

Scale-specific drivers of kelp forest communities

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Abstract Identifying spatial scales of variation in natural communities and the processes driving them is critical for obtaining a predictive understanding of biodiversity. In this study, we focused on diverse communities inhabiting productive kelp forests on shallow subtidal rocky reefs in southern California, USA. We combined long-term community surveys from 86 sites with detailed environmental data to determine what structures assemblages of fishes, invertebrates and algae at multiple spatial scales. We identified the spatial scales of variation in species composition using a hierarchical analysis based on eigenfunctions, and assessed how sea surface temperature (SST), water column chlorophyll, giant kelp biomass, wave exposure and potential propagule delivery strength contributed to community variation at each scale. Spatial effects occurring at multiple

scales explained 60% of the variation in fish assemblages and 52% of the variation in the assemblages of invertebrates and algae. Most variation occurred over broad spatial scales (> 200 km) consistent with spatial heterogeneity in SST and potential propagule delivery strength, while the latter also explained community variation at medium scales (65–200 km). Small scale (1–65 km) community variation was substantial but not linked to any of the measured drivers. Conclusions were consistent for both reef fishes and benthic invertebrates and algae, despite sharp differences in their adult mobility. Our results demonstrate the scale dependence of environmental drivers on kelp forest communities, showing that most species were strongly sorted along oceanographic conditions over various spatial scales. Such spatial effects must be integrated into models assessing the response of marine ecosystems to climate change.

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Introduction

Ecological communities are complex systems. Identifying the processes responsible for their spatial distribution is an enduring, yet important goal of community ecology (Leibold et al. 2004; Legendre and Legendre 2012). One of the main challenges in achieving this goal is that many ecological processes act across multiple spatial scales, resulting in complex spatial patterns of community structure. Although the importance of spatial scale in community ecology is widely recognized (Menge and Olson 1990; Levin 1992; Schneider 2001; Dungan et al. 2002), recent changes in global biodiversity (Dornelas et al. 2014; McGill et al. 2015; Newbold et al. 2015; García Molinos et al. 2016) highlight the need for a better understanding of how anthropogenic and natural processes interact at multiple scales to influence community structure and biodiversity conservation (Tzanopoulos et al. 2013; Socolar et al. 2016). Our ability to precisely quantify the effects of a given ecological process or environmental driver on biodiversity critically depends upon an understanding of the spatial scales over which they operate. Failure to account for this can lead to unproductive debates over the importance of a given process or driver on biodiversity loss (e.g., invasive species: Sax et al. 2002 and Vilà et al. 2011).

Beta diversity, the compositional variation among communities (*sensu* Anderson et al. 2011; Legendre and Legendre 2012), offers a way to account for varying spatial scales ranging from small areas to larger regions, and has provided novel insight into the processes driving community structure (Chase 2010; Chase and Myers 2011; Chase et al. 2011; Vellend et al. 2014). However, spatial variation among communities (commonly referred to as metacommunity structure) can also occur across multiple scales when the underlying processes generating this variation are themselves spatially structured. Complex and multiscale compositional variation among communities will ultimately arise when communities are controlled by multiple environmental factors that differ in their spatial structure (Legendre and Legendre 2012). A key assumption here is that dispersal limitation does not prevent species from tracking their environmental optimum, but instead allows them to be sorted along environmental gradients (Leibold et al. 2004). Not only does dispersal play a fundamental role in community ecology, as put forward by neutral theory (Hubbell 2001) and metacommunity theory (Leibold et al. 2004), but it can also strongly influence spatial variation among communities (Hubbell 2001) due to “true” spatial autocorrelation, the spatial variation due to dispersal limitation and/or local processes (Legendre 1993).

Spatial scales of measurement are frequently arbitrary and reflect either our perception of a system or practical sampling limitations. Multiscale modelling using eigenfunction analysis can be used as an objective tool to detect

and define hierarchical scales of spatial variation among communities (Borcard and Legendre 2002; Dray et al. 2006, 2012). This approach comprises a family of methods in which eigenvectors computed from matrices of the spatial arrangement among localities are used as predictors in multivariate analyses. These spatial proxies can further serve to decompose the total spatial variation among communities into the most relevant scales of variation and aid in characterizing the underlying drivers. Spatial eigenfunction analysis has been successfully applied to a variety of systems and has led to an improved understanding of metacommunity structure (Borcard et al. 2004; Laliberté et al. 2009; Declerck et al. 2011). More importantly, the integration of spatial scales into metacommunity theory has helped resolve the ways that niche-based processes (e.g., species sorting), stochastic processes, and spatial processes structure natural communities at different spatial scales (Laliberté et al. 2009; Meynard et al. 2013; Ryberg and Fitzgerald 2015). For instance, evidence suggests that broad-scale patterns in metacommunity structure tend to arise primarily due to niche-based processes, while biotic interactions and stochastic processes can generate smaller-scale variation that can be difficult to identify (Jones et al. 2006; Laliberté et al. 2009; Declerck et al. 2011).

The interplay between environmental heterogeneity and dispersal limitation on metacommunity structure has received much theoretical attention (Leibold et al. 2004; Leibold and McPeck 2006), but disentangling the relative importance of these processes across spatial scales in nature remains challenging. Uncertainty about the role of these processes is especially high in complex marine metacommunities consisting of species that vary widely in their mobility, dispersal abilities and environmental optimum. Many marine species have complex life cycles, with dispersive propagule stages that can remain in the plankton for several weeks. The resulting potential for long distance dispersal is often assumed to reduce the likelihood of dispersal limitation. In addition, environmental heterogeneity can be high in marine ecosystems and propagule survival and recruitment is often stochastic and unpredictable. Finally, marine species markedly differ in their dispersal abilities as adults. For instance, sessile algae and invertebrates remain stationary following recruitment, while mobile fishes have home ranges of widely varying size. Because of this multi-level complexity, the extent to which different environmental processes drive spatial variation in marine communities remains challenging to quantify (but see: Fraschetti et al. 2005; Terlizzi et al. 2007; MacNeil et al. 2009; Yeager et al. 2011; Menge et al. 2015).

Here we combined detailed community data collected from shallow subtidal reefs across a broad region in the northern portion of the Southern California Bight with environmental data obtained from satellite remote sensing and oceanographic models to understand the multiscale

patterns and drivers of kelp forest communities. Forests of the giant kelp *Macrocystis pyrifera* on rocky reefs in the study region are extremely productive ecosystems (Reed et al. 2008) whose dynamics are influenced by a range of environmental factors operating at different spatial scales (Cavanaugh et al. 2011, 2013; Bell et al. 2015). Thus, the communities inhabiting this iconic ecosystem experience a spatially complex environment, at scales ranging from the local reef ($\sim 1000 \text{ s m}^2$) to the regional Southern California Bight ($\sim 1000 \text{ s km}^2$). We seek to characterize the multiscale spatial patterns in kelp forest communities and understand the environmental conditions that underlie their variation across scales. The species included in this study span a wide variety of life history and dispersal abilities ranging from sessile to highly mobile adult forms and non-dispersive to highly dispersive propagules (Reed et al. 2000; Shanks et al. 2003). We investigated whether differences in adult dispersal abilities affect these scales of variability by comparing assemblages of extremely mobile fishes with benthic assemblages of weakly mobile and sessile invertebrates and algae. Although propagule dispersal in these two groups varies widely, it tends to be higher in fishes than in invertebrates and algae (Kinlan and Gaines 2003; Shanks et al. 2003), which is consistent with patterns of adult movement. Thus, we hypothesized that the strong environmental heterogeneity occurring in the study region should underpin compositional variation in the assemblages of these two functional groups at multiple spatial scales. If both types of assemblages display compositional variation along the same spatial scales, it would suggest that in kelp forest communities, the structuring effects of environmental sorting prevail over effects of dispersal limitation related to adult movement or propagule dispersal. We predicted that the metacommunity structure of both types of assemblages should vary across multiple scales due to the influence of regional oceanographic conditions at the Southern California Bight scale, and the effect of local kelp dynamics, wave disturbances or biotic interactions at smaller spatial scales. We tested this prediction using eigenfunction analyses aimed at: (1) characterizing the most important scales of variation in assemblages of kelp forest fish and benthic invertebrates and algae and (2) assessing the environmental driver(s) underlying each of these spatial scales.

Materials and methods

Ecological data

Our study area spans the mainland and offshore islands that bound the Santa Barbara Channel, the Santa Barbara Island and the San Nicolas Island to the south (Fig. 1a). It provides a uniquely advantageous setting for investigating the

multiscale structure of nearshore marine communities in a relatively small region (c.a. 200 km long) that is characterized by strong environmental heterogeneity. Here, the cool southward flowing California Current and the warm northward flowing Southern California Counter Current meet to create highly heterogeneous oceanographic conditions (Harms and Winant 1998; Henderikx Freitas et al. 2017), while the coastal topography and offshore islands generate much variability in wave exposure. Giant kelp forests in the region are spatially structured due to the patchy distribution of rocky habitat and environmental processes (e.g., oceanographic conditions, wave exposure, grazing and recruitment) operating across a range of scales (Cavanaugh et al. 2011, 2013; Castorani et al. 2015).

Kelp forest communities were surveyed annually at 86 sites (Fig. 1a) between summer to early autumn from 2005 to 2014 by four monitoring programs: (1) the National Park Service Kelp Forest Monitoring program (KFM, 33 sites, Kushner et al. 2013), (2) the Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO, 37 sites), (3) the Santa Barbara Coastal Long Term Ecological Research Project (SBC LTER, 11 sites, Reed 2016), and (4) the San Nicolas Island monitoring program (SNI, 5 sites, Kenner et al. 2013). We focused on 45 demersal fish species recorded at all 86 sites and 29 invertebrate and algal species that were recorded at 74 of the 86 sites (Electronic supplementary material Table S1, Fig. S1). We computed the annual mean density of each fish species at the site level based on visual counts of individuals in spatially defined transects established by each monitoring program. We similarly computed the annual mean density of 19 benthic species of invertebrates and algae at the site level based on replicate counts of individuals in defined areas of varying size ranging from 1 to 60 m^2 depending on the species and monitoring program. We examined the abundance of ten additional species of invertebrates and algae using percent cover data collected by random or uniform point contact sampling. The specific sampling methods used by each monitoring program to estimate the density or percent cover of each species is summarized in Table S1. Species that were not recorded by all four programs were rare, or not characteristic of rocky reef habitats were not included in the analysis.

Environmental variables

We used five variables to capture the spatial heterogeneity in oceanographic conditions and kelp forest structure across sites: (1) sea surface temperature (SST); (2) chlorophyll-*a* concentration in surface waters (a surrogate for phytoplankton biomass); (3) wave exposure; (4) potential propagule delivery strength and (5) giant kelp canopy biomass, which is known to influence assemblages of reef fishes,

Fish assemblages

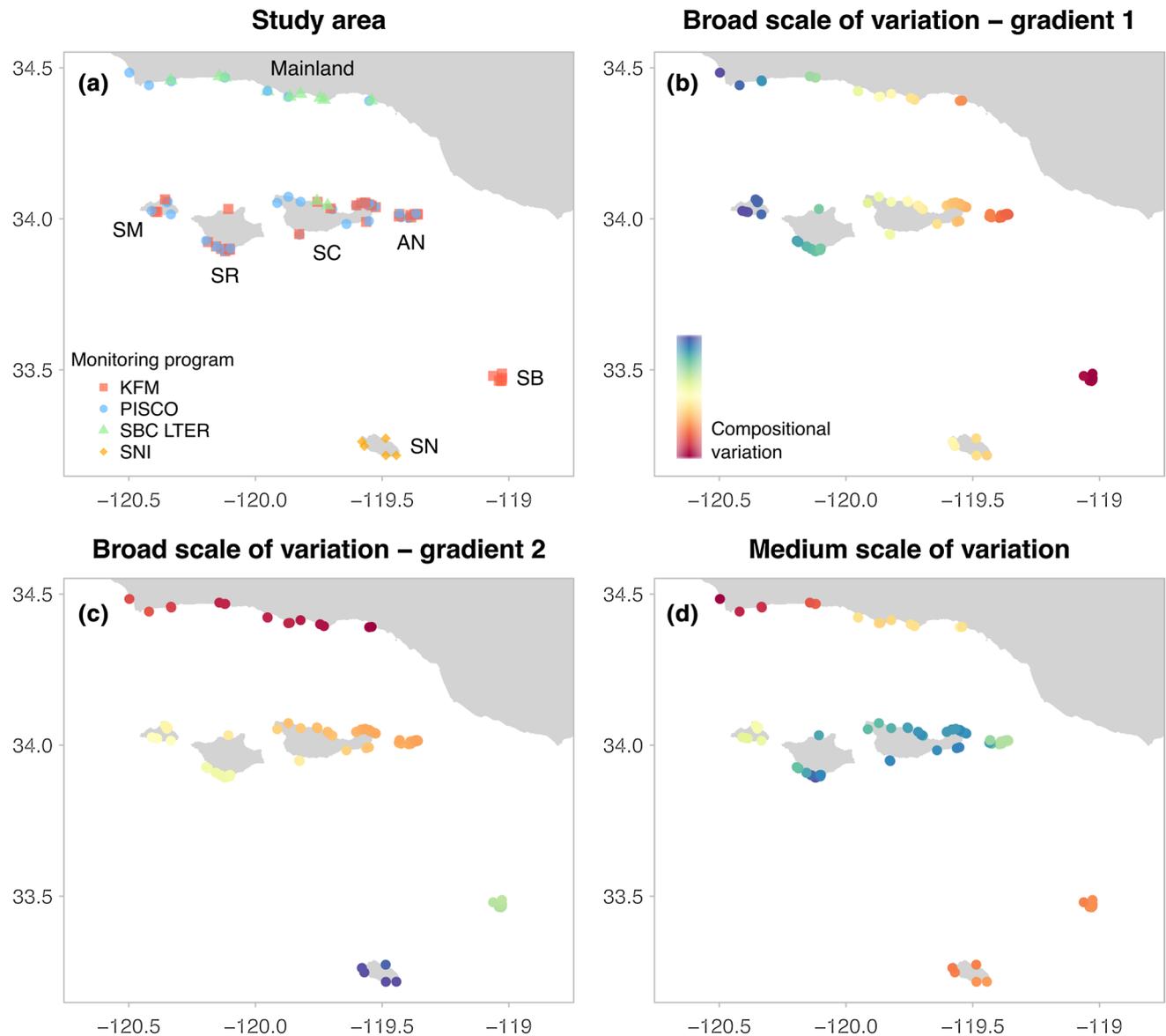


Fig. 1 Spatial variation in fish, invertebrate and alga assemblages at different scales. **a** Study area showing the Santa Barbara Channel. Islands correspond to San Miguel (SM), Santa Rosa (SR), Santa Cruz (SC), Anacapa (AN), Santa Barbara (SB) and San Nicolas (SN). East to West gradient (**b**) and North to South gradient (**c**) of the broad scale of variation in fish assemblages. **d** Medium scale (MS) of vari-

ation in fish assemblages. Each symbol represents one of the 86 sites, and colour scales with the variation in species composition (i.e. sites displaying similar colour have similar species composition at that scale). The small scale of variation is showed in Fig. S3 (colour figure online)

invertebrates and algae. The variables were each averaged over a 10-year period (2005–2014) for each study site.

SST and chlorophyll-*a* concentration

Coastal SST ($^{\circ}\text{C}$) and chlorophyll-*a* concentration (mg m^{-3}) were estimated using composite satellite measurements. SST was taken from the Multi-scale Ultra-high Resolution Sea

Surface Temperature dataset (MUR SST, <https://mur.jpl.nasa.gov/>), which provides daily SST values at 1 km spatial resolution. Chlorophyll-*a* concentration was based on Aqua MODIS, which provides monthly chlorophyll-*a* concentration at a 1.25 km spatial resolution (Henderikx Freitas et al. 2017). We extracted long-term SST and chlorophyll-*a* concentration values from the pixel overlaying each site to compute its average over the 10-year period.

Wave exposure

Maximum significant wave height at each site was estimated using data from the Coastal Data Information Program (CDIP; <https://cdip.ucsd.edu>). CDIP uses a wave propagation model to generate spatially explicit significant wave height (H_s ; mean height of the highest 1/3 of the waves) at 200 m resolution. Hourly estimates of H_s at a depth of 10 m were used to generate the daily maximum significant wave height (the top 1/3 of the hourly estimates). We extracted daily maximum significant wave height for each site as the value of the closest 200 m pixel to obtain the average over the 10-year period following Bell et al. (2015). We chose maximum daily values over mean daily values because extreme waves are more likely to influence kelp forests and their associated communities in the study region (Reed et al. 2008; Byrnes et al. 2011). In addition, these two variables were highly correlated among sites ($r = 0.99$).

Potential propagule delivery strength

A three-dimensional Regional Ocean Modeling System (ROMS) solution for the Southern California Bight (SCB) region (Dong et al. 2009) was used to estimate connectivity among sites via the delivery of propagules (i.e., spores and larvae) by ocean currents following methods discussed in Mitarai et al. (2009), Simons et al. (2013) and Siegel et al. (unpublished data). More than 500 million Lagrangian particles were released each month from 135 nearshore ROMS connectivity cells of approximately 80 km², every 5 m in depth from 5 to 30 m below the surface (Fig. S2). Spatial probability density function (PDF) distributions for each source connectivity cell and release month were computed for particle advection times ranging from 1 to 70 days. The PDFs were used to form monthly connectivity matrices for each advection time among every ROMS connectivity cell in the SCB network and were used to calculate mean Lagrangian particle transit times among each pair of cells for each month (Siegel et al. unpublished data). To quantify the relative “attractiveness” of a ROMS connectivity cell for propagule delivery, we computed the potential propagule delivery strength by summing the monthly connectivity evaluated at the mean transit time over all potential sources in the domain (i.e., excluding the focal ROMS cells; Siegel et al. unpublished data). Finally, we averaged monthly potential propagule delivery strength between January 1996 and December 2007 to estimate the long-term average potential propagule delivery strength for each ROMS connectivity cell. Both long-term annual, as well as the vernal, averages were determined since propagule production for many species tends to be highest in the spring. These two indices were not as highly correlated ($r = 0.65$) as the other long-term seasonal averages (all three seasons vs. yearly

average: $r > 0.94$), which suggested they convey different aspects of the seasonal variability in coastal oceanographic connectivity. Because we were interested in characterizing spatial patterns of diverse communities, we were not able to impose general propagule characteristics (e.g., planktonic larval duration, size of the propagule source) on particles, as can be done when modelling the distribution of a single species (Watson et al. 2011b). Consequently, our approach only captured the physical aspect of coastal oceanographic connectivity (Grober-Dunsmore et al. 2009).

Giant kelp biomass

Giant kelp forms a dense floating canopy at the sea surface that influences the species composition and abundance of reef fishes, invertebrates and algae (reviewed in Schiel and Foster 2015). Data on kelp canopy biomass at 30 m spatial resolution were derived from Landsat 5 Thematic Mapper and Landsat 7 Enhanced Thematic Mapper + satellite images and calibrated using in situ data collected by divers (Bell et al. 2017) following methods introduced by Cavanaugh et al. (2011). We assessed canopy biomass of giant kelp in a 2 km buffer area around each site every 1–2 months to compute long-term average kelp canopy biomass from 2005 to 2014. The choice of a 2-km radius was guided both by the spatial scales over which these remote sensing techniques are reliable and the fact that choosing larger (e.g., 3 km) or smaller (e.g., 1 km) buffer areas resulted in highly correlated indices ($r > 0.90$). Because kelp forests are extremely dynamic (Cavanaugh et al. 2011, 2013; Bell et al. 2015; Castorani et al. 2015), we also computed the temporal coefficient of variation of kelp canopy biomass within each buffer area to capture information on the temporal dynamics of kelp forests.

Space–time interaction

We hypothesized that kelp forest communities are primarily structured across space rather than time due to the strong spatial gradients in the oceanographic conditions of the Santa Barbara Channel (SBC). We tested for a space–time interaction in community composition using a multivariate analysis of variance by canonical redundancy analysis (RDA; Legendre and Anderson 1999; Legendre et al. 2010). Helmert contrasts were used to test for the main factors (space and time), while the space–time interaction was modelled based on the product of the first $s/2$ and $t/2$ spatial and temporal principal components neighbourhood matrix (PCNM) variables, respectively, following Legendre et al. (2010), where s stands for the number of sites and t the number of years. We used type III sums-of-squares due to unequal replication in our sampling design (9 and 20% of site by year combinations were missing for fish surveys

and invertebrate and algal surveys, respectively, resulting in space factors, time factors and space–time interaction factors that were not fully orthogonal: see Fig. S1). Despite significant space–time interactions in our analysis (see “Results”), the spatial component of the total variation in both types of communities was predominant. In addition, our results provided similar conclusions when modelled separately for each year (see Table S2). Thus, because we were primarily interested in understanding the spatial structure of communities, we focus on results of analysing ecological data at the site level using long-term averages over the 10-year period.

Spatial variables

Based on the sampling design of the 86 sites, we developed three groups of spatial variables to analyse the multi-scale spatial variation in fish assemblages and benthic assemblages of invertebrates and algae at broad scale (> 200 km), medium scale (65–200 km) and small scale (1–65 km), respectively. We performed a hierarchical analysis of the multiscale spatial variation of communities, whereby the spatial variation was modelled sequentially from the largest to the smallest spatial scale by means of partial RDA.

The broad scale of variation in the two assemblages was modelled using the geographic coordinates of each site as spatial variables to capture spatial trends at broad scales. We then used spatial eigenfunctions derived from a connection matrix of neighbouring sites, where the connection among sites was defined as the overwater distance, to analyse finer-scale spatial variation in both assemblages. This method corresponds to distance-based Moran’s eigenvector maps (dbMEM; Dray et al. 2006) previously referred to as PCNM (principal coordinates of neighbour matrices; Borcard and Legendre 2002; Borcard et al. 2004). dbMEM analysis provides a means of dissecting all the possible scales of variation encompassed by a sampling design. Each eigenfunction generated represents an orthogonal spatial variable that displays a given spatial correlation (Moran’s I ; Borcard and Legendre 2002; Dray et al. 2006). We first modelled the medium scale of variation in both assemblages based on eleven dbMEM variables obtained from the connection matrix among all sites, representing significant positive spatial structure at scales ranging from 65 km (i.e., the truncation distance Borcard and Legendre 2002) to the entire Channel (~ 200 km). We then modelled variation in both assemblages at the small scale (1–65 km), using a staggered matrix of dbMEM variables for spatially clustered sites following Declerck et al. (2011). In this analysis, we built dbMEM variables for each spatial cluster (i.e., the six islands and the coastline; Fig. 1a) independently and assembled them into a staggered matrix, arranging dbMEM variables in blocks corresponding to each spatial cluster. Within these blocks, sites from the other spatial clusters were assigned the

value 0 (Declerck et al. 2011). A dummy variable coding for the six spatial clusters was used to control for spatial differences among the six spatial clusters.

Lastly, we computed a multivariate spline correlogram to complement our hierarchical analysis for identifying the scales of variation in the two assemblages. The correlogram allowed us to investigate how spatial autocorrelation, measured as the Mantel statistic, varied as a function of overwater distance among sites. The confidence interval of the Mantel statistic was constructed based on bootstrap resampling with 999 replications (Bjørnstad and Falck 2001).

Spatial scales of variation in community composition and their underlying drivers

We used RDA to independently model the spatial structure of fish assemblages and benthic assemblages of invertebrates and algae as a function of the three groups of spatial predictors (broad, medium and small scales). For each group, we first pre-selected spatial variables by forward selection (Blanchet et al. 2008), performed RDAs, and tested the significance of the RDA axes through marginal tests (Legendre et al. 2011). Each significant RDA axis represents a distinct and significant pattern of spatial variation in the corresponding assemblage. The eigenvalue associated with each significant RDA axis was used to assess the variance explained by that scale as expressed by adjusted R^2 .

To determine the extent to which environmental variables explain different spatial scales of assemblage composition, we modelled the variation along significant RDA axes as a function of the five categories of environmental variables (SST, chlorophyll-*a* concentration, potential propagule delivery strength, giant kelp biomass and wave exposure) using variation partitioning (Borcard et al. 1992; Peres-Neto et al. 2006). This allowed us to quantify how much variation at each scale was explained by: (1) environmental heterogeneity, i.e., the overall contribution of the five categories of variables, and (2) each of the five variables. In the latter case, variation partitioning was used to partition the total contribution of one variable into its unique contribution and the portion of its contribution shared with the effect of other variables. Shared contribution among variables can occur when they are correlated, and can be negative.

We Hellinger-transformed our data prior to the analyses, so that RDA and variation partitioning preserve the Hellinger distance among sites, which is more appropriate for compositional data and give lower weights to rare species that were potentially more prone to sampling error (Legendre and Gallagher 2001). Kelp canopy biomass and chlorophyll-*a* concentration were square-root transformed. All statistical analyses were performed in R 3.0.2 (R Core Team 2014), using the *rda* and *varpart* functions of the *vegan*

package. The spatial correlogram was computed using the ncf package, adapted to accommodate overwater distances.

Results

Space, time and their interaction explained significant variation in the assemblages of fish and benthic invertebrates and algae ($P < 0.001$ for all terms; Table 1). However, space had a more prominent role in explaining variation in assemblages of fish ($R^2 = 0.560$) and of invertebrates and algae ($R^2 = 0.668$), compared to time ($R^2 = 0.047$ and $R^2 = 0.027$ for fish assemblages and invertebrate and algal assemblages, respectively) and the space–time interaction ($R^2 = 0.128$ and $R^2 = 0.120$, respectively). Hence, the following results focus on the long-term spatial variation in both assemblages.

Different ecological drivers can operate across multiple spatial scales, leading to complex and multiscale patterns of variation in kelp forest communities. Here we found that both assemblages were primarily structured over the broad spatial scale, which explained 39% of the total variation in fish composition ($F_{2,83} = 27.828$; $P = 0.001$; Figs. 1b, c, 3), and 23% of the total variation in invertebrate and algal composition ($F_{2,71} = 11.942$; $P = 0.001$; Figs. 2a, b, 4). Two significant RDA axes captured different facets of the broad scale of variation. The first axis of the broad scale of variation in fish assemblages ($F_{1,83} = 39.918$; $P = 0.001$) captured an east to west gradient (Fig. 1b), while the second ($F_{1,83} = 15.739$; $P = 0.001$) captured a north to south gradient (Fig. 1c), which explained 28 and 11% of the total variation in fish composition, respectively. Both gradients were accurately explained by the combination of all five environmental variables, which collectively accounted for 98.7% ($P < 0.001$) and 90.1% ($P < 0.001$) of the variation in fish species composition along the first and second gradients, respectively. SST and kelp biomass explained a large fraction of the east to west gradient when analysed independently (Fig. 5a, Table S3). However, the individual contribution of each variable was to a large extent shared with the contribution of other variables (Fig. 5a). For instance, only 33.3% of the 96.7%, contribution of SST to the east to west

gradient was unique, while the remaining fraction could also be attributable to other variables, notably kelp biomass and to a lesser extent to potential propagule delivery strength or chlorophyll-*a* concentration. In contrast, the explanation of the north to south gradient was less confounded. Potential propagule delivery strength was the best predictor of this gradient, explaining 70.0%, more than half of which was a unique contribution (Fig. 5b). Wave exposure also explained a large fraction of this gradient (36.6%), though most of its effect was shared with chlorophyll-*a* concentration and potential propagule delivery strength (Fig. 5b). Kelp biomass and SST did not contribute to the explanation of the north to south gradient.

The broad scale of variation in assemblages of invertebrates and algae was very similar to the one characterized for fishes. Indeed, two significant RDA axes also characterized the broad scale variation in invertebrates and algae and similarly captured an east to west gradient ($F_{1,71} = 17.918$; $P = 0.001$; Fig. 2a), and a north to south gradient in the species composition of invertebrates and algae ($F_{1,71} = 5.966$; $P = 0.001$; Fig. 1b), which explained 17.3 and 5.8% of the total variation, respectively. Here again, the five environmental variables collectively accounted for most of the variation in the first ($R_a^2 = 0.981\%$; $P < 0.001$) and second gradient ($R_a^2 = 0.907\%$; $P < 0.001$). SST and kelp biomass were tightly related to the east to west gradient in invertebrate and algal species composition, explaining 95.6 and 63.3% of this gradient, respectively, though most of their contributions were also confounded (Fig. 6a, Table S3). Indeed, only 27.7% and less than 1% of the contribution of SST and kelp biomass were unique contributions. Potential propagule delivery strength and wave exposure were tightly related to the north to south gradient, explaining 54.6 and 41.3% of the second gradient, half of the contribution of potential propagule delivery strength (32.8%) being unique (Fig. 6b, Table S3).

Eleven dbMEM variables were used to model the medium spatial scale (≥ 65 to ~ 200 km) of variation. Among these, three variables (#1, 2 and 8) for fishes and four variables (#1, 2, 3 and 5) for invertebrates and algae were retained following forward selection to capture the medium scale

Table 1 Spatio-temporal variation in fish assemblages and in assemblages of invertebrates and algae over a 10-year period (2005–2014) in the Santa Barbara Channel

Source	Fish assemblages				Invertebrate and alga assemblages			
	<i>df</i>	R^2	<i>F</i>	<i>P</i>	<i>df</i>	R^2	<i>F</i>	<i>P</i>
Space	85	0.560	13.849	0.001	73	0.668	24.041	0.001
Time	9	0.047	11.059	0.001	9	0.027	7.894	0.001
Space × time	215	0.128	1.253	0.001	215	0.120	1.463	0.001
Residuals	466				391			

The variance explained by each component (R^2) was tested using a multivariate analysis of variance by canonical RDA

P probability value

Invertebrate and algal assemblages

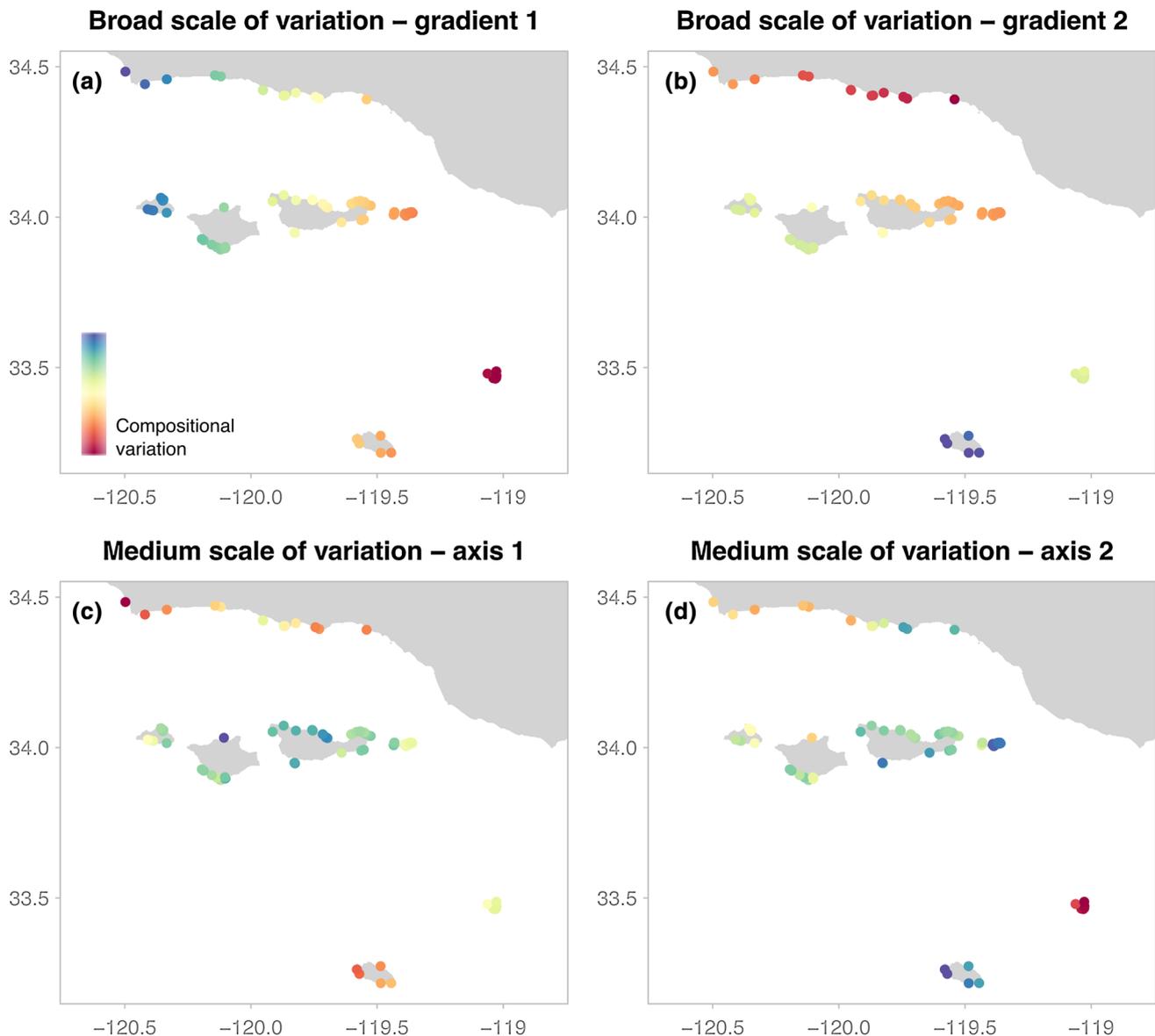


Fig. 2 Spatial variation in invertebrate and alga assemblages at different scales. East to West gradient (a) and North to South gradient (b) of the broad scale of variation in invertebrate and algal assemblages. First (c) and second (d) axis of the medium scale of variation in invertebrate and algal assemblages. Each symbol represents one of

the 74 sites, and colour scales with the variation in species composition (i.e., sites displaying similar colour have similar species composition at that scale). The small scale of variation is showed in Fig. S3 (colour figure online)

of variation. The latter explained 11.6% ($F_{3,80} = 7.434$; $P = 0.001$) of the total variation in fishes (Fig. 3), and 15.5% ($F_{4,67} = 5.464$; $P = 0.001$) of the total variation in invertebrates and algae, after controlling the broad scale (Fig. 4). Only the first RDA axis of the medium scale of variation in fish species composition was significant ($R_a^2 = 0.105$; $P = 0.001$; Fig. 1d). Variation along this significant axis captured additional non-linear variation in fish species composition occurring in the SBC, such as differences between the

mainland coastline and the islands, and among the islands and sides of islands (Fig. 1d). For instance, both the north-east side of Santa Cruz Island and the southern side of Santa Rosa Island displayed similar scores along this RDA axis. All environmental variables taken together explained 62.9% of the medium scale variation in fish species composition (Fig. 5c). Taken independently, each variable had a unique contribution (Fig. 5c, Table S3), but potential strength delivery strength was the strongest contributor, explaining 42.6%

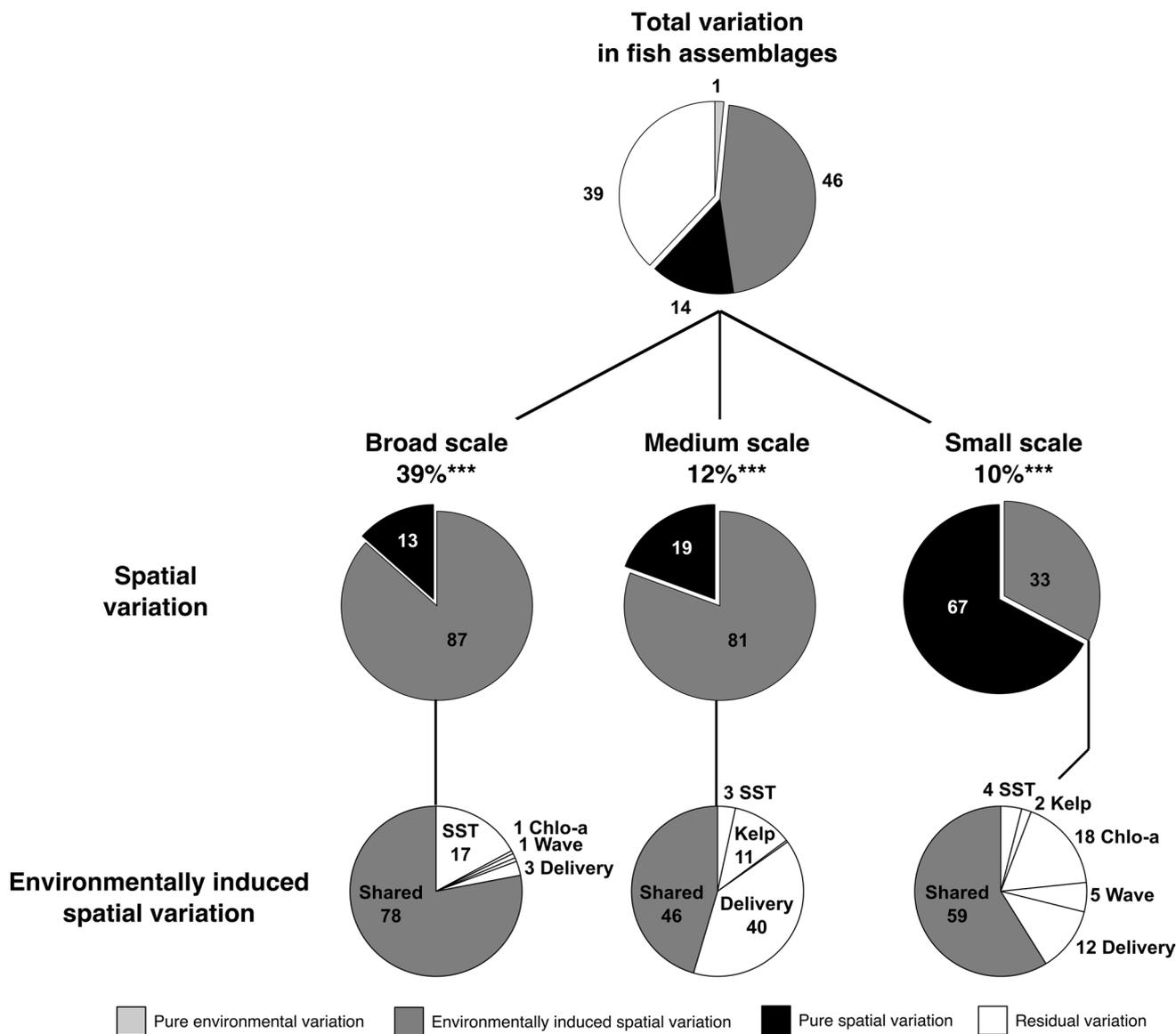


Fig. 3 Relative influence of spatial and environmental effects on the variation in fish assemblages at different spatial scales. The total variation is decomposed into purely spatial (black), environmentally induced spatial (dark grey), purely environmental (light grey) and residual (white) components. The total spatial variation (i.e., due to purely spatial effects and induced by the environment) is further

decomposed into different spatial scales. Finally, the environmentally induced spatial variation at each scale is decomposed into the contributions of the five environmental variables. Their total contributions are divided into a unique contribution (white) and a shared contribution. The importance of each effect is given by the percentage outside or inside the chart and is calculated based on adjusted R^2

of the variation in fish assemblages at this scale. Kelp biomass explained 11.3% of the variation at this scale, while all other variables had marginal contributions. By contrast, two RDA axes of the medium scale of variation in the assemblages of invertebrates and algae were significant ($R_a^2 = 0.109$; $P = 0.001$ and $R_a^2 = 0.029$; $P = 0.001$; Fig. 2c, d). All environmental variables collectively explained 37.4% of these two axes, with unique contributions by potential propagule delivery strength (15.3%) and kelp biomass (13.5%; Fig. 6c, Table S3).

The small scale (1–65 km) explained 10% of the total variation in fishes and 14% of the total variation in invertebrates and algae after controlling for the broad and medium scales (Figs. 3, 4). Two RDA axis of the small scale of variation in the fish assemblages were significant (axis 1: $R_a^2 = 0.032$; $P = 0.003$; axis 2: $R_a^2 = 0.026$; $P = 0.018$) and captured very small-scale features of the spatial variation occurring within islands or along the mainland coastline (Fig. S3a, b). However, all five environmental variables collectively explained only 32.2% of this small-scale variation (Fig. 5d).

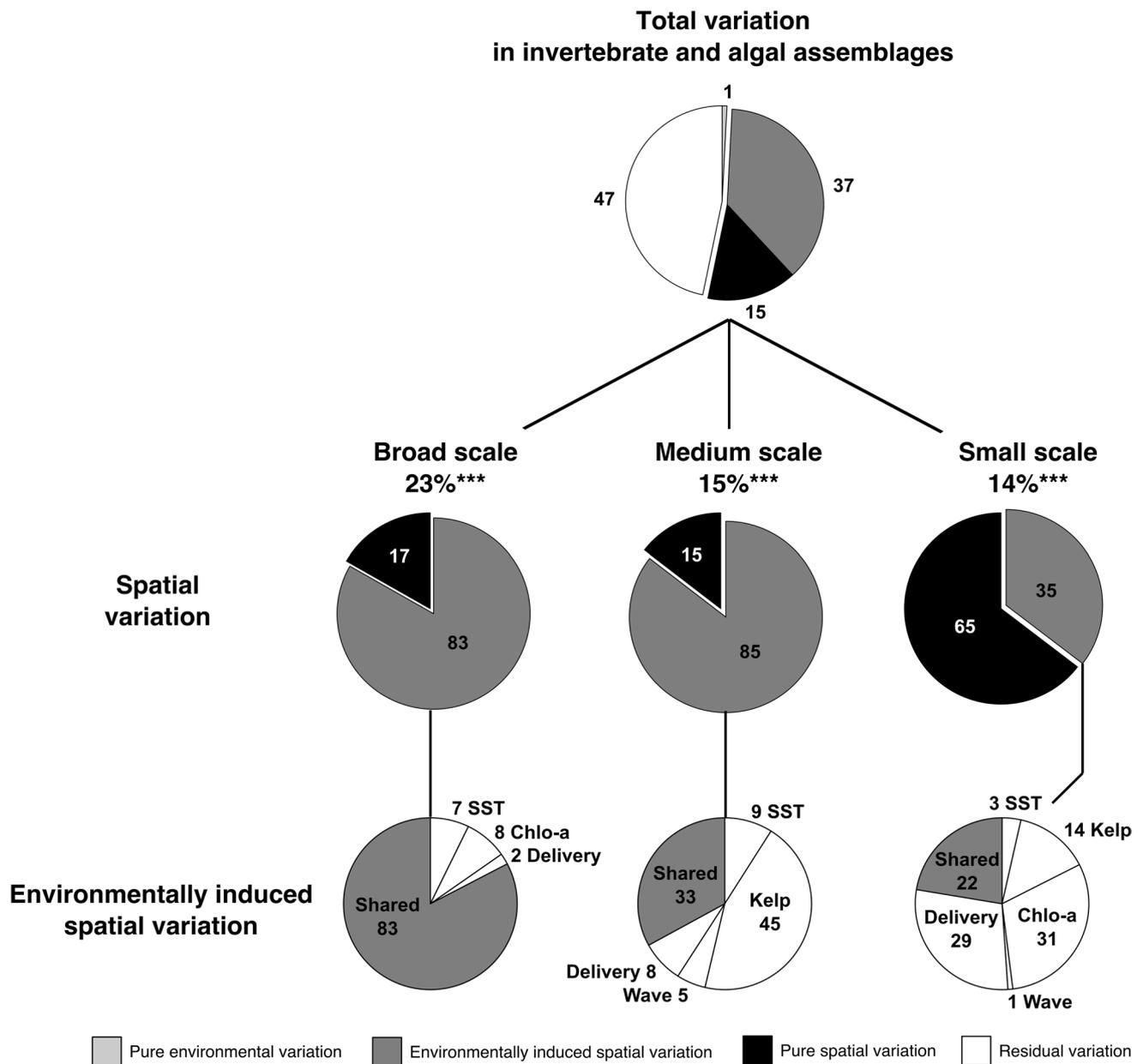


Fig. 4 Relative influence of spatial and environmental effects on the variation in invertebrate and algal assemblages. See Fig. 3 for legend description

Two RDA axis also explained the small scale of variation in invertebrate and algal assemblages (axis 1: $R_a^2 = 0.075$; $P = 0.001$; axis 2: $R_a^2 = 0.022$; $P = 0.043$; Fig. S3c, d), but were also poorly explained by the five environmental variables ($R_a^2 = 0.240$; $P = 0.001$; Fig. 6d). Of the five environmental variables, chlorophyll-*a* concentration had the highest contribution to the small scale of variation in assemblages of fishes (11.5%), and in assemblages of invertebrates and algae (9.5%).

Finally, 13, 19 and 67% of the broad, medium and small scales of variation in fish assemblages (Fig. 3),

and 17, 15 and 65% of the broad, medium and small scales of variation in invertebrate and algal assemblages (Fig. 4) were uniquely explained by our spatial variables. This corresponds to purely spatial effects attributable to either dispersal limitation or unmeasured variables. After controlling for broad, medium and small scale spatial variables, local scale effects of the five environmental variables explained ~ 1% of the total variation in the assemblages of fishes and assemblages of invertebrates and algae (Figs. 3, 4). The spatial multivariate correlogram further supported the identification of these scales

Fish assemblages

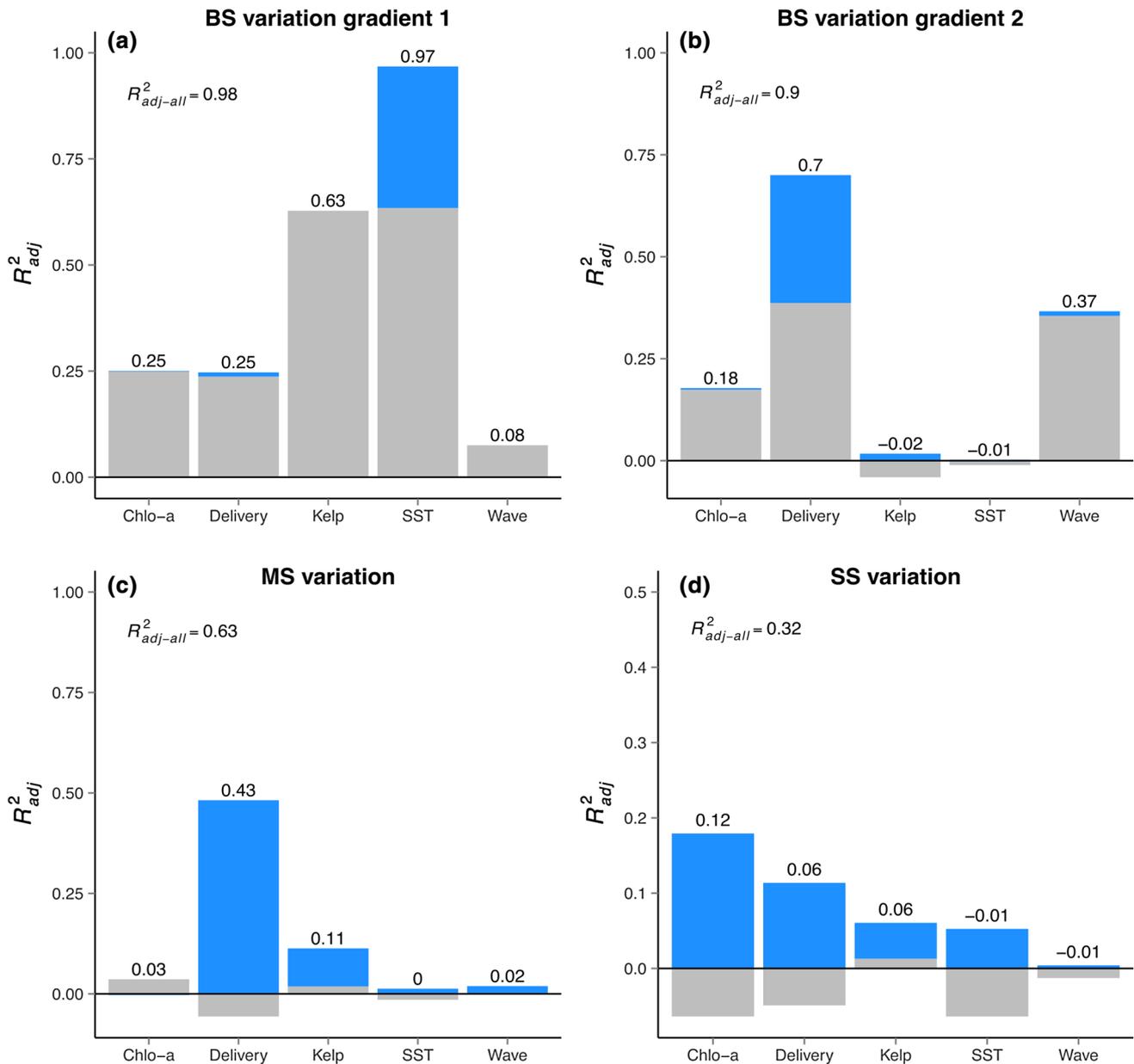


Fig. 5 Relationships between environmental variables and the variation in fish assemblages at different spatial scales. Each bar represents the contribution of an environmental variable to the variation in species composition at a given spatial scale. The total contribution of a variable is decomposed into a unique contribution (blue fraction) and a contribution that is shared with the other environmental variables (grey fraction). Negative shared contributions can emerge

when variables are correlated, in which case its unique contribution can be higher than its total contribution. The number above each bar corresponds to the total contribution of each variable. The five environmental variables are chlorophyll-*a* concentration (Chlo-*a*), potential propagule delivery strength (delivery), kelp biomass (Kelp), sea surface temperature (SST) and wave exposure (Wave). Note that the scale of the y-axis in (d) differs from (a–c) (colour figure online)

of variation in both assemblages (Fig. 7). The correlogram for fishes displayed significant positive spatial correlation at distances ranging from 0 to 33.7 km [95% confidence interval (28.4–40)], while the positive spatial correlation in invertebrates and algae was no longer significant for

overwater distances > 31.3 km [95% confidence interval (24.6–40.7)]. Beyond this distance, assemblages of fishes and assemblages of invertebrates and algae exhibited significant negative spatial correlation, suggesting that they were more dissimilar than expected by chance.

Invertebrate and algal assemblages

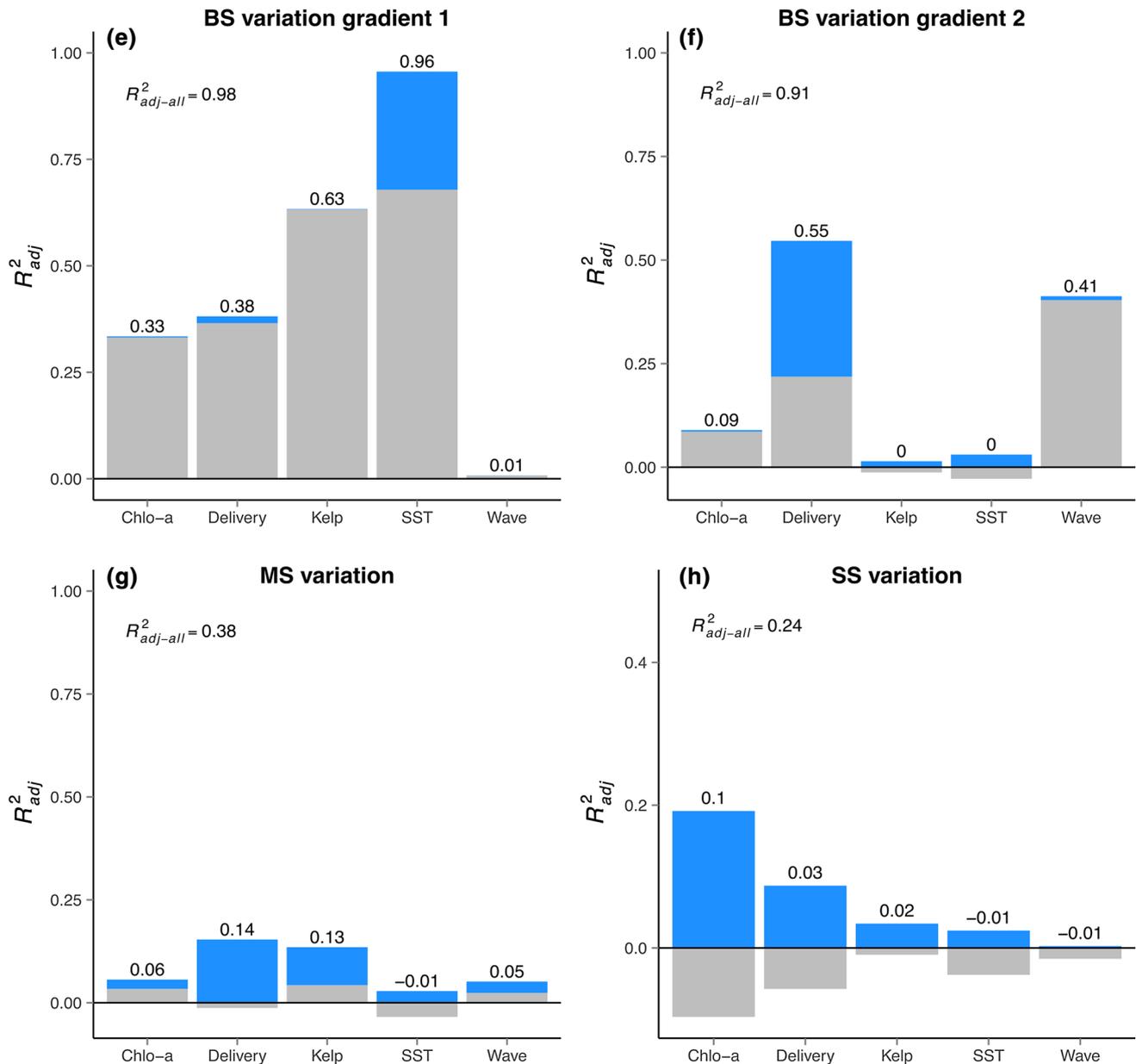


Fig. 6 Relationships between environmental variables and the variation in invertebrate and algal assemblages. See Fig. 5 for legend description

Discussion

Understanding the causes of spatial variation in natural communities can be extremely complex when the underlying processes vary across multiple scales. In coastal ecosystems, the importance of multiple biotic and abiotic processes (e.g., species interactions, dispersal and environmental forcing) in explaining the local composition of marine communities (Connell 1971; Dayton 1971) or their spatial structure (Paine 1974; Dayton et al. 1984; Underwood and Chapman 1996)

has been emphasized repeatedly. However, understanding precisely how these processes interact to shape the structure of coastal marine communities at multiple scales remains a challenge. Many assume that spatial variation will mainly arise over very broad scales because of presumed high connectivity in marine systems (Tittensor et al. 2010; Magurran et al. 2015), while some evidence suggests that spatial variability can also occur over very small spatial scales (Hughes et al. 1999; Edwards 2004). In this study, we used spatially extensive data from sustained monitoring efforts in the SBC

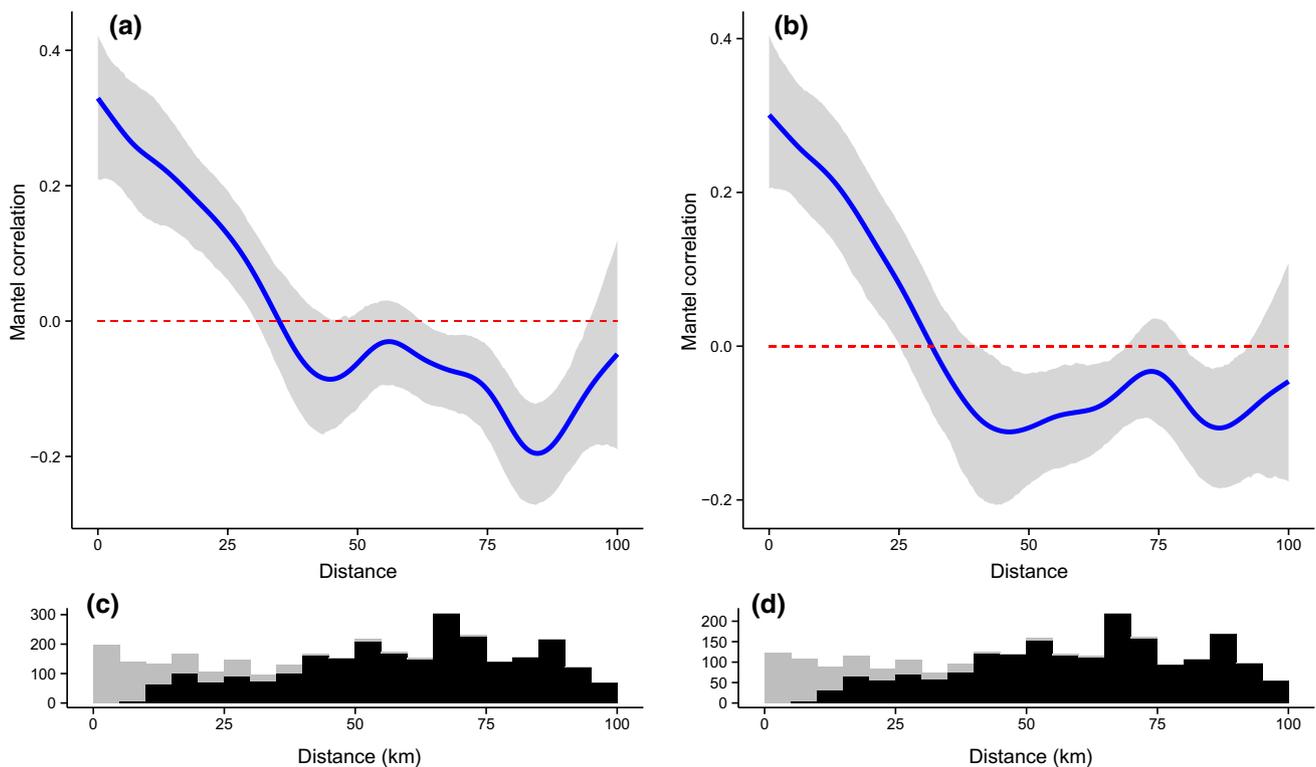


Fig. 7 Multivariate correlogram of fish assemblages (**a, c**) and of invertebrate and algal assemblages (**b, d**). The blue line corresponds to the mean spatial autocorrelation, while the grey area represents its 95% confidence interval. The lower panels (**c, d**) illustrate the num-

ber of site pairs used for each distance class. The grey bars show site pairs that belong to the same spatial clusters (islands or mainland), while the black bars represent site pairs that belong to distinct spatial clusters (colour figure online)

to show that the spatial variation in assemblages of mobile fishes and benthic invertebrates and algae can be complex and manifested at multiple spatial scales. Nonetheless, our results suggest that most of the spatial variation arises at broad spatial scales, especially for fishes. We found strong evidence that the broad scale of variation in the species composition of kelp forest communities in the SBC was driven by an SST gradient running from west to east, as well as by north to south variation in oceanographic connectivity. The major effect of SST is consistent with findings identifying ocean temperature as a predominant driver of marine communities globally (Tittensor et al. 2010) as well as in our study region (Blanchette et al. 2007, 2009). Previous studies have investigated determinants of spatial patterns in community composition in the SBC, focusing on specific aspects of the environmental variability (e.g., SST, physical disturbance), dispersal and oceanographic connectivity (Reed et al. 2000; Kinlan and Gaines 2003; Broitman and Kinlan 2006; Blanchette et al. 2009; Watson et al. 2011a). While these studies suggested that SST and oceanographic connectivity play a role in structuring reef communities, we found that they act at different spatial scales, and hence underlie two different gradients in the structure of kelp forest communities. Medium scale variation in both fishes and the

benthic assemblage of invertebrates and algae was closely associated with heterogeneity in oceanographic connectivity within the SBC. Small scale variation in both types of assemblages was significant, yet we could not accurately attribute it to any of the environmental variables included in our model. It is often difficult to attribute small-scale variation to environmental variables, in part due to biotic interactions, or variation in environmental factors that is smaller than the scale at which they are measured (Borcard et al. 2004). In our study, variation among sites in depth, substrate characteristics and species interactions undoubtedly account for some of the unexplained variation in our analyses. Site differences in coastal topography and morphology might also explain additional variation, as they can influence nutrient flux, wave exposure and propagule delivery (Broitman and Kinlan 2006; Lester et al. 2007). Small- and medium-scale effects might be more important for assemblages of sessile invertebrates and algae, for which broad scale drivers explained less variability than was the case for fishes.

By taking into account multiple spatial scales, one can evaluate how the relative influence of stochastic processes (e.g., dispersal limitation) and species sorting vary in space. Previous contributions have shown how stochastic processes can be a dominant force structuring metacommunities at one

scale, while environmental conditions can become predominant at either larger (Jones et al. 2006; Laliberté et al. 2009) or smaller (Declerck et al. 2011) spatial scales. In coastal marine systems, regional differences in climate are known to be important in structuring communities over large scales, whereas, a combination of factors including local stochastic perturbations, successional processes and ecological interactions can substantially shape communities at small scales. Among these processes, dispersal plays an important role in community organization and spatial variation. Species with short-distance dispersal tend to be primarily structured by spatial factors, reflecting the importance of stochastic processes such as dispersal limitation, whereas assemblages of species with a capacity for longer range dispersal tend to be more influenced by regional environmental conditions (Reed et al. 2000; Hubbell 2001; Flinn et al. 2010; Schroeter et al. 2015). Species examined in this study differed greatly in the dispersal abilities of their propagules and adult forms (Shanks et al. 2003). The fact that we found very similar spatial scales of variation in assemblages of fishes and of benthic invertebrates and algae, despite differences in their mobility (e.g., Reed et al. 2000; Kinlan and Gaines 2003), suggests that environmental conditions prevail over dispersal limitation in controlling the structure of these communities. The lack of a strong pure spatial effect at any of the spatial scales studied further suggests that adult mobility and limitations on propagule dispersal do not play an overwhelming role in structuring the kelp forest metacommunity in the SBC. Our study considered the importance of adult mobility by contrasting mobile fish with benthic invertebrates and algae. Although these groups likely differ on average in larval dispersal potential (with fish having potential for longer distance dispersal), pelagic larval duration is not known for many of these species. Our results suggest that dispersal limitation does not play a large role at the community level, but it is a potentially important predictor of the spatial distribution of the most dispersal limited species (Reed et al. 2000; Simons et al. 2016). A more detailed analysis of the roles of pelagic larval duration and the size of source populations on the spatial structure of rocky reef communities would be valuable especially for short dispersers.

Paradoxically, potential propagule delivery strength explained a large portion of the north to south gradient and of the medium scale variability in communities despite the overall lack of evidence for dispersal limitation effects. This suggests that dispersal limitation does not prevent species from tracking their environmental optima but that connectivity is still an important driver of metacommunity dynamics within the SBC. The effect of potential propagule delivery was due in large part to greater particle connectivity of the mainland sites compared with the island sites (Mitarai et al. 2009; Siegel et al. unpublished data). Here, we used the mean transit time for Lagrangian particles between two

sites to represent the physical connection between kelp forest habitats. In that respect, our index captured structural aspects related to the spatial configuration of the habitat in relation to oceanographic connectivity (Grober-Dunsmore et al. 2009; Olds et al. 2016). Integrating propagule dispersal abilities and movement of adult organisms among habitats has provided critical information on the demographic connectivity of single species (Watson et al. 2011b). Demographic connectivity has been shown to be a key process controlling metapopulations of giant kelp, which depend on the number of propagules available for dispersal as well as physical transport of those propagules (Castorani et al. 2015). However, further work is needed to fully understand the role connectivity in controlling kelp forest metacommunities that consist of a diverse array of species with different dispersal abilities (Melià et al. 2016; Magris et al. 2016).

Surprisingly, giant kelp biomass was not a good predictor of spatial community structure in SBC, especially at medium and small scales. Kelp biomass was an important predictor only at the largest scale (east to west gradient), although its influence was confounded with that of other variables, notably wave height and SST, which are known to influence kelp biomass in the region (Cavanaugh et al. 2011; Bell et al. 2015). Giant kelp is regarded as an important foundation species that provides habitat and food for many of the studied species (Graham 2004; Koenigs et al. 2015; Miller et al. 2015). However, fish are mobile; the home range of many species certainly exceeds the extent of a kelp forest, and metapopulations may shift between sites as a response to resource limitation or other factors. Alternatively, it could be that our definition of kelp canopy biomass does not capture the ecologically relevant aspects of giant kelp for fishes, and the relationship between kelp and its communities, or that kelp is more important for the temporal variability of rocky reef communities as patches of kelp come and go. Overall it suggests that kelp may not be as strong of a factor sorting fish species relative to SST and oceanographic connectivity.

This study benefited from the existence of four long-term programs designed to monitor temperate rocky reef ecosystems in the SBC. These data provided the large number of spatial replicates needed for multiscale analysis, and underscore the importance of long-term surveys (Hughes et al. 2017). Despite similar goals and sampling protocols, sampling effort varied across programs. To minimize potential resulting bias, we focused on the 74 species that could be appropriately compared across programs and standardized abundances to give less weight to rare species. Yet, we cannot disregard the possibility that combining data from several monitoring programs led to sampling bias that resulted in underestimating compositional changes at small scales, where changes can be more subtle. In addition, it is worth noting that grouping spatial variables into subsets to model different scales is a somewhat arbitrary process, as there is

no general rule for defining broad, medium or small scales. Yet this represents the most effective way to dissect the spatial structure of natural communities (Borcard and Legendre 2002).

Islands and the mainland coastline (our spatial clusters) were the most parsimonious spatial predictors of assemblage structure. Indeed, the spatial structure of both fishes and the benthic assemblage of invertebrates and algae matched quite well with regional geomorphological structure. The maximum distances between any two intra-island sites for San Nicolas, Santa Barbara, Anacapa and San Miguel islands did not exceed 17 km, far below the 34 and 31 km scale of variability characterized in the correlogram for the fish assemblages and the invertebrate and algal assemblage, respectively. In contrast, the larger Santa Cruz Island, Santa Rosa Island, and the mainland coast had sites that were separated by distances greater than these thresholds. Other processes in addition to connectivity likely contributed to the observed differences between island and mainland communities; for example, water clarity is typically greater around the islands than the mainland due to the lack of land-derived sediment around the islands (Ebeling et al. 1980; Henderikx Freitas et al. 2017). Declining water quality can have complex effect on coastal communities, as it can both directly influence recruitment, growth or survival of species as well as indirectly modulate species interactions (Airoldi 2003).

While some marine species can be primarily controlled by processes occurring over small spatial scales (e.g., Hughes et al. 1999; Edwards 2004), our results highlight the prominent role of large-scale environmental drivers on the spatial structure of kelp forest communities. The presence of the two broad-scale gradients indicate that SST and oceanographic connectivity act at scales even broader than the entire SBC, suggesting that the effects of global warming on kelp forest community structure should be evaluated at very large spatial scales (Wernberg et al. 2016; Krumhansl et al. 2016; Vergés et al. 2016). The coastal waters of California and the Santa Barbara Channel in particular, have been the focus of recent conservation efforts designed to protect its valuable marine resources from human exploitation (Saarman and Carr 2013). Our results suggest that much of the variability in the kelp forest communities of the SBC is induced by environmental heterogeneity occurring over broad scales that may conflict with conservation efforts aimed at smaller local scales. 26 sites were located within marine protected areas, yet after accounting for the strong environmental gradients, the protection status of these sites did not explain the spatial variation of species composition in kelp communities. This suggests that existing reserves may not be significantly structuring communities in space, even though their effect on harvested species is indisputable (Caselle et al. 2015). A better understanding of how natural processes and anthropogenic factors interact across different

spatial scales to affect biodiversity is needed to improve the effectiveness of conservation efforts. Ideally, the spatial scales at which conservation policies are developed should be matched with the scales at which relevant ecological processes occur (Socolar et al. 2016) and planned in ways that consider future changes in climate, which are predicted to greatly affect coastal marine communities including kelp forests (Wang et al. 2015; Coleman et al. 2017).

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Author contribution statement TL, DR, AR and RM designed the study, TL, AR, DS, LK, TB and RS processed the data and TL performed statistical analyses. TL wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

References

- Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. *Oceanogr Mar Biol* 41:161–236
- Anderson MJ, Crist TO, Chase JM et al (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecol Lett* 14:19–28
- Bell TW, Cavanaugh KC, Reed DC, Siegel DA (2015) Geographical variability in the controls of giant kelp biomass dynamics. *J Biogeogr* 42:2010–2021
- Bell TW, Cavanaugh KC, Siegel DA (2017) SBC LTER: time series of quarterly NetCDF files of kelp biomass in the canopy from Landsat 5, 7 and 8, 1984 - 2016 (ongoing). St. Barbara. Coast. LTER
- Bjørnstad ON, Falck W (2001) Nonparametric spatial covariance functions: estimation and testing. *Environ Ecol Stat* 8:53–70
- Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecology* 89:2623–2632
- Blanchette CA, Helmuth B, Gaines SD (2007) Spatial patterns of growth in the mussel, *Mytilus californianus*, across a major oceanographic and biogeographic boundary at Point Conception, California, USA. *J Exp Mar Biol Ecol* 340:126–148
- Blanchette CA, Raimondi PT, Broitman BR (2009) Spatial patterns of intertidal community structure across the California Channel Islands and link to ocean temperature. In: Proceedings of the 7th California Islands Symposium. Institute for Wildlife Studies, Arcata, CA, pp 161–173
- Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol Model* 153:51–68
- Borcard D, Legendre P, Drapeau P (1992) Partialling out the spatial component of ecological variation. *Ecology* 73:1045–1055
- Borcard D, Legendre P, Avois-Jacquet C, Tuomisto H (2004) Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85:1826–1832

- Broitman BR, Kinlan BP (2006) Spatial scales of benthic and pelagic producer biomass in a coastal upwelling ecosystem. *Mar Ecol Prog Ser* 327:15–25
- Byrnes JEK, Reed DC, Cardinale BJ et al (2011) Climate-driven increases in storm frequency simplify kelp forest food webs. *Glob Chang Biol* 17:2513–2524
- Caselle JE, Rassweiler A, Hamilton SL, Warner RR (2015) Recovery trajectories of kelp forest animals are rapid yet spatially variable across a network of temperate marine protected areas. *Sci Rep* 5:14102
- Castorani MCN, Reed DC, Alberto F et al (2015) Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system. *Ecology* 96:3141–3152
- Cavanaugh KC, Siegel DA, Reed DC, Dennison PE (2011) Environmental controls of giant-kelp biomass in the Santa Barbara Channel, California. *Mar Ecol Prog Ser* 429:1–17
- Cavanaugh KC, Kendall BE, Siegel DA et al (2013) Synchrony in dynamics of giant kelp forests is driven by both local recruitment and regional environmental controls. *Ecology* 94:499–509
- Chase JM (2010) Stochastic community assembly causes higher biodiversity in more productive environments. *Science* 328(80):1388–1391
- Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philos Trans R Soc B Biol Sci* 366:2351–2363
- Chase JM, Kraft NJB, Smith KG et al (2011) Using null models to disentangle variation in community dissimilarity from variation in α -diversity. *Ecosphere* 2:art24
- Coleman MA, Cetina-Heredia P, Roughan M et al (2017) Anticipating changes to future connectivity within a network of marine protected areas. *Glob Chang Biol* 23:3533–3542
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer PJ, Gradwell GR (eds) *Dynamics of populations*. PUDOC, pp 298–312
- Dayton PK (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol Monogr*:351–389
- Dayton PK, Currie V, Gerrodette T et al (1984) Patch dynamics and stability of some California kelp communities. *Ecol Monogr* 54:254–289
- Declerck SAJ, Coronel JS, Legendre P, Brendonck L (2011) Scale dependency of processes structuring metacommunities of cladocerans in temporary pools of High-Andes wetlands. *Ecography* 34:296–305
- Dong CM, Idica EY, McWilliams JC (2009) Circulation and multiple-scale variability in the Southern California Bight. *Prog Oceanogr* 82:168–190
- Dornelas M, Gotelli NJ, McGill B et al (2014) Assemblage time series reveal biodiversity change but not systematic loss. *Science* 344(80):296–299
- Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol Model* 196:483–493
- Dray S, Péliissier R, Couteron P et al (2012) Community ecology in the age of multivariate multiscale spatial analysis. *Ecol Monogr* 82:257–275
- Dungan JL, Perry JN, Dale MRT et al (2002) A balanced view of scale in spatial statistical analysis. *Ecography (Cop)* 25:626–640
- Ebeling AW, Larson TJ, Alevizon WS (1980) Habitat groups and island-mainland distribution of kelp-bed fishes off Santa Barbara, California. In: Power DM (ed) *Multidisciplinary symposium on the California Islands*. Santa Barbara Museum of Natural History, Santa Barbara
- Edwards MS (2004) Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. *Oecologia* 138:436–447
- Flinn KM, Gouhier TC, Lechowicz MJ, Waterway MJ (2010) The role of dispersal in shaping plant community composition of wetlands within an old-growth forest. *J Ecol* 98:1292–1299
- Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol Prog Ser* 296:13–29
- García Molinos J, Halpern BS, Schoeman DS et al (2016) Climate velocity and the future global redistribution of marine biodiversity. *Nat Clim Chang* 6:83–88
- Graham HM (2004) Effects of local deforestation on the diversity and structure of Southern California giant kelp forest food webs. *Ecosystems* 7:341–357
- Grober-Dunsmore R, Pittman SJ, Caldow C et al (2009) A landscape ecology approach for the study of ecological connectivity across tropical marine seascapes. In: Nagelkerken I (ed) *Ecological connectivity among tropical coastal ecosystems*. Springer, Dordrecht, pp 493–530
- Harms S, Winant CD (1998) Characteristic patterns of the circulation in the Santa Barbara Channel. *J Geophys Res* 103:3041–3065
- Henderikx Freitas F, Siegel DA, Maritorena S, Fields E (2017) Satellite assessment of particulate matter and phytoplankton variations in the Santa Barbara Channel and its surrounding waters: role of surface waves. *J Geophys Res Ocean* 122:355–371
- Hubbell SP (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton
- Hughes TP, Baird AH, Dinsdale EA et al (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* 397:59–63
- Hughes BB, Beas-Luna R, Barner AK et al (2017) Long-term studies contribute disproportionately to ecology and policy. *Bioscience* 67:271–281
- Jones MM, Tuomisto H, Clark DB, Olivas P (2006) Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. *J Ecol* 94:181–195
- Kenner MC, Estes JA, Tinker MT et al (2013) A multi-decade time series of kelp forest community structure at San Nicolas Island, California (USA). *Ecology* 94:2654
- Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology* 84:2007–2020
- Koenigs C, Miller RJ, Page HM (2015) Top predators rely on carbon derived from giant kelp (*Macrocystis pyrifera*). *Mar Ecol Prog Ser* 537:1–8
- Krumhansl KA, Okamoto DK, Rassweiler A et al (2016) Global patterns of kelp forest change over the past half-century. *Proc Natl Acad Sci* 113:13785–13790
- Kushner DJ, Rassweiler A, McLaughlin JP, Lafferty KD (2013) A multi-decade time series of kelp forest community structure at the California Channel Islands. *Ecology* 94:2655
- Laliberté E, Paquette A, Legendre P, Bouchard A (2009) Assessing the scale-specific importance of niches and other spatial processes on beta diversity: a case study from a temperate forest. *Oecologia* 159:377–388
- Legendre P (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology* 74:1659–1673
- Legendre P, Anderson MJ (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol Monogr* 69:1–24
- Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia* 129:271–280
- Legendre P, Legendre L (2012) *Numerical ecology*. Elsevier, Third Edit

- Legendre P, De Cáceres M, Borcard D (2010) Community surveys through space and time: testing the space–time interaction in the absence of replication. *Ecology* 91:262–272
- Legendre P, Oksanen J, ter Braak CJF (2011) Testing the significance of canonical axes in redundancy analysis. *Methods Ecol Evol* 2:269–277
- Leibold MA, McPeck MA (2006) Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410
- Leibold MA, Holyoak M, Mouquet N et al (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613
- Lester SE, Gaines SD, Kinlan BP (2007) Reproduction on the edge: large-scale patterns of individual performance in a marine invertebrate. *Ecology* 88:2229–2239
- Levin SA (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology* 73:1943–1967
- MacNeil MA, Graham NAJ, Polunin NVC et al (2009) Hierarchical drivers of reef-fish metacommunity structure. *Ecology* 90:252–264
- Magris RA, Trembl EA, Pressey RL, Weeks R (2016) Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. *Ecography* 39:649–664
- Magurran AE, Dornelas M, Moyes F et al (2015) Rapid biotic homogenization of marine fish assemblages. *Nature Com* 6:8405
- McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends Ecol Evol* 30:104–113
- Melià P, Schiavina M, Rossetto M et al (2016) Looking for hotspots of marine metacommunity connectivity: a methodological framework. *Sci Rep* 6:23705
- Menge BA, Olson AM (1990) Role of scale and environmental factors in regulation of community structure. *Trends Ecol Evol* 5:52–57
- Menge BA, Gouhier TC, Hacker SD et al (2015) Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. *Ecol Monogr* 85:213–233
- Meynard CN, Lavergne S, Boulangéat I et al (2013) Disentangling the drivers of metacommunity structure across spatial scales. *J Biogeogr* 40:1560–1571
- Miller RJ, Page HM, Reed DC (2015) Trophic versus structural effects of a marine foundation species, giant kelp (*Macrocystis pyrifera*). *Oecologia* 179:1199–1209
- Mitarai S, Siegel DA, Watson JR et al (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. *J Geophys Res Ocean* 114:C10026
- Newbold T, Hudson LN, Hill SLL et al (2015) Global effects of land use on local terrestrial biodiversity. *Nature* 520:45–50
- Olds AD, Connolly RM, Pitt KA et al (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. *Glob Ecol Biogeogr* 25:3–15
- Paine RT (1974) Intertidal community structure. *Oecologia* 15:93–120
- Peres-Neto PR, Legendre P, Dray S, Borcard D (2006) Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology* 87:2614–2625
- R Core Team (2014) R: a language and environment for statistical computing
- Reed DC (2016) SBC LTER: reef: kelp forest community dynamics: fish abundance. Santa Barbara Coastal LTER
- Reed DC, Raimondi PT, Carr MH, Goldwasser L (2000) The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. *Ecology* 81:2011–2026
- Reed DC, Rassweiler A, Arkema KK (2008) Biomass rather than growth rate determines variation in net primary production by giant kelp. *Ecology* 89:2493–2505
- Ryberg WA, Fitzgerald LA (2015) Landscape composition, not connectivity, determines metacommunity structure across multiple scales. *Ecography* 39:932–941
- Saarman ET, Carr MH (2013) The California marine life protection act: a balance of top down and bottom up governance in MPA planning. *Mar Policy* 41:41–49
- Sax DF, Gaines SD, Brown JH (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am Nat* 160:766–783
- Schiel DR, Foster MS (2015) The biology and ecology of giant kelp forests, 1st edn. University of California Press, California
- Schneider DC (2001) The rise of the concept of scale in ecology. *BioScience* 51:545–553
- Schroeter SC, Reed DC, Raimondi PT (2015) Effects of reef physical structure on development of benthic reef community: a large-scale artificial reef experiment. *Mar Ecol Prog Ser* 540:43–55
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:S159–S169
- Siegel DA, Watson JR, Simons RD et al. Characterizing particle transit time metrics in a coastal ocean network. *J Geophys Res* (**unpublished data**)
- Simons RD, Siegel DA, Brown KS (2013) Model sensitivity and robustness in the estimation of larval transport: a study of particle tracking parameters. *J Mar Syst* 119–120:19–29
- Simons RD, Page HM, Zaleski S et al (2016) The effects of anthropogenic structures on habitat connectivity and the potential spread of non-native invertebrate species in the offshore environment. *PLoS One* 11:e0152261
- Socolar JB, Gilroy JJ, Kunin WE, Edwards DP (2016) How should beta-diversity inform biodiversity conservation? *Trends Ecol Evol* 31:67–80
- Terlizzi A, Anderson MJ, Fraschetti S, Benedetti-Cecchi L (2007) Scales of spatial variation in Mediterranean subtidal sessile assemblages at different depths. *Mar Ecol Prog Ser* 332:25–39
- Tittensor DP, Mora C, Jetz W et al (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101
- Tzanopoulos J, Mouttet R, Letourneau A et al (2013) Scale sensitivity of drivers of environmental change across Europe. *Glob Environ Change* 23:167–178
- Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia* 107:212–224
- Vellend M, Srivastava DS, Anderson KM et al (2014) Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos* 123:1420–1430
- Vergés A, Doropoulos C, Malcolm HA et al (2016) Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. *Proc Natl Acad Sci* 113:13791–13796
- Vilà M, Espinar JL, Hejda M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708
- Wang D, Gouhier TC, Menge BA, Ganguly AR (2015) Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518:390–394
- Watson JR, Hays CG, Raimondi PT et al (2011a) Currents connecting communities: nearshore community similarity and ocean circulation. *Ecology* 92:1193–1200
- Watson JR, Siegel DA, Kendall BE et al (2011b) Identifying critical regions in small-world marine metapopulations. *Proc Natl Acad Sci* 108:E907–E913
- Wernberg T, Bennett S, Babcock RC et al (2016) Climate-driven regime shift of a temperate marine ecosystem. *Science* 353(80):169 LP–172
- Yeager LA, Layman CA, Allgeier JE (2011) Effects of habitat heterogeneity at multiple spatial scales on fish community assembly. *Oecologia* 167:157–168