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Dispersal synchronizes giant kelp forests

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Abstract

Spatial synchrony is the tendency for population fluctuations to be correlated among different locations. This phenomenon is a ubiquitous feature of population dynamics and is important for ecosystem stability, but several aspects of synchrony remain unresolved. In particular, the extent to which any particular mechanism, such as dispersal, contributes to observed synchrony in natural populations has been difficult to determine. To address this gap, we leveraged recent methodological improvements to determine how dispersal structures synchrony in giant kelp (*Macrocystis pyrifera*), a global marine foundation species that has served as a useful system for understanding synchrony. We quantified population synchrony and fecundity with satellite imagery across 11 years and 880 km of coastline in southern California, USA, and estimated propagule dispersal probabilities using a high-resolution ocean circulation model. Using matrix regression models that control for the influence of geographic distance, resources (seawater nitrate), and disturbance (destructive waves), we discovered that dispersal was an important driver of synchrony. Our findings were robust to assumptions about propagule mortality during dispersal and consistent between two metrics of dispersal: (1) the individual probability of dispersal and (2) estimates of demographic connectivity that incorporate fecundity (the number of propagules dispersing). We also found that dispersal and environmental conditions resulted in geographic clusters with distinct patterns of synchrony. This study is among the few to statistically associate synchrony with dispersal in a natural population and the first to do so in a marine organism. The synchronizing effects of dispersal and environmental conditions on foundation species, such as giant kelp, likely have cascading effects on the spatial stability of biodiversity and ecosystem function.

KEYWORDS
demographic connectivity, dispersal, kelp forest, matrix regression, metapopulation, Moran effect, nutrients, population dynamics, remote sensing, spatial synchrony, stability, wave disturbance

INTRODUCTION

Spatial synchrony is the tendency for populations in different locations to exhibit correlated fluctuations in abundance over time. Greater spatial synchrony (henceforth, synchrony) leads to greater regional population variability, reduced population stability, and increased extinction risk (Anderson et al., 2021; Heino et al., 1998). Synchrony has been extensively documented across numerous taxa and can occur over scales of centimeters to thousands of kilometers (Koenig & Liebhold, 2016; Liebhold et al., 2004; Post & Forchhammer, 2002; Walter et al., 2021). Spatial patterns of synchrony can vary in response to geographic variation in synchronizing forces (Anderson et al., 2018; Walter et al., 2017). Resolving patterns of synchrony and their underlying drivers is important to our fundamental understanding of population dynamics and for addressing applied challenges in conservation (Earn et al., 2000; Tack et al., 2015), ecosystem management (Forchhammer & Post, 2004; Post & Forchhammer, 2002), and epidemiology (Earn et al., 1998).

Synchrony is caused by three major factors. First, populations in different locations can respond similarly to synchronous fluctuations in environmental conditions, such as changes in disturbance or resources. This phenomenon is known as the Moran effect (Moran, 1953) and has been documented across a wide diversity of organisms (Liebhold et al., 2004). Second, species interactions such as predation, parasitism, and facilitation can cause one species to synchronize another (Bjørnstad et al., 1999; Liebhold et al., 2004). Third, the dispersal of individuals among populations can induce synchrony (Kendall et al., 2000; Vogwill et al., 2009). In contrast to Moran effects and synchronizing species interactions, the role of dispersal in structuring synchrony and its geographic variation is poorly resolved in nature, despite a strong theoretical basis (e.g., Abbott, 2011; Kendall et al., 2000; Lande et al., 1999). Here, we define dispersal as movement from a natal location, often by offspring or propagules (e.g., seeds, spores; Burgess et al., 2014). Empirical studies examining dispersal as a synchronizing force have largely been based on studies with laboratory microorganisms or aquatic mesocosms (reviewed in Yang et al., 2022; but see Anderson et al., 2018; Bunnell et al., 2010; Peltonen et al., 2002). Such research is particularly rare in marine ecosystems, despite the importance of dispersal for structuring coastal population dynamics and the high potential for geographic variation in dispersal (Burgess et al., 2014; Cheal et al., 2007; Gouhier et al., 2010; Lagos et al., 2007).

Consistent with the idea that dispersal is a major cause of synchrony, comparisons among species show that those with broader dispersal are more strongly synchronized than those with limited dispersal (Liebhold et al., 2004; Paradis et al., 1999). Likewise, in butterflies, the spatial scale of synchrony corresponds with typical dispersal distances (Sutcliffe et al., 1996). Prior studies of synchrony typically used distance between locations as a coarse proxy for dispersal potential (Bjørnstad et al., 1999; Bjørnstad & Falck, 2001). Instead, here we determined whether more realistic estimates yield stronger evidence for the importance of dispersal for determining patterns of synchrony. Specifically, we used spatiotemporally explicit models to estimate two dispersal metrics: (1) individual dispersal probabilities, describing the movement from a natal location i to a non-natal location j, and (2) demographic connectivity, a quantity incorporating fecundity of the natal location to yield the total number of propagules dispersing from i to j (*Methods*; Burgess et al., 2014; Castorani et al., 2015, 2017).

Theory suggests the Moran effect may be more important than dispersal in controlling synchrony (e.g., Haydon & Steen, 1997). Here, we examine this hypothesis. We focused our investigation on giant kelp *Macrocystis pyrifera*, a broadly distributed marine foundation species that has served as an effective system for studies of synchrony in natural populations (Castorani et al., 2022; Cavanaugh et al., 2013; Reuman et al., 2023; Walter et al., 2022, 2024). Giant kelp is patchily distributed on rocky reefs in shallow coastal seas and demographically linked by ocean currents that disperse kelp spores (Castorani et al., 2015, 2017; Reed et al., 2006). In addition to studying giant kelp dispersal, we investigated Moran effects via destructive storm-driven waves and nutrients delivered primarily by upwelling, whose effects vary geographically (Bell et al., 2015; Castorani et al., 2022; Young et al., 2016). In doing so, we accomplish three interrelated goals: (1) describe the geography of synchrony among giant kelp populations (i.e., giant kelp forests in different locations, see *Methods*); (2) determine how dispersal affects giant kelp synchrony and its geographic patterns using two dispersal metrics (individual dispersal probabilities and demographic connectivity); and (3) assess how the effect of dispersal on giant kelp synchrony varies between two subregions that differ in environmental conditions and geographic isolation (mainland and islands of southern California, USA; Bell et al., 2015; Castorani et al., 2017).

METHODS

Study system

Giant kelp is the most widely distributed kelp species (Graham et al., 2007). It forms highly productive forests

that substantially determine the structure and function of reef ecosystems within its range (Castorani et al., 2018, 2021; Graham et al., 2007; Miller et al., 2018). Giant kelp sporophytes (the large, habitat-forming stage) consist of a holdfast anchored to the seafloor, a bundle of buoyant vegetative fronds extending to the ocean's surface, and spore-producing reproductive blades near the base. Giant kelp is exceptionally well suited for studying synchrony because its floating surface canopy is measurable over large areas and decadal time spans using satellite remote sensing (Bell et al., 2020; Cavanaugh et al., 2011). Giant kelp is also an ideal study species because its populations are extremely dynamic, with fast growth and frequent reproduction. Short lifespans of plants (typically 2–3 years) and fronds (1–6 months), quick generation cycles (about one or more per year), and rapid growth (~2% per day) cause standing biomass to turn over six to 12 times per year (Rassweiler et al., 2018; Reed et al., 2008, 2011; Rodriguez et al., 2013). Therefore, giant kelp responds quickly to changes in environmental conditions (Bell et al., 2015; Edwards, 2019; Graham et al., 2007).

We focused on giant kelp populations across ~880 km of coastline along the mainland of southern California, USA, and the eight California Channel Islands (Figure 1). Populations in this region are patchily distributed among rocky reefs and are demographically linked by microscopic spores that are produced and released throughout the year by mature sporophytes and passively dispersed by ocean currents (Castorani et al., 2015, 2017; Edwards, 2022; Reed et al., 2006). Demographic connectivity is thought to be typically limited to several kilometers due to a relatively short duration of spore viability (hours to days) and high spore densities required for postsettlement fertilization (>1 spore mm^{-2}; Edwards, 2022; Reed, 1990).

Along the California coast, oceanographic conditions synchronize fluctuations of giant kelp canopy biomass across hundreds of kilometers (Castorani et al., 2022). Such synchrony is caused in part by severe storm-driven waves that destroy and dislodge sporophytes and by fluctuations in seawater nutrients that influence growth, survival, and recruitment (Castorani et al., 2022). Coastal upwelling delivers nitrate-rich water that fuels rapid growth (Fram et al., 2008), and periods of low nitrate have been associated with declines in giant kelp biomass, reduced recruitment, and delayed population recovery (Bell et al., 2015; Cavanaugh et al., 2011, 2019; Edwards, 2019). Therefore, spatial variation in nitrate concentrations and wave heights partly determine geographic patterns of giant kelp synchrony (Castorani et al., 2022; Reuman et al., 2023; Walter et al., 2022, 2024). Cavanaugh et al. (2013) speculated that dispersal may be an additional

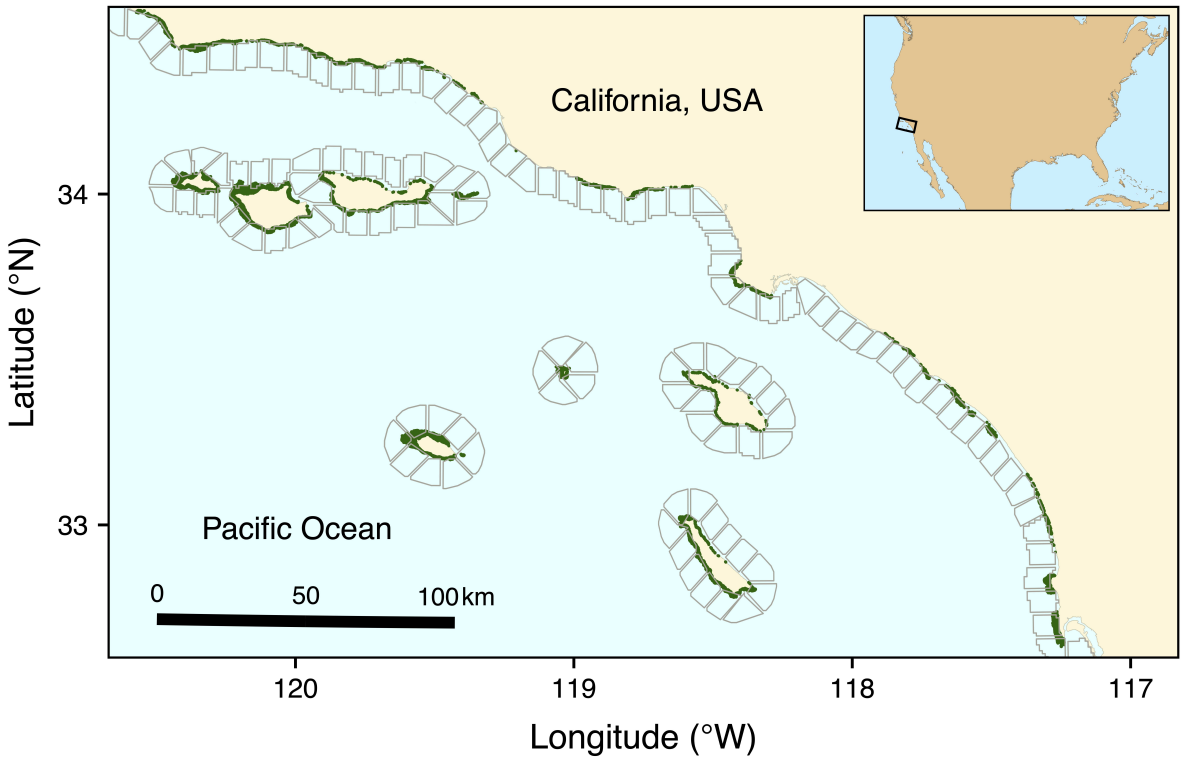

FIGURE 1 Map of study domain in southern California, USA. Green points show distribution of giant kelp *Macrocystis pyrifera* from Landsat satellite imagery, 1984–2021 (points not to scale). Polygons depict boundaries of cells in the ocean circulation model used to estimate dispersal of giant kelp spores (Regional Ocean Modeling System, ROMS). Of 135 ROMS cells, 117 contained kelp during the time series.

factor synchronizing giant kelp populations based on an observed rapid decay of synchrony with increasing distance that roughly coincided with the typical distances of giant kelp spore dispersal (up to several kilometers).

However, no studies have quantified the influence of dispersal on synchrony in giant kelp or any other marine organism. Moreover, it is not known whether the synchronizing effects of nutrients and waves on giant kelp (Moran effects) remain strong after controlling for the potentially synchronizing effects of dispersal (Castorani et al., 2022). Lastly, although patterns of giant kelp synchrony have been described for the California mainland (Castorani et al., 2022; Reuman et al., 2023; Walter et al., 2022), it is unknown whether patterns of synchrony and their drivers are similar for populations surrounding the California Channel Islands. These islands support 64% of southern California's kelp forests (measured as canopy biomass, 1984–2021; Bell, 2023) and are subject to patterns of nitrate supply, wave exposure, ocean currents, and geographic isolation that differ from those of the mainland (Bell et al., 2015; Castorani et al., 2017).

Giant kelp data

The primary data set used in this study was a field-validated satellite time series of giant kelp canopy biomass across the California coast from 1984 through 2021 (Bell, 2023). Surface canopy biomass (in kilogram wet) was estimated using 30-m-resolution multispectral imagery captured by Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus, and Landsat 8 Operational Land Imager satellites at least every 16 days. Briefly, kelp canopy cover was estimated from atmospherically corrected, radiometrically standardized Landsat reflectance data using multiple endmember spectral mixture analysis and correlated with diver measurements of canopy biomass (details and validation in Bell et al., 2020; Cavanaugh et al., 2011). Such estimates are frequently used to approximate the population size of adult sporophytes at scales of tens to thousands of kilometers (Bell et al., 2020; Castorani et al., 2015, 2017; Cavanaugh et al., 2019; Reed et al., 2006; Young et al., 2016).

We estimated giant kelp spore dispersal using a high-resolution ocean circulation model with polygon "cells" covering ~5 km of coastline (see details below). To match the kelp data to the spatial resolution of the circulation model outputs, we aggregated giant kelp biomass data to within the nearest cell (Figure 1) and averaged by quarter (January–March, April–June, July–September, October–December). Hereafter, we refer to cells containing kelp as giant kelp populations. When analyzing the geography of giant kelp synchrony, we analyzed all available data (36 years = 144 quarters; 1984–2021). When investigating the drivers of synchrony, we limited our analyses to an 11-year period (44 quarters) for which temporally explicit spore transport estimates were available (1996–2006).

Dispersal metric data

We characterized dispersal among giant kelp populations using two metrics: (1) the individual probability of kelp spore dispersal and (2) estimates of demographic connectivity that incorporate kelp fecundity (the number of spores dispersing; Burgess et al., 2014). We estimated dispersal using the Regional Ocean Modeling System (ROMS; Dong et al., 2009; Dong & McWilliams, 2007; Shchepetkin & McWilliams, 2005), a high-resolution (1 km horizontal), three-dimensional, empirically validated (Buijsman et al., 2012; Dong et al., 2009; Ohlmann & Mitarai, 2010) ocean circulation model that has been used to study giant kelp spore dispersal and metapopulation dynamics in southern California at scales of kilometers to hundreds of kilometers (Castorani et al., 2015, 2017). ROMS simulations estimated asymmetric, spatiotemporally explicit advection of Lagrangian particles—representing spores—released from 135 approximately rectangular nearshore coastal polygon cells (Figure 1; marginal shoreline width ~5 km; hereafter, "locations") across depths occupied by giant kelp (5–30 m; Graham et al., 2007; Young et al., 2016). Briefly, 63,000 simulated particles were released at each ROMS cell every 12 h from 1996 through 2006 (detailed methods in Mitarai et al., 2009; Simons et al., 2013). The resulting trajectories were used to estimate annual averages of the minimum transport time ($\tau_{ij,t}$) connecting each source location i with each destination location j in each year t (Castorani & Siegel, 2023).

The ROMS-estimated transport times do not account for the loss of giant kelp spores occurring during dispersal due to mortality or settlement in areas between source and recipient kelp forests. Daily loss rates of kelp spores are unknown, but lab studies suggest that giant kelp spores have limited periods of effective settlement competency (less than ~5 days; Reed et al., 1992). We considered proportional spore loss rates (μ) between 0.5 and 0.98 per day to represent a range of reasonable possibilities (Castorani et al., 2015, 2017; Edwards, 2022). A prior study using similar spore loss rates ($\mu = 0.5$–0.99) and the same ROMS transport data found that estimated spore dispersal probabilities were consistent with in situ dispersal measurements, population genetic estimates, and hydrodynamic models of giant kelp spore dispersal (Castorani et al., 2017, and references therein). Moreover, we found that our results on the effect of dispersal on kelp synchrony were highly robust to uncertainty in μ (Table 1 and Appendix S1: Tables S1 and S2). Because our synchrony analyses required a single, time-averaged

estimate of the dispersal probability or demographic connectivity among locations (see below), we defined the mean transport time connecting source location i and destination location j as $\tau_{ij} = \text{mean}_t(\tau_{ij,t})$ for all t years (1996–2006). We then calculated individual dispersal probabilities as

$$D_{ij} = (1-\mu)^{\tau_{ij}}. \quad (1)$$

Theory predicts that synchrony is related not simply to the individual probability of dispersal but to the degree of demographic connectivity between populations (Kendall et al., 2000), which incorporates the number of dispersing propagules (Burgess et al., 2014). Therefore, we estimated connectivity by multiplying the time-averaged probability of dispersal, D_{ij}, by the time average (1996–2006) of the annual population fecundity within the source location, $F_{i,t}$, which we estimated using a nonlinear seasonal relationship between canopy biomass and spore-producing tissue density (Castorani et al., 2017). Hence, we calculated connectivity as

$$C_{ij} = [\text{mean}_t(F_{i,t})] \times D_{ij}. \quad (2)$$

Because synchrony is a symmetric quantity (i.e., $\text{cor}(x_i,x_j) = \text{cor}(x_j,x_i)$ for population time series x_i and x_j associated with locations i, and j, respectively), and because we statistically compared dispersal–probability and connectivity matrices with synchrony matrices (see below), we use the maximum value between locations i

TABLE 1 Results of multiple regression on distance matrices (MRM) models with $\mu = 90\%$.

Locations	Dispersal metric	Dispersal transform	Synchrony transform	*p*			
				Dispersal	Distance	Waves	Nitrate
All	Dispersal probability	Linear	Logit	**0.001**	**0.001**	**0.001**	0.091
All	Dispersal probability	Linear	Linear	**0.001**	**0.001**	**0.001**	**0.036**
All	Dispersal probability	Log	Logit	**0.001**	**0.017**	**0.001**	**0.016**
All	Dispersal probability	Log	Linear	**0.001**	0.053	**0.001**	**0.006**
All	Connectivity	Linear	Logit	**0.001**	**0.001**	**0.001**	0.089
All	Connectivity	Linear	Linear	**0.001**	**0.001**	**0.001**	**0.05**
All	Connectivity	Log	Logit	**0.001**	**0.003**	**0.001**	**0.014**
All	Connectivity	Log	Linear	**0.001**	**0.009**	**0.001**	**0.004**
Mainland	Dispersal probability	Linear	Logit	**0.001**	0.237	0.443	0.169
Mainland	Dispersal probability	Linear	Linear	**0.001**	0.55	0.557	0.072
Mainland	Dispersal probability	Log	Logit	**0.001**	**0.017**	0.593	0.053
Mainland	Dispersal probability	Log	Linear	**0.002**	**0.03**	0.648	**0.032**
Mainland	Connectivity	Linear	Logit	**0.001**	0.184	0.411	0.195
Mainland	Connectivity	Linear	Linear	**0.001**	0.472	0.524	0.093
Mainland	Connectivity	Log	Logit	**0.001**	**0.015**	0.551	0.068
Mainland	Connectivity	Log	Linear	**0.002**	**0.034**	0.571	**0.034**
Islands	Dispersal probability	Linear	Logit	**0.001**	**0.001**	**0.001**	0.605
Islands	Dispersal probability	Linear	Linear	**0.001**	**0.001**	**0.001**	0.711
Islands	Dispersal probability	Log	Logit	**0.001**	0.765	**0.001**	0.465
Islands	Dispersal probability	Log	Linear	**0.005**	0.164	**0.001**	0.61
Islands	Connectivity	Linear	Logit	**0.001**	**0.001**	**0.001**	0.606
Islands	Connectivity	Linear	Linear	**0.001**	**0.001**	**0.001**	0.731
Islands	Connectivity	Log	Logit	**0.001**	0.319	**0.001**	0.279
Islands	Connectivity	Log	Linear	**0.001**	0.965	**0.001**	0.4

Note: Bold face denotes $p \leq 0.05$. Each row corresponds to a multiple regression on distance matrices (MRM) model predicting a giant kelp synchrony matrix as a function of multiple predictor matrices: (1) a dispersal metric (the individual dispersal probability or demographic connectivity), (2) distances between locations, and synchrony in (3) wave height, and (4) nitrate. *p*-values indicate the significance of model terms. Models differed in their location (all locations, mainland only, or islands only), whether they analyzed dispersal on a linear (untransformed) or natural-log transformed scale, and whether the giant kelp synchrony response matrix was analyzed on a linear (untransformed) or logit transformed scale. These models were calculated using a daily proportional spore loss rate, μ, of 90%, but results were similar for other loss rates (Appendix S1: Tables S1 and S2).

and j for matrices of dispersal probabilities and connectivity. In other words, whenever the i,j^{th} matrix element in one of these matrices was smaller than the j,i^{th} element in the same matrix, we replaced the i,j^{th} element by the j,i^{th} one.

We considered both untransformed and natural-log-transformed matrices of dispersal probabilities and connectivity in our statistical models below (Castorani et al., 2017).

Environmental data

In addition to these metrics of dispersal, we investigated two environmental variables as potential drivers of giant kelp synchrony via Moran effects: disturbance in the form of destructive waves and resources in the form of seawater nutrient availability. These factors were recently shown to induce synchrony in giant kelp populations across the California mainland (Castorani et al., 2022; Cavanaugh et al., 2013; Reuman et al., 2023; Walter et al., 2024), but such studies did not quantify effects at the California Channel Islands, nor did they control for the potential synchronizing effects of dispersal.

We characterized wave disturbance using coastal swell predictions (detailed methods in Bell et al., 2015). Briefly, a cross-validated model combined hourly in situ measurements and model outputs of significant wave height (i.e., the mean height of the highest one-third of waves; hereafter, "wave height") and direction (from the U.S. National Buoy Data Center and the U.S. Wave Information Study) with real-time and hindcast swell models from the Coastal Data Information Program (details and validation in Hanson et al., 2009; O'Reilly et al., 2016; Wingeart et al., 2001). The spatial resolution of the wave height data was finer than the ROMS cells, and so we averaged the maximum wave height data within each ROMS cell for each quarter from 1996 through 2006.

We characterized nutrient availability using nitrate concentrations (hereafter, "nitrate") estimated from sea surface temperature (SST). Briefly, using an empirical relationship (Snyder et al., 2020), we calculated daily surface nitrate from daily SST derived from the National Oceanic and Atmospheric Administration Coral Reef Watch version 3.1 global 5-km satellite SST data product (details and validation in Roberts-Jones et al., 2012; Maturi et al., 2017). Surface nitrate is highly predictive of nitrate availability at depths of 0–20 m ($R^2 = 73\%$; Castorani et al., 2022); nitrate data below 20 m were not available for this analysis, but in California >80% of giant kelp is distributed at 0–20 m (Young et al., 2016). As with wave height, we calculated quarterly mean nitrate for each ROMS cell from 1996 through 2006.

Analyses

We pretreated kelp biomass, wave height, and nitrate data to produce demeaned, detrended time series that were variance-standardized and made approximately normal through optimal Box-Cox transformation in R using the *wsyn* package (Reuman et al., 2021). We carried out this normalization because we calculated synchrony using Pearson correlation (see below).

Addressing our first goal—to describe the geography of giant kelp synchrony—we computed synchrony as Pearson correlations between all pairs of locations across the full quarterly giant kelp time series (1984–2021). We estimated the distance decay of synchrony using the Euclidean distance between locations and the spline correlogram methods of Bjørnstad and Falck (2001), implemented in R using the *ncf* package (Bjornstad, 2022). We used matrix heatmaps to visually represent the geography of giant kelp synchrony. Lastly, using *wsyn*, we implemented an adapted version (Walter et al., 2021) of the eigenvector-based clustering method of Newman (2006) to identify clusters of locations having relatively high within-group synchrony and relatively low between-group synchrony. To characterize differences in kelp dynamics between clusters, we produced mean cluster time series by averaging time series from all locations within each cluster.

Addressing our second goal—to determine how dispersal metrics affect giant kelp synchrony and quantify its geographic patterns—we used multiple regression on distance matrices (MRM; Legendre et al., 1994) in R using *ecodist* (Goslee & Urban, 2007). The MRM method is conceptually similar to multiple linear regression, but response and predictor variables in MRM models are matrices, with rows and columns indexed by locations and cells containing comparative information between locations. MRM models use permutation-based tests to determine the significance of regression coefficients. For each model term, we tested whether a MRM model containing the term explained significantly more variability in the response than a model lacking the term. In our context, for which the response variable was matrices of giant kelp synchrony and predictor variables included matrices of dispersal metrics (individual dispersal probabilities or demographic connectivity), MRM models could answer, for instance, whether pairs of locations that were more connected by dispersal were also more synchronous in kelp dynamics. Models could also control for the influence of predictors other than the two dispersal metrics.

We fit several MRM models analyzing subsets of the kelp and environmental data from the period for which spore transport estimates were available (1996–2006). We excluded locations (ROMS cells) that did not contain kelp

at any point in the time series; this left 117 locations with kelp and $n = 6786$ pairs of i, j locations ($i \neq j$) for analysis. Because we were interested principally in the potential effects of dispersal, all models included synchrony matrices of wave height and nitrate as predictors to control for these Moran effects. To control for geographic proximity per se, all models also included as a predictor a matrix of the Euclidean distances between locations. As a fourth predictor, each model used a matrix of either the dispersal probabilities or demographic connectivity (but not both). All models tested whether the dispersal metric matrix explained significant additional variation in the response synchrony matrix than what was already explained by the distance, wave height, and nitrate matrices.

To determine the robustness of our results to several statistical decisions, we fit separate MRM models with factorial combinations of (1) dispersal metrics expressed on the untransformed linear scale or natural-log-transformed scale; (2) the response variable—the synchrony matrix of giant kelp biomass—expressed on the untransformed linear scale (bounded from −1 to 1) or logit-transformed scale (bounded from $-\infty$ to ∞); and (3) dispersal metrics calculated with the daily proportional spore loss rate (μ) equal to 0.5, 0.9, or 0.98.

Addressing our third goal—to assess how the effects of dispersal on giant kelp synchrony may differ between mainland and island populations—we used additional MRM models. We fit the suite of models described above separately using data from all locations, only locations from the southern California mainland, or only locations surrounding the California Channel Islands.

In summary, we analyzed a total of 72 models by varying these five factors in a factorial manner: (1) the dispersal metric (individual dispersal probabilities or demographic connectivity) on (2) linear or natural-log scales; (3) the response variable synchrony matrix on linear [−1,1] or logit ($-\infty$,∞) scales; (4) the spore loss rate $\mu = 0.5$, 0.9, or 0.98; and (5) using data from all locations, mainland locations, or island locations. By comparing results from these alternatives, we determined whether results were sensitive to different methodological choices.

RESULTS

Geography of giant kelp synchrony

Addressing our first goal—to describe the geography of giant kelp synchrony—we found that synchrony declined rapidly with distances up to ~50 km and then declined slowly to ≥300 km (Figure 2). This pattern is consistent with earlier findings (Cavanaugh et al., 2013; Walter et al., 2022).

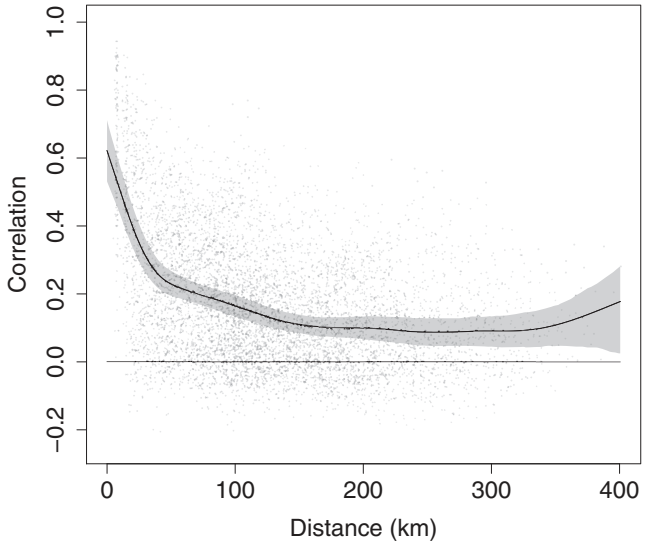

FIGURE 2 The synchrony of giant kelp biomass declines rapidly with distance between locations, up to about 50 km, and then declines slowly as distances continue to increase (to at least 300 km). Points correspond to Euclidean distances and correlations between all pairs of 117 locations containing giant kelp ($n = 6786$; see *Methods* and Figure 1). Black line shows fitted spline correlogram; shading shows 95% confidence interval.

Clustering based on kelp synchrony revealed distinct dynamics in two subregions. Clustering with data from all locations (mainland and islands) revealed one cluster roughly encompassing the more western portions of the islands and the mainland in the very northwest of our study region (near Santa Barbara and Point Conception) and a second cluster roughly encompassing the more eastern portions of the islands and the rest of the mainland (Figure 3a). Clusters based on locations only on the islands (Figure 3b) or only on the mainland (Figure 3c) yielded similar spatial patterns, evidence of robustness of clustering results. Visual examination of cluster-averaged time series (Figure 3d–f) suggested that clusters exhibited similar fluctuations on multiyear timescales (low-frequency oscillations), and therefore clustering may have been driven by differences between clusters in seasonal and year-to-year variability (high-frequency oscillations); such short-term variance was generally higher for the western clusters (blue points in Figure 3) than the eastern clusters (red points in Figure 3).

Effects of dispersal on giant kelp synchrony

Addressing our second goal—to determine how dispersal metrics affect giant kelp synchrony and quantify its geographic patterns—we found that individual dispersal probabilities and demographic connectivity were consistently

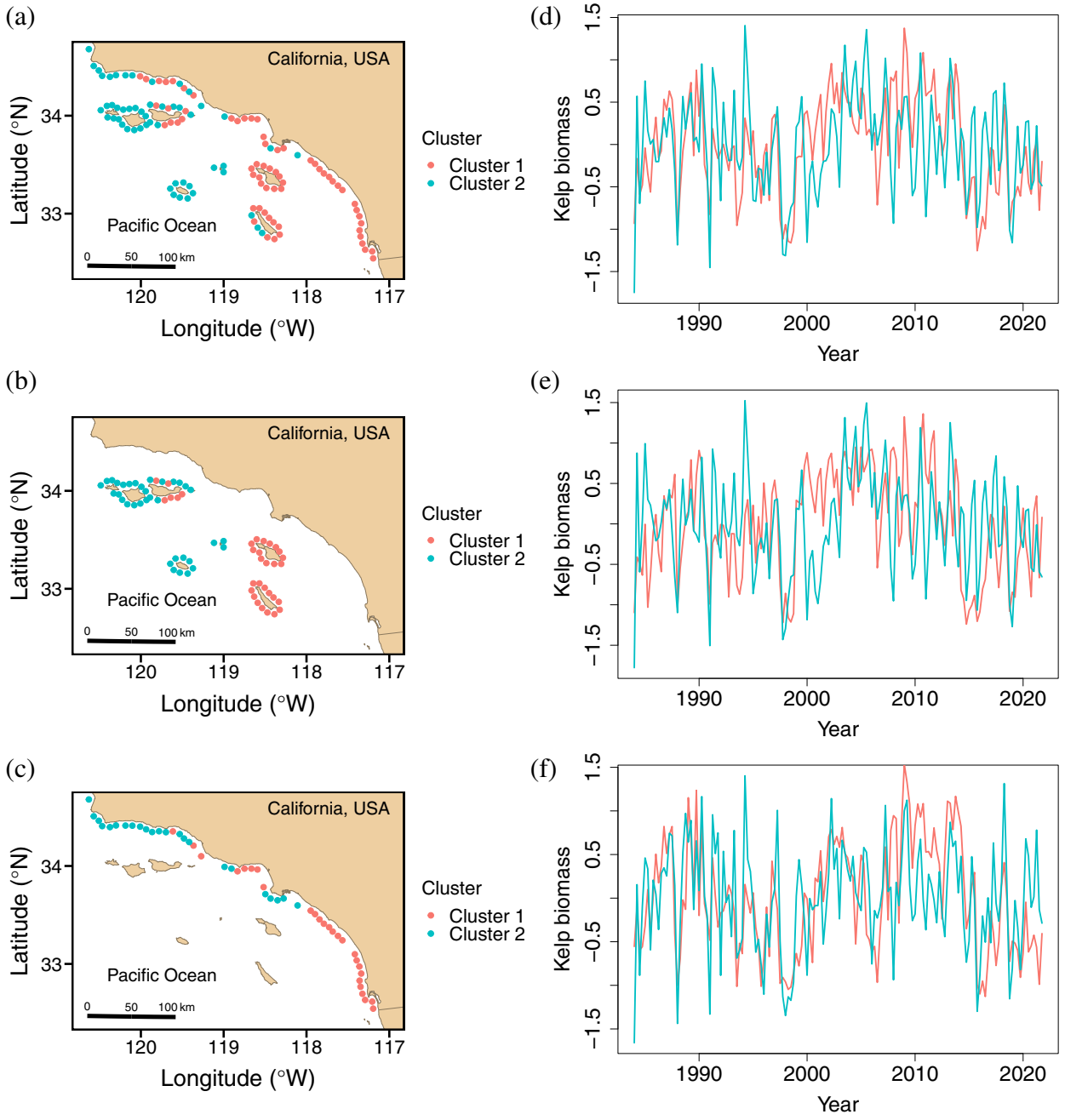

FIGURE 3 Clusters of synchrony for giant kelp biomass time series (a–c) and average time series for each cluster (d–f). Clusters (*Methods*) and cluster time series averages were computed separately based on data from all locations in southern California, USA (a, d), only locations surrounding the California Channel Islands (b, e), and only locations along the southern California mainland (c, f). Each point in panels (a), (b), and (c) represents a cell from the Regional Ocean Modeling System (ROMS; see *Methods*). Kelp biomass time series have been demeaned, detrended, and Box–Cox transformed (*Methods*).

important in our MRM models for explaining patterns of synchrony of giant kelp biomass ($p \leq 0.005$). Example matrices used in MRM models are visualized as heatmaps in Appendix S1: Figure S1. In particular, dispersal metrics were highly significant predictors of giant kelp synchrony for all 72 of the models we considered (Table 1; Appendix S1: Tables S1 and S2). In contrast, the influences of predictor matrices for the synchrony of nitrate, synchrony of wave height, and Euclidean distance in our MRM models were not uniformly significant. These results provide strong evidence that dispersal is highly important for structuring the geography of synchrony in giant kelp and so also an important cause of synchrony.

Still, when considering all locations in our study region, the synchrony of environmental conditions was generally an important driver of synchrony in giant kelp

and its geography. Wave height was a highly significant ($p \leq 0.002$) factor regardless of the scales of predictor or response variables or the daily proportional spore loss rate (μ; Table 1; Appendix S1: Tables S1 and S2). Evidence for nitrate as a synchronizing force ranged from very strong ($p = 0.003$) to marginal ($p = 0.1$), depending on the statistical choices made, but overall was significant ($p \leq 0.05$) in 83% (20/24) of the models fit to data from all locations (Table 1; Appendix S1: Tables S1 and S2).

Bivariate relationships between giant kelp synchrony and each predictor (Figure 4) suggested associations consistent with the statistical results (Table 1). These visual relationships do not replace the statistical results of Table 1 because the nonindependence of points within each panel of Figure 4 means that traditional tests of correlation are not appropriate. However, they do provide a visualization of our statistical tests based on MRM models, which were designed to deal with nonindependence arising from data based on pairwise comparisons among locations.

Geographic variation in effects of dispersal and environmental variables

Addressing our third goal—to assess how the effect of dispersal on giant kelp synchrony may vary between mainland and island locations—we found that dispersal metrics were strong and highly consistent drivers of giant kelp synchrony and its geography for both the mainland and islands ($p \leq 0.005$; Table 1; Appendix S1: Tables S1 and S2). By contrast, environmental drivers of synchrony (synchrony in nitrate and wave height) varied in their importance between the two subregions. Specifically, for all statistical choices, synchrony of giant kelp and its geography were partly attributable to synchrony in wave height along the islands ($p \leq 0.001$), but not along the mainland ($p \geq 0.36$; Table 1; Appendix S1: Tables S1 and S2). By contrast, synchrony in nitrate was not a cause of synchrony in kelp at the islands ($p \geq 0.16$), but the evidence for nitrate as a driver of kelp synchrony on the mainland was strong ($p \leq 0.038$) in one-third (8/24) of models and marginal ($p \leq 0.1$) in half (12/24) of models (Table 1; Appendix S1: Tables S1 and S2).

In summary, there was very strong ($p \leq 0.001$) to marginal ($p \leq 0.1$) evidence that synchrony in wave height and nitrate were drivers of synchrony in giant kelp at the regional scale (all locations; Table 1; Appendix S1: Tables S1 and S2). The analysis of mainland-only and island-only locations suggests that island locations drove the regional importance of wave height as a cause of kelp synchrony and mainland locations drove the regional importance of nitrate as a cause of kelp synchrony. In contrast, we found no evidence that the regional importance of dispersal metrics varied by subregion.

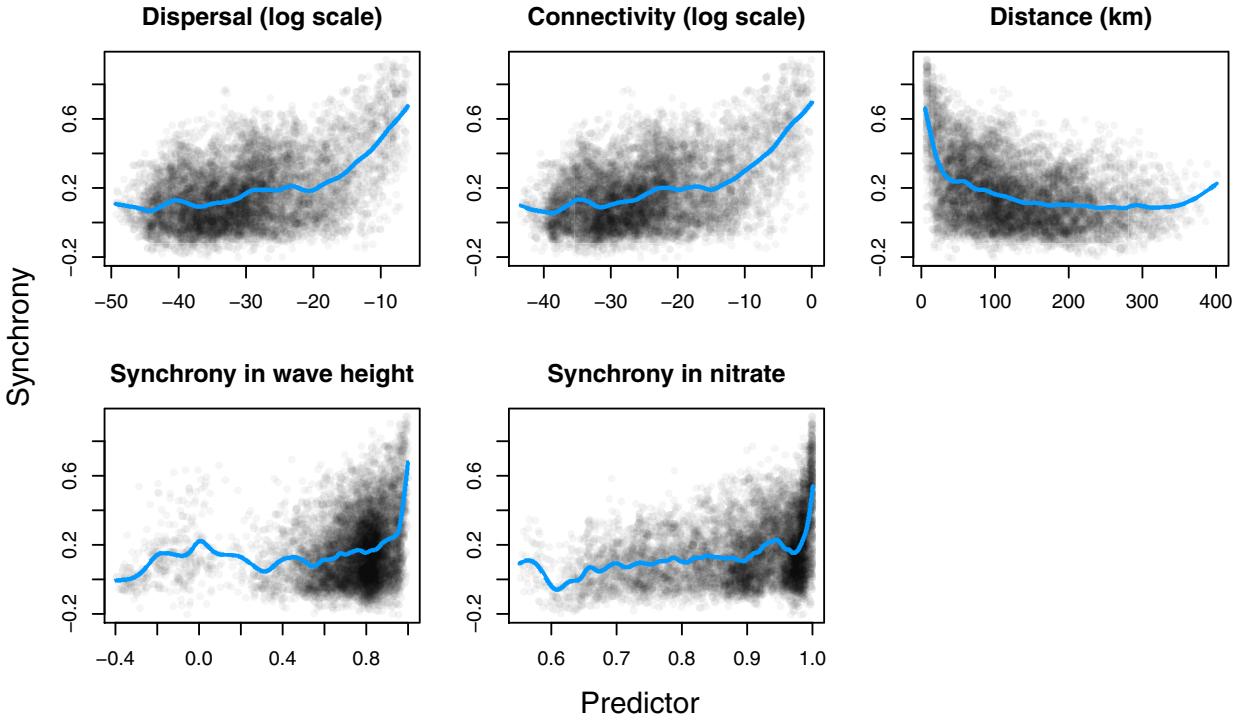

FIGURE 4 Predictors used in multiple regression on distance matrices (MRM) models plotted against synchrony of giant kelp biomass. Each point corresponds to a pair of locations, as in Figure 1. Blue lines show fitted splines. A relationship is visually apparent in each panel, supporting the statistical results reported in Table 1.

DISCUSSION

We determined how spatial patterns of synchrony in giant kelp are attributed to and structured by well-studied environmental mechanisms—resource fluctuations and disturbance (Liebhold et al., 2004)—and by the understudied mechanism of dispersal. Consistent with previous studies of giant kelp and other species, our results show that giant kelp synchrony tended to be stronger across shorter distances (Cavanaugh et al., 2013) and had geographic structure (Walter et al., 2022). We found that synchrony declined rapidly with distances up to about 50 km (and more gradually beyond this), but patterns of synchrony differed between two subregions (islands and mainland). Our results also revealed that two Moran drivers—storm-driven waves and seawater nutrients—synchronize giant kelp dynamics; this conclusion bolsters findings from a recent wavelet-based study of giant kelp synchrony along the mainland coast of California that did not control for the synchronizing effects of dispersal (Castorani et al., 2022).

Our results extended previous work on giant kelp synchrony in two important ways: (1) we included the California Channel Islands, which contain 64% of giant kelp forests in southern California (measured as canopy biomass, 1984–2021; Bell, 2023) and experience unique environmental conditions and patterns of isolation (Bell et al., 2015; Castorani et al., 2017); and (2) we quantified the influence of dispersal in the form of individual dispersal probabilities and demographic connectivity, which incorporates propagule production (i.e., fecundity) to yield the total number of propagules dispersing (Burgess et al., 2014; Castorani et al., 2015, 2017). After controlling for geographic distance and Moran effects, these dispersal metrics were both highly significant drivers of giant kelp synchrony across a broad suite of models with varying statistical choices. By contrast, the synchronizing effects of nutrients and wave disturbance varied among models. Consistent with this, waves were a strong and consistent driver of synchrony on the islands but not the mainland. This is likely because the orientation of the mainland coast relative to a large headland (Point Conception and Point Arguello) provides shelter from large northwest swells and the Channel Islands block swells originating from both the northwest and southwest (Bell et al., 2015). Likewise, the strength of evidence for nitrate as a synchronizing force varied between subregions (being stronger on the mainland than the islands), but also with various statistical decisions (e.g., the scale of the response and predictor variables). These results are consistent with a large-scale study that found that the effects of waves on giant kelp biomass dynamics were slightly stronger and the effects of nitrate were slightly weaker at the California Channel Islands than the southern California mainland (Bell et al., 2015). Our results also showed that, in contrast to wave height and nitrate, dispersal was a significant driver of the geography of giant kelp synchrony in both subregions and under all modeling decisions. Our findings may hold for giant kelp populations elsewhere and may apply broadly to other species that disperse moderate distances and are influenced by both resource fluctuations and disturbance.

Our study is among very few to statistically associate synchrony with dispersal in a natural population and the first to do so in a marine organism. There are three general mechanisms of synchrony: correlated environmental fluctuations (Moran effects), synchronizing species interactions (e.g., with predators, pathogens, or facilitating species), and dispersal among populations (Bjørnstad et al., 1999; Kendall et al., 2000; Liebhold et al., 2004; Moran, 1953). Of these mechanisms, dispersal remains the least well studied, despite several theoretical and lab-based investigations showing its strong potential to influence synchrony (Abbott, 2011; Kendall et al., 2000; Lande et al., 1999; Ranta et al., 1995, 1998; Yang et al., 2022). Dispersal is often difficult to estimate in nature due to the challenges associated with quantifying the movement of propagules or offspring among populations (Koenig et al., 1996). Because of this, only a few studies have directly measured the effects of dispersal on synchrony in unmanipulated natural populations (Anderson et al., 2018; Bunnell et al., 2010; Oliver et al., 2017). Instead, investigations of Moran effects have often tried to eliminate the potentially synchronizing effect of dispersal by experimentally manipulating dispersal (Ims & Andreassen, 2005) or selecting study systems in which dispersal is absent or extremely limited (Forchhammer & Post, 2004; Haynes et al., 2013). For instance, Grenfell et al. (1998) studied the synchrony of sheep inhabiting distant islands, and Rusak et al. (2008) studied the synchrony of zooplankton in separate lakes; in these cases, dispersal could not feasibly have affected synchrony. Our study also builds substantially on prior works that indirectly characterized the synchronizing effect of dispersal by comparing interspecific variation in dispersal and synchrony among species of insects (Peltonen et al., 2002; Sutcliffe et al., 1996) and birds (Bellamy et al., 2003; Paradis et al., 1999). Such studies demonstrated positive among-species associations between dispersal potential and synchrony but did not quantify or statistically attribute relationships for any specific taxa, as we accomplished here with giant kelp.

More generally, it has historically been difficult to statistically infer the causes of synchrony in natural populations (i.e., outside of theoretical models and controlled lab or mesocosm studies; Yang et al., 2022).

However, recent methodological developments, including the MRM methods used here, have overcome this problem, and our results provide an example of this success. Early papers used statistical techniques that provide little or no capability to deduce the causes of synchrony, instead focusing on how declines in population correlations change with distance (Abbott, 2007; Liebhold et al., 2004; Walter et al., 2017). As a result, prior to recent methodological improvements, it was only possible to examine mechanisms in special cases for which potential drivers could be ruled out (e.g., where dispersal was impossible and predators were absent; Grenfell et al., 1998; Tedesco et al., 2004) or in controlled experiments (Ims & Andreassen, 2005; Vasseur & Fox, 2009). With enough data, it is now possible to infer the causes of synchrony using several statistical approaches (Defriez & Reuman, 2017a, 2017b; Sheppard et al., 2016; Walter et al., 2017). For instance, MRM methods were used in a prior study to infer that precipitation acted as a Moran effect to control the synchrony of a defoliating moth (Haynes et al., 2013). Subsequently, MRMs were used to identify environmental factors (Bogdziewicz et al., 2021; Koenig et al., 2017; Walter et al., 2021) and dispersal (Anderson et al., 2018) as causes of synchrony in a few field systems (annual plants, trees, and freshwater plankton). Using MRMs and other modern analytical methods, we have shown that giant kelp synchrony is structured by dispersal (this study) and Moran effects (nutrients and wave disturbance, both underpinned by climate; Castorani et al., 2022). Other potential Moran effects deserve additional study, such as the influence of ocean warming and marine heatwaves that can cause kelp loss over large areas (Bell et al., 2023; Cavanaugh et al., 2019; Smale, 2020). Further work is also needed to understand the potential for giant kelp to be synchronized by species interactions—such as competition between understory macroalgae and early life stages of giant kelp (Beckley & Edwards, 2021; Edwards & Connell, 2012) and changes in the abundance (Pearse & Hines, 1979; Williams et al., 2021) or grazing behavior (Rennick et al., 2022; Smith et al., 2021) of sea urchins—and the spatial and temporal scales over which this may occur.

Our results indicate that the dispersal of giant kelp spores over scales of several kilometers induces synchrony among giant kelp populations. Little is known about the mortality experienced by planktonic marine propagules, including kelp spores, but our findings were robust to uncertainty about the loss rate of dispersing spores (proportional loss of 0.5–0.98/day). It is highly likely that synchrony attributed to dispersal was driven by spores released from mature kelp sporophylls near the bottom, rather than fertile sporophylls dislodged by storms and set adrift. Fertile drifters usually represent a small fraction of the reproductive population (Reed et al., 2004) and are fairly quickly transported out to sea or onto nearby beaches, spending relatively little time floating over suitable habitat several kilometers from their natal location (Reed et al., 2006). Moreover, due to their slow sinking speed and limited motility, kelp spores released from drifters would have difficulty traveling from the surface to the seafloor (Gaylord et al., 2012). Lastly, we investigated dispersal using a mesoscale ocean circulation model and described kelp synchrony at the scale of model outputs (marginal shoreline width ~5 km). The patterns and drivers of kelp spore dispersal and the effects on synchrony at smaller spatial scales warrant further investigation (Gaylord et al., 2012).

The causes of synchrony and the geography of synchrony do not necessarily coincide, but for the mechanisms that our results have revealed to operate, they are the same (Walter et al., 2017). In other words, our tests show that dispersal is an important driver of both synchrony and its geography for giant kelp. Geographies of synchrony can result from mechanisms that also cause synchrony itself and can result from mechanisms that are not also causes of synchrony. For instance, if the geography of synchrony of a species were inherited directly from the geography of synchrony of an environmental variable that influenced the species, then a Moran-like effect would be the mechanism for both synchrony and its geography. Examples of mechanisms of geography of synchrony that are not also causes of synchrony itself include spatial variation in density-dependent population regulation and spatial variation in the sensitivity of populations to environmental drivers (Walter et al., 2017). In such cases, synchrony would have geographic structure even if the operating environmental driver(s) causing synchrony were perfectly synchronized. However, our MRMs, precisely by demonstrating congruence between geographic patterns of kelp synchrony and geographic patterns of dispersal, indicate that dispersal is a major contributing factor to giant kelp synchrony. Our statistical tests show that such congruences are unlikely to have occurred by chance if dispersal were not among the causes of kelp synchrony. Buttressing this conclusion, prior studies indicated that spore dispersal was an important factor governing giant kelp extinction, colonization, and metapopulation dynamics (Castorani et al., 2015, 2017; Edwards, 2022; Reed et al., 2006; Young et al., 2016). Therefore, throughout this study, all drivers of the geography of synchrony established via our MRM models were also drivers of synchrony itself.

In conclusion, our results show that dispersal—quantified as either the individual probability of dispersal or demographic connectivity—is a mechanism of synchrony and its geography in southern California giant

kelp populations. These findings have implications for the stability, resilience, and recovery of giant kelp and associated ecosystems. Dispersal induces synchrony and in doing so has the potential to reduce the spatial stability of giant kelp and its ecological functions (Kremen, 2005). At the same time, dispersal is necessary for recolonization following local extirpation, leading to complex effects of dispersal on metapopulation persistence (Abbott, 2011; Fox et al., 2017). Giant kelp is a foundation species that strongly influences diversity and production on rocky reefs (Castorani et al., 2018, 2021; Miller et al., 2018) and nearby sandy beaches via detrital subsidies (Dugan et al., 2003); thus, giant kelp synchrony may cascade to reef and beach communities through species interactions (Walter et al., 2024). Therefore, our results not only provide a framework for using MRMs to evaluate dispersal and environmental drivers of synchrony in natural populations; they also hint at the unexplored possibility that dispersal in a foundation species may synchronize ecosystem structure and function across space and among ecosystems.

AUTHOR CONTRIBUTIONS

MCNC, DCR, and JAW conceived the study. MCNC, TWB, and MSW collected and compiled the data. DCR and JAW developed the statistical methods. MSW analyzed the data, with substantial contributions from DCR and JAW. All authors contributed to interpreting the results and writing the manuscript. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are publicly available from the Environmental Data Initiative (https://edirepository.org). Data on giant kelp biomass, wave height, and nitrate concentrations from Bell (2023) are available at https://doi.org/10.6073/pasta/c40db2c8629cfa3fbe80fdc9e086a9aa. Giant kelp spore transport time estimates from Castorani and Siegel (2023) are available at https://doi.org/10.6073/pasta/28a62732ad76625af1667c252187c8e3. R code to reproduce all results is publicly archived with Zenodo in Wanner et al. (2024) at https://doi.org/10.5281/zenodo.10558035.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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