Richness and distribution of sponge megabenthos in continental margin canyons off southeastern Australia

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ABSTRACT: Submarine canyons are spectacular topographical features that intersect the continental margins of the world's oceans. Canyons comprise unique habitats in terms of complexity, instability, material processing, and hydrodynamics, and they may support diverse assemblages of larger epibenthos. Yet, quantitative data on the biodiversity of the megabenthos in canyons are scant. Consequently, we quantified the diversity of sponges (a key and dominant group of the megabenthos) in 5 canyons located on the continental margin off southeastern Australia at depths from 114 to 612 m. The canyons harboured a rich sponge fauna, with a total of 165 species, belonging to 65 genera, 41 families, 10 orders, and 2 classes in 14 sled samples. Species richness declined with depth, but was positively linked to spatial heterogeneity of bottom types. Areas comprised of a broader range of bottom types (e.g. mixed rocky and sandy/muddy bottoms) contained more species than areas with more uniform substratum properties. Spatial patterns of the sponge assemblages were characterized by (1) high species turnover both between sites in individual canyons and between different canyons, and (2) low levels of site occupancy of the component species, with most species recorded from single canyons only. Variations in depth, substratum type and topographic relief resulted in heterogeneous environmental conditions of benthic habitats in canyons that corresponded to changes in the assemblage structure of sponges. A broad comparison with other abrupt topographical features in the bathyal zone of the region suggests that canyon assemblages may rival the diversity of sponges on seamounts. Site-to-site variation in diversity and species composition within individual canyons suggests that biological patterns may be finer-grained than the spatial scale of conventional geomorphological units. Consequently, from a perspective of conservation planning, a single or a few canyons are unlikely to accurately represent the regional faunal diversity, because of the strong biotic separation of communities between canyons and the limited distributional ranges of the component species.

KEY WORDS: Submarine canyons · Megabenthos · Porifera · Diversity · Species-range sizes

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INTRODUCTION

Submarine canyons are ubiquitous and spectacular features that incise the continental margins of the world's oceans. Canyons are topographically complex seascapes (Yoklavich et al. 2000), contain diverse bottom types (Kottke et al. 2003), and can be highly un-

stable environments due to active mass-wasting and high sediment loads (Okey 1997).

Canyons act as conduits for the passage of material down the continental slope, and profoundly modify the hydrodynamic regime of continental and island margins. Shallow-sourced material is exported in the form of sediments (Puig et al. 2003) and organic matter (Lin

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et al. 2005), including detached macrophytes such as kelp and seagrass (Okey 1997, 2003, Harrold et al. 1998, Vetter & Dayton 1999). Canyons can intensify mixing and the formation of cyclonic eddies (Allen et al. 2001), and are sites of both upwelling (Kämpf 2005), and downwelling (Wåhlin 2002). These hydrodynamic effects can propagate to pelagic consumers, manifested in increased plankton and nekton biomass in and around canyons (Cartes et al. 1994, Genin 2004).

Benthic infaunal biomass and density in canyons can be either higher (Gage et al. 1995, Vetter & Dayton 1998), lower (Maurer et al. 1994), or similar to the adjacent slope (Houston & Haedrich 1984). Whether macrofauna is more abundant and diverse inside canyons depends to some degree on the physical disturbance regime and the rate and quantity of organic matter deposition (Rowe et al. 1982, Okey 1997, Vetter & Dayton 1998, Okey 2003). Similarly, while several studies on the megabenthos have reported increased density or biomass in canyons (Headrich et al. 1975, Cartes et al. 1994, Sarda et al. 1994, Vetter & Dayton 1999), any 'canyon effect' on the larger epibenthos may be specific to individual taxa or functional groups (Vetter & Dayton 1999); it can also depend on the quantity and types of organic detritus inputs such as sunken macroalgae and eelgrass (Harrold et al. 1998, Vetter & Dayton 1999, Duineveld et al. 2001). Canyons can also be critical fish habitats (Brodeur 2001), acting as nursery areas (Stefanescu et al. 1994), preferred spawning sites (A. Williams unpubl. data), and refuges from bottom-contact fishing in areas of highly rugged topography (Yoklavich et al. 2000).

Sponges (Porifera) play a key structural and functional role in the marine benthos. Sponges can profoundly modify the physical properties of the seafloor and influence the composition, abundance, and distribution of the fauna (Bett & Rice 1992). The ecological significance of sponges arises from several traits and mechanisms including: (1) sponges can form dense aggregations ('sponge beds', 'sponge reefs', 'ostur') dominating the biomass of benthic communities (Klitgaard & Tendal 2004, Conway et al. 2005); (2) as structure-forming invertebrates they add structural complexity and increase the diversity and quality of fish habitat (Pirtle 2005, Tissot et al. 2006), a functional role equivalent to that of other large megabenthos such as corals; (3) sponges may also function as microhabitat islands in the deep sea (Beaulieu 2001); (4) sponges host a great diversity of other invertebrates that are either facultative or obligate endo- and epibionts (Henkel & Pawlik 2005); (5) sponges act as ecosystem engineers profoundly modifying the surrounding seafloor via current baffling, enhancement of bacterial biomass in sediments, sediment trapping, the creation of spicule mats, and the formation of biogenic structures and hard substratum in otherwise low-relief

habitats (McClintock et al. 2005), and (6) as suspension feeders of high biomass, they play a key role in benthopelagic coupling and benthic metabolism in both shallow and deep sea settings (Witte & Graf 1996). Sponges are also vulnerable to impacts by bottom trawling and other human disturbances (Freese 2001).

Although data on the abundance and biomass of the megabenthos in canyons are available for several sites worldwide (Headrich et al. 1975, Vetter & Dayton 1999), the diversity of the benthic assemblages is rarely documented and not known for the sponge fauna of any canyon. Thus, our chief objective in this study was to quantify levels of species richness of sponge assemblages in submarine canyons. In addition to documenting levels and patterns of sponge richness, we assessed (1) whether habitat type and complexity are linked to community composition and species turnover, and (2) to what extent different canyons share species (beta diversity). Finally we provide an example of how such survey data on species richness, range size, and species turnover can be employed conceptually to complement the broad spectrum of multi-faceted conservation planning tools for continental margins.

MATERIALS AND METHODS

Study area and field collections. Many (>100) submarine canyons incise the continental margin around southeastern Australia (Hill et al. 2005). These vary in overall morphology from relatively small features to large and complex features with many tributary or 'feeder' canyons that together span tens of kilometres in width (Hill et al. 2005). Canyons that have been completely mapped typically extend from the continental shelf edge (in about 150 to 200 m depth) to the abyss (>3000 m depth).

Collections of sponges for this study were made in 2004 during a 2 wk seabed mapping survey by Australia's National Facility research vessel FRV 'Southern Surveyor'. Samples were taken at 14 stations from 5 prominent southeastern Australian canyons: 3 intermediate-scale features off the west coast of Tasmania (King Island Canyons, Ling Canyon and Pieman Canyon), one intermediate-scale feature off the north-eastern coast of Tasmania (Banks Strait Canyon), and one large feature off eastern Victoria (Big Horseshoe Canyon; Figs. 1 & 2, Table 1). Each of these canyons extends from the continental shelf to abyssal depths, but sponge collections were limited to the upper sections at outer shelf and upper continental slope depths (mostly between 200 and 600 m, Table 1). Benthic samples were located below the prominent thermocline located between 70 and 120 m in the canyons (Fig. 2). One sample (Ho-88) was taken from rocky bottom on the shelf

Fig. 1. (a) Locations of canyon sampling sites off southeastern Australia; (b) King Island canyons; (c) Pieman canyon; (d) Ling Hole canyon. Depth contours are 200, 700 and 1000 m as labelled; locations of sled transects are shown as straight lines

immediately adjacent to the head of the Big Horseshoe Canyon at 116 m depth. Seabed bathymetry maps (Fig. 1), made for each canyon with a Simrad EM300 multi-beam sonar (MBS), assisted in identifying locations that could be sampled with a benthic sled. Our aim was to maximise diversity in our collections, and thus trawls were generally taken down the canyons from shallow to greater depth whenever possible.

The benthic sled used in the survey is described in detail by Lewis (1999). It has a mouth opening of 0.72 m² (600 × 1200 mm), and a robust construction enabling it to be used on steep, rugged seabed. It was towed with a 25 mm wire rope at an average speed of approximately 2 knots. Two sensors on the sled provided telemetry data to assist with positioning on the seabed: a pressure sensor and transducer (Scanmar System 400 depth sensor; model HC4-D12) were used to monitor height off the bottom as the sled descended, and a USBL (Ultra Short Baseline) acoustic beacon (Sonardyne) provided estimates of the sled's position relative to the vessel. The ac-

curacy of sled position estimates is determined by several factors including intrinsic data quality which decreases as the range to the beacon increases, dynamic errors in vessel sensors (motion reference unit measuring pitch and roll, and gyrocompass measuring vessel heading) which increase during rough sea state, sound velocity errors, and by undulating bottom when data transmission was interrupted. Overall, estimates of sled positions were estimated to be in the range of ±8 m at the shallowest site (~100 m depth) and ±50 m at the deepest site (~600 m depth). Sled tow tracks were overlaid on the MBS maps to estimate the ranges of seabed ('bottom') slope and hardness along each track. Bottom hardness is an index derived from acoustic backscatter (Kloser et al. 2001) measured in decibels (dB); 3 categories of bottom type ('soft', 'hard' and an intermediate 'mixed' type) are based on a simple classification with cut-off points at -33 and -31 dB. These cut-off points were determined from examination of acoustic data from locations validated with video data (CSIRO unpubl.

Fig. 2. Temperature and salinity profiles from CTD casts in the water columns of canyons sampled for sponges in (a) Ling Hole canyon, (b) King Island canyons, (c) Pieman canyon, and (d) Big Horseshoe canyon

data). MBS data were processed in the MB System software application (www.mbari.org/data/mbsystem) and mapped using a grid cell resolution of 20×20 m. A tow distance of approximately 900 m to 1200 m was attempted (15 to 20 min duration at ~2 knot tow speed), but this was not always possible over rough seabed. The depth range and distance of each tow were estimated from mapping data by overlaying the start and end points of tows from USBL data.

Sled samples were sorted on board to the lowest taxonomic resolution possible. The resolution achieved varied between taxonomic groups; some were not split be-

yond phyla (e.g. bryozoa, anthozoa), other groups, including sponges, were sorted to putative species. Sponges comprised a variable fraction of the total catch that ranged from about 5 to 270 kg total wet weight, but generally were among the dominant megabenthic groups that also included bryozoans, ascidians, echinoderms and decapod crustaceans. All sponge specimens were retained and each taxon was given a unique allocation number, photographed to record fresh colour, and preserved in 70% ethanol. Subsequent laboratory identification of sponges was done by the second author to species level in the laboratory of John Hooper, Queensland Museum, Brisbane.

Data analysis. The principal measure of alpha diversity employed here is the number of taxa recorded per individual sled sample at the level of species, genera, family, and order. The spatial scale over which alpha diversity is defined varies amongst authors. Here we follow the notation of Gray (2000) where richness per sled tow is termed 'sample' richness (SR_s), because a sampling gear towed along the seafloor for some distance effectively integrates specimens from smaller 'point' samples (*sensu* Gray 2000). This terminology is consistent with the use of pooled grabs ('point' richness) in the analysis of marine benthic assemblages (Ellingsen 2002, Ellingsen & Gray 2002). Species richness does not, however, directly reflect phylogenetic (or at least taxonomic) diversity (Warwick & Clarke 2001). Thus, 2 complementary measures of diversity were also included: (1) average taxonomic distinctness, $\Delta+$ (Warwick & Clarke 1995), and (2) variation in taxonomic distinctness, $\Delta+$ (Clarke & Warwick 2001). Taxa which occur at a single site only are termed 'spot endemics' (*sensu* Schlacher et al. 1998) or 'uniques' (*sensu* Colwell & Coddington 1994).

Patterns in sponge assemblages were assessed based on similarities in species composition using Bray-Curtis (B-C) resemblance coefficients (identical to the Sorensen or Dice coefficient for presence/absence data), followed by non-metric multidimensional scaling (Clarke 1993). For all statistical analysis, we used presence/absence data only for 3 reasons: (1) sponges can be colonial and thus estimates of abundance cannot be obtained consistently with accuracy from dredge and sled samples, (2) physical collections can contain fragments of sponges which are still valid for taxonomic identification but lower the accuracy of abundance estimates,

Table 1. Stations sampled for sponges in 5 submarine canyons off southeastern Australia

Stn	Latitude (S)	Longitude (E)	Trawl length (km)	Depth (m)
King Island				
Ki-25	39° 48.93'	143° 09.48'	0.74	224–359
Ki-27	39° 49.53'	143° 10.56'	1.25	205–338
Ki-29	39° 52.53'	143° 10.50'	1.61	240–415
Ki-30	39° 52.80'	143° 10.28'	0.92	391–464
Ki-35	39° 49.43'	143° 08.22'	1.97	480–612
Ling Hole				
Li-50	41° 22.27'	144° 24.51'	3.28	174–324
Li-51	41° 23.34'	144° 21.69'	2.17	359–429
Li-52	41° 20.60'	144° 19.44'	1.79	196–338
Pieman				
Pi-65	41° 45.97'	144° 33.78'	0.06	442–449
Pi-72	41° 46.69'	144° 34.50'	2.59	173–485
Pi-73	41° 45.23'	144° 33.78'	2.88	181–482
Banks Strait				
Ba-82	40° 39.27'	148° 47.61'	3.31	179–397
Big Horseshoe				
Ho-86	37° 57.21'	149° 14.76'	1.14	114–117
Ho-88	38° 09.06'	149° 20.58'	1.49	270–337

and (3) there may be unknown biases in abundance estimates of benthic organisms derived from towed sampling gears if catchability is uneven.

Relationships between faunal patterns and environmental variables were explored using the BIO-ENV procedure (Clarke & Ainsworth 1993). Environmental variables used in this analysis included depth, bottom type, and slope. This method essentially selects subsets of environmental variables that best match the faunal patterns, the degree of concordance being defined as rank correlation between abiotic matrices (calculated from normalised Euclidean distances) and biotic matrices (calculated from B-C coefficients) for all combinations of available environmental variables. The 'optimum subset' of environmental variables is usually selected based on the highest rank correlation, but a number of subsets can show correlation coefficients that differ only marginally from each other. Therefore, we also calculated the number of times an individual environmental variable was included in the 100 'best' subsets. In addition, we assessed how closely single environmental factors (excluding all other abiotic variables) related to station-to-station differences in species composition by assessing rank correlations between Euclidean distance matrices and biotic B-C similarity matrices using the RELATE routine implemented in the PRIMER software package (Clarke 1993, Warwick & Clarke 1993). The same method was used to test the match between the spatial separation of sites (geographic distance) and similarity in species composition.

Diagnostic checks. Due to operational constraints and sea conditions, sampling effort (measured as trawled distance on the seafloor) varied between sites (mean 1.8 km $\pm$ 0.26 SE; Table 1). Therefore, we carried out 3 diagnostic checks to test whether distribution of sampling effort was even across physical habitats, and whether species diversity and assemblage structure were influenced by effort. There was no evidence for systematic sampling bias for either response variable. (1) Environmental attributes: samples in deeper water were not significantly longer or shorter (Spearman rank correlation coefficient, r_s , between mean depth and trawl distance: $r_s = -0.07$, $p_{(2)} = 0.82$); trawls over hard ground were not significantly shorter or longer than on soft bottoms ($r_s = -0.19$, $p_{(2)} = 0.52$); and sampling effort did not vary systematically with the steepness of the seafloor ($r_s = -0.21$, $p_{(2)} = 0.46$). Therefore a consistent bias in sampling effort across habitat types is highly unlikely. (2) Alpha diversity: variation in sampling effort did not systematically bias sample values of sponge richness (correlations between trawled distance and sample richness: species: $r_s = 0.12$, $p_{(2)} = 0.69$; genera: $r_s = 0.05$, $p_{(2)} = 0.87$; families: $r_s = 0.13$, $p_{(2)} = 0.64$; orders: $r_s = 0.09$, $p_{(2)} = 0.74$). Similarly, taxonomic diversity across sites was not systematically biased by trawled distance ($\Delta+$: $r_s = 0.11$, $p_{(2)} = 0.71$; $\Lambda+$: $r_s = -0.26$, $p_{(2)} = 0.37$), nor was the number ($r_s = -0.12$, $p_{(2)} = 0.67$) or the proportion ($r_s = -0.17$, $p_{(2)} = 0.56$) of restricted range species ('spot endemics'). (3) Species composition: multivariate patterns in assemblage structure of sponges within and across canyons were not significantly related to differences in sampling effort (RELATE test between biotic and trawled distance matrix: $Rho = 0.043$, $p_{(2)} = 0.354$).

RESULTS

Environmental heterogeneity

Variations in depth, bottom type, and seafloor relief resulted in spatial heterogeneity of habitat attributes both within single canyons and among canyons (Fig. 3). Depth ranged from 114 to 612 m (Table 1; Fig. 3a). Most samples spanned a broad depth band between 200 and 400 m, but with considerable variation in depth coverage traversed by individual sled tows (Table 1, Fig. 3a). A single sample (Ki-35) was deeper than 600 m, and one was relatively shallow (Ho-86, Table 1). Fifty percent of sites had maximum sample depths >400 m, and 13 samples were deeper than 300 m (Table 1, Fig. 3a). Although soft sediments were the predominant bottom type at most sites, variability in sediment properties (estimated from acoustic backscatter) was evident at all scales

(Fig. 3b). Within a single trawl track, a diversity of substrata was often recorded, and half of all soft sediment samples also contained some mixed substratum (Fig. 3b). The seafloor at 2 sites in the Big Horseshoe canyon (Ho-86 & Ho-88) and at a deep collection in the Pieman canyon (Pi-65), consisted mostly of mixed substratum types, but also included hard, rocky patches as well as soft sections (Fig. 3b). By contrast, relatively uniform soft sediments of low substratum diversity were less frequent (Fig. 3b). The seafloor relief (as estimated from variation in slope along trawl tracks) indicated high topographic complexity, encompassing both relatively flat sections of low relief (e.g. Ho-86) as well as steep areas of high complexity (Ki-25). Average slope ranged from 3 to 12°, with steeper sections tending to be more topographically complex than flatter areas (Fig. 3c).

Alpha diversity

The canyons surveyed harboured a rich sponge fauna. A total of 165 sponge species, belonging to 65 genera, 41 families, 10 orders, and 2 classes were recorded from the 14 sled samples (Appendix 1; available at: www.int-res.com/articles/suppl/m340p73-88_app.pdf). Sample richness varied considerably among sites, ranging from a single species (Li-51) to 38 species (Ba-82) per bottom shot. Similarly, sample genus richness ranged from 1 to 26, while the maximum numbers of families and orders recorded per sample were 21 and 9, respectively. Ten samples had >10 species, 5 samples had >5 species, and 3 samples had ≥30 species. Alpha diversity declined with depth for species, genera, and families (Fig. 4a,b, Table 2). Bottom type per se (e.g. whether predominately soft, mixed, or hard) appears not to be an important driver of alpha diversity, but heterogeneity of bottom types is. Areas with a greater diversity and a range of substratum types (e.g. mixed rocky and sandy/muddy bottoms) harboured more sponge taxa than areas with more uniform substratum properties (Fig. 4c,d, Table 2). Richness of species and of genera were significantly higher in canyons located on the eastern shelf than in canyons on the western shelf after accounting for the possible influences of depth, bottom type, and relief (Table 3); this large-scale difference in sponge richness was found to a lesser degree for families and orders (Table 3).

Beta diversity

Species turnover was high, both between canyons and between sites within individual canyons. This re-

Fig. 3. Variation in (a) sample depth, (b) bottom type as assessed by acoustic backscatter, and (c) seafloor relief measured as standard deviation of bottom slope along trawl tracks. Box and whiskers denote interquartile range (box), medians (horizontal range in box) and ranges (whiskers). See Table 1 for list of canyons and sampling site codes

Fig. 4. Influence of depth (minimum sample depth, $D_{\min}$) and substratum diversity (SD of backscatter signals) on sample richness (n) of sponge species and genera (cf. Table 2 for other environmental factors and higher taxa)

Table 2. Correlations between habitat variables and alpha diversity for sponge assemblages in canyons. Measure of concordance is Spearman rank correlation, r_s ; *denotes coefficients with $p_{(2)} < 0.05$; and (*) denotes coefficients with $p_{(2)} < 0.10$, $n = 14$; measure of alpha diversity is richness per sample for each of 4 taxonomic levels

	Species	Genera	Families	Orders
Depth				
Mean	-0.34	-0.38	-0.35	-0.20
Median	-0.44	-0.49(*)	-0.47(*)	-0.30
SD	0.28	0.20	0.30	0.19
Min.	-0.56*	-0.51(*)	-0.51(*)	-0.32
Max.	-0.19	-0.27	-0.20	-0.15
Range	0.23	0.15	0.27	0.14
Bottom type (Acoustic backscatter)				
Mean	0.27	0.37	0.31	0.33
Median	0.32	0.43	0.37	0.38
SD	0.49	0.53*	0.43	0.49(*)
Min.	-0.17	-0.2	-0.20	-0.33
Max.	0.31	0.35	0.26	0.41
Bottom slope				
Mean	-0.16	-0.20	-0.12	-0.20
Median	-0.03	-0.13	-0.07	-0.16
SD	-0.15	-0.10	0.00	-0.07
Min.	-0.13	-0.12	-0.09	-0.20
Max.	-0.07	0.00	0.08	0.01

sulted in high beta diversity and low biotic similarities between samples. Species occurrence among canyons was highly disjunct, and canyons had on average only 10.3% of the species pool in common. The maximum fraction of shared species between any 2 canyons was equally low at 20.7%. At the scale of individual sites, species overlap was similarly narrow. Each site shared on average only 6.25% of its species with other sites. The maximum probability that a single species picked at random from the full data set found jointly in any pair of samples is 0.27.

No single environmental factor drove patterns in sponge assemblage structure (Fig. 5, Table 4). Rather, the biotic mosaic in sponge assemblages was most closely related to a suite of variables that included differences in depth, bottom type and diversity, and seafloor relief (Fig. 5, Table 4). Thus, variations in deep sea canyon sponge communities likely arose from biological responses to environmental conditions encompassing seafloor properties (relief and bottom type) and depth.

Distributional ranges

Canyon sponges had strongly compressed distributions. The vast majority of species (126 spp. or 76%) were 'spot endemics', occurring at single stations only (Table 5, Fig. 6). No species spanned the entire survey range, the maximum site occupancy being 7 sites (50%) for only 3 species (Table 5, Fig. 6). Similarly, 42% of genera, 29% of families, and 36% of orders had but a single site occurrence. Three-quarters of all sponge genera occupied 3 sites or less, and 75% of families occurred at 5 sites or less (Fig. 6b). This prevalence of highly compressed distributional ranges is also evident at the canyon scale: 79% of species and 46% of genera were found in single canyon systems only. No species was found in all 5 canyons sampled, and only 3 out of 65 genera were distributed across all canyons (Table 5).

DISCUSSION

A highly speciose canyon sponge fauna?

We found a rich sponge fauna in the canyons with a relatively small collecting effort; 14 sled samples yielded 165 species, 65 genera, 41 families, and 10 orders

Table 3. Summary of analysis of covariance (ANCOVA) contrasting mean sponge richness at 4 taxonomic levels (species, genera, families, and orders) between canyons situated on the East and West Shelves (cf. Fig. 1). Tabulated values ($F_{(1,13)}$) refer to tests for the main effect of location, i.e. the eastern versus western shelf. Not significant: ns; $p_{(2)} > 0.05$; * $p_{(2)} < 0.05$; ** $p_{(2)} < 0.01$

Covariates	Species	Genera	Families	Orders
Depth				
Mean	7.33* E > W	5.55* E > W	3.11 ^{ns}	3.49 ^{ns}
Median	7.72* E > W	5.92* E > W	3.27 ^{ns}	3.60 ^{ns}
SD	18.91** E > W	13.73** E > W	9.80** E > W	8.06* E > W
Min.	7.97* E > W	6.22* E > W	3.37 ^{ns}	3.59 ^{ns}
Max.	8.40* E > W	6.14* E > W	4.11 ^{ns}	4.68 ^{ns}
Bottom type (acoustic backscatter)				
Mean	10.47** E > W	6.01* E > W	4.04* E > W	3.79 ^{ns}
Median	9.97** E > W	6.04* E > W	3.90* E > W	3.69 ^{ns}
SD	5.37* E > W	2.51 ^{ns}	1.81 ^{ns}	1.57 ^{ns}
Min.	8.66* E > W	6.58* E > W	3.83 ^{ns}	3.60 ^{ns}
Max.	8.38* E > W	5.18* E > W	3.80 ^{ns}	2.68 ^{ns}
Bottom slope				
Mean	8.92* E > W	6.86* E > W	4.57 ^{ns}	4.38 ^{ns}
Median	8.97* E > W	6.61* E > W	4.01 ^{ns}	3.97 ^{ns}
SD	12.11** E > W	12.57** E > W	8.93* E > W	7.73* E > W
Min.	9.61* E > W	7.68* E > W	4.49 ^{ns}	4.43 ^{ns}
Max.	13.67** E > W	13.58** E > W	9.34* E > W	7.61* E > W

Table 4. Concordance between environmental data and spatial patterns in sponge assemblages. Degree of correspondence between environmental and biotic data (species composition per sample) assessed by defining the sets of permutations of environmental variables that were most strongly correlated with biotic similarities (BIO-ENV: combinations of environmental variables; times included in the 100 best matches), complemented by correlations of single factors to biotic data (RELATE: single variable matrix correlation).

*: included in the overall best match

	BIO ENV	RELATE	
		r_s	$p_{(2)}$
Depth			
Mean	50	0.293	0.068
Median	19	0.202	0.135
SD	9	0.122	0.214
*Min.	46	0.240	0.093
*Max.	89	0.237	0.112
Range (max.–min.)	60	0.130	0.223
Bottom type (acoustic backscatter)			
Mean	39	0.304	0.071
*Median	91	0.342	0.047
SD	0	0.204	0.061
*Min.	100	0.215	0.164
Max.	0	0.074	0.301
Bottom slope			
Mean	0	0.113	0.280
Median	0	0.128	0.247
*SD	96	0.092	0.259
Min.	0	0.049	0.392
Max.	0	–0.088	0.640

(Appendix 1). While density and biomass values for canyon megabenthos are available from several canyons worldwide (Headrich et al. 1975, Vetter & Dayton 1999), the richness of the canyon sponge fauna has not been quantified for any other submarine canyon system. Broad comparison with seamounts in the Tasman and Coral Seas indicate that the canyon megabenthos may rival or exceed that of seamounts in terms of sponge richness (Fig. 7). These comparative data from the seamounts were collected over similar depth ranges, using very similar or the same gear type, and employed the same taxonomic resolution. Seamounts are conventionally regarded as benthic hotspots in the deep sea, characterised by high levels of benthic biomass, diversity and endemism (Rogers 1994, Richer de Forges et al. 2000). The comparatively high levels of species richness found in the canyons would thus suggest a broader role of abrupt topographies in generating areas of high megabenthic biodiversity in the deep sea.

Strong currents in canyons (Wählin 2002) may enhance the food supply to filter feeders. Interactions between abrupt, sloping topographies, such as canyons, and impinging currents greatly amplify near-bottom flows, resulting in enhanced delivery of particulate food to sessile filter feeders (Genin et al. 1986, Genin 2004). This appears to be common in these habitats on seamounts, and is thought to be the main mechanism responsible for the localised concentrations in filter-feeder biomass (including sponges) (Genin et al. 1986, Richer de Forges et al. 2000). Records of benthic filter feeders in canyons are rarer, but typical megabenthic

filter feeders such sea whips, sponges, and basket stars have been found in high densities inside canyons (Rowe 1971, Brodeur 2001). This would suggest the presence of substantial near-bottom flows that deliver particulate food to filter feeders such as sponges. In a parallel study that used video mapping of the canyon seabeds, we did observe some ripple marks on the canyon seafloor indicative of strong near-bottom currents. These were,

Fig. 5. Ordinations (non-metric multidimensional scaling) of similarities in species composition of sponge assemblages between sites. Ordination plots are superimposed with (a) location, (b) minimum sample depth, (c) median backscatter signal, and (d) seafloor relief measured by the SD in bottom slope. For ease of visual interpretation, the environmental variables (depth, bottom type, slope) are denoted by different symbols based upon the quartile (Q1–Q4) in which individual site values fell

however, relatively rare (3% of 211 354 video frames scored for seabed features showed distinct ripple marks). Thus, while bottom currents may play a role in creating a favourable environment for sponges in some canyon localities, there is uncertainty as to whether suspended particulate food carried in such flows is the primary factor that leads to the establishment and maintenance of these highly speciose assemblages of filter feeders inside the canyons.

Increased densities and biomass of canyon benthos have been linked to spatial subsidies of the canyon food webs in settings where canyons trap and accumulate large quantities of detached macrophytes such as kelp and seagrass (Vetter 1995, Okey 1997, Harrold et al. 1998, Vetter & Dayton 1999). Our video mapping of the canyon bottoms showed detached seagrass and kelp in some places, but they were rare and only occurred as individual fronds or blades, not as large parcels. However, semi-amorphous material that appeared to consist of agglutinated detritus was observed on several canyon transects, often in association with sponge aggregations. The origin and composition of this material cannot be resolved from underwater images, but the possibility exists that it may constitute a food source to the benthos. The presence of such 'detrital flocs' does indicate that the canyon seafloor may receive inputs of phytodetritus from the overlaying water column that may supply food particles to sponges.

Sponges generally have a catholic diet. They feed unselectively on a variety of bacteria and smaller plankton and ingest a broad size spectrum of particles from 0.5 to 70 μm (Ribes et al. 1999). Detrital deposits observed on the canyon floor amongst sponges are an indication of a food-rich environment, but whether sponges consume these detrital flocs directly is unknown. Sponges are known to graze primarily on the ultra-plankton (plankton <5 μm) fraction of the water column (Pile & Young 2006), mainly because the upper size limit of ingestible food is set by the diameter of the ostia and the anatomy of the aquiferous system (Bergquist 1978). Thus, while sponges may not routinely ingest larger detrital aggregates, they have been shown to phagocytize large cells from a settling bloom of diatoms (Gaino et al. 1994, see also Ribes et al. 1999). Detritus could play an indirect role in the nutrition of canyon sponges when decaying detrital flocs release dissolved organic matter (DOM), which in turn promotes the growth of heterotrophic bacteria in the benthic boundary layer. Bacterivory is common in sponges, and bacteria are an excellent source of nutrients for sponges (A. Pile pers. comm.).

Apart from a few sponge families for which we have a reasonably good taxonomic knowledge worldwide (e.g. Microcionidae, Raspailiidae), assigning specimens to species remains very difficult, particularly for

Table 5. Distributional range size of sponge taxa expressed as (A) number of sites and (B) number of canyons occupied by members of each taxonomic level. Total number of sites surveyed was 14

No.	Species		Genera		Families		Orders	
	n	%	n	%	n	%	n	%
(A) Sites								
1 ^a	126	76	27	42	12	29	4	36
2	17	10	14	22	6	15		
3	11	7	8	12	6	15	1	9
4	2	1	3	5	3	7		
5	4	2	3	5	3	7	1	9
6	2	1	8	12	3	7		
7	3	2	1	2	4	10	1	9
8					3	7		
9							2	18
10								
11			1	2	1	2		
12							2	18
Total	165		65		41		11	
(B) Canyons								
1	130	79	30	46	13	32	3	27
2	20	12	15	23	9	22	1	9
3	10	6	7	11	4	10		
4	5	3	10	15	10	24	2	18
5			3	5	5	12	5	45
Total	165		65		41		11	
^a 'Spot endemics'								

most deep-living sponges. While it is likely that many of the canyon sponges collected by us are new to science, it is premature to present their exact taxonomic identity and biogeographic affinities in a global or regional context without further detailed taxonomic work that will take many years to complete. Consequently, reliable taxonomic and biogeographic comparisons with similar faunas can not be made at present, particularly when comparing our data with the pivotal studies of the rich bathyal seamount faunas south of New Caledonia (Lévi 1993 and references therein) and the recent, unpublished collections from the Tasman Sea obtained during the NORFANZ cruise (www.oceans.gov.au/norfan/). Nevertheless, some faunistic trends were apparent that suggest the canyon sponge fauna may be derived primarily from a sublittoral, coastal and continental shelf fauna rather than from representatives of the bathyal fauna, as documented for the New Caledonian region (Lévi 1993). A few of our species, e.g. *Dendrilla rosea*, *Holopsamma laminaefavosa*, and *Acanthella dendyi*, are common in the shallower waters of Bass Strait, and parts of southern Australia and New Zealand, where they occur at SCUBA depths (Hooper 1996). Many of the *Haliclona* species are probably also recruited from this fauna, given the preponderance of this genus in shallow waters. There are, however, some species in our collection

that have been recorded previously only from bathyal depths (>200 m) of southern Australia, the subantarctic islands and Antarctica, e.g. *Clathria* (*Axosuberites*) *nidificata*, *Clathria* (*Clathria*) *inanchorata*, and *Craniella* (*Tethyopsilla*) *stewartii*. Some genera are known chiefly from bathyal or hadal depths, such as *Phlyctenopora* (*Barbozia*) and *Lithoplocamia* (e.g. Lévi & Lévi 1983). Most of the specimens in our collection whose specific identities can be confirmed at this time, e.g. *Clathria* (*Thalysias*) *rubra*, *Clathria* (*Axosuberites*) *thetidis*, *C. (A.) canaliculata*, *C. (A.) cylindrica*, *Raspailia* (*Raspaxilla*) *compressa*, and *Mycrotylostylifer anomalus* have been recorded only from deeper coastal or mid-shelf waters (40 to 150 m), on the southeastern and southern continental shelf of Australia (Hooper 1996), with the present study greatly extending the published depth and geographic ranges of some species. This preliminary finding that the canyon sponge fauna is dominated by species from shallower waters is further supported by the absence of any Hexactinellida or 'Lithistid' sponges in our collections, even though they are known from similar depths on New Caledonian seamounts, with the latter particularly abundant and characteristic of seamount faunas (Schlacher-Hoenlinger et al. 2005).

Limited range size of canyon sponges

Canyon sponges had strongly compressed range sizes, with 76% of species being restricted to a single site, and 79% occurring in single canyons only (Table 5, Fig. 6). Very low levels of site occupancy are not uncommon for marine benthic assemblages; some examples include: (1) 20 to 50% of polychaete species on the abyssal plain of the Central Pacific were restricted to single sites (Glover et al. 2002); (2) on seamounts of the Norfolk Ridge, 25% of squat lobster species were recorded from single seamounts only (Samadi et al. 2006); (3) amongst the epifaunal megabenthos trawled on the island slope of New Zealand, 25% of species were found at single stations (Cryer et al. 2002); (4) macrobenthic assemblages on the Norwegian shelf showed compressed range sizes with 25 to 27% of species recorded from single stations only (Ellingsen 2001, 2002, Ellingsen & Gray 2002); (5) 42% of macrofaunal species sampled in a Pacific coral reef lagoon occurred at one site only (Schlacher et al. 1998); (6) 32% of mollusc species found in a very comprehensive sampling programme on a coral reef complex in New Caledonia were collected from single stations (Bouchet et al. 2002); and (7) among Australian shallow-water sponge assemblages, 48 to 60% of species were found at single sites within the reef complexes sampled (Hooper & Kennedy 2002, Fromont et al. 2006).

Fig. 6. (a) Range size of canyon sponges. Insert (b) shows cumulative site occupancy at increasing proportions of the regional taxon pool recorded in this survey, illustrated for 50 and 75% of taxa at the level of genera (G), families (F) and orders (O)

Arguably, our data on compressed sponge distributions could, potentially, be biased by sampling properties if either or both of 2 conditions are met: (1) limited spatial coverage of sampling sites results in underestimates of true site occupancy (Gaston & Blackburn 2000), and (2) if many species occur at low abundance, they may not be detected in all samples (MacKenzie et al. 2003). As the spatial coverage of sampling increases, more site records for previously known species are likely to be obtained, thus extending the estimated range sizes of the species that have already been found (e.g. the fraction of spot endemics is likely to decline). However, further sampling is likely to add new rare (i.e. sparsely distributed species) to the collection, which will produce sample estimates of very narrow range sizes (e.g. the relative abundance of spot endemics will increase). It is thus possible that the net effect of more comprehensive spatial sampling may produce no considerable change in the overall estimate of site occupancy, including estimates of spot-endemism. Thus,

sample estimates of highly restricted range sizes may not necessarily be strongly and consistently influenced by variation in sample coverage, but this has not been quantified for marine benthic communities.

Distributions of site occupancy (range size *sensu* Gaston 1991) are also sensitive to the spatial scale over which samples are taken or records obtained. Species range size distributions become markedly more right-skewed as the geographic scale and spatial grain of sampling and analysis are expanded (Gaston & Blackburn 2000). Also, large-scale mapping of species distributions generally produces patterns where most species are narrowly distributed and a few are widespread. In fact, studies embracing the entire geographical ranges of all, or at least the majority, of the species in a taxonomic assemblage tend to document species-range size distributions with a strong right-skew (Brown et al. 1996).

It is possible that many sponge species sampled by us do occur at low densities, and a high frequency of rare species characterizes the canyon communities. In fact, most species-abundance distributions show that natural communities generally do contain a few highly abundant species and a large number or rare species (Pueyo 2006). Such rare species are predicted to have a lower chance of inclusion in samples and, consequently, their ranges may be underestimated (MacKenzie et al. 2003). For deep-sea benthic assemblages,

it has been argued that such markedly right-skewed species abundance distributions may influence derived patterns of distributions and species turnover between localities (Glover et al. 2002). We are not aware, however, of any empirical or theoretical study that has quantified the effects of under-sampling on estimates of species-range sizes in marine benthic communities. Thus, the extent to which undersampling of potentially rare species may have biased our estimates of site occupancy for the canyon sponges remains unresolved.

Geographic distance (e.g. spatial separation) was found to be a poor predictor of biotic similarity in sponge assemblages at small and intermediate scales (Fig. 8). Sponge assemblages from different sites within the same canyon were just as distinct as assemblages in different canyons on the same shelf (Figs. 5 & 8). This pattern in biotic dissimilarity implies that there is no discernable spatial effect of 'canyon affinity' *per se* in structuring this fauna. Rather, differences in environmental characteristics that are manifested at

Fig. 7. Comparison of species accumulation curves between this data set (Tasmanian canyons) and deep-sea sponge surveys on seamounts in the neighbouring Coral and Tasman Seas and the northern Norfolk Ridge in New Caledonia

Fig. 8. Similarity of sponge assemblage composition in relation to geographic distance between sites at 3 spatial scales. (a) Summary plots of biotic similarity between sites pooled separately for each spatial scale. Box and whiskers denote interquartile range (box), medians (horizontal range in box) and ranges (whiskers). A, B and C in (a) are explained in (b). (b) Relationship between biotic similarity and distance amongst sites. r_s and associated p value refer to Spearman's rank correlation between geographic distance matrix and biotic similarity matrix tested with the RELATE procedure of Clarke & Ainsworth (1993)

multiple scales may be more important than geographic placement in an individual canyon. The processes which lead to such high levels of 'spot endemism' (sensu Schlacher et al. 1998) and high species turnover at multiple spatial scales in canyon sponges are currently unresolved, but could, hypothetically, involve 2 mechanisms that are not mutually exclusive: (1) very limited dispersal of sponge larvae, or (2) strong substratum selection by settling larvae in an environment that contains many different habitat patches (Fig. 3).

Sponge larvae are likely to have highly limited dispersal capabilities (Maldonado 2006). Thus, limited dispersal of sponge larvae appears a plausible mechanism for the small range sizes of adults found in this study. However, the validity of this 'restricted dispersal explanation' for canyon sponges has to be tested against other taxa with better larval dispersal capabilities (e.g. echinoderms, crustaceans). These data are not currently available for the megabenthos of canyons. There is insufficient evidence to generalize about whether settlement of sponge larvae is specific or catholic in terms of substratum choice (Maldonado 1996). Thus, the question whether larval settlement or post-settlement processes primarily drive the observed patterns in variation in assemblage composition across different combinations of seafloor characteristics in and between canyons remains unresolved (Fig. 5).

Links to spatial planning for biodiversity conservation and fishery habitat

Australia is presently introducing measures to protect deep-sea benthic biodiversity and benthic fishery habitats through marine protected areas (MPAs) (ANZECC 1999) and expanded regulation of deep-sea bottom fishing through spatial closures. MPAs are being designed using a 'CAR' approach (TFMPA 1999), reserving areas for the full range of ecosystems (comprehensive), of sufficient size and spatial distribution to ensure their ecological viability (adequate), that reflect the biodiversity of particular marine ecosystems (representative). Presently, however, the information needs of managers considerably exceed existing knowledge, especially for the outer continental shelf and continental slope, including features such as submarine canyons that have been little sampled. Initial studies from southeastern Australia (Bax & Williams 2001, Koslow et al. 2001), and elsewhere (Langton et al. 1995), demonstrate the need for information on habitat and animal distributions at multiple spatial scales (Williams et al. 2005a) for management strategies to be effective. Since our data identify biodiversity patterns in an important group of the megabenthos from

Table 6. Ranking of sites based on maximising 4 diversity criteria that could be employed to select target areas in conservation planning. For all biotic indices that showed significant correlations with environmental variables, both the raw values and values adjusted for the influence of environmental factors (depth and substratum adjusted) were used; these adjusted ranks are derived from residuals of non-linear regression models. **Bold**: top 5 sites for each criterion; * : top 3 ranked sites in each column). Criterion 1 (taxon richness): pooled rank over the number of species, genera, families and orders per site. Criterion 2 (taxonomic distinctness): combined rank of average taxonomic distinctness (Δ^*) and variation in taxonomic distinctness (Δ^+ , Warwick & Clarke 1995, Clarke & Warwick 2001b). Criterion 3 (endemic species): number of species found only at this single site, 'spot endemics' sensu Schlachter et al. (1998). Criterion 4 (species overlap): fraction of a site's species that is shared with all other sites ('species overlap')

Canyon	Stn	Depth (m)	Species (n)	Criterion 1			Criterion 2			Criterion 3			Criterion 4	
				Raw	Depth adj.	Substr. adj.	Rank of mean	Raw	Depth adj.	Rank of mean	Raw	Depth adj.	Rank of mean	Overall score
Banks Strait	Ba-82	308	38	12*	13*	13*	13*	8	6	7	13*	14*	14*	47*
King Island	Ki-30	442	26	9	10	11	10	12*	12*	12*	9	12*	10	43*
Pieman	Pi-72	281	33	13*	12*	14*	14*	3	3	3	11	10	10	41*
Big Horseshoe	Ho-88	303	29	14*	14*	8	12*	3	3	3	12*	13*	14*	40
King Island	Ki-27	246	19	10	10	12*	11	7	7	7	9	11	9	34
King Island	Ki-29	357	12	6	5	7	7	13*	13*	13*	3	4	4	33
Ling Hole	Li-52	277	16	8	7	9	8	8	9	9	4	3	4	31
Big Horseshoe	Ho-86	116	32	11	8	9	9	3	5	5	14*	9	12*	3
King Island	Ki-25	275	12	5	4	5	4	10	10	10	8	7	8	29
King Island	Ki-35	554	9	3	9	2	4	13*	13*	13*	1	6	4	27
Ling Hole	Ki-50	238	9	3	2	6	2	10	11	11	4	1	1	18
Pieman	Pi-65	446	5	2	6	3	2	6	7	6	4	8	7	17
Pieman	Pi-73	300	13	7	3	4	4	2	2	2	4	2	2	16
Ling Hole	Li-51	404	1	1	1	1	1	1	1	1	1	5	2	5

a largely unsampled environment (submarine canyons), it is of interest to explore how they can be applied to spatial planning initiatives.

Although conservation planning is a multi-faceted process that spans a wide spectrum of input parameters for site selection, measures of 'biodiversity' and of 'endemism' are almost ubiquitously employed in this process (Lamoreux et al. 2006). Here we present an approach that uses 3 complementary criteria of diversity (taxon richness, taxonomic distinctness, and species overlap) and the number of 'spot endemics' (sensu Schlachter et al. 1998) to rank candidate sites based on sponge diversity and species distributions (Table 6). Sponges form species-rich assemblages and can significantly enhance the habitat value for numerous invertebrates and fishes (Pirtle 2005). As such, sponges are predicted to serve as proxies for overall megabenthic diversity. The exact form and strength of the relationship between sponge richness and the diversity and biomass of larger epibenthos and fish in the canyons will, however, require nondestructive observational studies using landers, ROVs (remotely-operated vehicles) or submarines in the future. Our results (Table 6) show that the 5 top-ranked sites are from 4 of the 5 canyons surveyed, and the top 3 sites are from 3 different canyons. This indicates that it will be necessary to include several to many canyons in protected areas to capture a high fraction of the regional sponge biodiversity (i.e. to be representative). This result is unsurprising given the underlying patterns in the data, with high spot endemism, few species (21%) occurring in more than one canyon, and small-scale distributional patterns linked to several properties of the seabed (depth, slope, bottom type and diversity). Thus, topographically complex canyons are characterized by benthic environments with high spatial heterogeneity that appears to translate into a mosaic of different sponge communities sharing few species. These data confirm the importance of including submarine canyons as key habitats for positioning MPAs and achieving representativeness, certainly for sponges, and possibly for total megabenthos diversity if sponges represent a proxy for broader communities. Further, in relation to the adequacy of individual MPAs, our data show that it is important to include whole canyons due to the heterogeneity within them, and to ensure the shallowest areas are included because these contain the highest levels of alpha diversity. The biotic separation at larger scales (i.e. eastern versus western continental margins) suggests the need to include canyons from different bio-geographic provinces,

and it is consistent with the current approach being taken that aims to ensure comprehensiveness, i.e. reserving areas from a full range of ecosystems and bioregions (ANZECC 1999, TFMPA 1999).

The distribution and abundance of bathyal fishes is positively linked to biogenic structures of the seafloor (Auster 2005), where close associations of fishes have been demonstrated with large megabenthic invertebrates such as sea whips, corals and sponges (Pirtle 2005, Tissot et al. 2006). Off southeastern Australia, this has been demonstrated in one of our study sites (Big Horseshoe Canyon), where there is a positive association between the commercial cusk eel *Genypterus blacodes* and structured habitats characterized by abundant megabenthos dominated by sponges (Williams et al. 2005b). Thus, aspects of sponge aggregations (diversity and density) and sizes of individuals may serve as proxies for identifying the habitat value for canyon-associated species. As many sponges are typically soft-bodied and protrude above the sediment surface (e.g. erect forms), they are easily damaged or removed by mobile fishing gear (Freese 2001). Absence of sponges may therefore identify habitats lacking suitable environmental conditions for rich, structural megabenthos to develop, or habitats where large sessile invertebrates have been removed by mobile fishing gear.

Negative effects of bottom-contact fishing on marine benthic systems have been well documented, including reductions in biodiversity and biomass, homogenization of the substratum, and disruption of ecosystem processes (Thrush & Dayton 2002). Fishing activities have even been found to trigger sediment gravity flow in one canyon (Palanques et al. 2006). We found that canyons that experience most bottom fishing (Ling Hole and Pieman) rank lower in terms of sponge diversity compared with canyons that experience little bottom fishing (Banks Strait and King Island; Table 6). In the case of the Ling Hole canyon, removal of megabenthos, including sponges, is corroborated by seabed photography (authors' unpubl. data). This correlative pattern indicates a possible connection between the intensity of bottom fishing (estimated here from commercial logbook data) and sponge diversity, but does not necessarily demonstrate a cause and effect relationship. Photographic surveys at finer spatial resolution that map sponge distributions in relation to trawling effort may prove a useful tool to better establish links between putative fishing impacts and seabed diversity in this situation. Conserving sponge aggregations not only preserves the species forming the community but also habitat complexity and associated organisms that provide habitats and refuges for commercial species. These factors need to be considered in fishery closure planning, as well as the fact that

canyons can be considered as hot spots for fishery production in southeastern Australia, because they contain concentrated aggregations of commercial fishes (Williams et al. 2005b). Thus, integrating the independent processes of designing MPAs and fishery closures is necessary to conserve the benthic biodiversity of sponges and the ecosystem services they provide.

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