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SPECIAL TOPIC

High species density patterns in macrofaunal invertebrate communities in the marine benthos

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Abstract

Species density of macrofaunal invertebrates living in marine soft sediments was highest at the shelf-slope break (100–150 m) in Monterey Bay (449 m^{-2}). There were 337 species m^{-2} in the mid-shelf mud zone (80 m). There were fewer species along the slope: 205 m^{-2} from the lower slope (950-2000 m) and 335 m^{-2} on the upper slope (250-750 m). Species density was highest inside the bay (328-446 m^{-2}) compared to outside (336-339 m^{-2}), when examining samples at selected water depths (60-1000 m). There was little difference in local species density from 1 km of shoreline compared to regional species density along 1000 km of shoreline at both shelf and slope depths. The highest species densities worldwide in the literature are recorded along the Carolina slope in the Atlantic Ocean, where peak species density (436/0.81 m^2) at 800 m and values at the largest sample areas are similar to those on the Monterey Bay shelf. We speculate that the highest species densities occur where ocean water exchanges energy with shoaling topography at the continental margin, bringing more food to the benthos – areas such as the very productive waters in the upwelling system of Monterey Bay.

Introduction

Early ecologists wanted a term, or index, for species diversity that could reflect the complexity of biological interactions in a community and searched for models to embody this concept, settling on the idea that a community with a more even distribution of individuals among species allowed for a greater probability of interspecific encounters and was therefore more diverse. They borrowed the Shannon–Wiener (Weaver) equation (H') from information theory with a questionable analogy to interspecific encounter (Goodman 1975). H' became the most commonly cited measure of species diversity. Goodman (1975) reviewed the history of this measure and put into words what it does to the number of species and individuals: 'The Shannon–Weaver measure of species diversity is the negative logarithm of the geometric mean of the probability per individual of correctly guessing, in sequence, the species identity of each individual in a random ordering of an assortment of individuals whose relative species frequencies are given by $\{p_1\}$, when the 'guess' is carried out by picking some arbitrary ordering of this assortment of individuals'. He concluded: 'It is a dubious index. Whatever the index does measure seems to have no direct biological interpretation'. The measure of evenness (J), derived from H', suffers from the same problem. Hurlbert (1971) thought that the effort to represent the complexity of interactions in an encounter index and the use of H' rendered species diversity a nonconcept. He provided a realistic index of the probability of interspecific encounter (PIE), which H' was supposed to be, but was not. Hurlbert urged that PIE not be used as another measure of species diversity, but instead be called what it was, an index of interspecific encounter.

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Apparently few ecologists embraced the wisdom of Hurlbert's warnings. The effort to capture the complexity of biological interactions in a single index was doomed from the start. Since then the ambiguous 'species diversity' has engulfed the more general term diversity. It is now common for a mix of measures to be called species diversity, diversity, and richness and for the terms to be used interchangeably so that it is difficult to know what is actually being measured and presented (Spellerberg & Fedor 2003).

The two components of species diversity, richness and evenness, are still subsumed in the nonconcept, but are good metrics of community structure. Numerical species richness is commonly measured by the expected number of species, $E(S_n)$ (Sanders 1968; Hurlbert 1971), which estimates the number of species in a given number of individuals. It was first used to compare species number from benthic samples collected with an epibenthic sled, which does not collect a known area of bottom. Although it is now widely used with quantitative samples, comparisons are rarely made from equal areas (Levin *et al.* 2001), which is the primary reason for collecting quantitative samples. Aerial species richness, or species density, is the number of species from a given area. It can also refer to estimates of species number, essentially species lists, representing large biogeographic regions and is often limited to particular taxonomic groups (*e.g.* Rex *et al.* 2000). Since the number of species can be positively related to the number of individuals, there is an argument that an increase in the number of species per area is the result of having more individuals in the sample (Gotelli & Colwell 2001). Standardizing by number of individuals avoids this statistical problem. On the other hand, species–area plots show the actual number of species living in real and equal habitat areas over a range of areas, whether the number of individuals is large or small in different samples. The statistical relationship between species and individuals does not negate the reality of the species–area pattern, or the importance of comparing communities in a known spatial context. There are numerous papers expressing species number per number of individuals, despite comparing different areas of habitat. As a result, a recent contribution on continental margin biodiversity only shows patterns of numerical species richness and H' (Menot *et al.* 2010). It is much less common to find data on species density, particularly accumulated over a range of areas, allowing comparisons among marine benthic communities even when the basic quantitative sample unit is not the same area.

Our primary goals are to present species density patterns in benthic communities from the Northern and Central California margin, to show how these patterns differ on the shelf and adjacent slope, and to compare our results to high species densities from other locations around the world.

Study Site and Methods

We obtained estimates of soft-bottom species density and other community metrics by sampling benthic invertebrate communities in four major sampling programs along the upwelling coast of Central and Northern California (Fig. 1). Three of these programs were focused around the Monterey Bay area. In July and August 1999, samples were taken along four transects across the continental shelf and slope at water depths ranging from 10 to 2000 m. The four transects were potential routes for an underwater telecommunications cable proposed by MCI WorldCom (ABA Consultants 2000). Wave disturbance is most severe in the nearshore (Oliver *et al.* 1980) so we used samples from 30 to 2000 m depths in our analysis (Fig. 1: MCI). Five replicate 0.1-m^2 grabs were collected at each water depth along each transect. At least two of the replicates were processed from each station. In April 2004 and May 2005, NOAA collected single samples (0.1-m^2) along eight transects in water depths from 80 to 950 m (Fig. 1: NOAA). In June 2003, single 0.1-m^2 samples were collected at 49 shelf stations ranging in depth from 33 to 123 m, covering the largest geographic region of the four sampling programs. These grabs were taken for the U.S. Environmental Protection Agency's Western Environmental Monitoring and Assessment Program (WEMAP), and ranged from Point Conception to the Oregon border (Fig. 1: WEMAP). In September (2002) and October (2001, 2002, 2004–2006), one or two replicate 0.1-m^2 samples were collected at eight stations along the 80-m isobath, which is in the center of the mud band along the outer shelf (Griggs & Hein 1980). These stations, near and inside Monterey Bay, are part of a regional monitoring program (Central Coast Long-term Environmental Assessment Network, or CCLEAN; Fig. 1: CCLEAN). The four datasets are thus named MCI, NOAA, WEMAP, and CCLEAN throughout this paper and are distinguished as an easy means to discuss differences in species density as it relates to sampling effort, spatial scale, and water depth.

The macrofaunal invertebrate community was the focus of our comparison, rather than the larger megafauna, the smaller meiofauna or the microbial assemblages. Macrofaunal communities are much better sampled and described, and are the basis of all of the important past work on benthic marine diversity (*e.g.* Sanders 1968, 1969; Dayton & Hessler 1972; Rex 1981, 1983; Gray *et al.* 1997; Levin *et al.* 2001; Menot *et al.* 2010). To date, they are the best indicator of species density for the entire

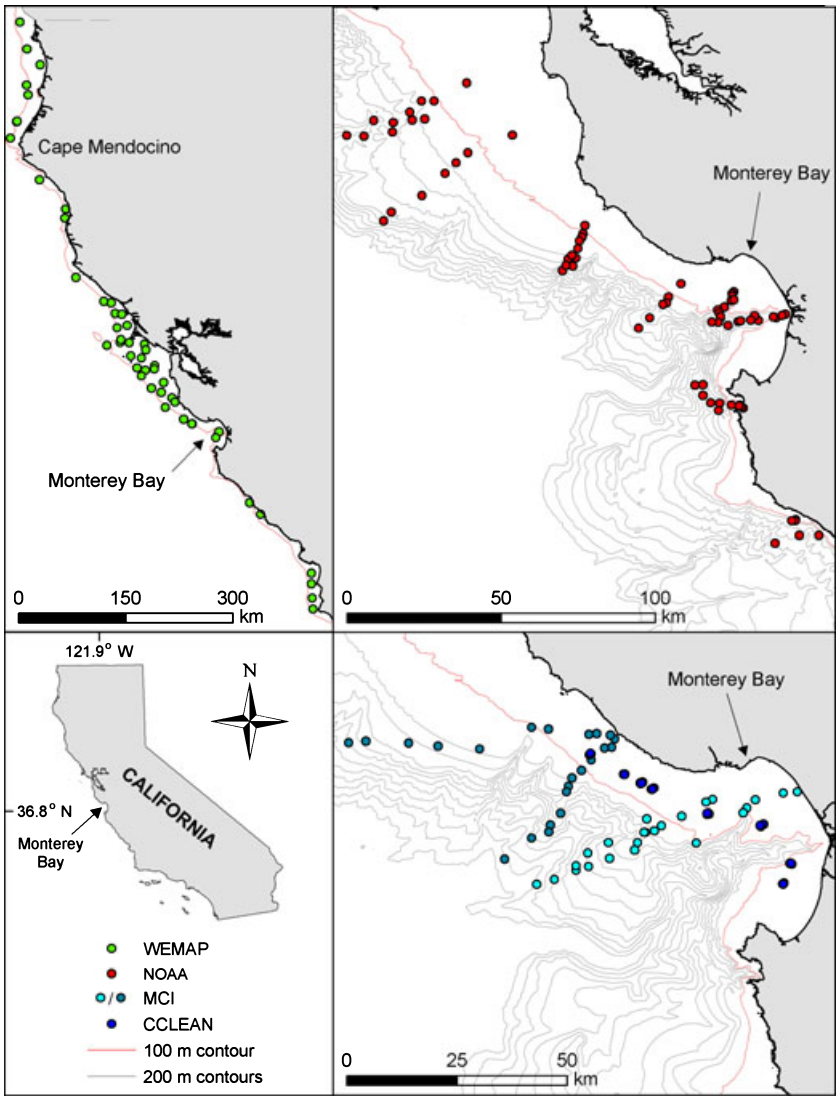

Fig. 1. Location of the four sampling projects along the Central and Northern California coast. MCI samples were taken along transects inside Monterey Bay (open squares) and outside the bay (filled squares).

benthic community. The megafauna (epifauna) includes far fewer species than the macrofauna and is thus a poor indicator of species density for the entire community. Meiofaunal community descriptions are too few, limited in sample area, and the taxonomy is more difficult compared to macrofauna. The species density of the microbial community has not been measured, although molecular techniques should provide realistic estimates that will allow comparisons at least among different microbial assemblages.

The 0.1-m^2 Smith–McIntire grab contents were washed over 0.5-mm screens, collecting the macroinvertebrate community. Residues were preserved in 10% buffered formalin for 48–72 h and transferred to alcohol. Animals were sorted from the debris, identified to the lowest possible taxon, and counted. Because data were generated over several years, we updated all taxonomy prior to beginning data analysis. A 0.5-mm screen was used along the slope rather than the smaller 0.3-mm mesh because qualitative assessments indicated little loss of macrofaunal individuals and no loss of species, probably because of the relatively large size of the macrofauna in the California upwelling system as well as the large volume of residue that clogged the screens and likely made the effective mesh size smaller (ABA Consultants 2000). We made these assessments for the outer shelf and slope by washing samples through both screens during the MCI survey, which was done before the NOAA slope sampling.

Despite a large number of small amphipod and other peracarid crustacean species at the shelf break, we found very few species and individuals on the smaller screen size. Along the slope, we found a few individuals of juvenile polychaetes in the 0.3-mm residues. All of the macrofaunal species found in the 0.3-mm screen residues were also present in the 0.5-mm fraction of the same sample.

Computations were conducted using the PRIMER v6 software package (Clarke & Gorley 2006). Smoothed species accumulation or species/area curves were generated using 999 random sample permutations for all projects combined and various subsets of samples by depth. PRIMER'S DIVERSE routine was used to calculate numbers of individuals, numbers of species, and Shannon–Wiener, Chao1 and Simpson's dominance (λ) indices for each sample. Means of indices were then calculated for all data and various subsets of samples by depth. Rarefaction curves were created in ECOSIM Professional v1.0 (Gotelli & Entsminger 2011).

Data from two Monterey Bay MCI transects inside the bay (Fig. 1) were used to generate a local estimate of species-area patterns to compare with samples collected over the entire geographic range of the four datasets (regional estimate). Because replication within transects was not identical, we used a subset of the data with equal replication throughout common water depths for both the local and regional comparisons (60, 90, 109, 150, 450, 700, 1000 m). The local samples were collected along a 1-km section of the shoreline. The regional samples were selected from the entire study area along 1000 km of shoreline. Data for regional curves were selected using Hawth's Analysis Tools for ARCGIS to randomly select sample positions in the appropriate depth range (30–150, 250–2000 m; Beyer 2004). In cases where multiple replicates were collected at a sample position (MCI, CCLEAN), a single replicate was randomly selected for use in the regional dataset.

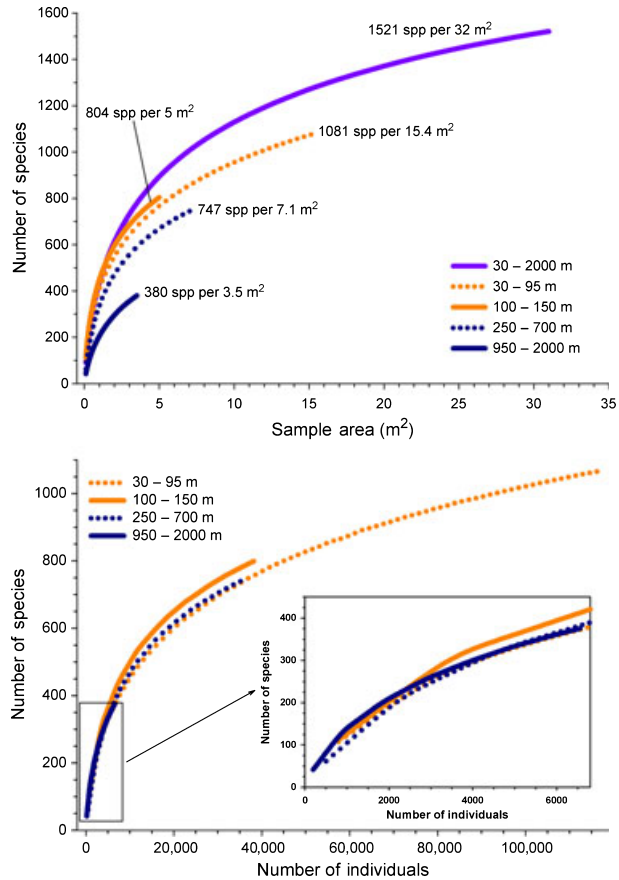

Fig. 2. Changes in species–area and rarefaction (numerical species richness) patterns in different water depths combining all four datasets. The top panel shows species–area curves for all depths and four depth ranges. The bottom panel shows rarefaction curves for four depth ranges with an inset that enlarges the area where all curves are present. Numbers next to curves in the top panel are the total species present in the largest sample area (sum of all samples for that depth range).

Results and Discussion

California upwelling system

There were distinct changes in species density among the four sampling programs, inside and outside Monterey Bay, and especially with water depth. The number of macrofaunal species in soft-bottom communities was highest on the continental shelf when all four datasets were combined (Fig. 2) and when they were examined separately (Fig. 3). The highest species density was observed at the shelf–slope break, and the lowest at deeper slope depths below the oxygen minimum zone (Fig. 2). The MCI transects in Monterey Bay had a higher species density than those sampled along the continental margin outside the bay (Fig. 4). Therefore, the Monterey Bay shelf was a local hot spot for species density, peaking at the shelf break. This pattern was not related to sampling effort in the Monterey Bay transects. The transect with the highest species density was based on 23 samples and the two transects from outside the bay were based on 26 and 20 samples (Fig. 4).

We examined each dataset separately because they represent different depth and geographic ranges (Fig. 1). Despite considerable variation in both depth and geographic area, species density was high throughout the study area (Fig. 3). However, the two datasets with the largest depth range (MCI and NOAA) had a higher number of species compared to the two programs sampling only the shelf (WEMAP and CCLEAN; Fig. 3). CCLEAN

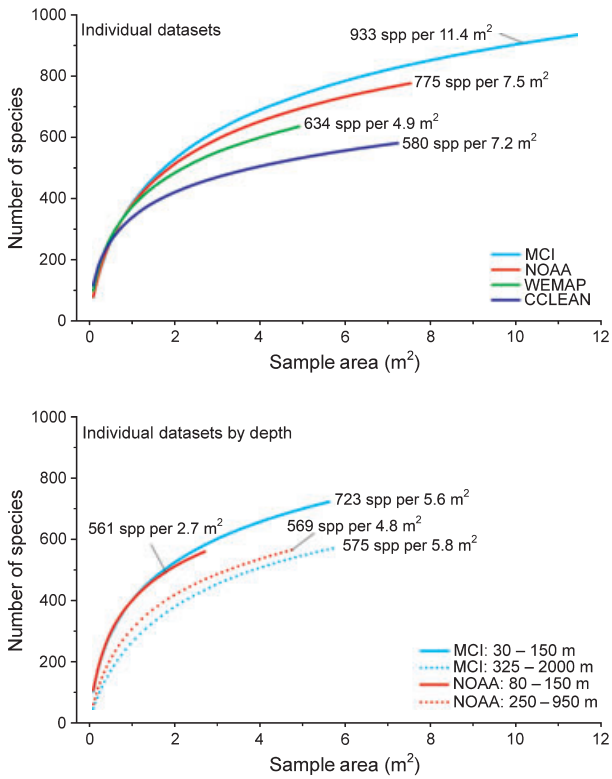

Fig. 3. Species–area patterns from each dataset (top panel) and then separated into shelf and slope depths for the two programs that sampled beyond the shelf (bottom panel, MCI and NOAA). Shown for each curve are the number of species present in the largest sample area (sum of all samples for that depth range).

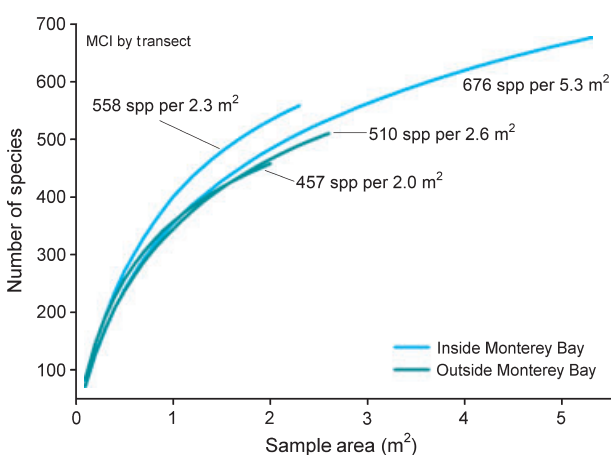

Fig. 4. Changes in species–area patterns among the four transects in the MCI sampling program. Data are from the same water depths on each transect. Shown for each curve are the number of species present in the total sample area.

had the lowest species number and included the fewest stations, all at one water depth (80 m) in the mud band (Griggs & Hein 1980) along the shelf (Figs 1 and 3).

Unlike water depth, there was no simple relationship between the total geographic area of a sampling program and species density. WEMAP samples were dispersed over the largest geographic area, but were limited to shelf depths with only a few samples at the shelf–slope break (Fig. 1). They had the third highest species density (Fig. 3). NOAA samples were dispersed over the next largest geographic area from 80 to 950 m (Fig. 1). They had the second highest species density (Fig. 3). MCI samples were mostly around the Monterey Bay area, from depths of 30–2000 m (Fig. 1). They had the highest species density (Fig. 3). Finally, CCLEAN samples were dispersed over the smallest geographic region, and they had the lowest species density (Fig. 3). We also examined the impact of geographic scale by estimating species density from a local area within Monterey Bay (along a kilometer of shoreline) and from a larger regional scale along 1000 km of shore, selecting samples to avoid differences in sampling effort. There was little difference between our estimates of local and regional species density on the shelf or the slope (Fig. 5).

Ideally we would compare species density from the largest area possible and thus at or closer to the asymptote (relatively flat top) of the species–area curves (Gotelli & Colwell 2001). Fortunately, the lower-bound of the expected number of species at the asymptote can be predicted with the Chao1 estimator (Chao 2005). The Chao1 estimators show the same general pattern of high species number on the shelf compared to the slope (Table 1). Although the Chao1 estimates are interesting and support the key depth and geographic patterns, we believe the sample data, not the model predictions, are more realistic and thus accurate metrics for describing community structure and making comparisons within

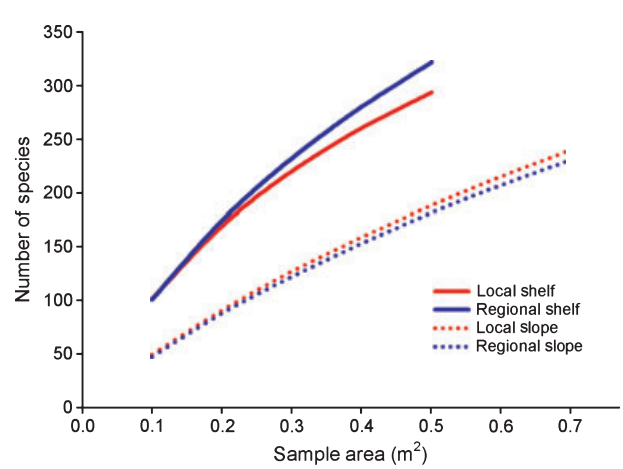

Fig. 5. Species–area patterns from local (1 km) and regional (1000 km) geographic sampling.

and between communities. The species–area curves crossed only at the smallest sample areas, where there was the greatest variability between single samples. Once samples were combined, the variability was reduced at larger sample areas and the relative differences among the curves persisted to the end of each curve (*e.g.* Fig. 3 top panel).

The presence of an oxygen minimum zone (OMZ) did not account for the lower species density on the slope compared to the shelf. The OMZ is between 500 and 1000 m in the study area (Mullins *et al.* 1985; Johnson *et al.* 1992). Although oxygen levels in the Central California coastline's OMZ are relatively low compared to some upwelling regions (Levin 2003), the center of the OMZ harbored a dense community of ampeliscid amphipods, forming a tube mat that was seen in ROV video footage along all four of the MCI depth transects (Fig. 1). We sampled in the tube mat from the center of the OMZ at 700 m and included these samples in the upper slope, where there was relatively high species density (Fig. 2). The lowest species densities were found below the OMZ at 1000–2000 m (Fig. 2).

In addition to higher species density on the shelf, we found a significant negative correlation between the number of species and dominance per grab sample (Fig. 6). The significant correlation persisted if we separated the data into shelf ($r^2 = 0.1$) and slope ($r^2 = 0.2$, $P < 0.0001$ for both). This negative relationship is present along the wave-swept inner shelf and in local wetlands as well (Oliver *et al.* 2008, 2009). Since there are usually higher numbers of individuals on the shelf compared to the slope, we observed a significant positive correlation between the number of species and individuals (Fig. 6). This correlation also persisted when the data were divided into shelf ($r^2 = 0.6$) and slope ($r^2 = 0.3$, $P < 0.0001$ for both).

Other indices

Changes in the Shannon–Wiener index followed the same pattern as species density: higher on the shelf than the slope, highest at the shelf break, and lowest along the deeper slope (Table 1). Simpson's dominance was lowest on the shelf and highest in the deepest water depths sampled (Table 1). We recommend that H' and J be retired from ecology and that other species diversity indices should be named for what they attempt to model, such as the probability of interspecific encounter (PIE), as Hurlbert (1971) recommended decades ago. Indices of dominance and evenness should be just that, and no longer components of species diversity. They are important summaries of relative abundance. Species diversity should also not be a model of the complexity of biological interactions. It should refer to the variety of species estimated by two types of structural metrics, species density and numerical species richness, with no ambiguity about which is being presented. Number of species increases with increasing habitat area in a non-linear manner, so quantitative sampling gear collects a standard area of bottom to allow direct comparisons among replicates and other sample collections. The gold standard for measuring species number should be the number per quantitative sample and thus area. Levin *et al.* (2001) found that species density and numerical species richness showed the same pattern with depth, but not in our sampling (Fig. 2). Although the shelf edge (100–150 m) had the

Table 1. Summary statistics for the total dataset and selected depth ranges. N is the number of samples in each depth range. S is the observed total number of species. Chao1 is a total species density estimator. H' is the Shannon–Wiener index and λ is Simpson's Dominance Index.

depth range (m)	N	S	Chao1	H'	λ
30–2000	310	1521	1714	3.420	0.085
30–95	154	1081	1293	3.675	0.057
100–150	50	804	998	3.680	0.064
250–700	71	747	942	2.981	0.130
950–2000	35	380	508	2.821	0.149

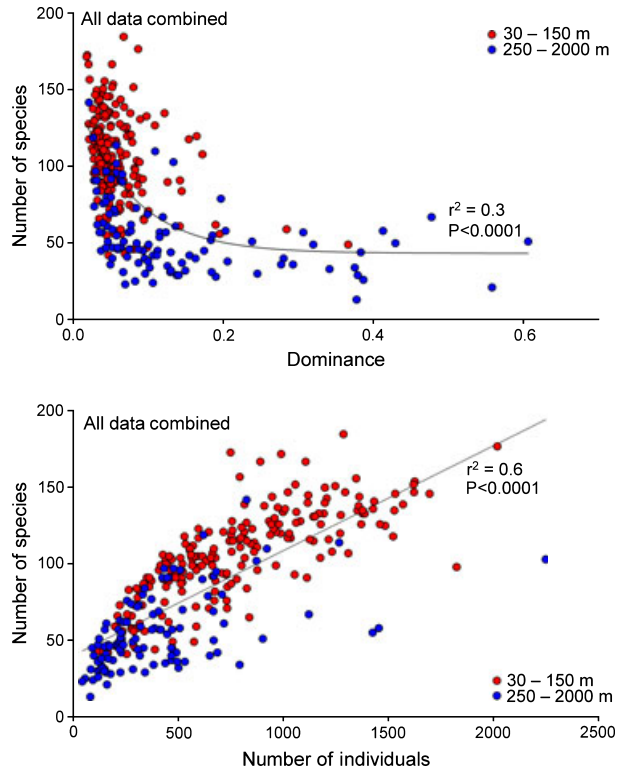

Fig. 6. The significant negative relationship between number of species and dominance and the significant positive correlation between number of species and individuals (all four datasets).

Table 2. Comparison of species density of soft-bottom macrobenthos from the upwelling coast of California and other soft-bottom communities with high species density.

sample area (m^2)	Central California continental shelf and slope species density							species density in worldwide studies			
	30–150 all data	250–2000 all data	30–150 MCI & NOAA	30–150 MCI	80–150 NOAA	33–123 WEMAP	80 CCLEAN	no. of species	depth (m)	sieve size (mm)	location
23.10	1286[a]							886	90–565	0.30	Santa Maria, CA, USA[1]
21.00	1286[a]							798	1500–2500	0.30	NJ & DE, USA[2]
17.19	1231[b]							952	250–2180	0.30	Georges Bank, USA[3]
13.50	1153	858[c]						1202	600–3500	0.30	Carolina Slope, USA (SACSAR)[4]
13.50	1153	858[c]						810	2160–3142	0.30	San Francisco, CA, USA[5]
13.30	1148	858[c]						1295	600–3500	0.30	Carolina Slope, USA (SACSAR)[6]
10.40	1069	853	957[d]					803	11–51	1.00	Bass Strait, Australia[7]
5.67	937[g]	706[g]	858[g]	723[e]		634[f]	549	599	1220–1350	0.30	New England, USA (NACSAR)[3]
2.50	652	512	653	568	549	531	447	511*	400–1800	0.42	Hebrides Slope, Scotland, UK[8]
1.25	487	364	493	440	436	405	362	314	1230	0.42	San Diego Trough, CA, USA[9]
0.81	418[h]	301[h]	401[h]	364[h]	366[h]	337[h]	310[h]	436	800	0.30	Charleston, SC, USA[4]
0.68	363	253	371	335	343	314	292	250	3600	0.30	New England, USA[10]

Total sample area (m^2) = [a]20.4, [b]17.2, [c]10.6, [d]8.3, [e]5.6, [f]4.9, [g]5.7, [h]0.80; *Peracarid crustaceans not identified.
[1]Hyland *et al.* (1991); [2]Grassle & Maciolek (1992); [3]Cited in Levin *et al.* (2001); [4]Blake & Grassle (1994); [5]Blake *et al.* (2009); [6]Hilbig (1994); [7]Gray *et al.* (1997); [8]Gage *et al.* (2000); [9]Jumars (1976); [10]Grassle & Morse-Porteous (1987).

highest numerical species richness and species density, numerical richness at the other depths were quite similar (Fig. 2). Therefore, we cannot always expect numerical species richness and species density to show the same depth and geographic patterns.

Numerical species richness often peaks along the slope (Rex 1981, 1983; Levin *et al.* 2001), but not always (Menot *et al.* 2010). Species density in the deep-sea may also be high along the slope, but there are high values from the shelf as well (Table 2). Although we did not observe high species density from the slope depths we sampled (Figs 2 and 3), there are high values along the slope outside San Francisco Bay (Table 2), which is only 100 km north of Monterey Bay (Fig. 1). The important similarity in all these data is that the highest values (species density and numerical species richness) are along the continental margins (Table 2, Menot *et al.* 2010). The species density data clearly show that slope and shelf communities both have extremely high values (Table 2).

If we could shrink ourselves and walk through the benthic community as we can walk through a forest, the number of species would clearly be higher on the shelf than on the slope (Figs 2 and 3). If we walked from the scale of a sample (0.1-m^2) to the local setting and through the regional geography, the variety of species would be higher on the shelf at all spatial scales (Figs 2–5). This is not reflected in numerical species richness, which showed little difference between the shelf and slope (Fig. 2). We would also encounter a much greater number of individuals and less dominance on the shelf (Fig. 6, Table 1). A higher species density (Fig. 2), larger number of animals (Fig. 6), and greater evenness of relative abundance (Fig. 6) would lead most naturalists to conclude that the complexity of biological interactions should be higher on the shelf (all other things being equal for the walk). There is no model (probability of interspecific encounter or other) that combines these fundamental community metrics into a single metric of community complexity (structure or function) without obscuring the most important ecological realities observed during our hypothetical walk. Numerical species richness is a fine addition to the three metrics and is especially useful if we do not have samples of a standard area. If quantitative samples are taken, species density should be measured and presented in species–area curves for community descriptions. Despite the statistical inconvenience of the correlation between the number of species and individuals (Fig. 6), the most realistic community description is done in a known spatial context, especially for comparisons among samples, community patches, and different communities.

Worldwide patterns

We compared our data with the highest species densities in soft sediments that we could find in the literature (Table 2). Species density from the continental shelf in Monterey Bay was very similar to levels reported from the Carolina slope, which has the highest species densities in the world reported to date, with a peak at 800 m (436/0.81 m^2; Table 2). The Carolina slope has a heterogeneous bottom with dynamic currents and likely high inputs of food (Blake & Grassle 1994). The second highest species density from the shelf was documented on the Australian side of Bass Strait between Australia and Tasmania (Gray *et al.* 1997). The species density was also high on the shelf and highest at the shelf break at the southern end of the California upwelling system (Hyland *et al.* 1991). It appears that the soft-bottom shelf communities with the highest species densities in the world were found in well-mixed and oxygenated waters with high production (Breaker & Broenkow 1994; Pennington & Chavez 2000; Fitzwater *et al.* 2003; McGinley 2008; Ryan *et al.* 2009). These general habitat characteristics are similar to the current-dominated Carolina slope with the highest species densities in the world (Blake & Grassle 1994).

Escaravage *et al.* (2009) documented a positive relationship between species density and productivity in soft bottoms from a compiled dataset covering the European coast (primarily from the shelf). They include two studies with moderately high species density: the highest with 1033 species in 34.4 m^2 from the Aegean. We found 1531 in 32 m^2 (Fig. 1). There are 952 in 17.19 m^2 along the Georgia Banks (Table 2), which is half the sample area from the Aegean. Table 2 does not include a number of other studies with moderately high species density (*e.g.* Gage 1979; Gray *et al.* 1997; Stora *et al.* 1999; Thiel *et al.* 2007; Dahle *et al.* 2009).

Differences between sampling methods and sample dispersion do not confound comparisons between our data and those from other parts of the world (Table 2). All the data in Table 2 come from quantitative samples. We are not comparing species density to numerical species richness (Abele & Walters 1979; Gray *et al.* 1997). The differences in screen size do not lead to unrealistic comparisons, but some must be qualified, especially the samples from Bass Strait. We found no loss of species between the 0.5- and 0.3-mm screens, so our data can be compared to samples that were washed through the smaller screen (most of the data in Table 2). Samples from two of the slope sites were washed through 0.42-mm screens, potentially losing some species that could be captured on a 0.3-mm mesh. The samples from Scotland do not include the peracarid crustaceans, so species density should be even higher here. We include the two 0.42-mm surveys because they found high species density despite their use of a larger sieve mesh size. Bass Strait samples were dispersed over a small geographic area and depth range and washed over a 1-mm screen, which could significantly depress species density. Despite these likely losses, Bass Strait has a high species density (Table 2, Gray *et al.* 1997). If the sampling included the entire shelf and a 0.5-mm screen, species density might be more similar to that in Monterey Bay and along the Carolina slope. Although there are considerable differences in the depth and geographic ranges of the data from other parts of the world, many of these differences are similar to the variation in our study, which includes samples from one depth, two depth zones on the shelf and slope, the shelf and slope combined, and several different geographic scales with different depth ranges. None of the differences discussed above invalidates the comparisons in Table 2.

Boundary effects

All of the communities with the highest species densities (Table 2) are located along continental margins, where there are dramatic changes in topography. The continental slope is probably the most extensive steep rise in topography in the ocean. The shelf–slope break is the most abrupt topographic change along the slope. Pelagic primary productivity at the ocean surface is often highest over the continental shelf and drops rapidly at the shelf break and over the slope (Kudela *et al.* 2008). However, we found a strikingly different pattern in benthic species density. The highest species density in our study occurred around the shelf–slope break (Fig. 2). We documented 804 species in 5 m^2 (Fig. 2, top panel) collected from 100 to 150 m. Four of the locations from other parts of the world reported about 800 species, but they were collected in sample areas that were two to four times larger than 5 m^2 (Table 2).

What is it about the shelf break that might cause such high species densities? Although the continental shelf is often characterized by an accumulation of fine material (a 'shelf mud belt'), the outer shelf and upper slope usually comprise coarser grained sediments, a relict from glacial low sea stands. Oceanographers have long discussed the reasons that the relatively abrupt change in topographic steepness at the shelf break might enhance currents and frictional dissipation of long-wavelength features such as tides and low-mode internal tides (Sverdrup *et al.* 1942). Abrupt topographic changes such as those found on Georges Banks or on the European shelf seas can cause tidal mixing fronts and intense, rapid exchange between the sea floor and near-surface waters (Houghton &

Ho 2001), and a seasonal shelf-break front is a common feature of the Northeastern Atlantic (Chapman & Lentz 1994). Although such features are not typically found over the continental shelves of California, they still serve to illustrate the sometimes dramatic changes in dynamics and energy near the shelf–slope break (see review, McPhee-Shaw 2006). Studies from the California margin demonstrate that interaction between internal tides and topography intensify cross-isobath currents over the upper continental slope and are associated with removal of fine sediments from the margin (Cacchione *et al.* 2002; McPhee-Shaw *et al.* 2004).

These variations in energy and dynamics can have an array of effects on benthic habitat. Intense up-slope and down-slope excursions associated with internal tides expose benthic organisms, which are fixed in space, to several hundred meters of vertical water column gradients of temperature and oxygen, and over brief time scales (<12 h). These water movements may also bring more food to the benthos. Energetic currents prevent the accumulation of fine material, and presumably allow greater penetration of oxygen and nutrients into the substrate. Thus, just as in freshwater ecosystems, where the well mixed and oxygenated gravel and mixed-substrate under medium-to-energetic streams have a much higher density of macroinvertebrates than the substrates under either very strong rivers or under the still waters of deep channels, ponds, and lakes (Karr & Chu 1999), the shelf–slope break and upper slope may be an ideal habitat for ocean benthic communities. Although more diffuse in space and larger in scale, the shelf break and upper continental slope may be analogous to the species-rich hard-bottom communities of coral reefs and ocean pinnacles, both of which have a topography that enhances water motion and the transport of food and nutrients to the sea floor (Genin *et al.* 1986; Koslow 1997; Leichter *et al.* 1998; Genin 2004).

Summary

1 We found 1521 species of macrofaunal invertebrates in 32 m^2 of bottom from the California upwelling system (Fig. 2), where soft-bottom species density is among the highest in the world (Table 2).

2 Species density was consistently higher along the shelf (30–150 m) than along the slope (250–2000 m; Figs 2 and 3), with the highest number of species at the shelf–slope break (Fig. 2: 100–150 m) coincident with breaking internal waves and in the Monterey Bay under an upwelling plume and production hot spot (Fig. 4).

3 Numerical species richness did not show the same depth pattern as species density, which we consider the best local and regional estimate of species number.

4 There was a significant negative correlation between the number of species and dominance.

5 Species density from the California shelf is remarkably similar to that reported from the Carolina slope, at both local (800 m compared to the shelf break) and regional scales (Table 2). Species density at these two sites is considerably higher than anywhere else in the world.

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