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ORIGINAL ARTICLE

Biogeographical patterns of rocky intertidal communities along the Pacific coast of North America

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ABSTRACT

Aim Our aim in this paper is to present the first broad-scale quantification of species abundance for rocky intertidal communities along the Pacific coast of North America. Here we examine the community-level marine biogeographical patterns in the context of formerly described biogeographical regions, and we evaluate the combined effects of geographical distance and environmental conditions on patterns of species similarity across this region.

Location Pacific coast of North America.

Methods Data on the percentage cover of benthic marine organisms were collected at 67 rocky intertidal sites from south-eastern Alaska, USA, to central Baja California Sur, Mexico. Cluster analysis and non-metric multidimensional scaling were used to evaluate the spatial patterns of species similarity among sites relative to those of previously defined biogeographical regions. Matrices of similarity in species composition among all sites were computed and analysed with respect to geographical distance and long-term mean sea surface temperature (SST) as a measure of environmental conditions.

Results We found a high degree of spatial structure in the similarity of intertidal communities along the coast. Cluster analysis identified 13 major community structure 'groups'. Although breaks between clusters of sites generally occurred at major biogeographical boundaries, some of the larger biogeographical regions contained several clusters of sites that did not group according to spatial position or identifiable coastal features. Additionally, there were several outliers – sites that grouped alone or with sites outside their region – for which localized features may play an important role in driving community structure. Patterns of species similarity at the large scale were highly correlated with geographical distance among sites and with SST. Importantly, we found community similarity to be highly correlated with long-term mean SST while controlling for the effects of geographical distance.

Main conclusions These findings reveal a high degree of spatial structure in the similarity of rocky intertidal communities of the north-east Pacific, and are generally consistent with those of previously described biogeographical regions, with some notable differences. Breaks in similarity among clusters are generally coincident with known biogeographical and oceanographic discontinuities. The strong correlations between species similarity and both geographical position and SST suggest that both geography and oceanographic conditions have a large influence on patterns of intertidal community structure along the Pacific coast of North America.

Keywords

Benthic marine organisms, biogeographical regions, conservation biogeography, environmental distance, geographical distance, north-east Pacific, rocky intertidal, species similarity.

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INTRODUCTION

Characterizing the distribution and abundance of species over scales of space and time has been a major focus of ecology and biogeography for many decades (Pielou, 1979; Cox & Moore, 1993). In the marine realm, there have been several efforts to broadly characterize biogeographical regions on large (whole ocean) scales to examine latitudinal patterns in diversity and the abundance of particular taxa (Eckman, 1953; Thorsen, 1957; Sanders, 1968; Glemarec, 1973; Pielou, 1979; Gaines & Lubchenco, 1982; Gee & Warwick, 1996). Although these studies have covered coarse spatial scales, they have been mainly descriptive and based on analyses of existing presence/absence data sets for particular taxa. Recent efforts have begun to address the need for more quantitative estimates of abundance across a variety of taxa by examining patterns of community similarity in coastal marine species at mesoscales (tens to hundreds of kilometres). These mesoscale studies have attempted to correlate community structure patterns with oceanographic and abiotic processes. Studies along the coast of South Africa (Bustamante & Branch, 1996; Sink *et al.*, 2005), Chile (Broitman *et al.*, 2001), New Zealand (Menge *et al.*, 1999, 2003), the US west coast (Connolly & Roughgarden, 1998; Schoch *et al.*, 2006; Blanchette & Gaines, 2007), Japan (Nakaoka *et al.*, 2006), British Columbia, Canada (Zacharias & Roff, 2001) and Santa Cruz Island, California, USA (Blanchette *et al.*, 2006) all support a strong link between oceanographic conditions and geographical variation in species assemblages.

Recent conservation efforts have highlighted the need for more quantitative information on the patterns of coastal species distribution. One of the most important applications of this line of research is the generation of knowledge necessary to achieve adequate and representative conservation of biodiversity. Despite the great economic importance of coastal marine ecosystems in terms of fishing, recreation and other services (Costanza *et al.*, 1997; IPCC, 2001), little is known about the biogeographical patterns of coastal marine species. It is widely thought that representative protected areas need to be established within each principal biogeographical coastal region if marine biodiversity is to be conserved (Attwood *et al.*, 1997; Hockey & Branch, 1997; Airame *et al.*, 2003; Roberts *et al.*, 2003a,b). This knowledge is critical to the management of coastal areas in the context of human use and is also critical to predicting and forecasting the potential impacts of climate change. There is a strong scientific consensus that coastal marine ecosystems, along with the goods and services they provide, are threatened by anthropogenic global climate change (Hays *et al.*, 2005; Hsieh *et al.*, 2005; Harley *et al.*, 2006; Helmuth *et al.*, 2006b; Parmesan, 2006; Harvey, 2007). Intertidal communities are particularly sensitive to the potential effects of changing climate, due to the fact that they are exposed to a wide range of environmental conditions at the extreme edge of both the marine and terrestrial environment (Harley *et al.*, 2006; Helmuth *et al.*, 2006b).

Temperature has been one of the most well-studied environmental factors in biogeography and provides a useful and easily quantifiable metric of ocean conditions. Temperature has long been thought to play a key role in determining species distributions in the marine environment. Abundant fossil evidence demonstrates that marine faunas shifted polewards as sea surface temperatures (SSTs) rose, e.g. during the Pleistocene–Holocene transition (Hubbs, 1960; Addicott, 1969; Moore *et al.*, 1980). Short-term pulses of increased temperatures, such as those during ENSO events, can also have an impact on species distributional limits (Pearcy & Schoener, 1987; Tanasichuk & Cooper, 2002; Zacherl *et al.*, 2003; Keister *et al.*, 2005; Lluch-Belda *et al.*, 2005). Likewise, it is important to consider the present and future patterns of environmental stress in the context of biogeographical distributions. Present temperatures and predicted near-future increases in thermal stress do not necessarily vary consistently with latitude in coastal marine systems (Helmuth *et al.*, 2002, 2006a), and organisms could be most at risk in hotspots well removed from their current biogeographical range edge.

In this paper we focus on the role of ocean temperature and geography in the determination of the non-random geographical distribution patterns of the biota of intertidal rocky shores along the west coast of North America. We sampled benthic communities at 67 sites, spanning 35 degrees of latitude and 5500 km across the Pacific coast of North America (Fig. 1). Biogeographical patterns of species distribution and community composition of these systems have never been described at this continental scale. Previous large-scale biogeographical analyses have been based on presence-or-absence data from single taxa (e.g. molluscs), while we focus here on the quantitative relative abundance of species across a wide variety of benthic taxa. The sampling effort here is unique and unprecedented in both spatial scale and the use of consistent field methodology and personnel to reduce taxonomic and other sampling-related biases.

The study region spans two major coastal biogeographical provinces: the Oregonian and Californian (sometimes referred to as the San Diegan) (Valentine, 1966). The Oregonian province extends primarily from south-eastern Alaska to Point Conception, and is part of the Eastern Boreal Pacific Region (Briggs, 1974; Newman, 1979). The Oregonian province also extends southward beyond Point Conception along the outer islands of southern California, and in part reappears in upwelling areas off Baja California (Hubbs, 1948; Lluch-Belda *et al.*, 2003). The Californian province extends from Point Conception, California, to Punta Eugenia, Baja California Sur (Briggs, 1974). However, in warm-regime years, some Californian province species extend their ranges northward (Burton, 1998; Hellberg *et al.*, 2001). Beyond Punta Eugenia to the south is another region sometimes referred to as the California Transition Zone, extending from Punta Eugenia to the southern tip of Baja at Cabo San Lucas (Roy *et al.*, 1994, 2000). This subtropical region spans the area between the Californian province and the tropical Panamic province, which extends from the southern tip of Baja down to the equator.

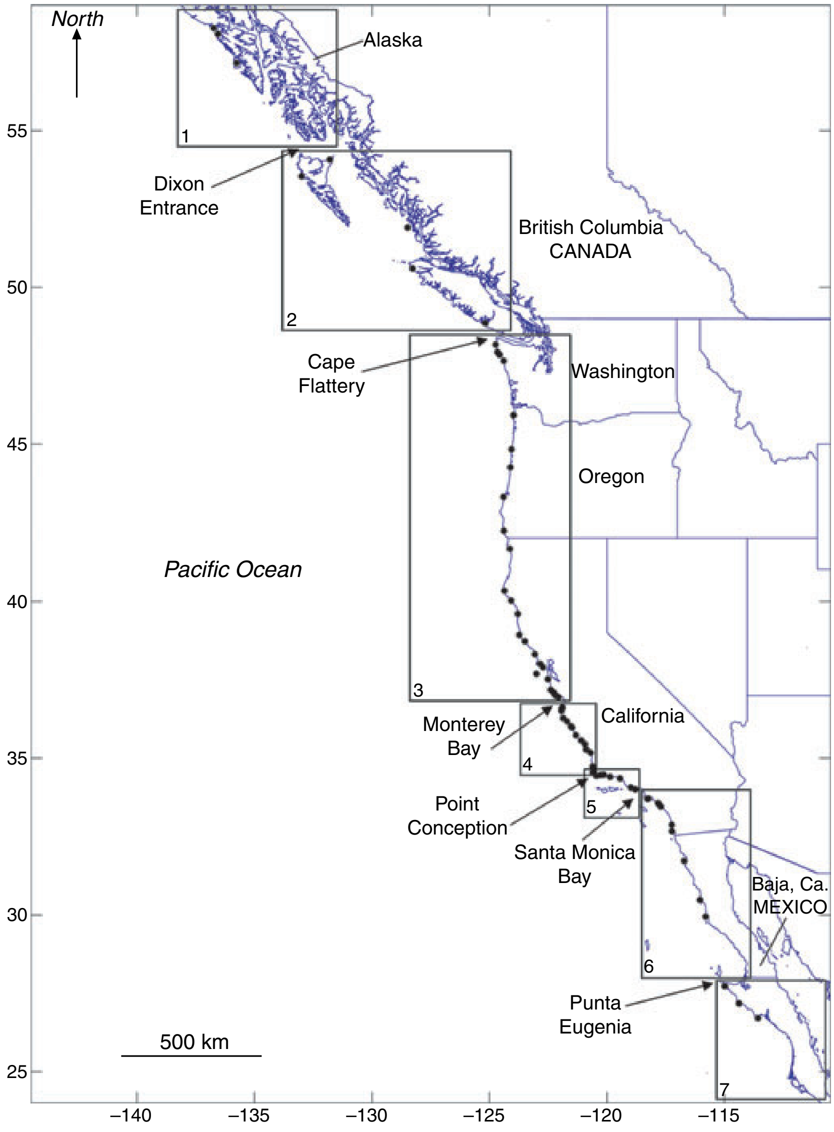

Figure 1 Map of the study area along the Pacific coast of North America. The locations of biogeographical regions and major coastal features delimiting regions are shown. The boxes with numbers correspond to biogeographical regions in Table 1, and are individually highlighted in Fig. 2.

These large biogeographical provinces have been defined primarily on the basis of where clusters of range boundaries occur for particular groups of species, and vary somewhat depending on the taxa of interest. In this study we attempt to characterize biogeographical patterns based on communities comprising many taxa varying widely in life-history attributes and dispersal capabilities. For many species, geographical range limits often correspond to major oceanographic or coastal features such as capes, bays and islands. Several of these prominent coastal features define smaller biogeographical regions, which have been described as biogeographical breaks for several marine taxa. These regions (see regions and regional boundaries in Table 1) follow the proposed provincial systems of Hall (1960, 1964) and Valentine (1966), based on molluscs and are also generally applicable to the shallow water marine algae (Abbott & Hollenberg, 1976). They provide a useful starting point for the exploration of intertidal community biogeographical regions since both molluscs and marine algae are two of the dominant groups of space occupiers in these communities.

Table 1 Biogeographical regions and geographical boundaries as referenced in Fig. 1 and based on the provincial systems of Hall (1960, 1964) and Valentine (1966).

Region	Region name	Region boundaries
1	Aleutian	Prince William Sound to Dixon Entrance
2	Columbian	Dixon Entrance to Cape Flattery
3	Mendocinian	Cape Flattery to Monterey Bay
4	Montereyan	Monterey Bay to Point Conception
5	Southern Californian	Point Conception to Santa Monica Bay
6	Ensenadian	Santa Monica Bay to Punta Eugenia
7	Magdelenan	Punta Eugenia to Cabo San Lucas

In a seminal paper on the analysis and interpretation of spatial patterns in species composition, Nekola & White

(1999) proposed that the factors affecting the spatial structure of ecological communities can be studied by analysing the degree of similarity of species composition between sites ('species similarity'). They argued that species similarity decreases with increasing distance between the sites, and that this 'distance decay' reflects the combined effects of two fundamental factors: niche relationships and dispersal processes. Niche relationships produce a decay of species similarity with geographical distance because environmental conditions are always spatially autocorrelated, so that nearby sites tend to be more similar in their environmental conditions than distant sites (Legendre, 1993). The spatial decay in environmental similarity leads to a corresponding decay in species similarity (Steinitz *et al.*, 2006). Here we describe the biogeographical patterns of intertidal rocky shores along the Pacific coast of North America and examine patterns of species similarity relative to both geographical and environmental distance. Our specific objectives were: (1) to assess patterns of intertidal community structure and spatial scales of community correlation; (2) to compare these to previously described biogeographical regions; (3) to identify potential associations between spatial patterns of intertidal community structure and measures of large-scale oceanographic conditions; and (4) to identify characteristic taxa that account for similarities within regions.

METHODS

Study region

We conducted quantitative surveys at 67 rocky intertidal sites (Fig. 1) distributed along the Pacific coast of North America from south-eastern Alaska, USA, to central Baja California Sur, Mexico, spanning seven previously described biogeographical regions (Fig. 2, Table 2). Sites were all sampled during a 5-year period between January 2001 and January 2006. These sites were all gently sloping (0°–20°) rocky benches and were selected to be as similar as possible in terms of geomorphology, wave exposure and habitat type.

Biological sampling design

We used a point-intercept sampling method to quantify percentage cover of sessile invertebrate and macrophyte species at each site based on methods described in detail in Murray *et al.* (2006). A representative shore section 30 m long was designated as the site. A 30-m baseline tape was laid out along the upper edge of the highest intertidal barnacle zone, parallel to the shore. A point-intercept transect was then surveyed perpendicular to the horizontal tape at each 3-m interval, for a total of 11 transects per site. These vertical transects extended from the upper edge of the barnacle zone to about the 0.0 m mean lower low water tidal datum (MLLW) level predicted by the tide tables (generally the surfgrass zone). Along each vertical transect, the species or taxon located under each point at a pre-determined interval along the tape was scored sequentially. The transect sampling interval at each site depended on the size and topography of the bench and was calculated to provide at least 100 sampling points per transect. For each point, we sampled the taxa directly under the point, including layering and epibionts. Percentage cover estimates reported here are based on the primary taxa (including any layering) attached to rock located directly under each point.

Sea surface temperature analyses

We followed the approach of Broitman *et al.* (2005) and Blanchette *et al.* (2006) and characterized oceanographic conditions at each site through spatial and temporal patterns of SST from the Advanced Very-High Resolution Radiometer (AVHRR) of a nominal resolution of 1.1 km averaged over 5 days. From the AVHRR data set we selected the pixels corresponding to the locations of our 67 intertidal sites and averaged the first three cross-shelf pixels to obtain time series with 80% to 97% of valid observations. Cross-shelf averaging was imposed to improve temporal coverage; missing pixels were common in the near shore. Long-term means were derived directly from the resulting time series from 1985 to 2001. We chose to use satellite-based SST for this analysis due to the availability of long-term data for all of our study locations. One of the great advantages of using remotely sensed observations is that one can explore biophysical relationships in many parts of the world where satellite-based data are available, but long-term data from *in situ* physical instrumentation are not. Long-term satellite data also provide a much better index of the persistence of oceanographic regimes over extended periods of time and across broad spatial scales.

Data analysis

To examine geographical patterns of community similarity, we used the multivariate methods of Clarke (1993) and the PRIMER 6.1.3 (Plymouth Routines in Multivariate Ecological Research) software package. The data matrix of taxon abundances was square-root transformed to reduce the contribution of very abundant species and increase that of rare species. A similarity matrix was constructed using the Bray–Curtis similarity coefficient and cluster analysis was performed using a hierarchical method with group-average linking. We used two-dimensional, non-metric multidimensional scaling (nMDS) to examine regional segregation among communities (Kruskal & Wish, 1978). A SIMPROF test using 10000 permutations was run for the dendrogram to indicate significant group structure at the 0.1% level.

Variance and similarity both measure differences between samples and can be modelled as a function of intersample distance. Here we follow the approach of Nekola & White (1999) to model the shape of that relationship. Regression of similarity against distance produces a direct estimate of the rate of distance decay and thus the rate of composition change through space.

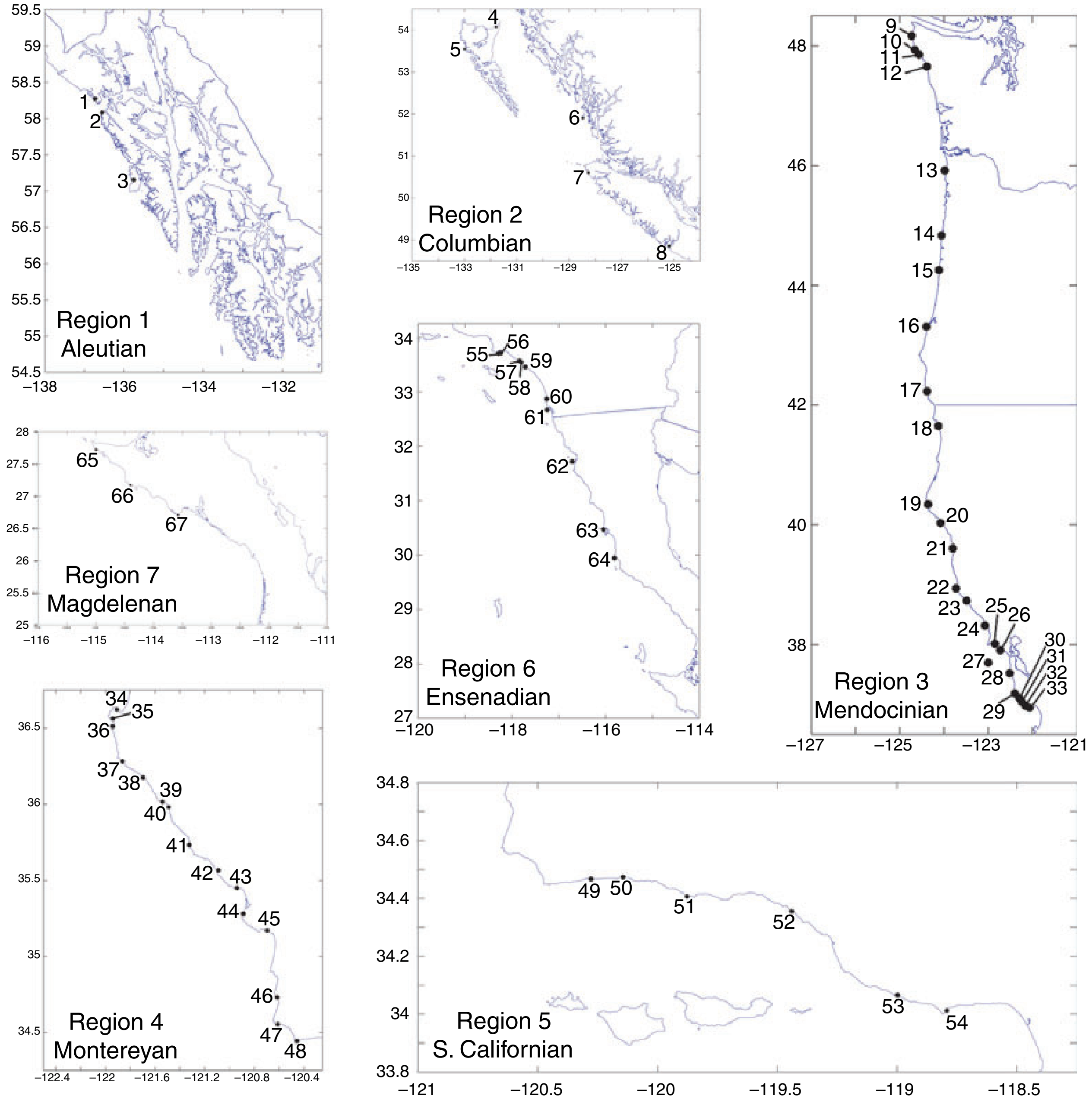

Figure 2 Map of each biogeographical region and numbered study sites within each region as referenced in Table 2.

We used Mantel tests to examine the correlation between the matrices of community similarity and coastal distances among sites and differences in long-term mean SST among sites (Legendre, 1993; Legendre & Legendre, 1998; Legendre *et al.*, 2005). The results of these analyses enabled us to test the prediction that community similarity is correlated with both geographical distance and oceanographic climate. However, two variables may appear to be correlated simply because they are both linked to a third, common variable, such as location in space. Thus, in the presence of autocorrelation, it is necessary to remove the effect of this third variable before concluding that the original two variables are indeed correlated, similar to a partial correlation. This can be done with the partial Mantel test (Smouse *et al.*, 1986; Legendre & Troussellier, 1988; Fortin & Payette, 2002). A significant coefficient of correlation (r) for the partial Mantel test (with spatial effects removed) indicates that the relationship that exists between the two variables is not related to a common spatial structure (Legendre & Fortin, 1989). We used a partial Mantel test to examine the correlation between community similarity and SST while controlling for the effects of geographical location. The Mantel and partial Mantel tests were based on 10,000 random permutations with a Pearson correlation coefficient at a significance level of $\alpha = 0.05$. All Mantel tests were done using zt software (Bonnet & Van De Peer, 2002).

Table 2 Names and locations of all rocky intertidal field sites. Site numbers refer to the map in Fig. 2.

Site no.	Province	Site name	Latitude	Longitude
1	Aleutian	Graves Harbor, AK	58°16′16″ N	136°43′52″ W
2	Aleutian	Yakobi, AK	58°04′55″ N	136°33′18″ W
3	Aleutian	Port Mary, AK	57°09′14″ N	135°45′18″ W
4	Columbian	Tow Hill, BC	54°04′41″ N	131°47′42″ W
5	Columbian	Hippa Island, BC	53°32′46″ N	132°59′46″ W
6	Columbian	Duck Island, BC	51°54′18″ N	128°28′52″ W
7	Columbian	Palmerston, BC	50°36′04″ N	128°16′16″ W
8	Columbian	Little Ohiat, BC	48°51′11″ N	125°10′59″ W
9	Mendocinian	Cannonball Island, WA	48°10′16″ N	124°44′10″ W
10	Mendocinian	Chilean Memorial, WA	47°56′06″ N	124°39′47″ W
11	Mendocinian	Taylor Point, WA	47°51′07″ N	124°34′05″ W
12	Mendocinian	Starfish Point, WA	47°39′11″ N	124°23′31″ W
13	Mendocinian	Ecola, OR	45°55′05″ N	123°58′44″ W
14	Mendocinian	Fogarty Creek, OR	44°49′52″ N	124°03′36″ W
15	Mendocinian	Bob Creek, OR	44°15′14″ N	124°06′47″ W
16	Mendocinian	Cape Arago, OR	43°18′29″ N	124°24′04″ W
17	Mendocinian	Burnt Hill, OR	42°13′41″ N	124°23′13″ W
18	Mendocinian	Damnation Creek, CA	41°39′11″ N	124°07′48″ W
19	Mendocinian	Cape Mendocino, CA	40°20′28″ N	124°21′47″ W
20	Mendocinian	Shelter Cove, CA	40°01′52″ N	124°04′44″ W
21	Mendocinian	Kibesillah, CA	39°36′14″ N	123°47′53″ W
22	Mendocinian	Stornetta Ranch, CA	38°56′17″ N	123°43′44″ W
23	Mendocinian	Sea Ranch, CA	38°43′48″ N	123°29′17″ W
24	Mendocinian	Bodega, CA	38°19′05″ N	123°04′23″ W
25	Mendocinian	Santa Maria Creek, CA	38°00′43″ N	122°50′56″ W
26	Mendocinian	Bolinas Point, CA	37°54′14″ N	122°43′37″ W
27	Mendocinian	Mussel Flat Farallons, CA	37°41′46″ N	123°00′11″ W
28	Mendocinian	Fitzgerald Reserve, CA	37°31′19″ N	122°31′01″ W
29	Mendocinian	Pigeon Point, CA	37°11′06″ N	122°23′49″ W
30	Mendocinian	Ano Nuevo, CA	37°06′29″ N	122°17′38″ W
31	Mendocinian	Scott Creek, CA	37°02′42″ N	122°14′13″ W
32	Mendocinian	Sand Hill, CA	36°58′52″ N	122°09′18″ W
33	Mendocinian	Terrace Point, CA	36°56′53″ N	122°03′54″ W
34	Montereyan	Hopkins, CA	36°37′16″ N	121°54′25″ W
35	Montereyan	Stillwater Cove, CA	36°33′40″ N	121°56′24″ W
36	Montereyan	Point Lobos, CA	36°30′40″ N	121°56′28″ W
37	Montereyan	Andrew Molera, CA	36°16′52″ N	121°51′47″ W
38	Montereyan	Partington Point, CA	36°10′26″ N	121°41′49″ W
39	Montereyan	Lucia, CA	36°00′50″ N	121°32′28″ W
40	Montereyan	Mill Creek, CA	35°58′48″ N	121°29′28″ W
41	Montereyan	Point Sierra Nevada, CA	35°43′52″ N	121°19′26″ W
42	Montereyan	Rancho Marino, CA	35°33′50″ N	121°05′24″ W
43	Montereyan	Cayucos, CA	35°26′56″ N	120°56′24″ W
44	Montereyan	Hazards, CA	35°16′44″ N	120°53′17″ W
45	Montereyan	Shell Beach, CA	35°10′08″ N	120°41′46″ W
46	Montereyan	Stairs, CA	34°43′52″ N	120°36′54″ W
47	Montereyan	Boat House, CA	34°33′14″ N	120°36′40″ W
48	Montereyan	Government Point, CA	34°26′31″ N	120°27′22″ W
49	S. Californian	Alegria, CA	34°28′01″ N	120°16′41″ W
50	S. Californian	Arroyo Hondo, CA	34°28′26″ N	120°08′38″ W
51	S. Californian	Coal Oil Pt, CA	34°24′25″ N	119°52′41″ W
52	S. Californian	Mussel Shoals, CA	34°21′18″ N	119°26′24″ W
53	S. Californian	Old Stairs, CA	34°03′58″ N	118°59′53″ W
54	S. Californian	Paradise Cove, CA	34°00′43″ N	118°47′35″ W
55	Ensenadian	Whites Point, CA	33°42′54″ N	118°14′10″ W
56	Ensenadian	Point Fermin, CA	33°42′25″ N	118°17′10″ W
57	Ensenadian	Crystal Cove, CA	33°34′16″ N	117°50′17″ W
58	Ensenadian	Shaw's Cove, CA	33°32′42″ N	117°47′56″ W

Table 2 Continued

Site no.	Province	Site name	Latitude	Longitude
59	Ensenadian	Dana Point, CA	33°27′36″ N	117°42′50″ W
60	Ensenadian	Scripps, CA	32°52′16″ N	117°15′11″ W
61	Ensenadian	Cabrillo Zone I, CA	32°40′08″ N	117°14′42″ W
62	Ensenadian	La Bufadora, BCN	31°43′26″ N	116°42′50″ W
63	Ensenadian	La Chorera, BCN	30°28′12″ N	116°02′49″ W
64	Ensenadian	Punta Baja, BCN	29°56′56″ N	115°48′43″ W
65	Magdelenan	Punta Rompiente, BCS	27°43′34″ N	114°59′42″ W
66	Magdelenan	Punta San Roque, BCS	27°10′37″ N	114°23′53″ W
67	Magdelenan	Punta Abreojos, BCS	26°42′18″ N	113°34′34″ W

RESULTS

Species composition and abundance

We identified a total of 296 taxa, consisting of 167 algae, 127 invertebrates and two species of seagrasses. We found no evidence of a geographical or latitudinal pattern of taxon richness along the coast. Average taxon richness across all sites was 55; however, there were a few regions where taxon richness was particularly low (richness values of 25–27 at sites 51 and 52 in the Santa Barbara Channel) or relatively high (richness values of 76–78 at sites 20 and 23 on the northern Californian coast).

The patterns of distribution and abundance for many of the most common species reflected a relatively patchy distribution of abundance throughout the study region. Although various taxa with more northern (e.g. *Alaria nana*, *Semibalanus cariosus*, *Hedophyllum sessile*) or southern (e.g. *Caulacanthus ustulatus*, *Tetraclita rubescens*, *Chondracanthus canaliculatus*) biogeographical affinities, based on their geographical range limits as described in Barry *et al.* (1995) and Sagarin *et al.* (1999), were relatively common near the northern and southern extremes of the study area, many cosmopolitan species (e.g. *Mytilus californianus*, *Balanus glandula*, *Phyllospadix scouleri*) dominated space in varying abundances throughout the large study region (Fig. 3). Many of these species were distributed unevenly across the geographical range of this study, and similar to the findings of Sagarin & Gaines (2002), very few of these species reflected an 'abundant centre' distribution.

Cluster analysis and non-metric multidimensional scaling

Hierarchical cluster analysis and two-dimensional nMDS ordination were used to explore community similarity among sites along the geographical gradient and among biogeographical regions. The dendrogram illustrates the high degree of spatial structure among groups of sites (Fig. 4). The SIMPROF test identified 13 significantly different groups of sites and four sites (sites 4, 9, 12 and 63) as outliers. Apart from these outliers, groups of sites generally corresponded to previously described biogeographical regions, with some important exceptions. The Aleutian sites clustered together as a distinct group (group 1), and all but one of the Columbian sites comprised another distinct cluster (group 2). The Mendocinian sites were spread across six different groups (groups 3–8), which included sites 37–39 from the Montereyan region, all of which are located along the Big Sur, California coast. The Mendocinian groups that included mainly northern sites (groups 3–5) grouped most closely with the Columbian sites, while sites in the more southern portion of the Mendocinian region (groups 6–8) grouped more closely with Montereyan sites. The majority of the Montereyan sites all formed one distinct group (group 9), including one site (64) from the Ensenadian region. Interestingly, site 64 (Punta Baja) sits along the northern Baja coast, in a well-known strong upwelling region (Castelao *et al.*, 2006; Legaard & Thomas, 2006; Pérez-Brunius *et al.*, 2006), and the intertidal species assemblages are visually remarkably similar to those of the strong upwelling areas along the Montereyan region of the central Californian coast. The southern Californian sites all clustered together (group 10). The Ensenadian sites fell out together in two distinct groups (groups 11 and 12), and the Magdelenan sites all formed another group (group 13).

The two-dimensional structure among sites and the relative spatial separation among sites coded by regions are revealed in the nMDS plot (Fig. 5). Sites within regions generally cluster close together, although there is some scatter, particularly within the Mendocinian region due to its large size and the existence of several distinct groups of sites within this region. The nMDS is useful for determining which sites form the most cohesive groups (e.g. groups 1 and 4). The general geographical configuration of sites from north to south is apparent in the nMDS plot, going from left (northern sites) to right (southern sites).

Distance decay in similarity and environmental correlates

Community similarity among sites decreased significantly with geographical distance (Mantel $r = -0.619$, $P < 0.0001$) and with long-term mean SST (Mantel $r = -0.691$, $P < 0.0001$) (Fig. 6). Since we found the geographical distance to be highly correlated with long-term mean SST (Mantel $r = 0.807$, $P < 0.0001$) we used a partial Mantel test to examine the

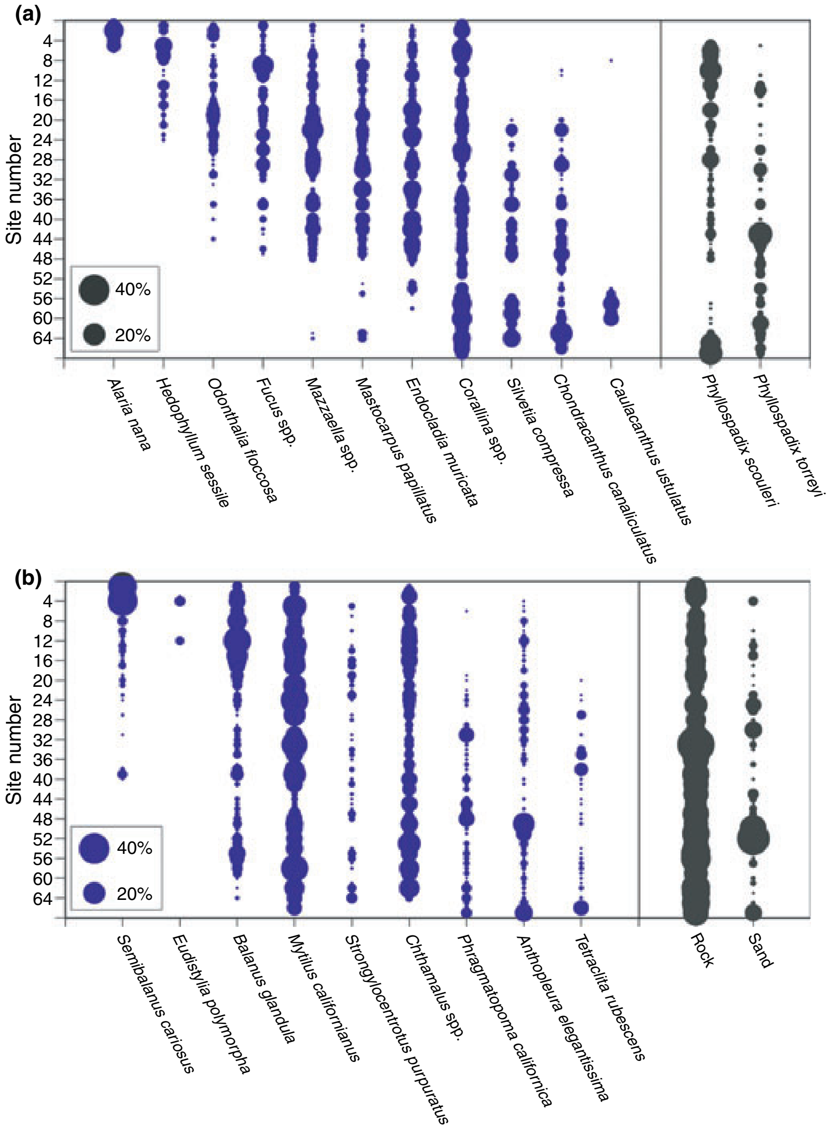

Figure 3 Geographical pattern of distribution and abundance for the most common species throughout the study area (as listed in Appendix S1), and species unique to northern and southern regions of the study area. Sites are represented from north to south and site numbers are referenced in Table 2. The size of each bubble depicts the relative percentage cover for each species at each site. (a) Distribution and abundance pattern for marine algae in the left panel and surfgrasses in the right panel. (b) Distribution and abundance pattern for sessile invertebrates in the left panel and substrate (rock and sand) in the right panel.

relationship between community similarity and ocean conditions while controlling for the effect of geographical distance. We found community similarity to be significantly correlated with long-term mean SST independent of geographical location (Mantel $r = -0.416$, $P < 0.0001$).

Characteristic species

Characteristic taxa for each of the major biogeographical regions are depicted in Fig. 3 and fully described in Appendix S1 in the Supplementary Material. The communities of the Aleutian region were characterized by the barnacles *Semibalanus cariosus* and *Balanus glandula* and the kelp *Alaria nana*, articulated coralline algae *Corallina* spp. and the red alga *Odonthallia floccosa*, as well as a large amount of bare space. Site 4 (Tow Hill), an outlier from the Columbian region, overlapped in species composition with the Aleutian sites, with high *A. nana* and *S. cariosus* cover. This similarity to Aleutian sites is apparent in the placement of Tow Hill in both the dendogram and nMDS. Barnacle cover at Tow Hill was exceptionally high, at 45% (10% *B. glandula* and 35% *S. cariosus*). Regional similarity in the Columbian region was characterized by *Corallina* spp., the brown alga *Hedophyllum sessile*, the surfgrass *Phyllospadix scouleri*, and the mussel *Mytilus californianus*. In the Mendocinian province (the largest geographically), communities were characterized by the mussel *M. californianus*, barnacles in the genus *Chthamalus*, and several species of red algae including *Mazzaella* spp., *Corallina* spp., *Endocladia muricata* and *Mastocarpus papillatus,* and high cover of bare rock. These taxa and substrate were common in both the northern and southern Mendocinian 'sub-regions', but varied in order of importance. One outlier from the Mendocinian region, site 12 (Starfish Point), had nearly equally high barnacle cover to that of Tow Hill, at 40% (30% *B. glandula*, 10% *Chthamalus dalli*/*fissus*). Tow Hill and Starfish Point also shared the distinction of being the only

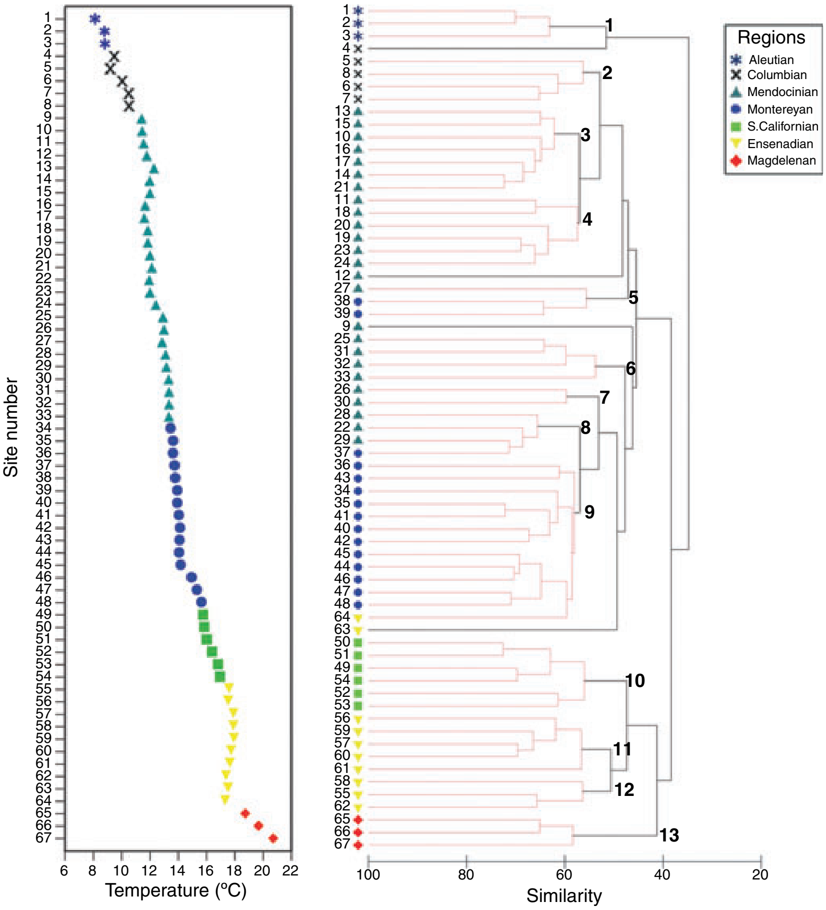

Figure 4 (a) Long term mean sea surface temperature at each site coded by region. (b) Dendrogram depicting sites numbered 1–67 from north to south. Regions are coded by different symbols. Solid lines indicate significant group structure at the 0.1% level. Numbers at the right-hand horizontal terminus of each vertical line indicate the clusters of sites represented in each of the 13 groups. Sites 4, 9, 12 and 63 are relatively unique and do not group with any other sites.

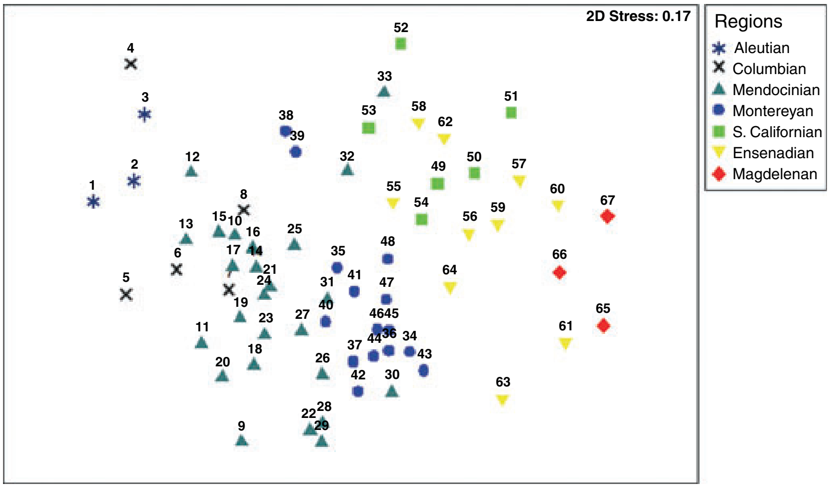

Figure 5 Non-metric multidimensional ordination plot (stress = 0.17) based on the square-root transformed taxon abundance data for each of the 67 sites within the seven biogeographical regions.

two sites where the tube worm, *Eudistylia polymorpha*, was common. Communities in the Montereyan region were characterized by bare rock, red algae such as *Corallina* spp., *E. muricata*, *Petrocelis* spp. and encrusting coralline algae as well as *M. californianus*. The southern Californian region was mainly dominated by abundant amounts of bare rock and sand, *M. californianus*, *Chthamalus* spp. and the sand-tolerant anemones *Anthopleura elegantissima* and *Anthopleura sola*. The Ensenadian province was also dominated by a high proportion of bare space as well as articulated and encrusting coralline algae, *M. californianus*, *Chthamalus* spp. and the fucoid alga *Silvetia compressa*. Finally, the Magdelenan region was characterized by a high proportion of bare rock and the surfgrasses *Phyllospadix scouleri* and *Phyllospadix torreyi*, articulated and encrusting coralline algae and the anemone *A. elegantissima*.

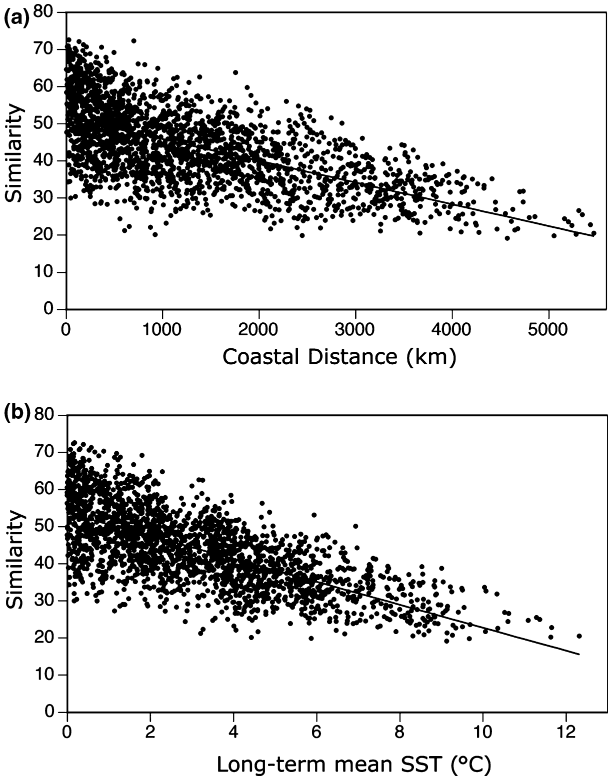

Figure 6 Relationship between community similarity and (a) coastal distance and (b) long-term mean sea surface temperature (SST) difference.

DISCUSSION

The overall results of this study indicate that geographical and environmental distances interact in determining patterns of community similarity, and build upon previous work showing that rates of decay in community similarity are influenced by the climatic characteristics of the region as well as the dispersal properties of the species. The strength of the relationship between community similarity and SST was highly significant, even after accounting for the high degree of spatial autocorrelation in patterns of SST. Although a decay of community similarity with geographical distance may result from other, unmeasured, environmental factors that are spatially autocorrelated (e.g. day length, rainfall, etc.), long-term mean SST provides a reasonable index of oceanographic conditions known to influence benthic community structure (Broitman *et al.*, 2005; Blanchette *et al.*, 2006).

The distribution and abundance of marine species on large geographical scales is governed by large-scale dispersal and influenced by oceanographic conditions (Hubbs, 1948; Druehl, 1978, 1981; Bolton, 1986; Broitman *et al.*, 2001; Schiel *et al.*, 2004; Blanchette *et al.*, 2006). Most invertebrates have a planktonic larval phase and larval dispersal is strongly influenced by oceanographic conditions (Roughgarden *et al.*, 1988; Shanks, 1995; Caley *et al.*, 1996; Connolly *et al.*, 2001). Benthic communities are thus inextricably linked to the broader oceanographic environment through the delivery of food, nutrients, propagules and larvae. The oceanographic processes that drive the delivery of these constituents span large spatial scales and thereby connect distant onshore communities (Dayton & Tegner, 1984; Gaines & Roughgarden, 1985; Bustamante *et al.*, 1995; Polis & Hurd, 1996; Connolly *et al.*, 2001). Recent studies from around the world support a strong coupling between coastal oceanography and nearshore benthic community structure, particularly in regions of strong upwelling and oceanographic variability (Bustamante *et al.*, 1995; Menge *et al.*, 1997a,b, 1999; Broitman *et al.*, 2001).

The overall spatial patterns of community similarity found here are generally consistent with biogeographical regions previously described by Hall (1960, 1964) and Valentine (1966) for molluscs and agree with notable marine biogeographical boundaries (i.e. Point Conception, Monterey Bay) described by Abbott & Hollenberg (1976) for marine algae. These biogeographical patterns largely reflect shifts in relative abundance of taxa, rather than wholesale changes in species assemblages among regions. Many of the most abundant species described here and those characterizing regions were not absent from any region, but had large and consistent differences in abundance among regions. However, there are several exceptions to these general grouping patterns, suggesting that while similar processes may influence the distribution and abundance of species across a broad range of taxa and life histories, there are also important local features such as topography, geology and wave exposure as well as species interactions that may be important drivers of the composition of rocky intertidal communities.

Overall, previously described biogeographical regions were good predictors of site grouping structure. Sites within the Aleutian, southern Californian and Magdelenan regions grouped exclusively with other sites from their respective regions. However, these were also among the smallest groups in both site number and latitudinal coverage (for sites sampled in this study), which may have contributed to their tight group structure, as the amount of within-region variability is more likely to be small with smaller sample sizes. The Columbian, Montereyan and Ensenadaian regions were also well-supported by the grouping structure of sites, although there were some outliers.

These outliers may give us an important insight into the local features of an area that can override the large-scale processes that drive regional grouping patterns. Some of these were complete outliers (sites 4, 9, 12 and 63), grouping with no other sites. These sites had unique physical features that were strikingly different from other sites in their respective regions. For example, site 4 (Tow Hill) was an isolated bench surrounded by sand. This high sand influence is reflected in the types of species that were abundant at the site, which included the sand-tolerant anemone, *Anthopleura elegantissima* and *Acrosiphonia* spp. Other outliers grouped with sites outside their region, and again highlight the importance of localized site features in driving community structure. For example, sites in the Montereyan region form a single cluster along with one additional site, 64 (Punta Baja), from the Ensenadian region (group 6). The oceanographic environment in the Montereyan region is characterized by strong and continuous upwelling (Huyer, 1983; Strub & James, 1995; Lynn *et al.*, 2003; Huyer *et al.*, 2005; Pickett & Schwing, 2006). The northern coast of Baja is also characterized by strong upwelling (Lluch-Belda *et al.*, 2003; Castelao *et al.*, 2006; Legaard & Thomas, 2006; Pérez-Brunius *et al.*, 2006), and Punta Baja is located at one of the major upwelling centres on the coast of northern Baja. Clustering of these upwelling-dominated sites supports the strong contribution that oceanographic conditions make to community structure.

All of the biogeographical regions referred to in this paper are delimited by coastal features associated with transitions in oceanographic conditions and/or changes in geomorphology (i.e. long stretches of sandy beaches, changes in coastline orientation). Our results support the existence of traditionally described biogeographical boundaries functioning as boundaries to species similarity at the community level. For example, Point Conception, which is a well-established biogeographical boundary in the traditional sense, may also function as a boundary to community similarity for species whose ranges do not end in this region. Our results show a clear break between the Montereyan and southern Californian regions, and although some species distributions end in this region, the transition in community structure around Point Conception is due mainly to a more gradual shift in the relative dominance of wide-ranging species. Out of the 296 taxa recorded in our surveys, only 127 were found exclusively north, and 47 exclusively south, of Point Conception.

The identification of distinct benthic marine biogeographical regions has important implications for conservation, particularly to ensure that representative sites and their characteristic assemblages within regions are protected. Marine reserves are becoming an important tool for conservation worldwide, and among their many purposes are intended to protect biodiversity and ecosystem functions as well as individually targeted species. At the present time in the USA, the state of California is embarking on the design of a large group of marine protected areas which will span much of the west coast of the USA. The community-based approach to understanding biogeographical pattern is particularly relevant to conservation planning because regional differences in the abundance of some taxa may reflect important ecological differences, such as contrasting trophic patterns, that may indicate important ecosystem processes. The concept of ecosystem-based management explicitly recognizes the importance of these tight connections among species and habitats and their importance for ecosystem functions. The inclusion of different community assemblages in marine protected areas is likely to include the distinct smaller and/or rarer taxa, which are usually not well sampled or studied.

Understanding the processes underlying coastal biogeographical patterns is also essential for forecasting the impacts of climate change. This study provides evidence that temperature plays a key role in the observed biogeographical patterns, and future changes in SST may alter the structure of these communities in unpredictable ways. Many climate change scenarios predict geographically patchy temperature changes (IPCC, 2001; Helmuth *et al.*, 2006b) and may act to further divide biogeographical regions or alternatively to homogenize large regions. The knowledge gained from the present study of the distribution and abundance of coastal marine species will help to provide a baseline across a large geographical scale against which the potential anthropogenic and natural changes of the future may be assessed.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Characteristic taxa (top 10) for each of the biogeographical regions as determined by SIMPER analysis

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2008.01913.x (This link will take you to the article abstract).

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