Environmental controls on spatial patterns in the long-term persistence of giant kelp in central California

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Abstract. As marine management measures increasingly protect static areas of the oceans, it is important to make sure protected areas capture and protect persistent populations. Rocky reefs in many temperate areas worldwide serve as habitat for canopy-forming macroalgae and these structure-forming species of kelps (order Laminariales) often serve as important habitat for a great diversity of species. *Macrocystis pyrifera* is the most common canopy-forming kelp species found along the coast of California, but the distribution and abundance of *M. pyrifera* varies in space and time. The purpose of this study is to determine what environmental parameters are correlated with and their relative contribution to the spatial and temporal persistence of *M. pyrifera* along the central coast of California and how well those environmental parameters can be used to predict areas where this species is more likely to persist. Nine environmental variables considered in this study included depth of the seafloor, structure of the rocky reef, proportion of rocky reef, size of kelp patch, biomass of kelp within a patch, distance from the edge of a kelp patch, sea surface temperature, wave orbital velocities, and population connectivity of individual kelp patches. Using a generalized linear mixed effects model (GLMM), the persistence of *M. pyrifera* was significantly associated with seven of the nine variables considered: depth, complexity of the rocky reef, proportion of rock, patch biomass, distance from the edge of a patch, population connectivity, and wave orbital velocities. These seven environmental variables were then used to predict the persistence of kelp across the central coast, and these predictions were compared to a reserved dataset of *M. pyrifera* persistence, which was not used in the creation of the GLMM. The environmental variables were shown to accurately predict the persistence of *M. pyrifera* within the central coast of California ($r = 0.71$, $P < 0.001$). Because persistence of giant kelp is important to the community structure of kelp forests, understanding those factors that support persistent populations of *M. pyrifera* will enable more effective management of these ecosystems.

Key words: *foundation species; generalized linear mixed effects models; giant kelp; GLMM;* Macrocystis pyrifera; *population connectivity; spatial persistence; wave climate.*

Introduction

Populations of species are spatially patchy throughout ecosystems, and understanding the environmental causes of this patchiness is a central focus in ecology (Wright 1931, MacArthur and Wilson 1967, Levins 1969). Island biogeography theory and the theory of metapopulation dynamics have helped to understand and quantify ecological dynamics over broad spatial scales (Hanski and Simberloff 1997) but many of these studies are conducted over short time periods and with consideration for few

environmental drivers. Because the persistence of metapopulations over broad scales is reliant on both the spatial configuration of habitat and population dynamics (Hanski 1997), incorporating the combination of habitat attributes and population factors can help to better explain species distributions and persistence over patchy landscapes.

Understanding species distributions over broad scales, especially the distribution of persistent populations, is important as management measures increasingly protect static areas (Gaston et al. 2002, Claudet et al. 2008). Persistence refers to the continued existence of a species through time, signifying that a population does not go extinct or, if it does, that it recolonizes during a given period of time (Connell and Sousa 1983). Of particular importance is the persistence of foundation species:

species such as terrestrial forests, kelp forests, coral reefs, and seagrasses that define and provide food and habitat for entire ecological communities (Jones et al. 1997, Connell 2003, Ellison et al. 2005). However, the presence of foundation species varies in space and time, and this variability impacts the structure of the communities they support (Levin and Hay 1996, Thompson et al. 1996). Therefore, understanding the environmental factors correlated with the persistence of habitat-forming species could improve our understanding of community dynamics across landscapes and enable more effective management of these ecosystems. The majority of studies that have looked at the broad-scale distribution of species over long time periods were conducted in terrestrial landscapes mostly with plant communities and forests (e.g., Kouki et al. 2004, Mas et al. 2004, Marini et al. 2012). A likely reason for the focus on plant communities and forests is they consist of large patches and are discernible using remote sensing technology. Unfortunately, the time scales of these studies do not capture multigenerational persistence of species and focus more on the effect of human land use rather than ecological drivers of persistence.

By contrast, many foundation species in marine systems, particularly macroalgae, have much shorter generation times. In particular, rocky reefs in many temperate areas worldwide serve as substrate for canopy-forming macroalgae (e.g., kelp; Schiel 1988, Graham et al. 2007, Connell and Irving 2008, Springer et al. 2010, Carr and Reed 2015) and these structure-forming kelp species often serve as important habitat for numerous other species (Foster and Schiel 1985, Steneck et al. 2002, Graham et al. 2007, Carr and Reed 2015). Giant kelp, *Macrocystis pyrifera,* is the world's most widely distributed kelp species (Graham et al. 2007), has a generation time of between 3 and 7 yr, and is the foundation species for one of the most productive ecosystems on earth (North 1971, Dayton 1985, Foster and Schiel 1985, DeMartini and Roberts 1990, Steneck et al. 2002). Along the Pacific coast of North America from central California to Baja California, *M. pyrifera* is the most common and competitively dominant canopy-forming kelp species (Bushing 2000, Graham et al. 2007, Carr and Reed 2015), but its presence and abundance varies spatially and temporally (Dayton et al. 1992, Edwards 2004, Edwards and Estes 2006). The purpose of this study is to determine the environmental correlates of the spatial and temporal persistence of *M. pyrifera* along the central coast of California and their relative contribution to persistence.

Understanding the distribution and persistence of *M. pyrifera* throughout its range is important to understanding the community dynamics within these kelp forests (Bushing 2000, Arkema et al. 2009, Byrnes et al. 2011). In this study, we define persistence as the number of years *M. pyrifera* is present in a spatial location. Although *M. pyrifera* tends to persist in certain areas, it is spatially patchy and temporally variable throughout its range (Reed et al. 2006). This variability is believed to be caused by a number of abiotic and biotic conditions including effects of currents, temperature, substrate, depth, nutrient availability, swell intensity, size of kelp patch, species assemblages within the forest, and planktonic distribution (Dayton 1985, Dayton et al. 1992).

Many of the processes responsible for the temporal and spatial heterogeneity of patterns of marine organisms occur over longer time periods and broader spatial scales than can be captured in the typical design of studies done in small, homogenous areas (Foster 1990, Carpenter et al. 1995, Dayton et al. 1999). Therefore, the use of classical field sampling techniques makes it difficult to look at broadscale patterns in coastal marine ecosystems (Cavanaugh et al. 2010). With an increase in the availability of high resolution remote sensing technology, however, there is now the potential to make observations over broad spatial and temporal scales (Jensen et al. 1980, Belsher and Mouchot 1992, North et al. 1993).

Because forests of *M. pyrifera* often form dense surface canopies, satellite images can be used to derive biomass estimates, which are verified through diver-based measurements, to map the temporal and spatial extent of estimated *M. pyrifera* biomass (Cavanaugh et al. 2010, 2011). Biomass estimates allow *M. pyrifera* persistence to be quantified over long time periods and over broad spatial scales, which can be combined with environmental information to determine what variables drive the distribution and persistence of *M. pyrifera* over its entire range. For example, Cavanaugh et al. (2011) found that wave disturbance and sea-surface temperature were the primary factors correlated with variations in kelp biomass within the Santa Barbara Channel. In addition, previous studies have linked the distribution and persistence of *M. pyrifera* to attributes of the seafloor habitat such as bottom relief and wave action (Bushing 2000), but these studies have been done using low resolution data at broader spatial scales. These studies have also been limited to Southern California kelp forests, and it is unknown whether the same factors are important in other regions along the range of *M. pyrifera*. Furthermore, spatial heterogeneity of the seafloor including susceptibility to disturbance (Sousa 1984) and variation in structural complexity (Pearsons and Li 1992) could also play a significant role in kelp persistence.

Most previous studies into factors affecting the persistence or distribution of *M. pyrifera* have focused on one or two environmental variables over short time periods. The purpose of this study is to explore the relationship between the long-term persistence of *M. pyrifera* and known environmental relationships to determine which environmental factors are most important to persistence across multiple generations and if a combination of variables can be used to accurately predict persistence over large geographic scales. In this study, we use fine scale seafloor habitat variables derived from multibeam bathymetry along with other environmental

factors to determine what habitat attributes are correlated with and their relative contribution to the temporal and spatial persistence of *M. pyrifera* along the central coast of California. The general hypothesis is that *M. pyrifera* persistence will vary predictably with depth, variations in the structure of the rocky reef, patch characteristics including the size and biomass of individual patches, distance from the edge of the patch, variations in wave orbital velocities, changes in sea-surface temperature (SST), and the connectedness of a kelp patch. Specifically, the following relationships are predicted based on previous findings in the literature. First, *M. pyrifera* persistence will have a nonlinear (hyperbolic) relationship with depth; persistence will be greatest at intermediate depths, decreasing with shallower depths due to increases in swell intensity and irradiance (Graham 1996, Swanson and Druehl 2000) and deeper depths due to decreases in irradiance (Cribb 1954, Foster and Schiel 1985, Graham 1997, Graham et al. 2007). Second, *M. pyrifera* persistence will decrease with increases in topographic complexity of the rocky reef (Deysher et al. 1998, Grove et al. 2002). Third, *M. pyrifera* persistence will increase with higher proportions of rocky substratum as they require hard substrate for attachment (Cribb 1954, Foster and Schiel 1985, Westermeier and Möller 1990, Schiel et al. 1995, Carr and Reed 2015) and can be disturbed with increases in sediment (Devinny and Volse 1978, Shaffer and Parks 1994, Spalding et al. 2003, Shepherd et al. 2009, Geange et al. 2014). Fourth, *M. pyrifera* found in larger patches, more abundant patches, and further toward the center of a patch will increase in persistence because kelp patches have a moderating effect on currents (Jackson and Winant 1983, Jackson 1984, Rosman et al. 2007) and increased recolonization potential with higher densities (Reed et al. 2004). Fifth, *M. pyrifera* persistence will increase with the population connectivity of a kelp patch (Reed et al. 2004, Alberto et al. 2011). Sixth, *M. pyrifera* persistence will decrease with increases in wave orbital velocities due to higher disturbance potential (Seymour et al. 1989, Edwards 2004). Seventh, *M. pyrifera* persistence will decrease with increases in SST because increased temperatures are correlated with decreased nitrate availability (Zimmerman and Robertson 1985, Hernández-Carmona et al. 2001). Finally, we predict that strong relationships between *M. pyrifera* and some combination of environmental variables will allow for accurate predictions of *M. pyrifera* persistence.

We tested for these relationships using a spatially explicit, predictive modeling approach to determine what combination of habitat variables are important to the persistence of *M. pyrifera* and the relative contribution of each significant variable. We then used these predictions to forecast the persistence of *M. pyrifera* across the region and compared our results to a reserved dataset to see how well a combination of habitat and population variables can determine the persistence of *M. pyrifera*.

Methods

Study location

The study area for this project was along the central coast of California, which extends from Pigeon Point in the north (37°10′57″ N, 122°23′38″ W) to Point Conception in the south (34°26′55″ N, 120°28′14″ W). *M. pyrifera* has a patchy and variable distribution along this section of the California coast (Fig. 1) and there is variation in seafloor substrate complexity, depth, currents, temperature, and wave orbital velocities, making it an ideal area to determine the relative extent to which these different environmental parameters correlate with the persistence of *M. pyrifera*.

Using satellite data to estimate kelp canopy biomass and persistence

Macrocystis pyrifera forms distinct and dense floating canopies at the ocean surface, which are distinguishable with satellite imagery (Jensen et al. 1980, Belsher and Mouchot 1992, North et al. 1993). Using the methods developed by Cavanaugh et al. (2010, 2011), we used high-resolution multispectral satellite imagery to quantify *M. pyrifera* biomass along the central coast of California from May 1984 to September 2011. Using cloud-free imagery, we were able to estimate *M. pyrifera* biomass every 1–2 months. To calculate persistence, as defined in this study, we converted those estimates of *M. pyrifera* biomass for each of the 30-m resolution Landsat 5 Thematic Mapper pixels within the region to binary presence/absence maps derived from the annual mean biomass for the 28 yr used in this study. With absence assigned a value of "0" and presence assigned a value of "1", we collated these binary maps (summed) to produce a map of the number of years that *M. pyrifera* was present in each of the Landsat pixels (values ranged from 1 to 29 yr; Fig. 2). This definition of persistence (the number of years kelp is present in a Landsat pixel) differs from patch-based persistence values used by Reed et al. (2006) and Castorani et al. (*in press*), since we are only interested in presence and not extinction. We derived a centroid point from each of the Landsat pixels within the region from the persistence maps and used these persistence points as the response variable in the predictive models.

Environmental variables

Seafloor structure variables.—Multibeam data coverage is available for the majority of the region under study at 2-m resolution within the depth range of kelp distribution (California State Mapping Program [CSMP]; *available online*).[7] There is a gap in data coverage between the shore and where multibeam data starts (anywhere between the 2-m and 10-m contour). This gap exists because multibeam data cannot be acquired using traditional, ship-based mapping methods where navigation
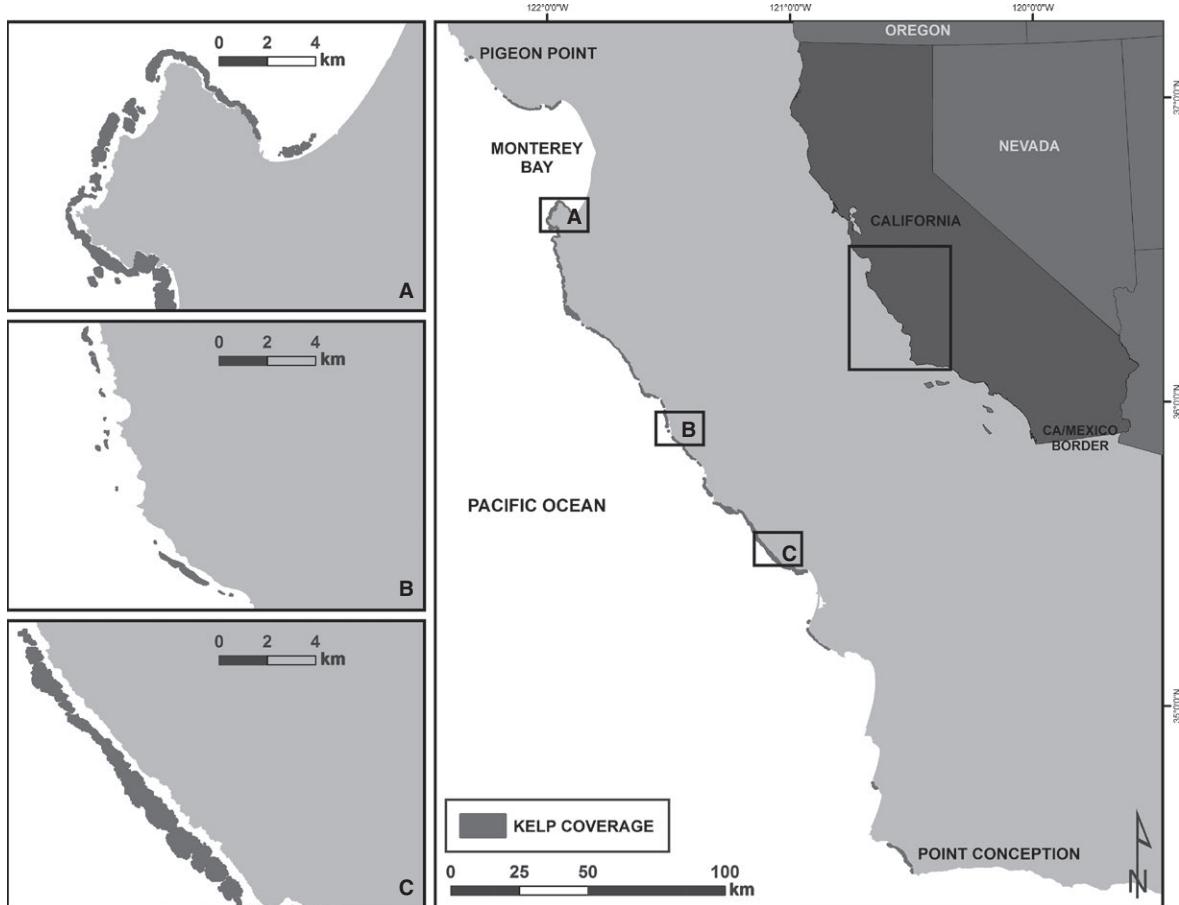
Fig. 1.   The study region is shown in the map on the right, which extends from Pigeon Point in the north to Point Conception in the south along the central coast of California. *Macrocystis pyrifera* coverage derived from the Landsat imagery is shown in dark gray. Boxes (A), (B), and (C) display the patchy distribution of kelp along small sections of the coastline.

hazards such as breaking waves and exposed rocks are present. Therefore, we limited the analyses in this study to the region where multibeam data are available. Where available, multibeam data provide full coverage depth values for the seafloor, which were converted into 2 m resolution digital elevation models (DEMs). We used the resulting DEMs to provide depth information and derive other structure variables likely to be of importance to the distribution and persistence of *M. pyrifera* within the central coast region of California.

The first variable we derived from the multibeam data was the complexity of the rocky reef. More complex reef is likely to have more variation in physical conditions (e.g., light, sediment cover, water motion, etc.; Toohey et al. 2007), which can influence the presence of algae (Seymour et al. 1989, Thomson et al. 2012). In this study, complexity of the rocky reef is based on the slope of slope of the terrain (rate of change of slope) and was calculated within ArcGIS 10.x using the Spatial Analyst toolbox (ESRI 2014). First, the slope was computed for the DEM, and then slope was computed again on the resulting slope raster to provide the rate of change in

slope or slope of slope. Previous work has shown that slope of slope is an adequate measure of complexity for better understanding distributions of marine species (Pittman and Brown 2011).

The amount of hard substrate is likely to be important to the persistence of *M. pyrifera*. With only a few exceptions, kelp forests occur on hard substrates where holdfasts more firmly attach (Dayton 1985, Smith et al. 2004). Additionally, greater spatial coverage of rock reduces the amount of soft sediment in the area that could potentially result in burial of hard substrate (Storlazzi et al. 2011, 2013), which can negatively affect recruitment (Devinny and Volse 1978, Geange et al. 2014). Increased sediment could also result in increases in turbidity and reduced irradiance and, as a result, affect the abundance and depth distribution of kelp (Shepherd et al. 2009). We therefore used the rock/sediment substrate maps developed through the CSMP to calculate the proportion of hard substrate within each of the Landsat pixels. The resulting layer provides a measure of available suitable habitat within each of the Landsat pixels.
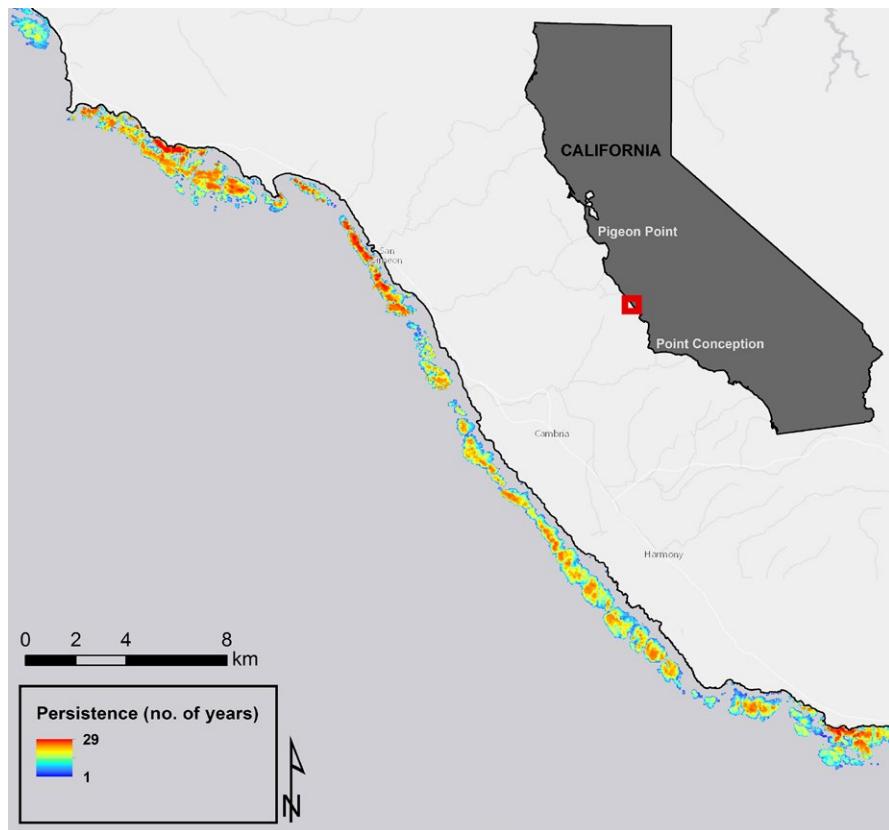
Fig. 2. The persistence of *Macrocystis pyrifera* along a small portion of the central coast of California. The warmer colors represent higher persistence (greater number of years when *M. pyrifera* is present in a certain location) compared to the cooler colors, which represent areas where *M. pyrifera* is less persistent. Persistence is measured at 30-m resolution (the resolution of the Landsat data). Service Layer Credits for ESRI grayscale background image: Copyright 2013 Esri, DeLorme, NAVTEQ.

We scaled all of the above 2-m resolution seafloor habitat variables to the 30-m resolution Landsat pixels by using the "Focal Statistics" tool within ArcGIS Spatial Analyst. We computed the mean and standard deviation of the 2-m resolution maps for depth and complexity with a 30 × 30 m moving window.

Patch-based variables.—The size and structure of kelp patches themselves are also likely to influence persistence of *M. pyrifera*. For example, the structure of kelp plants has been shown to buffer against currents from the edge and toward the center of a kelp patch (Jackson and Winant 1983, Jackson 1984, Rosman et al. 2007, 2010). Rosman et al. (2007) and Gaylord et al. (2007) found that currents are reduced at a rate correlated with the coverage of surface canopy. The greater distances from the edge of a kelp patch could also be related to an increase in spore delivery (Gaylord et al. 2006). In addition to the inward distance from the edge of the kelp patch (i.e., toward the center), the overall size of a kelp patch and abundance within the patch is potentially correlated with the persistence of *M. pyrifera* due to increased density leading to higher probability of recolonization (Reed 1990). To include the effect of the individual patches on

the persistence of *M. pyrifera*, we defined contiguous kelp patches for the region. To define the kelp patches, we designated Landsat pixels that contained *M. pyrifera* at any time during the duration of this study as "kelp presence," and contiguous "presence" pixels were combined to form individual patches (Fig. 3A). Once the patches were defined, we used the "Euclidean Distance" tool within the "Spatial Analyst Tools" toolbox to find distance from the edge of these patches and the "Calculate Geometry" tool to calculate area of each of these patches. To account for patch abundance, we computed average annual biomass for each Landsat pixel across the entire region and then summed these values within individual patches to estimate total biomass of each patch for the time period of the study.

Connectivity of kelp populations.—In previous work, Cavanaugh et al. (2014) developed a framework using graph theory and spatial autocorrelation for distinguishing "subpatches" (subpopulations) within contiguous "megapatches" of *M. pyrifera* off the coast of southern California. The dynamics of subpatches within these megapatches match theoretical expectations better than any other scale of patches and, therefore,
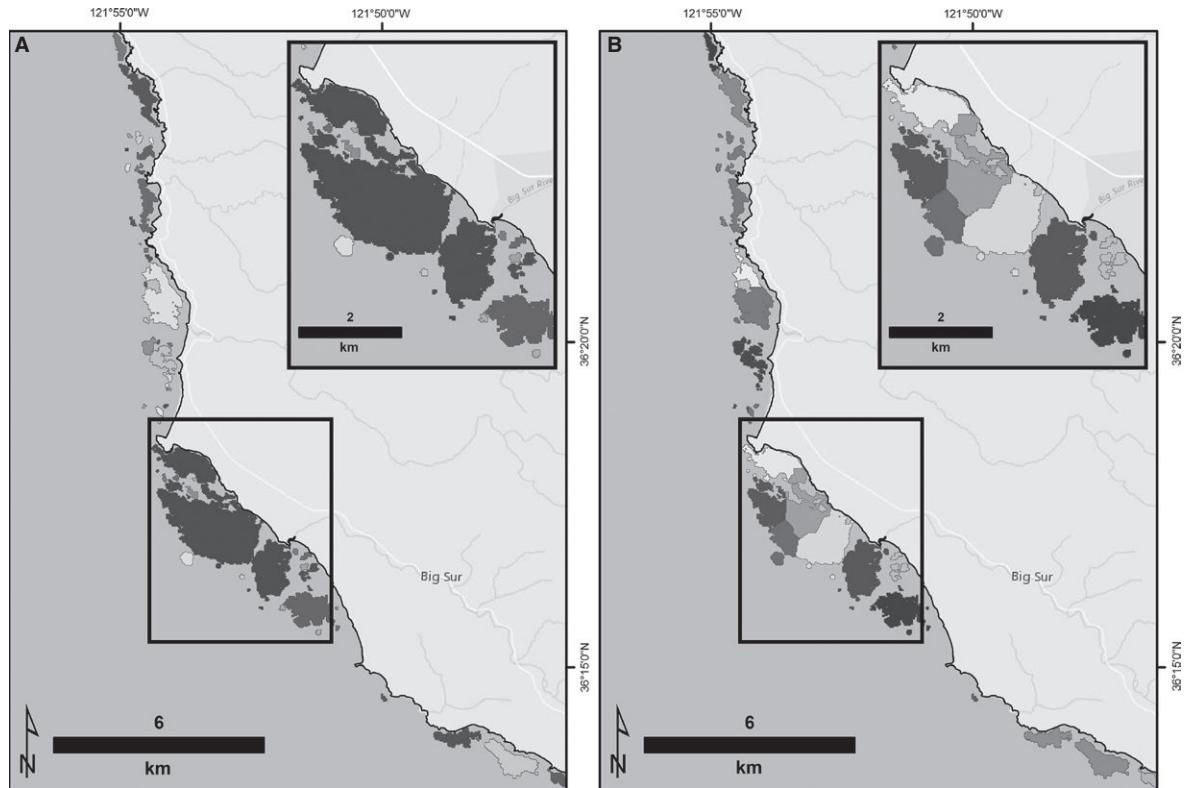
Fig. 3. Examples of (A) the contiguous patches used to calculate the patch variables and (B) the subpatches used to calculate the connectivity between the subpopulations. The different levels of gray in both maps represent different patches and the inset maps show a close-up view of one area of patches to highlight the variation in the different methods for defining patches within the central coast of California. Service Layer Credits for ESRI grayscale background image: Copyright 2013 Esri, DeLorme, NAVTEQ.

likely represent subpopulations within metapopulations (Cavanaugh et al. 2014). We employed these methods in the central California region to delineate patches of *M. pyrifera* representing subpopulations within the overall metapopulation (Fig. 3B) and we used them to determine the relative connectivity of *M. pyrifera* subpopulations across the study region.

Connectivity of kelp patches based on spore transport times using oceanographic models has proven an effective tool for understanding gene flow across populations of *M. pyrifera* (Alberto et al. 2011). To estimate connectivity between kelp patches, we used a three-step process (Castorani et al., *in press*). The first step was to determine biomass for patches of *M. pyrifera* in central California. We computed patch biomass using Landsat information for 30×30 m pixels aggregated into patches of coherent synchrony as described by Cavanaugh et al. (2014). Because biomass is strongly related to spore production, we used biomass as a measure of transportable individuals in the metapopulation context. The second step was to determine the typical number of days it would take a spore to transit among pixels. We calculated the spore connection times using output from a Regional Ocean Modeling Systems (ROMS) simulation for the central coast study region. The model is realistically configured over a domain extending from Mexico to Washington State at one-third degree horizontal resolution. Details of the model implementation and evaluation, and its application to larval transport studies in the California Current System can be found in Drake et al. (2011, 2013). For this investigation, we used 7 yr (2000–2006) of bidaily, springtime releases to calculate mean connection times following Mitarai et al. (2009; their eq. 13) between near-coastal cells extending 10 km cross-shore and 30 km alongshore. Larvae were assumed to be passive (i.e., exhibiting no larval behavior) but influenced by turbulent mixing as they were transported for up to 90 d by the full three-dimensional current field. Because the near-coastal cells are much larger than kelp patches, and because there can be multiple kelp patches within a cell, we evaluated the relationship between mean connection time and distance in separate analyses for upcoast and downcoast transit. To do this we calculated mean connection time and mean distance (along coast) between all pairs of cells. The times were modeled as a function of distance and had very strong fits ($R^2 > 0.9$) for transits to the north and to the south. As a result, we used these relationships to estimate the connection time between all the subpatches of kelp. In most ROMS modeling simulations, particles are immortal and never settle or die, which is clearly not realistic. Thus, the third step was to incorporate a reasonable loss rate of spores during tran-

sit between patches due to both settlement and mortality. We used a rate of 90% per d, which is consistent with the results of Reed et al. (1988), who showed that swimming in spores ended within 24 h, indicating a loss of lipid reserves also necessary for successful settlement and metamorphosis. Using this three-step process, we developed a measure of the relative connectivity of each subpatch by estimating the sum of the products of biomass, connection time (between the recipient and donor patch), and loss rate for all other patches in central California.

Sea-surface temperature (SST).—Nitrate limitation is one of the key factors that has been found to reduce the productivity of kelp (Jackson 1977, Dayton et al. 1999), and ocean temperature is correlated with an absence of detectable nitrogen in waters at 16°C or greater in southern California and, therefore, can be used as a proxy for nitrate availability (Jackson 1977, Zimmerman and Robertson 1985, Reed et al. 1997, Tegner et al. 1997). We downloaded SST data from the National Oceanic and Atmospheric Administration (NOAA) website using the Marine Geospatial Ecology Toolbox (MGET) within ArcGIS (Roberts et al. 2010). The SST data used in this study comes from the NOAA Advanced Very High Resolution Radiometer (AVHRR) satellite data, which provides monthly averaged daytime SST data for the region of interest at a resolution of 4.5 km². These monthly averages were used to calculate annual averages to match the temporal resolution of the kelp data. Because the 4.5-km² resolution of the SST was much coarser than the resolution of the habitat variables and kelp persistence data, the SST data were binned into 1°C intervals and treated as a categorical variable in order to preserve the resolution of the other variables.

Wave orbital velocity.—Wave exposure is often one of the main environmental factors affecting the distribution of marine organisms (Denny 1988, Utter and Denny 1996, Sundblad et al. 2014) and has been shown to affect the distribution and persistence of kelp in many regions throughout the world (Foster and Schiel 1985, Graham et al. 1997, 2007, Reed et al. 2011). Wave-induced velocities and acceleration can tear *M. pyrifera* stipes away from the remainder of the plant or remove entire plants, affecting persistence (Koehl and Wainwright 1977, Seymour et al. 1989).

Patterns of wave orbital velocities along the California coast were simulated with the numerical wave model SWAN (Simulating WAves Nearshore). SWAN is a third-generation spectral wave model capable of simulating wind-wave growth, propagation, refraction, dissipation, and depth-induced breaking (Booij et al. 1999, Ris et al. 1999). A set of 15 SWAN model grids were developed and used to simulate wind-wave growth and propagation across the inner portion of the California continental shelf. All grids were curvilinear, with an average cross- and along-shore resolution of 30–50 m and 60–100 m, respectively, in the shallow inshore regions. Model grid cells were smaller in the cross-shore direction, in shallow water, and around complex bathymetry to enable accurate wave refraction and shoaling. Latitudinal extents were defined based on local geography and computation limitations. The offshore extent of the model grids were defined by 64 Wave Information System (WIS; *available online*)[8] model output stations located approximately 20 km offshore along the entire California coast. Wave parameters (significant wave heights, peak wave period, and mean wave direction) derived from the WIS database were applied at the boundaries of the 15 SWAN grids. Thirty-two years of WIS data (1980 through 2011) were used to calculate seasonal (arithmetic) mean and extreme (arithmetic mean of highest 5%) conditions. Seasons were defined as: winter, December through February; spring, March through May; summer, June through August; and fall, September through November.

Parametric wave descriptors (wave heights, periods, and wave direction) derived from the WIS database were applied along the open boundaries of the SWAN domains. Winds from the most centrally located WIS station of each grid were applied uniformly across the domains to allow for inclusion of locally wind-generated waves in addition to (usually greater) energy contributions from distantly generated swell waves. In shallow water, the orbital motions of water particles induced by surface waves extend down to the seabed. The resulting wave-induced orbital velocities near the seabed are considered to be a representative measure of how waves influence the sea floor and as such are a focus of this study.

Tests of hypotheses

Tests of assumptions of analyses.—Prior to testing hypotheses regarding the relationship between *M. pyrifera* persistence and habitat variables, we tested for violations of assumptions of the analyses (e.g., independence, normality, linearity, homogeneity of variance) following the guidelines of Zuur et al. (2009a,b). We used Cleveland dotplots to determine if any of the variables required transformation. We applied multipanel scatterplots, Spearman's rank correlation coefficients, and variance inflation factors (VIFs) to test for collinearity between explanatory variables. Those paired variables that had a correlation coefficient >0.50 or a VIF >3, which is a conservative approach, were not included in models together (Zuur et al. 2009a,b). The only variable that required a square root transformation was the measure of mean topographic complexity (slope of slope). Relationships between *M. pyrifera* persistence and depth and wave orbital velocity were hyperbolic, so we used a quadratic function within the models for both of these variables. We used Moran's *I* to test for spatial autocorrelation among the *M. pyrifera* persistence values. We detected significant spatial autocorrelation in the response variable (*M. pyrifera* persistence) and used

[8] http://wis.usace.army.mil/

a modeling approach that accounted for it (see *Modeling Approach*).

Modeling approach.—To test the hypothesized relationships between persistence of *M. pyrifera* and habitat variables, we applied a generalized linear mixed effects model (GLMM). The persistence data met the assumptions of the Poisson distribution, so we used a GLMM with a Poisson distribution and a log-link function. The GLMM was trained using half of the persistence observations to determine the relationship between persistence and the environmental variables (30785 points were used to train the models while 30784 points were reserved to test the accuracy of the predictions). We used a GLMM because this modeling approach allows for datasets that are hierarchically structured and accounts for dependencies within those hierarchical groups by the use of random effects (Pinheiro and Bates 2000, Zuur et al. 2009*a*,*b*). Persistence of *M. pyrifera* was spatially autocorrelated within subpatches. To account for the spatial autocorrelation of *M. pyrifera* persistence in subpatches, we used subpatch as a random effect in the GLMM. We used a spline correlogram of the Pearson residuals to verify that the spatial autocorrelation was accounted for in the GLMM. The spline correlogram used was smoothed using the spline function (Bjornstad and Falck 2001, Zuur et al. 2009*a*,*b*; see RESULTS). The relative variance explained by variables in the GLMM cannot be modeled for fixed effects using restricted maximum likelihood approximation; therefore, the relative importance of the variables is ranked by their absolute values of the Z scores, reflecting the likelihood of their explanatory value.

The "lme4" package (Bates et al. 2014) in R v3.1.0 (R Development Core Team 2012) was used to run the GLMM. Prior to running the GLMM, we standardized all of the variables using the "scale" function in R. Standardizing coefficients removes the unit of measurement for the variables and allows for comparison of coefficients across a variety of scales (Zuur et al. 2009*a*,*b*). Once standardized, we ran a series of GLMM models to determine the best model for explaining the persistence of kelp along the central coast of California by using Akaike's information criterion (AIC) model selection and the significance of variables. We then chose the best model and used the "predict" function to produce predicted persistence values across the central coast and compared these to the actual values within the reserved persistence points to determine the accuracy of the model in predicting kelp persistence.

RESULTS

Using satellite data to estimate kelp canopy biomass and persistence

Landsat data for the central coast of California estimated 61.4 km² of *M. pyrifera* canopy cover within the shallow subtidal on hard substrate within the 5–30 m depth range. Annual persistence (number of years) of *M. pyrifera* varied throughout this region, ranging from 1 to 29 yr, but was fairly persistent throughout the region with over 60% of the Landsat pixels containing kelp for 15 or more years (Fig. 2; yellow, orange and red hues). From the Landsat data, there were a total of 61569 points of *M. pyrifera* observations within the study region that overlapped with the environmental variables.

Environmental variables

Seafloor structure variables.—The depth distribution of *M. pyrifera* in the central coast region varied from 0.1 to 50 m with an average depth of 15.1 m, and the majority of the kelp, as predicted, occurred in the intermediate 10–20 m depth range (Fig. 4A). Within these depths, *M. pyrifera* was found on rock substrate. The average proportion of rock found within each Landsat pixel was 0.58 with an increase in *M. pyrifera* occurrences as the proportion of rock increases (Fig. 4B). *M. pyrifera*, however, was found on rock substrate of varying complexity with mean slope of slope values of 40.1 (moderate complexity) with a range of 0.4 (very low complexity) to 139.2 (very high complexity) (Fig. 4C).

Patch-based variables.—There were a total of 409 contiguous patches defined within the central coast study region and, along with the seafloor structure variables, the frequency of *M. pyrifera* occurrences varied with changes in each of the variables derived from these patches. The distance from the edges of patches ranged from 0 to 566 m with an average distance of 75.2 m (Fig. 4D). The size (area) of the contiguous kelp patches varied from 0.01 to 2.47 km², with average kelp patch size of 0.89 km² (Fig. 4E). Biomass within kelp patches varied from 33 kg to 6 864 400 kg. However, the distribution was highly skewed to the right, with many more pixels at lower levels of biomass and a median biomass across all patches of 808 717 kg (Fig. 4F).

Connectivity of kelp populations.—The definition of subpatches across the study region resulted in a total of 168 individual subpatches (or subpopulations) within the metapopulation. The relative connectivity values computed for these subpatches ranged from almost no connectivity (<0.001) to complete connectivity (1.00, a patch's connectedness with itself) with a 90% rate of spore loss (Fig. 4G).

Sea surface temperature (SST).—Where kelp was present, SST for the central coast region generally ranged from just over 11°C to just under 15°C with an average temperature of 13.6°C. SST, however, was not included as an explanatory factor in the GLMM for explaining variation in persistence of *M. pyrifera* because it was not significant.

Wave orbital velocity.—*Macrocystis pyrifera* is found across a variety of wave environments from areas where
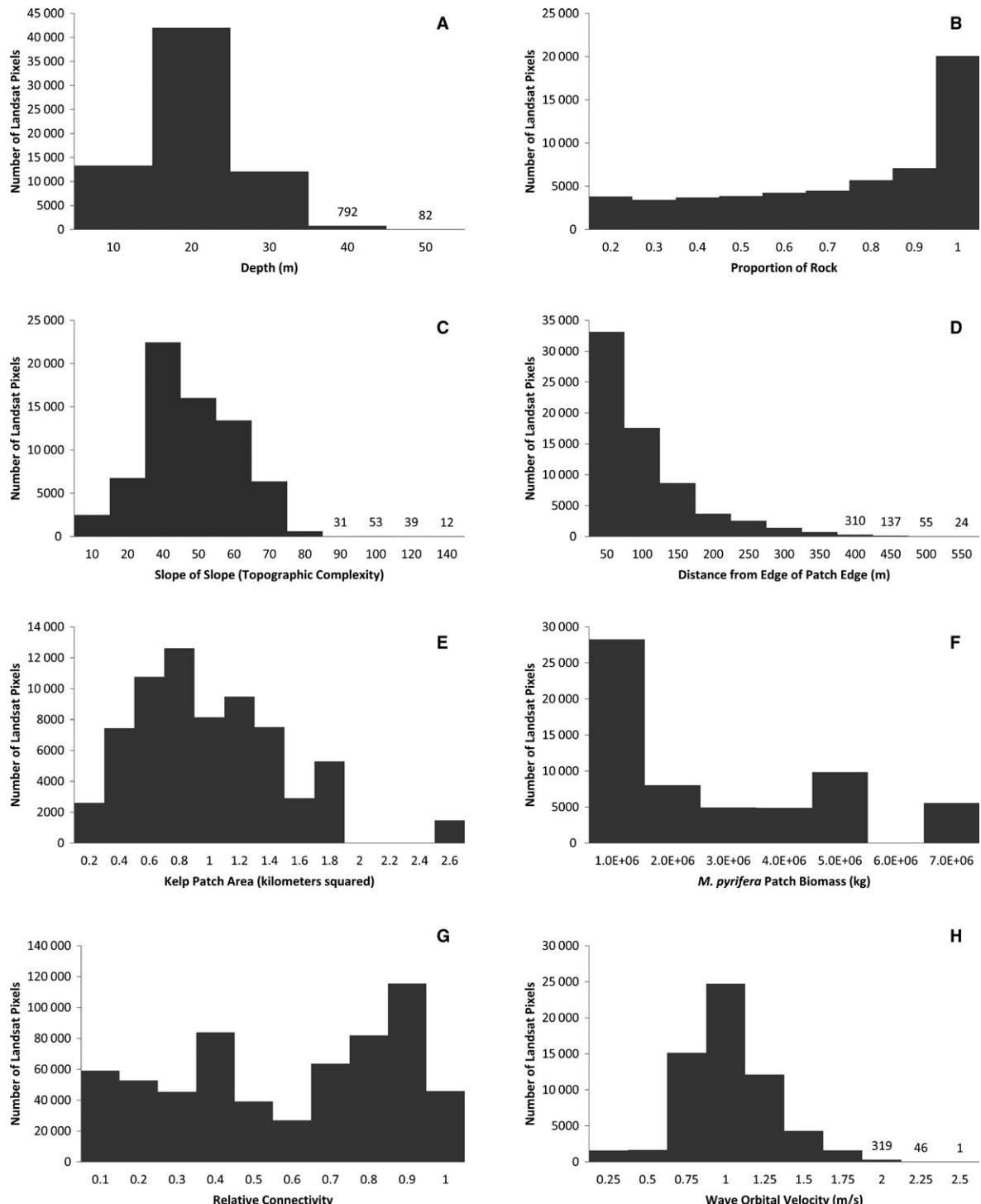
Fig. 4. Frequency distributions of the occurrence of *Macrocystis pyrifera* in relation to (A) variation in depth, (B) propor-tion of rock, (C) slope of slope or topographic complexity, (D) distance from edge of kelp patch, (E) kelp patch area, (F) total biomass within a kelp patch, (G) the relative connectivity of the patch, and (H) the wave orbital velocity. Vertical axes are the number of Landsat pixels where kelp is present within each of the categories of geomorphic structure.

the wave orbital velocity values are close to 0 m/s to areas where the velocity reaches 2.27 m/s. The average orbital velocity value where *M. pyrifera* occurs is 0.89 m/s (Fig. 4H).

Results of modeling approach

Comparison of spatial autocorrelation of residuals from a generalized linear model (GLM) with spatial

autocorrelation of residuals of the GLMM indicated that spatial autocorrelation was better modeled and adequately accounted for in the GLMM (Fig. 5). The best GLMM (i.e., with lowest AIC containing all significant variables) generated from the restricted subset of the dataset to explain persistence of *M. pyrifera* included depth (quadratic function), topographic complexity, top 5% orbital velocity (quadratic function), distance to the edge of the patch, relative connectivity, area of the patch, and proportion of rock (Table 1).

The relationship between *M. pyrifera* persistence and distance inward from the edge of patches was highly significant (GLMM: $P < 0.001$) and was the most important variable in the model (Z score = 100.68; Table 1). The persistence of *M. pyrifera*, therefore, increases towards the center of a kelp patch. Depth was the second most important variable of those tested (Z score = 37.91; Table 1) and, as predicted, the relationship between persistence and depth was non-linear (hyperbolic) and highly significant (GLMM: $P < 0.001$). The relationship between persistence and geomorphic complexity was
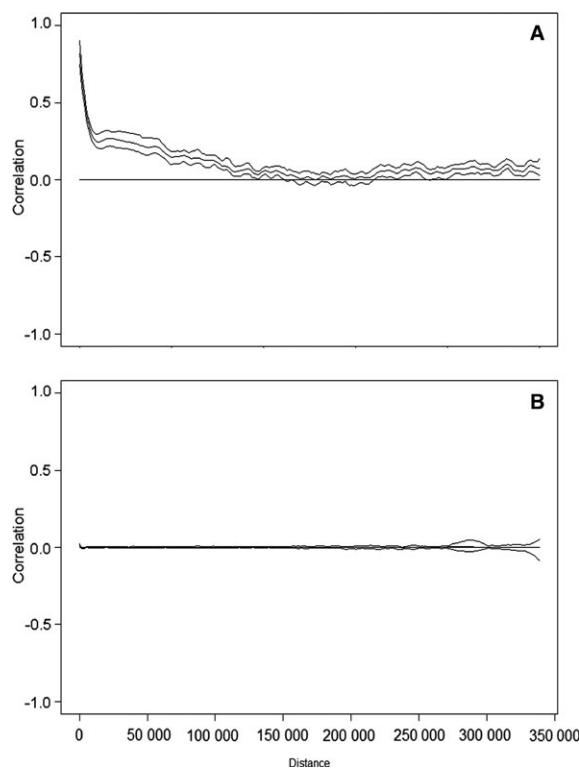

Fig. 5. Spline correlograms with 95% pointwise bootstrap confidence intervals showing the comparison of (A) the spatial autocorrelation of the residuals of a generalized linear model (GLM), which does not take into account spatial autocorrelation, and (B) the spatial autocorrelation of the residuals from the generalized linear mixed model (GLMM). The correlation of the residuals at close distances (measured in meters) in the GLM were significantly correlated, whereas there is almost no spatial autocorrelation at any distance class in the GLMM.

also highly significant (GLMM: $P < 0.001$) and the third most important variable of those tested (Z score = 35.44; Table 1). Contrary to our prediction based on the literature, we detected a positive relationship between persistence and complexity with increased persistence in higher complexity areas. The relationship between persistence and patch biomass was also highly significant (GLMM: $P < 0.001$) and the fourth most important variable of those tested (Z score = 29.06; Table 1), with persistence increasing in patches with higher average biomass. We detected collinearity between the mean and the top 5% wave orbital velocity, so only one of the variables from that pair was included in the different GLMM runs, and the best model included the top 5% wave orbital velocity. As the fifth most important variable in the model (Z score = 14.89; Table 1), the relationship between *M. pyrifera* persistence and top 5% wave orbital velocity was highly significant (GLMM: $P < 0.001$) but the relationship was not as predicted. *M. pyrifera* persistence increased with both decreases and increases in wave orbital velocity (hyperbolic relationship). The relationship between *M. pyrifera* persistence and proportion of rock cover was also significant (GLMM: $P = 0.006$) and the sixth most important variable in explaining variation in persistence (Z score = 3.46; Table 1). As previously shown, *M. pyrifera* persistence increases with increases in rocky substrate. Finally, the relationship between *M. pyrifera* persistence and connectivity of a patch was significant (GLMM: $P = 0.006$) and the least important variable in the model (Z score = 2.76; Table 1) with persistence increasing with greater connectivity. When the best GLMM (Table 1) was used to predict the spatial patterns of *M. pyrifera* persistence using a dataset not used in the creation of the model, the predictions from the GLMM and the actual observed persistence in the reserved dataset were strongly and significantly correlated ($R = 0.71$, $P < 0.001$; Fig. 6).

Discussion

Macrocystis pyrifera is an important, well-studied foundation species in many parts of the world, but no previous studies have looked at the relative contributions of environmental parameters in defining the long-term persistence of patches of this species. Although the relationship between *M. pyrifera* distribution and the variables used in this study has previously been explored individually, the combination of all of these environmental variables (i.e., seafloor structure, patch dynamics, population connectivity, oceanography) into a single model allows us to better understand how much each of the variables contributes to the long-term ($\approx$30 yr) persistence of *M. pyrifera* in the central coast region of California. Understanding the spatial and temporal patterns of *M. pyrifera* persistence and the factors responsible for its persistence is critical to understanding the distribution and abundance of the highly diverse and economically important species that

TABLE 1. The results from the best GLMM for predicting the persistence of kelp on the central coast of California based on AIC and deviance explained.

Fixed effects			
	Coefficient	abs (Z score)	P-value
(Intercept)	3.067	85.72	<0.001
Distance to edge of patch	0.162	100.68	<0.001
Depth	−0.019	37.91	<0.001
Mean complexity	0.125	35.44	<0.001
Patch biomass	0.152	29.06	<0.001
(Depth)^2	−0.022	17.71	<0.001
Wave orbital velocity	−0.033	14.89	<0.001
(Wave orbital velocity)^2	−0.011	11.75	<0.001
Proportion rock	0.011	3.46	0.001
Subpatch connectivity (survivorship = 0.10)	0.152	2.76	0.006
Random effects			
		Variance	SD
Subpatch (168 individual subpatches)		0.151	0.389

Notes: The variables used as fixed effects are shown with their corresponding Z scores and P values. Variance and standard deviation of the random effect used (Subpatch) is shown.

associate with forests of giant kelp and the communities they constitute (Foster and Schiel 1985, Carr and Reed *in press*). We found that persistence of *M. pyrifera* is significantly correlated with many environmental variables including depth, structural complexity of the seafloor, proportion of rock in an area, distance from the edge of a kelp patch, biomass of a kelp patch, oceanographic connectivity of the subpopulations, and wave environment. These variables can be used to accurately predict locations where kelp is likely to be more persistent and projections from these predictions can be used to help support the design and evaluation of marine protected areas and potentially predict where kelp may persistently occur in the future as the environment changes with the effects of climate change (Snyder et al. 2003).

As expected, *M. pyrifera* persistence increased with the distance from the edge of a kelp patch. The moderating effect of kelp on currents (Gaylord et al. 2003, Rosman et al. 2010) and waves (Rosman et al. 2013) and higher colonization potential (Reed 1990) are probably responsible for this pattern. In addition, the biomass of the patch significantly increases persistence with higher biomass patches more likely to experience greater reproductive and recruitment potential (Reed 1990). Although the size of a patch was included as a variable in the GLMM, it did not come out as significant. Therefore, the abundance within a kelp patch appears to be more important to persistence than the overall size of a patch.

The non-linear, hyperbolic relationship between kelp persistence and depth was expected based on previous knowledge of the depth distribution of *M. pyrifera*. As depth increases, *M. pyrifera* becomes less abundant as irradiance decreases (Graham et al. 2007, Carr and Reed 2015). On the other hand, the inshore limit of kelp is related to an increase in wave action (Dayton et al. 1992) and irradiance (Graham 1996, Swanson and Druehl 2000).

In contrast to other studies that have looked at the relationship between kelp persistence and complexity of hard substrate and found kelp is more persistent on lower relief, less complex rocky habitat (Deysher et al. 1998, Grove et al. 2002), our results here indicate that *M. pyrifera* persistence increases with increased structural complexity of the substrate. These contrasting results are likely due to differences in rocky substrate in southern California, where the majority of *M. pyrifera* studies have been done, vs. central California. In southern California, the majority of hard substrate is made up of low relief, sedimentary rock whereas central California is made up of granitic rocky reef of much higher and more varying topographic complexity and is much less susceptible to erosion than the sedimentary formations in southern California. Complexity of the rocky reef may also increase the number of microhabitats, allowing for higher rates of colonization (Sousa 1984, Pearsons and Li 1992).

The significant, non-linear (hperbolic) relationship between *M. pyrifera* persistence and wave orbital velocity was not expected. We predicted that *M. pyrifera* persistence would increase as wave orbital velocity decreases because waves are the most frequent disturbance responsible for tearing out plants (Graham 1997). The results from this study show, however, that *M. pyrifera* occurs across the range of wave orbital velocities along the central coast of California but is most abundant in a moderate wave environment (average 0.86 m/s wave orbital velocity). One explanation for this pattern could be the temporal resolution at which the data were analyzed. Because persistence in this study was defined as the annual persistence of *M. pyrifera*, even if the waves do remove kelp temporarily (i.e., during winter storms) there is still the potential for recovery throughout the year. Therefore, those areas that have strong recovery rates after disturbance events will have high persistence by our measure. Another reason for this result could be an increase in nutrient delivery to kelp plants in areas of higher wave orbital velocities. Water velocity through a kelp forest determines the amount of nutrient uptake by individual plants (Wheeler 1988, Hurd 2000).

Increases in the proportion of rock were significantly correlated with persistence of *M. pyrifera*. *Macrocystis* requires rocky substrate for attachment (Cribb 1954, Foster and Schiel 1985, Westermeier and Möller 1990, Schiel et al. 1995), and the increase in the proportion of rock also reduces the amount of soft sediment near the reef. Areas of lower sediment cover are less likely to experience periodic burial and scouring (Devinny and Volse 1978,
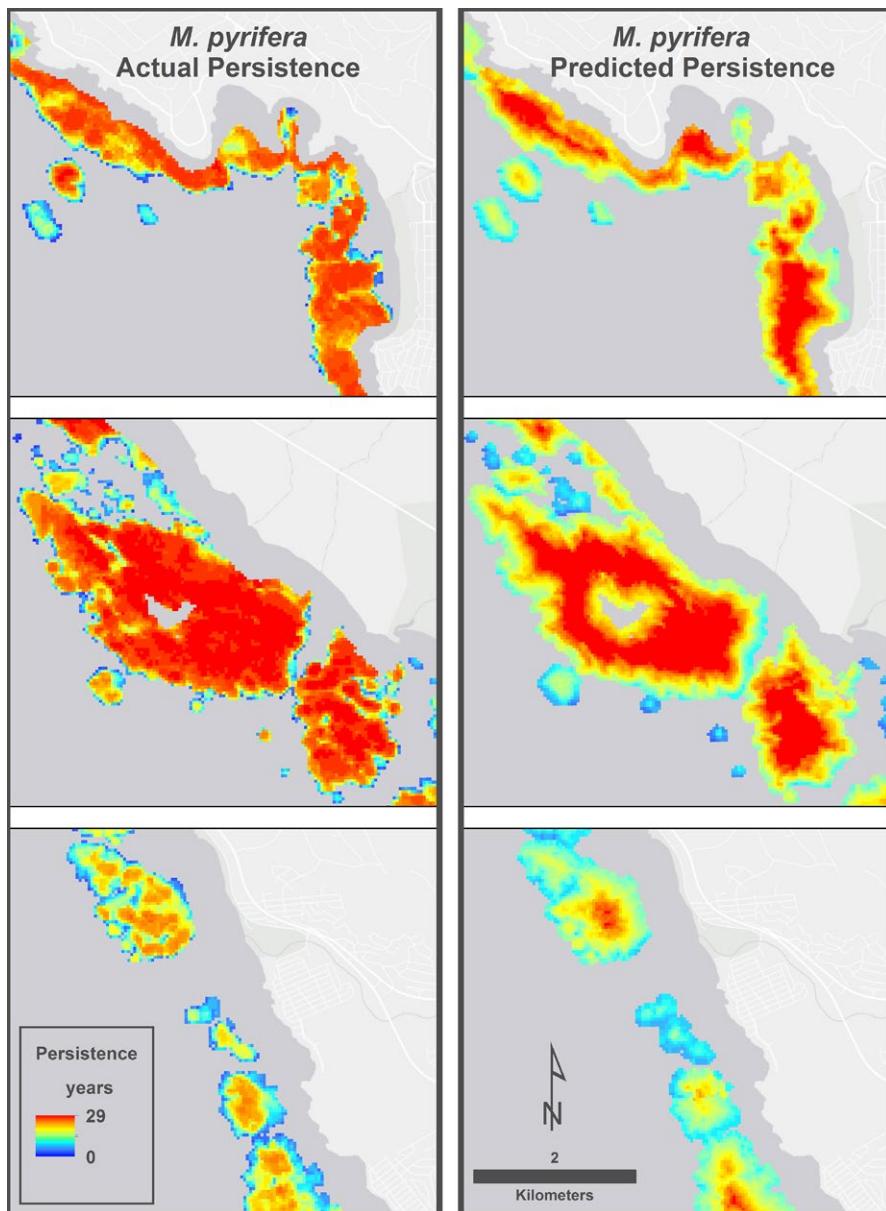
Fig. 6. Comparison of actual *Macrocystis pyrifera* persistence (left panel) and persistence predicted from the GLMMs (right panel) in three locations along California's central coast. Persistence is given in number of years with the warmer colors (reds, oranges) representing areas of higher persistence and cooler colors (blues) representing areas of lower persistence. Both the actual and predicted persistence maps are at 30-m resolution. Service Layer Credits for ESRI grayscale background image: Copyright 2013 Esri, DeLorme, NAVTEQ.

Storlazzi et al. 2013, Geange et al. 2014) and sediment in the water column, which results in higher turbidity and lower irradiance (Shaffer and Parks 1994, Spalding et al. 2003, Shepherd et al. 2009).

Population connectivity between the subpatches was also found to be a significant variable in the model. Previous studies have shown that the population connectivity of marine species within the coastal environment is linked to the "oceanographic distance" between populations, as measured by oceanographic currents (Mitarai et al. 2009,

Alberto et al. 2011, Castorani et al., *in press*). In this study, using a loss rate of 90% (Reed et al. 1988, 2006), we found that those subpatches at closer oceanographic distances were more persistent than those subpatches that were more isolated. Population connectivity is, understandably, an important factor in the persistence of kelp, because those patches that are more "connected" to the rest of the patches are more likely to experience more consistent spore recruitment and greater persistence through time.

One of the main limitations on the distribution of *M. pyrifera* throughout the world is nutrient availability, most commonly nitrate (Ladah et al. 1999, Hernández-Carmona et al. 2000, Edwards 2004, Graham et al. 2007). Because nitrate availability has been linked to the ocean temperature in previous studies (Zimmerman and Robertson 1985, Tegner et al. 1996, Hernández-Carmona et al. 2001), we used SST as a proxy for nitrate. Along the central coast of California, however, SST had a limited range during our study and did not have a significant effect on the persistence of kelp. In southern California, south of Point Conception, it is more likely that nitrate would play a role in the persistence of kelp populations because there is more variability and greater temperature extremes within that region (Carr and Reed 2015). In fact, previous studies have shown a correlation between *M. pyrifera* and SST within the Santa Barbara Channel in southern California (Cavanaugh et al. 2011). Sea surface temperature and nitrate concentration may become more important factors in central California if changing climate conditions alter upwelling timing or duration (Snyder et al. 2003).

Another factor that is often linked to the presence of kelp but was not explored in this study is the abundance of grazers. In many parts of the world, kelp populations are dramatically affected by the overgrazing by marine organisms (Graham et al. 2007), and *M. pyrifera* can be greatly affected by the presence of grazers (Dayton 1985, Foster and Schiel 1985, Estes and Duggins 1995, Steneck et al. 2002). Along the coast of California, sea urchins are one of the main grazers of kelp (Carr and Reed 2015) and could be contributing to variation in persistence as was previously shown in the central coast by Pearse and Hines (1979). In this study, however, the presence of grazers was not taken into consideration due to the lack of detailed temporal data on urchin abundance across the region. Additionally, there is a population of sea otters that overlaps with the range of this study (Tinker et al. 2006, 2008). Sea otters forage on urchins, greatly diminishing their abundance (Reed et al. 2011, Carr and Reed 2015) and possibly limiting their effects on *M. pyrifera* persistence. For example, previous studies in central California have shown that sea otter predation on sea urchins increased algal abundance (McLean 1962, Laur et al. 1988). However, incorporating species interactions, both herbivores as well as competitive species (e.g., *Nereocystis luetkeana*), into our model might account for some of the unexplained variation and provide further understanding of what drives kelp persistence.

Previous studies have shown that giant kelp is highly variable on short time scales (Graham et al. 2007), which was not accounted for in this study. The processes responsible for short-term variability, including the drivers of mortality and recovery (e.g., wave disturbance and connectivity, respectively), are closely tied with long-term persistence. Those populations that have low short-term variability are likely to persist over the long term. Kelp forests in central California are highly persistent when compared to other populations throughout the world (Carr and Reed 2015) and, therefore, the mechanisms for long-term persistence in this study are likely closely tied to the mechanisms that define short-term variability in persistence.

Conclusion

Overall, this study shows that the persistence of *M. pyrifera* along the central coast of California has predictable relationships with a suite of environmental variables and that these environmental variables can be used to predict areas where this important structure-forming kelp species is likely to persist. In addition, the incorporation of oceanographic variables including wave environment, currents affecting the connectivity between kelp patches, and SST allows us to forecast how changes in the ocean environment due to climate change are likely to affect the persistence of *M. pyrifera*. As a foundation species that can support upwards of 1000 different species (Foster and Schiel 1985), understanding those factors that support persistent populations of *M. pyrifera* are important when managing and protecting marine communities.

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