



ORIGINAL ARTICLE

# Assemblage structure, but not diversity or density, change with depth on a northeast Pacific seamount

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## Keywords

Alpha-diversity; assemblage structure; bathymetric; beta-diversity; density; species turnover.

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## Abstract

Although depth-related patterns in assemblage structure are documented in several deep-sea systems, variation in diversity, assemblage structure, and abundance with depth on individual seamounts remains unexplored. Knowledge of alpha- and beta-diversity on single seamounts is needed for any robust generalization about large-scale biodiversity patterns on seamounts. Here, we explore bathymetric variation in benthic megafauna, based on ROV video transects, on Davidson seamount (1246–3656 m) in the Northeast Pacific Ocean. We found that substantial change in assemblage structure can occur over vertical scales on an individual seamount. Changes of 50% in assemblage composition (beta-diversity, faunal turnover) were observed over as little as a ~1500 m depth interval down the flanks of the seamount, although bathymetric clines in composition were not uniform across major taxa. Diversity and density exhibit no consistent bathymetric pattern and can vary greatly on a single isobath. Our findings suggest that ecological and evolutionary processes may vary considerably on a single seamount. As such, seamounts should be viewed as patchworks of habitats where high beta-diversity may ultimately increase total biodiversity.

## Introduction

Biodiversity, irrespective of taxa, is distributed heterogeneously across all landscapes (Ricklefs & Schluter 1993) including the deep sea (Rex 1973; Rex *et al.* 2000; Levin *et al.* 2001). Given that many environmental and biological drivers vary with depth, it is unsurprising that the deep-sea literature is brimming with explorations of various ecological metrics, such as alpha-diversity, beta-diversity, standing stock, body size, genetic structure, and trophic diversity, over bathymetric gradients on the continental slope and rise (Rex 1973; Jumars *et al.* 1990; Carney 2005; Etter *et al.* 2005; McClain 2005; McClain *et al.* 2005; Rex *et al.* 2006). Previous studies suggest several macroecological rules, albeit with exceptions, for the deep-sea benthos: (i) diversity typically displays a unimodal relationship with depth, with diversity highest at intermediate depths (~2000–

3000 m), (ii) the presence of considerable species zonation with depth, (iii) density and biomass decrease exponentially with depth, (iv) and an overall reduction in body size with increasing depth (reviewed in McClain *et al.* 2009b,c). These patterns likely reflect multiple processes, working in concert (McClain & Barry 2009). Factors such as oxygen, sediment grain size, topographic complexity, disturbance, ocean chemistry (Etter & Grassle 1992; Levin *et al.* 2001; McClain & Rex 2001; Levin 2003; McClain 2005; McClain *et al.* 2009b,c) and particularly spatial and temporal variation in food availability (Rex 1981; Snelgrove *et al.* 1992; Levin *et al.* 2001; Gooday 2002; Ruhl & Smith 2004; Rex *et al.* 2006; Johnson *et al.* 2007; Smith *et al.* 2008) remain key explanations. However, little support exists for some hypotheses of bathymetric clines such as geometric constraints, temperature, and area (Rex 1981; Pineda & Caswell 1998; McClain & Etter 2004).

Central to the discussion of seamount biodiversity is the pattern of beta-diversity with depth on single seamounts. Such information is important for clarifying whether the hypothesized heightened diversity of seamounts (Samadi *et al.* 2006) reflects greater faunal turnover or greater species coexistence. Questions concerning the contribution of seamount faunas to regional and global diversity also require an understanding of faunal turnover across individual seamounts. Faunal dissimilarity between seamounts (de Forges *et al.* 2000) may simply reflect bathymetric differences between them as opposed to geographic distance. The global biodiversity on seamounts would be lower if faunas were replicated among seamounts at the same depth. More generally, bathymetric gradients on seamounts may provide natural experiments in which hypotheses about the maintenance of deep-sea diversity can be tested and refined. Seamounts provide opportunities for depth and key environmental factors to be uncorrelated. For example, on continental margins, carbon flux typically decreases with increasing depth, correlating in part with distance from high productivity coastal regions (Johnson *et al.* 2007). Seamounts far from productive coastal waters may exhibit weaker relationships of flux with depth.

Despite the reasons for gaining an understanding of bathymetric changes in biodiversity on seamounts, studies explicitly examining such changes are rare (although see Lundsten *et al.* 2009a,b). Most studies on seamount biodiversity address patterns of beta-diversity among seamounts (de Forges *et al.* 2000). This may reflect the difficulty of gaining adequate bathymetric coverage on a single seamount due to the prohibitive cost of obtaining multiple samples, difficulty of sampling a predominantly hard substrate, and a host of other issues more general to oceanographic fieldwork. Here we capitalize on an intensive field program to quantify biodiversity at Davidson Seamount off the central California coast (Lundsten *et al.* 2009a,b; McClain *et al.* 2009a), utilizing video transects conducted with remotely operated vehicles. We test for decreases in density, a unimodal diversity relationship, and significant faunal change with depth among the Davidson seamount benthic megafauna.

## Material and Methods

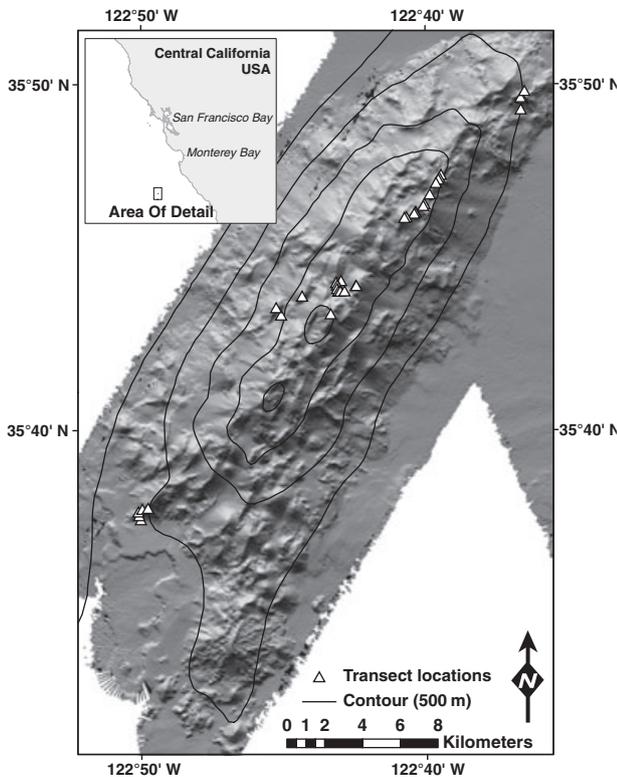
### Collection of megafaunal assemblage data

Seamount communities were sampled using video transects collected by MBARI's ROV *Tiburón*. Video transects were conducted using high definition (HD) video cameras and recorded onto D5-HD video tape. We collected specimens for taxonomic determinations using ROV

manipulator arms and suction samplers. Video transects were annotated in detail using MBARI's Video Annotation and Reference System, VARS (Schlining & Jacobsen-Stout 2006).

All megafauna were identified to the species level or equivalent by trained video annotators using *in situ* video frame grabs and/or voucher specimens that were identified by taxonomists (see Acknowledgements). Every effort was made to assign organisms that were morphologically distinct (*i.e.* morphospecies) with an appropriate Latin binomial. Voucher specimens were not collected for organisms that could be identified easily from video and are known from the Californian shelf and Monterey Canyon. In some instances, voucher specimens were not obtainable and video frame grabs, digital still images, and/or video segments of the organisms in question were reviewed by taxonomists with expertise in that particular taxonomic group. Recently, the usage of video and still images in biogeographic, ecological, and taxonomic studies of deep-sea species has become a common and vital tool for describing both species and faunas in habitats logistically difficult to sample like the deep sea (Matsumoto *et al.* 2003; Haddock 2004; Braby *et al.* 2007; Cairns 2007; Lundsten *et al.* 2009a,b; Williams & Lundsten 2009).

A total of 33 quantitative video transects were collected at Davidson Seamount in 2006 (Fig. 1). The total number of transects reflects the maximum number feasible during our total allotted remotely operated vehicle dives. Transect placement was chosen to maximize depth coverage, minimize ship and ROV transit time, and satisfy multiple dive objectives spanning across several research projects. Two parallel, 640-nm red lasers were placed 29 cm apart and used to estimate transect width. Transect length was calculated in ARCVIEW® 3.2 using the Animal Movement Analysis Extension, Version 2, which was used to calculate successive distance between transect start and end points (Hooge & Eichenlaub 1997). Transect distance ranged from 93 m to 444 m with the mean and majority of transects being near 200 m and transect width between 1 and 3 m. For each transect the total area was calculated and included as a factor in the analyses. For multivariate analyses, density per meter squared was used to calculate similarities using abundance. Davidson Seamount was sampled over 96.8% of its depth from summit at 1246 m to base at 3289 m (transects at 1299, 1477, 1546, 1602, 1655, 1664, 1671, 1674, 1677, 1681, 1692, 1693, 1698, 1719, 1719, 1725, 1725, 1742, 1747, 1764, 1769, 2043, 2219, 2464, 2491, 2664, 2675, 2790, 2927, 2949, 3068, 3190, and 3276 m). More on the features, geology, and habitat of Davidson Seamount can be found in Davis *et al.* (2002).



**Fig. 1.** Map showing location of Davidson Seamount off the central Californian coast. Points represent locations of video transects.

### Statistical analyses

For each megafauna video transect, species richness ( $S$ ), Shannon's diversity index ( $H'$ ), Pielou's evenness ( $J'$ ), and  $\log_{10}$  density per meter squared were calculated using EstimateS (Colwell 2009). Log values were used to normalize the data to meet the assumptions of the statistical tests. Each of these variables was plotted against depth and Type 1 regression analysis using the statistical software JMP (1989–2007, SAS Institute Inc., Cary, NC, USA).

To examine how similarity among assemblages changes with depth across Davidson Seamount, we employed the distance decay of similarity method as described by Nekola & White (1999). Similarity between transects was quantified as Bray–Curtis similarity on presence/absence data as utilized in other studies (Nekola & White 1999; Soininen *et al.* 2007) to measure change in composition rather than change in dominance of species. Decay was measured as change in similarity from both the shallowest and deepest assemblages on Davidson Seamount. Exponential functions were fitted to the relationships ( $Sim = a * Depth * Separation^b$ ). The similarity half-life, the amount of depth

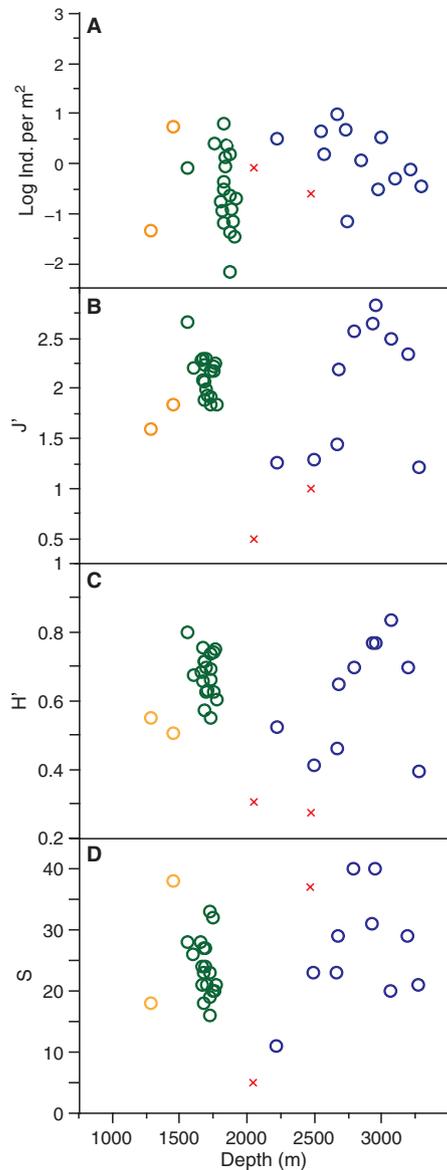
required to see a 50% change in similarity, was calculated by dividing  $\ln 2$  by the slope of the exponential fit ( $half\ life = \ln 2 / b$ ).

Several multivariate analyses were conducted using routines in PRIMER v6 (Clarke & Gorley 2006). Bray–Curtis similarity was calculated between transects using both presence/absence and log-transformed abundance data. Utilizing both presence/absence and log-transformed abundances allows us to explore bathymetric changes in both species composition and the species dominance. Nonmetric multidimensional scaling (MDS) plots were used to visualize faunal turnover between transects in a reduced multivariate space. MDS plots were conducted with a standard 25 restarts and allowing dissimilarities which are equal to be represented in the final ordination by distances which are not. Cluster analyses, using group averages, were also conducted on both the log-transformed and presence/absence-based similarity matrices. The SIMPROF routine in PRIMER was used to test the null hypothesis that sets of transects not divided by depth do not differ from each other in multivariate structure. This routine allows 'communities' in the cluster analysis to be identified (significance level set at  $P < 0.05$ ). The SIMPER routine in PRIMER was used to quantify the contribution of each species to the Bray–Curtis similarities within and among transect groups identified by the cluster analyses. Using the RELATE test in PRIMER, analogous to a Mantel test, we tested the correlation between the faunal similarity matrices and a model similarity matrix based only on differences in depths between transects, *i.e.* that faunal similarities are related to depth differences among transects. Analyses were conducted for total megafaunal assemblages and individual higher taxa. The 2STAGE routine in PRIMER was used to explore how bathymetric changes among different taxa were related. 2STAGE conducts an MDS on a similarity matrix comprising correlation coefficients between varying similarity matrices.

### Results

#### Density, evenness, and alpha-diversity

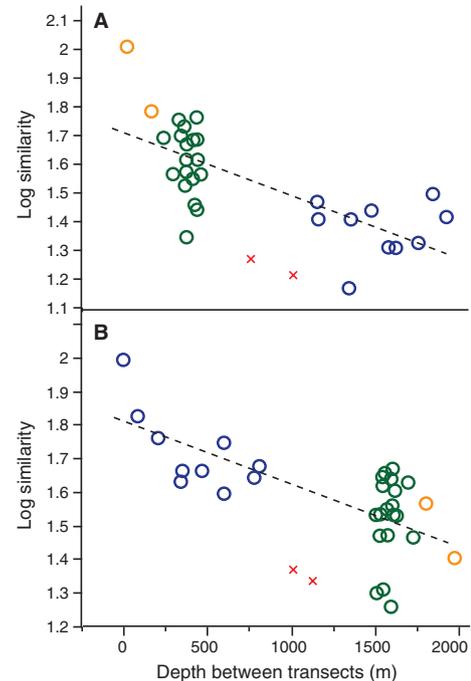
Density did not decline significantly with depth over Davidson Seamount ( $P = 0.2911$ ,  $df = 32$ , Fig. 2A). Overall, there appears to be little bathymetric variation in species richness ( $S$ ), evenness ( $J'$ ), or diversity ( $H'$ ) (Fig. 2B–D). Linear or quadratic regressions of all three metrics across Davidson Seamount were not significant ( $P = 0.2140$ – $0.9392$ ,  $df = 32$ ). Transect area was not a significant predictor of density,  $S$ ,  $J'$ , or  $H'$  ( $P = 0.357$ ,  $P = 0.184$ ,  $P = 0.746$ ,  $P = 0.859$ ).



**Fig. 2.** Bivariate plots of faunal metrics *versus* depth. Symbols represent substrate type (X: soft, o: hard). Colours correspond to the faunal zones as identified in the cluster analysis (Fig. 5). (A) Log density (individuals per meter squared). (B) Pielou's evenness ( $J'$ ). (C) Shannon's diversity index ( $H'$ ), and (D) Species richness ( $S$ ).

#### Assemblage composition and structure

Faunal similarity between stations decays exponentially with increasing separation of transects on the depth gradient (Fig. 3A,B), whether measured as changes from the shallowest (Similarity =  $1.80\text{Depth}^{-0.0005}$ ,  $R^2 = 0.53$ ,  $P < 0.0001$ ,  $df = 32$ ) or changes from the deepest transects (Similarity =  $1.71\text{Depth}^{-0.0004}$ ,  $R^2 = 0.48$ ,  $P < 0.0001$ ,  $df = 32$ ). The similarity half-lives, the amount of depth required to observe a 50% difference in composi-

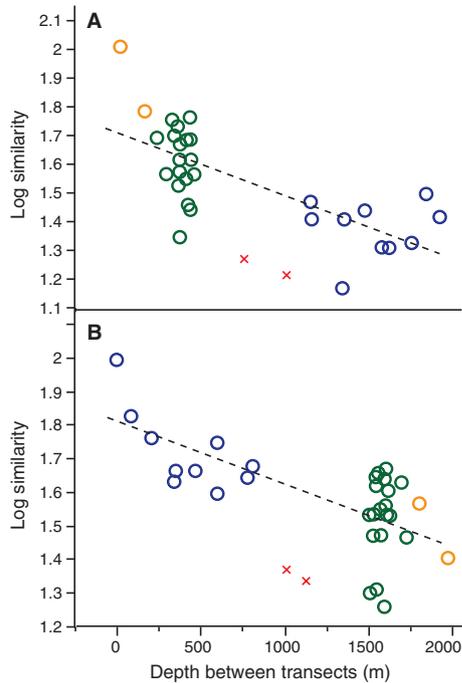


**Fig. 3.** (A) Distance decay, measured as Bray–Curtis similarity based on presence/absences from the deepest transect (Similarity =  $1.71\text{Depth}^{-0.0004}$ ,  $R^2 = 0.48$ ,  $P < 0.0001$ ). (B) Distance decay, measured as Bray–Curtis similarity based on presence/absence from the shallowest transect (Similarity =  $1.80\text{Depth}^{-0.0005}$ ,  $R^2 = 0.53$ ,  $P < 0.0001$ ).

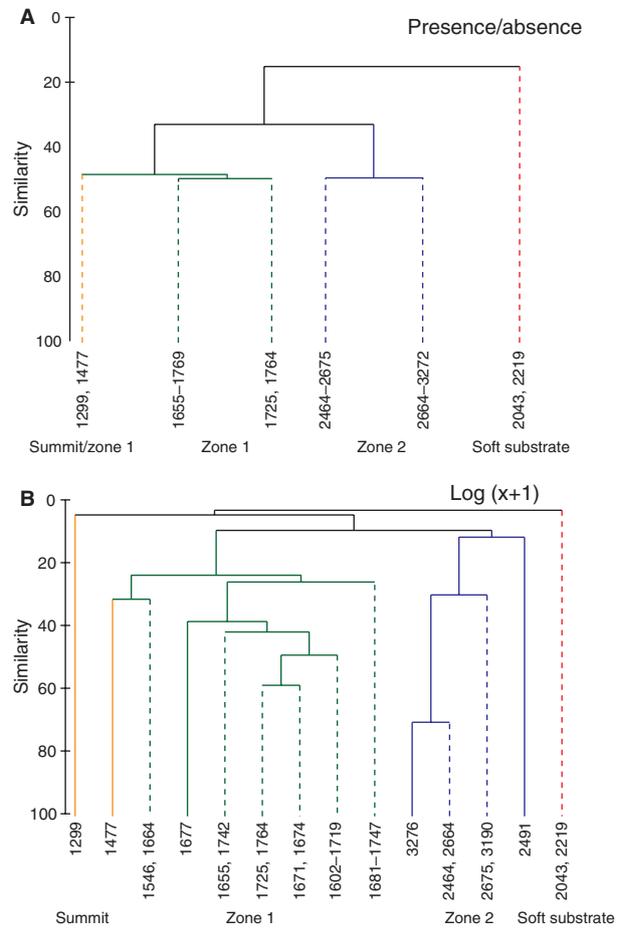
tion, are 1733 m and 1386 m, calculated from the deepest and shallowest transects, respectively. Transects at the opposite end of the depths sampled here have only 20–30% similarity in species composition.

An MDS plot of the similarity of megafauna based on depth alone yields a horseshoe pattern in multivariate space (Fig. 4B,C). This horseshoe feature is to be expected for a linear gradient in a 2-D MDS plot (Fig. 4A). MDS plots for all megafauna based on both presence/absence (Fig. 4B) and log-transformed (Fig. 4C) data also exhibit a similar horseshoe shape, implying that assemblage structure changes considerably over depth at Davidson Seamount in terms of composition and the relative abundances among species. Correlations between a model similarity matrix based on depth and the similarity matrix based on presence/absence data were significant and highly correlated ( $Rho = 0.65$ ,  $P < 0.001$ , Table 1). Correlations with log-transformed data that include species abundances are slightly weaker but significant ( $Rho = 0.53$ ,  $P < 0.001$ ).

The MDS and cluster analyses suggest four broad groupings of transects (hereafter referred to as 'zones'), with both species composition and dominance analyzed (Fig. 5). The transects 1299 and 1477 m form a Summit



**Fig. 4.** (A) Nonmetric multidimensional scaling (MDS) based on Bray–Curtis similarity of depth differences alone. MDS plots based on Bray–Curtis similarity of (B) presence/absence and (C) log-transformed data. Numbers indicate transect depth. For clarity, not all points are labeled. Lines indicate increasing depth. Note that visual similarities between subplots B and C to A indicate importance of depth in structuring these communities.



**Fig. 5.** Cluster analyses based on Bray–Curtis similarity of (A) presence/absence and (B) log-transformed data. Dotted lines contain multiple transects and further branches (not shown) are not significant different from random.

**Table 1.** Rank correlations between Bray–Curtis similarity matrices based on megafaunal data and a model matrix based on depths alone.

transformation	group	Rho	P-value
Presence/Absence	Davidson Total	<b>0.65</b>	<b>0.001</b>
	Actinopterygii	−0.02	0.544
Log (x + 1)	Davidson Total	<b>0.53</b>	<b>0.001</b>
	Cnidaria	<b>0.36</b>	<b>0.003</b>
	Hexacorallia	0.05	0.278
	Cerianthipatharia	<b>0.23</b>	<b>0.010</b>
	Octacorallia	<b>0.41</b>	<b>0.002</b>
	Decapoda	−0.08	0.786
	Echinodermata	<b>0.54</b>	<b>0.001</b>
	Holothuroidea	0.05	0.255
	Crinoidea	<b>0.20</b>	<b>0.031</b>
	Asteroidea	<b>0.28</b>	<b>0.003</b>
Porifera		<b>0.56</b>	<b>0.001</b>
	Hexactinellida	<b>0.68</b>	<b>0.001</b>
	Demospongiae	<b>0.30</b>	<b>0.001</b>

Values in bold indicate significant correlations.

Zone assemblage sharing 60.7% similarity in species composition (Table 2). The summit zone is characterized by the presence of the anthozoan *Paragorgia arborea*; hexactinellids *Farrea occa*, *Heterochone calyx*, and *Chonelasma* sp.; and the echinoderms *Ceramaster patagonicus* and *Gorgoncephalus* sp. (Table 2). Although transects 1299 and 1477 m form a summit zone for presence/absence data, 1477 m groups more closely with the deeper zone (Fig. 5B) when species abundances are considered. This is driven largely by differences in the bubblegum coral *P. arborea*. The Zone 1 assemblage, occurring on Davidson’s flanks, includes depths of 1546–1769 and is on average 58.3% compositionally similar and 37.7% similar when species abundances are accounted for (Table 2, Fig. 5). The compositional similarity of the Zone 1 assemblage is driven by the abundant hexactinellid sponges *Sclerothamnopsis* sp., Hexactinellidae sp. A, and

**Table 2.** List of species that characterize each depth zone.

zone	presence/absence		Log (x + 1)	
	species	contribution %	Species	contribution %
Summit	<b>Average Similarity</b>	<b>60.7</b>		
1299–1477 m	Octocorallia: <i>Anthomastus ritteri</i>	5.9		
	Octocorallia: <i>Paragorgia arborea</i>	5.9		
	Asteroidea: <i>Ceramaster patagonicus</i>	5.9		
	Ophiuroidea: <i>Gorgonocephalus</i> sp.	5.9		
	Hexactinellida: <i>Chonelasma</i> sp.	5.9		
	Demospongiae: <i>Asbestobluma</i> sp. nov.	5.9		
	Hexactinellida: <i>Farrea occa</i>	5.9		
	Hexactinellida: <i>Heterochone calyx</i>	5.9		
	Total	47.0		
Zone 1	<b>Average Similarity</b>	<b>58.3</b>		<b>37.7</b>
1655–1769 m	Hexactinellida: Hexactinellida sp. A	6.6	Hexactinellida: <i>Sclerothamnopsis</i> sp.	66.8
	Hexactinellida: <i>Sclerothamnopsis</i> sp.	6.5	Hexactinellida: Hexactinellida sp. A	10.4
	Hexacorallia: <i>Actinaria</i> sp.	5.2	Hexactinellida: <i>Chonelasma</i> sp.	6.5
	Crinoidea: <i>Florometra serratissima</i>	5.0		
	Hexactinellida: Hexactinellida sp. B	4.5		
	Ophiuroidea: <i>Gorgonocephalus</i> sp.	4.4		
	Octocorallia: <i>Anthomastus ritteri</i>	3.9		
	Bivalvia: Pectiniidae sp. A	3.7		
	Octocorallia: <i>Corrallium</i> sp.	3.3		
	Antipatharia: <i>Lillipathes</i> sp.	3.2		
	Hexactinellida: <i>Farrea occa</i>	2.3		
	Octocorallia: <i>Acanella</i> sp.	1.7		
	Total	50.2		83.7
Zone 2	<b>Average Similarity</b>	<b>54.0</b>		<b>21.5</b>
2464–3276 m	Hexacorallia: <i>Actinaria</i> sp.	6.5	Demospongia: <i>Poecilosclerida</i> sp.	61.7
	Crinoidea: <i>Bathycrinus</i> sp.	6.5	Crinoidea: <i>Florometra serratissima</i>	24.8
	Crinoidea: <i>Florometra serratissima</i>	6.5		
	Crinoidea: <i>Hyocrinus</i> sp.	6.5		
	Octocorallia: <i>Lepidisis</i> sp.	5.2		
	Antipatharia: <i>Umbellapathes</i> sp.	5.0		
	Octocorallia: <i>Chrysogorgia pinnata</i>	2.1		
	Demospongiae: <i>Poecilosclerida</i> sp.	2.1		
	Maxillopoda: Scapellidae sp.	2.0		
	Hexactinellida: <i>Saccocalyx pedunculata</i>	1.8		
	Antipatharia: <i>Trissopathes pseudotrística</i>	1.4		
	Asteroidea: <i>Ceramaster patagonicus</i>	1.3		
	Octocorallia: <i>Chrysogorgia monticola</i>	1.3		
	Total	48.2		86.5
Soft	<b>Average Similarity</b>	<b>37.5</b>		<b>0.0</b>
2024, 2219 m	Holothuroidea: <i>Pannychia moseleyi</i>	43.2	Holothuroidea: <i>Pannychia moseleyi</i>	67.8
	Holothuroidea: <i>Laetomogone</i> sp.	33.3		
	Asteroidea: <i>Ceramaster patagonicus</i>	22.4		
	<b>Total</b>	<b>99.0</b>		<b>67.8</b>

List was constructed by determining how much each species significantly contributed (%) to the within group similarity based on both presence/absence and density [Log(x + 1)] between stations in each zone as determined by the SIMPER routine in PRIMER. The average Bray–Curtis similarity among stations within a zone is given in bold.

*Chonelasma* sp. The appearances of the corals, *Acanella* sp., *Lillipathes* sp., and *Corrallium* sp., as well as the crinoid *Florometra serratissima*, also characterize the assemblage of this zone. The deeper Zone 2 assemblage, 2464–3276 m on Davidson's base, is characterized by its high

abundances of a stalked glass sponge *Poecilosclerida* sp. and the crinoid *F. serratissima*. Some similarity to the Zone 1 assemblage occurs in the presence of *F. serratissima* and *Actinaria* sp. The Zone 2 assemblage also includes the crinoids *Bathycrinus* sp. and *Hyocrinus* sp.,

as well as corals *Lepidisis* sp., *Umbellapathes* sp. *Chyrsogorgia pinnata*, *Chyrsogorgia monticola*, and *Trissopathes pseudotristicha*.

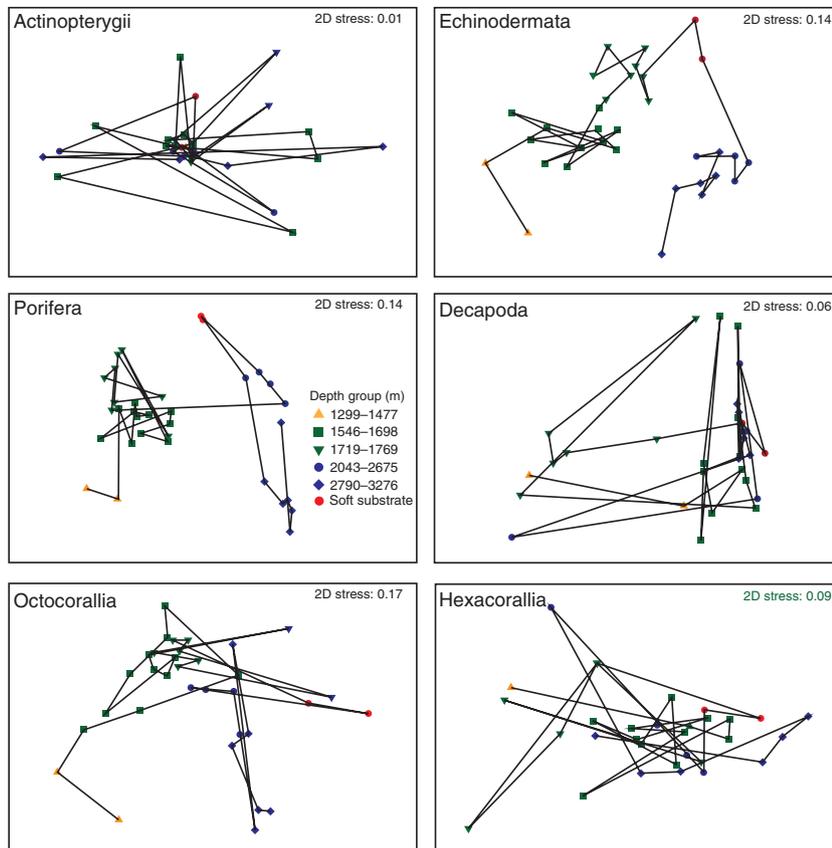
The MDS and previous analyses reveal two outliers, transects 2219 m and 2043 m. These transects are characterized by lower diversity and density which are considerably different from the other transects in the study. Both transects occurred in a sediment pond Seamount with a substrate consisting of coarse sands that were dominated numerically by the holothurians *Pannychia moseleyi* and *Laetomogone* sp., which occurred rarely or never on other transects.

Individual faunal groups exhibit varying bathymetric responses in assemblage structure (Table 1). Porifera, both as a phylum and separated by classes, exhibited the strongest depth signal (Table 1, Figs 6 and 7). Changes in Echinodermata as a whole, and crinoids and asteroids, also correlate strongly with depth. Cnidarians as a whole, Octacorallia, and Cerianthipatharia also displayed significant changes over depth. Holothurioidea, Decapoda, Hexacorallia, and Actinopterygii exhibit no significant, depth variation (Table 1).

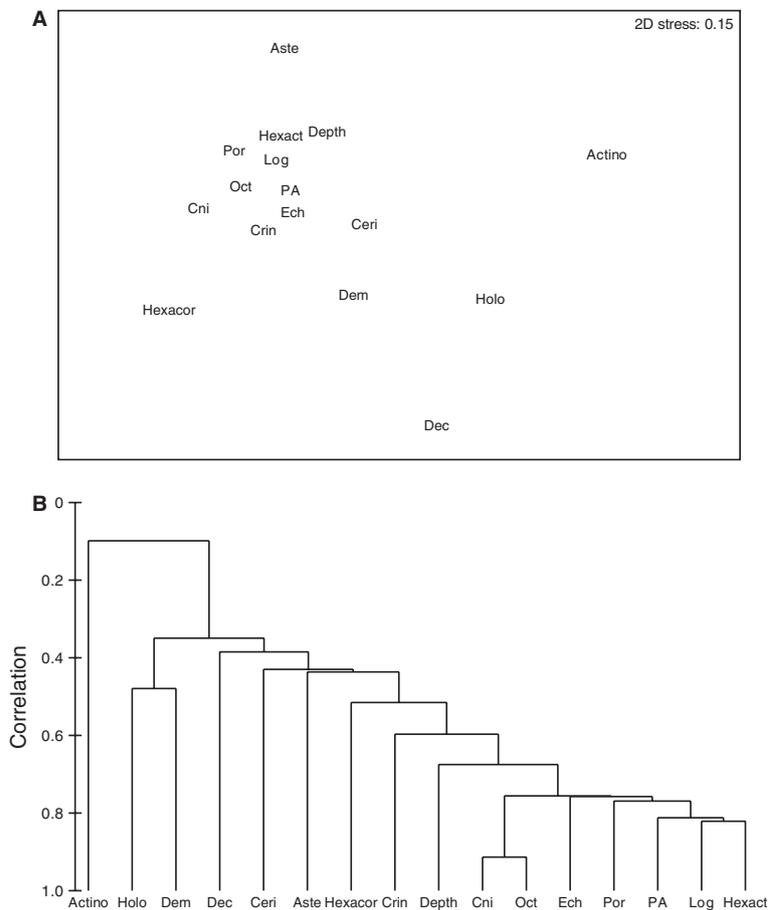
An MDS of correlations between the similarity matrices calculated for different taxa also indicates that octocorals, hexactinellids, and echinoderms drive much of the difference among transects at Davidson, and that hexactinellids drive much of the depth pattern (Fig. 7). Holothurians, asteroids, cerianthiparians, and actinopterygians seem to have much less influence on bathymetric or spatial variation.

**Discussion**

Much of the dialogue and research on seamounts focuses on the richness of, and the compositional changes between, seamounts (reviewed in Wilson & Kaufmann 1987; reviewed in Rogers 1994; de Forges *et al.* 2000; Moore *et al.* 2001). The context of variation in alpha-diversity and spatial patterns of beta-diversity on single seamounts is needed for generalizations about large-scale biodiversity gradients on seamounts. Unexpectedly, our exploration indicates little bathymetric pattern in diversity or density on Davidson Seamount as has been demonstrated on continental margins for megafauna over similar



**Fig. 6.** Nonmetric multidimensional scaling (MDS) plots based on Bray–Curtis similarity of log-transformed data for individual taxa. Lines indicate increasing depth.



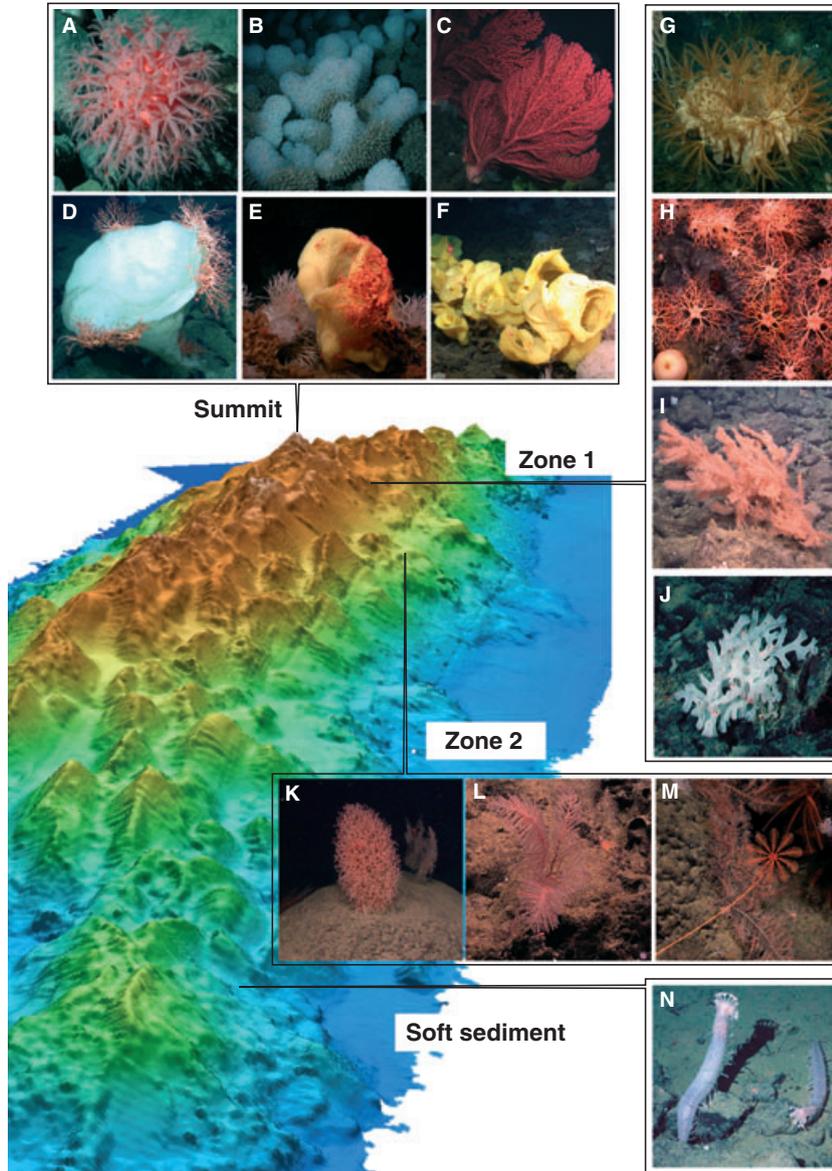
**Fig. 7.** (A) Non-metric multidimensional scaling (MDS) plots and (B) cluster diagrams based on correlations between Bray–Curtis similarity matrices for different transformations and faunal components. PA: presence/absence, Log:  $\log(x + 1)$  transformation, Depth: depth model matrix, Ech: Echinodermata, Aste: Asteroidea, Holo: Holothuroidea, Crin: Crinoidea, Cni: Cnidaria, Oct: Octacorallia, Hexacor: Hexacorallia, Ceri: Cerianthipatharia, Dec: Decapoda, Por: Porifera, Dem: Demospongiae, and Hexact: Hexactinellida.

depth intervals (Polloni *et al.* 1979; Rex 1981; Rex *et al.* 2006; Mc Clain, Rex *et al.* 2009b and c). Our results do indicate that considerable species turnover, upwards of 70%, can occur across the flanks of an individual seamount.

Despite the prominent bathymetric trends in diversity and density that characterize deep-sea megabenthos (Polloni *et al.* 1979; Rex 1981; Rex *et al.* 2006; McClain *et al.* 2009b,c), it is surprising to observe no clear bathymetric gradients on Davidson Seamount. At this point, we hesitate to suggest that the lack of bathymetric gradients in diversity or density is a common feature of seamounts, as work examining these patterns is rare. The reasons, although speculative, for the lack of clear bathymetric signal in diversity or density may reflect the proximity of Davidson to highly productive coastal waters fueled by coastal upwelling (Field *et al.* 1998). This contrasts with the relatively strong gradients in overhead production that characterize many other studies (Field *et al.* 1998).

This may mitigate the productivity gradient needed to generate such relationships. In addition, Rex (1981) demonstrated that soft-bottom, benthic megafaunal invertebrates and fishes exhibited weaker unimodal diversity curves with depth ( $R^2 = 0.48\text{--}0.53$ ) compared with macrofaunal groups ( $R^2 = 0.68\text{--}0.78$ ). This, combined with limited sampling, may also limit our power to detect these relationships. Of course, variation in productivity need not be reflected in density if changes occur in body size or population turnover.

A significant shift in species composition and relative abundances of species occurs with depth. A 50% change in composition is observed for approximately every 1500 m. Davidson Seamount summit and base assemblages share as little as 20–30% of their species. A consistent bathymetric gradient in compositional change occurs across the flanks of the seamount, as demonstrated by the RELATE tests and the distance-decay analysis. In addition, transects group into three distinct depth zones that



**Fig. 8.** Illustration of major zones and taxa within each zone for Davidson Seamount. *In situ* images of typical organisms from each zone: (A) *Anthomastus ritteri*, (B) *Farrea occa*, (C) *Paragorgia arborea*, (D) *Chonelasma* sp. with attached *Gorgonocephalus* sp., (E) *Staurocalyptus* sp., *Farrea occa*, *Asbestopluma* sp., and *Gorgonocephalus* sp., (F) *Staurocalyptus* sp., (G) dense *Florometra serratissima* upon *Heterochone calyx*, (H) dense *Gorgonocephalus* sp. and *Actiniaria* sp., (I) *Lillipathes* sp., (J) *Sclerothamnopsis* sp., (K) *Chrysogorgia monticola*, (L) *Umbellapathes* sp., (M) *Bathycrinus* sp., (N) *Pannychia moseleyi*.

correspond to the summit, flanks, and base of Davidson (Fig. 8). Much of the compositional pattern appears to be driven by compositional changes in octocorals, hexactinellids, asteroids, and crinoids, with hexactinellids contributing the most to bathymetric variation in species dominance.

The strong correlations occurring in the habitat-forming groups, *i.e.* Hexactinellida, Demospongiae, and Octocorallia (particularly *Paragorgia arborea*), relate in part to

their decreasing density with depth (Lundsten *et al.* 2009a). Bathymetric trends in beta-diversity in these groups may reflect the particular chemical and physical requirements (such as temperature, pressure, current velocity, oxygen concentration, aragonite concentration, *etc.*) that vary among taxa. For example, the dominance of octocorals *versus* scleractinians may be driven by aragonite saturation depth and oxygen saturation (Lundsten *et al.* 2009a; Tittensor *et al.* 2009). Observed patterns of

depth zonation in asteroids may also be related to predator/prey interactions. For example, many of the asteroids that we observed are corallivores (Mah *et al.* 2010) and therefore their distribution would necessarily be related to prey taxa (e.g. octocorals).

However, not all taxa show similar depth patterns. Four taxa, Hexacorallia, Decapoda, Actinopterygii and Holothuroidea, displayed no bathymetric variation in composition or abundance structures. A lack of pattern for Actinopterygii may reflect the overall lower densities of fish on Davidson compared to surrounding seamounts (Lundsten *et al.* 2009b). Wilson & Kaufmann (1987) also described a trend towards cosmopolitan species with broader depth distributions that increases with depth and distance from shore on seamounts. This appears to be true for Actinopterygii (Lundsten *et al.* 2009b) and may also contribute to the lack of compositional differences across depths.

Substrate differences may also lead to differences in assemblage composition. The two transects at Davidson Seamount at 2043 m and 2219 m are dominated almost completely by a surface deposit-feeding, elapsid holothurian, *Pannychia moseleyi*. On these two transects, patches of course-grained sediment occur between volcanic hard substrate, providing ample habitat for *P. moseleyi*. These findings are consistent with our previous work, demonstrating faunal differences between sedimentary and hard substrata on seamounts (Lundsten *et al.* 2009a).

Considerable variation in assemblage structure can occur over vertical scales on an individual seamount. This change in composition and assemblage structure across depth on a single seamount is similar to that reported among seamounts several hundred of kilometers distant (de Forges *et al.* 2000). Interestingly, despite the noticeable change in assemblage structure with depth, considerable variation in species diversity and density, and species composition can occur at any given depth. In light of our findings, we caution that interpretations of high beta-diversity among seamounts must account for bathymetric differences among samples. We also advise against viewing seamounts as homogeneous biogeographic units with equally uniform ecological and evolutionary processes. To borrow from the view that originated from Grassle & Sanders (1973) for the deep-sea soft benthos, seamounts are a mosaic of habitats and communities.

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## References

- Braby C.E., Rouse G.W., Johnson S.B., Jones W.J., Vrijenhoek R.C. (2007) Bathymetric and temporal variation among *Osedax* boneworms and associated megafauna on whale-falls in Monterey Bay, California. *Deep-Sea Research I*, **54**, 1773–1791.
- Cairns S.D. (2007) Calcaxonian Octocorals (Cnidaria, Anthozoa) from Eastern Pacific Seamounts. *Proceedings of the California Academy of Sciences*, **58**, 511–541.
- Carney R.S. (2005) Zonation of deep biota on continental margins. *Oceanography and Marine Biology Annual Review*, **43**, 211–278.
- Clarke K.R., Gorley R.N. (2006) *Primer*. Primer-E, Plymouth: ???-???
- Colwell R.K. (2009) EstimateS: Statistical estimation of species richness and shared species from samples.
- Davis A.S., Clague D., Bohron W.A., Dalrymple G.B., Greene H.G. (2002) Seamounts at the continental margin of California: a different kind of oceanic intraplate volcanism. *GSA Bulletin*, **114**, 316–333.
- Etter R.J., Grassle J.F. (1992) Patterns of species diversity in the deep sea as a function of sediment particle size diversity. *Nature*, **360**, 576–578.
- Etter R.J., Rex M.A., Chase M.R., Quattro J.M. (2005) Population differentiation decreases with depth in deep-sea bivalves. *Evolution*, **59**, 1479–1491.
- Field C.B., Behrenfeld M.J., Randerson J.T., Falkowski P. (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, **281**, 237–240.
- de Forges B.R., Koslow J.A. *et al.* (2000) Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature*, **405**, 944–947.
- Gooday A.J. (2002) Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography*, **58**, 305–332.

- Grassle J.F., Sanders H.L. (1973) Life histories and the role of disturbance. *Deep-Sea Research*, **34**, 313–341.
- Haddock S. (2004) A golden age of gelata: past and future research on planktonic cnidarians and ctenophores. *Hydrobiologia*, **530/531**, 549–556.
- Hooge P.N., Eichenlaub B. (1997) *Animal movement extension to ArcView*. Alaska Science Center-Biological Science Office, U.S. Geological Survey, Anchorage, AK: ???–???
- Johnson N.A., Campbell J.W., Moore T.S., Rex M.A., Etter R.J., McClain C.R., Dowell M.D. (2007) The relationship between the standing stock of deep-sea macrobenthos and surface production in the western North Atlantic. *Deep-Sea Research I*, **54**, 1350–1360.
- Jumars P.A., Mayer L.M., Deming J.W., Baross J.A., Wheatcroft R.A. (1990) Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philosophical Transactions of the Royal Society of London A*, **331**, 85–101.
- Levin L.A. (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanography and Marine Biology: an Annual Review*, **41**, 1–45.
- Levin L.A., Etter R.J., Rex M.A., Gooday A.J., Smith C.R., Pineda J., Stuart C.T., Hessler R.R., Pawson D.L. (2001) Environmental influences on regional deep-sea species diversity. *Annual Review of Ecology and Systematics*, **32**, 51–93.
- Lundsten L., Barry J.P., Caillet G.M., Clague D.A., DeVogelaere A.P., Geller J.B. (2009a) Benthic invertebrate communities on three seamounts off Southern and Central California. *Marine Ecology Progress Series*, **374**, 23–32.
- Lundsten L., McClain C.R., Barry J.P., Caillet G.M., Clague D.A., DeVogelaere A.P. (2009b) Ichthyofauna on three seamounts off Southern and Central California, USA. *Marine Ecology Progress Series*, **389**, 223–232.
- Mah C., Nizinski M., Lundsten L. (2010) Phylogenetic Revision of the Hippasterinae (Goniasteridae; Asteroidea): systematics of Deep Sea Corallivores, including one new genus and three new species. *Zoological Journal of the Linnean Society*, in press, ???, ???–???
- Matsumoto G.I., Raskoff K.A., Lindsay D.J. (2003) *Tiburonia granrojo* n. sp., a mesopleagic scyphomedusa from the Pacific Ocean representing the type of a new subfamily (class Scyphozoa: order Semaestomeae: Family Ulmaridae: Subfamily Tiburoniinae subfam. nov.). *Marine Biology*, **143**, 73–77.
- McClain C.R. (2005) Bathymetric patterns of morphological disparity in deep-sea gastropods from the western North Atlantic Basin. *Evolution*, **59**, 1492–1499.
- McClain C.R., Barry J. (2009) Habitat heterogeneity, biogenic disturbance, and resource availability work in concert to regulate biodiversity in deep submarine canyons. *Ecology*, in press, ??, ???–???
- McClain C.R., Etter R.J. (2004) Mid-domain models as predictors of species diversity patterns: bathymetric diversity gradients in the deep sea. *Oikos*, **109**, 555–566.
- McClain C.R., Rex M.A. (2001) The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: an application of quantile regression. *Marine Biology*, **139**, 681–685.
- McClain C.R., Rex M.A., Jabbour R. (2005) Deconstructing bathymetric patterns of body size in deep-sea gastropods. *Marine Ecology Progress Series*, **297**, 181–877.
- McClain C.R., Lundsten L., Ream M., Barry J., DeVogelaere A. (2009) Endemicity, biogeography, composition, and community structure on a Northeast Pacific seamount. *PLoS ONE*, **4**, e4141.
- Moore J.A., Vecchione M. et al. (2001) Biodiversity of Bear Seamount, New England Seamount Chain: results of exploratory trawling. *Journal of the Northwest Atlantic Fishery Science*, **31**, 363–372.
- Nekola J.C., White P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.
- Pineda J., Caswell H. (1998) Bathymetric species-diversity patterns and boundary constraints on vertical ranges. *Deep-Sea Research II*, **45**, 83–101.
- Polloni P., Haedrich R. et al. (1979) The size-depth relationship in deep ocean animals. *Internationale Revue des Gesamten Hydrobiologie*, **64**, 39–64.
- Rex M.A. (1973) Deep-sea species diversity: decreased gastropod diversity at abyssal depths. *Science*, **181**, 1051–1053.
- Rex M.A. (1981) Community structure in the deep-sea benthos. *Annual Review of Ecology and Systematics*, **12**, 331–353.
- Rex M.A., Stuart C.T., Goyne G. (2000) Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 4082–4085.
- Rex M.A., Etter R.J., Morris J.S., Crouse J., McClain C.R., Johnson N.A., Stuart C.T., Thies R., Avery R. (2006) Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Marine Ecology Progress Series*, **317**, 1–8.
- Ricklefs R.E., Schluter D. (1993) *Species Diversity in Ecological Communities: Historical and Geographical Communities*. University of Chicago Press, Chicago: 1–414.
- Rogers A.D. (1994) The biology of seamounts. *Advances in Marine Biology*, **30**, 304–360.
- Ruhl H.A., Smith K.L. (2004) Shifts in deep-sea community structure linked to climate and food supply. *Science*, **305**, 513–515.
- Samadi S., Botton L., Macpherson E., De Forges B.R., Boisselier M.-C. (2006) Seamount endemism questioned by the geographic distribution and population genetic structure of marine invertebrates. *Marine Biology*, **149**, 1463–1475.
- Schlining B., Jacobsen-Stout N. (2006) MBARI's Video Annotation and Reference System. MTS/IEEE Oceans 2006.
- Smith C.R., De Leo F.C., Bernardino A.F., Sweetman A.K., Arbizu P.M. (2008) Abyssal food limitation, ecosystem structure and climate change. *Trends in Ecology and Evolution*, **23**, 518–528.

- Snelgrove P.V.R., Grassle J.F., Petrecca R.F. (1992) The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. *Limnology and Oceanography*, **37**, 1543–1550.
- Soininen J., McDonald R., Hillebrand H. (2007) The distance decay of similarity in ecological communities. *Ecography*, **30**, 3–12.
- Tittensor D.P., Baco-Taylor A.R., Brewin P., Clark M.R., Consalvey M., Hall-Spencer J., Rowden A.A., Schlacher T., Stocks K., Rogers A.D. (2009) Predicting habitat suitability for stony corals on seamounts. *Journal of Biogeography*, **36**, 1111–1128.
- Williams G.C., Lundsten L. (2009) The nephtheid soft coral genus *Gersemia* Marenzeller, 1878 with the description of a new species from the northeast Pacific and a review of two additional species (Octocorallia: Alcyonacea). *Zoologische Mededelingen Leiden*, **83**, 1067–1081.
- Wilson R.R., Kaufmann R.S. (1987) Seamount biota and biogeography. In: Keating B.H. *et al.* (Eds), *Seamounts, Islands, and Atolls*. American Geophysical Union, Washington, DC: 227–237.