Ecological processes can synchronize marine population dynamics over continental scales

Tarik C. Gouhier, Frédéric Guichard, and Bruce A. Menge

Determining the relative importance of local and regional processes for the distribution of population abundance is a fundamental but contentious issue in ecology. In marine systems, classical theory holds that the influence of demographic processes and dispersal is confined to local populations whereas the environment controls regional patterns of abundance. Here, we use spatial synchrony to compare the distribution of population abundance of the dominant mussel Mytilus californianus observed along the West Coast of the United States to that predicted by dynamical models undergoing different dispersal and environmental treatments to infer the relative influence of local and regional processes. We reveal synchronized fluctuations in the abundance of mussel populations across a whole continent despite limited larval dispersal and strong environmental forcing. We show that dispersal among neighboring populations interacts with local demographic processes to generate characteristic patterns of spatial synchrony that can govern the dynamic distribution of mussel abundance over 1,800 km of coastline. Our study emphasizes the importance of dispersal and local dynamics for the distribution of abundance at the continental scale. It further highlights potential limits to the use of “climate envelope” models for predicting the response of large-scale ecosystems to global climate change.

Synchronized fluctuations in abundance among spatially segregated populations are common in nature and can be used to quantify and understand the distribution of abundance in space and time (1). Synchrony can be induced by local intrinsic processes such as dispersal among populations and strong interactions with mobile predators or regional extrinsic processes such as spatially correlated environmental variability (1). Although these processes are well known, identifying their relative contribution to patterns of synchrony remains a challenge (1). Recent work has shown that when the processes that contribute to synchrony can be studied in isolation, it is via natural barriers to dispersal among populations (2, 3) or experimental manipulation (4), synchrony patterns can be ascribed to their underlying cause. However, when intrinsic and extrinsic causes of synchrony co-occur, as is the case in most systems, assigning synchrony patterns to any specific causal process becomes onerous (1). Here, we show that in marine populations experiencing both intrinsic and extrinsic sources of synchrony, the shape of spatial synchrony patterns can be used to infer the cause of synchrony and explain the regional distribution of abundance.

Marine population theory has relied mostly on the environment to explain the regional (>1,000 km) dynamics of populations. This focus is motivated by the lengthy pelagic larval stage commonly found in marine organisms, during which the larvae can be transported over large distances by strong nearshore currents (5). The potential for large-scale transport, along with the difficulties associated with measuring larval dispersal, has prompted many studies to assume either completely closed (no exportation of larvae to other populations) or completely open (no coupling between larval production and recruitment) demography (5, 6, but see refs. 7, 8). This assumption, typically associated with equilibrium dynamics at the local scale, has emphasized the effect of large-scale heterogeneity in nearshore environmental conditions on recruitment (i.e., supply-side theory) to explain the regional dynamics of marine populations (6, 9). However, recent progress on the quantification of larval dispersal distance has motivated the relaxation of demographic openness in several marine species (10–12). In light of these recent developments, we relax the assumptions of demographic openness and local equilibrium dynamics and compare the distribution of population abundance, predicted by dynamical metapopulation models undergoing different dispersal and environmental treatments, to that of the dominant mussel Mytilus californianus, observed along the West Coast of the United States, to assess the relative importance of nearshore environmental heterogeneity and dispersal.

Results and Discussion

Role of the Environment in Natural Mussel Populations. We first focus on the role of environmental heterogeneity by quantifying the strength and the consistency of the relationship between nearshore environmental conditions and the abundance (% cover) of M. californianus. Although nearshore environmental conditions have a strong effect on patterns of recruitment (13, 14), that effect seems lost on the regional distribution of M. californianus cover (15) (Fig. 1A). Indeed, the spatial correlation between the environmental conditions and the mean annual M. californianus cover is relatively weak and inconsistent through time (Fig. 1A), regardless of the temporal lag used (Fig. S1), the temporal scale over which the environment is averaged (Fig. S2) or whether the analysis explicitly accounts for the spatial heterogeneity observed in nearshore conditions (Fig. S3). This weak spatial correlation reflects the mismatch between the persistent spatial gradient in the environment and the spatiotemporal variability in the cover of M. californianus (Fig. S3). This mismatch leads to local correlations whose strength and sign vary in space and time (Fig. S3). Once spatially averaged, these highly variable local correlations lead to weak and inconsistent spatial correlations at the regional scale (Fig. L4 and Fig. S2). Spatial synchrony, which measures the correlation in the time series of pairs of sites as a function of the lag distance that separates them (Materials and Methods), more succinctly reveals the same discrepancy between the persistent spatial gradient in nearshore environmental conditions and the more complex spatiotemporal patterns in the cover of M. californianus (Fig. 1B). All environmental variables undergo a slow and statistically significant linear decrease in synchrony with increasing lag distance (Fig. 1B, see Materials and Methods and Table 1 for statistical details). However, the cover of M. californianus shows a statistically significant nonlinear pattern.

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oscillating between synchrony and asynchrony with increasing lag distance (Fig. 1B and Table 1). This discrepancy suggests that intrinsic processes (i.e., dispersal and species interactions) rather than local nearshore environmental conditions may control the spatial synchrony patterns exhibited by _M. californianus_.

**Effect of Dispersal and Species Interactions on Natural and Model Mussel Populations.** To elucidate how dispersal and species interactions can generate the complex spatial synchrony patterns observed in natural _M. californianus_ populations, we develop metapopulation models that describe disturbance–succession (16, 17) and predator–prey (18–20) dynamics in a network of mussel populations connected by dispersal. Dispersal was implemented as a symmetrical kernel in the successional model (Materials and Methods) and as a symmetrical and uniform nearest-neighbor process in the predator–prey model (SI Text). We subjected these metapopulation models to environmental variability treatments based on the nearshore environmental conditions observed along the West Coast of the United States by varying mussel fecundity (21) according to a linear spatial gradient (i.e., spatial environmental variability) and a linear spatial gradient with normally distributed white noise (i.e., spatiotemporal environmental variability; Materials and Methods).

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When there is no dispersal (i.e., full local retention of larvae), regional mussel dynamics are strictly controlled by environmental heterogeneity. Under this scenario, the model metapopulations experiencing either spatial or spatiotemporal environmental variability predict a weak and inconsistent spatial correlation between the mussel cover and the 1-year lagged environmental conditions (Fig. 2A and B). This weak and inconsistent relationship is compatible with the results from our survey data (Fig. 1A and previously published accounts (15). However, model metapopulations predict that environmental variability induces a rapid decay in the spatial synchrony pattern of the mussel cover, which is incompatible with the nonlinear spatial synchrony pattern observed in natural populations of _M. californianus_ (Fig. 2C and D). We now introduce dispersal among populations and vary the environment and the scale of dispersal to determine their relative contribution to spatial synchrony.

When dispersal is limited to neighboring populations (herein “limited dispersal”; 8.6% of the spatial domain for results in Figs. 3 and 4), model metapopulations undergoing either spatial or spatiotemporal environmental variability predict a weak and inconsistent relationship between mussel cover and 1-year lagged environmental conditions (Fig. 3A and C) that is similar to the one observed in the survey data (Fig. 1A). However, regional dispersal (44% of the spatial domain in Figs. 3 and 4) leads to a strong and dynamical relationship between the mussel cover and the environment (Fig. 3B and D) that is inconsistent with the weak spatial correlation observed between populations of _M. californianus_ and nearshore environmental conditions (Fig. 1A). This suggests that limited dispersal between fluctuating populations might be an important driver of abundance in natural populations of _M. californianus_. Indeed, this role of limited dispersal is made more evident through the analysis of spatial synchrony.

In metapopulations experiencing limited dispersal, both the successional model (Fig. 4A, C, and E) and the predator–prey model (Fig. S4 A, C, and E) accurately predict the nonlinear spatial synchrony pattern observed in natural populations of _M. californianus_, regardless of environmental variability. In contrast, in metapopulations undergoing regional dispersal, both the successional model (Fig. 4B, D, and F) and the predator–prey model (Fig. S4 A, C, and E) predict that the spatial synchrony pattern displayed by mussels will match the quasilinear decay displayed by the environment, despite the strong but inconsistent spatial correlation between the environment and mussel cover (Fig. 3B and D). Hence, in successional and predator–prey metapopulation models, limited dispersal is critical for the emergence of nonlinear

*Fig. 1.* The dynamics of _M. californianus_ cover and the environment along the West Coast of the United States. (A) The correlation between the mean annual _M. californianus_ cover and the 1-year lagged mean annual (i) sea surface temperature (SST, dark blue squares), (ii) chl-a concentration (chl-a, green diamonds), (iii) upwelling index (light blue triangles), and (iv) the first axis of the principal component analysis of all three environmental variables (PCA axis 1, red circles) at each site. (B) Spatial synchrony of the mean annual (i) _M. californianus_ cover (red circles), SST (dark blue squares), chl-a (green diamonds), and upwelling index (light blue triangles). The curves correspond to nonlinear (_M. californianus_) and linear (chl-a, SST, and upwelling index) statistical models fitted to each data set (Materials and Methods). Full circles indicate statistical significance (α = 0.05).

<table>
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<tr>
<th>Data set</th>
<th>n</th>
<th>G value</th>
<th>R²</th>
<th>AICc</th>
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<th>G value</th>
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spatial synchrony patterns that are compatible with those observed in natural populations of *M. californianus*. Nonlinear spatial synchrony patterns arise because limited dispersal (Fig. S5) couples neighboring populations and thus allows local fluctuations (Fig. S6) to scale up and generate complex, nonstationary spatiotemporal patterns at the regional scale (Figs. S7 and S8) that are robust to environmental forcing (Fig. 4B, D, F, and Figs. S4 B, D, and F). This cross-scale interaction between local population dynamics and limited dispersal is a general property of metapopulations (Fig. 4 and Fig. S4) that merely requires that local populations undergo sustained fluctuations (Fig. S6) and that the average dispersal distance represents 3–10% of the spatial domain (Fig. S5). Regional dispersal prevents these cross-scale interactions by spatially synchronizing population fluctuations across the entire metapopulation and thus generating regular regional oscillations characterized by stationary and quasilinear spatiotemporal synchrony patterns (Fig. 4 B, D, F, and Figs. S4 B, D, and F and Figs. S9 and S10). The shape of spatial synchrony can thus be used to determine the relative influence of cross-scale interactions and environmental forcing on the distribution of abundance in space and time. This can be achieved by fitting nonlinear and linear statistical models representing, respectively, cross-scale interactions and environmental forcing to the observed spatial synchrony patterns and then comparing their performance using model selection (Data Analysis and Fig. S5).

**Using Spatial Synchrony to Quantify the Scale of Dispersal in Natural Populations.** Our metapopulation models show that the shape of nonlinear spatial synchrony patterns can be used to quantify the scale of dispersal. Indeed, the spatial range, defined as the lag distance at which synchrony first reaches zero (22), is systematically associated with the average dispersal distance in both our successional model (Fig. 4A, C, and E) and our predator–prey model (Fig. S4 A, C, and E) when dispersal is limited. Applying this result to our survey data, we estimate that the scale of dispersal of *M. californianus* is \( \approx 100 \) km (i.e., 6% of the domain). This estimate falls within the 95% confidence interval of dispersal distances documented for other bivalve species (72–220 km, see ref. 11) and is very similar to the scale of dispersal (97–115 km) of more closely related *Mytilus* species in other systems (11). Our estimate is based on the number of recruits that survive to the adult stage and is smaller than the 250-km estimate derived empirically by measuring the density of settlers in the same system (23). This is because spatial synchrony estimates integrate postsettlement processes that can limit the effective scale of dispersal.

**Spatial Synchrony Reveals the Relative Influence of Intrinsic and Extrinsic Processes on the Distribution of Population Abundance.** Theory has shown that local dynamics and limited dispersal can lead to complex spatial (24, 25) or spatiotemporal (26, 27) patterns at the regional scale that can promote coexistence (28), stability (27, 29), persistence (26, 29, 30), and functioning (24, 25) in spatial ecological systems. Similar complex spatiotemporal patterns have also been used to describe insect (31) and epidemic (32) outbreaks at regional and continental scales. However, linking local dynamics and limited dispersal to regional patterns has typically required extensive time series and characteristic spatial signatures such as Turing structures (24, 25), traveling waves (26, 31), or power laws (33). Here, we extend these theories by showing that in systems lacking these characteristic spatial signatures, the shape of spatial synchrony patterns can be used to infer the joint effect of local dynamics and dispersal on the regional distribution of abundance. Hence, our framework moves away from the use of correlations between abundance and the environment to infer the causal effect of abiotic processes on biological patterns. Instead, by partitioning
long nonstationary time series into smaller quasistationary time series and applying spatial synchrony analysis, we show that the distribution of species abundance at small spatial scales (≤200 km) whereas climate dominates at larger spatial scales (>200 km) (34). Here, we have shown that despite strong regional environmental forcing, local dynamics interact with limited dispersal to control the distribution of population abundance at scales that are much larger (>1,000 km) than that of dispersal (~100 km). Hence, our work suggests that processes occurring at small spatial scales can interact synergistically to control the distribution of population abundance at large spatial scales. Such cross-scale interactions demonstrate the limitations of adopting climate envelope models based on hierarchical frameworks to understand the distribution of species abundance and predict the effects of global climate change.

Overall, by applying spatial synchrony analysis to a large data set of mussel populations along the West Coast of the United States, our study provides unique evidence that limited connectivity among local populations affects the dynamic distribution of abundance over >1,000 km. Our work supports the suggested shift toward a more dynamical approach to regional conservation, one that emphasizes patterns and processes across scales instead of those limited to the scale of the environment or dispersal.

Materials and Methods

Data Collection. Abundance (percent cover) of *M. californianus* was quantified annually from 1999 to 2004 at 48 sites located along the West Coast of the United States and stretching from southern California to Washington (39) (32.7 °N to 48.4 °N). For each site, the cover of *M. californianus* was surveyed in 10 randomly placed 0.25 m² quadrats for each of three 50-m transects located within the midintertidal zone. Mean annual sea surface temperature (SST, °C), chlorophyll-a concentration (chl-a, in mg/m³), and upwelling index (in m²/s/100 m of coastline) data from 1997 to 2003 occurring within a 0.2 degree radius (1 degree radius for upwelling) of each of the 48 sites were obtained, respectively, from the advanced very high resolution radiometer (NOAA), the sea-viewing wide field-of-view sensor (NASA), and sea level pressure maps (Pacific Fisheries Environmental Laboratory). These environmental data series were validated by comparing them to in situ buoy measurements (see Data Validation in SI Text).

Data Analysis. Before conducting spatial synchrony analysis, all variables were detrended by subtracting the global mean time series from each site's time series to remove any bias caused by common large-scale trends (40). The distances between all pairs of sites were then computed and used to group the detrended time series data into equally spaced distance bins (66 km wide). The coefficient of synchrony for each bin was calculated by computing the correlation coefficient between the time series of all pairs of sites within the bin. The extent of the spatial synchrony analysis was restricted to half of the spatial domain to avoid large discrepancies in the number of pairs of sites within each bin (22). Statistical significance was determined by using a one-tailed test (α = 0.05) on 10,000 Monte Carlo randomizations (22). Specifically, for each bin, the P value was calculated by shuffling the data pairs within the bin 10,000 times, computing the coefficient of synchrony for each randomization, and then calculating the proportion of randomizations with a coefficient of synchrony greater than or equal to that obtained with the original data. The same one-tailed randomization technique was used to assess the statistical significance of the correlation between the annual cover of *M. californianus* at year i and each environmental variable at year i−1 (1-year lag). We used a 1-year lag because it corresponds to the temporal scale at which the correlation between the annual cover of *M. californianus* and each nearshore environmental variable is statistically significant (Fig. S1).

We used model selection to detect linear and nonlinear spatial synchrony patterns in the environmental (SST, chl-a, and upwelling index) and *M. californianus* data sets. For each data set, we fit a linear statistical model $m_{\text{linear}}$ and a nonlinear statistical model $m_{\text{nonlinear}}$ to the spatial synchrony pattern:

$$m_{\text{linear}} = a \cdot d + b \quad [1]$$
where \( L \) is the lag distance vector, \( a, b \) represent fitted coefficients and \( 3\pi \) is the normalized lag distance vector scaled to the domain \([0, 3\pi]\). This scaling of the lag distance vector allows the cosine function in the nonlinear model to fit modal patterns of spatial synchrony over the spatial domain. For each statistical model, we calculated the Akaike information criterion corrected for small samples (41):

\[
AIC_c = -2\log(L) + 2K + \frac{2K(K + 1)}{n - K - 1},
\]

where \( L \) represents the maximum likelihood, \( K = 3 \) represents the number of parameters in each statistical model, and \( n \) represents the number of samples. The statistical model with the smallest AIC value was selected for each data set (41).

Successional Model. The successional model describes local disturbance and recovery dynamics in a network of mussel populations that are connected by dispersal (17). Within populations, the successional dynamics observed in natural intertidal systems (16, 42) are represented as a mean-field implementation of a spatial process affecting the proportional abundance of (i) the dominant mussel \( m \), (ii) the wave disturbance \( w \), and (iii) the empty substrate \( s \) (43). A maximum fraction \( \alpha_0 = 0.1 \) of the proportional abundance of the dominant mussel species \( m \) can be displaced by wave disturbances \( w \). A proportion \( 1 - \beta_0 \) of disturbances displaces mussels through a density-dependent contact process with aggregation (Moore neighborhood, \( q = 8 \)), whereas a proportion \( \beta_0 = 10^{-3} \) of disturbances is density independent. This disturbance dynamic is based on the assumption that wave disturbances destroy the byssal thread attachments of mussels around the edges of disturbed areas, thus making them temporarily more susceptible to further disturbance (43, 44). Hence, newly disturbed areas allow the local propagation of wave disturbances to adjacent mussel beds. Once the disturbance has propagated away from the newly disturbed area, the area transitions from the “wave disturbed” state to the “empty substrate” state. Similarly to disturbance, a maximum fraction \( \alpha_2 = 0.65 \) of the empty substrate \( s \) can be colonized by mussels. A proportion \( \alpha_0 = 0.1 \) of colonization occurs through a density-independent process, whereas the remaining colonization is density dependent \( 1 - \beta_2 \). Mussel colonization also depends on the production and recruitment of larvae. Within populations \( x \), larval production is a function of local mussel proportional abundance \( n_x \) and fecundity \( f_x \) \((f = 5 \pm 25)\). The recruitment rate \( C_{ij} \) is described by a Poisson process \((45) C_{ij} \sim 1 - e^{-x_{ij}} \), where \( p_{ij} \) integrates \((i)\) the total number of larvae produced and recruited in populations \( x \) at time \( t \) and \((ii)\) the total number of larvae produced in other populations \( y \) and dispersed to populations \( x \) at time \( t \). The dynamics of the model are represented by the following integro-difference equation system for populations \( x \) in a metapopulation consisting of \( n = 256 \) populations:

\[
\begin{align*}
w^{t+1}_x &= a_m m_x (\delta_0 + (1 - \delta_0) (1 - \left(1 - w_{x}^{t} \right)^2)) \\
\delta^{t+1}_x &= w_{x}^{t} + \delta_{x}^{t} - \alpha_2 C^{t}_{xy} \delta_{y}^{t} (\delta_2 + m_x^{t} (1 - \delta_2)) \\
m^{t+1}_x &= 1 - w_{x}^{t} - \delta_{x}^{t}
\end{align*}
\]

with:

\[
C_{ij} \sim 1 - e^{-x_{ij}} \\
p_{ij} &= m_{x}^{t} f_{x} (1 - d) + \int m_{y}^{t} f_{y} dD(x | y) \\
D(x | y) &= \left( \begin{array}{c}
2x_{ij} - x_{ij}^2 \ni e^{-x_{ij}^2} \\
x = \text{int} \left( \frac{L}{L - 1} \right)
\end{array} \right) \\
L &= \left\{ \begin{array}{cl}
0 & x = \text{int} \left( \frac{L}{L - 1} \right) \\
\vdots & \\
n - 1 & 
\end{array} \right.
\]

where \( D \) is the symmetrical mussel dispersal kernel resulting from larval transport at a constant speed and with a time-dependent settlement rate (double Weibull distribution) \((46)\), \( d \) represents the proportion of larvae being dispersed, \( u \) represents the scale of dispersal, and \( L \) represents a zero-based vector of population locations. We vary dispersal by manipulating \( d \), the proportion of larvae being dispersed \( (d = 0 \text{ means that all larvae are retained locally}) \), whereas \( d = 1 \text{ means that all larvae are dispersed}) \), and \( u \), the scale of dispersal \((u = 2 \text{ corresponds to regional dispersal and } u = 0 \text{ corresponds to limited dispersal}) \). We assumed periodic boundary conditions for all simulations and set the dispersal rate to \( d = 1 \text{ (i.e., no local retention}) \) unless otherwise specified (i.e., Fig. 2 where \( d = 0 \)). All successional model simulations were performed for \( 256 \) populations and the results were analyzed over \( 2,000 \) posttransient time steps. Because our goal was to test the importance of local ecological processes and dispersal, all parameter values detailed above were selected to be representative of the broad parameter space characterized by spatiotemporal heterogeneity \((17, 47)\). Here, we further assess the model’s sensitivity to dispersal distance and to fecundity \( f \) as a means to determine the role of environmental variability in marine metapopulations.

Environmental variability can have a significant impact on the productivity of intertidal populations \((21, 48)\). Here, we implement this effect by varying mussel fecundity spatially and spatiotemporally. Specifically, the spatial environmental treatment consists of varying the mussel fecundity \( f \) linearly from 3 to 7.5 over the entire spatial range \((f = 5.25)\). We generate the spatiotemporal environmental treatment by adding normally distributed white noise with zero mean and variance \( \sigma^2 = 2.7 \) to the previously described spatial variation in fecundity \((f = 5.25)\). The spatial and spatiotemporal environmental treatments thus preserve the same mean fecundity as the successional model undergoing no environmental variability. These spatial and spatiotemporal treatments were chosen to roughly mimic the spatial and spatiotemporal properties of the environment along the West Coast of the United States. Applying the same spatial and spatiotemporal treatments to the mussel growth rate \( \alpha_2 \) yields qualitatively similar results.

Model Analysis. We applied the spatial synchrony and model selection methods (Data Analysis) used on the survey data to the posttransient time series of the successional and the predator–prey (SI Text) models to assess their ability to generate nonlinear spatial synchrony patterns that are compatible with those observed in natural populations of \( M. californiana \). Specifically, the model time series \((2,000 \text{ posttransient time steps}) \) was split into 10-time step windows and spatial synchrony analysis was conducted over each window. We chose 10-time step windows to approximate the temporal extent of our intertidal survey data. However, our results are robust to window size (Fig. S5 B, D, and F). For each time window, we fit the same linear \((m_{\text{linear}})\) and nonlinear \((m_{\text{nonlinear}})\) statistical models described in Data Analysis to the spatial synchrony patterns generated by the metapopulation models. For each time window, the nonlinear statistical model was selected if \( AIC_{\text{nonlinear}} < AIC_{\text{linear}} \) (41). The model spatial synchrony patterns presented in all figures were computed by averaging the spatial synchrony patterns from all 10-time step windows in which the nonlinear statistical model was selected. When no compatible synchrony pattern exists for the entire model time series (i.e., for the regional dispersal treatment), the spatial synchrony patterns from \( n \) randomly selected time windows are computed and averaged (where \( n \) corresponds to the number of compatible synchrony patterns for the limited dispersal treatment). This allows for unbiased comparisons across dispersal treatments.

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Supporting Information

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SI Text

Data Validation. We used remote sensing data to quantify sea surface temperature (SST), chlorophyll a concentration (chl-a), and upwelling currents (upwelling index) instead of in situ measurements because the former had greater temporal and spatial coverage. Additionally, the broad spatial extent of remote sensing data can often better reflect the spatially integrated environmental conditions experienced by intertidal populations (1). Both the SST and chl-a data had a nominal resolution of 4 km, whereas the upwelling index had a coarser resolution of 1 degree (~111 km). Because remote sensing data are prone to errors due to cloud cover and aerosols that can influence captured irradiance, we excluded low-quality data points characterized by high cloud/aerosol cover from the analysis (2). Additionally, outliers were removed from the remote sensing data series by computing the filtered mean (2) of each variable for each site:

\[ \frac{\sum_{i=1}^{p}[(X - 1.5\sigma_X) \leq X \leq (X + 1.5\sigma_X)]}{N}, \]

where \( P \) represents the total number of points within 0.2 degrees (1 degree for upwelling) of the site, \( N \) is the total number of points within 1.5 SD of the mean \( X \). These filtered environmental data series were then validated by using reduced major axis regression (2) to relate them to in situ buoy measurements (chl-a: \( R^2 = 0.42, P \) value = 0, \( n = 583 \); SST: \( R^2 = 0.60, P \) value = 0, \( n = 536 \)).

Quantifying the Relationship Between M. californianus and the Environment. In many marine species, individuals begin their lives as water-borne planktonic larvae and eventually settle onto the intertidal to become sessile adults. This bipartite lifecycle has important implications for identifying the relative influence of pre- and postsettlement processes on population dynamics and community structure. Nearshore current patterns such as coastal upwelling, which describes the offshore transport of the warm top water layer and the consequent rise of cold and nutrient-rich water to the surface, has been identified as a potentially critical process controlling recruitment in intertidal communities located along the coasts of New Zealand (3), Chile (4), and the West Coast of the United States (5). Along the West Coast of the United States, the pronounced spatial gradient in coastal upwelling has been linked to patterns of recruitment (5–7). Indeed, offshore transport due to coastal upwelling is weaker and less persistent north of Cape Blanco (43°N) than it is south of Cape Blanco (5, 6). This major spatial discontinuity in coastal upwelling conditions has led to the hypothesis that environmental conditions affecting presettlement processes are more likely to play an important role in adult intertidal communities south of Cape Blanco, where recruitment is environmentally limited, than they are north of Cape Blanco, where recruitment is not environmentally limited (5–7).

We tested this hypothesis by examining the relationship between the mean annual cover of M. californianus and 1-year lagged, multiyear averaged environmental conditions in each region. We chose a 1-year lag because it corresponds to the temporal scale at which the correlation between the cover of M. californianus and each environmental variable is statistically significant (Fig. S1). In both regions, the spatial correlation between the environment and the cover of M. californianus varies in time, regardless of whether the environmental conditions are averaged over 2 or 3 years (Fig. S2). The spatial correlation between the growth of the mean annual M. californianus cover and the environment is equally variable in time for both regions. This indicates that the relationship between M. californianus cover and the environment is inconsistent in both regions. However, this inconsistency could be the product of the coarse division of the study system into a nonenvironmentally limited northern region and an environmentally limited southern region. To test this hypothesis, we further examined this relationship by relating the 1-year lagged mean annual environmental time series to the mean annual M. californianus cover time series at each of the 48 sites (Fig. S3). Although all environmental variables show a persistent spatial structure (Fig. S3 A, C, and E), the sign and strength of the local correlation between the environmental time series and the M. californianus time series is highly variable in space (Fig. S3 B, D, and F). Once averaged spatially, these variable local correlations lead to weak and inconsistent spatial correlations at the regional scale (Fig. S2). Overall, these results indicate that the persistent latitudinal gradient seen in all environmental variables is not reflected in the cover of M. californianus.

Identifying the Necessary Conditions for the Occurrence of Cross-Scale Interactions Between Local Fluctuations and Limited Dispersal. Cross-scale interactions in a predator–prey metapopulation. We have shown that local fluctuations and limited dispersal interact across spatial scales ranging from that of local ecological processes to the scale characterizing the regional distribution of abundance. Such cross-scale interactions lead to nonlinear patterns of spatial synchrony that are robust to both spatial and spatiotemporal environmental variability affecting either growth or fecundity in the discrete time successional model (Fig. 4). Now, we examine the generality of this phenomenon in metapopulation models by adopting a spatially explicit version (8, 9) of the continuous time Rosenzweig-MacArthur predator–prey model (10):

\[
\frac{dM_i}{dt} = r_i M_i \left(1 - \frac{M_i}{K_i}\right) - \frac{a M_i P_i}{b + a M_i} - c M_i \sum_{i \neq x} M_i,
\]

\[
\frac{dP_x}{dt} = \frac{a M_i P_i}{b + a M_i} - P_x (m + c) + \frac{c}{r_{i \neq x}}\sum_{i \neq x} P_i,
\]

where the prey (mussels \( M_i \)) at site \( x \) has growth rate \( r_i = 0.5 \), carrying capacity and the predator \( P_x \) at site \( x \) has mortality rate \( m = 0.1 \), encounter rate \( a = 0.2 \) and half saturation constant \( b = 1 \). Both the predator and the prey migrate to their \( n \) nearest neighbors with a migration rate of \( c = 0.1 \). We used these parameter values to illustrate the spatial dynamics of Eq. 2 and detail the generality of our results in the next sections. We assume symmetrical dispersal, equal dispersal scales for the predator and the prey, and periodic boundary conditions. All simulations were run for 100 sites and the results were analyzed over 2,000 posttransient time steps using the model selection methods described in Model Analysis in the main text. We adopted the same spatial and spatiotemporal treatments used in the successional model. Specifically, the spatial environmental treatment consisted of varying the mussel growth rate \( r \) linearly from 0.2 to 0.8 over the entire spatial range (\( r = 0.5 \)). We generated the spatiotemporal environmental treatment by adding normally distributed white noise with zero mean and variance \( \sigma^2 = 0.2 \) to the previously described spatial variation in the mussel growth rate (\( r = 0.5 \)). The spatial and spatiotemporal environmental treatments thus preserved the same mean mussel growth rate as the predator–prey model undergoing no environmental variability. As with the successional model, we vary...
dispersal and the environment to determine their relative influence on spatial synchrony patterns of mussel abundance in natural and model metapopulations.

We show that in the predator–prey model, limited dispersal is critical to the occurrence of nonlinear spatial synchrony patterns of mussel abundance that are compatible with those observed in natural populations along the West Coast of the United States (Fig. S4). In the absence of any environmental variability, nonlinear spatial synchrony patterns arise because of the cross-scale interaction between local mussel population fluctuations and limited dispersal (Fig. S4A). These patterns are robust to both spatial (Fig. S4C) and spatiotemporal (Fig. S4E) environmental variability. Regional dispersal, however, prevents the occurrence of cross-scale interactions and leads to regional synchrony in the absence of environmental variability (Fig. S4B). Regional dispersal also facilitates environmental forcing in response to either spatial (Fig. S4D) or spatiotemporal (Fig. S4F) variability.

Hence, even though the successional model and the predator–prey model have fundamental differences in terms of their ecological structures (populations vs. communities), mathematical properties (continuous vs. discrete), dispersal mechanisms (nearest neighbor vs. dispersal kernel), connectivity rates (10% dispersal rate vs. 100% dispersal rate), perturbation types (biotic vs. abiotic), and spatial extents (256 sites vs. 100 sites), they both predict the occurrence of nonlinear spatial synchrony patterns in response to the cross-scale interaction between local fluctuations and limited dispersal.

Relation between dispersal and cross-scale interactions. We have shown that the cross-scale interaction between limited dispersal and local fluctuations yields nonlinear spatial synchrony patterns, whereas regional dispersal and environmental forcing lead to linear spatial synchrony patterns (Fig. 4 and Fig. S4). Hence, the linearity of spatial synchrony patterns can be used to ascertain the relative importance of cross-scale interactions and environmental forcing in natural populations. However, because the nonlinear spatial synchrony patterns are also nonstationary (Figs. S7 and S8), one must not rely on the specific characteristics of any single spatial synchrony pattern, but rather identify the nonlinear properties that describe a family of spatial synchrony patterns. Here, we use model selection (Data Analysis) to determine the relative importance of cross-scale interactions and environmental forcing by detecting nonlinearities in the spatial synchrony patterns of metapopulation models for a range of dispersal scales.

Our results show that in the successional and predator–prey models, nonlinear spatial synchrony patterns occur over the same limited range of dispersal scales (Fig. S5 A, C, and E). Indeed, regardless of environmental variability, the nonlinear model is selected when the scale of dispersal is less than 10–15% of the spatial domain and systematically rejected when dispersal occurs over more than 10–15% of the spatial domain (Fig. S5 A, C, and E). Hence, model selection methods based on linearity can be used to determine whether spatial synchrony patterns are the product of (i) the cross-scale interaction between limited dispersal and local intrinsic fluctuations or (ii) regional dispersal and environmental forcing.

Relation between local fluctuations and cross-scale interactions. We have shown that cross-scale interactions between local fluctuations and limited dispersal can occur in both the successional and the predator–prey model. Their occurrence is dependent upon the scale of dispersal, which must be limited to 3–10% of the spatial domain (Fig. S5 A, C, and E). Additionally, cross-scale interactions depend upon the existence of strong local fluctuations. We now demonstrate this dependence by analyzing the dynamics of the predator–prey model. Under spatially homogeneous conditions (i.e., zero net migration and identical environmental conditions across all sites), the predator–prey metapopulation model can be analyzed as a series of uncoupled predator–prey populations. The stability of each predator–prey population can be ascertained by deriving the zero net growth isolines (ZNGI) of the predator ($M^*$) and the prey ($P^*$):

$$ P^* = \frac{L}{\alpha}(mK + M(aK - b) - aM^*) $$

$$ M^* = \frac{\alpha}{\alpha + \beta}(a + \beta) $$

[3.1, 3.2]

The equilibrium dynamics of this predator–prey system depends on the modal shape of the prey ZNGI and where the prey and predator ZNGIs intersect. When the predator and prey ZNGIs intersect in the ascending section of the prey ZNGI ($\partial P/\partial M > 0$), the equilibrium is unstable and the system undergoes stable limit cycles. When the ZNGIs intersect in the descending section of the prey ZNGI ($\partial P/\partial M < 0$), the equilibrium is stable (11). We now identify the conditions under which the system transitions from stable equilibrium dynamics to stable limit cycles (i.e., the Hopf bifurcation point) by differentiating Eq. 3.1 and solving $\partial P^*/\partial M = 0$:

$$ \frac{\partial P^*}{\partial M} \bigg|_{M = M^*} = \frac{r}{aK} (aK - b - 2a(m b a (1 - m))) = 0. $$

[4]

The sign of the derivative and the stability of the system depend upon the bracketed term in Eq. 4. After some algebra, it is possible to transform the bracketed term and show that the stability of the system is linked to the critical parameter $K_{\text{critical}}$:

$$ K_{\text{critical}} = \frac{b(m + 1)}{a(1 - m)} $$

[5]

The dynamics of the system thus directly depend on the carrying capacity $K$: when $K > K_{\text{critical}}$, the system undergoes stable limit cycles whereas when $K < K_{\text{critical}}$, the system reaches a stable equilibrium. For our particular model parameterization ($b = 1$, $a = 0.2$, $m = 0.2$), $K_{\text{critical}} = 7.5$. By varying $K$ across the $K_{\text{critical}} = 7.5$ threshold, we show that cross-scale interactions, as manifested by the occurrence of compatible nonlinear spatial synchrony patterns, are directly linked to the system’s transition from stable equilibrium dynamics to stable limit cycles (Fig. S6).

Our results are thus robust to the specifics of our models: cross-scale interactions merely require that local populations undergo sustained fluctuations (Fig. S6) and that dispersal occurs over 3–10% of the spatial domain (Fig. S5 A, C, and E).

Robustness of Nonlinear Spatial Synchrony Patterns to Window Size. All spatial synchrony analyses of the model data were performed over 10-time step windows to approximate the temporal extent of our survey data. However, our results are robust to window size. Indeed, regional dispersal never leads to nonlinear spatial synchrony patterns in either the successional or the predator–prey model, regardless of environmental variability or window size (Fig. S5 A, C, and E). However, when dispersal is limited, the predator–prey and successional models generate nonlinear spatial synchrony patterns for a range of window sizes (Fig. S5 B, D, and F). Hence, regardless of window size, nonlinear spatial synchrony patterns remain a signature of metapopulations experiencing limited dispersal. The robustness of spatial synchrony to window size means that the occurrence of cross-scale interactions can be detected in natural systems for which data availability is limited to short temporal scales that do not integrate many cycles of abundance fluctuations.

Dispersal Mediates Pattern Formation in Dynamical Metapopulations. Dispersal is a key process that has important consequences for the regional distribution of abundance. In marine systems, dispersal has been shown to directly mediate the correlation between predator abundance and prey recruitment. Indeed, predator abundance and prey recruitment of nondispersing predator and prey species pairs were strongly correlated, whereas no relationship existed between predator abundance and prey re-
mentally mediated spatial waves do not affect the nonstationary at sites with high fecundity (i.e., central sites) that slowly prop-
leads to the formation of spatial waves of high mussel abundance
addition of spatiotemporal (Fig. S8) environmental variability
distance at which synchrony
are nonstationary, the spatial range of synchrony (i.e., the lag
scales (Fig. S7
spatial synchrony patterns characterized by different spatial
B
D
Metapopulations characterized by regional dispersal and no environmental variability undergo synchronized regional fluctuations (Fig. S9) that lead to stationary and uniform patterns of spatial synchrony (Fig. S9 B–D). It is important to note that even though these metapopulations undergo strongly synchronized regional fluctuations (Fig. S9), spatial synchrony analysis shows very low levels of synchrony across the entire spatial range (Fig. S9 B–D). This is because the mussel abundance time series was detrended by removing the mean regional time series before performing spatial synchrony analysis. Hence, our spatial synchrony analysis focuses on the spatial trends of synchrony instead of the absolute strength of synchrony. The addition of spatiotemporal environmental variability (Fig. S10) leads to the formation of fronts that originate from highly fecund central sites. These fronts propagate extremely rapidly across the entire metapopulation and lead to stationary and linear spatial synchrony patterns (Fig. S10 B–D).
These results thus show how dispersal modulates pattern formation in metapopulations. Furthermore, they show that spatial synchrony can be used to quantify complex spatiotemporal patterns and link them to their underlying mechanisms.
Fig. S1. Temporal structure of the correlation between the annual cover of *M. californianus* and the environment for all 48 sites. Spatial correlation (red circles) between the annual cover of *M. californianus* and mean annual (blue curves) (A) SST, (B) chl-a, and (C) upwelling index across all sites as a function of lag time (number of years). The vertical dashed line indicates the 1-year lag used to correlate the cover of *M. californianus* in year \( i \) to the environmental conditions in year \( i-1 \). Full circles indicate statistical significance (\( \alpha = 0.05 \)).
Fig. S2. Time series of the correlation between the annual *M. californianus* cover and the multiyear average environment at 48 sites located along the West Coast of the United States. The correlation between mean annual *M. californianus* cover and each 1-year lagged, (A, C, and E) 2-year averaged, or (B, D, and F) 3-year averaged environmental variable for (A and B) all 48 sites, (C and D) sites located north of Cape Blanco (43°N), and (E and F) sites located south of Cape Blanco. The 1-year lagged, multiyear averaged environmental variables are SST (dark blue squares), (ii) chl-a (green diamonds), (iii) upwelling index (light blue triangles), and (iv) the first axis of the principal component analysis of all three environmental variables (red circles). Full circles indicate statistical significance ($\alpha = 0.05$).
Fig. S3. The spatial structure of both the environment and the correlation between the environment and the annual *M. californianus* cover time series at 48 sites located along the West Coast of the United States. (A, C, and E) The spatial structure of the mean annual (A) chl-a, (C) SST, and (E) upwelling index from 1999 to 2002 (dark blue circles, 1999; red squares, 2000; light blue triangles, 2001; black diamonds, 2002). The vertical dashed line depicts an upwelling index of zero. (B, D, and F) The spatial structure of the correlation between the mean annual *M. californianus* cover time series and the 1-year lagged mean annual time series of (B) chl-a, (D) SST, and (F) upwelling index. Blue circles indicate negative correlations and red circles indicate positive correlations. The size of each circle is proportional to the absolute value of the correlation, with the largest circle representing a correlation of 0.95.
Fig. S4. Spatial synchrony of annual mussel cover in the predator–prey model for metapopulations undergoing different environmental and dispersal treatments. (A and B) No environmental variability and either (A) limited or (B) regional dispersal. (C and D) Spatial environmental variability and either (C) limited or (D) regional dispersal. (E and F) Spatiotemporal environmental variability and either (E) limited or (F) regional dispersal. Spatial synchrony in the predator–prey model annual mussel cover is represented in blue solid curves (mean ± SE), whereas that of the 1-year lagged environment is represented in green dashed curves (mean ± SE). The spatial synchrony of the annual *M. californianus* cover from the West Coast of the United States is also depicted to facilitate comparisons (red circles). The scale of dispersal is represented by the vertical dotted line. The spatial extent of the limited dispersal treatment corresponds to 6% of the domain, whereas that of the regional dispersal treatment corresponds to 80% of the domain. Full circles indicate statistical significance (α = 0.05).
Fig. S5. Using model selection to detect nonlinear spatial synchrony patterns in the mussel cover time series of metapopulation models. (A, C, and E) The percentage of nonlinear models selected as a function of the scale of dispersal for successional (blue) and predator–prey (red) metapopulations undergoing (A) no environmental variability, (C) spatial environmental variability, or (E) spatiotemporal environmental variability. (B, D, and F) The percentage of nonlinear models selected as a function of the size of the time window for successional (blue solid curve) and predator–prey (red dashed curve) metapopulations undergoing limited dispersal and (B) no environmental variability, (D) spatial environmental variability, or (F) spatiotemporal environmental variability.

Fig. S6. The occurrence of nonlinear spatial synchrony patterns in the mussel cover time series of the predator–prey metapopulation model. The percentage of nonlinear spatial synchrony models selected in a predator–prey metapopulation undergoing limited dispersal (6% of the spatial domain) and no environmental variability (blue solid curve) and the minimum/maximum mussel abundance across the entire metapopulation (red circles) as a function of the critical parameter \( K \). The transition from stable equilibrium dynamics to stable limit cycles occurs for \( K > K_{\text{critical}} = 7.5 \) and coincides with the selection of nonlinear spatial synchrony models.
Fig. S7. The time series of the mussel cover from the successional model with sample spatial synchrony analyses for a metapopulation undergoing limited dispersal and no environmental variability. (A) The time series of the metapopulation mussel cover (color bar) and sample synchrony profiles (B–D) taken at three randomly selected 10-time step windows indicated by the red outlines. (B–D) The blue solid curve indicates the spatial synchrony of the mussel cover and the blue vertical dotted line indicates the scale of dispersal.

Fig. S8. The time series of the mussel cover from the successional model with sample spatial synchrony analyses for a metapopulation undergoing limited dispersal and spatiotemporal environmental variability. (A) The time series of the metapopulation mussel cover (color bar) and sample synchrony profiles (B–D) taken at three randomly selected 10-time step windows indicated by the red outlines. (B–D) The blue solid curve indicates the spatial synchrony of the mussel cover, the green dashed curve indicates the spatial synchrony of the environment, and the blue vertical dotted line indicates the scale of dispersal.
Fig. S9. The time series of the mussel cover from the successional model with sample spatial synchrony analyses for a metapopulation undergoing regional dispersal and no environmental variability. (A) The time series of the metapopulation mussel cover (color bar) and sample synchrony profiles (B–D) taken at three randomly selected 10-time step windows indicated by the red outlines. (B–D) The blue solid curve indicates the spatial synchrony of the mussel cover and the blue vertical dotted line indicates the scale of dispersal.

Fig. S10. The time series of the mussel cover from the successional model with sample spatial synchrony analyses for a metapopulation undergoing regional dispersal and spatiotemporal environmental variability. (A) The time series of the metapopulation mussel cover (color bar) and sample synchrony profiles (B–D) taken at three randomly selected 10-time step windows indicated by the red outlines. (B–D) The blue solid curve indicates the spatial synchrony of the mussel cover, the green dashed curve indicates the spatial synchrony of the environment, and the blue vertical dotted line indicates the scale of dispersal.