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Assemblage structure is related to slope and depth on a deep offshore Pacific seamount chain

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Bathymetry; beta diversity; distance decay; diversity; productivity; seamount.

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Abstract

Scientific study has generated a range of hypotheses about the ecological structure and function of seamounts. Interpretations of these ideas and data are vital to understanding how seamount communities will respond to anthropogenic impacts. Here, we examine how diversity and structure of seamount assemblages vary with depth and slope of the sea floor. We conducted ROV video transects on three seamounts of the Taney Seamount Chain in the Northeast Pacific Ocean. Depth and slope were both related to assemblage structure on the Taney seamounts. Depth differences were seen in alpha- and beta-diversity but not density. Beta-diversity and density but not alpha-diversity varied with slope. Overall, slope and depth together explained 14–31% of beta-diversity. The findings suggest that differences in beta-diversity as related to depth gradients may differ among onshore and offshore and/or between shallow and deep summit seamounts. Specifically, we hypothesize that differences in productivity and depth gradients among seamounts may generate different patterns of beta-diversity.

Introduction

From the abyssal plain over 4 km deep, 100,000 seamounts are estimated to arise from the sea floor (Wessel *et al.* 2010). As noted by Rowden *et al.* (2010a): ‘despite their vast number and widespread distribution, the biota of very few seamounts have been well sampled.’ Nonetheless, limited scientific study has generated a range of hypotheses about the ecological structure and function of seamounts. Many of these seamount hypotheses stem from the idea that the ecological, evolutionary and oceanographic processes on seamounts may differ from surrounding deep-sea habitats (Wilson & Kaufmann 1987; Rogers 1994; McClain 2007; Clark *et al.* 2010; Shank 2010), increasing gamma-diversity in the deep-sea (*e.g.* McClain *et al.* 2009).

Earlier theories of a highly endemic seamount fauna have found little support (Samadi *et al.* 2006; O’Hara 2007; O’Hara *et al.* 2008; Brewin *et al.* 2009; Lundsten *et al.* 2009a,b; McClain *et al.* 2009; Thoma *et al.* 2009; Howell *et al.* 2010; Narayanaswamy *et al.* 2013). How-

ever, the contribution of seamounts to total global biodiversity and many hypotheses regarding the processes maintaining seamount biodiversity remain to be determined (McClain 2007; Lundsten *et al.* 2009a,b; Clark *et al.* 2010; Rowden *et al.* 2010a,b). For example, the elevated biomass seen on many seamounts may support greater species richness (Samadi *et al.* 2006; McClain 2007; Rowden *et al.* 2010a,b). Common seamount habitat types, *e.g.* hard substratum, may provide niches that are absent or rare on continental margins or the abyssal plain (*e.g.* Stocks 2004; O’Hara 2007; O’Hara *et al.* 2008; McClain *et al.* 2009). Dense aggregations of habitat-forming coral and sponges on seamounts may also enhance habitat-complexity, thereby increasing diversity (Roberts & Hirshfield 2004). Whether serving as productive oases or providing unique habitats, seamounts may also export propagules to marginal habitats in the adjacent deep sea (McClain *et al.* 2009).

The lack of knowledge about the processes underlying assemblage structure on seamounts is alarming given the

current and potential anthropogenic impacts to seamount biodiversity. Resource exploitation on seamounts tends to be concentrated in small areas, thus impacts can be relatively severe (Clark *et al.* 2010). Over the last 50 years, approximately 2 million metric tons of deep-sea species were extracted from seamounts (Clarke *et al.* 2007). Hundreds to thousands of trawls are estimated to have been taken on seamounts in the Southwest Pacific (Clark *et al.* 2010), with every square kilometer, on average, trawled 130 times (O'Driscoll & Clark 2005). Increased interest and types of mining mineral-rich deposits provides additional threats to seamount species (Clark *et al.* 2010; Van Dover 2011). Impacts from resource extraction include reduced structural complexity, biomass, diversity, and alteration of assemblage structure and function (reviewed in Clark *et al.* 2010). Further anthropogenic impacts to seamounts are of even greater concern if seamounts are deemed essential habitats for supporting and maintaining global marine biodiversity. For example, the distinctive oceanographic setting of seamounts may provide refugia from previous anoxic events (Galil & Zibrowius 1998) and future refugia against ocean acidification (Tittensor *et al.* 2010).

New synthetic and sampling efforts have stimulated re-examinations of old hypotheses and the formulation of

new ideas with regard to seamounts (*e.g.* McClain *et al.* 2009; Clark *et al.* 2010; Howell *et al.* 2010; Rowden *et al.* 2010a,b; Shank 2010; Tittensor *et al.* 2010). However, much work remains to understand the processes governing seamount assemblage structure. While changes in beta-diversity occur with depth, bathymetric patterns of alpha-diversity and density may not, a finding in stark contrast to continental margins (McClain *et al.* 2010). The same study also found considerable variation in assemblage structure beyond that described by depth, suggesting that small-scale substratum and topographic complexity on a single seamount also play a role. Here, we examine the role of depth and slope on three seamounts of the Taney Seamount Chain approximately 270 km west of San Francisco in the Northeast Pacific Ocean.

Methods

Study area

Taney Seamounts (Figs 1 and 2) consist of five aligned volcanoes (TA–TE) located on the Pacific Plate, west of San Francisco (Clague *et al.* 2000). The largest volcano, Taney A, is estimated to be 26 Ma in age, roughly the

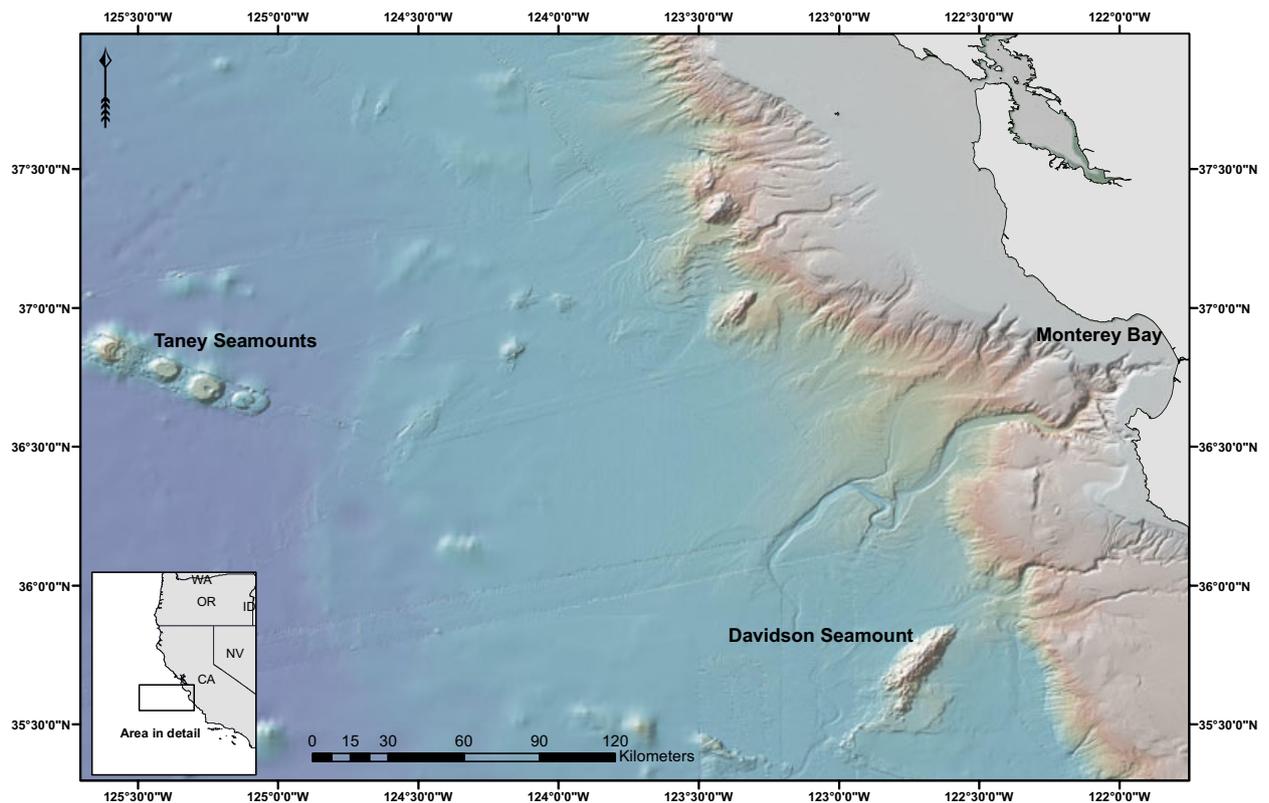


Fig. 1. Map showing location of the Taney Seamounts in the Northeast Pacific Ocean.

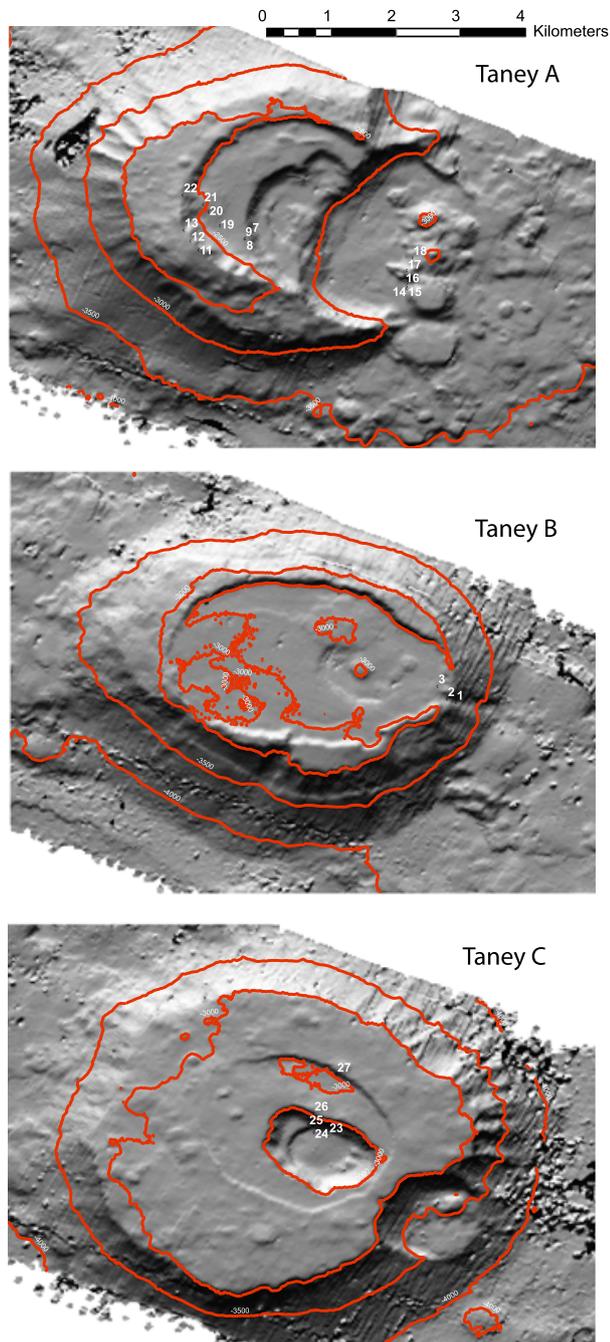


Fig. 2. Map of bathymetry of Taney Seamounts A, B, and C. Bold numbers on maps indicate locations of video transects.

same age as the underlying sea floor, and is ~15 km in diameter and 1990 m in height. The southeastern flank of Taney A has been heavily modified by three successive caldera collapses. Taney B has a large, ovoid caldera with a basal length of 12 km and a height of 1300 m, with a distinct caldera rim which varies in height up to ~150 m tall. Taney C has a circular caldera that is ~12 km across

at its base and 1310 m in height. Taney C has a relatively flat summit but contains three calderas; two central calderas nested within each other and the third, which truncates the southeastern flank. For a complete description of the Taney Seamounts see Clague *et al.* (2000).

Sampling

Taney Seamounts A, B and C were surveyed 5–14 August 2010 using the Monterey Bay Aquarium Research Institute (MBARI) remotely operated vehicle (ROV) *Doc Ricketts*. High definition video of each dive was recorded onto D5 tape. During this survey, seven ROV dives were conducted, resulting in the collection of 54 h of video and 24 megafauna video transects (~100 × 1 m). Details of each transect can be found in the Appendix 1. The width of the video transect was determined using two parallel red laser beams (640 nm) positioned 29 cm apart. The ROV pilots ensured that the ROV maintained a consistent height off the bottom. To further ensure transects were near a 1-m swath, the camera operator also used camera zoom controls. Actual transect length and width were calculated using transect start and end points within ARCGIS 10.1. Area was tested as a factor in all analyses and was not significant. Video transects were collected from various depths at each seamount. Taney Seamount A was sampled from its summit at 2135 m to its base at a depth of 3176 m at (n = 16), Seamount B was sampled from its summit at 2313 m to a depth of 3187 m on its eastern flank (n = 3, and Seamount C was sampled from its summit at 2934 m to a depth of 3314 m within the collapsed caldera (n = 5).

High-resolution bathymetry and side-scan data of Taney and Davidson seamounts were collected with a hull-mounted 30-kHz sonar. Bathymetric data for all seamounts was gridded at 30 m resolution within ARCGIS 10.1. The Spatial Analyst extension within ARCGIS 10.1 (ESRI 2011) was used to calculate slope values (degrees of slope angle) for the gridded bathymetric data. These data were extracted and joined to each observation recorded during every transect, giving a slope value for each unique observation. Slope values for observations on each transect were then averaged, giving an estimate of average slope for each transects.

Analyses

Video transects were annotated in detail using the MBARI Video Annotation and Reference System (VARS; Schlining & Jacobsen-Stout 2006). Within VARS, all benthic and demersal organisms were identified to the lowest possible taxonomic rank. For animals that were unknown to the authors, voucher specimens were collected using

the ROV manipulator arm, suction sampler or push cores. Voucher specimens were not collected for organisms that could be identified easily from video and that were known to occur on the California shelf or Monterey Canyon. Although every effort was made to identify organisms to the lowest possible level, assignment to species was not always possible. For organisms that were morphologically distinct but not identified at the species level, an operational taxonomic unit was used within the VARS database (e.g. Echinoidea sp. 1).

For each megafauna video transect, species richness (S), Shannon's diversity index (H'), Pielou's evenness (J'), and log₁₀ density per meter squared were calculated using the *vegan* R package (Solymos *et al.* 2013). 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 general linear models were performed using JMP (1989–2007; SAS Institute Inc., Cary, NC, USA). We used Akaike's information criterion corrected for small-sample sizes (AICc) to evaluate the strength of support for the various models. We ranked models based on AICc scores (Δ AICc). All models with Δ AICc ≤ 2 were considered to have strong support.

To examine how similarity among assemblages changed with depth at each seamount, we employed the distance decay of similarity method as described by Nekola & White (1999). For comparison, we included distance decay estimates from Davidson Seamount as reported by McClain *et al.* (2010). Similarity between transects was quantified as Bray–Curtis similarity on presence/absence data as utilized in other studies (Nekola & White 1999; McClain *et al.* 2010) to measure change in composition rather than change in dominance of species. Decay was measured as change in similarity from the shallowest transect. Exponential functions were fitted to the relationships (Similarity = $a \cdot \text{DepthDifference}^b$). The similarity half-life, the amount of depth required to observe 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 allowed us to explore depth changes in both species composition and the species dominance. Cluster analyses, using group averages, were also conducted on log-transformed and presence/absence-based matrices.

The SIMPROF routine in PRIMER was used to test the null hypothesis that sets of transects that are not divided by environmental factors do not differ 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. We used distance-based redundancy analysis (dbRDA) to calculate the effects of depth and slope on generating assemblage structure differences. Analyses were conducted for total megafaunal assemblages and individual higher taxa. The 2STAGE routine in PRIMER was used to explore how depth changes among different taxa were related. 2STAGE conducts a multidimensional scaling (MDS) on a similarity matrix comprising correlation coefficients between varying similarity matrices.

Results

Density, evenness, and alpha diversity

In no case was transect area a significant predictor of density (I), diversity (H') or evenness (J'). For density, the best fit model included estimates for the linear and quadratic forms of slope ($I = -0.13 + 0.01\text{Slope} + (\text{Slope} - 17.74)^2$, F ratio = 8.03, df = 24, $P = 0.0026$, Table 1). This model described 43% of the variance and, in terms of R^2 values, was only outcompeted by a full model. The highest densities occurred on transects with the greatest slopes ($>30^\circ$, Fig. 3) and lowest densities occurred at intermediate slopes values ($\sim 20^\circ$).

For H' and J', the quadratic fit to depth yielded the best support (Fig. 3, Table 1). Highest H' and J' values were seen at intermediate depths at ~ 2600 m. For H', the quadratic depth model explained 36% of the variance [$H' = 3.84 - 0.0007\text{depth} - 0.000002(\text{depth} - 2790.3)^2$, F ratio = 5.93, df = 24, $P = 0.0091$]. For J', the best model as determined by AICc values was a model that included only depth². However, the full quadratic fit with depth [$J' = 2.86 - 0.0005\text{depth} - 0.000007(\text{depth} - 2790.3)^2$, F ratio = 4.02, df = 24, $P = 0.0334$] and a model only including seamount as a factor had Δ AICc within 2. The best models described 23–36% of the variance. The failure of the model to determine between models for J' may stem from the fact that all of the deepest transects lie on two seamounts (Taney B and C), whereas the shallowest transects lie on Taney A only. It is worth noting that the quadratic fits with depth for H' and J' did not exist if the transects were limited to only Taney A.

Assemblage composition and structure

Among all five Taney seamounts, faunal similarity decayed exponentially with increased depth separation of transects (Fig. 4) as measured from the shallowest transect (Similarity = $4.03\text{depth}^{-0.0008}$, $R^2 = 0.54$, $P < 0.0001$,

Table 1. Results from specific hypothesis models. AICc values and R² are given for each model. Models with lowest AICc values are indicated in bold. All models with ΔAICc ≤ 2 were considered to have strong support.

Dependents	Independent	R ²	AICc
H'	Seamount, Area, Depth, Depth ² , Slope	0.44	37.78
	Area, Depth, Depth ²	0.37	28.70
	Seamount, Depth, Depth ²	0.44	29.30
	Slope, Depth, Depth ²	0.36	28.88
	Depth, Depth²	0.36	25.65
	Depth ²	0.17	28.92
	Depth	0.15	29.46
	Area	0.00	35.79
	Seamount	0.25	32.04
	Slope	0.01	33.24
	J'	Seamount, Area, Depth, Depth ² , Slope	0.40
Area, Depth, Depth ²		0.28	20.01
Seamount, Depth, Depth ²		0.40	19.13
Slope, Depth, Depth ²		0.29	19.63
Depth, Depth²		0.28	16.93
Depth²		0.24	15.33
Depth		0.23	15.67
Area		0.00	24.13
Seamount		0.36	16.57
Slope		0.08	19.73
Log (Ind. m ⁻²)		Seamount, Depth, Depth ² , Slope, Slope ²	0.54
	Seamount, Depth, Depth ²	0.25	42.65
	Seamount, Slope, Slope ²	0.50	35.02
	Slope, Depth, Depth ²	0.22	39.74
	Slope, Slope ² , Depth, Depth ²	0.52	32.01
	Depth, Depth ²	0.05	41.28
	Slope, Seamount	0.33	36.24
	Slope, Slope²	0.43	31.59
	Slope²	0.30	31.03
	Depth ²	0.04	38.68
	Depth	0.04	40.95
	Seamount	0.21	37.06
	Slope	0.22	33.62

df = 23). A similar pattern was also seen among only Taney A transects (Similarity = $3.99\text{depth}^{-0.0006}$, R² = 0.43, P = 0.0082, df = 15). Compared with the hard substrate transects of Davidson Seamount (McClain *et al.* 2010), greater faunal change occurred over depth at Taney A [Taney A slope: confidence interval (CI) = -0.0006 to 0.0010, Taney A, B, C: CI = -0.0008 to 0.0011] than Davidson Seamount even when limited to just deeper samples (Davison slope: CI = -0.0002 to 0.0003, Davidson Deep slope: CI = -0.0004 to 0.0005). The distance decay half-lives, the amount of depth required to observe a 50% difference in composition, was 866 m (CI = 611–1485) among all the Taney Seamounts and 1155 m (CI = 712–3045) for just Taney A, compared with 3465 m (CI = 3466–5506) for all transects at Davidson Seamount or 1607 m (CI = 1527–1696) just for deeper transects.

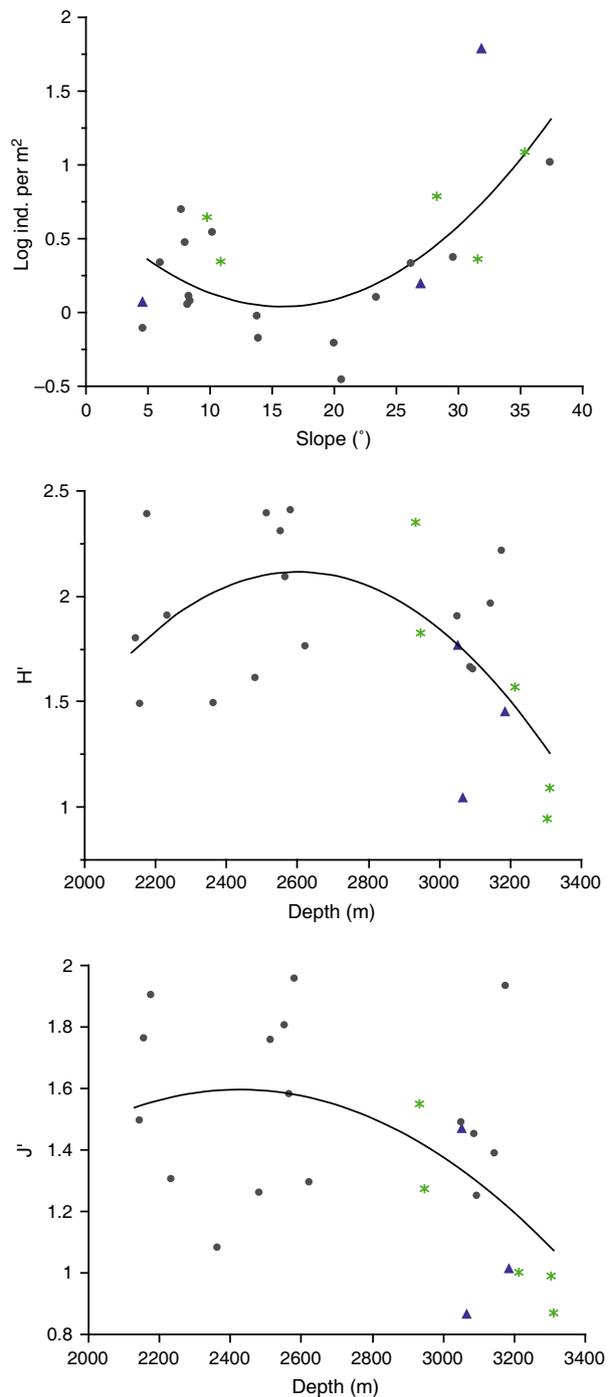


Fig. 3. Bivariate plots of faunal metrics versus depth and slope. Taney Seamount A, gray-filled circles; Taney Seamount B, purple triangles; Taney Seamount C, green asterisk. (Top) Log density (individuals per meter squared) versus slope. (Middle) Shannon's diversity index (H') versus depth (meters). (Bottom) Pielou's evenness (J') versus depth meters.

A cluster and SIMPROF analysis (Fig. 5) yielded eight major groupings of transects. These groupings roughly corresponded to depth bins but clear discrepancies

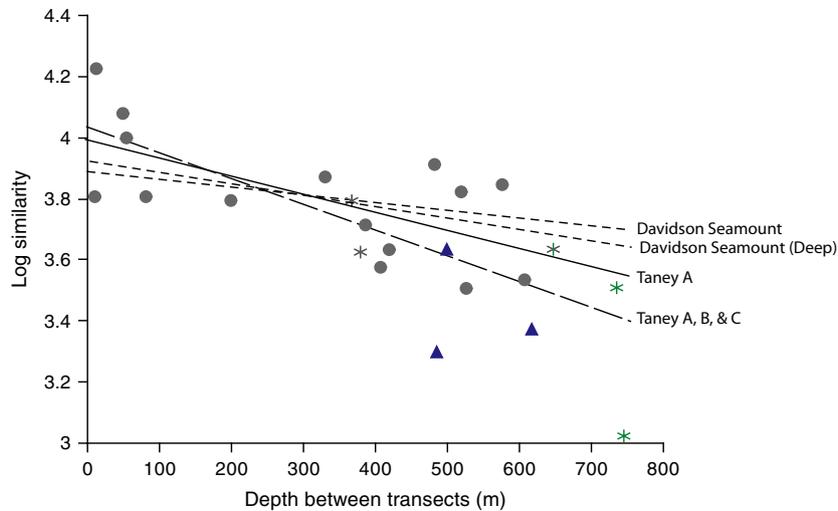


Fig. 4. Distance decay, measured as Bray–Curtis similarity based on presence/absences from the shallowest transect. Taney Seamount A, gray-filled circles; Taney Seamount B, purple triangles; Taney Seamount C, green asterisk. Decay lines are provided for Taney A transects separately and all transects across Taney A, B, and C. For reference the decay line is also given for Davidson Seamount and for deeper transects at Davidson (2043–3276 m).

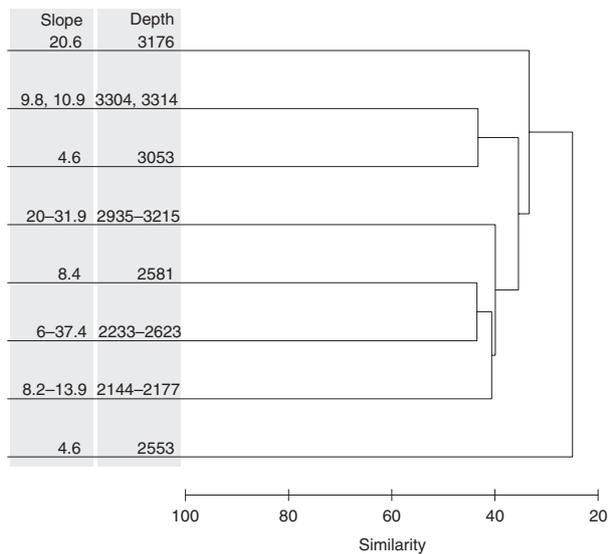


Fig. 5. Cluster analyses based on Bray–Curtis similarity on log-transformed data. Tips that present ranges of slope and depth represent multiple transects and further branches (not shown) that are not significantly different from random.

existed, e.g. 3053, 3304, 3314, and 3176 m, which likely corresponded to differences in slope.

Using distance-based redundancy analysis (dbRDA), we specifically tested for the affect of slope and depth on beta-diversity (Fig. 6). The dbRDA analyses identified both depth and slope as significant predictors of Taney seamount assemblage structure (Table 2). Analyses based on Log X+1 yielded two major axes that explained 63.57% and 36.43% of the variation. Depth correlated strongly with axis 1 (−0.97) and explained 16.1% of the variation ($P = 0.001$). Slope correlated strongly with axis 2 (0.97) and explained 9.2% of the variation ($P = 0.001$).

If the analysis is constrained just to transects of Taney A, a very similar result is obtained. Depth explained 15% of the variations and slope 8.5%. Analyses based on presence/absence data also yielded similar results. The two major axes accounted for 71.4% and 28.6%, respectively. Depth correlated with axis 1 (−0.99) and explained 18.3% of the variation ($P = 0.001$). Slope correlated with axis 2 (0.99) and explained 7.3% ($P = 0.002$). Individual groups showed varying relationships with depth and slope. Cnidaria assemblage structure correlated poorly with both variables in comparison with other groups (Table 2). Dominant taxa, largely Echinoderms and Poriferans, correlated the most strongly with slope. Non-dominant taxa, *i.e.* those species contributing <10% to total abundance, showed the strongest depth influence.

A cluster of the correlations between the similarity matrices (2NDSTAGE) calculated for different taxa also indicate that the depth patterns are primarily driven by non-dominant taxa (Fig. 7). The similarity between the non-dominant taxa and differences in depth was 53%. Porifera (43%) and Echinodermata (62%) contributed most to the dominant taxa and drove turnover in terms of both abundance (Log X+1) and species composition (presence/absence). Differences in slope were around 15%, similar to other groups.

Based on a cluster analysis we defined three major depth groups. We used the SIMPER routine to identify the major faunal constituents of each group (Appendix 1). The 2000–2500 m group had an average similarity of 51.25%. The 2500–3000 m group had an average similarity of 49.89%, and the 3000–3500 m group an average similarity of 48.61%. Ophiuroidea and Asteroidea were commonly observed in all depth groupings; however, drivers of groupings included numerous poriferan OTUs, the gastropod mollusk *Calliostoma* sp., several

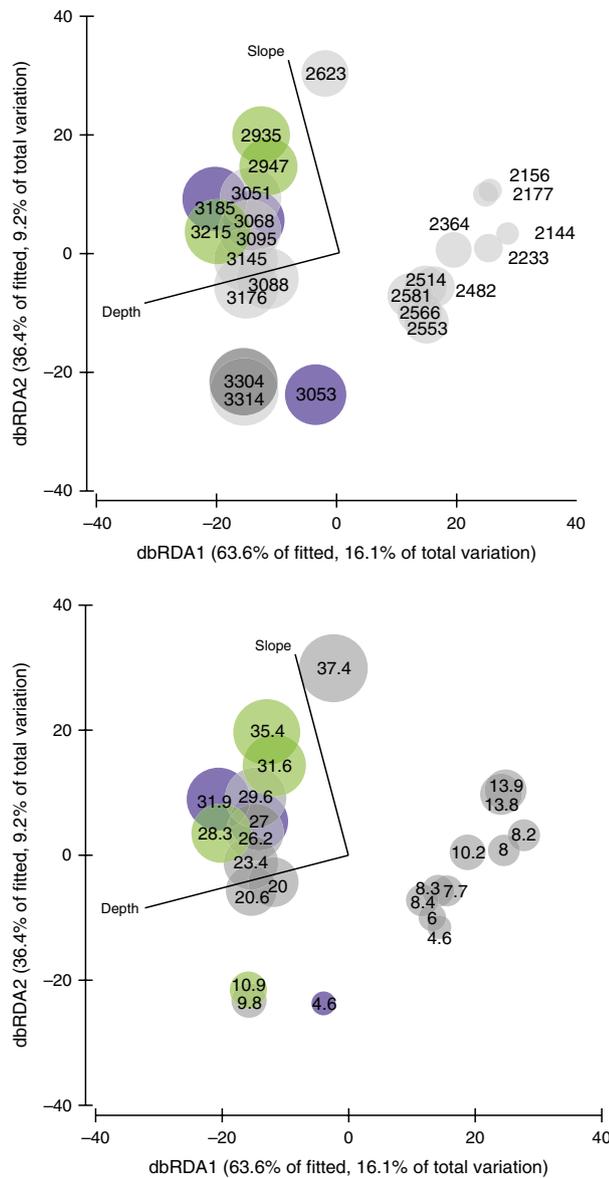


Fig. 6. Distance-based redundancy analysis for transects across the Taney Seamounts. (Top) Scale of circles and numerical labels correspond with depth. (Bottom) Scale of circles and numerical labels correspond with degree of slope. Taney Seamount A, gray; Taney Seamount B, purple; Taney Seamount C, green.

echinoderms (e.g. Comatulidina, *Pentametrocrinus paucispinus*), Paguroidea, *Laetmonice* sp. and Serpulidae polychaete worms, as well as Torquaratoridae enteropneusts. Holothurians and other invertebrate taxa contributed to these groupings as well.

A SIMPER analysis was also used to identify shared species in the four major slope related assemblage groups (Appendix 1). The highest average similarity (56.74%) was found on slopes of 30° and steeper. Ophiuroids,

Comatulida crinoids, Asteroidea, Holothuria, and numerous poriferan OTUs were drivers of this grouping. A 20–30° slope group had a 48.43% average similarity with cerianthid anemones, *Calliostoma* sp., *P. paucispinus*, Asteroidea, and numerous poriferan OTUs, contributing to the differences in assemblage composition. A grouping of 10–20° slopes showed a 48% average similarity and had the lowest number of taxa contributing to assemblage composition. Ophiuroidea, Asteroidea, *Calliostoma* sp., poriferans and a rare genus of urchin, *Pilematechinus*, were drivers of this group. A 0–10° slope group had a 48.02% average similarity and showed high diversity in a broad group of invertebrate taxa; however, the numerous poriferan OTUs seen in the steeper slope groups were largely absent.

Discussion

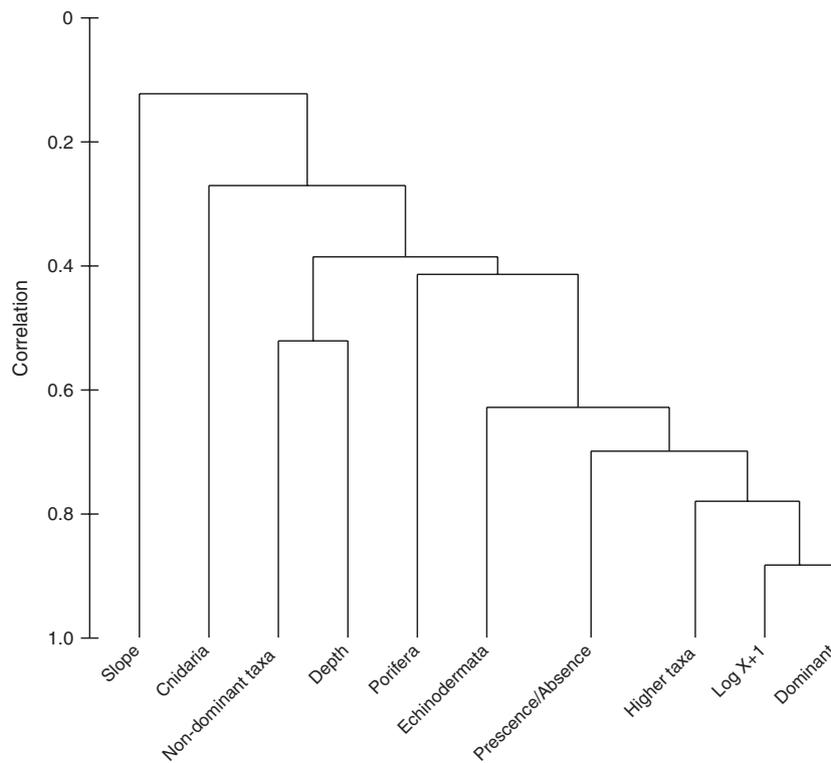
Changes in depth and slope were associated with significant changes in assemblage structure on seamounts. Depth differences were seen in alpha- and beta-diversity but not density. Slope differences were seen in beta-diversity and density but not alpha-diversity. Slope and depth together explained 14–31% of beta-diversity.

Our finding that density did not change with depth is in agreement with previous work for nearshore seamounts (McClain *et al.* 2010) but contrasts with research from Southern Ocean seamounts, where density peaked between 2000- and 2500 m (Thresher *et al.* 2011), and exponential decreases in density for the deep continental margins (Rex *et al.* 2006). The densities for the Taney Seamounts (mean: 5.3 ind. m⁻², range: 0.4–60.3) were much lower than the maximum reported ~200 ind. m⁻² for the Southern Ocean seamounts (Thresher *et al.* 2011) but comparable to those seen at nearshore seamounts off California (Lundsten *et al.* 2009a; McClain *et al.* 2010). One potential reason why density decreases with depth may be uncommon on seamounts is that low metabolic demand and long-lived individuals of Cnidaria and Porifera dominate the assemblages. The combination of these factors may decouple population sizes from temporal and spatial environmental variability (Holyoak & Baillie 1996; Sæther *et al.* 2005).

In contrast to the nearshore Davidson Seamount (McClain *et al.* 2010), species diversity and evenness on the Taney seamounts varied with depth. Peak diversity occurred at intermediate depths, ~2600 m, and was roughly equivalent to depths of peak diversity seen for fauna of continental margins (Rex 1981). This unimodal relationship between diversity and depth has been largely attributed to variation in productivity (Tittensor *et al.* 2011). However, the lack of change in density with depth suggests that the diversity–depth relationship does not

Table 2. Percent variation of faunal turnover among transects explained by depth and slope as identified by dbRDA. Results are presented for different transformations and faunal components.

Group	Transformation	% Variation explained by epth	% Variation explained by slope	% Total variation explained
All species	Presence/Absence	18.3	7.3	25.6
All species	Log X+1	16.1	9.2	25.3
All species Taney A	Log X+1	15.0	8.5	23.5
Higher Taxa	Log X+1	18.3	5.8	24.1
Dominant Taxa	Log X+1	17.4	13.9	31.3
Non-Dominant Taxa	Log X+1	23.0	4.2	27.2
Echinodermata	Log X+1	13.8	7.4	21.2
Porifera	Log X+1	17.2	7.2	24.4
Cnidaria	Log X+1	8.2	5.3	13.5

**Fig. 7.** Cluster diagram based on correlations between Bray–Curtis similarity matrices for different transformations and faunal components.

simply reflect increased energy allowing for greater abundances, in turn allowing for more species above some minimal viable population size (*i.e.* the More Individuals Hypothesis, *e.g.* Hurlbert 2004). The lack of change in density also argues against Allee effects, *i.e.* density reaches a minimum threshold such that local extinction becomes more probable (*e.g.* Rex *et al.* 2005). The decrease of diversity at shallower depths may occur because increased guild competition with increasing resources suppresses diversity (McClain & Barry 2010). At deeper depths, low diversity may simply reflect the attrition of taxa that are physiologically ill-equipped to deal with lower food availability, calcium carbonate disso-

lution rates, etc. (McClain 2005; Lundsten *et al.* 2009a,b; McClain *et al.* 2010). Indeed, corals were generally observed in low abundance at Taney Seamounts when compared with shallower and nearshore seamounts off California (Lundsten *et al.* 2009a,b; McClain *et al.* 2009, 2010). The deeper parts of the Taney Seamounts, simply, may not be optimal habitat for corals (Tittensor *et al.* 2009). We noticed, at least anecdotally, that a diverse assemblage of poriferan OTUs may have been filling the niches normally occupied by corals at other surveyed seamounts in the region.

Depth explained 8.2–23% of faunal turnover among transects on the Taney Seamounts. Interestingly, this was

not driven by dominant taxa but rather by those taxa constituting <10% of total abundance. As abundance and geographic range are often positively correlated (e.g. Gaston *et al.* 1997), dominant taxa are expected to have greater niche breadth and increased geographic and depth ranges. This would result in lower turnover across these and other environmental gradients. Rarer taxa may have narrower depth ranges, and potentially more limited niches, thus exhibiting greater turnover across an environmental gradient.

The findings suggest that differences in beta-diversity over depth gradients may be different between onshore and offshore seamounts or, alternatively, between seamounts with different summit heights. Distance decay rates were greater at Taney A than at Davidson, *i.e.* greater beta-diversity with depth at Taney A. The half-life, *i.e.* the depth difference required to obtain a 50% change in fauna, was 1155 m (CI = 712–3045) at Taney A and 3465 m (CI = 3466–5506) at Davidson. Even when distance decay estimates were limited to a similar depth range at Davidson, the half-life estimate was 1607 m (CI = 1527–1696) and still greater than that of Taney A. That the half-life on Taney was smaller than on Davidson even when similar depths were compared, argues against a purely summit effect on these relationships.

Abiotic factors such as temperature, salinity, and oxygen were similar between Davidson and Taney A Seamounts (Appendix 1). Oxygen concentrations are slightly greater at Davidson below the oxygen minimum zone, but differ by <0.25 ml·l⁻¹ (Appendix 1). These environmental similarities between Davidson and Taney A narrow the likely candidates to explain differences in beta-diversity on these seamounts to either differences in currents or carbon flux between these seamounts. In the region of study, carbon flux is generally higher nearshore due to the productive California current and in general decreases with increasing longitude west. For example, at 2000-m carbon flux is near 0.3–0.5 mol Org. C·m⁻²·year⁻¹ at 125° W, the approximate location of the Taney Seamounts (Martin *et al.* 1987). At 122° W, the location of Davidson Seamount, the value is higher, at 0.5–1.0 mol Org. C·m⁻²·year⁻¹ (Martin *et al.* 1987). The shallower summit depth of Davidson Seamount may also contact the lower reaches of diurnally migrating species, providing greater carbon availability to summit species (Rowden *et al.* 2010a,b). Likewise, higher chlorophyll concentrations often occur over shallow seamounts (Rowden *et al.* 2010a,b). This provides support for the idea that productivity input to Davidson and Taney seamounts may differ and in turn create distinctive patterns in beta-diversity.

Additionally, we find that the slope or pitch had a significant impact on assemblage structure. Although alpha-diversity did not vary with degree of slope, density

exhibited a minimum at intermediate grades. At slopes <10° and <23°, density was highest. The lowest densities were seen at ~20° and the highest at >35°. The degree of slope also explained 4.2–13.9% of faunal turnover among transects. The decline in density may occur because organisms are either horizontal or vertical specialists. Intermediate slopes may prove to be a non-optimal habitat for both kinds of specialists. In shallow water marine systems, major faunal differences occur between horizontal and vertical orientation of hard substrates (Miller & Etter 2011). Differences in turnover with slope were largely driven by dominant taxa including numerous Poriferan OTUs, suggesting filter feeding may be important. Prior work has tied high densities of filter-feeding taxa such as sponges and corals to the higher currents occurring on summits and ledges, which in turn provide greater filter-feeding opportunities (Genin *et al.* 1986).

The 69–86% unexplained variance implies that other drivers of assemblage structure and a multitude of assemblages exist on a seamount. Individual seamounts likely incorporate a vast array of habitat types. Over a single seamount a variety of substrates and structures, ranging from soft sediments to cobble to volcanic crusts, can occur on a back drop of varying depths, topographic grades, and currents (Clague *et al.* 2000; Davis *et al.* 2002; McClain *et al.* 2010). Thus, seamounts are unlikely to be single homogeneous biogeographic units with equally uniform assemblages and underlying ecological processes (McClain *et al.* 2010). For example, previous work has demonstrated that considerable variation in assemblage structure occurs with depth (McClain *et al.* 2010) and rivaled assemblage differences seen among seamounts hundreds of kilometers distant (de Forges *et al.* 2000). However, along single isobaths, considerable differences in assemblages still occur and are potentially related to topographic and sediment characteristics (McClain *et al.* 2010). Grassle & Sanders (1973) originally proposed that the soft bottom benthos of the deep sea was a mosaic of habitats and communities. When combined with prior work these findings suggest that the patch mosaic hypothesis, as broadly defined, should potentially be extended to seamounts as well.

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Supporting Information

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

Data S1. List of transects, collection dates, location, and size.