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Latitudinal regionalization of epibenthic macroinvertebrate communities on rocky reefs in the Gulf of California

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ABSTRACT
We report on a latitudinal pattern in the structure and species composition of epibenthic macroinvertebrate communities on rocky reefs along a gradient of eight degrees of latitude in the Gulf of California. We provide quantitative evidence of a prominent shift in the taxa dominating these communities, particularly the sessile taxa (Cnidaria, Bivalvia, Annelida, Asciacea and Porifera). This pattern was not found in non-sessile taxa (Echinodermata, Decapoda, Cephalopoda, Gastropoda and Polycladida). Based on Bray-Curtis similarity and indicator species analysis we found that the macroinvertebrates of rocky reefs in the Gulf of California are distributed in three broad regions, indicating that sessile taxa are creating such a structure and are related to environmental changes tied to latitude. The northern region (>28° N) was a temperate zone with the coolest water in winter and highest chlorophyll a concentrations, where Octocorallia of the genus Muricea were the dominant taxa. The central region (∼24–28° N) had a mix of oceanographic features of the northern and southern regions and was dominated by Echinodermata in terms of species richness and density. The southern region (<24° N) is a subtropical zone with typically warm and clear water, and dominated by Hexacorallia (stony corals). The southern area was less diverse and had lower densities than the central and northern areas. These three communities correspond to known oceanographic discontinuities in the Gulf of California. This implies that future coastal management plans and conservation efforts in the Gulf of California must be regionalized to support their distinct ecological communities.

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Introduction
Marine benthic macroinvertebrates have long been used for monitoring the health of marine ecosystems because of their wide geographic distribution, high biodiversity as a group, and their sensitivity to environmental perturbations (Clarke & Warwick 2001; Thrush et al. 2009). Large-scale biodiversity and abundance studies of macroinvertebrates such as cnidarians, sponges, molluscs and echinoderms are increasingly relevant because they allow researchers to correlate these biological variables to external factors and explain, in physiological terms, how tolerance ranges are determined by environmental conditions (Begon et al. 2006). Furthermore, they are powerful indicators of the health of their environments and may reflect habitat degradation, pollution from land development, overexploitation and global warming. However, these studies are uncommon in tropical and subtropical marine regions, such as the Gulf of California (Hendrickx & Brusca 2007).

The Gulf of California is one of the world’s hotspots of marine biodiversity (Roberts et al. 2002), spanning a latitudinal gradient of eight degrees, providing a unique conformation characterized by a semi-enclosed sea with a transition between temperate and tropical waters; hence, a natural laboratory to analyse distribution patterns of marine fauna. This region is rich in marine habitats and includes feeding grounds, areas of reproduction and nurseries for over 6000 reported marine species, of which 4852 are marine invertebrates (Brusca et al. 2005). Previous macroinvertebrate studies covered large spatial scales but focus on single taxa,
such as sea stars (Caso 1994), macrocrustaceans (Hendrickx et al. 2002) or molluscs and echinoderms (Honey-Escandón et al. 2008). Other studies of species assemblages are restricted to small areas (González-Medina et al. 2006; Holguín-Quiñones et al. 2008), showing that a comprehensive and integrative perspective on the spatial structure of the macroinvertebrate communities is lacking. Clearly, an analysis of the macroinvertebrate benthos of a large geographically important area could show prevailing patterns of community structure and their relationship with oceanographic conditions that occur in the Gulf of California, and provide a comparative baseline for future studies.

In this study, we focus on the question: Does the macroinvertebrate community of rocky reefs exhibit a latitudinal pattern in its structure in the Gulf of California, that is, do the communities have a pattern of regionalization? If so, (1) what is the pattern for diversity and density among regions? (2) Which species characterize each community? Finally (3), is there an association between the observed community structure and its environmental features among these regions?

**Methods**

Dive surveys of 80 rocky reefs along the east coast of the Baja California Peninsula and offshore islands in the Gulf of California were conducted during summer (July–September) in 2009 and 2010. The mainland coast is almost entirely composed of sandy beaches; therefore, it was not surveyed (Figure 1). Survey sites ranged from the northernmost island (29°33′18.64′′N, 113°33′38.074′′W) to the tip of the peninsula (22°52′32.3′′N, 109°53′34.275′′W) (Table SI, supplementary material). At each site, four replicates of 1 × 30 m belt transects were surveyed at depths of ~5 m and another four at ~20 m, depending on the presence of rocky substrate. During each transect, scuba divers identified to species level, whenever possible,
counted, and measured body size of all conspicuous epibenthic macroinvertebrates > 1 cm. As part of our standard survey method, rocks or habitat-forming structures were not removed during the survey. Within each transect, the area covered by live colonial invertebrates, such as zooxanthellate scleractinian corals (stony corals) was estimated according to Chippalone & Sullivan (1991), which assumes that colonies are circular. For each site, average density per species was calculated, using the replicate transects at each depth. For live stony corals, an average percentage of covered area per square metre was estimated at both depths. In total, 28,565 m² were surveyed in 985 belt transects in two years.

To identify if any latitudinal patterns were present and obtain a broad view of the community structure of epifauna on rocky reefs, we estimated the level of dominance of each species per degree of latitude, regardless of whether the species were colonial or solitary, using the Olmstead–Tukey method (Sokal & Rohlf 1981). The method classifies a species as dominant (density and relative frequency of species presence on transects above its mean values), common (only relative frequency of species presence on transects above its mean), occasional (only density above its mean), or uncommon (density and relative frequency below its mean).

To determine the similarity of communities among the survey sites along the latitudinal gradient, taxa densities per survey site were fourth-root transformed to compensate for the high density of very abundant species and low density of uncommon species (Clarke & Gorley 2006). Data were arranged on a Bray–Curtis similarity matrix and used to perform a non-metric multidimensional scaling (nMDS) ordination plot (PRIMER 6.1 software). Once groups were identified among our survey sites, a multi-response permutation procedure (MRPP) was performed to test if these community structures differed significantly from multiple pairwise comparisons by a Mantel test (PC-ORD 4.26 beta). Species were also classified using a simultaneous ordination with survey sites by a hierarchical two-way cluster analysis using the Bray–Curtis link method and the Flexible Beta distance was $\beta = 0.25$, using PC-ORD 4.26 beta (McCune & Grace 2002).

To determine the featured species for each community, we used the indicator species analysis (ISA). The ISA measures the fidelity of taxa occurrence within a particular group of survey sites. The procedure scores for species in each group from 0 (no group indicator) to 100% (perfect group indicator). Statistical significance for each species was tested with a Monte Carlo randomization technique, using PC-ORD 4.26 beta (Dufrene & Legendre 1997; McCune & Grace 2002; Gómez-Gutiérrez et al. 2007).

Sample-based rarefaction curves were estimated to compare species richness between the groups resulting from previous analyses (Sanders 1968, modified by Hurlbert 1971; Gotelli & Colwell 2001). This procedure provides robust estimates of species richness when samples are different in size (Gotelli & Colwell 2001), which was our case. Rarefaction curves and their confidence intervals were estimated with a Monte Carlo method with 5000 replicates, using R statistical software (R Development Core Team 2014).

Macroinvertebrate species richness and density patterns were related to sea surface temperature (SST) as a relevant physiological stress indicator, and chlorophyll $a$ (Chl-$a$) as an index of energy input available for local communities at our survey sites. Since benthic macroinvertebrates are relatively long-lived, we obtained environmental data from January 1998 to December 2010 to assess mean SST and Chl-$a$ conditions during the period of analysis. Satellite data were retrieved from the CoastWatch repository.

Monthly averages from 1998 to 2009 of SST data were obtained from the AVHRR-Pathfinder satellite with a resolution of 18 km². SST data for 2010 are from the Aqua-MODIS sensor, which has a resolution of 4 km². We averaged four pixels around each site to provide the same resolution as the AVHRR-Pathfinder sensor. We created an SST time series for each of the 80 sites by extracting the value from the corresponding pixel, and estimated the seasonal mean (winter, spring, summer, autumn) and maximum, minimum and range of the SST.

Chlorophyll $a$ concentration of monthly averages was obtained from January 1998 to December 2010 from the SeaWiFS at a resolution of 9 km². We extracted a time series for each site from the corresponding pixel and calculated the seasonal mean and maximum, minimum and range of Chl-$a$. Long-term series of satellite-based data are readily available and provide a better index of persistence of marine regimes over extended periods and large areas (Blanchette et al. 2008).

Both environmental variables at each site were normalized and used to create an nMDS ordination plot based on an Euclidean distance similarity matrix, which was linked to the species matrix. Because the biota matrix has Bray–Curtis similarity units and the environmental variables have Euclidean distance units, the scaling methods do not allow for direct comparisons, although their ranks can be compared through a rank correlation coefficient. These
procedures were performed with the BEST Routine (BVSTEP method, forward- and backward-stepping, to arrive at a putative optimal set), with the weighted Spearman rank correlation and permutation test of 999 random samples, using PRIMER 6.1.16 software (Clarke & Warwick 2001).

Results
We identified and measured 142,606 individual macroinvertebrates during the surveys of 2009 and 2010. These were classified into 140 taxa, among eight phyla and 15 classes, subclasses and/or orders. About 68% were identified to species level, 28% to genus level, 2% to family level, 1% to order level and 1% to class level (Table SII, supplementary material). Phylum Cnidaria was the most diverse, with subclasses Octocorallia (32 taxa) and Hexacorallia (23 taxa), and the class Hydrozoa (six taxa). Phylum Mollusca was the second most diverse, with three classes: Gastropoda (20 taxa), Bivalvia (10 taxa) and Cephalopoda (one taxon). Phylum Echinodermata was third, with four classes: Asteroidea (13 taxa), Echinoidea (six taxa), Holothuroidea (three taxa) and Ophiuroidea (two taxa) (Figure 2a).

The four most abundant phyla on rocky reefs in the gulf were Cnidaria, Echinodermata, Porifera and Chordata. Cnidaria accounted for 55% of total density, of which 29% were Octocorallia (e.g. sea fans), 23% were Hexacorallia (e.g. stony corals, sea anemones and black coral) and hydrozoans constituted only 3% of overall density. Echinodermata represented 20%, of which 6% were Asteroidea (sea stars), 13% were Echinoidea (sea urchins), 0.5% were Holothuroidea (sea cucumbers) and 0.3% were Ophiuroidea (brittle stars). Porifera (sponges) and Chordata (ascidians) represented 6% each. Phylum Mollusca was rich in species (31 taxa), but not abundant, representing 5.5% of total density, of which 3.04% were Gastropoda, 2.4% were Bivalvia and 0.05% were Cephalopoda (Figure 2b).

Each degree of latitude had more than 50 taxa. The highest species richness occurred from 24°N to 30°N, with more than 80 taxa (Figure 3a). In terms of densities, higher values of taxa occurred from 24°N to 30° N, followed by 22°N to 24°N; the highest densities were within 27°–29°N (Figure 3b), where unexpected and unexplained, high densities of small individuals (2 to 4 cm in diameter) of the sea urchin Arbacia stellata (Blainville, 1825; ?Gmelin, 1791) (Echinodermata) were observed (up to 60 urchins per m²). We also found latitudinal clines in density for ascidians, declining to the south, sponges and hexacorals, declining to the north and octocorals, depending on the genus (Figure 3b).

We found no evidence of a difference in distribution with depth for 105 of the 140 species. Only 35 species of octocorals, including four species of the genus Lepi togorgia, showed a preference for shallow water, eight species of the genus Pacificgoria and 13 species of the genus Muricea with a preference for deeper water (Figure 4a), and 10 species of stony coral showed a significant difference with depth (Figure 4b). Coverage of live stony coral has a latitudinal cline from south to north and has a preference for shallow waters, regardless of latitude (Figure 4b). Porites panamensis Verrill, 1866, the only stony coral present at 28°–30°N, was found mainly in shallow waters (~5 m deep). At 25°–28°N (the central region) six of the 10 species of stony coral are present, but they had the lowest area coverage of live coral, especially in deeper water. All 10 species with the highest area coverage inhabited the southern areas (22°–24°N), mainly in shallow waters.
water. *Pocillopora elegans* Dana, 1846 and *Pocillopora damicornis* (Linnaeus, 1758) had the largest area of coverage, nearly 30% of the transect area at some survey sites.

The analysis of dominance, applied to each species arranged per degree of latitude, showed that dominant taxa varied with latitude and were mostly sessile taxa (sponges, ascidians, hexacorals and octocorals), and 62 species (~45% of the total) were uncommon (Table SII). Sponges of the genus *Aplysina* and stony corals of the genus *Pocillopora* were dominant at 22°–24°N and declined northward. At higher latitudes (28°–29°N), hexacorals were less common and only *Ceratopogonid fransiscana* Durham & Barnard, 1952 and *Epizoanthus* sp. were dominant. Octocorals of the genus *Muricea* were dominant at 27°–30°N, with a cline to the south, while *Leptogorgia* and *Pacificorgia* were dominant at 22°–25°N, both with a cline to the north. Octocorals, as a

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**Figure 3.** (a) Distribution of macroinvertebrate taxa per degree of latitude. (b) Mean macroinvertebrate densities per degree of latitude. Phyla are:  
- Black: Annelida,  
- Green: Ascidiacea,  
- Light blue: Cnidaria,  
- Yellow: Crustacea,  
- Blue: Echinodermata,  
- Red: Mollusca,  
- Purple: Platyhelminthes and  
- Tan: Porifera.

**Figure 4.** (a) Mean density per genus of octocorals per degree of latitude and at two depths. Genera are:  
- Blue: *Leptogorgia*,  
- Green: *Pacificorgia* and  
- Light blue: *Muricea*. (b) Mean coral cover percentages per degree of latitude and at two depths. Species are:  
- Red: *Pavona gigantea*,  
- Peach: *Pavona varians*,  
- Green: *Pocillopora capitata*,  
- Light blue: *Pocillopora damicornis*,  
- Orange: *Pocillopora effusus*,  
- Yellow: *Pocillopora elegans*,  
- Dark yellow: *Pocillopora meandrina*,  
- Blue: *Porites panamensis*,  
- Light green: *Psammocora binghami* and  
- Dark green: *Psammocora stellata.*
group, was the only one that showed mixed latitudinal clines in their dominance patterns. The sea star *Phataria unifascialis* (Gray, 1840) was the only dominant species throughout the gulf without a latitudinal pattern.

*Porites panamensis* Verrill, 1866 was dominant at all latitudes; however, colonies at higher latitudes were typically smaller than those at lower latitudes. In their central and southern distribution, they were a conspicuous component of the marine landscape because of their large size and abundance (Table SII and Figure 4b).

Survey site classification (Figure 5 and the respective dendrogram Figure S1, supplementary material) consistently grouped our sites into three clusters, indicating the presence of three distinct macrobenthos communities at 41.5% of the Bray–Curtis similarity coefficient and with a 0.11 stress level in the nMDS ordination, which is considered regular. The 41.5% similarity was selected as our threshold since it is the maximum similarity value that provides a parsimonious classification of survey sites while maintaining spatial coherence.

The northern region covers 28° to 30°N (except for site 19 at 27.8°) (see Table SI). The central region covers 24°–28°N. The southern region covers 22°–24°. These three regions differ significantly between them according to pairwise comparison by MRPP (all pairwise comparisons have a $P < 0.005$).

To determine which taxa contributed the most to community structure, we developed Bray–Curtis dendrograms for visual interpretation with classification matrices that excluded one taxon group at a time. Sessile taxa (Cnidaria, Bivalvia, Annelida, Asciidiacea and Porifera), which represent ~75% (106,924) of the individuals and ~62% of species, generated a site classification similar to the three regions found during our previous analyses (41.5% of the Bray–Curtis similarity index; Figure 6a). Classification of sites with non-sessile taxa only (Echinodermata, Decapoda, Cephalopoda, Gastropoda and Polycladida) represented 25% (35,682) of all individuals (~38% of species reported) and did not show coherent spatial structure at any level of similarity (Figure 6b).

**Figure 5.** nMDS ordination plot of survey sites based on macroinvertebrate species composition. Grey boxes indicate the division between regions. Similarity lines indicate the division of the three regions by Bray-Curtis similarity at 41.5% (see Figure S1, supplementary material).
We assessed latitudinal complexity in species richness for the three regions, using rarefaction curves (Figure 7). Species richness reached an asymptote at about 90 species after sampling 3000 m² in the northern and central regions. The southern region stabilized at a lower species richness, about 60 species, after sampling 2500 m². The presence of the asymptote in the rarefaction curves is an indication of sufficient sample size. The southern region was the least diverse, while the other two regions had similar levels of species richness, but their species composition was distinctly different.

Two-way clustering (Figure 8) shows the three clusters, as observed in nMDS, and the species composition and density values associated with them. This figure also shows the decreasing species richness toward the southern region, and a similar high species richness, but different structure, in the northern and central regions. The northern region is dominated by Cnidaria and the central region by Echinodermata and Mollusca. The central region shares species with the adjacent regions; hence, we considered it a transitional region in the benthic macroinvertebrate components of coastal rocky habitats (Table SII). The regional affinity of species resulting from ISA analysis showed that groups that are abundant in a region also are statistically significant ($P < 0.005$). Sponges and stony corals are associated with the southern region, ascidians with the northern region and octocorals with the northern and southern regions, depending on the genus. For the central region, there is no affinity class or subclass, only a mix of species (Table SII).

The annual average SST declines, although its range increases, from south to north. From 1998 through 2010, the three regions had the same high SST during summer (mean: 30°C). During winter, the
The lowest mean SST was 16.31°C in the northern region and 21.8°C in the southern region. The central region had a winter mean of 19.63°C. The northern region had a maximum range in SST (17°C); the southern region had the lowest range in SST (<12°C); and the central region had a range of 14°C (Figure 9a).

Concentrations of chl-α did not show a latitudinal pattern as strong as the SST. Low concentrations occurred in the southern region (annual average 0.51 mg m⁻³). High concentrations occurred in the northern region (annual average 1.65 mg m⁻³). The chl-α time series did not show a consistent trend at season scale, but the southern region is consistently the least productive and the northern region was consistently the most productive. The central region was transitional for SST and chl-α values (Figure 9a).

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We found a significant correlation between the similarity matrices of abiotic variables at our survey sites with species similarity matrices (ρ = 0.731), based on the BVSTEP method. The nMDS of survey sites with the abiotic matrix (Figure 9c) also showed the presence of three regions, similar to the nMDS results with the fauna matrix. These results suggest that the environmental variables influence the structure of the communities in the three regions. These results do not demonstrate a definitive causal relationship because the correlation method does not necessarily imply causality.

**Discussion**

Our analysis of community structure and density of species shows that the macroinvertebrate fauna of the rocky reefs in the Gulf of California are mainly dominated by corals, octocorals and echinoderms that are distinct in the three latitudinal regions along the east coast of the Baja California Peninsula. These regions decline in species richness toward the south, with the southern region having the lowest species richness and densities. This is contrary to literature that indicates that tropical zones have more species diversity than higher latitudes (Sanders 1968; Gray 2001; Clarke & Crame 2010). A plausible explanation for low species richness in the specific case of macroinvertebrates may be as a result of a decrease in area of rocky habitats in the southern part of the Peninsula (Sala et al. 2002), and strong substrate competition from zooxanthellate hexacorals, which is also reflected in their large area coverage per sample transect (~30% of the transects). The northern and central regions are similar in species richness, but their density and composition of species are different; echinoderms and molluscs dominate the central region, and cnidarians (mainly octocorals) dominate the northern region. Octocorals are known to be highly tolerant of thermal stress (Prada et al. 2010), which explains their high species diversity in the northern region. Of particular
note, the southern and northern regions shared very few species; the central region is composed of overlapping northern and southern communities, suggesting that this region is a transitional zone.

Ascidians, sponges, hexacorals (mainly stony corals) and octocorals showed marked latitudinal differences. Ascidians are more abundant at northern latitudes, having a tolerance for a wider range of temperature

Figure 8. Two-way clusters showing classification across survey sites and density per species from a Bray–Curtis similarity matrix. Site codes are arranged by latitude and are given in Table S1; species ID labels are in Table S2 (supplementary material). Bubble colours indicate minimum (white) to maximum (dark blue) species density.

Figure 9. (a) Annual mean SST and (b) chlorophyll $a$ from January 1998 through December 2010 separated per degree of latitude. Grey boxes indicate the division between regions. (c) nMDS ordination plot of survey sites based on the normalized abiotic variables, of SST and chlorophyll $a$ concentration. Similarity cluster lines indicate the separation of the three regions by a Euclidean distance of similarity.
(Lambert 2005). The most common species found here, *Rhopalaea birkelandii* Tokioka, 1971, is a successful species that is found as far south as Panama (Bullard et al. 2011). The possible explanation for the low density of ascidians in the southern region is from substrate competition with stony corals and sponges (Davis et al. 1991; Stoner 1994; Green et al. 2002), which are present at high densities in the southern region.

Sponges, specifically the most common genus *Aplysina*, have a marked preference for the southern latitudes, from the middle of the peninsula to its tip. It reflects the Aplysiniidae family’s tropical and subtropical biogeographic affinity (Friedrich et al. 1999). Many common reef sponges (including some species of the Aplysiniidae family), like most shallow coral reef scleractinians, possess photosynthetic endosymbionts, such as zooxanthellae or cyanobacteria (Rützler 1990; Vicente 1990; Friedrich et al. 1999; Freeman & Thacker 2011). Primary production from photosymbionts provides crucial nutrition to reef sponges similar to corals. It is an important adaptation of sponges to the oligotrophic coral reef environment, increasing sponge growth and competitive ability, enabling them to inhabit nutrient-poor tropical waters (Hentschel et al. 2006; Taylor et al. 2007; Erwin & Thacker 2008; Brümmer et al. 2008), which are attributes of the southern region. To our knowledge there are no studies of photosymbionts in sponges in the Gulf of California; however, the high abundance of sponges in the nutrient-poor southern region could be explained by the presence of photosymbionts.

Zooxanthellate stony corals are typically found in shallow, warm, clear tropical waters (Spalding et al. 2001). They had the largest area coverage at the southern end of the peninsula (22°–23°N), where these conditions prevail as a result of a strong influence of tropical water currents (Spalding et al. 2001; Lluch-Cota et al. 2007). Their coverage declines at higher latitudes.

Dominance of octocoral genera varied with latitude. *Muricea* declines in the lower latitudes and is rare or absent in the southern region, but is dominant and diverse at depths of 5 and 20 m in the northern region and at depths of 20 m in the central region. Van-Oppen et al. (2005) state that some species of *Muricea* are azooxanthellates, and their distribution is not limited by environmental factors. Prada et al. (2010) state that octocorals are highly tolerant of thermal stress. The highest concentration of chl-α and the widest range of SST in the Gulf of California may explain the predominance of *Muricea* in the northern region.

On the other hand, the octocoral genus *Pacificgoria* is absent or rare at northern latitudes, but diverse and abundant at southern latitudes, at depths of 20 m, as is *Leptogorgia*, but mainly in shallow water. Imbs et al. (2009) found biomarkers of photosymbionts on azooxanthellate octocorals, proposing that this is an indication of an association in azooxanthellate octocoral with phototrophic bacteria, particularly cyanobacteria, having the same role as endosymbiotic zooxanthellate algae in corals; this could possibly explain the dominance of *Pacificgoria* and *Leptogorgia* species in the oligotrophic water of the southern region. Clearly, this subject requires further research to test this hypothesis.

The three communities of macroinvertebrates are significantly correlated with SST and chl-α concentration. Not surprising, the matrix of sites with these variables has a similar classification pattern as that based on macroinvertebrates (i.e. three regions).

The northern region has the lowest winter SST (15°C), the widest annual range of SST (15–30°C) and high salinity (based on high evaporation rates) (Thomson & Gilligan 2000). This region also has the shallowest mean depth (~200 m), and produces high loads of suspended sediments generated by extreme tidal range (~10 m) that generates strong currents. This also contributes to high primary productivity (Lluch-Cota et al. 2007), which is consistent with the high chlorophyll a values found there. The dominant taxa here (*Muricea* octocorals) are usually cold-water dwellers, with a tolerance to high salinity and wide-ranging temperature (Prada et al. 2010). High primary productivity in the north also reduces light penetration and could limit the occurrence of phototrophic corals (Halfar et al. 2006; Álvarez-Borrego 2012). This scenario is a plausible explanation for the limited presence of stony corals. For instance, the only light-dependent stony coral (*Porites panamensis*) occurs in shallow water in this area. We conclude that species in this region face the strongest environmental seasonal change, but are highly diverse and abundant (particularly sessile, suspension-feeding species) because of high productivity.

The central region appears to be a transitional region in terms of coastal rocky inhabitants, as found in our two-way cluster (Figure 8). The macroinvertebrates are a mix of northern and southern taxa, dominated by echinoderms. Summer temperatures are similar to the northern region, but winter temperatures do not drop below 17°C (Figure 9a). This region has greater depths than the northern region, moderate tidal range (Thomson & Gilligan 2000) and mesotrophic primary productivity (Figure 9b).
The southern region is the warmest, with an average annual SST of 25°C and has the warmest winter SST (20°C) (Figure 9a). This region has a narrow continental shelf, and it is near a deep ocean basin; thus, it is strongly influenced by oceanographic conditions from the open ocean (Lluch-Cota et al. 2007). Tidal range is less than 2 m, and the water is the clearest from the open ocean (Lluch-Cota et al. 2007). Tidal flow strongly influences the open ocean (Lluch-Belda et al. 2001; Espinosa-Carreón & Valdez-Holguín 2007). This is consistent with our findings (Figure 9b). Taxa in this region are not subject to wide temperature changes and have many attributes of tropical areas, including coral reefs. Coral reefs, with their structural heterogeneity, provide other habitats for species associated with them and create a different landscape than in the other two regions. In summary, the species in this region face less seasonal change than in the other regions, and as a result of the low productivity, autotrophs, such as stony corals, dominate these rocky reefs.

In regard to our initial question, there seems to be a latitudinal pattern in the macroinvertebrate community, displayed as three distinct regions characterized by different species composition in terms of diversity and density. This regionalization is displayed by sessile taxa only, while non-sessile taxa display no latitudinal zonation. Clearly, sessile invertebrates have to be adapted to the variability of their local environment, while motile invertebrates have a measure of control, capable of retreating from unfavourable conditions (Begon et al. 2006).

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Our results show that there is a gap in our understanding of the role that photosymbiotic organisms, zooxanthellates and others, play in the creation and maintenance of the structure and function of rocky reef benthic macroinvertebrate communities along the coast in the Gulf of California. There is accumulating evidence of these symbionts in host taxa, including turbellarians, sea anemones, ascidians, tridacnid clams and sponges (Venn et al. 2008). Similarly, the reproductive strategies and larval development times and dispersal patterns must be relevant factors for colonization of species in the narrow shelf of rocky reef habitats along the east coast of the peninsula.

This broad view of structure and composition of the epibenthic macroinvertebrate communities strengthens our knowledge, not only from a theoretical standpoint, but from an applied standpoint, because rocky reefs are quite important to the local fishing communities. Understanding latitudinal changes in abundance of these taxa, along with their environmental differences, will help identify threats to marine biodiversity from climate change and coastal development, and further conservation efforts of coastal biodiversity in the Gulf of California by providing a baseline to avoid the ‘shifting baseline syndrome’ (Pauly 1995).

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