DOI: 10.1111/maec.12453

ORIGINAL ARTICLE

WILEY marine ecology

Biogeographic patterns of communities across diverse marine ecosystems in southern California

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Funding information
MPA Grants via California Sea Grant through the California Marine Protected Areas Baseline Program; Southern California Coastal Water Research Project; National Science Foundation-Santa Barbara Coastal Long Term Ecological Research, Grant/Award Number: OCE-9982105, OCE-0620276 and OCE-1232779; PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans) funded by the David and Lucille Packard Foundation; University of Southern California (USC) Sea Grant, Grant/Award Number: 10-069; National Oceanic and Atmospheric Administration (NOAA) Restoration Center and the Montrose Settlements Restoration Program; United States Navy Commander, US Pacific Fleet; California Ocean Science Trust; California Department of Fish & Wildlife; California Ocean Protection Council; The Bay Foundation; Resources Legacy Fund Foundation; Keith Campbell Foundation for the Environment; Lisa and Douglas Goldman Foundation; State Coastal Conservancy; Annenberg Foundation; UCSB Associated Students Coastal Fund

Abstract

Integrating results from monitoring efforts conducted across diverse marine ecosystems provides opportunities to reveal novel biogeographic patterns at larger spatial scales and among multiple taxonomic groups. We investigated large-scale patterns of community similarity across major taxonomic groups (invertebrates, fishes or algae) from a range of marine ecosystems (rocky intertidal, sandy intertidal, kelp forest, shallow and deep soft-bottom subtidal) in southern California. Because monitoring sites and methods varied among programs, site data were averaged over larger geographic regions to facilitate comparisons. For the majority of individual community types, locations that were geographically near or environmentally similar to one another tended to have more similar communities. However, our analysis found that this pattern of within community type similarity did not result in all pairs of these community types exhibiting high levels of cross-community congruence. Rocky intertidal algae communities had high levels of congruence with the spatial patterns observed for almost all of the other (fish or invertebrate) community types. This was not surprising given algal distributions are known to be highly influenced by bottom-up factors and they are important as food and habitat for marine fishes and invertebrates. However, relatively few pairwise comparisons of the spatial patterns between a fish community and an invertebrate community yielded significant correlations. These community types are generally comprised of assemblages of higher trophic level species, and additional ecological and anthropogenic factors may have altered their spatial patterns of community similarity. In most cases pairs of invertebrate community types and pairs of fish community types exhibited similar spatial patterns, although there were some notable exceptions. These findings have important implications for the design and interpretation of results of long-term monitoring programs.

KEYWORDS
algae, biogeography, cross-community congruence, ecosystem-based management, fish, invertebrate

1 | INTRODUCTION

Understanding linkages among patterns and processes operating at large spatial scales across multiple ecosystems and taxonomic groups represents a key question for the implementation of ecosystem-based management approaches in conservation and management. One common ecosystem-based management strategy is the implementation of marine protected areas (MPAs). MPAs are place-based tools for biodiversity protection (e.g., Edgar, Barrett, & Stuart-Smith, 2009; Weeks, Russ, Alcala, & White, 2010), fisheries conservation (e.g., Lauck, Clark, Mangel, & Munro, 1998) and in some cases, fisheries or biodiversity enhancement (e.g., Dayton, Sala, Tegner, & Thrush, 2000; Dugan & Davis, 1993; McClanahan & Mangi, 2000). California, USA, has recently completed a massive MPA implementation process, beginning in the Northern Channel Islands of southern California and continuing statewide (Botsford, White, Carr, & Caselle, 2014). Currently over 132 MPAs protecting >15% of coastline are in place in the State. MPAs are often touted as ecosystem based tools, yet monitoring and assessment rarely include coordinated data analysis across multiple habitats within an MPA or network, even when multiple habitats are being monitored (Day, 2008; Fox et al., 2014).

The Marine Life Protection Act (MLPA), a California state law passed in 1999, required the implementation of a network of MPAs throughout the State. The science-based MPA network design process took place sequentially in five "Study Regions" throughout the State (Botsford et al., 2014). Briefly, scientific guidelines for MPA and network design included habitat representation (e.g., every "key" marine habitat should be represented in the network) and habitat replication (e.g., "key" marine habitats should be replicated in multiple MPAs across large environmental gradients or geographic divisions), as well as minimum size and maximum spacing guidelines (Botsford et al., 2014; Saarman et al., 2013). MPA planning for southern California, i.e., the "South Coast Study Region" (SCSR), where the present study took place, was initiated in 2008 and this network was implemented on 1 January 2012. The South Coast Study Region is larger, and more diverse both within and among marine ecosystems, than other Study Regions in the State. For this reason, early models grouping similar community structure across multiple habitats delineated four biogeographic provinces into which MPAs were located (CA MLPA, 2009). We build on that work here.

Once in place, the MLPA specifies that monitoring of the MPA network must be conducted. An initial baseline assessment of key species and habitats was carried out from 2011–2013 to inform design and development of long-term MPA monitoring for the SCSR. Field-based assessments took place across the entire SCSR, in all major habitats and incorporating key species from invertebrates to birds. This large-scale sampling effort created a novel opportunity to compare patterns in community structure across multiple community types from different marine ecosystems in a very diverse study region.

Lying in a transitional zone between the cold temperate fauna fueled by the California Current to the north and the warm temperate fauna associated with the Southern California Countercurrent flowing from the south (Figure 1; Bograd & Lynn, 2003; Horn & Allen, 1978; Horn, Allen, & Lea, 2006), the Southern California Bight (SCB) is a complex marine biogeographic region with very high biodiversity. The SCB is influenced by a recirculation pattern of the California Current, which flows equatorward into the Bight deflecting slightly offshore at Pt Conception (Bray, Keyes, & Morawitz, 1999; Hickey, 1993). The region is characterized by a shallow, broad continental shelf, deep ocean basins and canyons, and several large offshore islands. Offshore islands contain more high relief rocky habitat, while the mainland coast is dominated by sand, interspersed with generally lower relief rocky reefs (Pondella, Williams et al., 2015). Human activities [e.g., sedimentation and pollution from urban runoff from the Los Angeles and San Diego metropolitan areas (North, 1964; Schiff, 2003; Sikich & James, 2010)] exert a far greater influence on the mainland coast. Key ecological differences among the islands and the mainland (Ebeling, Larsen, & Alevzion, 1980; Pondella & Allen, 2000), as well as environmental gradients from north to south add to the region's biodiversity. For example, the northwestern most Channel Islands (San Miguel, Santa Rosa and San Nicolas Islands) lie at the boundary between the bioregions, with cooler waters, more frequent disturbances, and a mix of San Diegan and Oregonian species (Hamilton, Caselle, Malone, & Carr, 2010; Pondella, Gintert, Cobb, & Allen, 2005). Further south and east, the islands experience warmer waters and less frequent disturbances. These strong gradients in environmental and anthropogenic conditions underlie the observed ecological patterns observed across the SCB.

A number of important biological communities in the SCB are highly spatially structured, including rocky reef fish communities (Hamilton et al., 2010; Pondella et al., 2005), rocky and sandy intertidal invertebrates (Blanchette et al., 2008; Blanchette, Raimondi, &

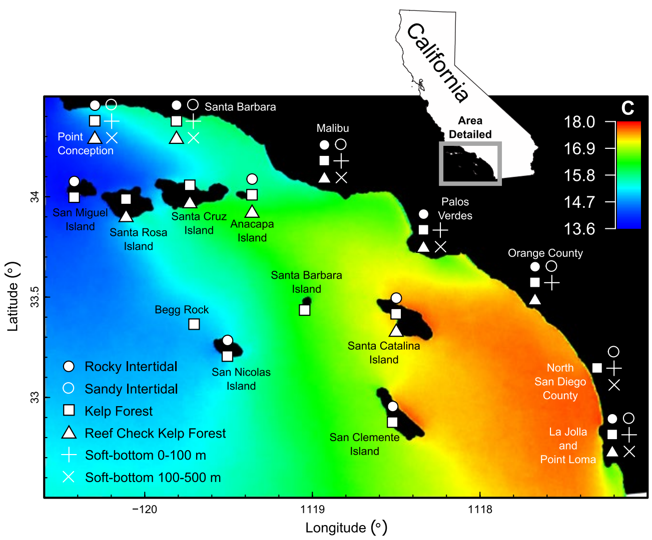

FIGURE 1 Map of available ecosystem-specific data within each of the 16 Regions with mean sea surface temperature (MODIS SST) from 2000–2012. Note that data from each ecosystem were typically available for multiple community types (e.g., invertebrates, fishes; Table 1)

Broitman, 2009; Seapy & Littler, 1980; Wenner, Dugan, & Hubbard, 1993), rocky intertidal algae (Murray & Littler, 1981) and subtidal macro-invertebrate communities (Zahn, Claisse, Williams, Williams, & Pondella, 2016). These spatial patterns have been directly or indirectly related to the strong gradient in sea surface temperature across the region in the majority of studies. Other oceanographic features have also explained some patterns of marine biogeography in the SCB including temperature fronts (Gosnell, Macfarlan, Shears, & Caselle, 2014), wave exposure (Reed et al., 2011) and circulation patterns affecting larval dispersal (Cowen, 1985; Watson et al., 2011). For example, Watson et al. (2011) found that for nearshore subtidal (kelp forest) and rocky intertidal communities, two metrics derived from ocean circulation modeling (oceanographic distance and oceanographic asymmetry) explained patterns of community structure better than thermal structure. While the drivers of community structure in marine ecosystems are likely to be complex, the question remains: do different communities in close proximity respond in the same way to the combined set of environmental and anthropogenic factors that they experience?

Here we investigate whether 12 different "community types" (Table 1) are responding to these overarching drivers in the same way across marine systems in the SCB. Each community type encompasses an assemblage from a different taxonomic group (invertebrates, fishes or algae) residing in one of five marine ecosystems (rocky intertidal, sandy intertidal, subtidal kelp forest, shallow and deep soft-bottom subtidal). We first quantify large-scale spatial patterns of community similarity for each of the 12 different community types individually. We then examine levels of cross-community congruence for each pair of community types. In this context, cross-community congruence refers to patterns of similarity in one community type also being observed in the other community type. For example, do pairs of large areas (i.e., islands, large sections of coastline) that have similar rocky intertidal sessile invertebrate communities also have similar kelp forest fish communities? While these methods have previously been aimed at using one taxon or community to predict patterns at specific sites for other taxonomic groups (e.g., Gioria, Bacaro, & Feehan, 2011; Jackson & Harvey, 1993), this study is intended to provide a broad first look at these patterns over larger spatial scales across multiple different marine ecosystems. While data gathered in this study came from a baseline assessment of an MPA network, we do not explicitly consider protection as a factor here because most MPAs had only been established for 0–3 years during data collection, and within-Region data from sites are pooled across open and protected areas.

2 | MATERIAL AND METHODS

2.1 | Monitoring program dataset descriptions (community type)

Data for our analyses were generated by integrating datasets from five MPA baseline monitoring programs in southern California (Table 2, Figure 1). Because monitoring sites and methods varied among those programs, site data were pooled into 16 geographic "Regions" (i.e., islands or sections of coastline between major submarine canyons) to facilitate comparisons over a large spatial scale.

2.1.1 | Rocky Intertidal (Sessile Algae, Sessile Invertebrates, Mobile Invertebrates)

The abundance of sessile and mobile species was sampled at 44 rocky intertidal sites across 12 Regions (Table 2, Figure 1, Appendix 1) between 2009–2014 using a biodiversity survey protocol (for more details on protocols see Blanchette et al., 2008, 2009). This dataset contained three community types: Sessile Algae (range: 20–81 taxa), Sessile Invertebrates (range: 12–38 taxa), Mobile Invertebrates (range: 21–62 taxa; Table 1). At each site a sampling grid was established. The grid is bound by two permanent 30-m horizontal baselines (parallel to the shoreline), the upper baseline placed in the high zone above the upper limit of marine biota, such as barnacles, while the lower baseline is within the low zone of biota at that site. A series of 11 parallel transect lines at 3-m intervals is then extended perpendicular to the shoreline, vertically between these baselines. Each vertical transect was uniformly divided into approximately 100 sampling points, and all taxa that fell directly under each point were identified using the point intercept method to determine the relative abundance (percent cover) of sessile algae and invertebrates. The abundances of mobile invertebrates were determined in 50 × 50 cm quadrats located randomly in each of three zones: the low zone (the area below the mussels), the mid-zone included the mussels and the rockweeds, and the high zone was dominated by barnacles and littorine snails. The tidal elevations vary widely across the sites depending on site characteristics (e.g., swell, aspect). The lowest points sampled are approximately −2.0 m below mean lower low water (MLLW), and the highest points are approximately 3.0 m above MLLW. Species percent cover (sessile) or densities (mobile) were averaged across transects or quadrats and then across years for each site.

2.1.2 | Sandy Intertidal (Mobile Invertebrates)

The intertidal macroinvertebrate communities on sandy beaches were sampled at 12 sites across six mainland Regions (Table 2, Figure 1, Appendix 2) during daytime spring low tides during fall of 2011 (for more details on protocols see Dugan et al., 2003, 2015; Schooler, Dugan, & Hubbard, 2014). This dataset contained a single community type: Mobile Invertebrates (range: 29–52 taxa; Table 1). At each site, sampling was conducted on three vertical format (shore-normal) transects that extended from the lower edge of terrestrial vegetation or the bluff to the lowest level exposed by swash at the time of low tide. The distances between transects were randomly selected and a 10-m buffer zone was added between transects to minimize disturbance of the mobile fauna in the lower beach in adjacent transects. A series of 150 core samples (0.0078 m^2, 10-cm diameter taken to a depth of 20 cm) was taken at uniform spacing along each transect with the top core corresponding to the lower edge of the terrestrial vegetation or the bluff toe and the lowest core corresponding to the low swash level. For this analysis data were pooled across all cores at each

TABLE 1 Range and count of taxa observed for each community type by Region

Community type	Range	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	Begg Rock	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Point Conception	Santa Barbara	Malibu	Palos Verdes	Orange County	North San Diego County	La Jolla and Point Loma
Rocky Intertidal Sessile Algae	20–81	33			48		53		64	57	20	35	49	41	79	45	81
Rocky Intertidal Sessile Invertebrates	12–38	20			18		27		31	31	12	30	30	27	38	27	31
Rocky Intertidal Mobile Invertebrates	21–62	26			32		40		58	38	21	37	35	45	58	37	62
Sandy Intertidal Invertebrates	29–52										36	52	46		29	40	43
Soft-bottom Invertebrates 0–100 m	11–53										11	43	47	53	49	39	50
Soft-bottom Invertebrates 100–500 m	37–66										46	64	47	39		37	66
Kelp Forest Fishes	7–55	39	39	55	41	7	15	25	40	32	37	47	44	48	33	28	36
Kelp Forest Invertebrates	15–44	39	38	43	34	15	15	33	34	27	32	36	35	44	25	23	31
Reef Check Kelp Forest Fishes	14–27		19	26	24				27		14	24	21	25	19		22
Reef Check Kelp Forest Invertebrates	15–21		17	21	21				19		16	15	17	20	20		17
Soft-bottom Fishes 0–100 m	27–51										28	51	44	27	41	38	39
Soft-bottom Fishes 100–500 m	32–51										45	51	40	44		32	37

TABLE 2 Sampling summary. Number of sites sampled in each of the 16 Regions for each of the six datasets. We also report the mean sea surface temperature (SST) value (°C) for each Region and dataset (average MODIS SST across sites sampled with the Region). Note that datasets may contain more than one community type

	Rocky Intertidal		Sandy Intertidal		Kelp Forest		Reef Check Kelp Forest		Soft-bottom 0–100 m		Soft-bottom 100–500 m	
Years sampled	2009–2014		2011		2011–2012		2011–2013		2013		2013	
Region	Sites	Mean SST	Sites	Mean SST	Sites	Mean SST	Sites	Mean SST	Sites	Mean SST	Sites	Mean SST
San Miguel Island	2	14.05			4	14.05						
Santa Rosa Island					3	14.94	3	15.22				
Santa Cruz Island					10	15.53	6	15.66				
Anacapa Island	2	15.91			4	15.83	5	15.81				
Begg Rock					1	14.98						
San Nicolas Island	3	15.3			1	14.93						
Santa Barbara Island					5	16.44						
Santa Catalina Island	5	17.56			14	17.5	7	17.59				
San Clemente Island	5	16.91			12	17.13						
Point Conception	1	15.21	2	15.46	3	15.14	1	15.6	2	15.34	10	14.54
Santa Barbara	3	15.69	2	15.61	3	15.69	3	15.59	18	15.67	19	15.44
Malibu	6	16.06	2	16.12	5	16.14	3	16.39	19	16.36	8	16.12
Palos Verdes	3	16.85			14	16.89	6	16.91	11	16.96	7	17.01
Orange County	6	17.39	1	17.33	4	17.43	7	17.4	11	17.42		
North San Diego County	2	17.76	3	17.62	5	17.67			8	17.62	6	17.69
La Jolla and Point Loma	6	17.3	2	17.77	6	17.37	5	17.5	9	17.21	9	17.58

site, yielding a total sampling area of 3.5 m^2. Sediments were removed from the core samples by sieving in a mesh bag with an aperture of 1.5 mm in the swash zone. All animals retained on the sieves were identified and enumerated. Means of abundance of all beach macroinvertebrates were calculated and then expressed as numbers/m of shoreline (a vertical meter-wide strip of intertidal beach) based on the core interval for each transect as suggested by Brown and McLachlan (1990).

2.1.3 | Kelp Forest (Fishes, Invertebrates)

Fish and invertebrate assemblages were sampled annually in summer or fall of 2011 and 2012 using standard underwater visual belt survey methods (for more details on the protocol see Caselle, Rassweiler, Hamilton, & Warner, 2015; Hamilton et al., 2010; Pondella, Caselle et al., 2015; Zahn et al., 2016). Ninety-four sites were sampled across all 16 Regions (Table 2, Figure 1, Appendix 3). This dataset contained two community types: Fishes (range: seven–55 taxa), Invertebrates (range: 15–44 taxa; Table 1). Each site consists of approximately 250 m of coastline. At each site, eight to 16 fish transects were conducted that measured 30 × 2 × 2 m at multiple levels in the water column: benthic, midwater, and kelp canopy (when present). At each level in the water column, one SCUBA diver per transect counted and estimated the total length of all fish, excluding small cryptic fishes. Transects are laid out across a site in a stratified random design, with multiple non-permanent transects located in fixed strata (i.e., deep, outer, middle and inner edges of the reef) to ensure surveys capture variation in species occurrence across these gradients. Pelagic species and highly mobile species not characteristic of kelp forest systems (e.g., northern anchovy [*Engraulis mordax*], Pacific barracuda [*Sphyraena argentea*]) were excluded from the dataset. The abundance of conspicuous (≥2.5 cm) mobile and sessile macroinvertebrates was quantified along 30 × 2 m benthic transects, with typically six to eight transects per site per year. Smaller invertebrates (<2.5 cm) as well as encrusting and colonial species such as tunicates, bryozoans and most sponges were not recorded in this method and are not included here. Species densities were averaged across transects and then across years for each site.

2.1.4 | Reef Check Kelp Forest (Fishes, Invertebrates)

Fish and invertebrate assemblages were sampled by Reef Check California staff and volunteers (citizen scientists) annually in summer or fall of 2011 and 2012 using standard underwater visual belt survey methods (for more details on the protocol and species list see Freiwald & Wisniewski, 2015; Gillett et al., 2012). Reef Check California is a program of the Reef Check Foundation, a 501(c)3 non-profit developed with the goal of involving the public in the scientific monitoring of California's rocky reefs and kelp forests to inform marine resource management. Forty-six sites were sampled across 10 Regions (Table 2, Figure 1, Appendix 4). This dataset contained two community types: Fishes (range: 14–27 taxa), Invertebrates (range: 15–21 taxa; Table 1). Each site consists of approximately 250 m of coastline. At each site, 18 fish transects were conducted that measured 30 × 2 × 2 m along the bottom. At each transect, a SCUBA diver counted and estimated the total length of 35 fish species in three size categories. Exact locations for transects were chosen at random, but potential locations are stratified in space and between two depth zones to ensure even coverage of the reef. The abundance of 33 conspicuous (≥2.5 cm) mobile and sessile macroinvertebrates were quantified along 30 × 2 m benthic transects at six transects per site per year. The six invertebrate transects were co-located with six of the fish transects, with the additional 12 fish-only transects also being performed in the vicinity. The invertebrate species identified and counted do not include smaller (<2.5 cm) mobile, encrusting or colonial invertebrate species such as tunicates, bryozoans and most sponges. Species densities were averaged across transects and then across years for each site.

2.1.5 | Soft-bottom (Invertebrates 1–100 m, Invertebrates 100–500 m, Fishes 1–100 m, Fishes 100–500 m)

Fish and invertebrate assemblages were sampled from July through September 2013. Samples were collected with 7.6 m head-rope semi-balloon otter trawls with 1.25 cm cod-end mesh (for more details on the protocol see Allen et al., 2011; Williams, Pondella, & Schiff, 2015). One hundred and thirty-seven sites were sampled across seven mainland Regions (Table 2, Figure 1, Appendices 5, 6). This dataset contained four community types: Invertebrates 1–100 m (range: 11–53 taxa), Invertebrates 100–500 m (range: 37–66 taxa), Fishes 1–100 m (range: 27–51 taxa), Fishes 100–500 m (range: 32–51 taxa; Table 1). These shelf zones (depth ranges) are bathymetric life zone divisions of the continental shelf and slope along the west coast of North America (Allen, 2006; Allen & Smith, 1988; Williams et al., 2015). Each site consists of a single co-ordinate selected by a stratified random sampling design and categorized by depth (1–100 or 100–500 m). At each site, a trawl net was towed along isobaths for 10 min at 0.8–1.0 m/s covering an estimated distance of 600 m. All fish and megabenthic invertebrates from assemblage trawls were identified and enumerated. Megabenthic invertebrates were defined as epibenthic species with a minimum dimension of 1 cm; specimens <1 cm were excluded from the analysis. Other invertebrates excluded were pelagic, infauna or small species that are better sampled by other methods. Infaunal, pelagic and colonial species, as well as unattached fish parasites (e.g., leeches, cymothoid isopods) were not processed. Fish and invertebrates were identified to species and all individuals were counted.

2.2 | Data analysis

2.2.1 | Individual community type patterns

We first quantified spatial patterns of community similarity for each of 12 different community types individually at the Region scale.

For each community type separate analyses were performed using a similarity matrix constructed with transformed taxon-specific values and the Bray–Curtis similarity co-efficient. With monitoring programs sampling at different sites, site means were averaged across years, then across sites within each Region to facilitate eventual comparisons among geographic Regions between community types (Table 2, Figure 1). Taxa densities were square-root transformed, and Sandy Intertidal Invertebrates was fourth-root transformed. A relatively weak square-root transformation was chosen for most data sets in order to emphasize the numerically dominant taxa in defining patterns of community similarity, and limit the influence of rare taxa, which would be more sensitive to unbalanced levels of sampling effort among Regions. A stronger transformation was chosen for the Sandy Intertidal Invertebrate dataset, which was scaled differently, i.e., abundance/m of coastline, and contained relatively extreme single-species abundance values that would have otherwise overly influenced the results. We used two-dimensional (2d), non-metric multidimensional scaling (nMDS) to examine patterns of community similarity among Regions using the “metaMDS” function in the “vegan” package (Oksanen et al., 2013) in R (R Core Team, 2015). Different shapes were used for island and mainland Regions on nMDS plots to visualize these general habitat differences. To provide an environmental context to the observed relationships among Regions, patterns of sea surface temperature (SST) were also visualized across the nMDS plots using the “ordisurf” function in the R package “vegan” (Oksanen et al., 2013; function defaults used), which fits a smooth surface using generalized additive modeling with thin plate splines (Oksanen et al., 2013; Wood, 2003). Long-term averages of SST for all sites was obtained from merged MODIS 1-km resolution data from MODIS-Aqua and MODIS-Terra composited over 15-day intervals by the California Current Ecosystem Long-term Ecological Research program based at Scripps Institution of Oceanography (available from: http://spg.ucsd.edu/Satellite_data/California_Current/). Due to inconsistencies with the availability of 1-km cell values close to shore, values were averaged for each 15-day layer across cells within 4 km of the point locations for a given site. These values were then averaged across the entire period available from 24 February 2000 through 31 December 2012 and Region-specific values were obtained for each community type by averaging across all sites sampled within each Region (Figure 1, Table 2).

We also investigated spatial and environmental relationships of regional community similarity for each community type individually using Mantel tests (Legendre & Legendre, 1998). We examined the correlation between the matrices of community similarity and geographic distances among Regions or differences in SST among Regions using the “mantel” function in the R “vegan” package (Oksanen et al., 2013). Geographic distance and SST are correlated at this scale (Figure 1; Blanchette et al., 2009; Zahn et al., 2016), but due to low sample size of Regions for many community types, we did not run Partial Mantel tests (Legendre & Legendre, 1998) in an attempt to quantify the correlation with each variable separately after the effect of the other variable has been removed (e.g., Blanchette et al., 2009).

2.2.2 | Pairwise community congruence

We also investigated the level of community congruence between all pairwise combinations of community types. In this context community congruence refers to patterns of community similarity among Regions in one community type also being observed in the other community type. These pairwise analyses necessitate datasets being reduced to Regions both community types have in common. We used two somewhat similar analyses to quantify these relationships. Mantel tests were used to test for correlations between the similarity matrices (Gioria et al., 2011; Su, Debinski, Jakubauskas, & Kindscher, 2004) using the “mantel” function in the R “vegan” package (Oksanen et al., 2013). We then used PROTEST, i.e., Procrustean analysis of congruence (Gioria et al., 2011), using the “protest” function in the R “vegan” package (Oksanen et al., 2013). The Procrustes test or PROTEST is an alternative to Mantel tests that uses reduced space (i.e., the 2d nMDS ordinations) instead of the complete dissimilarity matrices. PROTEST uses a rotational-fit algorithm to minimize the total sum-of-squared residuals between the two ordinations and runs a permutation test of the significance of the correlation. Note that the PROTEST correlation statistics will be greater than the Mantel statistics because dimensionality and noise is reduced in the 2d ordination space compared to the original dissimilarity matrix. Gioria et al. (2011) suggest using multiple methods when investigating cross-taxa relationships given the advantages and drawbacks with each method, and this seems particularly applicable for this study given the differences between each dataset (e.g., sampling frameworks, site selection) and our goal to examine large-scale general patterns.

3 | RESULTS

3.1 | Individual community types

Our investigation of spatial and environmental relationships of regional community similarity for each individual community type revealed robust patterns. For the majority of community types in this study, Regions tended to be more similar that were geographically closer together (i.e., spatial autocorrelation) or had similar SSTs (significant Mantel tests, Table 3). This included all of the fish community types, with the exception of Reef Check Kelp Forest Fishes, and the communities of Rocky Intertidal Sessile Algae, Sandy Intertidal Invertebrates, Soft-bottom Invertebrates 100–500 m and Kelp Forest Invertebrates (Table 3). For these community types, these patterns were also well represented visually in the 2d ordination space of the nMDS plots (Figures 2 and 3), where the pattern of points (Regions) on the nMDS plots appears similar to that of the points on the map legend, and the SST surfaces fitted to those points exhibit clear gradients (i.e., parallel lines that span a relatively large range of temperatures). In individual cases where Mantel tests were not significant, examination of their nMDS plots was informative. For example, the regional community similarities of Rocky Intertidal Mobile and Sessile Invertebrates were not significantly related to SST (Figure 2b,c). This was due to communities in some Regions being more different than

TABLE 3 Mantel tests to examine the correlations between taxonomic group community dissimilarity and geographic distance or between taxonomic group community dissimilarity and differences in long-term mean sea surface temperature (SST) among Regions

Community type	Distance	SST
Rocky Intertidal Sessile Algae	0.66**	0.66**
Rocky Intertidal Sessile Invertebrates	0.43**	0.19
Rocky Intertidal Mobile Invertebrates	0.35*	0.09
Sandy Intertidal Invertebrates	0.70**	0.70**
Soft-bottom Invertebrates 0–100 m	0.29	0.17
Soft-bottom Invertebrates 100–500 m	0.71*	0.75*
Kelp Forest Fishes	0.36*	0.45**
Kelp Forest Invertebrates	0.54**	0.61**
Reef Check Kelp Forest Fishes	0.23	0.2
Reef Check Kelp Forest Invertebrates	0.36	0.41*
Soft-bottom Fishes 0–100 m	0.45*	0.53*
Soft-bottom Fishes 100–500 m	0.66**	0.56*

Mantel *r* statistic value is reported and statistically significant values are indicated by *($p < .05$) and **($p < .005$). Note that because dissimilarity is used, positive *r* values indicate communities are more different as the difference in geographic distance or SST between Regions increases.

their associated differences in SST. In their nMDS plots (Figure 2b,c) the points for the Point Conception and Santa Barbara Regions were relatively far from the points for Anacapa Island and San Nicolas Island, while they had similar SST values (Table 2). Additionally, the points for the La Jolla/Point Loma and North San Diego County Regions (Figure 2b,c) were also relatively far from each other while their SST values were similar (Table 2). Finally, for all community types that included both island and mainland Regions (i.e., those from the rocky Intertidal and kelp forest datasets), clear separation in regional communities was observed between these habitat types in the nMDS plots (Figures 2 and 3), with the exception of Reef Check Kelp Forest Fishes where island points surrounded mainland points (Figure 3c).

3.2 | Pairwise community congruence

Next we investigated the level of cross-community congruence between all pairwise combinations of community types. Community congruence refers to patterns of similarity between Regions in one community type also being observed in the other community type. We used two similar analyses of congruence, Mantel tests and PROTEST with each pairwise combination of two community types. These patterns can also be observed by visually comparing pairs of nMDS plots (Figures 2 and 3). Rocky Intertidal Sessile Algae, the only non-animal community type, exhibited significant pairwise relationships with almost all other community types (Table 4). There were, however, relatively few significant relationships between pairs of community types that included a fish community and an invertebrate community. Typically neither, or in some cases only one, of the two tests were significant. Only two of these community type pairings had both the Mantel and PROTEST tests significant: Kelp Forest Fishes and Kelp Forest Invertebrates, and Reef Check Kelp Forest Fishes and Rocky Intertidal Mobile Invertebrates (Table 4).

The patterns of community similarity among Regions for pairs of invertebrate community types typically exhibited significant congruence. For example, Rocky and Sandy Intertidal invertebrate community types had significant pairwise relationships with each other in almost all cases (Table 4). Significant relationships were also observed between the communities of Sandy Intertidal Invertebrates and the shallow Soft-bottom Invertebrates 0–100 m, both community types which only occur along the mainland (Figure 2b,d). However, there were some notable examples of non-congruence. None of the spatial patterns observed in the rocky intertidal or subtidal (kelp forest) invertebrate communities were significantly related to the spatial patterns in the communities of shallow Soft-bottom Invertebrates 0–100 m. Major contributors to this lack of congruence appear to include the relatively large differences between the communities in two pairs of adjacent Regions in the Soft-bottom Invertebrates 0–100 m that were more similar in the rocky habitat communities, i.e., Point Conception and Santa Barbara, and Orange County and North San Diego County (pattern visually apparent in Figure 2e; relatively large PROTEST residual for one Region in the pair). This lack of geographic community structure for Soft-bottom Invertebrates 0–100 m was also evident in the non-significant correlation with geographic distance (Table 3). The patterns of similarity among Regions for the deeper Soft-bottom Invertebrates 100–500 m had significant correlations with those patterns in shallow Soft-bottom Invertebrates 0–100 m and all of the Rocky Intertidal community types (Table 4).

Kelp forest invertebrate communities (including Reef Check) exhibited congruence with patterns among Regions in Rocky Intertidal Sessile Invertebrates, but did not yield significant congruence with the communities of mobile invertebrates found in the rocky or sandy intertidal, or with either of the shallower or deeper soft-bottom invertebrate communities (Table 4). In both kelp forest datasets, the invertebrate communities found in the two Regions farthest apart geographically, Point Conception and La Jolla/Point Loma, were relatively more similar to each other (Figure 3b,d) compared to the intertidal and soft-bottom invertebrate community types where these Regions tend to have the least similar communities (Figure 2c–f). Additionally, the warmer islands (Santa Catalina and San Clemente) tended to have very different kelp forest invertebrate communities than the colder northern islands, while they were not as different in the communities of Rocky intertidal Mobile Invertebrates.

Similar patterns across Regions were observed among fish communities in shallow water habitats. There were significant pairwise relationships among Kelp Forest Fishes and Soft-bottom Fishes 0–100 m, including Kelp Forest Fishes (sampled by professional academic researchers) and Reef Check Kelp Forest Fishes (sampled by trained

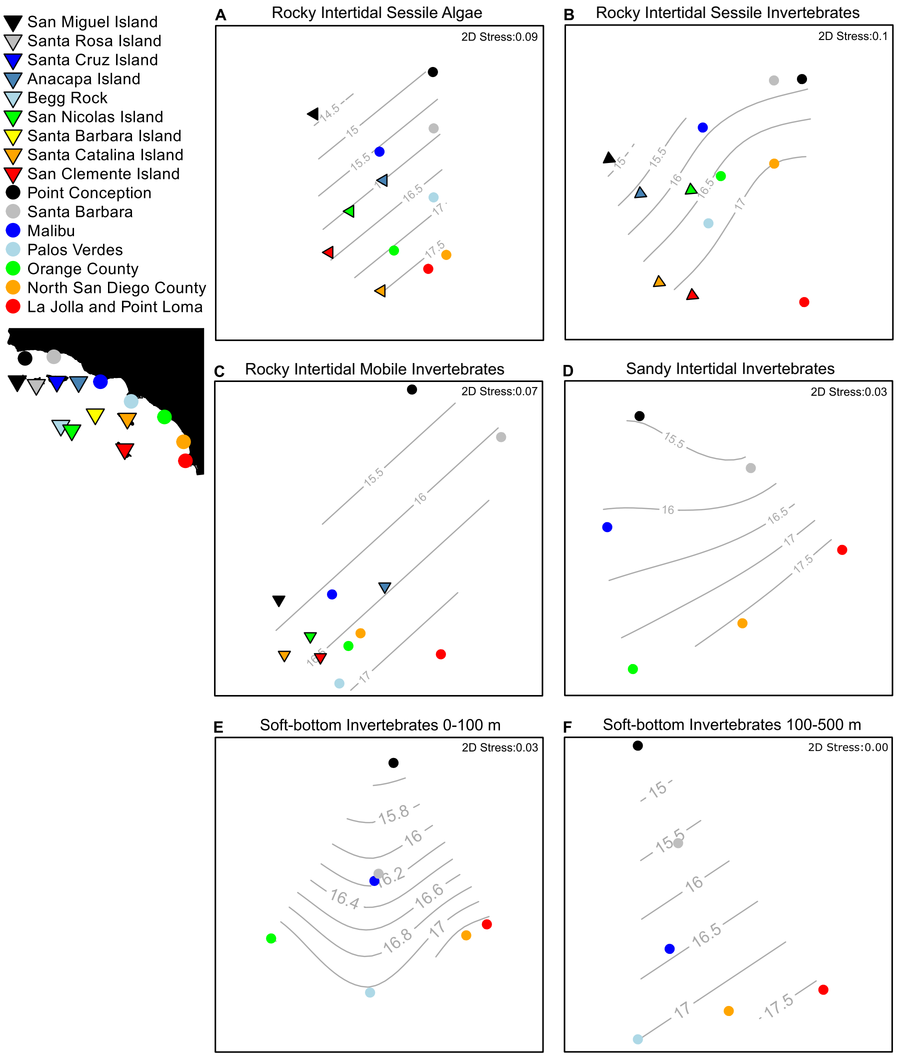

FIGURE 2 Non-metric multidimensional ordination plot for each community type using Bray–Curtis similarity based on the square-root transformed species density or percent cover (exception: Sandy Intertidal Invertebrates were fourth-root transformed) for each of the Regions where data were available overlaid on a fitted sea surface temperature surface (gray contour lines; °C)

citizens; Table 4). However, the communities of deeper Soft-bottom Fishes 100–500 m did not have significant correlations with the spatial community patterns in shallow soft-bottom or kelp forest fishes sampled by either group. A major contributor to this lack of congruence appears to be that for Soft-bottom Fishes 100–500 m, two Regions adjacent in space, North San Diego County and La Jolla/Point Loma, had the most distinct communities (pattern visually apparent in Figure 3f; relatively large PROTEST residuals for one Region in the pair).

4 | DISCUSSION

Our results illustrate how integrating biogeographic data from multiple baseline monitoring efforts can reveal novel patterns at larger spatial and taxonomic scales than would otherwise be possible. Our analyses of large-scale patterns of biotic community similarity across different taxonomic groups from very different marine ecosystems provide insight into regional processes and environments. As expected, for the majority of individual community types, pairs of Regions (islands or sections of coastline between major submarine canyons) tended to have more similar communities when they were geographically close (i.e., spatially autocorrelated) or more environmentally (i.e., mean SST) similar to one another. However, this did not result in all pairs of the community types exhibiting high levels of cross-community congruence.

The patterns observed may be indicative of the relative importance of bottom-up and top-down forces in structuring spatial patterns for different community types. The high levels of congruence of Rocky Intertidal Sessile Algae communities with almost all of the other (fish or invertebrate) community types were not surprising. As primary producers, sessile algae thrive in cold nutrient-rich water, and they are often the key taxa defining regions of biogeographic similarity (Blanchette et al., 2009). The local abundances of various algal species are highly influenced by bottom-up factors, including differences

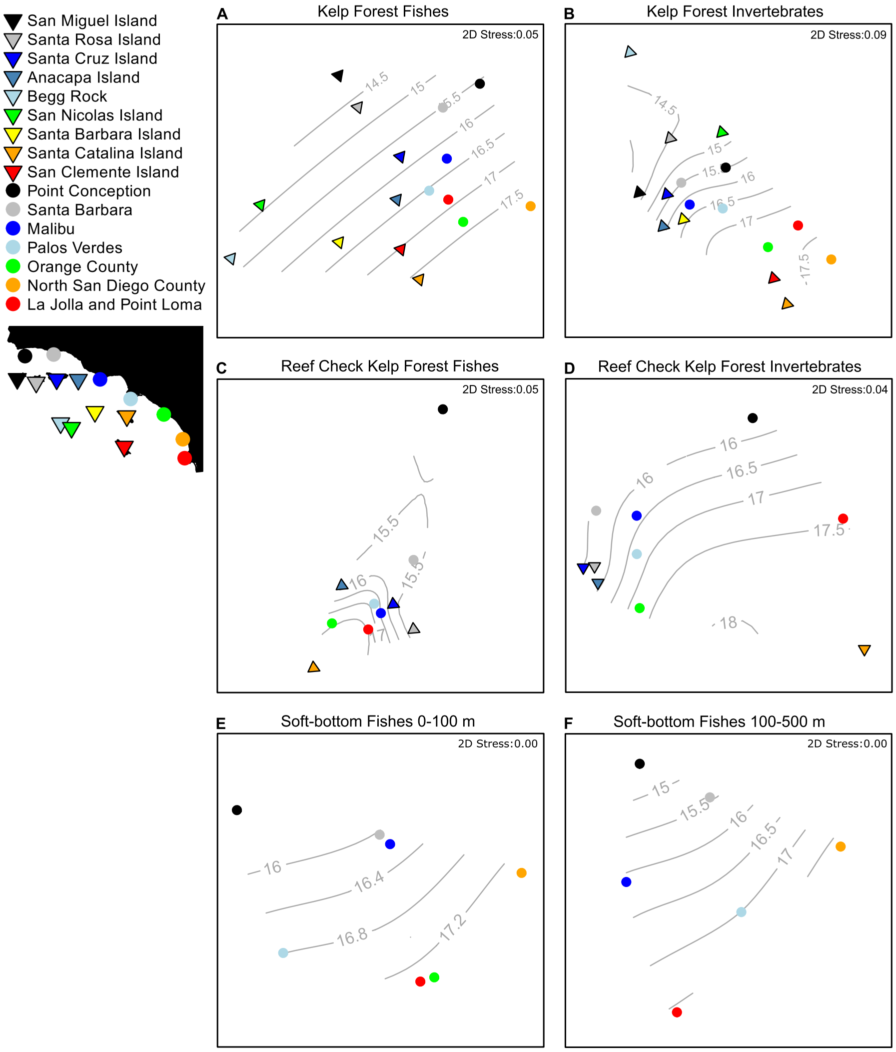

FIGURE 3 Non-metric multidimensional ordination plot for each community type using Bray–Curtis similarity based on the square-root transformed species density data for each of the Regions where data were available overlaid on a fitted sea surface temperature surface (gray contour lines; °C)

in water temperature and nutrients (Barry, Baxter, Sagarin, & Gilman, 1995; Schiel, Steinbeck, & Foster, 2004). Algae and drift macrophytes are also important as food and habitat for marine invertebrates and fishes (e.g., Dugan, Hubbard, McCrary, & Pierson, 2003; Graham, 2004; Schiel et al., 2004). Strong associations between these algae and consumers would likely contribute to the significant pairwise correlations between their spatial patterns of community similarity.

In contrast, there were relatively few significant relationships between pairs of community types that included a fish community and an invertebrate community, with the primary exception being kelp forest fishes and invertebrates. These invertebrate and fish community types are generally comprised of assemblages of higher trophic level species (Blanchette et al., 2015; Pondella, Caselle et al., 2015), for which additional ecological and species interaction factors operate, including direct human interactions via fishing (Dayton, Tegner, Edwards, & Riser, 1998) and intensive coastal development and management (e.g., Dugan et al., 2003; Dugan, Hubbard, Rodil, Revell, & Schroeter, 2008). These factors may have altered patterns of community similarity and resulted in the reduced level of congruence observed between spatial patterns in those assemblages of higher level and, in some cases, human exploited or impacted taxa (Jackson & Harvey, 1993; Rooney & Bayley, 2012).

Pairs of invertebrate community types also tended to exhibit similar spatial patterns. This included pairs of Rocky and Sandy Intertidal Invertebrate communities, and the Sandy Intertidal Invertebrates with the shallow Soft-bottom Invertebrates 0–100 m. An exception was that the shallow Soft-bottom Invertebrate 0–100 m community was not significantly correlated with Rocky Intertidal or with Kelp Forest Invertebrate communities. This result appears to be due to a lack of geographic community structure in the shallow Soft-bottom Invertebrates 0–100 m (Table 3), where pairs of Regions adjacent in space had relatively low community similarity (Figure 2e). Notably, the soft-bottom datasets (Sandy Intertidal, 0–100 m, and 100–500 m) were based on relatively fewer Regions (six or seven; Table 2) than

TABLE 4 Mantel and PROTEST pairwise community correlation results among Regions

	Test	Rocky Intertidal Sessile Algae	Rocky Intertidal Sessile Invertebrates	Rocky Intertidal Mobile Invertebrates	Sandy Intertidal Invertebrates	Soft-bottom Invertebrates 0–100 m	Soft-bottom Invertebrates 100–500 m	Kelp Forest Fishes	Kelp Forest Invertebrates	Reef Check Kelp Forest Fishes	Reef Check Kelp Forest Invertebrates	Soft-bottom Fishes 0–100 m
Rocky Intertidal Sessile Invertebrates	Mantel	0.54**										
	PROTEST	0.80**										
Rocky Intertidal Mobile Invertebrates	Mantel	0.50**	0.61**									
	PROTEST	0.76**	0.77**									
Sandy Intertidal Invertebrates	Mantel	0.59*	0.51**	0.57*								
	PROTEST	0.75	0.82	0.88*								
Soft-bottom Invertebrates 0–100 m	Mantel	0.31	0.28	0.17	0.56**							
	PROTEST	0.67	0.62	0.66	0.92*							
Soft-bottom Invertebrates 100–500 m	Mantel	0.69**	0.61*	0.84**	0.42	0.60*						
	PROTEST	0.93**	0.80*	0.93**	0.86	0.92**						
Kelp Forest Fishes	Mantel	0.49**	0.22	0.1	0.29	0.14	0.44					
	PROTEST	0.83**	0.70*	0.60*	0.63	0.74*	0.57					
Kelp Forest Invertebrates	Mantel	0.59**	0.27*	0.07	0.44	0.02	0.17	0.62**				
	PROTEST	0.73**	0.65*	0.41	0.76	0.56	0.74	0.58*				
Reef Check Kelp Forest Fishes	Mantel	0.61**	0.4	0.67*	−0.1	0.29	0.79*	0.77**	0.41*			
	PROTEST	0.86**	0.78**	0.82*	0.64	0.72*	0.72	0.85**	0.5			
Reef Check Kelp Forest Invertebrates	Mantel	0.50*	0.43*	0.2	0.02	0.39	0.31	0.38	0.71**	0.51*		
	PROTEST	0.64	0.69	0.42	0.73	0.65	0.48	0.59	0.84**	0.53		
Soft-bottom Fishes 0–100 m	Mantel	0.45*	0.19	0.34	0.1	0.33	0.38	0.56*	0.26	0.76*	0.09	
	PROTEST	0.81**	0.7	0.6	0.53	0.53	0.48	0.76*	0.73	0.96	0.63	
Soft-bottom Fishes 100–500 m	Mantel	0.60*	0.60*	0.15	0.24	0.14	0.37	0.42	0.56*	0.41	0.43	0.12
	PROTEST	0.73	0.71	0.59	0.58	0.54	0.71	0.74	0.62	0.79	0.6	0.67

Pairwise Mantel r statistic value and PROTEST m^2 statistic are reported and statistically significant values are indicated by *($p < .05$) and **($p < .005$) and in bold text. Increasing r and m^2 values indicate that the same patterns of similarity between Regions in one community type are also observed in the other community type.

other community types. Analyses of pairwise cross-community congruence can only include Regions that both community types have in common, and the relative influence of any difference in a pair of Regions becomes magnified with smaller sample sizes.

A second exception in patterns involving pairs of invertebrate community types was that spatial patterns in the kelp forest invertebrate communities, from both the dataset collected by professional academic researchers (PAR) and the dataset that included a reduced set of taxa collected by Reef Check trained citizens (RCCA), were not similar to the patterns in any of the other mobile invertebrate communities (i.e., rocky and sandy intertidal, and the shallow and deeper soft-bottom subtidal; Table 4). This lack of congruence appears to be driven by relatively high similarity of kelp forest invertebrate communities found in the two Regions that were farthest apart geographically (Point Conception and La Jolla/Point Loma). This similarity despite geographic distance might be related to similarity in their benthic habitat characteristics. Both of these Regions have relatively flat (low relief) cobble or bedrock reefs, compared with the more high relief reefs found at the outer islands and other mainland regions such as Palos Verdes (Pondella, Williams et al., 2015).

Spatial patterns in fish community similarity were congruent across shallow habitats between the kelp forest (both PAR and RCCA) and shallow Soft-bottom 0–100 m communities. However, the community of deeper Soft-bottom Fishes 100–500 m was not significantly correlated with any of the other fish communities. Again, this is not surprising given the environmental differences between the shallow and deeper marine ecosystems, with seasonal variability in temperature, salinity, productivity and turbulence declining with depth (Allen, 2006). Generally, soft-bottom fish species distributions and the associated species assemblages are highly depth stratified (Allen, 2006; Allen & Smith, 1988; Williams et al., 2015). In our analyses, Soft-bottom Fishes 100–500 m in North San Diego County and La Jolla/Point Loma had the most distinct communities despite being adjacent to each other, and this appears to be a major contributor to the lack of congruence overall (Figure 3). A sampling issue, also relating to depth stratification, likely contributed to this difference, with more trawls coming from the shallower or deeper ends of the depth range in these two Regions, respectively. This difference was further magnified by the relatively low number of Regions sampled for these fishes.

This study also gave us an opportunity to compare invertebrate and fish communities in kelp forest ecosystems collected by two methods, by PAR and by RCCA. Citizen science, also called public participation in scientific research is growing in popularity in the US and Europe and has the potential for expanding scientific data both spatially and temporally (Foster-Smith & Evans, 2003; Schmeller et al., 2009; see Freiwald et al. this issue). However, rigorous comparisons are necessary in order to validate the quality of data collected by non-scientists. Gillett et al. (2012) compared fish, invertebrate and habitat data from the same two kelp forest monitoring programs based on a smaller subset of southern California reefs in 2008. In that study, both fish and invertebrate community structure exhibited generally similar spatial patterns, although the less detailed taxonomic resolution used by RCCA resulted in differences in relative abundance. Physical habitat as measured by the divers (not compared here) was very different across the two programs.

The RCCA kelp forest monitoring program targets a reduced number of taxa [maximum taxa observed: 55 (PAR) to 27 (RCCA) for fishes, and 44 (PAR) to 21 (RCCA) for invertebrates]. The reduced list of target species in the RCCA protocol (i.e., 35 fish species, 33 invertebrate taxa) likely contributes to the lack of differentiation among regions seen in the RCCA fish data (Figure 3c), as compared to the PAR data (Figure 3a). The Point Conception Region fish community in particular appears to drive this pattern and it had the fewest taxa observed (14) of any Region in the RCCA dataset. This Region was only represented by one site (Refugio State Beach) in the RCCA data set (Appendix 4) and therefore lower sampling effort probably also reduced the number of species observed. There was also a lack of significant correlation with geographic distance and SST for the RCCA fish data (Table 3). This might be driven by the selection of species counted by RCCA. For this statewide monitoring program, species were selected that are likely to be found in many geographic regions potentially reducing the ability to identify region-specific assemblages. However, even with the reduced level of taxonomic breadth, it was reassuring to find a high level of congruence between spatial patterns in the kelp forest community types collected with the different methods. This provided additional general support that the patterns observed across the community types were not an artefact of the differences in methodology, but are reflective of the biogeographic patterns. Comparisons such as these can inform the extent to which taxonomic coverage of the species assemblages is required to delineate biogeographic patterns, and ultimately may help to design long-term monitoring protocols and programs. It also highlights the need for clear objectives (e.g., informing marine resource management, detecting biogeographic patterns, characterizing species assemblages or diversity) of monitoring programs as the targeted taxa may affect the conclusions that can be drawn from the monitoring data.

Our analyses of spatial patterns for individual community types were consistent with those described in previous studies of many of the same taxonomic groups in the SCB. Primarily, (i) Regions that were geographically closer together or had similar SSTs tended to be more similar and (ii) there was clear separation between the communities found on the mainland and the offshore islands (see summary in the Introduction for citations). A notable difference in our study was that data were pooled across sites within Regions to facilitate comparisons between community types. In some previous studies (Blanchette et al., 2009; Zahn et al., 2016) community similarity was found to have stronger correlation with mean SST than with geographic distance compared to what was observed here. This difference was likely due to the coarser spatial resolution of our data with sites averaged within Regions. In particular, there are relatively large differences in mean SST on opposite sides of each of the offshore islands (Figure 1), a characteristic that is lost when averaging data from sites on both sides of an island. Monitoring site coordination in future studies or monitoring programs could help resolve this issue (e.g., Gioria et al., 2011; Jackson & Harvey, 1993). The relative impact of other oceanographic features (e.g., temperature fronts, wave exposure, circulation patterns affecting larval dispersal) on various community types in these different ecosystems remains to be examined more closely.

Our study provides a broad view of patterns of community congruence across different marine ecosystems over a large spatial scale. This is in contrast to typical studies examining cross-taxa congruence that are often focused on identifying biodiversity surrogates or bioindicators for a specific ecosystem. The goal of these studies is often to find ways to effectively monitor ecosystems with a limited budget. Surrogates may be individual species or communities that can be monitored relatively easily and provide insights into the state of other populations and communities at a specific site or the overall environmental conditions of the local system (Gioria et al., 2011; Rooney & Bayley, 2012; Su et al., 2004). Our study indicates that intertidal sessile algal communities exhibit high levels of congruence with other fish and invertebrate community types. For this reason, it will be important to include these algal communities in long-term monitoring programs, as changes in algal assemblages will likely influence invertebrate and fish communities and may be indicative of impacts from climate change (Barry et al., 1995; Schiel et al., 2004). However, because fish and invertebrate communities do not exhibit high levels of congruence, they may be responding differently to changes in oceanographic regimes or large-scale management actions as a result of additional ecological interactions at these higher trophic levels. A previous study examining community congruence in assemblages of wetland plants, invertebrates, and birds found that congruence was lower in sites more impacted by humans (Rooney & Bayley, 2012). A similar hypothesis could be tested in marine ecosystems where an increased level of cross-community congruence might be observed with in MPAs as communities recover from the impacts of fishing, compared with those outside of MPAs that remain open to fishing. Testing this hypothesis will require long-term monitoring data to be obtained from multiple community types at a sufficient number of well-coordinated sites inside and outside MPAs over sufficient time spans to allow impacted populations to recover.

ACKNOWLEDGEMENTS

A dedicated Integrative Baseline Project within the SCSR provided an opportunity to make use of the SCSR MPA baseline monitoring data and a framework for developing synthesis products based on collaborations across projects. This and the other MPA baseline data collection projects were funded by MPA Grants via California Sea Grant through the California Marine Protected Areas Baseline Program. We would like to thank all organizations and everyone (particularly students and volunteers) involved in funding, collecting, entering, processing and managing the South Coast MPA Baseline and Bight '13 data for the projects involved in this study. We would also like to thank the following organizations for their funding and/or support of these monitoring programs: the Southern California Coastal Water Research Project for support of the 2013 Bight Program, an integrated, collaborative regional monitoring program (sccwrp.org); National Science Foundation-Santa Barbara Coastal Long Term Ecological Research (Award Nos OCE-9982105, OCE-0620276, OCE-1232779); PISCO (Partnership for Interdisciplinary Studies of Coastal Oceans) funded by the David and Lucille Packard Foundation; University of Southern California (USC) Sea Grant under grant no. 10-069 issued by the California Coastal Conservancy; National Oceanic and Atmospheric Administration (NOAA) Restoration Center and the Montrose Settlements Restoration Program; United States Navy Commander, US Pacific Fleet (additional support and facilitation were provided by Naval Facilities Engineering Command Southwest, the findings and conclusions in this paper reflect those of the authors and do not necessarily represent the views of the US Navy); California Ocean Science Trust; MPA Monitoring Enterprise; California Department of Fish & Wildlife; California Ocean Protection Council; The Bay Foundation; Resources Legacy Fund Foundation; the Keith Campbell Foundation for the Environment; the Lisa and Douglas Goldman Foundation; the State Coastal Conservancy; the Annenberg Foundation; the University of California, Santa Barbara (UCSB) Associated Students Coastal Fund.

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How to cite this article: Claisse JT, Blanchette CA, Dugan JE, et al. Biogeographic patterns of communities across diverse marine ecosystems in southern California. *Mar Ecol*. 2018;39:e12453. https://doi.org/10.1111/maec.12453

APPENDIX 1

Sites Sampled for the Rocky Intertidal Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Anacapa Island	S Frenchys Cove	34.00655	−119.41104	Palos Verdes	Point Vicente	33.74101	−118.40947
Anacapa Island	Middle West	34.00584	−119.39643	Palos Verdes	Abalone Cove	33.73778	−118.37612
La Jolla and Point Loma	La Jolla Caves	32.84861	−117.26535	Palos Verdes	Point Fermin	33.70679	−118.28614
La Jolla and Point Loma	Wind and Sea	32.83285	−117.28231	Point Conception	Alegria	34.46714	−120.27818
La Jolla and Point Loma	Sea Ridge	32.80799	−117.26793	San Clemente Island	Graduation Point	33.03327	−118.57560
La Jolla and Point Loma	Navy North	32.69278	−117.25306	San Clemente Island	North Head	33.03287	−118.60057
La Jolla and Point Loma	Cabrillo 1	32.66943	−117.24541	San Clemente Island	West Cove	33.01477	−118.60613
La Jolla and Point Loma	Cabrillo 3	32.66490	−117.24282	San Clemente Island	Boy Scout Camp	33.00112	−118.54832
Malibu	Old Stairs	34.06622	−118.99810	San Clemente Island	Eel Point	32.91801	−118.54668
Malibu	Deer Creek	34.06069	−118.98221	San Miguel Island	Cuyler Harbor	34.04861	−120.33642
Malibu	Sequit Point	34.04323	−118.93700	San Miguel Island	Crook Point	34.02207	−120.37924
Malibu	Lechuza Point	34.03446	−118.86179	San Nicolas Island	Thousand Springs	33.28491	−119.52972
Malibu	Paradise Cove	34.01200	−118.79214	San Nicolas Island	Tranquility Beach	33.26567	−119.49210
Malibu	Point Dume	34.00036	−118.80703	San Nicolas Island	Marker Poles	33.21870	−119.49575
North San Diego County	Cardiff Reef	32.99984	−117.27867	Santa Barbara	Ellwood	34.43519	−119.93078
North San Diego County	Scripps	32.87140	−117.25321	Santa Barbara	Coal Oil Point	34.40686	−119.87829
Orange County	Buck Gully South	33.58825	−117.86736	Santa Barbara	Carpinteria	34.38704	−119.51408
Orange County	Crystal Cove	33.57086	−117.83785	Santa Catalina Island	Bird Rock	33.45167	−118.48761
Orange County	Muddy Canyon	33.56576	−117.83314	Santa Catalina Island	Big Fisherman Cove	33.44645	−118.48526
Orange County	Shaws Cove	33.54473	−117.79974	Santa Catalina Island	Two Harbors	33.44435	−118.49888
Orange County	Heisler Park	33.54259	−117.78928	Santa Catalina Island	Goat Harbor	33.41680	−118.39407
Orange County	Dana Point	33.45994	−117.71461	Santa Catalina Island	Avalon Quarry	33.32200	−118.30520

APPENDIX 2

Sites Sampled for the Sandy Intertidal Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
La Jolla and Point Loma	Blacks	32.88792	−117.25303	North San Diego County	San Elijo	33.02460	−117.28659
La Jolla and Point Loma	Scripps	32.86415	−117.25464	Orange County	Crystal Cove	33.57810	−117.84797
Malibu	Leo Carillo	34.04697	−118.94820	Point Conception	Gaviota	34.47109	−120.22788
Malibu	Dume Cove	34.00608	−118.80167	Point Conception	Arroyo Quemado	34.47039	−120.11952
North San Diego County	San Clemente	33.40074	−117.60329	Santa Barbara	East Campus	34.41053	−119.84205
North San Diego County	Carlsbad	33.11060	−117.32302	Santa Barbara	Isla Vista	34.40930	−119.87373

APPENDIX 3

Sites Sampled for the Kelp Forest Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Anacapa Island	AI - West Isle	34.01693	−119.43079	San Clemente Island	SCLI - Station 1	32.93640	−118.49825
Anacapa Island	AI - East Isle	34.01672	−119.36571	San Clemente Island	SCLI - Eel Point	32.90469	−118.53910
Anacapa Island	AI - Lighthouse Reef	34.01237	−119.36510	San Clemente Island	SCLI - Purseseine Rock	32.86900	−118.41043
Anacapa Island	AI - Middle Isle	34.00862	−119.39041	San Clemente Island	SCLI - Lost Point	32.84186	−118.49016
Begg Rock	SNI - Begg Rock	33.36237	−119.69495	San Clemente Island	SCLI - Lil Flower	32.83663	−118.36587
La Jolla/Point Loma	Children's Pool	32.85167	−117.27829	San Clemente Island	SCLI - Pyramid Cove	32.81550	−118.37115
La Jolla/Point Loma	Matlahuayl	32.85116	−117.27018	San Clemente Island	SCLI - China Point	32.80065	−118.42918
La Jolla/Point Loma	South La Jolla	32.81593	−117.28372	San Miguel Island	SMI - Harris Point Reserve	34.05986	−120.35069
La Jolla/Point Loma	Point Loma Central	32.71210	−117.26302	San Miguel Island	SMI - Cuyler	34.05405	−120.35042
La Jolla/Point Loma	Point Loma South	32.67649	−117.25615	San Miguel Island	SMI - Tyler Bight	34.02714	−120.40928
La Jolla/Point Loma	Cabrillo National Monument	32.66371	−117.24424	San Miguel Island	SMI - Crook Point	34.01647	−120.33518
Malibu	Deep Hole East	34.04522	−118.95920	San Nicolas Island	SNI - Boilers	33.27600	−119.60693
Malibu	Leo Carrillo East	34.03996	−118.92427	Santa Barbara	Naples	34.42353	−119.95266
Malibu	Encinal Canyon East	34.03505	−118.87098	Santa Barbara	IV Reef	34.40401	−119.86915
Malibu	Little Dume West	34.00654	−118.79097	Santa Barbara	Horseshoe Reef	34.39166	−119.55003

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Malibu	Point Dume	33.99884	−118.80659	Santa Barbara Island	SBI - Graveyard Canyon	33.47471	−119.02679
North San Diego County	San Mateo Kelp	33.36900	−117.61058	Santa Barbara Island	SBI - Southeast Sealion	33.46878	−119.02882
North San Diego County	South Carlsbad	33.09845	−117.32315	Santa Barbara Island	SBI - Sutil	33.46585	−119.04821
North San Diego County	Leucadia	33.06360	−117.30932	Santa Barbara Island	SBI - Cat Canyon	33.46442	−119.04408
North San Diego County	Swami's	33.03574	−117.30134	Santa Barbara Island	SBI - Southeast Reef	33.46293	−119.03127
North San Diego County	San Elijo	33.01818	−117.28882	Santa Catalina Island	SCAI - Indian Rock	33.46887	−118.52617
Orange County	Crystal Cove	33.56275	−117.83770	Santa Catalina Island	SCAI - Ship Rock	33.46302	−118.49140
Orange County	Heisler Park	33.54039	−117.79189	Santa Catalina Island	SCAI - Bird Rock	33.45217	−118.48767
Orange County	Laguna Beach	33.53115	−117.78048	Santa Catalina Island	SCAI - Blue Cavern	33.44802	−118.47947
Orange County	Dana Point	33.46160	−117.72145	Santa Catalina Island	SCAI - Iron Bound Cove	33.44750	−118.57515
Palos Verdes	Ridges North	33.78848	−118.42323	Santa Catalina Island	SCAI - West Quarry	33.44250	−118.47017
Palos Verdes	Ridges South	33.78631	−118.42641	Santa Catalina Island	SCAI - Ripper's Cove	33.42815	−118.43547
Palos Verdes	Rocky Point North	33.78093	−118.42999	Santa Catalina Island	SCAI - Cat Harbor	33.42609	−118.51181
Palos Verdes	Rocky Point South	33.77638	−118.43160	Santa Catalina Island	SCAI - Twin Rocks	33.41788	−118.38917
Palos Verdes	Lunada Bay	33.77180	−118.43030	Santa Catalina Island	SCAI - Italian Gardens	33.41073	−118.37576
Palos Verdes	Resort Point	33.76650	−118.42742	Santa Catalina Island	SCAI - Hen Rock	33.40010	−118.36690
Palos Verdes	Underwater Arch	33.75144	−118.41655	Santa Catalina Island	SCAI - Lover's Cove	33.34358	−118.31705
Palos Verdes	Hawthorne Reef	33.74662	−118.41657	Santa Catalina Island	SCAI - China Point	33.33032	−118.46975
Palos Verdes	Point Vicente West	33.73974	−118.41369	Santa Catalina Island	SCAI - Salta Verde	33.31458	−118.42152
Palos Verdes	Abalone Cove Kelp West	33.73922	−118.38789	Santa Cruz Island	SCRI - Painted Cave	34.07297	−119.87009
Palos Verdes	Long Point East	33.73595	−118.40122	Santa Cruz Island	SCRI - Hazards	34.05645	−119.82174
Palos Verdes	Bunker Point	33.72465	−118.35317	Santa Cruz Island	SCRI - Cavern Point	34.05384	−119.56949
Palos Verdes	Whites Point	33.71531	−118.32486	Santa Cruz Island	SCRI - Forney	34.05358	−119.91427
Palos Verdes	Point Fermin	33.70667	−118.29928	Santa Cruz Island	SCRI - Scorpion	34.05032	−119.55051

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Point Conception	Arroyo Quemado	34.46804	−120.12116	Santa Cruz Island	SCRI - Coche Point	34.04387	−119.60290
Point Conception	Bullito	34.45683	−120.33170	Santa Cruz Island	SCRI - Pelican	34.03166	−119.69668
Point Conception	Cojo	34.44435	−120.41927	Santa Cruz Island	SCRI - Yellowbanks	33.99283	−119.55903
San Clemente Island	SCLI - Castle Rock	33.03732	−118.61528	Santa Cruz Island	SCRI - Valley	33.98320	−119.64183
San Clemente Island	SCLI - Northwest Harbor	33.03225	−118.58382	Santa Cruz Island	SCRI - Gull Island	33.94833	−119.82489
San Clemente Island	SCLI - Reflector Reef	33.02639	−118.56347	Santa Rosa Island	SRI - Cluster Point	33.92908	−120.19083
San Clemente Island	SCLI - Boy Scout Camp	33.00208	−118.54826	Santa Rosa Island	SRI - Johnson's Lee South	33.89726	−120.10359
San Clemente Island	SCLI - South Range	32.96762	−118.57756	Santa Rosa Island	SRI - South Point	33.89344	−120.12148

APPENDIX 4

Sites Sampled for the Reef Check Kelp Forest Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Anacapa Island	Landing Cove	34.01747	−119.36240	Palos Verdes	120 Reef	33.73792	−118.39201
Anacapa Island	Cathedral Cove	34.01650	−119.36839	Palos Verdes	Abalone Cove	33.73615	−118.37632
Anacapa Island	Cathedral Wall	34.01575	−119.37150	Palos Verdes	White Point	33.71351	−118.31810
Anacapa Island	Goldfish Bowl	34.01473	−119.43750	Point Conception	Refugio State Beach	34.46333	−120.07032
Anacapa Island	Light House	34.01263	−119.36420	Santa Barbara	Naples Reef	34.42185	−119.95150
La Jolla/Point Loma	La Jolla Cove	32.85217	−117.26987	Santa Barbara	Sandpiper	34.41747	−119.89673
La Jolla/Point Loma	Windansea	32.83660	−117.28800	Santa Barbara	IV Reef	34.40305	−119.86608
La Jolla/Point Loma	South La Jolla	32.81345	−117.28577	Santa Catalina Island	Lions Head	33.45124	−118.50210
La Jolla/Point Loma	North Hill Street	32.72862	−117.26500	Santa Catalina Island	Bird Rock	33.45080	−118.48754
La Jolla/Point Loma	Broomtail Reef	32.69423	−117.26807	Santa Catalina Island	Isthmus Reef	33.44832	−118.49060
Malibu	Big Rock	34.03517	−118.60809	Santa Catalina Island	WIES Intake Pipes	33.44700	−118.48485
Malibu	Lechuza	34.03403	−118.87132	Santa Catalina Island	Long Point West	33.40840	−118.36740
Malibu	Paradise Point	34.00413	−118.79290	Santa Catalina Island	Torqua	33.38300	−118.35000
Orange County	Little Corona Del Mar	33.58980	−117.86870	Santa Catalina Island	Casino Point	33.34917	−118.32497
Orange County	Crystal Cove	33.57135	−117.84110	Santa Cruz Island	Cueva Valdez	34.05500	−119.81000
Orange County	Seal Rock North Crescent Bay	33.54555	−117.80370	Santa Cruz Island	Frys Anchorage	34.05416	−119.75600

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Orange County	Shaws Cove	33.54396	−117.79986	Santa Cruz Island	Scorpion Anchorage	34.04852	−119.55230
Orange County	Divers Cove	33.54317	−117.79658	Santa Cruz Island	Pelican Anchorage	34.03565	−119.70250
Orange County	Heisler Park	33.54225	−117.79500	Santa Cruz Island	Yellowbanks	33.99880	−119.55050
Orange County	Salt Creek	33.47715	−117.72736	Santa Cruz Island	Sandstone Pt.	33.99067	−119.55440
Palos Verdes	Malaga Cove	33.80365	−118.39835	Santa Rosa Island	Elk Ridge	33.95333	−119.96909
Palos Verdes	Christmas Tree Cove	33.76040	−118.42105	Santa Rosa Island	East Point	33.94397	−119.96478
Palos Verdes	Hawthorne Reef	33.74700	−118.41589	Santa Rosa Island	Johnsons Lee	33.90155	−120.10340

APPENDIX 5

Sites Sampled for the Shallower Soft-Bottom 0–100 m Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
La Jolla/Point Loma	B13-9052	32.82374	−117.34121	Orange County	B13-9177	33.54831	−117.82495
La Jolla/Point Loma	B13-9040	32.78135	−117.26930	Orange County	B13-9173	33.52456	−117.79534
La Jolla/Point Loma	B13-9037	32.76383	−117.31984	Orange County	B13-9171	33.52140	−117.76980
La Jolla/Point Loma	B13-9034	32.74076	−117.31480	Orange County	B13-9168	33.51414	−117.77943
La Jolla/Point Loma	B13-9012	32.58938	−117.26361	Orange County	B13-9166	33.51182	−117.77133
La Jolla/Point Loma	B13-9008	32.55110	−117.14986	Orange County	B13-9161	33.50506	−117.77313
La Jolla/Point Loma	B13-9007	32.55081	−117.19931	Orange County	B13-9159	33.50056	−117.75367
La Jolla/Point Loma	B13-9006	32.54924	−117.14077	Orange County	B13-9152	33.47427	−117.73662
La Jolla/Point Loma	B13-9005	32.53761	−117.15511	Palos Verdes	B13-9257	33.82949	−118.40126
Malibu	B13-9383	34.12507	−119.19268	Palos Verdes	B13-9245	33.73300	−118.12150
Malibu	B13-9377	34.11371	−119.18046	Palos Verdes	B13-9239	33.72266	−118.15526
Malibu	B13-9372	34.10112	−119.15082	Palos Verdes	B13-9229	33.69541	−118.29616
Malibu	B13-9342	34.02646	−118.57065	Palos Verdes	B13-9221	33.65956	−118.13065
Malibu	B13-9341	34.02321	−118.59282	Palos Verdes	B13-9219	33.65450	−118.05838
Malibu	B13-9339	34.02205	−118.86736	Palos Verdes	B13-9217	33.64800	−118.14950
Malibu	B13-9336	34.01948	−118.74305	Palos Verdes	B13-9214	33.64300	−118.07835
Malibu	B13-9331	34.01320	−118.67019	Palos Verdes	B13-9204	33.62780	−117.98720
Malibu	B13-9326	34.00509	−118.76663	Palos Verdes	B13-9200	33.60346	−118.09545
Malibu	B13-9323	34.00126	−118.82445	Palos Verdes	B13-9199	33.60185	−118.05647
Malibu	B13-9321	34.00042	−118.81508	Point Conception	B13-9487	34.46470	−120.17971
Malibu	B13-9320	33.99917	−118.86887	Point Conception	B13-9482	34.44309	−120.28516
Malibu	B13-9319	33.99744	−118.49182	Santa Barbara	B13-9471	34.40395	−119.81211

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Malibu	B13-9316	33.99528	−118.63280	Santa Barbara	B13-9470	34.40100	−119.83280
Malibu	B13-9303	33.96250	−118.47620	Santa Barbara	B13-9468	34.39975	−119.87481
Malibu	B13-9292	33.94372	−118.51978	Santa Barbara	B13-9467	34.39839	−119.86476
Malibu	B13-9286	33.93486	−118.53976	Santa Barbara	B13-9466	34.39548	−119.66218
Malibu	B13-9271	33.89793	−118.53699	Santa Barbara	B13-9465	34.39505	−119.85862
Malibu	B13-9266	33.86038	−118.44805	Santa Barbara	B13-9458	34.36812	−119.54012
North San Diego County	B13-9131	33.26991	−117.56485	Santa Barbara	B13-9456	34.36084	−119.84922
North San Diego County	B13-9130	33.26882	−117.53942	Santa Barbara	B13-9454	34.35930	−119.84950
North San Diego County	B13-9129	33.26553	−117.53393	Santa Barbara	B13-9449	34.34408	−119.56258
North San Diego County	B13-9121	33.17566	−117.38149	Santa Barbara	B13-9448	34.34384	−119.77376
North San Diego County	B13-9111	33.10513	−117.36191	Santa Barbara	B13-9447	34.34247	−119.45800
North San Diego County	B13-9105	33.08807	−117.35098	Santa Barbara	B13-9433	34.27832	−119.58315
North San Diego County	B13-9104	33.08343	−117.34265	Santa Barbara	B13-9424	34.25487	−119.47649
North San Diego County	B13-9094	33.03384	−117.31726	Santa Barbara	B13-9421	34.24441	−119.37034
Orange County	B13-9194	33.58976	−117.89469	Santa Barbara	B13-9409	34.21832	−119.29504
Orange County	B13-9192	33.58086	−117.86846	Santa Barbara	B13-9397	34.17867	−119.34686
Orange County	B13-9187	33.56822	−117.85659	Santa Barbara	B13-9382	34.12460	−119.25856

APPENDIX 6

Sites Sampled for the Deeper Soft-Bottom 100–500 m Dataset

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
La Jolla/Point Loma	B13-9056	32.83149	−117.35914	Point Conception	B13-9476	34.42003	−120.26919
La Jolla/Point Loma	B13-9053	32.82544	−117.36599	Point Conception	B13-9459	34.36839	−120.11302
La Jolla/Point Loma	B13-9051	32.82160	−117.36852	Point Conception	B13-9457	34.36268	−120.01034
La Jolla/Point Loma	B13-9035	32.74149	−117.42695	Point Conception	B13-9450	34.34424	−120.36861
La Jolla/Point Loma	B13-9026	32.69385	−117.39582	Point Conception	B13-9436	34.28711	−120.45557
La Jolla/Point Loma	B13-9023	32.67006	−117.42091	Point Conception	B13-9435	34.28456	−120.42371
La Jolla/Point Loma	B13-9014	32.59843	−117.32876	Point Conception	B13-9427	34.26002	−120.28113
La Jolla/Point Loma	B13-9013	32.59770	−117.35125	Point Conception	B13-9400	34.18317	−120.35129
La Jolla/Point Loma	B13-9011	32.58567	−117.34110	Point Conception	B13-9399	34.18235	−120.40732
Malibu	B13-9354	34.05085	−119.21575	Point Conception	B13-9387	34.14379	−120.17822
Malibu	B13-9350	34.04406	−119.05558	Santa Barbara	B13-9455	34.36050	−119.89146
Malibu	B13-9348	34.04114	−119.19721	Santa Barbara	B13-9444	34.31988	−119.75113

Region	Site name	Latitude	Longitude	Region	Site name	Latitude	Longitude
Malibu	B13-9325	34.00459	−119.05596	Santa Barbara	B13-9441	34.31380	−119.88421
Malibu	B13-9314	33.99155	−118.85703	Santa Barbara	B13-9432	34.27781	−119.71827
Malibu	B13-9309	33.97742	−118.87639	Santa Barbara	B13-9431	34.27751	−119.65789
Malibu	B13-9300	33.95711	−118.59303	Santa Barbara	B13-9426	34.25859	−119.81040
Malibu	B13-9287	33.93551	−118.59212	Santa Barbara	B13-9419	34.24006	−119.66910
N. San Diego County	B13-9125	33.22069	−117.51202	Santa Barbara	B13-9414	34.22508	−119.73198
N. San Diego County	B13-9107	33.09375	−117.41715	Santa Barbara	B13-9407	34.21626	−119.60595
N. San Diego County	B13-9100	33.06657	−117.36748	Santa Barbara	B13-9403	34.20641	−119.63271
N. San Diego County	B13-9092	33.02686	−117.33666	Santa Barbara	B13-9398	34.17889	−119.61204
N. San Diego County	B13-9091	33.01823	−117.34053	Santa Barbara	B13-9396	34.17124	−119.87676
N. San Diego County	B13-9073	32.91015	−117.29773	Santa Barbara	B13-9394	34.16870	−119.54170
Palos Verdes	B13-9251	33.76682	−118.46048	Santa Barbara	B13-9391	34.15836	−119.82763
Palos Verdes	B13-9237	33.72141	−118.41792	Santa Barbara	B13-9388	34.14562	−119.77009
Palos Verdes	B13-9235	33.70335	−118.39750	Santa Barbara	B13-9385	34.13268	−119.36990
Palos Verdes	B13-9228	33.69409	−118.34651	Santa Barbara	B13-9380	34.12281	−119.33129
Palos Verdes	B13-9223	33.67587	−118.33247	Santa Barbara	B13-9379	34.11821	−119.62891
Palos Verdes	B13-9185	33.56469	−118.01844	Santa Barbara	B13-9374	34.10717	−119.31902
Palos Verdes	B13-9179	33.55625	−118.02254				