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Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls

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Abstract. Populations of many species display spatially synchronous fluctuations in abundance. Synchrony is most commonly attributed to three processes: factors that influence recruitment (e.g., dispersal, early survival), large-scale environmental variability, and spatially autocorrelated trophic interactions. However it is often difficult to link population synchrony to a specific dominant process, particularly when multiple synchronizing forces are operating. We utilized a new satellite-based data set of giant kelp (*Macrocystis pyrifera*) canopy biomass to examine population synchrony in southern California kelp forests on spatial scales ranging from 50 m to 300 km and temporal scales ranging from 1 to 11 years. We examined the relationship between synchrony and distance for adult kelp populations, kelp recruits, sea urchin abundance (a major grazer of kelp), and environmental variables known to influence kelp population dynamics. Population synchrony in giant kelp decreased with distance between populations: an initial rapid exponential decrease between 50 m and 1.3 km was followed by a second, large-scale decrease between distances of 1.3 km and 172 km. The 50-m to 1.3-km spatial scale corresponded to the scales of synchrony in the abundance of sea urchins and young kelp recruits, suggesting that local drivers of predation and recruitment influence small-scale synchrony in kelp populations. The spatial correlation patterns of environmental variables, particularly wave height, were similar to the synchrony–distance relationship of kelp populations from 1.3 km to 172 km, suggesting that regional environmental variability, i.e., the Moran effect, was the dominant process affecting synchrony at larger spatial scales. This two-step pattern in the relationship between kelp biomass synchrony and distance was apparent in each of the 11 years of our study. Our results highlight the potential for synthesizing approaches from both landscape and population ecology in order to identify the multiple processes that generate synchrony in population dynamics.

Key words: giant kelp; Landsat; Macrocystis pyrifera; *Moran effect; population dynamics; remote sensing; southern California; spatial autocorrelation; synchrony; time series; wave disturbance.*

Introduction

Understanding how and why populations vary in space and time is a central challenge in ecology. A great deal of theoretical work has addressed how various processes interact to create spatial and temporal patterns in population abundance (Kareiva and Wennergren 1995, Bascompte and Solé 1998). Testing this theory with empirical data has been challenging because there are few species for which long-term abundance data across large spatial scales are available.

One commonly observed spatiotemporal pattern in ecology is synchrony, the tendency of populations to fluctuate together through time (Buonaccorsi et al.

2001). Synchrony is most commonly calculated as the correlation between two populations through time (Bjørnstad et al. 1999a). Such trends have been observed in a variety of animal (Hanski and Woiwod 1993, de Valpine et al. 2010) and plant (Koenig and Knopes 2000) populations. Covariance in population dynamics is generally attributed to three types of mechanisms: regional stochasticity (often in the form of environmental variability), recruitment processes (such as dispersal), and trophic interactions. In his classic study of the Canadian lynx, P. A. P. Moran hypothesized that spatially separated populations are synchronized by regional, density independent variability in temperature, a mechanism later termed the Moran effect (Moran 1953). If local dynamics among populations are similar and not highly nonlinear, the Moran effect predicts that population synchrony will mirror environmental synchrony (e.g., Bjørnstad 2000). Dispersal can also

synchronize populations through the movement of individuals or reproductive stages (Ranta et al. 1995). Finally, trophic interactions such as predation and parasitoidism have been invoked as a mechanism to synchronize populations at spatial scales corresponding to the scale of synchrony of the predator population (Ims and Andreassen 2000).

Theoretical studies have shown that associating synchrony with a particular forcing process can be difficult. For example, dispersal can generate synchrony over distances longer than the scale of dispersal (Lande et al. 1999, Gouhier et al. 2010) and interactions between dispersal and environmental effects can reduce each factor's synchronizing effect (Kendall et al. 2000). However, the degree to which synchronizing processes can be differentiated will depend on the particular system in question. If one factor is substantially more influential than others or if the factors operate on very different spatial scales, then population dynamics may display "characteristic spatial scales of regulation" (Bjørnstad et al. 1999b), making it easier to link pattern with process (de Roos et al. 1991). Also, in many species, autocorrelation in population dynamics declines with increasing distance. The rate of this decline and the distance at which spatial autocorrelation falls to zero can serve as tools for identifying synchronizing mechanisms.

However, analyzing patterns of population synchrony in isolation is typically not sufficient to draw conclusions about the processes producing these patterns (Abbott 2007). One must also evaluate the spatial autocorrelation of environmental controls, dispersal, and trophic interactions. If populations are autocorrelated over long distances relative to dispersal and exhibit a decline in synchrony with distance comparable to that of large-scale environmental controls, then environmental fluctuations are potentially the cause of the large-scale correlation (Peltonen et al. 2002). On the other hand, rapid decreases in synchrony over relatively short distances may be driven by dispersal or local trophic interactions (de Roos et al. 1991). For sessile organisms, rapid decreases in synchrony can also reflect small-scale variability in environmental processes that control recruitment success (e.g., topography, soil type, elevation, light). In most cases the relationship between synchrony and distance in populations will likely be controlled by a combination of processes, and very few empirical studies have simultaneously examined the roles of multiple processes in causing spatial autocorrelation in population dynamics. Still, caution is warranted when inferring causality by matching patterns of synchrony among populations with the patterns of their potential regulating factors. For example, Lande et al. (1999) demonstrated that small-scale dispersal could induce synchrony at large scales in the presence of environmental correlation when the dispersal rate is much larger than the strength of density regulation.

During the past decade the significance of synchrony–distance relationships has been examined in several species using novel statistical techniques (Bjørnstad et al. 1999b, Bjørnstad and Falck 2001, de Valpine et al. 2010). Still, the spatial resolution and/or extent of these studies have been limited. Either the spatial resolution of observations was equal to or coarser than the dispersal distance of the species under investigation (Bjørnstad et al. 1999b, Peltonen et al. 2002) or the extent was too small to observe spatial variability in environmental factors (de Valpine et al. 2010). As a result, most past studies of synchrony have not been able to fully evaluate how the roles of different synchronizing processes vary across spatial scales (but see Gouhier et al. 2010).

We utilized a new long-term, large-scale, high-resolution remotely sensed data set of giant kelp (*Macrocystis pyrifera*) canopy biomass in the coastal waters of southern California (Cavanaugh et al. 2011) as a case study to examine patterns of spatial synchrony across scales ranging from tens of meters to hundreds of kilometers. Compared to other habitat-structuring primary producers, giant kelp forests are exceptionally dynamic. Short life spans of both kelp fronds (4–6 months) and entire kelp plants (2–3 years) combine with rapid growth (~2% of total biomass per day) to produce a standing biomass that turns over 6–7 times per year (e.g., Reed et al. 2008, 2011). Growth and mortality of giant kelp is strongly influenced by environmental factors such as light, wave height, and nutrient levels (reviewed in Graham et al. 2007). Therefore, we expected to observe at least some synchrony in kelp dynamics due to seasonal cycles in these controls. Hence, our analyses focused on how patterns of synchrony in giant kelp populations declined with distance, and how these patterns varied over time. In order to identify the most important synchronizing processes, we compared the synchrony–distance curve of giant kelp to patterns of autocorrelation in environmental variables, predator abundance, and giant kelp recruitment. We examined synchrony in changes of kelp biomass rather than raw biomass in order to emphasize autocorrelation patterns in the growth and mortality of giant kelp populations. Using changes in biomass also has the benefit of removing long-term trends that can induce spurious correlation (Bjørnstad et al. 1999a, Koenig 1999).

Sea surface temperature (used as a proxy for nutrient levels in this region) and storm-driven wave disturbance, two important environmental controls of kelp biomass, are correlated on scales much larger than the scale of kelp dispersal (Reed et al. 2006a, Cavanaugh et al. 2011; see also *Results: Spatial synchrony in giant kelp, environmental, and urchin data*). Therefore any decreases in synchrony observed over large distances would likely reflect a large-scale Moran effect, while decreases over very short distances could be due to dispersal or other local processes that influence giant kelp recruitment (e.g., bottom irradiance, local currents, competition).
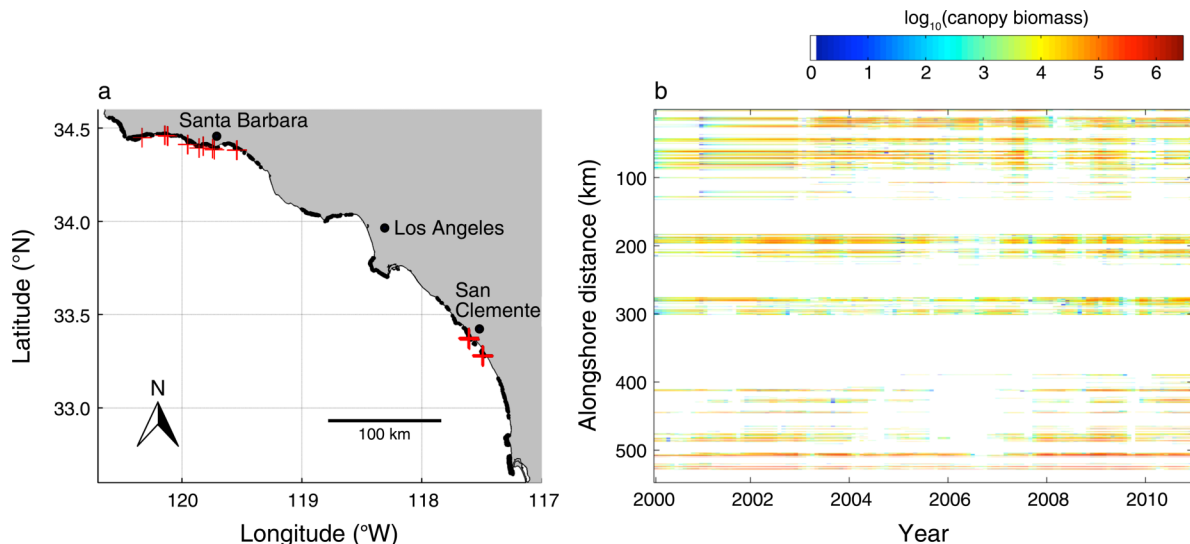
log$_{10}$(canopy biomass)

Fig. 1. (a) Map of the study area in coastal southern California, USA, and (b) time series of along-coast canopy biomass of giant kelp (*Macrocystis pyrifera*) binned into 50-m coastline segments between 2000 and 2010. The black shaded areas in panel (a) represent the areas where kelp appeared at least once during 2000–2010. The red crosses in panel (a) represent the locations of the urchin and kelp recruit transects. Offshore islands are not shown in panel (a). The *y*-axis in panel (b) gives the alongshore distance starting from the northwest corner of panel (a). The color key shows log-transformed kelp biomass, originally measured in kilograms.

Grazers could induce synchrony in kelp populations on scales corresponding to the scales of synchrony in grazer abundances. Unlike regional-scale environmental factors such as waves and nutrients, we did not have much a priori knowledge of the spatial scales of synchrony in patterns of kelp recruitment or grazer abundance.

The strength and timing of the seasonal cycle in kelp abundance varies a great deal among years (Cavanaugh et al. 2011), and so we might expect that the patterns of synchrony in kelp populations also vary substantially among years. To explore this inter-annual variability we examined the relationship between kelp biomass synchrony and distance separately for each year from 2000 to 2011. We show that by combining large-scale, high-spatial-resolution data of giant kelp with data characterizing environmental variables and grazer abundance, it may be possible to identify the effects of multiple synchronizing processes on the relationship between kelp synchrony and distance. The availability of long-term time series data from satellite sensors such as Landsat TM has increased dramatically in recent years, and so these methods can be used to characterize synchrony across multiple space and time scales in a variety of habitats where changes in abundance can be tracked from satellite imagery.

METHODS

Giant kelp data

We tracked giant kelp canopy biomass along the mainland California coast from Pt. Sal to the United States/Mexico border (~550 km; Fig. 1) from January 2000 to January 2011 using 30-m resolution multispec-

tral Landsat 5 TM satellite imagery. Methods used to process and calibrate the Landsat 5 TM imagery into kelp canopy biomass (in kilograms) are detailed in Cavanaugh et al. (2011). All of the following statistical analysis and spatial modeling activities were performed using the MATLAB (2011) and R (R Development Core Team 2011) software packages. We estimated canopy biomass from Landsat images taken approximately once every 1–2 months and interpolated the canopy biomass time series onto a regular 1-month time scale using a cubic spline (MATLAB function "spline"). To facilitate the calculation of alongshore synchrony, we binned the kelp data into 50-m alongshore coastline segments by assigning each pixel of kelp canopy to the closest coastline segment. Each 50-m coastline segment was considered a site for later statistical analysis.

In order to confirm that changes in giant kelp canopy biomass accurately reflected the population dynamics of giant kelp throughout the entire region, we compared canopy biomass to the density of adult plants determined from diver surveys collected as part of a 5-year study of kelp forests near San Clemente, California (Reed et al. 2006b). Each summer from 2000 to 2004 divers measured the density of adult kelp plants in six 40 × 40 m modules at seven sites ($N = 210$). Each year we selected the Landsat image closest in time to the diver survey and compared the satellite estimates of canopy biomass at each site to the diver-measured adult plant density. There was a very strong linear relationship between canopy biomass and adult plant density ($r^2 = 0.85$, $P < 0.001$, slope $= 2.24 \times 10^{-4}$ plants·m^{-2}·kg^{-1}, *y*-intercept $= 0.06$ plants/m^2, $F_{1,35} = 183$), indicating that

our Landsat time series of canopy biomass accurately represented the population dynamics of adult giant kelp.

Environmental data

Limited nutrient levels, specifically nitrogen, have been shown to limit kelp growth in southern California (Jackson 1977, Gerard 1982). Although kelp growth appears not to be influenced by water temperature per se (North and Zimmerman 1984), local sea surface temperature (SST) and nutrients (specifically nitrate + nitrite) show a strong negative linear relationship in southern California (Fram et al. 2008, Lucas et al. 2011). Therefore, we used satellite observations of local SST as a proxy for nitrate/nitrite levels. Monthly mean SST was assessed using merged MODIS Terra and MODIS Aqua daytime 1-km-resolution satellite observations (Kahru et al. 2009). This SST data set covered the entire region for which we had kelp data (Fig. 1a). To place the SST data on the same grid as the kelp canopy biomass data, we found the MODIS pixel that was closest to the center of each 50-m coastline segment. Because the SST data were coarser than the kelp canopy data (1 km vs. 50 m), the resolution of the synchrony–distance analysis for SST was limited to 1 km.

Large waves associated with storm events are a major source of disturbance for kelp populations in southern California (Dayton and Tegner 1984, Reed et al. 2008). Wave events can also induce synchrony in the recovery of kelp populations by removing existing canopy, thereby reducing shading and promoting juvenile growth (Graham et al. 1997). We calculated local wave disturbance using significant wave height measurements from the Coastal Data Information Project's (CDIP) swell model (*available online*).[7] This swell model used a linear refraction–diffraction wave propagation model to transform offshore deep-water buoy measurements of the wave field to locations along the coast at a 10-m depth (O'Reilly and Guza 1993). The model provided hourly data at 10-m depth for points spaced 1 km apart across our entire study area. We calculated the maximum significant wave height in each month at each model analysis location. Maximum significant wave height was used rather than mean significant wave height because extreme wave events have the greatest effect on kelp populations (Denny 1988). As we did with the SST data, we matched each model analysis location with the nearest 50-m coastline segment.

Urchin data

Sea urchins are responsible for the vast majority of kelp biomass lost to herbivory (Harrold and Pearse 1987); grazing rates of other fish and invertebrates in California kelp forests are generally low (Foster and Schiel 1985). Red and purple sea urchins (*Strongylocentrotus francis-*

canus, S. purpuratus) are by far the most abundant species of urchin in southern California and account for most of the kelp grazing in this region (Foster and Schiel 1985). Spatial autocorrelation in sea urchin abundance, and by extension rates of kelp grazing, could cause synchrony in kelp populations at scales corresponding to the scales of autocorrelation in urchin abundance. However, causality could also operate in the opposite direction, as consumer synchrony could be driven by producer abundance. In either case we would expect correspondence between the scales of synchrony in changes in kelp and urchin abundances. We used data from annual surveys of the combined density of red and purple sea urchins at 32 transects along the Santa Barbara coastline and 18 transects along the San Clemente coastline (red crosses in Fig. 1a) to examine synchrony in herbivore dynamics. The 50 transects were located between 20 m and 300 km apart, and the median pairwise distance between transects was 60 km. Red and purple urchins were counted by divers in six 1-m^2 quadrats uniformly spaced along fixed 40 × 2 m transects. Surveys were conducted at each transect once per year during the summer; 11 years of data (2000–2010) were collected at the Santa Barbara sites and 8 years of data (2000–2007) were collected at the San Clemente sites. Sea urchins are long lived, and so annual sampling is sufficient to characterize their population dynamics (Ebert and Southon 2003). Kelp forests that are heavily impacted by urchin grazing often display relatively low and stable levels of kelp abundance (i.e., dampened seasonal cycles in abundance) for multiple years (Lawrence 1975). Therefore, long-term changes in urchin dynamics have the potential to influence synchrony measured on monthly to seasonal time scales.

Giant kelp recruitment data

While the macroscopic stage of giant kelp is sedentary and firmly anchored to the bottom, its microscopic spores disperse freely in the water column and typically travel distances on the order of meters to kilometers before settling to the seafloor (Reed et al. 2006a). Once spores settle to the bottom, they require firm substrate and sufficient light and nutrients for successful recruitment (Graham et al. 2007). The amount of light and nutrients available to recently settled spores can vary greatly in space and time (Deysher and Dean 1986). Therefore spatial autocorrelation in these variables could create spatial patterns in kelp recruitment, which could in turn impact synchrony in adult populations (Nisbet and Bence 1989). If this is the case, then patterns of synchrony in kelp recruitment should resemble those of adult density as determined by Landsat imagery. We used annual surveys of the density of giant kelp juveniles <1 year old (defined as all individuals with fewer than three fronds) from 32 transects along the Santa Barbara coastline and 18 transects along the San Clemente coastline (red crosses in Fig. 1a) to examine synchrony in recruitment at scales of 50 m–300 km. Surveys were

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[7] http://cdip.ucsd.edu

conducted along the same transects used for the urchin surveys previously described.

Synchrony analysis

Synchrony between sites is usually measured as the pairwise correlation between time series of abundances or changes in abundances (Bjørnstad et al. 1999a). In this study we used first-differenced time series of log(canopy biomass + 1) in order to examine synchrony in growth and mortality of giant kelp populations. Log transformations were used to normalize the abundance data. Sites (50-m coastline segments) that did not have any kelp during the study period were not included in the analysis. Sea surface temperature, maximum wave height, urchins, and kelp recruit abundance are all likely to affect kelp growth rates directly, so for these explanatory variables we examined pairwise correlations in abundance/magnitude rather than changes in abundance/magnitude. We used spatial autocorrelation techniques and the nonparametric correlation function (NCF, "Sncf" function in R [Bjørnstad et al. 1999b]) to examine and model the relationship between synchrony and distance for the giant kelp canopy biomass, SST, wave height, urchin, and kelp recruit data sets (Sokal and Oden 1978). While the largest along-coast distance between two sites of giant kelp in our study area was 547 km, sample sizes were much larger for distances <300 km, so we used 300 km as the maximum distance for all analyses.

The NCF uses a smoothing spline to estimate a continuous function describing synchrony as a function of distance (Bjørnstad et al. 1999a). We used the square root of n, where n is the number of sampling locations for each variable, as the degrees of freedom for each NCF (this is the default value in the Sncf package). Conventional parametric approaches for estimating statistical significance and confidence intervals for pairwise correlations could not be used because of spatial autocorrelation in the data. Therefore we calculated confidence intervals using bootstrap resampling with 1000 iterations. For the kelp biomass synchrony analysis we used the temporal bootstrapping method described in de Valpine et al. (2010) in order to account for variability in the temporal process as well as spatial sampling variability. This method recreates the data set by resampling contiguous three-month blocks of data with replacement. We quantified the spatial scale of synchrony in our variables using three different methods. First, we calculated the distance at which synchrony was no longer significantly greater than zero. However, many of our variables displayed significant positive synchrony across the entire study area. In these instances we calculated the distance at which synchrony was equal to the regional mean of the NCF. Where possible, we also modeled each NCF as an exponential or double exponential decay function using least-squares fits as follows:

$$a + b(1 - \exp[-3x/c]) \tag{1}$$

for the exponential function and

$$a + b(1 - \exp[-3x/c]) + d(1 - \exp[-3x/f]) \tag{2}$$

for the double exponential function (Chiles and Delfiner 1999), where x is the distance between pixels and a, b, c, d, and f are the fit parameters. The variable a represents the modeled y-intercept value. The c and f parameters provide a measure of the length scale of synchrony.

We modeled the synchrony–distance correlation function of the giant kelp canopy biomass data, first using the entire 11-year time series, and then again separately for each year in order to examine how the correlation function changed through time. Giant kelp populations often experience annual cycles driven by seasonal changes in wave energy, nutrients, and light availability; however, the timing and strength of these cycles vary a great deal from year to year (Cavanaugh et al. 2011). Therefore, annual correlation functions (i.e., correlation functions created from monthly data from a single year) should capture the spatial scale of similarity in these annual cycles. We also calculated the annual correlation functions for SST and wave height and compared these to the kelp annual correlation functions. The urchin and kelp recruit data were collected annually so we were not able to calculate annual correlation functions for these variables.

RESULTS

Spatial synchrony in giant kelp, environmental, and urchin data

Synchrony in giant kelp canopy biomass changes decreased with increasing distance following a double exponential decay function with steps at two very different spatial scales: $c = 1.3 \pm 0.15$ km (all values expressed as mean and 95% confidence interval) and $f = 172 \pm 10$ km (Fig. 2; Appendix A: Table A1). The double exponential function provided a substantially better fit than the single exponential ($r^2 = 0.99$ vs. 0.88; Appendix A: Table A1). An F test demonstrated that the improved fit provided by the double exponential model was statistically significant ($F_{2,59} = 216$, $P \ll 0.01$). Mean synchrony among adjacent sites was high (0.53 ± 0.01), but the spatial correlation function decayed exponentially out to a distance of 1.3 km, where the mean pairwise correlation was 0.22 ± 0.03 (Fig. 2b). The second exponential decrease occurred on a much larger scale, flattening at 172 km, with a pairwise correlation of 0.04 ± 0.03 (Fig. 2a). Between distances of 172 km and 300 km synchrony was low, but significantly greater than 0. The regional mean synchrony in kelp biomass between 0 and 300 km was 0.08 ± 0.03, and the synchrony–distance curve fell below this regional mean level at a distance of 74 ± 15 km (Fig. 2a).

SST and significant wave height exhibited high levels of autocorrelation across the study area, but the magnitude of synchrony for both variables generally
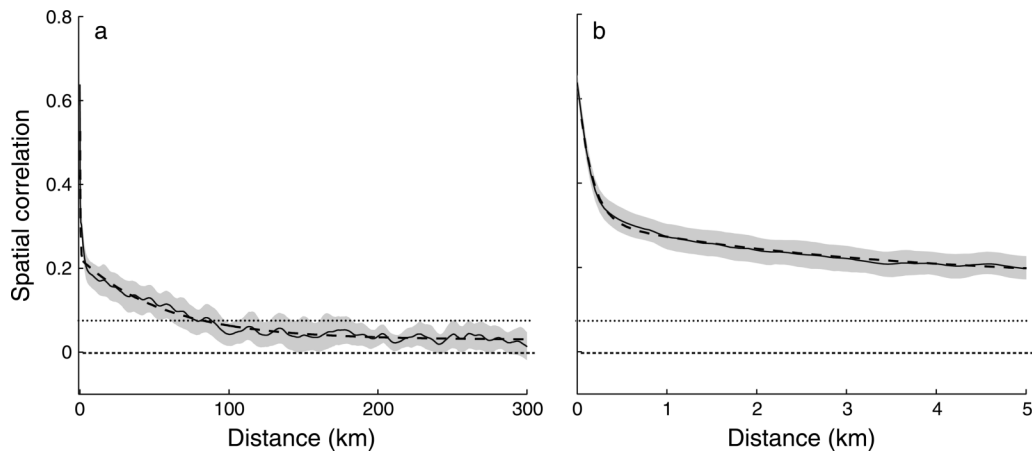
Fig. 2. Nonparametric spatial correlation functions (NCF) and modeled double exponential fit for changes in log(kelp biomass + 1). Panels (a) and (b) show the same data, but panel (b) has a different x-axis scale. In each plot, the solid black line represents the NCF, and the gray-shaded areas give the 95% bootstrap confidence intervals. The dashed curve represents the modeled double exponential fit for the NCF. The dotted horizontal line gives the regional mean correlation, and the short-dashed horizontal line represents 0 synchrony.

declined with increasing distance (Fig. 3a, b). The SST NCF decreased linearly between 0 and 300 km with a y-intercept of 0.98 and slope of -2×10^8 (Fig. 3a). The initial decrease in the wave height NCF between 0 and 120 km was well modeled by the exponential decay function (Fig. 3b; see Appendix B: Table B1 for exponential model parameters). Over this range the wave height NCF decreased from 0.98 ± 0.02 to 0.83 ± 0.03. The wave height NCF then increased slightly between 120 and 240 km.

We observed moderate positive synchrony in sea urchin abundance at distances <60 km (Fig. 3c). Synchrony declined from 0.37 ± 0.16 to 0.12 ± 0.12 between 0 and 11 km, and this initial decrease followed the exponential decay function (Appendix B: Table B1). Between 11 and 70 km, synchrony appeared to increase slightly; however, the confidence intervals at these distances were large (because of limited sample size) and so we cannot reject the hypothesis that the synchrony–distance relationship is flat across these distances.

Synchrony in the annual abundance of kelp recruits decreased exponentially between 0 and 10 km, falling from 0.25 ± 0.12 to 0.08 ± 0.09 (Fig. 3d). Kelp recruit synchrony was not significantly different from 0 at distances >10 km. The spatial coverage of both the urchin and kelp recruit data sets was limited, and so it was difficult to determine the significance of changes in synchrony in these variables at scales >25 km (as shown by the rug plots and large confidence intervals in Fig. 3c, d).

Temporal variability in giant kelp spatial synchrony

In each of the 11 years of our study, giant kelp synchrony displayed a two-step decrease with distance: an initial rapid decline at small scales (0–5 km) was followed by a more gradual decline at large scales (5–200 km; Fig. 4; Appendix D: Fig. D1). Table 1 lists the NCF

pairwise correlations at 0, 5, and 70 km for each year; in all years synchrony decreased significantly between these distance classes. While all years displayed this stepwise decrease in synchrony, the magnitude of correlation at each distance class and the distance at which the NCF reached the regional mean synchrony level varied across years (Table 1). Local correlation, ρ(0), and correlation at 5 km were relatively consistent, ranging from 0.63 to 0.74 and 0.21 to 0.48, respectively (coefficients of variation = 0.06 and 0.21). The correlation at 70 km was more variable: it ranged from 0.01 to 0.37 and had a coefficient of variation of 0.76. The length scale of kelp synchrony, defined here as the distance at which the NCF reached the regional synchrony level, also ranged widely from 28 to 102 km. This pattern indicates that much of the temporal variability in the annual spatial correlation functions occurs at larger, regional scales. We compared the annual length scales of kelp synchrony to the annual length scales of SST and wave height (Appendix C: Table C1), but did not find a significant relationship with either variable ($P = 0.40$ and $P = 0.48$, respectively). Defining the length scales of kelp, SST, and wave height as the distance at which kelp synchrony reached 0 or as the flattening parameters of the modeled exponential functions (c and f from Eqs. 1 and 2) did not change these results.

DISCUSSION

Researchers have long called for more interaction between the fields of population and landscape ecology (Levin 1992, Wiens 1997). This study demonstrates how remote sensing and geospatial analysis techniques, widely used by landscape ecologists, can be combined with time series analysis of population dynamics to analyze spatial autocorrelation in populations. This approach can help address the well-recognized problem that many conclu-
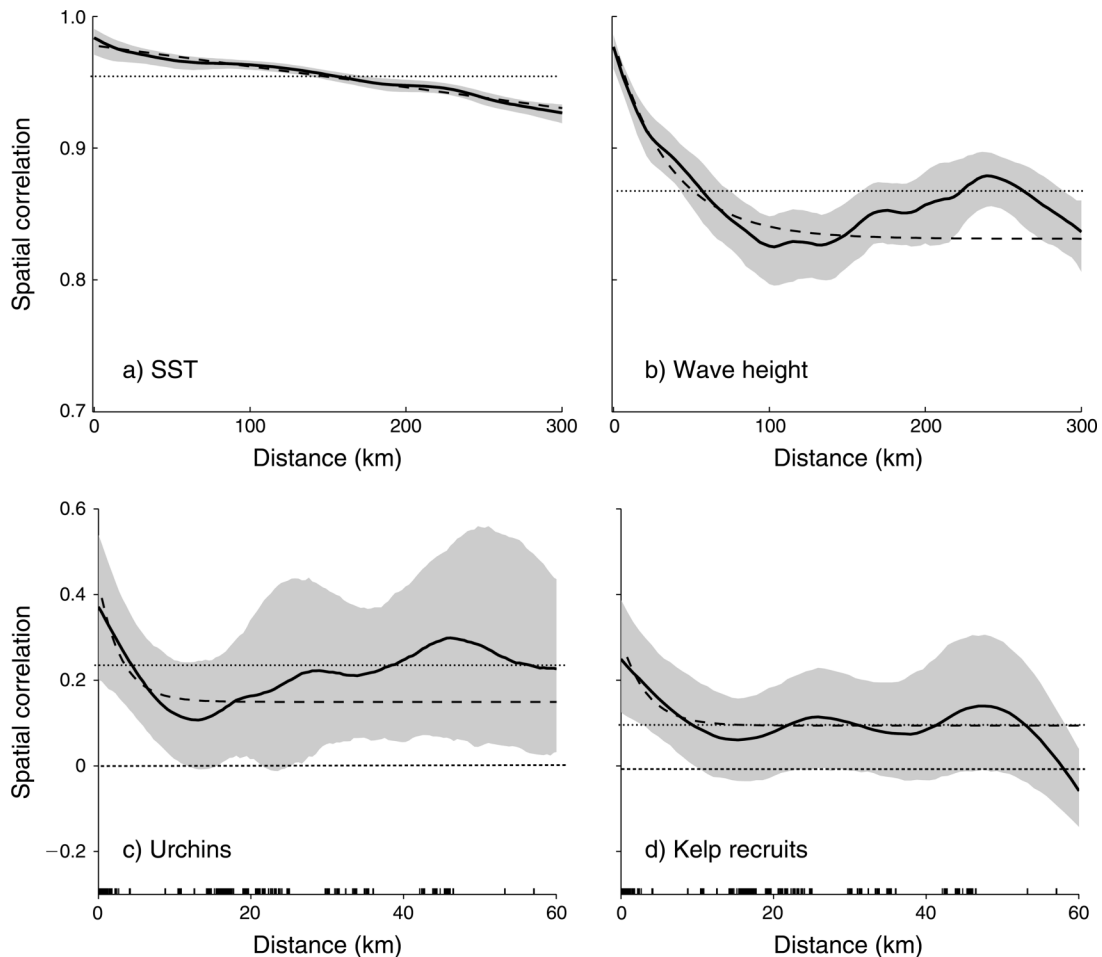
Fig. 3.   Nonparametric spatial correlation functions (NCF) for changes in (a) sea surface temperature, SST, (b) wave height, (c) $\log_{10}$(urchin abundance + 1), and (d) log(kelp recruit abundance + 1). Note the different scales in panels (a, b) vs. (c, d). The gray-shaded areas in each plot represent the 95% bootstrap confidence intervals. The dashed line in panel (a) represents the modeled linear fit for the SST NCF curve; the dashed curves in panels (b–d) represent the modeled exponential decay fits for the wave height, urchin, and kelp recruit NCFs, respectively. The dotted horizontal lines give the regional mean correlation, and the short-dashed horizontal lines represent 0 synchrony. Rug plots (dashes on x-axis) on panels (c) and (d) show the pairwise distances between sample sites.

sions regarding spatial population dynamics are limited by the scale of the study design (Wiens 1989, Bjørnstad et al. 1999b). Landsat TM provides relatively uninterrupted coverage from 1984 to 2011, and so these methods can be applied to examine long-term synchrony patterns in other habitats where changes in species abundance can be quantified from satellite imagery (e.g., seagrasses, coral reefs, wetlands, grasslands). However, the ability to observe synchrony over multiple generations will depend on the life span of the species in question, and so these techniques may not be applicable for habitats made up of long-lived species (e.g., pine forests). In these cases it may be more informative to examine synchrony in phenology or recruitment.

The spatial resolution (50 m) and extent (550 km) of our study spanned over five orders of magnitude. The spatial resolution was fine enough to cover the spatial scales of dispersal for this species (meters to kilometers [Reed et al. 2006a, Alberto et al. 2010]), while the extent was large enough to examine the spatial structure of large-scale environmental controls that are known to influence giant kelp populations (Graham et al. 2007). The temporal resolution and extent were sufficient to capture intra-annual as well as interannual variation in kelp biomass. Between 2000 and 2011 we identified a two-step decrease in synchrony with distance: an initial exponential decrease between 50 m and 1.3 km, followed by a large-scale exponential decrease between 1.3 and 172 km. The large difference in the spatial scales of these two patterns suggests that multiple processes are responsible for synchronizing giant kelp populations. Lande et al. (1999) demonstrated that small-scale dispersal could induce synchrony on much larger scales if the dispersal rate (roughly speaking, the fraction of the local popula-
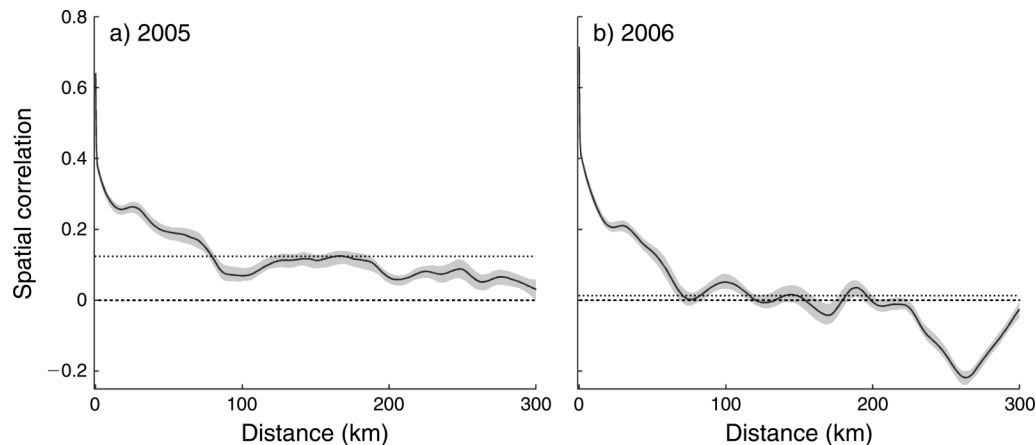
Fig. 4. Annual nonparametric spatial correlation functions for changes in log(biomass + 1) of kelp in 50-m alongshore coastline sites using monthly data from (a) 1 January 2005–31 December 2005 and (b) 1 January 2006–31 December 2006. The gray-shaded areas in each plot represent the 95% bootstrap confidence intervals. The dotted horizontal lines give the regional mean correlation, and the short-dashed horizontal lines represent 0 synchrony. Annual NCFs for other years are given in Appendix D: Fig. D1.

tion that disperses per unit time) is large relative to the strength of density dependence. However, only the spores of giant kelp disperse, so that, as a fraction of biomass, the dispersal rate (sensu Lande et al. 1999) is quite small. Since giant kelp dispersal is limited to relatively short distances (meters to kilometers [Reed et al. 2006a, Alberto et al. 2010]), and there are a variety of density-dependent processes acting at the local scale that impact the growth and mortality of giant kelp (reviewed in Schiel and Foster 2006), we do not think that dispersal is playing a major role in long-range synchrony.

Grazing by sea urchins and local processes that influence recruitment of giant kelp likely explain some of the initial exponential decrease in kelp canopy biomass synchrony between 50 m and 1.3 km. Synchrony in both urchin abundance and kelp recruitment was positive and significant at small scales, but declined rapidly on spatial scales similar to the initial exponential decrease in kelp synchrony (Fig. 3c, d). Grazing may induce synchrony in kelp populations by causing

mortality that is spatially autocorrelated at local scales. The processes controlling recruitment include dispersal limitation of planktonic spores, bottom irradiance, sedimentation, competition, and grazing. Fertilization in giant kelps occurs after dispersal and requires dense spore settlement (>1 spore/mm^2), thereby limiting the effective dispersal distance in giant kelp (Reed et al. 1991). Reed et al. (2006b) performed a series of empirical and modeling studies of spore dispersal and estimated that the scale of dispersal in giant kelp is on the order of meters to kilometers. This result agrees with theoretical diffusive models of dispersal that show exponential decreases in spatial autocorrelation with distance on spatial scales similar to the scale of average dispersal (Bjørnstad et al. 1999b, Okubo and Levin 2002: Chapter 5). While we were not able to quantify the spatial autocorrelation of local environmental factors such as bottom irradiance, sedimentation, and the effects of competition, many of these features vary on small scales and are important determinants of recruitment success

TABLE 1. The magnitude of spatial synchrony in giant kelp (*Macrocystis pyrifera*) biomass data at different distances, and the length scale of kelp synchrony in coastal California, USA.

	$\rho(0)$		$\rho(5)$		$\rho(70)$		Length scale (km)	
Year	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
2000	0.70	0.67–0.73	0.37	0.33–0.41	0.26	0.23–0.30	102	101–104
2001	0.64	0.62–0.68	0.39	0.34–0.42	0.08	0.05–0.10	85	61–107
2002	0.72	0.70–0.75	0.41	0.37–0.46	0.33	0.29–0.36	85	81–90
2003	0.67	0.65–0.69	0.35	0.32–0.37	0.10	0.08–0.11	37	34–39
2004	0.65	0.63–0.67	0.29	0.26–0.32	0.02	0.00–0.04	65	62–68
2005	0.64	0.62–0.66	0.29	0.26–0.33	0.17	0.15–0.19	74	67–77
2006	0.71	0.69–0.74	0.30	0.28–0.32	0.01	−0.01–0.04	62	57–65
2007	0.74	0.72–0.76	0.48	0.46–0.49	0.37	0.36–0.39	95	85–115
2008	0.67	0.65–0.69	0.31	0.29–0.33	0.14	0.13–0.16	85	71–88
2009	0.65	0.63–0.67	0.34	0.32–0.37	0.14	0.13–0.15	80	76–83
2010	0.63	0.61–0.65	0.21	0.19–0.23	0.10	0.08–0.12	28	25–62

Notes: The length scale was calculated as the distance at which the nonparametric correlation function reached the regional mean synchrony level. The variable $\rho(0)$ represents the *y*-intercept of the nonparametric correlation function.

for giant kelp (reviewed in Graham et al. 2007). It was not possible for us to separate the roles of dispersal, local environmental variability, and grazing in synchronizing kelp populations at small scales using these observational data; manipulative studies are needed to address this issue.

We hypothesize that the large-scale decrease in giant kelp synchrony is primarily due to large-scale environmental controls (i.e., the Moran effect), particularly wave disturbance. The Moran effect predicts that the synchrony of populations controlled by large-scale environmental perturbations should decline in an identical or parallel manner to the synchrony of the environmental variables (Moran 1953). The length scale of this large-scale decrease (74 km when calculated as the distance where the NCF reaches its regional mean synchrony level) corresponded to the length scale of the wave height NCF (61 km; compare Fig. 2 to Fig. 3b). In addition, the double exponential and exponential models of the kelp and wave height NCFs flattened at similar length scales, 172 km and 120 km, respectively. The most probable mechanism by which wave disturbance influences kelp synchrony is by causing spatially correlated mortality on scales corresponding to the scales of wave height autocorrelation. However, large wave events may also induce spatially correlated recruitment and growth of kelp populations. Wave disturbance can clear space and create light conditions that promote the recruitment and juvenile growth of a new cohort of giant kelp (Graham et al. 1997). Synchrony in changes in SST, a proxy for nutrients, also declined with distance over large scales, and so may be contributing to the large-scale decline in kelp synchrony. Nutrient levels can strongly influence giant kelp growth rates (Jackson 1977, Gerard 1982), and prolonged low-nutrient conditions, such as those associated with El Niño events, can cause regional-scale mortality events (Dayton and Tegner 1984). However, SST synchrony did not demonstrate an exponential decline, and SST was highly autocorrelated over the entire study area; we therefore hypothesize that wave-driven disturbance plays a larger role than nutrients in setting the spatial scale of regional kelp synchrony. These results are consistent with those of other studies that have found nutrient availability and wave disturbance to be important in accounting for regional differences in the dynamics of giant kelp (Dayton et al. 1999, Edwards 2004, Reed et al. 2011). Sea urchins, the major grazer of kelp, did show some positive synchrony in population dynamics at scales of up to 60 km (Fig. 3c), and so urchins could also play a role in large-scale kelp synchrony.

The stepwise pattern in the kelp biomass NCF was significant in each of the 11 years of the study (Table 1 and Appendix D: Fig. D1), demonstrating that this pattern is evident on annual as well as interannual time scales. It is important to note that the NCF created from the entire time series (2000–2011; Fig. 2) represents the long-term pattern in synchrony, and that this decadal-scale pattern in unlikely to be observed in a given year. The relatively high variability in both the magnitude of synchrony at large spatial scales and the length scale of synchrony for the annual kelp correlation functions (Table 1 and Appendix D: Fig. D1) indicates that much of the temporal variability in patterns of giant kelp synchrony occurs on the larger spatial scales that appear to be regulated by environmental factors. However, we were unable to explain the variability in the length scale of giant kelp using the length scale of SST or wave height. The lack of a significant relationship between these variables may be partly due to the complexity of the annual kelp correlation functions. This complexity makes it difficult to quantify the length scale of kelp synchrony. The annual kelp correlation functions do not all follow a double exponential decline, and the point where the NCF reaches the mean level of synchrony did not fully capture the shape of the NCF (Appendix D: Fig. D1). Also, the relationship between the length scale of kelp synchrony and its driving factors is probably complex and nonlinear on short time scales. For instance, a single large storm event can induce large-scale synchrony in kelp populations by removing all the kelp in a very large region (Edwards 2004). The relationship between annual maximum wave height and kelp mortality saturates at high wave heights (Cavanaugh et al. 2011), and so as long as the wave heights across a given region are all above a certain threshold, mortality will be high and consistent across that entire region, even if there is spatial variability in wave height across the region. Over longer time periods the effect of these short-term discrepancies in scale are likely averaged out by repeated cycles of disturbance and recovery.

It is especially important to understand how multiple processes synchronize populations for systems that function as metapopulations (see Reed et al. 2006a for a discussion of giant kelp as a metapopulation). The metapopulation concept refers to a collection of local populations linked by limited dispersal, and has been used to describe a wide variety of terrestrial (Hanski and Gilpin 1997) and marine (Kritzer and Sale 2006) ecosystems. Synchrony is especially important in these systems because metapopulation theory predicts that higher levels of synchrony in local population dynamics will lead to a higher probability of extinction of the metapopulation (Heino et al. 1997, Liebhold et al. 2004). If local subpopulations fluctuate together, then they will tend to go extinct at the same time. On the other hand, if spatial synchrony is low, then abundant subpopulations can contribute propagules that recolonize neighboring extinct patches, thereby increasing the persistence of the metapopulation. For example, in an analysis of wintering North American birds, Koenig (2001) found a significant positive relationship between spatial autocorrelation at short distances and the length of extinctions of resident species. However, theoretical studies have also shown that the degree to which spatial synchrony impacts metapopulation persistence is highly dependent on the spatial distribution of the subpopulations (Adler and Nuemberger 1994). Johst and Drechs-

ler (2003) modeled metapopulations of various spatial configurations and found that increased habitat clustering increased metapopulation persistence in both static and dynamic landscapes. More empirical work is needed to understand how the spatial distribution of subpopulations, the length scale of dispersal, and the length scale of synchrony interact to control extinction risk in real-world metapopulations.

LITERATURE CITED

Abbott, K. C. 2007. Does the pattern of population synchrony through space reveal if the Moran effect is acting? Oikos 116:903–912.

Adler, F. R., and B. Nuemberger. 1994. Persistence in patch, irregular landscapes. Theoretical Population Biology 45:41–75.

Alberto, F., P. T. Raimondi, D. C. Reed, N. C. Coelho, R. Leblois, A. Whitmer, and E. A. Serrão. 2010. Habitat continuity and geographic distance predict population genetic differentiation in giant kelp. Ecology 91:49–56.

Bascompte, J., and R. V. Solé. 1998. Spatiotemporal patterns in nature. Trends in Ecology and Evolution 13:173–174.

Bjørnstad, O. N. 2000. Cycles and synchrony: two historical "experiments" and one experience. Journal of Animal Ecology 69:869–873.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. Environmental and Ecological Statistics 8:53–70.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999a. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427–432.

Bjørnstad, O. N., N. C. Stenseth, and T. Saitoh. 1999b. Synchrony and scaling in dynamics of voles and mice in northern Japan. Ecology 80:622–637.

Buonaccorsi, J. P., J. S. Elkinton, S. R. Evans, and A. M. Liebhold. 2001. Measuring and testing for spatial synchrony. Ecology 82:1668–1679.

Cavanaugh, K. C., D. A. Siegel, D. C. Reed, and P. E. Dennison. 2011. Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. Marine Ecology Progress Series 429:1–17.

Chiles, J. P., and P. Delfiner. 1999. Geostatistics, modelling spatial uncertainty. Wiley-Interscience, New York, New York, USA.

Dayton, P. K., and M. J. Tegner. 1984. Catastrophic storms, El Nino, and patch stability in a southern California kelp community. Science 224:283–285.

Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser. 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. Ecological Monographs 69:219–250.

Denny, M. W. 1988. Biology and the mechanics of the wave-swept environment. Princeton University Press, Princeton, New Jersey, USA.

de Roos, A. M., E. McCauley, and W. G. Wilson. 1991. Mobility versus density-limited predator–prey dynamics on different spatial scales. Proceedings of the Royal Society B 246:117–122.

de Valpine, P., K. Scranton, and C. P. Ohmart. 2010. Synchrony of population dynamics of two vineyard arthropods occurs at multiple spatial and temporal scales. Ecological Applications 20:1926–1935.

Deysher, L. E., and T. A. Dean. 1986. Interactive effects of light and temperature on sporophyte production in the giant kelp Macrocystis pyrifera. Marine Biology 93:17–20.

Ebert, T. A., and J. R. Southon. 2003. Red sea urchins (Strongylocentrotus franciscanus) can live over 100 years: confirmation with A-bomb ^{14}carbon. Fishery Bulletin 101:915–922.

Edwards, M. S. 2004. Estimating scale-dependency in disturbance impacts: El Ninos and giant kelp forests in the northeast Pacific. Oecologia 138:436–447.

Foster, M., and D. Schiel. 1985. The ecology of giant kelp forests in California: a community profile. United States Fish and Wildlife Service Biological Report 85(7.2).

Fram, J. P., H. L. Stewart, M. A. Brzezinski, B. Gaylord, D. C. Reed, S. L. Williams, and S. MacIntyre. 2008. Physical pathways and utilization of nitrate supply to the giant kelp, Macrocystis pyrifera. Limnology and Oceanography 53:1589–1603.

Gerard, V. A. 1982. Growth and utilization of internal nitrogen reserves by the giant kelp Macrocystis pyrifera in a low-nitrogen environment. Marine Biology 66:27–35.

Gouhier, T. C., F. Guichard, and B. A. Menge. 2010. Ecological processes can synchronize marine population dynamics over continental scales. Proceedings of the National Academy of Sciences USA 107:8281–8286.

Graham, M. H., C. Harrold, S. Lisin, K. Light, J. M. Watanabe, and M. S. Foster. 1997. Population dynamics of giant kelp Macrocystis pyrifera along a wave exposure gradient. Marine Ecology Progress Series 148:269–279.

Graham, M. H., J. A. Vasquez, and A. H. Buschmann. 2007. Global ecology of the giant kelp Macrocystis: from ecotypes to ecosystems. Oceanography and Marine Biology: an Annual Review 45:39–88.

Hanski, I. A., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Hanski, I., and I. Woiwod. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology 62:656–668.

Harrold, C., and J. S. Pearse. 1987. The ecological role of echinoderms in kelp forests. Pages 137–233 in M. Jangoux and J. M. Lawrence, editors. Echinoderm studies. A.A. Balkema, Rotterdam, The Netherlands.

Heino, M., V. Kaitala, E. Ranta, and J. Lindstrom. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society B 264:481–486.

Ims, R. A., and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature 408:194–196.

Jackson, G. A. 1977. Nutrients and production of giant kelp, Macrocystis pryifera, off southern California. Limnology and Oceanography 22:979–995.

Johst, K., and M. Drechsler. 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? Oikos 103:449–456.

Kahru, M., R. Kudela, M. Manzano-Sarabia, and B. G. Mitchell. 2009. Trends in primary production in the

California Current detected with satellite data. Journal of Geophysical Research 114: C02004.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Kendall, B. E., O. N. Bjørnstad, J. Bascompte, T. H. Keitt, and W. F. Fagan. 2000. Dispersal, environmental correlation, and spatial synchrony in population dynamics. American Naturalist 155:628–636.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology and Evolution 14:22–26.

Koenig, W. D. 2001. Spatial autocorrelation and local disappearances in wintering North American birds. Ecology 82:2636–2644.

Koenig, W. D., and J. M. N. Knopes. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist 155:59–69.

Kritzer, J. P., and P. F. Sale. 2006. Marine metapopulations. Academic Press, San Diego, California, USA.

Lande, R., S. Engen, and B. Sæther. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. American Naturalist 154:271–281.

Lawrence, J. M. 1975. On the relationships between marine plants and sea urchins. Oceanography and Marine Biology Annual Review 13:213–286.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the Robert H. MacArthur Award Lecture. Ecology 73:1943–1967.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution, and Systematics 35:467–490.

Lucas, A. J., C. L. Dupont, V. Tal, J. L. Largier, B. Palenik, and P. J. S. Franks. 2011. The green ribbon: multiscale physical control of phytoplankton productivity and community structure over a narrow continental shelf. Limnology and Oceanography 56:611–626.

MATLAB. 2011. MATLAB version 7.12. MathWorks, Natick, Massachusetts, USA.

Moran, P. A. P. 1953. The statistical analysis of the Canadian lynx cycle. II. synchronization and meteorology. Australian Journal of Zoology 1:291–298.

Nisbet, R. M., and J. R. Bence. 1989. Alternative dynamic regimes for canopy-forming kelp: a variant on density-vague population regulation. American Naturalist 134:377–408.

North, W. J., and R. C. Zimmerman. 1984. Influences of macronutrients and water temperatures on summertime survival of Macrocystis canopies. Hydrobiologia 116-117:419–424.

Okubo, A., and S. A. Levin. 2002. Diffusion and ecological problems. Springer, New York, New York, USA.

O'Reilly, W., and R. Guza. 1993. A comparison of two spectral wave models in the Southern California Bight. Coastal Engineering 19:263–282.

Peltonen, M., A. M. Liebhold, O. N. Bjørnstad, and D. W. Williams. 2002. Spatial synchrony in forest insect outbreaks: roles of regional stochasticity and dispersal. Ecology 83:3120–3129.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ranta, E., V. Kaitala, J. Lindstrom, and H. Linden. 1995. Synchrony in population dynamics. Proceedings of the Royal Society B 262:113–118.

Reed, D., B. Kinlan, P. Raimondi, L. Washburn, B. Gaylord, and P. Drake. 2006a. A metapopulation perspective on the patch dynamics of giant kelp in Southern California. Pages 352–386 in J. Kritzer and P. Sale, editors. Marine metapopulations. Academic Press, San Diego, California, USA.

Reed, D. C., M. Neushul, and A. W. Ebeling. 1991. Role of settlement density on gametophyte growth and reproduction in the kelps *Pterygophora californica* and *Macrocystis pyrifera* (Phaeophyceae). Journal of Phycology 27:361–366.

Reed, D. C., A. Rassweiler, and K. K. Arkema. 2008. Biomass rather than growth rate determines variation in net primary production by giant kelp. Ecology 89:2493–2505.

Reed, D. C., A. Rassweiler, M. H. Carr, K. C. Cavanaugh, D. P. Malone, and D. A. Siegel. 2011. Wave disturbance overwhelms top-down and bottom-up control of primary production in California kelp forests. Ecology 92:2108–2116.

Reed, D. C., S. C. Schroeter, and D. Huang. 2006b. An experimental investigation of the use of artificial reefs to mitigate the loss of giant kelp forest habitat. A case study of the San Onofre Nuclear Generating Station's artificial reef project. California Sea Grant College Program, San Diego, California, USA.

Schiel, D. R., and M. S. Foster. 2006. The population biology of large brown seaweeds: ecological consequences of multiphase life histories in dynamic coastal environments. Annual Review of Ecology, Evolution, and Systematics 37:343–372.

Sokal, R. R., and N. L. Oden. 1978. Spatial autocorrelation in biology: 1. Methodology. Biological Journal of the Linnean Society 10:199–228.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3:385–397.

Wiens, J. A. 1997. Metapopulation dynamics and landscape ecology. Pages 43–68 in I. A. Hanski and M. E. Gilpin, editors. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

SUPPLEMENTAL MATERIAL

Appendix A

A table providing the exponential and double exponential decay function parameters for the giant kelp biomass nonparametric spatial correlation functions (*Ecological Archives* E094-041-A1).

Appendix B

A table providing the exponential decay function parameters for wave height, urchin abundance, and kelp recruit abundance nonparametric spatial correlation functions (*Ecological Archives* E094-041-A2).

Appendix C

A table providing the length scales of sea surface temperature and wave height synchrony for each year from 2000 to 2011 (*Ecological Archives* E094-041-A3).

Appendix D

A figure showing the annual nonparametric spatial correlation functions for changes in giant kelp biomass for each year from 2000 to 2011 (*Ecological Archives* E094-041-A4).