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The biogeography and community structure of kelp forest macroinvertebrates

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Abstract

Understanding species distributions and their community structure is increasingly important when taking an ecosystem-based approach to conservation and management. However, knowledge of the distribution and community structure of species in mid-range trophic levels (*e.g.* macroinvertebrates) is lacking in most marine ecosystems. Our study aimed to examine the spatial distribution and community-level biogeographic patterns of common kelp forest–rocky reef macroinvertebrates in Southern California and to evaluate the effects of environmental gradients on these communities. Quantitative SCUBA surveys were used to estimate macroinvertebrate densities at 92 sites from 2008–2012. Non-metric multidimensional scaling was used to evaluate spatial patterns of macroinvertebrate communities among Regions. We found that kelp forest–rocky reef macroinvertebrate communities are distinct among different island and mainland regions, and their community patterns exhibited a strong relationship with an environmental gradient (*i.e.* sea surface temperature) even after controlling for geographic distance between sites. High abundances of urchin species (*Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus*) were strong drivers of regional differences. Macroinvertebrate community patterns were driven by characteristic species that were typically more prevalent at warmer or colder sites. Our results provide the first quantitative analysis of macroinvertebrate community structure within the California kelp forest ecosystem. We also describe the distribution and abundance of 92 conspicuous kelp forest-rocky reef macroinvertebrates among nine pre-defined Regions. This study provides important preliminary information on these macroinvertebrate species that will be directly useful to inform management of invertebrate fisheries and spatial protection of marine resources.

Introduction

As ecologists move towards an ecosystem-based approach to spatial (e.g. Marine Protected Areas) and fisheries management (Lester *et al.* 2013), understanding species ranges and distributions is increasingly important (Airamé *et al.* 2003; Lourie & Vincent 2004). Understanding the ranges of species at each trophic level within an ecosystem as well as how oceanographic variables influence those spatial distributions is essential information for proper management of marine resources (Smith & Jon 1999; Blanchette *et al.* 2009).

In the Southern California Bight (SCB), biogeography has been a key topic of interest because the region spans a major environmental gradient and represents one of the most important oceanographic discontinuities on the west coast of North America (Burton 1998). This area ranges from Point Conception to the US–Mexico border, and contains a number of inter-mixing circulation patterns (Dong *et al.* 2009). These currents are domi-

nated from the north by the California current, a southeastern boundary current that brings strong coastal upwelling particularly in the northern portion of the SCB (Bray *et al.* 1999). The SCB is influenced from the south by the Southern California counter-current and the presence of the eight Channel Islands, which further complicates current patterns (Dong & McWilliams 2007). These complex current systems create a wide range of temperatures within relatively small geographic areas. Largely due to its location in the middle of the oceanographic transition zone between the cold Oregonian and warm San Diegan marine provinces, the SCB is home to a diverse assemblage of rocky reef fishes, invertebrates and algae (Dayton 1985; Pondella *et al.* 2005). The majority of these species live in giant kelp (*Macrocystis pyrifera*) forests, which are critical habitats for most marine species along the California coast (Dayton 1985; Holbrook *et al.* 1990). The benthic macroinvertebrate community within this system is dynamic and its structure is influenced heavily by temperature, geography, reef geomorphology, larval distribution, kelp canopy and understory algal cover, and other community dynamics (Tegner & Dayton 1981; Gaines *et al.* 1985; Steneck *et al.* 2003; Lafferty 2004; Levenbach 2008; Arkema *et al.* 2009; Hamilton *et al.* 2010). The community structure of benthic macroinvertebrates has not yet been studied extensively; however, this knowledge is increasingly important in understanding kelp forest ecosystem dynamics.

Hewatt (1946) recognized the potential importance of biogeography and the varied temperature regimes within the SCB, particularly around the Channel Islands. Subsequent studies have related patterns of biogeography to the major sea surface temperature (SST) gradients across the SCB for kelp forest fishes (Pondella *et al.* 2005; Hamilton *et al.* 2010), rocky inter-tidal invertebrates (Seapy & Littler 1980; Broitman *et al.* 2005; Blanchette *et al.* 2006, 2008, 2009) and inter-tidal macroalgae (Murray *et al.* 1980; Blanchette *et al.* 2008). Much of the work carried out on inter-tidal invertebrate community structure in relation to SST has been focused studies on Santa Cruz Island (Broitman *et al.* 2005; Blanchette *et al.* 2006), which is part of the Northern Channel Island chain and is located at the confluence of warm and cold ocean current systems. For inter-tidal filter-feeding invertebrates, a strong positive correlation was found with increased SST (Broitman *et al.* 2005; Blanchette *et al.* 2006), whereas inter-tidal macroalgae were found to be in highest abundance where average SST was persistently low (Blanchette *et al.* 2006). There has been extensive long-term monitoring of kelp forest communities focused on the Channel Islands National Marine Sanctuary in the northern part of the SCB. This has been conducted by the U.S. National Park Service since 1982 (Kushner *et al.* 2013) and by The Partnership for Interdisciplinary Studies of Coastal Oceans (PISCO) since 1999 (www.piscoweb.org). However, very limited information exists on the marine invertebrate community structure on nearshore rocky reefs along the southern part of the SCB mainland coast and the Southern Channel Islands.

In general there has been a lack of published information on the distribution and abundances of most kelp forest–rocky reef macroinvertebrate species, which is problematic when we are aiming to conserve biodiversity [*i.e.* one goal of California's Marine Life Protection Act, passed in 1999, see CDFG (2008)]. From a fisheries standpoint, kelp forest invertebrates now make up a large percentage of the commercial fishing catch value in California (Kildow & Colgan 2005); two fisheries alone account for a large portion of this total: California spiny lobster (*Panulirus interruptus*) and red sea urchin (*Strongglocentrotus franciscanus)* (CDFW 2013). The majority of these fisheries' landings occurs in Southern California; the red sea urchin fishery is largely restricted to the southern portion of the state due to the sea otter's range to the north (Rogers-Bennett 2013), whereas the California spiny lobster's range is only south of Point Conception. In recent years, commercial fisheries for other invertebrate species have emerged in Southern California ['emerging fishery species' – *e.g.* giant keyhole limpet (*Megathura crenulata*), Kellet's whelk (*Kelletia kelletii*) and wavy turban snail (*Megastraea undosa*), as well as sea cucumbers (*Parastichopus parvimensis* and *Parastichopus californicus*)]. This has raised concerns from resource managers due to the general paucity of life history, abundance and distributional data on these species (CDFG 2001, 2010). Therefore, baseline information on these species is needed to further understand benthic structure, community dynamics and large-scale ecological processes within California kelp forests.

This study assessed whether there are distinct macroinvertebrate communities within the SCB and its varied habitats and environments. To address this question, nine 'regions' within the study area were defined *a priori* based on geographic location (island *versus* a mainland area), and known biogeographic and habitat breaks. A study with similar analyses was performed with fish communities separated out into distinct island 'Regions' in the Northern Channel Islands (Hamilton *et al.* 2010). Hamilton *et al.* (2010) demonstrated a statistical benefit of incorporating biogeography *(i.e.* Region-scale community differences) into an evaluation of the impacts of Marine Protected Areas (MPAs) on species-level densities. This type of information will be important for future assessments in regards to spatial protection (*i.e.* MPAs) and associated changes in population abundances. The kelp forest–rocky reef macroinvertebrate analyses pro-

vided here are central to knowledge of the baseline community structure of these important species (both to fisheries and ecologically) in the SCB.

We expected macroinvertebrate communities to exhibit a high degree of spatial structure that relates to large-scale patterns in SST, similar to what has been observed in kelp forest fishes and inter-tidal invertebrates across the SCB (Pondella *et al.* 2005; Blanchette *et al.* 2008, 2009; Hamilton *et al.* 2010). In this study we explored (i) the spatial distributions, abundances and community structure of kelp forest–rocky reef macroinvertebrate species within nine predefined regions. We then (ii) tested for community differences among regions and described characteristic species that define each region. Finally, (iii) we explored the relationship between long-term patterns in SST and community structure across the study area.

Methods

Study area and data set

We conducted quantitative surveys using a standardized comprehensive monitoring protocol using SCUBA (for details of methods see Gillett *et al.* 2011; MME 2011; Claisse *et al.* 2012; Pondella *et al.* 2015). Surveys were conducted during annual summer/fall field seasons from 2008 through 2012. In rare cases the field season extended until January or early February of the following calendar year. These were part of multiple large spatial scale sampling efforts (Bight'08 2008; Claisse *et al.* 2012) including the baseline sampling in 2011 and 2012 for the new network of MPAs in the study area (MME 2011; Pondella *et al.* 2015). The 2012 surveys occurred during the year just following MPA implementation and thus the decreased fishing effort within MPAs was assumed to not be impacting the results. Ninety-two reef sites were sampled for between 1 and 4 years each. Forty one of these sites were distributed over four islands, San Nicolas, Santa Barbara, Santa Catalina, and San Clemente Islands, and another 50 sites were on the mainland coast from Malibu to Point Loma as well as one offshore pinnacle reef (Begg Rock) located 12.8 km northwest of San Nicolas Island (Fig. 1).

Sampling at each site followed a stratified random sampling design in which randomly located transects were sampled within fixed reef zones separated out by depth: inner (~5 m), middle (~10 m), outer (~15 m) and deep (~25 m). Only zones with rocky reef habitat were sampled at a given site. All sites used in these analyses included at least two depth zones. Two 30 m by 2 m (60 m^2) benthic band transects were completed per zone,

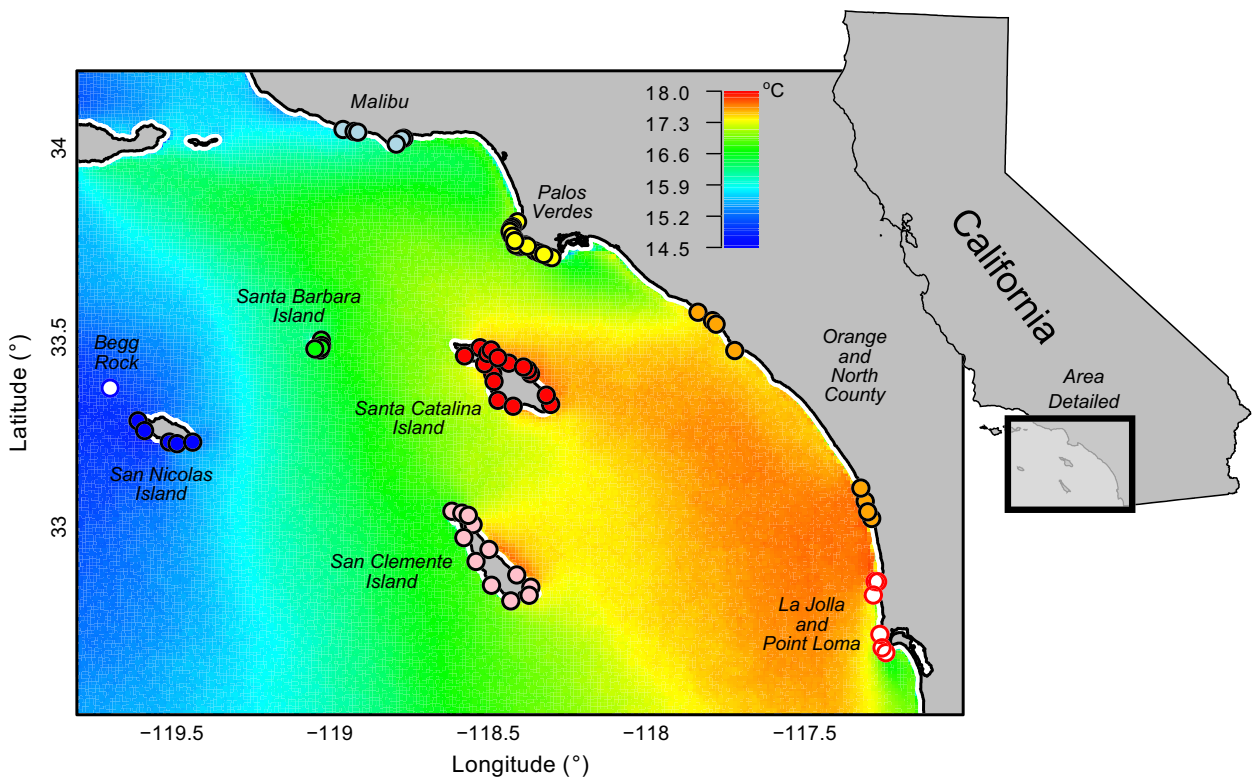

Fig. 1. Map of the 92 sites in each of the nine regions with mean sea surface temperature (Moderate Resolution Imaging Spectroradiometer, MODIS SST) from 2000–2012.

recording the densities of conspicuous (≥2.5 cm) mobile and sessile macroinvertebrates. This follows the standardized CRANE (Cooperative Resource Assessment of Nearshore Ecosystems) protocol for long-term monitoring developed specifically for these habitats (Bight'08 2008; Hamilton *et al.* 2010; Gillett *et al.* 2011; Claisse *et al.* 2013; Pondella *et al.* 2015). Cracks and crevices were searched within the transect area; any organism with more than half of its body inside the transect area was counted. 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. No organisms were removed from the substrate during sampling. The species listed in Table 1 represent all macroinvertebrates (≥2.5 cm) counted on transects that were identified to species in this data set (some groups identified to genus only were removed from analyses). We calculated mean macroinvertebrate species site-specific densities by first averaging transect densities within zones, then zones across years (on rare occasions not every zone was sampled each year), then zones within each site. We also report the means and standard errors of sites within each region. Raw and summarized data are available upon request from the corresponding author.

Data analysis

To examine geographic patterns in the macroinvertebrate communities, a similarity matrix was constructed using square root-transformed density and the Bray–Curtis similarity co-efficient. Two-dimensional, non-metric multidimensional scaling (nMDS) was used to examine patterns among communities at sites using the 'metaMDS' function in the 'vegan' package (Oksanen *et al.* 2013) in R (R Core Team 2013). This was followed by testing for significant differences among regions using the 'adonis' permutational multivariate analysis of variance (PERMANOVA) function and testing for homogeneity of multivariate dispersions with the 'betadisper' function, both functions from the 'vegan' package. PERMANOVA *post-hoc* tests for significant pairwise differences among regions were also performed. Characteristic species for each region were identified using similarity percentage (SIMPER) breakdown analyses (Clarke 1993). Owing to lack of site replication (n = 1), the Begg Rock region was not included in the analyses comparing regions.

SST analyses

Long-term averages of SST for all sites were obtained from merged Moderate Resolution Imaging Spectroradiometer (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 (LTER) (available from http://spg.ucsd.edu/Satellite_data/California_Current/). We averaged these over the entire period available: 24 February 2000 through 31 December 2012 (Fig. 1). Patterns of SST were also visualized across the nMDS ordination 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 (Wood 2003; Oksanen *et al.* 2013). We then used Mantel tests to examine the correlations between macroinvertebrate community similarity and geographic distance or between macroinvertebrate community similarity and differences in long-term mean SST among sites using the 'mantel' function in the R 'vegan' package. Due to clear autocorrelation between SST and geographic distance, this was followed by partial Mantel tests (Legendre & Legendre 1998) using the 'mantel.partial' function in the same package. This test permits controlling for a third factor (here either SST or geographic distance) when examining the correlation between two other factors (here either SST or geographic distance with macroinvertebrate community similarity) (Fortin & Payette 2002; Blanchette *et al.* 2009).

Results

Species composition and regional differences

We identified a total of 92 species of kelp forest–rocky reef macroinvertebrates from six different phyla and 12 classes on transects (Table 1). There were significant community level differences among regions [R adonis PERMANOVA: $F_{8,83} = 11.9$, partial $R^2 = 0.53$, Pr(>F) = 0.001]. However, there were no significant differences in the dispersions among sites within regions [R betadisper: $F_{7,83} = 0.68$, Pr (>F) = 0.70], *i.e.* variances were homogeneous, and therefore the PERMANOVA results can be interpreted without additional caution (Anderson 2006). Further, all region pairs were significantly different from each other (Table 2). In the nMDS plot, sites within regions generally clustered together (Fig. 2). The regions in the nMDS plot were also generally arranged in similar patterns as they are found in geographic space, with regions ordered north to south (Fig. 1) being arranged left to right in the nMDS plot (Fig. 2).

Relationship between SST and invertebrate community structure

While sites that are closer together tend to have a more similar average SST (Fig. 1), SST appears to have a stronger relationship with community similarity among sites than with geographic distance. Both SST (Mantel r = 0.5201, P = 0.0001) and geographic distance (Mantel

Table 1. Mean density (individuals·100 m^{-2}) with SE (across site variability) in parentheses for each macroinvertebrate species in each of the nine regions. Further description of sampling effort per region is provided in Table S1.

species	Begg Rock	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Malibu	Palos Verdes	Orange and North County	La Jolla and Point Loma
Acanthodoris lutea							0.01 (0.01)	0.02 (0.02)	
Anthopleura artemisia			0.02 (0.02)	0.01 (0.01)		0.05 (0.05)	0.13 (0.06)	0.12 (0.07)	0.04 (0.03)
Anthopleura elegantissima	1581.94 (NA)	109.12 (106.85)	92.59 (92.59)			0.19 (0.14)	2.43 (2.30)		0.02 (0.02)
Anthopleura sola	15.14 (NA)	31.04 (16.92)	6.23 (0.88)	0.11 (0.09)	0.02 (0.02)	3.08 (1.76)	19.57 (4.93)	1.86 (0.75)	0.33 (0.16)
Anthopleura xanthogrammica							0.04 (0.04)		
Aplysia californica			0.65 (0.20)	0.1 (0.08)	0.02 (0.02)	0.14 (0.14)	0.35 (0.10)		0.02 (0.02)
Aplysia vaccaria			0.28 (0.28)	0.08 (0.05)			0.04 (0.02)		
Astrometis sertulifera			0.14 (0.11)	0.08 (0.03)				0.02 (0.02)	
Astropectin armatus						0.12 (0.08)	0.04 (0.02)		
Baptodoris mimetica							0.03 (0.01)		0.21 (0.17)
Berthella californica			0.1 (0.10)				0.01 (0.01)		0.02 (0.02)
Cadlina flavomaculata							<0.01 (<0.01)		
Cadlina limbaughorum							<0.01 (<0.01)		
Cadlina luteomarginata							0.03 (0.02)		0.03 (0.03)
Calliostoma annulatum							0.01 (<0.01)		
Cancer anthonyi							<0.01 (<0.01)	0.03 (0.03)	
Centrostephanus coronatus			5.77 (2.13)	33.96 (8.04)	16.44 (6.58)	0.09 (0.09)	0.02 (0.01)	0.07 (0.05)	0.02 (0.02)
Ceratostoma foliatum				0.1 (0.05)	0.02 (0.02)		<0.01 (<0.01)		0.03 (0.03)
Chromodoris macfarlandi				0.01 (0.01)			<0.01 (<0.01)		
Craniella arb			0.02 (0.02)		0.02 (0.02)		0.16 (0.05)	0.07 (0.07)	0.17 (0.07)
Crassedoma giganteum	62.64 (NA)	0.67 (0.39)	1.27 (0.55)	1.2 (0.34)	0.7 (0.23)	0.19 (0.14)	0.28 (0.09)	1.06 (0.60)	0.06 (0.04)
Cryptochiton stelleri					0.01 (0.01)				
Cypraea spadicea	7.36 (NA)	0.33 (0.33)	0.73 (0.35)	0.17 (0.13)	0.05 (0.04)	0.19 (0.19)	0.2 (0.07)	0.17 (0.11)	0.11 (0.09)
Dermasterias imbricata	2.64 (NA)	0.38 (0.25)				0.28 (0.28)	<0.01 (<0.01)		0.07 (0.07)
Diaulula sandiegensis							0.12 (0.06)	0.03 (0.03)	0.14 (0.14)
Doriopsilla albopunctata	0.42 (NA)	0.08 (0.08)				0.14 (0.14)	0.03 (0.02)		
Doris montereyensis							<0.01 (<0.01)	0.03 (0.03)	0.02 (0.02)
Epiactis prolifera							<0.01 (<0.01)	0.07 (0.07)	
Eugorgia rubens				1.27 (1.27)	0.73 (0.28)		0.88 (0.58)		
Flabellina iodinea			0.22 (0.11)	0.03 (0.02)			0.37 (0.10)		0.05 (0.04)
Haliotis corrugata				0.32 (0.08)	0.49 (0.16)		0.02 (0.01)	0.05 (0.04)	0.14 (0.07)
Haliotis fulgens				1.26 (0.35)	0.05 (0.02)		<0.01 (<0.01)	0.07 (0.05)	0.31 (0.17)
Haliotis kamtschatkana assimilis							<0.01 (<0.01)		0.02 (0.02)
Haliotis sorenseni							0.01 (0.01)		
Henricia leviuscula	0.28 (NA)	0.63 (0.40)	0.06 (0.04)	0.16 (0.07)	0.58 (0.24)	0.09 (0.06)	0.25 (0.08)	0.03 (0.03)	0.59 (0.27)
Hermissenda crassicornis	0.42 (NA)		0.14 (0.10)	0.01 (0.01)	0.02 (0.02)		0.16 (0.07)		
Holothuria zacae				0.01 (0.01)					

Table 1. Continued

species	Begg Rock	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Malibu	Palos Verdes	Orange and North County	La Jolla and Point Loma
Janolus barbarensis				0.01 (0.01)					
Kelletia kelletii			0.21 (0.18)	0.76 (0.22)	0.12 (0.04)	5.14 (2.66)	7.72 (0.77)	1.55 (0.58)	1.44 (0.44)
Leptogorgia chilensis			7.2 (2.88)	0.37 (0.14)	3.94 (1.45)	1.37 (0.52)	3.64 (1.36)	0.1 (0.07)	0.43 (0.28)
Limacia cockerelli							0.01 (0.01)		
Linckia columbiae	0.56 (NA)		0.2 (0.13)	1.02 (0.20)	1.24 (0.30)		0.08 (0.04)	0.33 (0.13)	0.02 (0.02)
Lithopoma gibberosum			0.09 (0.09)	0.01 (0.01)			0.03 (0.01)		
Loxorhynchus grandis							0.02 (0.01)		
Lytechinus anamesus			4.61 (3.67)		0.02 (0.02)	0.67 (0.36)	3.34 (2.98)		
Mediaster aequalis			0.03 (0.03)						
Megastraea undosa		0.5 (0.20)	2.04 (0.74)	11.65 (3.16)	1.66 (0.40)	0.09 (0.06)	1.82 (0.45)	7.29 (3.64)	1.94 (0.47)
Megathura crenulata	3.89 (NA)	0.79 (0.25)	1.29 (0.71)	4.27 (1.44)	2.14 (0.56)	1.37 (0.64)	2.22 (0.42)	2.07 (0.61)	2.34 (1.15)
Metridium senile	3970 (NA)								
Mexichromis porterae							0.02 (0.02)		
Muricea californica			1.56 (0.43)	6.68 (1.67)	9.09 (3.64)	26.18 (5.10)	15.49 (3.03)	22.31 (4.55)	0.43 (0.23)
Muricea fruticosa			0.28 (0.12)	7.31 (2.30)	0.71 (0.18)	5.76 (2.22)	1.29 (0.48)	2.99 (0.93)	
Navanax inermis					0.01 (0.01)		0.02 (0.02)		
Norrisia norrisi			0.36 (0.16)	0.73 (0.25)	0.76 (0.25)		0.39 (0.11)	0.31 (0.13)	0.14 (0.05)
Octopus bimaculoides	0.14 (NA)		0.05 (0.05)	0.07 (0.03)	0.02 (0.01)		0.05 (0.02)	0.09 (0.04)	0.03 (0.03)
Octopus rubescens							<0.01 (<0.01)		
Okenia rosacea							0.01 (0.01)		
Ophioderma panamense			0.07 (0.07)				0.28 (0.13)		
Ophioplocus esmarki							0.03 (0.02)		
Orthasterias koehleri			0.02 (0.02)				0.04 (0.02)		0.13 (0.05)
Pachycerianthus fimbriatus			0.82 (0.50)	1.06 (0.52)	0.2 (0.07)	1.81 (1.37)	1.85 (0.35)	0.85 (0.43)	0.05 (0.04)
Pandalus danae							<0.01 (<0.01)		
Panulirus interruptus			0.54 (0.33)	3.47 (0.75)	8.03 (3.83)		0.27 (0.06)	1.46 (0.53)	3.03 (1.01)
Parastichopus californicus		0.17 (0.17)		0.18 (0.14)	0.01 (0.01)	0.19 (0.14)	0.21 (0.08)		
Parastichopus parvimensis		3.08 (2.02)	4.12 (1.03)	2.72 (0.94)	3.45 (0.97)	1.67 (1.36)	3.08 (0.45)	2.2 (1.92)	0.11 (0.09)
Patiria miniata	1.39 (NA)	20.21 (2.81)	17.77 (7.52)	0.02 (0.01)	0.02 (0.02)	30.25 (7.40)	32.6 (4.30)	1.32 (0.78)	11.3 (5.71)
Peltodoris nobilis			0.17 (0.17)				0.44 (0.10)		0.13 (0.07)
Phyllactis bradleyi			23.22 (17.26)				0.05 (0.04)		0.05 (0.05)
Pisaster brevispinus						7.04 (4.03)	0.61 (0.14)	0.03 (0.03)	0.25 (0.23)
Pisaster giganteus	6.53 (NA)	10.5 (2.07)	7.48 (2.22)	1.68 (0.43)	2.75 (0.87)	17.85 (2.12)	15.9 (1.58)	3.37 (0.54)	4.73 (1.91)
Pisaster ochraceus	187.22 (NA)	0.83 (0.53)	2.65 (2.03)	0.02 (0.02)		4.31 (4.03)	5.47 (0.89)	0.03 (0.03)	
Pododesmus macroschisma				0.04 (0.02)			<0.01 (<0.01)		
Polycera tricolor							<0.01 (<0.01)		
Prostheceraeus bellostriatus								0.02 (0.02)	
Pugettia producta							0.04 (0.02)		
Pugettia richii						0.07 (0.07)			

Table 1. Continued

species	Begg Rock	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Malibu	Palos Verdes	Orange and North County	La Jolla and Point Loma
Pycnopodia helianthoides		3.71 (1.34)	0.05 (0.05)			0.12 (0.08)	0.29 (0.07)		0.02 (0.02)
Sclerasterias heteropaes							0.01 (0.01)		
Strongylocentrotus franciscanus	6.94 (NA)	95.17 (47.35)	308.36 (65.47)	9.62 (2.08)	44.13 (11.18)	110.72 (30.42)	58.12 (10.01)	21.11 (12.12)	8.43 (2.67)
Strongylocentrotus purpuratus	153.47 (NA)	116.96 (51.73)	777.46 (389.03)	4.26 (1.40)	9.5 (3.14)	199.31 (116.71)	415.52 (86.93)	9.32 (6.13)	13.46 (9.87)
Styela montereyensis		0.71 (0.32)				23.31 (9.31)	1.26 (0.36)	0.69 (0.50)	0.24 (0.17)
Taliepus nuttallii				0.02 (0.01)					0.05 (0.05)
Tegula regina		0.08 (0.08)	2.43 (1.84)	0.04 (0.02)	0.02 (0.02)		0.19 (0.05)		0.03 (0.03)
Tethya californiana	4.58 (NA)	12.04 (3.67)	1.84 (0.89)	0.09 (0.08)	2.01 (1.13)	6.18 (2.34)	7.44 (1.28)	1.51 (0.50)	2.46 (0.98)
Tetilla sp. B							0.14 (0.05)		0.02 (0.02)
Trikentrion catalinae							<0.01 (<0.01)	0.03 (0.03)	0.05 (0.05)
Triopha catalinae							0.02 (0.01)		
Tritonia festiva							<0.01 (<0.01)		
Tylodina fungina								0.02 (0.02)	
Urticina columbiana			0.14 (0.14)				<0.01 (<0.01)		
Urticina lofotensis	1.25 (NA)	31.25 (19.40)	0.03 (0.03)	0.01 (0.01)			<0.01 (<0.01)		
Urticina mcpeaki		0.21 (0.21)	6.75 (5.78)	0.04 (0.03)	0.07 (0.04)		0.29 (0.06)	0.3 (0.13)	0.68 (0.28)

NA = not estimated due to there only being one site in this Region.

Table 2. Permutational multivariate analysis of variance R^2 statistics from pairwise *post-hoc* tests of significant differences in community structure between regions. Statistically significant values are indicated by * [Pr (>F) < 0.05] and ** [Pr(>F) < 0.005].

	San Nicolas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Malibu	Palos Verdes	Orange and North County
Santa Barbara Island	0.40**						
Santa Catalina Island	0.49**	0.44**					
San Clemente Island	0.49**	0.42**	0.13**				
Malibu	0.38**	0.39**	0.44**	0.43**			
Palos Verdes	0.16**	0.15**	0.47**	0.37**	0.10*		
Orange and North County	0.50**	0.50**	0.24**	0.25**	0.36**	0.28**	
La Jolla and Point Loma	0.47*	0.51**	0.28**	0.28**	0.46**	0.26**	0.22**

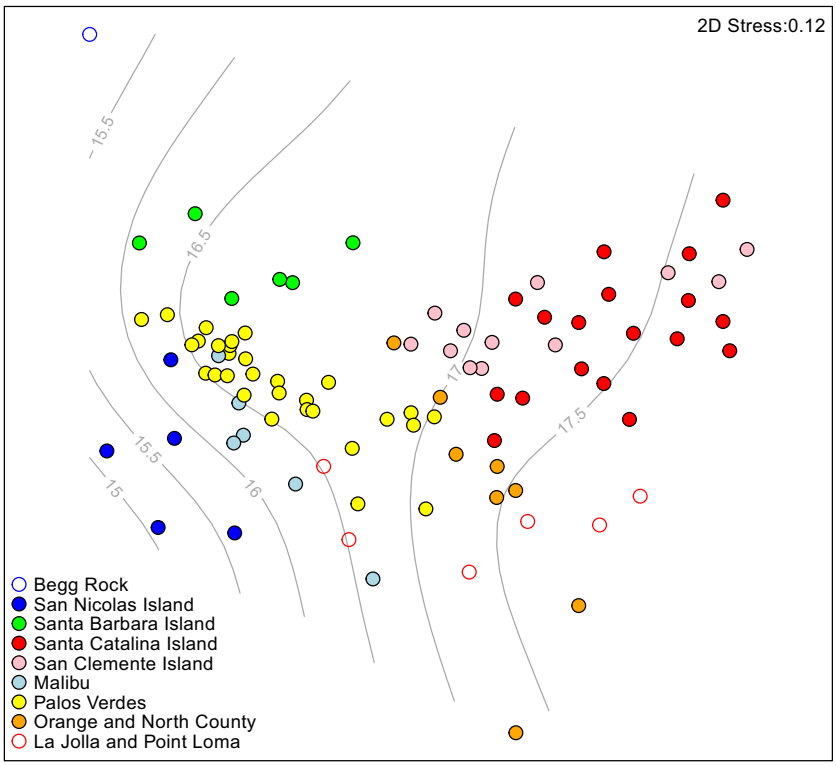

Fig. 2. Non-metric multidimensional scaling ordination plot of invertebrate communities using Bray–Curtis similarity based on the square root-transformed species density data for each of the 92 sites across the nine regions overlaid on a fitted sea surface temperature surface (gray contour lines: °C).

r = 0.3769, P = 0.0001) were significantly correlated with community similarity. However, using a partial Mantel test to examine the relationship between community similarity and SST while controlling for geographic distance, the correlation statistic remained relatively high (partial Mantel r = 0.4099, P = 0.0001). Furthermore, examining the relationship between community similarity and geographic distance while controlling for SST, the correlation was reduced more dramatically (partial Mantel r = 0.1467, P = 0.002).

Characteristic species

Characteristic macroinvertebrate species varied among regions (Table 3). In many cases urchins (*Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus*) made the highest contributions to a regional cluster, meaning that within a given region, urchins tended to have similar densities among sites (Table 3). Urchin abundances were in general higher at sites with a lower average SST, varying substantially among regions (Fig. 3, Table 1). *Strongylocentrotus purpuratus* ranged from a high of 777.5 ± 389 individuals·100 m^{-2} at Santa Barbara Island to a low of 4.25 ± 1.39 individuals·100 m^{-2} at Santa Catalina Island (Table 1, Fig. 3). Palos Verdes also had particularly high *S. purpuratus* densities, 415.5 ± 86.9 individuals·100 m^{-2} (Table 1, Fig. 3). For the commercially important red sea urchin (*S. franciscanus*), Santa Barbara Island showed the highest densities (308.4 ± 65.4 individuals·100 m^{-2}), with two other colder regions, San

Table 3. Characteristic species (top 90%) that contributed to the non-metric multidimensional scaling clustering for each region as determined by similarity percentage analysis (SIMPER) in PRIMER. The ranking is determined by S_i, the average contribution of each species to the overall similarity of a region. % contribution is the per cent that a given species contributes to the overall clustering of a region. Cumulative % is the cumulative per cent contribution of a species to the region's overall average similarity (S).

characteristic species	S_i	% contribution	cumulative %
Region – San Nicolas Island (S = 60.78)			
Strongylocentrotus purpuratus	14.35	23.6	23.6
Strongylocentrotus franciscanus	8.65	14.22	37.83
Patiria miniata	8.07	13.28	51.1
Anthopleura sola	6.37	10.49	61.59
Urticina lofotensis	6.04	9.93	71.53
Pisaster giganteus	5.32	8.75	80.27
Tethya californiana	4.94	8.13	88.4
Pycnopodia helianthoides	2.31	3.8	92.2
Patiria miniata	3.33	6.34	84.02
Urticina mcpeaki	1.38	2.64	86.65
Muricea californica	0.88	1.68	88.34
Henricia leviuscula	0.86	1.64	89.98
Haliotis fulgens	0.77	1.47	91.45
region – Santa Barbara Island (S = 60.33)			
Strongylocentrotus purpuratus	19.95	33.07	33.07
Strongylocentrotus franciscanus	17.66	29.27	62.34
Anthopleura sola	2.88	4.77	67.11
Pisaster giganteus	2.50	4.15	71.26
Patiria miniata	2.14	3.54	74.8
Parastichopus parvimensis	2.02	3.35	78.14
Centrostephanus coronatus	1.90	3.15	81.29
Leptogorgia chilensis	1.85	3.06	84.36
Phyllactis bradleyi	1.33	2.2	86.55
Muricea californica	1.14	1.9	88.45
Tethya californiana	1.06	1.76	90.21
region – Santa Catalina Island (S = 55.50)			
Centrostephanus coronatus	10.93	19.69	19.69
Megastraea undosa	6.13	11.05	30.73
Strongylocentrotus franciscanus	5.41	9.75	40.49
Muricea californica	4.82	8.68	49.16
Panulirus interruptus	4.44	8.0	57.17
Muricea fruticose	3.78	6.82	63.99
Strongylocentrotus purpuratus	2.26	4.08	68.06
Parastichopus parvimensis	2.13	3.85	71.91
Pisaster giganteus	2.13	3.83	75.74
Linckia columbiae	2.02	3.64	79.38
Haliotis fulgens	1.97	3.55	82.93
Crassedoma giganteum	1.94	3.49	86.42
Megathura crenulata	1.86	3.35	89.76
Kelletia kelletii	1.57	2.83	92.59
Strongylocentrotus purpuratus	15.53	25.41	25.41
Strongylocentrotus franciscanus	8.38	13.71	39.12
Patiria miniata	6.09	9.97	49.08
Pisaster giganteus	5.12	8.37	57.45
Kelletia kelletii	3.70	6.06	63.51
Muricea californica	3.44	5.63	69.14
Anthopleura sola	2.89	4.73	73.87
Tethya californiana	2.78	4.54	78.41
Pisaster ochraceus	1.87	3.06	81.47
Parastichopus parvimensis	1.84	3.01	84.48
Megathura crenulata	1.54	2.52	87
Megastraea undosa	1.10	1.79	88.79
Pachycerianthus fimbriatus	0.96	1.58	90.37
region – San Clemente Island (S = 57.41)			
Strongylocentrotus franciscanus	11.94	20.79	20.79
Centrostephanus coronatus	5.65	9.84	30.64
Panulirus interruptus	5.05	8.8	39.44
Muricea californica	5.02	8.75	48.19
Strongylocentrotus purpuratus	4.53	7.89	56.08
Megastraea undosa	3.28	5.71	61.79
Leptogorgia chilensis	3.08	5.37	67.16
Parastichopus parvimensis	2.88	5.01	72.17
Pisaster giganteus	2.48	4.32	76.49
Linckia columbiae	2.41	4.2	80.7
Megathura crenulata	2.23	3.88	84.58
Norrisia norrisi	1.49	2.6	87.18
Muricea fruticose	1.49	2.6	89.78
Crassedoma giganteum	1.47	2.56	92.34
region – Malibu (S = 61.87)			
Strongylocentrotus franciscanus	12.51	20.22	20.22
Strongylocentrotus purpuratus	10.48	16.94	37.15
Muricea californica	7.43	12.01	49.17
Pisaster giganteus	6.71	10.84	60.01
Patiria miniata	6.54	10.58	70.59
Styela montereyensis	5.27	8.51	79.1
Muricea fruticose	2.85	4.61	83.71
Tethya californiana	2.67	4.32	88.03
Kelletia kelletii	2.14	3.46	91.49
region – Palos Verdes (S = 61.12)			
Strongylocentrotus purpuratus	15.53	25.41	25.41
Strongylocentrotus franciscanus	8.38	13.71	39.12
Patiria miniata	6.09	9.97	49.08
Pisaster giganteus	5.12	8.37	57.45
Kelletia kelletii	3.70	6.06	63.51
Muricea californica	3.44	5.63	69.14
Anthopleura sola	2.89	4.73	73.87
Tethya californiana	2.78	4.54	78.41
Pisaster ochraceus	1.87	3.06	81.47
Parastichopus parvimensis	1.84	3.01	84.48
Megathura crenulata	1.54	2.52	87
Megastraea undosa	1.10	1.79	88.79
Pachycerianthus fimbriatus	0.96	1.58	90.37
region – Orange and North County (S = 54.38)			
Muricea californica	13.21	24.29	24.29
Pisaster giganteus	5.87	10.8	35.09
Strongylocentrotus franciscanus	5.10	9.38	44.47
Megastraea undosa	4.10	7.55	52.02
Strongylocentrotus purpuratus	3.53	6.5	58.52
Megathura crenulata	3.06	5.63	64.15
Kelletia kelletii	3.04	5.58	69.73
Tethya californiana	2.83	5.21	74.93
Muricea fruticose	2.66	4.9	79.83

Table 3. Continued

characteristic species	S_i	% contribution	cumulative %
Anthopleura sola	2.40	4.41	84.24
Panulirus interruptus	1.95	3.59	87.83
Pachycerianthus fimbriatus	1.47	2.71	90.54
region – La Jolla and Point Loma (S = 52.46)			
Strongylocentrotus franciscanus	9.13	17.4	17.4
Panulirus interruptus	5.66	10.78	28.18
Strongylocentrotus purpuratus	5.42	10.32	38.5
Pisaster giganteus	5.13	9.78	48.28
Megastraea undosa	4.38	8.36	56.64
Megathura crenulata	4.06	7.74	64.38
Kelletia kelletii	3.53	6.73	71.11
Tethya californiana	3.44	6.56	77.67
Patiria miniata	3.33	6.34	84.02
Urticina mcpeaki	1.38	2.64	86.65
Muricea californica	0.88	1.68	88.34
Henricia leviuscula	0.86	1.64	89.98
Haliotis fulgens	0.77	1.47	91.45

Nicolas Island and Malibu, also having high densities (95.17 ± 47.4 and 110.72 ± 30.4 individuals·100 m^{-2}, respectively), whereas lower densities were generally found in the warmer regions of La Jolla and Point Loma (8.43 ± 2.67 individuals·100 m^{-2}) and Santa Catalina Island (9.62 ± 2.08 individuals·100 m^{-2}) (Table 1, Fig. 3). However, the lowest regional value was found at Begg Rock (6.94 individuals·100 m^{-2}), a cold-water, offshore pinnacle reef.

The distribution of other individual species also showed distinct patterns related to SST. Invertebrate communities at the southernmost islands of Santa Catalina and San Clemente were characterized by higher densities of warmer-water associated species such as California spiny lobster (*Panulirus interruptus*) (3.47 ± 0.75 and 8.03 ± 3.83 individuals·100 m^{-2}, respectively) and crowned sea urchin (*Centrostephanus coronatus*) (33.9 ± 8.03 and 16.4 ± 6.58 individuals·100 m^{-2}, respectively) (Fig. 4A,B, Table 1). The crowned sea urchin also showed elevated densities at Santa Barbara Island. Overall, this species was seen more at the island sites than in the mainland regions. Colder regions (*e.g.* Palos Verdes and San Nicolas Island) were characterized by higher densities of bat stars (*Patiria miniata*) and solitary green anemones (*Anthopleura sola*) (Fig. 4C,D, Table 1).

In general, the emerging fishery species were more abundant in the mainland Regions than at the islands (Table 1). The highest density values for giant keyhole limpet (*Megathura crenulata*) were seen in the La Jolla and Point Loma, Orange and North County, and Palos Verdes regions: 2.33 ± 1.15, 2.06 ± 0.61 and 2.21 ± 0.41 individuals·100 m^{-2}, respectively. For Kellet's whelk (*Kelletia kelletii*), the highest densities were observed in the Palos Verdes, La Jolla and Point Loma, and Orange and North County regions: 7.71 ± 0.77, 1.44 ± 0.44 and 1.55 ± 0.85 individuals·100 m^{-2}, respectively. The wavy turban snail (*Megastraea undosa*) was the only exception to this mainland dominance pattern, with its highest density found at Santa Catalina Island (11.65 ± 3.16 individuals·100 m^{-2}), although the next highest values were in the Orange and North County, and La Jolla and Point Loma regions: 7.29 ± 3.64 and 1.94 ± 0.47 individuals·100 m^{-2}, respectively.

Discussion

This study represents the first quantitative description of kelp forest–rocky reef macroinvertebrate community biogeography in Southern California. Communities within the *a priori* defined mainland and island regions were significantly different from each other. Across the study area, while sites closer to each other tended to have similar communities, site differences were also correlated with long-term patterns in SST after controlling for geographic distance between sites. These findings are consistent with

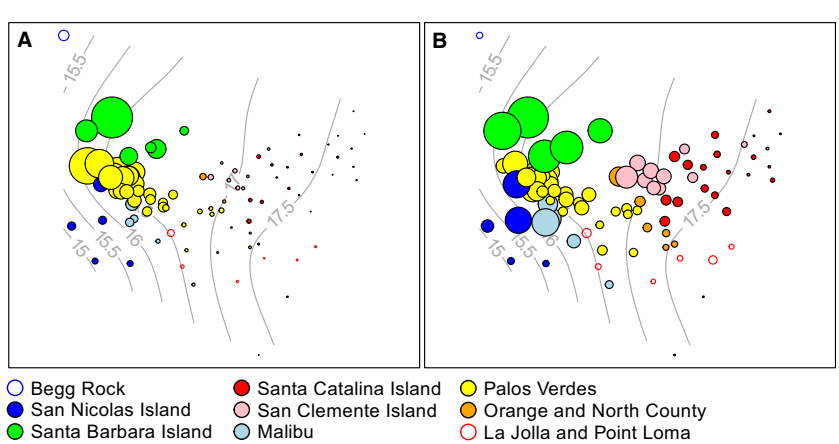

Fig. 3. Non-metric multidimensional scaling ordination plot of invertebrate communities with circles scaled to the square root-transformed density of (A): *Strongylocentrotus purpuratus* and (B): *Strongylocentrotus franciscanus* for each of the 92 sites across the nine regions overlaid on a fitted sea surface temperature surface (gray contour lines: °C).

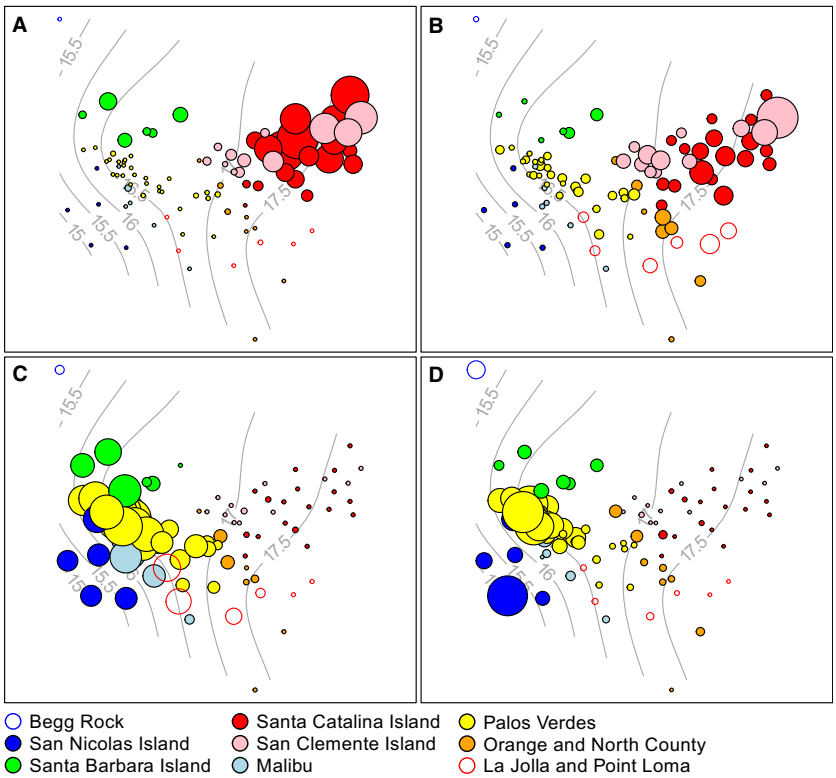

Fig. 4. Non-metric multidimensional scaling ordination plot of invertebrate communities with circles scaled to the square root-transformed density of two warm water-associated species, (A): *Centrostephanus coronatus* and (B): *Panulirus interruptus*, and two cold water-associated species, (C): *Patiria miniata* and (D): *Anthopleura sola*, for each of the 92 sites across the nine regions overlaid on a fitted sea surface temperature surface (gray contour lines: °C).

those for other rocky reef-associated marine taxa in the SCB that have linked SST to community structure, including fishes (Pondella *et al.* 2005; Hamilton *et al.* 2010) and inter-tidal invertebrates (Blanchette *et al.* 2006, 2008).

While local oceanographic conditions (*e.g.* SST) can shape local invertebrate community structure, potentially by impacting post-settlement processes, larval dispersal patterns also play an important role in determining the community structure of marine invertebrates on nearshore rocky reefs. Many of the macroinvertebrates observed in this study have a planktonic larval stage; their dispersal can be related to their pelagic larval duration (PLD), as well as oceanographic conditions and current patterns circulating around islands and mainland headlands within the SCB (Reed *et al.* 2000; Blanchette *et al.* 2006; White *et al.* 2010; Haupt *et al.* 2013). Connections between current patterns, which drive the average SST, and patterns of invertebrate larval recruitment can be significant, and the spatial variability that this causes in larval transport can have a large effect on benthic community structure (Wing *et al.* 1995; Gaylord & Gaines 2000). Larval settlement of crabs (genus *Cancer*) and urchins (*Strongylocentrotus* spp.) is positively correlated with increased SST, as well as with oceanographic relaxation events following periods of upwelling in Northern California (Wing *et al.* 1995). Pelagic larval duration (PLD) can vary greatly among species (Kelly & Palumbi 2010), and this can have a significant effect on dispersal potential (Reed *et al.* 2000). Wavy turban snails (*Megastraea undosa*) have a short 5–10-day PLD and estimated average dispersal distance of 3 km or less (Haupt *et al.* 2013). White *et al.* (2010) found that for Kellet's whelk (*Kelletia kelletii*), which has a much longer PLD of around 40–60 days, a model of larval dispersal based on ocean currents was a much better predictor of genetic population structure than the physical distance between sites.

One group of benthic macroinvertebrates, sea urchins (*Strongylocentrotus purpuratus* and *Strongylocentrotus franciscanus*), have been the focus of much research in Southern California for several reasons, including: (i) the existence and persistence of urchin barrens and their associated dynamics within and among kelp forest habitats (Graham 2004; Byrnes *et al.* 2013), (ii) their importance ecologically within kelp forest systems as key players in community dynamics and trophic cascades (Tegner & Dayton 2000; Rogers-Bennett 2013; Steneck 2013), and (iii) the importance of the red sea urchin (*S. franciscanus*) fishery in California (Kalvass & Hendrix 1997). Urchin abundances (particularly *S. purpuratus*) were extremely high at many sites, which drove the benthic community structure within several Regions. This study also found high abundances of *S. purpuratus* at Santa Barbara Island and Palos Verdes, which had been

previously reported (Shears *et al.* 2012; Claisse *et al.* 2013) and is most likely due to the prominent urchin barrens established on many reefs within those regions. High urchin densities can alter their behavior (algae consumption rates), which has implications for the persistence of urchin barrens over time (Byrnes *et al.* 2013). In general, urchin densities were higher in cold-water regions, with the exception of Begg Rock, an offshore pinnacle reef that is completely devoid of urchin macroalgal food resources.

California has the largest fishery for red sea urchin (*Strongylocentrotus franciscanus*) on the west coast of North America, and despite decreases in commercial catches since the early 1990s, the fishery continues to be within the top five statewide in terms of value (Rogers-Bennett 2013). This fishery targets the roe (gonads), which are directly affected by the presence of drift algae available for consumption. Because of this, urchin barren/kelp forest habitat community dynamics can directly affect the fishery's value (Claisse *et al.* 2013). The results provided here for fished and ecologically important macroinvertebrates may help to explain how fished species respond to spatial protection. Most prey species (such as urchins) respond to spatial protection in different ways than do higher trophic level predators (*e.g.* fishes). Shears *et al.* (2012) showed that although individuals of the fished *S. franciscanus* were consistently larger, and had higher biomass and reproductive output within reserves in the Northern Channel Islands compared with unprotected areas, densities were similar between protected and unprotected sites. As such, for a mid-trophic level species such as *S. franciscanus*, density estimates alone will not be sufficient to assess changes to populations over time. By contrast, unfished *S. purpuratus* will likely decrease in density within MPAs as predator species recover (Shears *et al.* 2012). This different response to spatial protection shows the importance of looking at macroinvertebrates on a species (*versus* genus) level basis, when assessing reserve efficacy for these species.

Temperature has also been shown to influence the physiological processes of some macroinvertebrate species, which in turn may influence their spatial distribution. Lobsters (*Panulirus spp.*) have been shown to have higher larval settlement, juvenile metabolism and specific growth rates at warmer water temperatures (Belman & Childress 1973; Arteaga-Ríos *et al.* 2007; Perera *et al.* 2007; Kemp & Britz 2008), consistent with the higher California spiny lobster abundances that we observed at warmer sites. Higher water temperatures have also been shown to increase urchin (*Strongylocentrotus purpuratus*) algal ingestion, assimilation and absorption of nutrients (Azad *et al.* 2011). Although we did not find higher urchin abundances at warmer sites, high urchin densities combined with increasing SST due to climate change (which could potentially affect urchin behavior) may have an impact on urchin barren dynamics in the future. The crowned sea urchin, *Centrostephanus coronatus*, is a benthic grazer particularly common around the Southern Channel Islands (Vance 1979; Lissner 1980); however, it is not associated with urchin barrens in the SCB. The genus *Centrostephanus* is represented mainly in tropical regions where another species, *Centrostephanus rodersii*, is found in much higher abundances (Andrew & Byrne 2007). *Centrostephanus rodersii* is associated with urchin barrens in tropical parts of New Zealand and Australia, and population increases there have been linked to increased SST, potentially due to climate change (Pecorino *et al.* 2013).

Another influence of benthic community structure on rocky reefs is habitat stability, which can in turn affect substrate type. Several of the reefs in some of the regions that we analysed here show different levels of habitat instability through scouring and portions of the reefs being buried in sand. Storlazzi *et al.* (2013) found *Anthopleura sola* to be at higher abundances at sites in Central California with increased scouring and dynamic sediment movement, whereas bat stars (*Patiria miniata*) were more abundant in stable (less scoured) environments. In our study, *A. sola* and *Pat. miniata* were found at high abundances in sites that were dominantly urchin barren habitats (more dynamic, disturbed systems), many of which were in the Palos Verdes region (Fig. 4C,D). Habitat instability through reef burial may have contributed to the high abundances of these species at some sites within this region.

As the regions surveyed in this analysis included different depth zones, some of the differences recorded among regions may be related to depth-specific habitat preferences of macroinvertebrates (*e.g.* Alfaro & Carpenter 1999; Blamey & Branch 2012; Bertelsen 2013; Claisse *et al.* 2013). Reef sites varied greatly in substrate composition, reef relief and substrate cover (*e.g.* understory or encrusting algae), all of which can influence the macroinvertebrate benthic community present at a given site. Future studies incorporating these metrics into large-scale analyses will give us a more comprehensive picture of ecosystem structure. As so many factors influence kelp forest-rocky reef macroinvertebrate community structure in the SCB, large-scale studies are required to determine what is driving local differences among Regions.

Megathura crenulata, *Kelletia kelletii* and *Megastraea undosa*, as well as sea cucumber species (*Parastichopus parvimensis* and *Parastichopus californicus*), are all the subjects of important emerging fisheries in Southern California. Abalone species (*Haliotis* spp.) were overfished in the SCB for decades and the fishery has been closed since 1996 (CDFG 2001). In the present study, *Haliotis* spp. in general had very low densities at sites within the SCB; however, the

green abalone (*Haliotis fulgens*) had higher densities at a select number of sites within two regions (La Jolla/Point Loma and Santa Catalina Island), indicating some potential population recovery. The SIMPER results show that all of these species were important to the regional clustering of several different regions (Table 3).

Kelletia kelletii was found to be more abundant on mainland reefs. This may be associated with habitat preference as this species tends to be found buried partially in sand, around cobble–sand interfaces (Zacherl *et al.* 2003). Previous studies have shown higher abundances of *K. kelletii* at mainland sites such as Point Dume (Malibu), Palos Verdes, and Point Loma, San Diego, than at Santa Catalina Island (Zacherl *et al.* 2003; Simmonds *et al.* 2014). In our study, *Megathura crenulata* and *Megastraea undosa* showed no considerable mainland *versus* island patterns. However, both species were more abundant around the warmer islands of Santa Catalina and San Clemente, as well in the southern mainland regions (La Jolla and Point Loma; Orange and North County), indicating that temperature may also play a role in these species' distributions. A previous study on *M. undosa* found higher growth rates and delayed onset of reproduction in populations with higher SST in Baja California (Martone & Micheli 2012). A genetic study of *M. undosa* indicated that Southern California populations may be a more recent expansion of the range of this species (end of last glacial maximum); the majority of its genetic diversity is centered in Baja California Sur with very low genetic diversity in SCB populations (Haupt *et al.* 2013). This has implications for fishery management and spatial protection of *M. undosa* and further justifies the importance of studying its abundances and distribution in the northern portion of its range – the SCB. Combining this life-history information with the baseline density and distributional data provided by this study will be useful to assess how these emerging fisheries are affecting population structures. Furthermore, it is important to consider the effects of physical factors such as SST as a driving factor in species' range expansions due to climate change – both in the past (*e.g.* Haupt *et al.* 2013) and in the future.

As mentioned above, the sea cucumber (*Parastichopus parvimensis* and *Par. californicus*) fishery is another of emerging importance; it has recently become one of the top fisheries in California yet very little life history and abundance information has been gathered (Rogers-Bennett & Ono 2006). *Parastichopus parvimensis*, the warty sea cucumber, was relatively abundant in several regions in the present study, particularly the islands. It was also a top characteristic species contributing to the clustering of the Santa Barbara Island, Santa Catalina Island, San Clemente Island and Palos Verdes regions (Tables 1 and 3). Baseline information on *Parastichopus* spp. populations and their current abundances will be useful to future management of this rapidly expanding fishery. The green abalone (*H. fulgens*) was an important contributing species to the clustering of both the La Jolla and Point Loma and the Santa Catalina Island regions (Table 3). As this species is listed federally as a 'species of concern', with a closed fishery, its regional importance in these areas may indicate some promising recovery of these populations.

The new network of MPAs in the SCB provides unique opportunities to assess the effectiveness of marine spatial management in looking at changes in kelp forest community structure over time. These results will provide important preliminary information on kelp forest–rocky reef macroinvertebrate community structure around baseline reserve establishment (2012). Marine reserves around the Northern Channel Islands (established in 2003) were shown to increase trap yield in the California spiny lobster (*Panulirus interruptus*) fishery after only 6 years, with increases in populations both inside and outside the reserve boundaries (Kay *et al.* 2012). This has implications for similar recoveries of fished California spiny lobster populations in the study area; baseline data from the present study can be used for future analyses to assess recovery. The *S. franciscanus* fishery (Northern Channel Islands) also shows preliminary benefits from reserve establishment in that *S. franciscanus* in reserves there had larger sizes and higher reproductive output (larger gonad sizes) than urchins taken from outside reserve boundaries (Shears *et al.* 2012).

Conclusions

This study provides important baseline information on the densities, distribution and community structure of kelp forest–rocky reef macroinvertebrates across a large range of habitats represented within the SCB. This study provides data on the kelp forests of some of the lesser studied islands and mainland areas of the SCB. Furthermore, as the SCB is the major warm to cold water transition zone on the Pacific coast of North America the influence of SST on these benthic communities may change over time as we start to see greater impacts of climate change along the California coast. The results presented here provide a baseline biogeographic assessment of these invertebrate communities from which we can monitor changes to inform future conservation and management.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of sampling effort. Regions, site names, location coordinates, year sampled, and the number of transects completed in each of the four depth zones.