. This suggests that physiological thermal thresholds play a more important role than local adaptations in range-edge responses to heat waves in kelp, which is similar to findings in Australian *Ecklonia* forests (Wernberg et al. 2016), but contradicts findings from other kelp studies (Bennett et al. 2015, Smale et al. 2019).

Given its near-global distribution, the dominance of studies on *Macrocystis* (e.g., a Google Scholar search finds 26,200 articles discussing *Macrocystis*) is understandable. Much insight into kelp forest dynamics and the response of kelp to environmental factors has resulted from this work, especially on the North American west coast (Estes and Duggins 1995, Dayton et al. 1999, Byrnes et al. 2011). However, much of the work on kelp responses to climate change has focused on just a few, relatively long-lived (perennial), canopy-forming species such as *Macrocystis*, *Ecklonia radiata*, and *Saccharina latissima* (Wernberg et al. 2010, Witman and Lamb 2018, Cavanaugh et al. 2019). To build theory for how kelps and seaweeds more broadly will respond to

climate change, we also need to examine how kelps with different life history strategies respond to stressors. The bull kelp *Nereocystis luetkeana* (hereafter *Nereocystis*) is one such species. Although this species is also a canopy-forming kelp with surface expression, the life history strategy of *Nereocystis* differs in many respects from giant kelp. It is a ruderal species that has an annual life cycle and incredibly high fecundity (Springer et al. 2010). *Nereocystis* tends to be an early-succession species and flourishes in more wave-exposed, disturbed environments than does giant kelp (Dayton et al. 1984, Springer et al. 2010). It is also the dominant canopy-forming kelp along the west coast of North America from northern California to Alaska (Springer et al. 2010). Considering how costly and spatially limited subtidal diving-based surveys of kelps are, and consequently how few long-term studies exist for most kelp species, using remote sensing to build regional-scale, long-term time series of *Nereocystis* can expand our theories of how kelps and seaweeds—beyond long-lived, late-succession species— will respond to climate change.

Several prior studies have investigated whether satellite imagery could be used to identify and track *Nereocystis* populations reliably. Nijland et al. (2019) and Schroeder et al. (2019) both focused on quantifying the accuracy with which imagery from various satellites could identify *Nereocystis* populations in British Columbia. They found that Landsat, the satellite used most often in *Macrocystis* studies, had challenges identifying *Nereocystis* because of its relatively coarse spatial resolution (30 m). *Nereocystis* has relatively less biomass present at the water's surface than *Macrocystis*, and Landsat's coarse resolution is more likely to miss small or sparse patches of *Nereocysti*s than *Macrocystis*. Additionally, Landsat imagery is not useful for identifying kelp within 30 m of shore because the spectral signal of kelp is similar to the spectral signal of land-based vegetation, which presents challenges along topographically complex coastlines like British Columbia (Nijland et al. 2019). Pfister et al. (2018), however, used 20-yr of aerial surveys to derive insights about mixed forests of *Nereocystis* and *Macrocystis* in the Strait of Juan de Fuca. They found evidence that *Nereocystis* and *Macrocystis* were not competing in that region and that both species responded negatively to the Pacific Decadal Oscillation and positively to the North Pacific Gyre Oscillation (Pfister et al. 2018). That is, increases in kelp abundance were associated with climatically driven cold temperatures. These studies show the limitations as well as the potential for using satellite imagery to derive insights into the population dynamics and ecology of *Nereocystis*.

In the past 5 yr, understanding of *Nereocystis* population dynamics has taken on additional importance, because *Nereocystis* forests in northern California were decimated by the combined direct effects of a marine heat wave (MHW; i.e., thermal stress and nutrient depletion) and indirect effects of sea star wasting (SSW; i.e., loss of sea star predators and their control of sea

urchins, a primary kelp grazer; Rogers-Bennett and Catton 2019). In the aftermath of these two events, vast stretches of sea urchin barrens caused a loss of fisheries worth $47 million to the Northern California coastal economy (Rogers-Bennett and Catton 2019). Oregon's *Nereocystis* forestslie just to the north of these populations but have received very little study, largely because the difficulty of regularly conducting subtidal diving surveys in the turbulent coastal waters typifying this area. Historical data on Oregon *Nereocystis* populations are limited to a few aerial surveys undertaken by the Oregon Department of Fish and Wildlife (ODFW) in the 1990s. Oregon, however, is an ideal place to use the relatively coarse-resolution Landsat imagery—Oregon's *Nereocystis* populations are relatively dense and mostly located offshore, and its coastline is relatively linear. In this study, we examined (1) whether Landsat imagery could be used to build a decades-long time series of Oregon's *Nereocystis* populations, and if so; (2) what long-term changes are evident in *Nereocystis* populations across the state; (3) how *Nereocystis* populations responded to the 2014–2016 MHW; and (4) what environmental drivers were associated with changes in these populations. We hypothesized that (1) Landsat imagery could be used to identify historical *Nereocystis* extent in Oregon; (2) *Nereocystis* populations were mostly stable over the last 35 yr; but (3) declined post 2014, as did those in Northern California; and (4) that climate indices and nutrient availability would be important environmental drivers.

Methods

Remote sensing of kelp canopy

We based our methods on similar work that used satellite imagery to estimate California *Macrocystis* canopy area (Cavanaugh et al. 2011, Bell et al. 2020). Canopy-forming kelps, like *Macrocystis and Nereocystis,* float at the ocean's surface and can be detected in satellite imagery because photosynthetically active vegetation has a different spectral signature than seawater. For the remote sensing of kelp canopy, we utilized the Collection 1 Level 2 Surface Reflectance Product for Landsat 5 Thematic Mapper (TM), Landsat 7 Enhanced Thematic Mapper + (ETM+), and Landsat 8 Operational Land Imager (OLI) sensor data.[5] Together, these satellites gathered multispectral images of Oregon at a 30-m resolution at least once every 16 d from 1984 to 2018. We used ArcMap 10.6.1 to draw an outline of the Oregon coast manually, which we used to mask land, beaches, estuaries, and intertidal zones from Landsat imagery (ESRI 2018). To ground-truth the accuracy with which this Landsat imagery captured *Nereocystis* canopy, we compared Landsat-derived estimates of kelp area to high-resolution (~1-m) aerial color-infrared photographs taken by Bergman Photographic, Inc. as part of an effort by the Oregon Department of Fish and Wildlife to survey kelp

populations statewide. These images were taken for several years in the 1990s in late summer and early fall at neutral tides. For a more complete description of the aerial photography, see Fox et al. (1996). We used 11 of these photographs of Orford Reef, Cape Blanco Reef, and Rogue Reef (provided by D. Fox and A. Merems, ODFW) that had a corresponding Landsat 5 TM or Landsat 7 ETM + image of the same reef taken within 7 d of the aerial photograph (Appendix S1: Table S1). We georeferenced the aerial photographs, manually removed rocks and islands, and identified kelp canopy in each pixel by calculating normalized difference vegetation index (NDVI; Eq. 1):

$$NDVI = \frac{(NIR - Red)}{(NIR + Red)} \qquad (1)$$

where NIR stands for the near-infrared spectral signal and the Red for the red-band spectral signal. Once kelp canopy was identified, we binned pixels in the aerial photos into 30-m cells corresponding to the 30-m grid of a Landsat image and summed the percentage of each 30-m cell that was covered in kelp (Appendix S1: Fig. S1). To quantify the percentage of each Landsat pixel covered in kelp, we used a kelp-identification algorithm to derive *Nereocystis* canopy area from satellite images. This algorithm quantifies kelp canopy presence and density using (1) a binary decision tree that determines whether a pixel contains kelp, seawater, cloud, or exposed rock/land based on blue, green, red, near-infrared, and short-wave infrared reflectance; and (2) sub-pixel-level multiple endmember spectral mixing analysis that estimates kelp and water fractional cover within pixels that contain kelp. For more detailed information on the algorithm see Bell et al. (2020). We applied a two-dimensional Gaussian filter ($\sigma = 0.5$) to both images to account for potential changes in current direction, which can shift the canopy between image dates. We then compared per-pixel estimates of canopy cover derived from the aerial photos to the fractional canopy coverage derived from the Landsat images. We quantified the algorithm's accuracy using linear regression and by calculating the rate at which the algorithm misidentified kelp as water and vice versa. To minimize spatial autocorrelation in our algorithm validation statistics, we only included pixels that were >150 m apart, because prior work has shown kelp populations to be highly autocorrelated closer than 150 m (Cavanaugh et al. 2013). We also excluded pixels estimated to contain ≤1% kelp cover by either NDVI (for aerial photos) or the kelp-detection algorithm (for Landsat images). For more on the ground-truthing process, see Supplementary Materials. After ground-truthing the accuracy of our kelp-detection algorithm, we used this algorithm to derive *Nereocystis* canopy area in all available Landsat images from 1984 to 2018 along the Oregon coast.

Prior work has shown that tides and currents bias aerial estimates of kelp canopy cover, because tides can

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[5] https://earthexplorer.usgs.gov/

immerse the canopy and currents can pull surface biomass below the surface of the water (Britton-Simmons et al. 2008, Bell et al. 2020). A direct test of the influence of tide height on canopy estimation was not possible here because all aerial photographs were taken near mid–low tide. However, we were able to test tide height effects using satellite-estimated kelp canopy. We pooled all satellite estimates of kelp canopy area into a single sample and grouped estimates into a "high-tide" and "low-tide" group based on the tide height when the image was taken. We then used a one-tailed Student's *t* test to test for significant differences between kelp canopy area between the high-tide and low-tide group as we changed the tide height cutoff between the groups. Once we found the resulting high-tide group that had significantly lower canopy estimates, we used that tide height as the cutoff to exclude images taken at that tide height or higher. Although this approach may miss more subtle differences in kelp area estimates based on tide height, it did eliminate nearly a third of the available Landsat images. Furthermore, given the high levels of interannual variability exhibited by *Nereocystis*, we posit that the remaining bias in canopy area estimates is probably small compared to the species' inherent variability.

Intensity of the marine heat wave

We used NOAA's high-resolution sea surface temperature (SST) data set (available at https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html) to compare the intensity of the 2014–2016 marine heat wave (MHW) in northern California (longitude = 123.8°W, latitude = 38.92°N) and southern Oregon (longitude = 124.6°W, latitude = 42.83°N). We used the Hobday et al. (2016) definition of a MHW, that is, periods of five or more consecutive days when daily SST was greater than the 90th percentile based on historic SST (Hobday et al. 2016). We calculated "historic" SST using SST data from 1984 to 2013 to identify mean temperature and percentiles for each day of the year by averaging the mean temperature within 10 d of each date over the previous 30 yr. We then calculated mean monthly temperature, maximum mean monthly temperature, the number of heat-wave days, mean monthly temperature anomaly, and maximum mean monthly temperature anomaly (Cavanaugh et al. 2019). A one-tailed *t* test was used to test the significance between mean monthly temperature and mean monthly temperature anomaly and a one-tailed binomial test was used for the number of heat-wave days.

Environmental data

To assess the relationship between *Nereocystis* canopy and the environment, we identified abiotic factors in the literature that were frequently associated with regional-scale fluctuations in kelp population size (e.g., Reed et al. 2011, Pfister et al. 2018). Specifically, we quantified

1.. Seawater nitrate concentration (μmol/L) using a negative nonlinear nitrate/temperature relationship derived from nearshore oceanographic cruise data taken from 1997 to 2004[6] (Appendix S1: Fig. S2). We used this relationship to estimate historic seawater nitrate concentrations during the growing season using NOAA high-resolution SST data.[7] For more information on how we derived this relationship see Supplementary Materials.

2.. Maximum wave height (m) for the winter and growing season, defined as the 95th percentile of wave height, using hindcasted significant wave height data from the Wave Watch III model for 1984–2004[8] and for 2005–2018.[9] For more information on how we ground-truthed this wave-height model see Supplementary Materials.

3.. Upwelling intensity during the growing season from the Bakun index of daily upwelling values ($m^3 \cdot s^{-1} \cdot 100$ m of coastline^{-1}) at 45° N, 125° W and 42° N, 125° W.[10]

4.. Climatic variability using the (1) multivariate El Nino southern oscillation (ENSO) index (MEI),[11] (2) Pacific decadal oscillation (PDO) index,[12] and (3) Northern Pacific gyre oscillation (NPGO) index.[13]

We defined the "growing season" as March–August because March is approximately when *Nereocystis* sporophytes begin growing, although the literature on *Nereocystis* growth is limited (Springer et al. 2010). We defined "winter" as the October–February prior to that year's growing season (e.g., "winter" maximum wave height for the 2003 growing season would cover October 2002–February 2003).

Statistical analyses

We conducted statistical analyses in R (R Studio Team 2015) and used nonparametric tests to address the positively skewed distribution of the canopy area data. Environmental drivers of kelp population size were identified from the literature and included mean strength of the ENSO, PDO, and NPGO during the growing season, mean and standard deviation of estimated seawater nitrate concentration and upwelling strength during the growing season, maximum wave height during the previous winter and current growing season, year, and, when

[6] http://globec.whoi.edu/jg/dir/globec/nep/ccs/ltop
[7] https://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html
[8] https://polar.ncep.noaa.gov/waves/hindcasts/nopp-phase2.php
[9] https://polar.ncep.noaa.gov/waves/hindcasts/prod-multi_1.php
[10] https://www.pfeg.noaa.gov/products/PFEL/modeled/indices/upwelling/NA/data_download.html
[11] https://www.esrl.noaa.gov/psd/enso/mei/
[12] http://research.jisao.washington.edu/pdo/PDO.latest.txt
[13] http://www.o3d.org/npgo/npgo.php

applicable, reef. We explored the relationship between summer kelp canopy cover and environmental variables using linear models, after verifying the normality assumption using the residuals of the linear models. Because climate change is altering the way organisms relate to their environment, we wanted to examine if the factors influencing bull kelp abundance might be changing over time. Thus we conducted two sets of linear models, the first using data from the entire time series (1984–2018) and a second using data from only the most recent two-thirds of the time series (1996–2018). We chose the latter period (1996–2018) to balance our desire to have enough data points to pick up kelp–environment relationships while also limiting the time series to be representative of more recent conditions. We examined variance inflation factors (VIF) before conducting each model in order to avoid highly correlated predictor variables. Only PDO was excluded from the analysis, because it regularly had VIF > 5 and was strongly correlated with several other metrics, including El Niño and nutrient concentration. To choose "best" models, we used backwards and forwards AIC stepwise model selection to identify important predictor variables and then sequentially removed variables with large P values to observe their effect on model significance and explanatory power. We settled on a "best" model once (1) all the terms in the model were significant at the $P = 0.05$ level, or (2) all terms were close to significance and excluding any terms from the model resulted in large changes in model significance or explanatory power.

RESULTS

Ground-truthing the kelp-detection algorithm

Landsat-based estimates of kelp canopy were strongly related to verified kelp cover documented in the 11 high-resolution aerial photos ($r^2 = 0.779$, $P < 0.001$, slope = 1.03; Fig. 1A). Furthermore, the algorithm (1) almost never identified kelp in a pixel that was purely water (<1% of the time) and (2) identified kelp ~70% of the time in pixels that contained kelp. To characterize the 30% of pixels that were misidentified as water, we plotted the odds of pixel misidentification as a function of kelp cover within that pixel and found that the miss rate declined exponentially as kelp cover increased (Fig. 1B). Above ~15% kelp cover the miss rate dropped to <10%.

Because most pixels missed by the kelp-detection algorithm had sparse kelp cover, we quantified the extent to which misidentifying these pixels as seawater impacted estimates of total canopy size. When we summed the canopy area in all misidentified pixels and compared that to the total area in the correctly identified pixels, we found that about 4.6% of the total canopy shown in aerial images was mistaken for water and about 5.6% for exposed rocks closely fringed by kelp. Overall, the kelp-detection algorithm missed ~10.2% of the total canopy shown in aerial photographs, and thus, identified ~90%
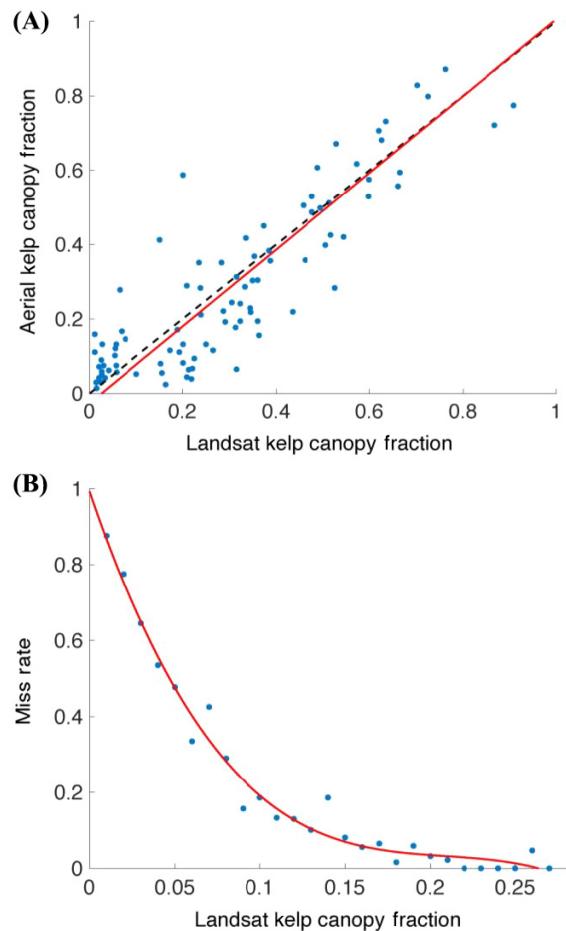

FIG. 1. (A) Relationship between aerial photography-derived canopy density and Landsat-derived canopy density. The red line is the best-fit linear relationship and the dashed black line a 1:1 line. Units are the percentage of each 30 × 30 m pixel that was covered by kelp. (B) Misidentification rate as function of Landsat kelp canopy fraction. The red line shows the best-fit nonlinear relationship.

of the kelp canopy present. Based on this relatively high level of accuracy, we felt justified using this algorithm to create a time series of kelp canopy area in Oregon over the last 35 yr.

When the kelp-detection algorithm was used on all available Landsat images, we created a time series of >12,000 Landsat pixels along the Oregon coast that contained emergent canopy at some point over the last 35 yr. We found 2,754 dates with cloud-free Landsat imagery from 18 November 1982 to 31 December 2018, but on most days cloud cover obstructed large swaths of the coast. We found that estimated canopy area was significantly smaller for images taken at a tidal height >1.5 m than those taken at tidal height <1.5 m. Therefore, we excluded estimates made on 757 d when Landsat images were taken at a ≥1.5-m tide. Between clouds and tides, we were able to estimate canopy extent from October to April about once every 6 months and from
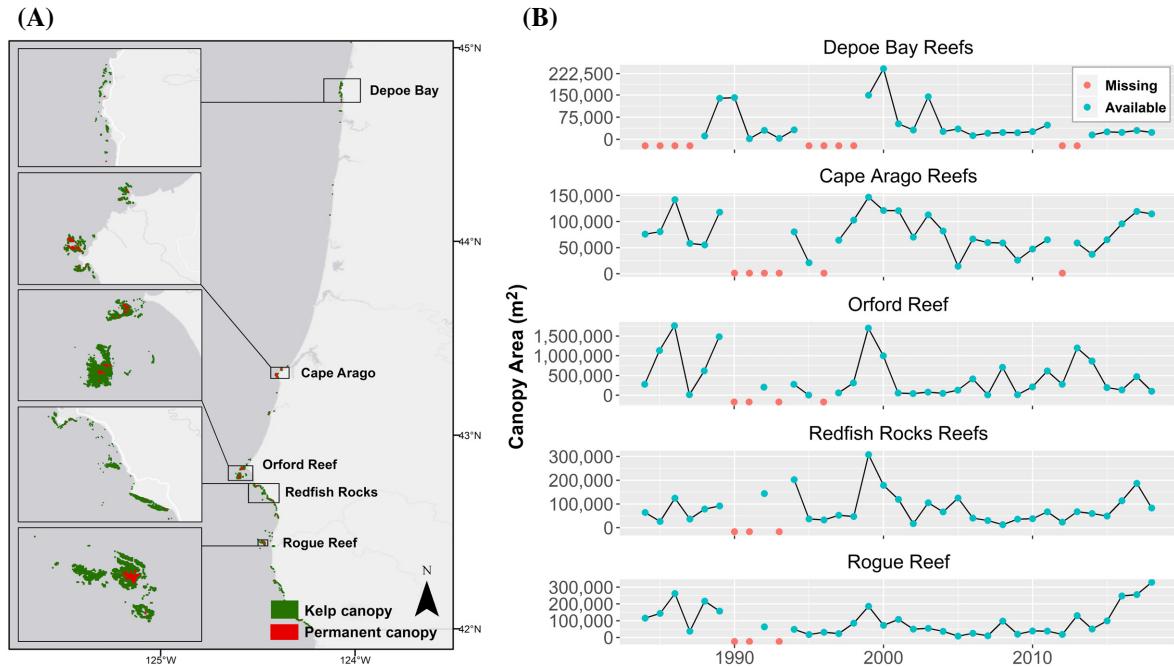
FIG. 2. (A) Map of all kelp detected in Oregon in at least 1% of the available Landsat images (green) and all "permanent" canopy (red), which we defined as being present in 80% of the summers for which an Landsat image was available. The five largest reefs in Oregon are labeled. (B) Time series of maximum detected summer kelp canopy area (m^2) for the five largest reefs in Oregon from 1984 to 2018. Note that the y-axis scale varies between reefs. Blue (pink) points represent summers when canopy area could (could not) be estimated, usually because of lack of cloud-free Landsat imagery or imagery taken at high tide.

May to September (when cloud cover is low) about every 3 months (Appendix S1: Fig. S2).

Although the frequency of estimates declined in fall and winter, we suggest this is less important when examining *Nereocystis* because it is an annual kelp. As an annual, the majority of the emergent canopy does not reach the surface and become visible in satellite images until July (Maxell and Miller 1996, Springer et al. 2010). Because cloud-free imagery and emergent canopy are most abundant from July–September, we focused our analyses of long-term trends and environmental correlates on maximum canopy extent in summer and early fall (Appendix S1: Fig. S5).

Spatial and temporal trends

The majority of kelp canopy in Oregon is present in the southern third of the state, with 95% of the median summer canopy present from Cape Arago south to the California border(Fig. 2A). In fact, 76% of the median summer canopy area is contained in just five reefs (Depoe Bay, Cape Arago, Orford, Redfish, and Rogue reefs), and thus we focused our temporal and environmental analyses on these reefs. Time series of canopy area at these reefs show three important patterns 2B. First, canopy area varied dramatically among years. For example, between 1986 and 1987 Orford Reef dropped from an estimated maximum summer canopy

extent of 1,761,900 m^2 to a mere 12,300 m^2 (0.7% of the area present the year before). Second, we see high variability in the trends in population size at these five reefs from 1984 to 2018. For two reefs, Depoe Bay and Orford Reef, year had a small negative correlation with canopy size in linear models run from 1984 to 2018 (but not for models run from 1996 to 2018), indicating declining populations over the last 35 yr. For two other reefs, Cape Arago and Redfish Rocks, population sizes over the last 5 yr remain well within the range of sizes seen regularly over the last 35 yr. Finally, at Rogue Reef, population sizes in 2018 are in fact greater than at any point over the last 35 yr and were positively related to year in our 1996–2018 linear model. Third, surprisingly, unlike northern California, kelp cover at these major reefs did not decline dramatically after 2014. At Depoe Bay and Orford Reef, a Wilcoxon rank sum test detected no changes in maximum summer canopy area for 2015–2018 compared to the prior 10 yr. Additionally, at Cape Arago, Redfish Rocks, and Rogue Reef, kelp area actually increased in 2015–2018 compared to the previous decade (*P* value = 0.006, 0.054, 0.004).

The 2014–2016 MHW in California and Oregon

The mean monthly temperature anomaly and the number of heat-wave days from 2014 to 2016 did not

differ between northern California (latitude = 38.92°, mean temperature anomaly = 0.983°C) and southern Oregon (latitude = 42.83°, mean temperature anomaly = 0.605°C), although the mean monthly temperature anomaly was about 0.3° higher for northern California (P value = 0.10) (Table 1). The maximum monthly temperature anomaly was very similar between the two places. However, the mean monthly absolute temperature during this period was higher for northern California (13.08°C) than Oregon (12.06°C) (P value = 0.002) and the maximum mean monthly temperature was about 1.5° higher in northern California.

Environmental drivers

Environmental factors explained 35% of the variance in summer canopy area across all five reefs together in both the 1984–2018 and 1996–2018 best linear model (P values for both periods <0.0001; Table 2). The 1984–2018 model identified El Niño and mean estimated nitrate concentration as having strong negative relationships with canopy area and a positive interaction between mean estimated nitrate concentration and Orford Reef. The 1996–2018 model included these same environmental factors with similar coefficients, but also identified maximum winter wave height as having a strong positive relationship and mean upwelling a small positive relationship.

To test if a single model across all five reefs might mask spatial patterns in environmental predictor strength, we identified a best linear model for each reef for the 1984–2018 and 1996–2018 time frames. Reef-specific models explained anywhere between 16% (at Redfish Rocks and Rogue Reef for 1984–2018) to 53% (at Cape Arago for 1996–2018) of the variation in summer kelp canopy area. The 1984–2018 models were quite similar to the 1996–2018 models. Both sets included a strong negative relationship between El Niño and kelp canopy area at each reef, a moderate negative relationship with estimated seawater nitrate concentration at the majority of reefs (three reefs in the 1984–2018 models and four reefs in the 1996–2018 models), and a strong positive relationship with winter wave height at several reefs (two reefs in the 1984–2018 models and three reefs in the 1996–2018 models; Fig. 3). The main difference between the earlier and later models was that the 1996–2018 models did not find a negative impact of year at any reef, whereas in the 1984–2018 models, year was identified as having a negative relationship with canopy area at Orford Reef and Depoe Bay. NPGO had opposing relationships at Rogue Reef (negative) and Depoe Bay (positive) in the 1984–2019 models, upwelling variability a small positive relationship and growing season wave height a moderate negative relationship in both models for Cape Arago, and year a positive relationship in the Rogue Reef 1996–2018 model.

DISCUSSION

Our data indicate that Landsat satellite imagery can indeed be used for long-term surveys of Oregon *Nereocystis* populations. Using our 35-yr time series of kelp canopy area, we identified long-term population changes and associated these with potential environmental drivers. Our time series revealed mixed long-term trends in population size, higher resistance to the 2014–2015 MHW and SSW than was seen in northern California, and unique environmental drivers. We address each of these results and their implications below.

Population dynamics

During the 35 yr surveyed, we found that three of the five largest reefs in Oregon (Cape Arago, Redfish, and Rogue) remained within historically normal levels and in fact, Rogue Reef reached its highest documented canopy area in 2018. In contrast, Depoe Bay has experienced sustained low populations levels for the past 15 yr and Orford Reef has shifted to somewhat smaller, less variable populations over the last 20 yr. These long-term changes are similar to those found in the Strait of Juan de Fuca, where most *Macrocystis* and *Nereocystis* populations remained near historical sizes (Pfister et al. 2018). However, the declining reefs in that study were closer to human population centers, which was suggested to play a role in their declines. Since Oregon's coastal human population density is relatively low, coastal development is less likely to be driving Oregon's declining reefs. These results, that is, general stability over long time periods combined with some declines in particular regions, also match trends in southern and central California *Macrocystis* elucidated by Landsat-derived time series (Bell et al., 2018).

Given the collapse in northern California *Nereocystis* associated with MHW and SSW (Rogers-Bennett and Catton 2019), we expected to see similar declines in Oregon after 2015. This was not observed, raising the question of why these geographically close (~200 km) populations responded so differently. One answer could lie in the differences in the intensity of the MHW in each area. Analysis of sea surface temperature shows the maximum monthly mean temperature in northern California during the heat wave was nearly 1.5°C higher than that in Oregon (Table 1). Local adaptation to temperature might be expected to be more important to a species like *Nereocystis* with an annual, ruderal life history strategy, especially considering *Nereocystis* is thought to have higher fecundity than *Macrocystis* (California Department of Fish and Game 2001). If *Nereocystis* did have more locally adapted populations then we might expect deviations from local temperature regimes to be increasingly important to the performance of *Nereocystis*. It follows then that relative metrics of heat wave (e.g., temperature anomalies) would be more informative than absolute ones (e.g., actual temperature) in predicting
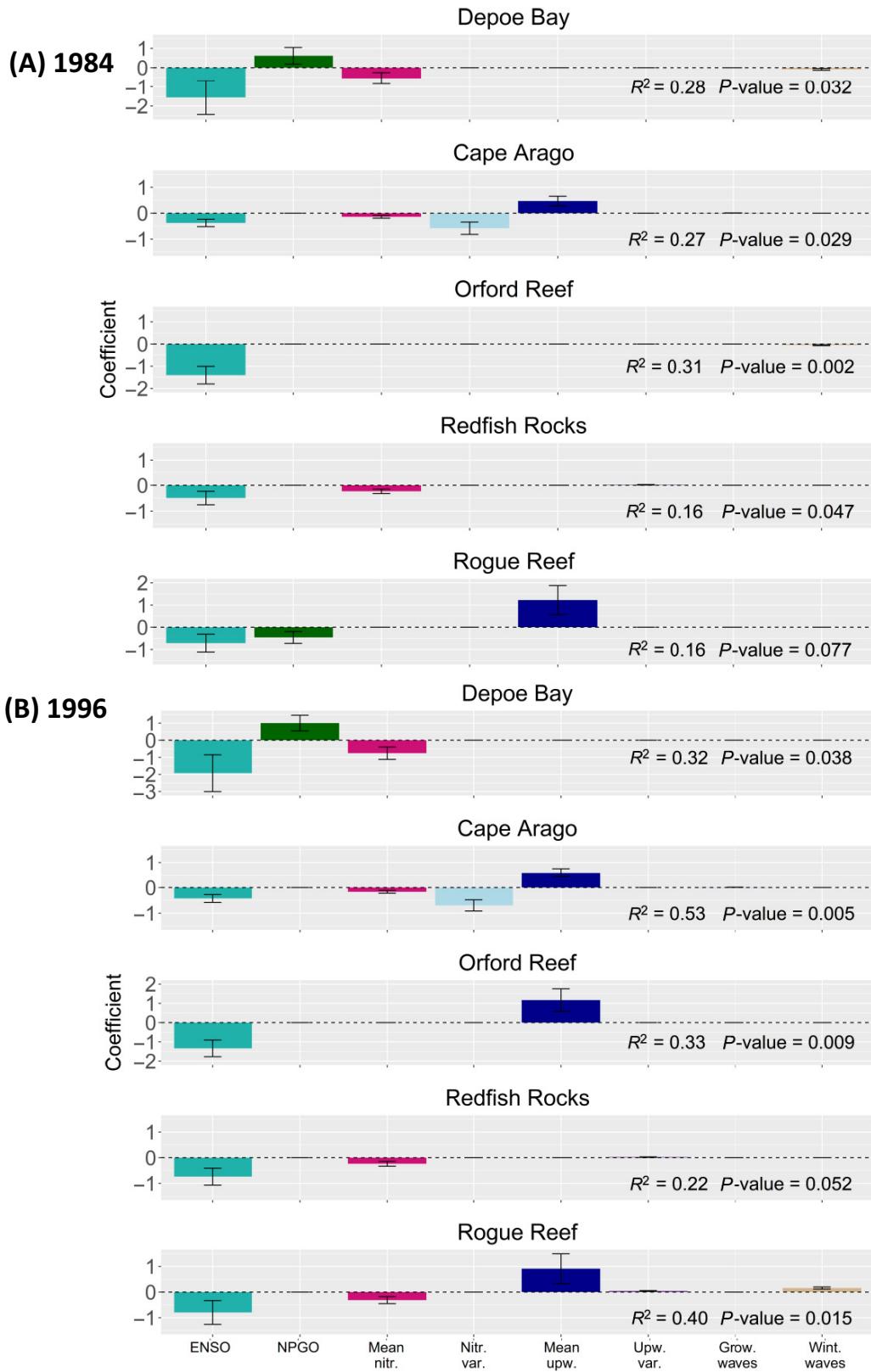
Fig. 3. Bar charts of the estimated coefficient for each variable identified in a best-fit linear model of kelp canopy cover for each of the five biggest reefs in Oregon from (A) 1984–2018 and (B) 1996–2018. Reefs are arranged from north (top) to south (bottom)

and model R^2 and P value are displayed on the bottom right of each graph. Abbreviations for environmental variables are ENSO = El Niño southern oscillation, NPGO = North Pacific gyre oscillation, Mean nitr. = mean estimated seawater nitrate, Nitr. var. = variability in seawater nitrate concentrations, Mean upw. = mean upwelling, Upw. var. = upwelling variability, Grow. waves = maximum growing season waves height, Wint. waves = maximum winter waves height.

responses to MHWs. Indeed, in prior studies, anomalies have been found to be more important in explaining kelp responses to MHWs than absolute temperature (e.g., Bennett et al. 2015). In this case, however, the difference in *Nereocystis* population responses to the 2014–2016 MHW cannot be explained by differences in the relative intensity of the MHW in the two areas. Mean monthly

TABLE 1. Table listing metrics of the heat-wave intensity of the 2014–2016 marine heat wave (MHW) in northern California (latitude = 38.92°) and southern Oregon (latitude = 42.83°).

MHW metric	Northern California	Southern Oregon	Difference significant?
Mean monthly anomaly	0.983	0.605	No ($P = 0.10$)
Maximum monthly anomaly	3.1	3.08	–
Total number of MHW days	300	315	No ($P = 0.29$)
Mean monthly temperature	13.06	12.08	Yes ($P = 0.002$)
Maximum monthly temperature	16.00	14.56	–

Notes: All temperatures are in degrees Celsius. Significance testing for the mean monthly anomaly and temperature was conducted using a one-tailed t test and for total number of MHW days using a one-tailed binomial test.

TABLE 2. Environmental variables present in the best-fit statewide linear models of maximum summer canopy area for the five largest reefs in Oregon for 1984–2018 and 1996–2018, the estimate coefficient for each variable, and the P value of each term.

Year	Model P value	R^2	Variable	Coefficient (m^2)	P value
1984–2018	<0.0001	0.35	El Niño	−110,816	0.0007
			Mean nitrate concentration	−24,370	0.32
			Orford Reef: mean nitrate concentration	63,692	0.034
1996–2018	<0.0001	0.35	El Niño	−119,189	0.001
			Mean nitrate concentration	−32,783	0.16
			Orford Reef: mean nitrate concentration	60,729	0.035
			Maximum winter wave height	83,965	0.049
			Mean upwelling	2,064	0.10

Notes: All variables represent growing-season (defined as March–August) data, except for maximum winter wave height. A categorical variable for all five reefs was included in the models, but only the effect of Orford Reef was significant.

temperature anomaly over these years did not differ between northern California and Oregon ($P = 0.10$) and the maximum monthly anomaly was very similar in the two places.

The total number of MHW days, another metric that has been tied to kelp responses to MHWs, was also not different between the two places (P value = 0.29; Smale et al. 2019). The only metric of MHW intensity we examined that was higher in northern California was the mean monthly temperature, which was nearly 1.5°C warmer in northern California than southern Oregon (P value = 0.002). Mean monthly temperature is a measurement of the absolute intensity of a MHW rather than relative intensity. Similarly, Cavanaugh et al. (2019) found that this metric, maximum mean monthly temperature, was most closely related to *Macrocystis* resistance to the 2014–2016 heat wave near its equatorward range limit. Thus, for two different species and two locations separated by nearly 1,000 km, kelp responses to the 2014–2016 MHW in North America were best explained by absolute temperature, rather than relative thermal anomalies.

It should be noted, however, that the MHW was not the only disturbance to impact these kelp ecosystems at this time. Urchin populations increased in both places, likely because of release from top-down predation by the sunflower star *P. helianthoides* via SSW (Appendix S1: Fig. S6; Rogers-Bennett and Catton 2019). Unfortunately, it is difficult to draw conclusions about whether the increase in urchin populations was quantitatively different between the two places, because long-term data on purple urchin populations in Oregon is limited. Anecdotally, however, Oregon urchin populations did not seem to reach the incredibly high densities seen in California immediately after SSW.

Environmental drivers

The modeled environmental drivers of *Nereocystis* abundance both confirm and challenge our prior understanding of North American kelp forest drivers, based heavily on *Macrocystis* studies. For example, El Niño was strongly negatively correlated with *Nereocystis* abundance both in the statewide model and on each reef. Negative El Niño impacts have been documented before in both *Macrocystis* and *Nereocystis* and are usually attributed to warmer, less nutrient-rich waters, and increased storms (Dayton and Tegner 1984, Bell et al. 2015, Pfister et al. 2018).

However, other potential environmental drivers we identified in this analysis complicate this explanation for the mechanism behind El Niño's strong negative impact. For example, the negative association of *Nereocystis*

abundance with nitrate concentration contradicts the negative correlation between abundance and El Niño. Although studies on *Macrocystis* in California have found that nutrient concentration is often a primary determinant of kelp forest abundance, intermittent upwelling keeps Oregon's nitrate levels mostly in the 5–15 μmol/L range throughout the growing season (Jackson 1977, Reed et al. 2011). These nitrate concentrations may not limit *Nereocystis* growth, as they are similar to the concentrations at which closely related kelps maximize growth rates (~2–5 μmol/L for *Macrocystis*, (Zimmerman and Kremer 1986, Kopczak et al. 1991) and ~5–10 μmol/L for several *Saccharina* species (Chapman et al. 1978, Wheeler and Weidner 1983)). Studies on intertidal kelp populations in Oregon have found evidence that kelp are nutrient-replete and that light limitation by plankton blooms negatively impact kelp growth rates at high nutrient levels (Kavanaugh et al. 2009). However, very little physiological work has been done on *Nereocystis* responses to nutrient concentration. This calls for further inquiry into nutrient requirements, utilization, and storage in *Nereocystis* to understand better if this species and annual kelps in general utilize nutrients differently than better-studied perennial species.

The positive relationship between winter wave height and *Nereocystis* abundance also differs from the generally accepted mechanism behind the negative impacts of El Niño on North American kelp populations. Extensive literature has found strong negative impacts of waves on *Macrocystis* (Dayton and Tegner 1984, Reed et al. 2011). Although *Nereocystis*, like *Macrocystis*, is often dislodged and effectively killed by storm events, considering its life history strategy illuminates why interannual *Nereocystis* abundance may not have a negative relationship with wave height. Although *Nereocystis* thalli are regularly ripped out by fall and winter waves, as a mostly annual species these populations are adapted to decreasing dramatically during the winter after reproduction has taken place, followed by spring regrowth of kelp beds from a new generation of sporophytes. Conversely, *Macrocystis* populations are perennial and reproduction occurs year-round (although with some seasonality), and thus plant mortality from winter storms decreases the standing population size and reproductive output (Anderson and North 1967).

Although life history differences may explain a neutral relationship between *Nereocystis* and winter wave height, it does not necessarily explain the positive relationship. As one alternative, hypothetically, the positive relationship could be an indirect effect of waves on *Nereocystis* that is transmitted by biotic interactions such as competition or predation. As only winter wave height (rather than growing season wave height) was consistently related to *Nereocystis* abundance, these effects may be imposed on the juvenile life stages rather than the adults. *Nereocystis* grows particularly well in wave-exposed environments and is a poor competitor with many other algae (Springer et al. 2010). It is possible that *Nereocystis* tolerates high wave action better than other competitively dominant algae and thus gains a competitive edge when high wave action in the winter precludes other algae from settling (Dobkowski et al. 2019). Alternatively, urchin grazing can be intense on juvenile kelp (Dean et al. 1984) and if large wave events in Oregon force urchins to seek shelter, intense wintertime wave action may limit urchin grazing on juvenile *Nereocystis* and allow for increased survival to adulthood (Ebeling et al. 1985). It should also be noted that in our statewide models, the positive effects of winter wave height and upwelling were absent in the 1984–2018 model but emerged in the more recent 1996–2018 model. This suggests that these factors may have become more important in controlling *Nereocystis* populations in recent years, and is particularly interesting considering that upwelling and wave height have been increasing in Oregon under climate change (Dello and Mote 2010, Ruggiero et al. 2010).

Overall, our study illustrates how the power of remote sensing studies can supplement laboratory and field experiments to help us build broader, more useful theory on how kelp communities will respond to climate change. For example, our work offers insights into the effect of temperature on *Nereocystis*, particularly when combined with laboratory studies. Muth et al. (2019) found that, in the laboratory, *Nereocystis* reproduction largely failed when temperatures were increased from 12° to 18°C. Our study may put a more precise number on that thermal threshold. During the MHW, maximum monthly sea surface temperature in northern California was roughly 16°C, whereas in Oregon it was 14.5°C. Considering the vastly different responses by these two populations to the 2014–2016 MHW, this may suggest that a physiological thermal threshold for *Nereocystis* may lie somewhere between these two temperatures. Additionally, if supported by subsequent research, the hypothesized impact of waves on *Nereocystis* populations suggests how differences in life-history strategy should be incorporated into our theoretical understanding of how kelp communities respond to climate change. Many models project that ocean storms will intensify under climate change and Ruggiero et al. (2010) have shown that significant wave height is increasing in the Pacific Northwest. Although increased storminess could be deadly for *Macrocystis* forest communities (Byrnes et al. 2011), no one has yet investigated how changes in storm frequency and severity could impact species like *Nereocystis* and the communities living amongst them.

Remote sensing efficacy

These ecological insights regarding the historical variability of *Nereocystis* populations, population stability in the wake of a marine heat wave and SSW, and the unique relationships between estimated seawater nitrate concentrations, winter wave height, and *Nereocystis* population size testify to the usefulness of remote sensing in studying kelp population dynamics. Remote

sensing has the potential to vastly increase our understanding of canopy-forming kelps in many parts of the world where long-term data sets are unavailable (e.g., Friedlander et al. 2018). However, although Landsat imagery worked well for estimating *Nereocystis* area in Oregon, where *Nereocystis* is often found in dense offshore forests, it may not be useful everywhere due to its relatively coarse pixel resolution (30 m). Landsat imagery will be less useful in areas where *Nereocystis* or other canopy-forming kelp occur in sparser, smaller forests or closer to the shore. For example, in areas like British Columbia where the coastline is very complex and *Nereocystis* occurs within meters of the shore, Landsat pixels often include land and kelp within a single pixel, which are more difficult to distinguish between than water and kelp (Nijland et al. 2019).

Because identification of *Nereocystis* canopy from Landsat imagery will be limited in many contexts, scientists should take advantage of more recent technologies to map and monitor canopy-forming kelp. For example, the European Space Agency's Sentinel satellites, which have a 10-m resolution and were launched in 2015, can greatly improve estimates of canopy-forming kelps over Landsat in many contexts. Additionally, drones can be used to do very high-resolution mapping, although they require trained personnel to be physically present in a location as opposed to the ease of remotely downloading imagery from a website. Although aerial mapping of kelp, whether by satellites, planes, or drones, is useful in understanding the population dynamics of canopy-forming kelp, it cannot (currently) tell us anything about the state of the kelp forest lying beneath the surface. These long-term aerial maps will be most useful when paired with subsurface monitoring to tie together the surface-level and subsurface ecosystem dynamics.

Conclusions

This study builds upon previous remote sensing work to show that Landsat imagery can be used to generate multidecade, regional time series of *Nereocystis* population dynamics, particularly when conducted in a region with relatively large, offshore kelp forests. The resulting time series unveiled both expected and unexpected insights into the regional ecology of *Nereocystis* populations. This study expands our understanding of regional-scale, multidecadal population dynamics beyond that of perennial, late-succession species like *Macrocystis* and *Ecklonia*. When analyzed with environmental parameters, the 35-yr time span of the new data set enable insights into the response of *Nereocystis* to climate-related variability as expressed in climate modes such as ENSO and NPGO, as well as variation in nutrients and wave height. We found that major recurrent perturbation as expressed in ENSO had negative effects on *Nereocystis* similar to those observed in California for *Macrocystis*. However, we also identified potential environmental drivers that had opposite relationships to

Nereocystis abundance than would be expected based on literature, particularly the negative relationship with nutrients and the positive relationship with wave height. Although the apparent nutrient relationship may be spurious because nutrient availability will rarely be limiting in Oregon, the positive relationship with waves is not wholly unexpected when one considers this kelp's annual life history strategy. This demonstrates the value of incorporating key life history characteristics in our mechanistic understanding of kelp forest drivers. Finally, we suggest that our approach may greatly expand our understanding of long-term dynamics of global populations of kelp with surface expression, and thereby provide deeper insight into how climate change is impacting these crucial ecosystem engineers and help us build theory to predict how it will continue to do so into an uncertain future.

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