Biodiversity and Conservation **11:** 851–885, 2002.

Biodiversity 'hotspots', patterns of richness and endemism, and taxonomic affinities of tropical Australian sponges (Porifera)

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Received 6 December 2000; accepted in revised form 21 May 2001

Key words: Australia, Biodiversity, Endemism, 'Hotspots', Marine sponges, Porifera, Richness, Taxonomic relationship

Abstract. 'Hotspots' of biodiversity (taxonomic richness, endemism, taxonomic affinities between communities) at small (α), medium (β) and larger (γ) scales of diversity were examined for marine sponge populations throughout tropical and subtropical Australia, with the faunas of Vanuatu, Palau and Thailand used as outgroups for comparison. Spatial and numerical (ordination) models and hierarchic classifications delineated 37 β and 13 γ scale faunas from 1343 investigated localities using a pool of 2324 species. The Australian taxonomic literature was ignored completely to avoid the many still unresolved taxonomic problems and to allow equal treatment of collecting localities. Richness and endemism varied considerably between marine areas, for species and genera at all spatial scales, with gradients strongly corroborated by hierarchic taxonomic relationships between faunas. Richness and endemism were equally effective indicators of biodiversity 'hotspots', whereas species-level vs. genus-level data produced differing patterns, with the latter substantially underestimating biodiversity and marine area relationships, and consequently a poor 'surrogate' for species data. Patterns of taxa shared between adjacent areas were more informative than richness and endemism data alone, as they more accurately reflect the processes in these areas. Latitudinal gradients in sponge diversity were not evident, whereas various environmental factors were prominent at α scales and biogeographic factors were prominent at β and γ scales of diversity. An example of a small (α) scale diversity fauna revealed substantial spatial heterogeneity (mean of 41 spp/locality, 33% apparently endemic, and a total fauna of 226 spp) containing few ubiquitous species (40% or 78 spp), with adjacent reefs having relatively low faunal similarity (mean 33%). Faunas at the medium (β) scale of diversity were less heterogeneous (mean 127 spp/region, 27% apparently endemic to a particular region, with a total fauna of 2324 spp), containing a significantly larger dataset (829 spp) found in >1 region to assess taxonomic affinities. At the larger (γ) scale of diversity faunas were far more heterogeneous (mean 263 spp/region, 47% apparently endemic to a particular region) containing a smaller dataset (only 588 spp or 26% of the fauna with >1 species/region) to assess taxonomic affinities. Consequently, sponge faunas at the α and γ scales of diversity are ineffective and inappropriate as biodiversity models, respectively, with γ scale diversity also less relevant as a practical tool for marine resource management and marine area conservation.

Abbreviations: GBR – Great Barrier Reef, MDS – non-metric 2D multidimensional scaling ordination, NSW – New South Wales, NT – Northern Territory, Qld – Queensland, SSBA – surface supplied breathing apparatus, WA – Western Australia.

Introduction

The decline of biodiversity is a fundamental global concern (Wilson 1992). In marine ecosystems, for example, it has been claimed that about 30% of the biota has disappeared over 30 years (WWF for Nature, reported in Butler 2000). The number of species threatened globally with extinction, however, far outstrips the current resources available for their conservation (Myers et al. 2000). This has produced conservation strategies that attempt to focus research resources more 'cost-effectively', such as 'biodiversity hotspots' strategies (e.g., Balmford and Long 1996; Myers et al. 2000). Conversely, it is questionable whether there are sufficient data to recognise 'hotspots' in the first place (Mace et al. 2000), such that priorities identified for one taxon may fail to reflect the diversity of others (Kerr 1997). Conservation priorities that truly represent 'biodiversity hotspots' require at least an adequate baseline knowledge of the diversity of species that form them, their dynamics and interdependencies, their interactions and responses to environmental factors (including impacts of invasive species), and investigations conducted at appropriate spatial scales (Jensen et al. 1999).

Unfortunately for marine ecosystems we simply do not have many of these data. We are still uncertain even of the magnitude of marine biodiversity (Kohn 1997), let alone the rate of its decline or the various factors responsible for widespread spatial heterogeneity amongst marine communities (Blanchard and Bourget 1999). Moreover, several established marine biodiversity models, such as latitudinal and bathymetric gradients in diversity, are now being questioned as to their validity across a broad range of marine taxa and environments (Poore and Wilson 1993; Gray 1997). We are also only just beginning to understand that the patterns and processes of speciation, dispersal, recruitment and succession in marine ecosystems are very different from those on land (Crame and Clarke 1997; Kohn 1997; Butler and Connolly 1999; Barber et al. 2000), such that conservation strategies designed for terrestrial species and ecosystems may be completely ineffective and inappropriate for marine systems.

How can marine resources be protected and conserved without adequately knowing what they contain or the processes that maintain them? Marine faunas are generally far more diverse than most of those on land (Crame and Clarke 1997), yet even in the most 'well-known' shallow coastal zones information on biodiversity is sparse at best (Anonymous 1997). For example, it has been widely assumed that the tropical Indo-Pacific generally contains a consistently highly diverse fauna living in a more-or-less uniform environment (Taylor 1997), yet coral reefs in particular, and many other marine environments in general (ranging from the intertidal to the deep sea and seamounts) are substantially heterogenous in their species diversity and faunal composition (e.g., Huston 1985; Grassle 1991; Guichard and Bourget 1998), often with little taxonomic overlap between geographically adjacent areas (Richer De Forges et al. 2000). For some marine taxa, such as scleractinian corals, fishes and some groups of molluscs we at least have adequate inventories of faunas (species and genera) at various spatial scales, with some corroborative molecular data to support their reported conspecificity to provide an informed assessment of their diversity, composition, and to address associated regional conservation issues (Veron 1993; Gray 1997; Meyer and Paulay 2000; Roberts et al. 2000). For most marine phyla, however, we still have too few reliable data on their diversity, endemism or biogeography – especially at larger spatial scales – to make any comparable sorts of assessments. This category includes the sponges (Porifera), with only about 30% of the estimated 15 000 species described so far worldwide (Hooper and Lévi 1994; Hooper and Wiedenmayer 1994). The phylum is not only more diverse but also far more widely distributed (geographically and ecologically) than scleractinian corals, for example. Moreover, current estimates of sponge diversity may be conservative given that only recently we have obtained good empirical support to show that populations of some allegedly widely distributed or 'cosmopolitan' species consist of several genetically distinct, cryptic sibling species (e.g., Solé-Cava et al. 1992; Klautau et al. 1994). In fact it is now generally recognised that most if not all phyla of sessile clonal marine invertebrates are grossly underestimated in their biodiversity, with sibling species being discovered at an increasing rate (Kohn 1997).

Meanwhile, species continue to disappear at alarming rates (e.g., Medlin 1998); our methods and abilities to enumerate them are cumbersome and ''presently impractical'' (Williams et al. 1997; Bridgewater 2000); and capabilities to achieve these goals continue to diminish as our taxonomic resources decline (Walker and Farquhar 1998; Possingham 1999; Fauchald 2000). Surrogates and umbrella species have been used to achieve more rapid strategic biodiversity assessments (Vane-Wright et al. 1991; Williams et al. 1997), but often with only limited success (Kerr 1997). The limitation of these 'surrogate' data as accurate biodiversity tools is illustrated by the debate over the relative importance of endemism vs. species richness data in identifying 'hotspots', where patterns of endemism and richness are often not the same (Kerr 1997 and references therein). Consequently, species-based approaches are still fundamental despite their acknowledged shortcomings of not being inclusive of all levels of biodiversity (Ormond et al. 1997; Maddock and Du Plessis 1999). This leaves us with the challenge to develop authentic quantitative datasets based on real measures of diversity from 'unweighted species richness data' (Williams et al. 1994).

Here we provide a comprehensive analysis of 2324 species of sponges from 1343 investigated localities throughout tropical and warm temperate Australian waters. These analyses are based exclusively on museum taxonomic collections (i.e., authenticated by voucher specimens). It ignores the published literature completely as many of the early species records for tropical Australia still contain unresolved taxonomic problems, requiring substantial resources to reconcile many nominal taxa with living populations (Hooper and Wiedenmayer 1994). Ignoring this literature also allows us to apply equal treatment to collecting localities, not biased by historical data and collection effort. We also use higher level (genus) classifications to test species level assessments, and we examine biodiversity assessment at different spatial scales (α, β and γ diversity). We compare the 'relative wealth' (richness, endemism, taxonomic similarities) of Australian faunas using outgroup comparisons with Vanuatu (southwest Pacific), Palau (central western Pacific) and Thailand faunas (Gulf of Thailand and Andaman Sea).

Although the biogeographic literature on sponges is expanding (e.g., van Soest and Hajdu 1997 and references therein) there are still relatively few evaluations of regional relationships or 'hotspots' of endemism and diversity. Several studies have compared small faunas (α and β scales of diversity) based on such data (Hooper 1994; De Voogd et al. 1999; Lehnert and Fischer 1999; Kennedy and Hooper, unpublished data), and a few have provided similar data at larger (γ) scales (van Soest 1993; van Soest and Hajdu 1997; Hooper et al. 1999). Only one has explored sponge diversity at the continental scale (as defined by IMCRA Technical Group 1998) (van Soest 1994), although its conclusions regarding sponge 'hotspots' are equivocal given that it was restricted to a subset of about 400 widely distributed species in 220 genera, disregarding the other 4000–5000 published species. Moreover, Van Soest's (1994) sole intention was to derive a model for biogeographic (marine area) relationships whereas the present study uses a much more substantial and authenticated taxonomic database (i.e., underpinned by voucher specimens) to determine biodiversity 'hotspots' and not a biogeographic model *per se*. Several biogeographic studies have been attempted for the Australian sponge fauna (Hooper and Lévi 1994; Hooper 1996) but their conclusions remain equivocal largely due to our inability to resolve marine area relationships, especially as they pertain to sponges. Other general references to Australian marine biogeography include Bunt 1987; Pearce and Walker 1991; Poore 1995; Veron 1995.

Our primary aim in this work is to ascertain patterns of sponge faunal relationships and biodiversity 'hotspots' using richness, endemism and taxonomic relationships between marine areas, at species and genus levels of diversity, and assessing the effectiveness of our data at different spatial scales. We do not attempt a congruency analysis to test whether similar patterns apply across a range of other phyla, although such an analysis is sorely needed to develop an accurate model of marine centres of maximum diversity and species origins (e.g., Roberts et al. 2000).

Methods

Definitions

In this work 'species diversity' refers to species richness. It does not include a measure of abundance of species populations frequently used to derive a synthetic diversity measure (see Clifford and Stephenson 1975). Similarly, the terms 'species endemism' and 'generic endemism' refer to geographically restricted taxa that were not recorded outside a particular region relative to other regions investigated, at all spatial scales of diversity. It does not necessarily imply a wider phylogenetic interpretation of 'endemism', which for the marine biome, and for sponges in particular, is still highly contentious (Hooper 1994; van Soest 1994; van Soest and Hajdu 1997). The concept of 'hotspots' refers to areas of maximum richness, endemism and not to threatened areas identified as deserving conservation priority (Myers et al. 2000).

Similarly, the terms α, β and γ scales of diversity (Gray 1997) correspond to 'local', 'regional' and 'provincial' scales of diversity, respectively (Hooper et al. 1999). This latter terminology is abandoned because it potentially confuses biodiversity analyses with biogeographic datasets. α Diversity refers to within-habitat diversity, where species are presumed to interact and compete for similar limiting resources; β diversity refers to between habitat diversity, where community boundaries are crossed, and sampling covers more than one habitat or community; and γ diversity refers to landscape diversity, where evolutionary processes become increasingly important (Gray 1997). This terminology is consistent with the IMCRA Technical Group (1998) classification that includes ecological patterns that occur at site (α), local (β), regional (γ) and continental scales (this entire study).

Sponge collections

Analyses were based on sponge collections from 1343 localities throughout tropical and subtropical Australian waters, from the Houtman–Abrolhos in the west (29° S, SE Indian Ocean) across the north of the continent to the Sydney region in the east (34° S, SW Pacific Ocean), with the Vanuatu (14–18° S), Palau (7–8° N) and Thailand faunas (8–13° N) included as comparative outgroups (Figures 1 and 2, Table 1). Localities were selected to include only those areas where ‘complete’ faunal inventories were undertaken by the authors during the past 15 years, as opposed to surveys that only selectively collected species for ‘interesting purposes’ (such as bioprospecting samples >1 kg wet weight for pharmaceutical testing, samples targeted specifically for molecular analysis, surveys of dominant (larger) life forms, etc.). This strategy, unfortunately, excluded several highly diverse faunas that we have investigated over the past decade (especially the Philippines, Papua New Guinea, Indonesia) for which there are still no comprehensive sponge biodiversity inventories. To include these limited datasets, lying as they do at the centre of marine diversity (e.g. Veron 1995), would have biased analyses unacceptably, such as species richness vs. collection effort.

Specimens were collected using SCUBA and surface supplied breathing apparatus (SSBA) diving, benthic trawls and by hand. They concern the predominantly shallow faunas at 0–70 m depth. All specimens used in analyses were photographed alive, identified, registered, databased and are housed in the collections of the Queensland Museum (Brisbane) (QM) and the Northern Territory Museum (Darwin) (NTM). Identifications of all species were made to the lowest possible taxonomic level, although most species (>70%) could not be assigned to a known taxon given that most southern hemisphere sponge faunas remain largely undescribed (Hooper and Wiedenmayer 1994; Hooper et al. 2000). Conspecificity or uniqueness (‘apparent endemism’) of species from all areas was determined from the QM species knowledge base containing comprehensive descriptions and illustrations of the pertinent morphological, histological, skeletal and living characteristics of every specimen collected, assigning each morphospecies to a unique (albeit predominantly still unnamed) taxon, in addition to containing relevant locality and habitat data. This knowledge base now contains ca. 4000 morphospecies, although only 2324 species are included in the present study for reasons mentioned previously.

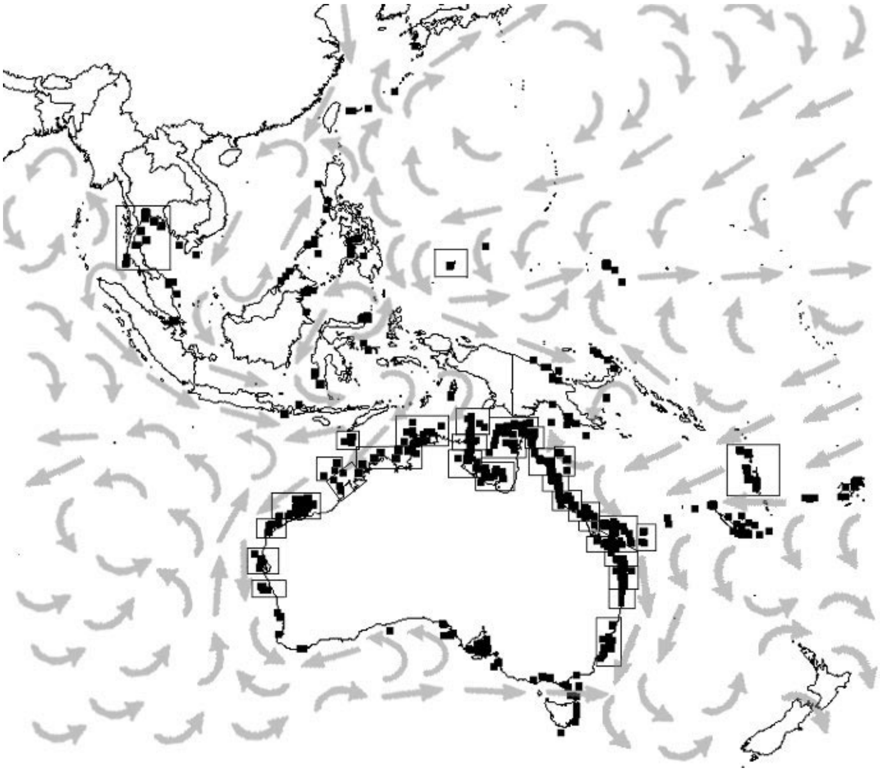

Figure 1. Individual collection sites generated from QM and NTM collection database records (solid squares). Sites included in this study are grouped together into faunas at the β scale of diversity (boxes), with groupings determined by computer similarity analysis of taxonomic affinities between faunas. Summer sea surface currents are also indicated (arrows), with current data redrawn from the National Geographic Society (2000) based on United States Hydrographic Office (1947).

Numerical analyses

Museum databases were initially interrogated for each of the 1343 investigated localities to compile α scale faunal inventories. Small (α) scale marine areas were defined by discrete clusters of collecting stations more-or-less contiguous with each other. Faunas within these α scale regions were determined by interrogating the computer database using quadrants of 5 min intervals of latitude and longitude. Faunal assemblages at larger β and γ scales of diversity were subsequently defined by numerical similarity analysis of species composition between all α scale faunal inventories, and not by arbitrary assumptions such as prior knowledge of regional geography, geomorphology or unique species diversity. The limits or extent of these β and γ scale faunas are therefore related to the extent of species distributions themselves, and not to any *a priori* assumption based on arbitrary grid quadrants.

Species richness (number of species) and ‘apparent endemism’ (number of unique

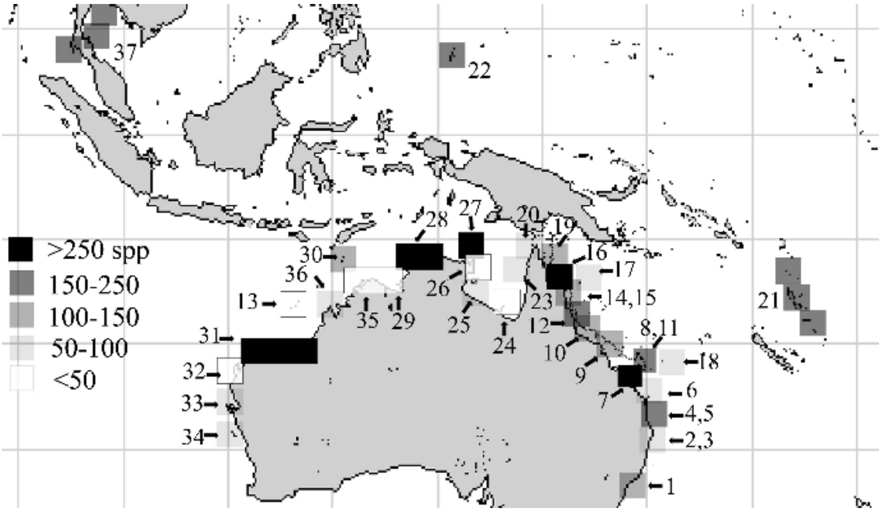

Figure 2. Species richness of sponge faunas at the β scale of diversity (regions determined by computer similarity analysis of taxonomic affinities between the 1343 individual collection sites). Refer to Table 1 for key to faunas.

species) were calculated by cross-tabulating presence/absence of species in each fauna (at all spatial scales). These similarity analyses produced 37 faunal regions at the β scale (Queensland Museum database), and subsequently 13 faunal regions at the γ scale of diversity (see below). We use the term 'apparent endemism' because many sponge faunas in the Indo-west Pacific remain largely unexplored, or their faunas virtually unpublished, or their published species records are so antiquated as to be practically useless for identifying living faunas (Hooper and Wiedenmayer 1994). Absolute levels of endemism for some or all of these areas may eventually fall or rise as their faunas become better known. This initial analysis produced information on species richness and species endemism, and these data were used to define the boundaries of faunas themselves at larger β and γ scales of diversity (Figure 2, Table 1).

Affinities between faunas were calculated using the Jaccard index of dissimilarity. This index was selected over the many other available coefficients of similarity as it neglects conjoint absences (0–0 matches), and is most suited to heterogeneous localities that possess a few species common to each, with the remainder restricted to few localities (Clifford and Stephenson 1975). This index is most appropriate to sponge data given the relatively high heterogeneity in species composition, even between closely adjacent localities, at small and medium scales (Hooper 1994; Hooper et al. 1999; Kennedy and Hooper, unpublished data). The Jaccard dissimilarity algorithm is a ratio of the number of co-occurrences divided by the total number of occurrences at either locality (i.e., $a/(a+b+c)$, where a = the number of species at both localities (positive–positive matches), b = the number of species at one locality (positive–negative matches), and c = the number of species at the other

Table 1. List of regional sponge faunas at β and γ scales of diversity.

Region (β scale)	Region (γ scale)	Region name	Latitude range	Longitude range	No. of localities sampled	No. of species	No. of endemic species	Endemic species (%)	No. of genera	No. of endemic genera	Endemic genera (%)
1	1	Sydney, Illawarra, Newcastle regions	33°00′–35°00′ S	150°00′–154°00′ E	42	134	95	71	66	4	6
2	2	Northern NSW–Byron Bay	28°05′–29°00′ S	153°30′–154°30′ E	9	55	9	16	33	1	3
3	2	Gold Coast–Tweed River	27°50′–28°05′ S	153°00′–154°30′ E	3	35	14	40	22	0	0
4	2	Moreton Bay, Stradbroke, Moreton Is	26°50′–27°50′ S	153°00′–154°00′ E	58	170	56	33	78	3	4
5	2	Sunshine Coast (Noosa–Mooloolaba)	26°00′–26°50′ S	153°00′–154°00′ E	22	226	71	33	92	1	1
6	2	Hervey Bay	24°30′–26°00′ S	152°00′–154°00′ E	12	52	8	15	39	1	3
7	4	Capricorn-Bunker Group	23°00′–24°30′ S	151°30′–153°00′ E	67	315	123	39	118	5	4
8	4	Swain Reefs	21°30′–23°00′ S	151°00′–153°00′ E	21	198	28	14	93	1	1
9	5	Northumberland Group	21°30′–22°20′ S	149°00′–151°00′ E	1	36	7	19	29	0	0
10	3	Whitsunday Group	20°00′–21°00′ S	148°00′–149°30′ E	22	126	26	21	69	0	0
11	4	Pompey Group	20°30′–21°30′ S	149°50′–151°50′ E	12	167	32	19	77	0	0
12	4	Townsville region (Orpheus, Palm, Slashers, Myrmedon, Broadhurst, Hook, Old, Stanley Reefs)	18°00′–20°00′ S	146°00′–150°50′ E	25	173	23	13	77	0	0
13	12	Rowley Shoals	17°00′–18°00′ S	118°45′–119°45′ E	23	23	6	26	20	2	10
14	3	Cairns region (Batt, Oyster, Sudbury, Opal Reefs)	16°30′–18°00′ S	145°30′–147°00′ E	47	117	29	25	65	3	5
15	3	Low Isles	16°00′–16°30′ S	145°20′–146°30′ E	27	108	29	27	62	1	2
16	4	Lizard, Direction Is, Ribbon, NoName, Yonge Rfs	14°00′–16°00′ S	144°30′–146°00′ E	102	272	82	30	104	1	1
17	7	Osprey, Bougainville Reefs	13°30′–16°00′ S	146°30′–147°30′ E	16	85	33	39	51	0	0
18	4	Wreck, Cato, Saumarez Reefs	20°00′–23°00′ S	153°00′–157°00′ E	15	94	28	30	62	1	2
19	3	Far Northern GBR reefs (Cockburn, Flinders, Howick Reefs, Turtle Group, Shelburne Bay)	11°00′–14°30′ S	142°30′–144°30′ E	58	119	13	11	71	1	1

20	9	Torres Straits	09°30′–11°00′ S	141°30′–143°30′ E	18	62	13	21	41	0	0
21	6	Vanuatu	11°00′–20°00′ S	165°00′–170°00′ E	53	193	112	58	91	5	5
22	8	Palau	05°00′–10°00′ N	132°00′–136°00′ E	24	212	155	73	86	2	2
23	9	East Gulf of Carpentaria	11°00′–15°00′ S	139°00′–142°30′ E	52	93	13	14	56	1	2
24	9	South Gulf of Carpentaria	15°00′–18°00′ S	135°00′–142°00′ E	36	48	12	25	31	0	0
25	9	West Gulf of Carpentaria	13°00′–15°00′ S	135°00′–139°00′ E	37	52	14	27	27	0	0
26	10	Gove region	12°00′–13°00′ S	135°00′–138°00′ E	17	39	0	0	25	0	0
27	10	Wessel Islands	10°45′–12°00′ S	135°00′–137°00′ E	133	315	69	22	116	3	3
28	10	Darwin and Cobourg Peninsula regions	10°45′–13°00′ S	130°00′–135°00′ E	87	274	39	14	111	1	1
29	11	Joseph Bonaparte Gulf	13°00′–15°30′ S	127°00′–130°30′ E	14	19	2	11	17	0	0
30	12	Ashmore, Cartier, Hibernia Reefs	11°00′–13°30′ S	122°00′–124°10′ E	39	125	32	26	77	2	3
31	10	Dampier and Port Hedland regions, Northwest Shelf	18°00′–22°30′ S	115°00′–120°00′ E	168	344	127	37	129	6	5
32	11	Exmouth Gulf	21°00′–23°00′ S	113°00′–115°00′ E	10	20	0	0	16	0	0
33	11	Shark Bay	23°00′–27°00′ S	112°00′–115°00′ E	15	57	18	32	38	3	8
34	11	Houtman Abrolhos	27°00′–29°00′ S	112°00′–115°00′ E	5	73	32	44	49	2	4
35	11	Joseph Bonaparte Archipelago	13°00′–15°30′ S	124°10′–127°00′ E	6	12	4	33	9	0	0
36	10	Broome region	15°25–18°00′ S	121°00′–125°30′ E	6	81	16	20	48	3	6
37	13	Thailand (Gulf and Andaman Sea)	08°00′–13°00′ N	097°00′–103°00′ E	141	196	130	66	73	4	5

Faunas were differentiated by computer similarity analysis of taxonomic affinities, including their location within tropical and subtropical Australia (and Indo-west Pacific outgroups), the number of collections, numbers of species/genera, and numbers and proportions of apparently endemic taxa.

locality (negative–positive matches), thus ignoring negative–negative matches. Taxonomic endemism for both species and genera, richness and collection effort data were compared using logarithmic transformations to compensate for heteroscedasticity, allowing values of Y to be measured more accurately at low than at high values of X (Zar 1999).

Frequency distributions of species at all spatial scales were used to assess the contribution of unique species and genera to biodiversity assessments, whereby the higher the level of endemism (i.e., taxa occurring in only one region) produces a smaller pool of species (i.e., taxa occurring in >1 region) available to assess affinities with other faunas at the same spatial scales, potentially biasing the accuracy of taxonomic relationships between these faunas (see Figure 5).

Classification of taxonomic affinities between sponge communities, as defined by observed similarities in species composition between regions, was firstly investigated using hierarchical cluster analysis, additive-tree cluster analysis and non-metric 2D multidimensional scaling ordination (MDS) based on the Jaccard dissimilarity matrix. These methods were chosen for comparative purposes to describe community groupings over other indices, for reasons described above. Hierarchical cluster analysis was undertaken by group-average linkages using Euclidean distance. All calculations were performed using Systat 9.0 (SPSS 1999).

Finally, hierarchical analyses were based on computer cladistics tools (Paup version 4.0b4a; Swofford 2000) to test faunal relationships at all spatial scales, having the advantage over purely phenetic tools in its capability to test patterns of similarities/faunal affinities against the possibility that chance events might produce similar patterns (bootstrap analysis). Optimality criteria were set to distance and analysed using a heuristic search, a randomly generated seed and 100 bootstrap replicates. Only bootstrap consensus values of $>50\%$ were considered in the resulting analyses, where bootstrap values of $>85\%$ are apparently equivalent to 95% confidence limits (Hillis and Bull 1993), in these cases providing strong support for taxonomic affinities between faunas.

Results

Biodiversity at the species level

Species richness

α Scale biodiversity. Only a single small scale, α diversity fauna, is presented here as an example (Kennedy and Hooper, unpublished data). This example was chosen over the other 1343 collecting localities as it represents an important (diverse, highly endemic) but potentially threatened fauna adjacent to a major metropolitan area. This fauna contained 226 species from 10 more-or-less adjacent reefs, with 22 individual collection sites investigated, on the Sunshine Coast, Southeast Qld (Table 1). Mid-shelf reefs had the highest diversity of sponges, diminishing closer to the shore (inner reefs ~2 km from the coast) and further seawards (outer reefs ~15 km from the coast). Adjacent reefs were highly heterogeneous in species composition to each other containing many apparently endemic species, but still broadly differentiated into these two groups of communities. The maximum diversity of any single reef was 83 species (mean of 41 species for all reefs), of which an average of 34% of species were found on only one reef. Moreover, about 60% of species were rare or unique, with the consequence that assessment of taxonomic affinities of sponge faunas between these reefs was based on only 40% of the fauna.

β Scale biodiversity. Throughout tropical and warm temperate Australia, and including the faunas of Vanuatu, Palau and Thailand as outgroup comparisons, 2324 species of sponges from 272 genera were recorded from 1343 separate localities, with similarity analyses recognising 37 faunas at the β scale of diversity (Table 1). Species richness varied considerably between these faunas (Figure 2), containing both relatively depauperate faunas (e.g., Joseph Bonaparte Archipelago (region 35), Joseph Bonaparte Gulf (region 29), Rowley Shoals (region 13) and Exmouth Gulf, WA (region 32)), and exceptionally rich faunas. Five of these regions contained faunas consisting of >250 spp (Figure 2) (Dampier–Port Hedland regions, WA (region 31), Capricorn–Bunker Group, GBR (region 7), Lizard Island region, GBR (region 16), Wessel Island and Darwin regions, NT (regions 27–28)), with a mean of 127 species per region. In some cases species richness data were clearly biased by collection effort (Table 1), whereas regression analysis of these data (i.e., number of sites collected vs. species richness in each region) showed a moderately strong positive relationship ($R^2 = 0.62$; Figure 3), suggesting that other environmental variables are involved in addition to collection effort.

γ Scale biodiversity. β Scale diversity faunas were amalgamated into 13 faunas at the γ scale of diversity based on similarity analysis of species richness data, with an average 263 species for each of the 13 regions. These analyses showed that there were three biodiversity 'hotspots', each containing >600 species: (1) mid- and outer-reefs of the GBR, including the Marion Plateau and oceanic reefs; (2) the 'Top End', NT (Wessel Islands to Port Darwin); and (3) the Northwest Shelf of WA and adjacent coastal reefs such as the Dampier Archipelago and Monte Bello Islands (Figure 4).

Frequency distributions of species (Figure 5) showed that a high proportion of sponge faunas, at all spatial scales, consisted of species apparently endemic to a single region. At the α scale, with a pool of 226 species, 60% were apparently endemic to only a single locality, and thus only 78 species (40%) were available to assess taxonomic relationships between adjacent localities (Kennedy and Hooper, unpublished data). Similarly, at the β scale, with a pool of 2324 species, 64% were apparently endemic, leaving 829 species (36%) available for inter-regional comparisons. In contrast, at the γ scale significantly higher levels of apparent species endemism (74%) were found, of which only 588 species (26%) provided informative data on marine area relationships. These data indicate that faunas at the β scale of diversity are more effective (i.e., contain the most information) of all scales of biodiversity to analyse faunal affinities based on species composition (see below).

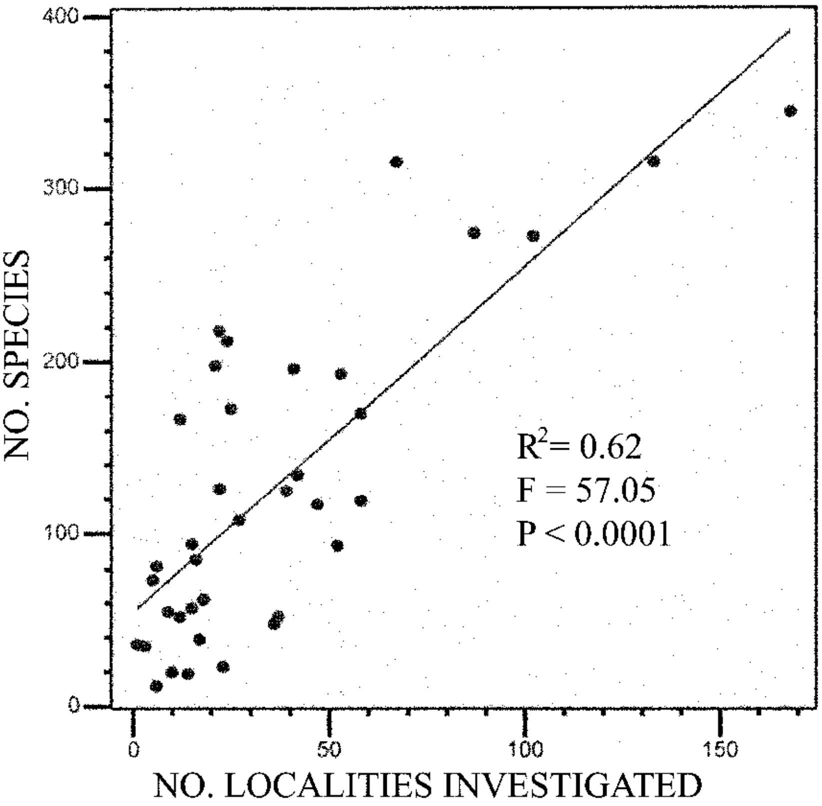

Figure 3. Analysis of collection effort for sponge faunas at the β scale of diversity (regression of species richness vs. number of localities investigated per region).

Species endemism

Similarly, levels of apparent endemism varied considerably between faunas at the β scale, ranging from zero (Gove, NT, and Exmouth Gulf, WA, without any apparent endemic species relative to other regions) to 155 species (Palau, with 73% of species apparently endemic to this region) (Table 1), and with an average of 27% apparent endemic species for all 37 regions. In this context 'endemism' refers to unique species contained within particular regions that were not found in any of the other regions investigated. This figure was higher (47% species apparently endemic) for the 13 amalgamated faunas at the γ scale of diversity, with a range of 19–73%.

In general there was also a strong positive correlation between species richness and species endemism ($R^2 = 0.62$; $P < 0.0001$) (Figure 6), such that regions with high species richness (>100 spp) tended also to contain a large number of geographically restricted taxa, although once again this richness–endemism relationship was geographically variable and likely influenced significantly by distance between nearest-neighbour regions.

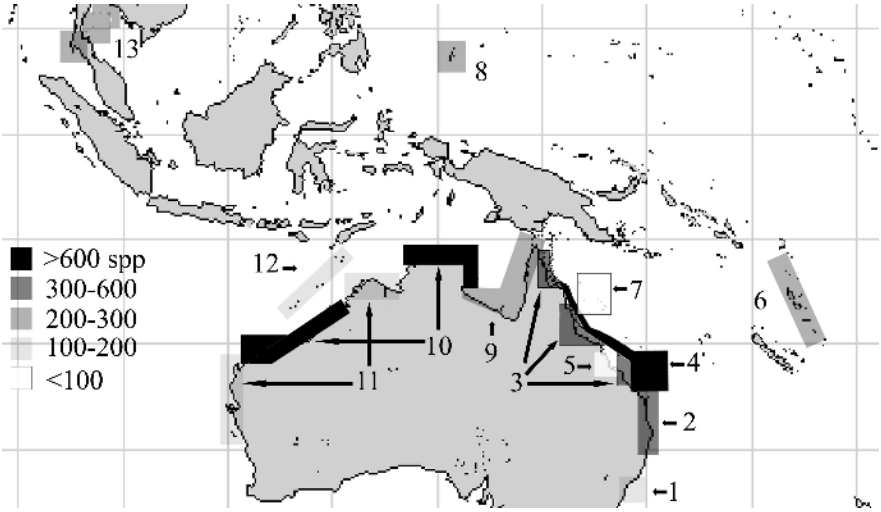

Figure 4. Species richness of sponge faunas at the γ scale of diversity (regions determined by computer similarity analysis of taxonomic affinities between the 37 faunas at the β scale). Refer to Table 2 for key to faunas.

Faunal affinities

Two complementary methods were used to test faunal affinities: (1) cluster analyses (additive and cluster trees analyses and distance matrix classification), and (2) MDS ordination. Cluster analyses (not shown), and distance matrix classification (Figure 7) broadly grouped species into four major faunas at the β scale of diversity, although distance matrix classification did not have high bootstrap support for these groups (52–63%), possibly reflecting high levels of heterogeneity existing between adjacent faunas. These major faunas consisted of: Group 1: the inner continental reefs, islands, embayments and coastal communities of WA and NT; Group 2: the carbonate platform reefs of both western and eastern tropical Australia; Group 3: the southern Qld and northern NSW coastal reefs and embayments; and Group 4: the non-reefal fauna of the Sydney–Newcastle–Illawarra region, southern NSW. The outgroups of Thailand, Palau and Vanuatu were more similar in their species assemblages to the carbonate platform faunas than to any other regions.

MDS ordination analysis produced a similar pattern (Figure 8; stress of configuration = 0.2108), but one that appears to be influenced equally by both environmental factors and genetic connectivity. Group A: western and southwestern WA (largely sandy terrigenous substrates, temperate high latitude reefs, and turbid environments); Group B: northwestern WA, northern NT and northeastern Gulf of Carpentaria and Torres Strait, Qld (tropical, largely terrigenous sediments, sand, mud or muddy sand, and including highly turbid reefs); Group C: carbonate platforms in northeast Qld and the Coral Sea (tropical reefs, clear water, high energy environments); Group D: mid- and southeastern Australia, Qld and NSW (high latitude reefs, terrigenous sediments, and including non-reefal localities); and Group E: the

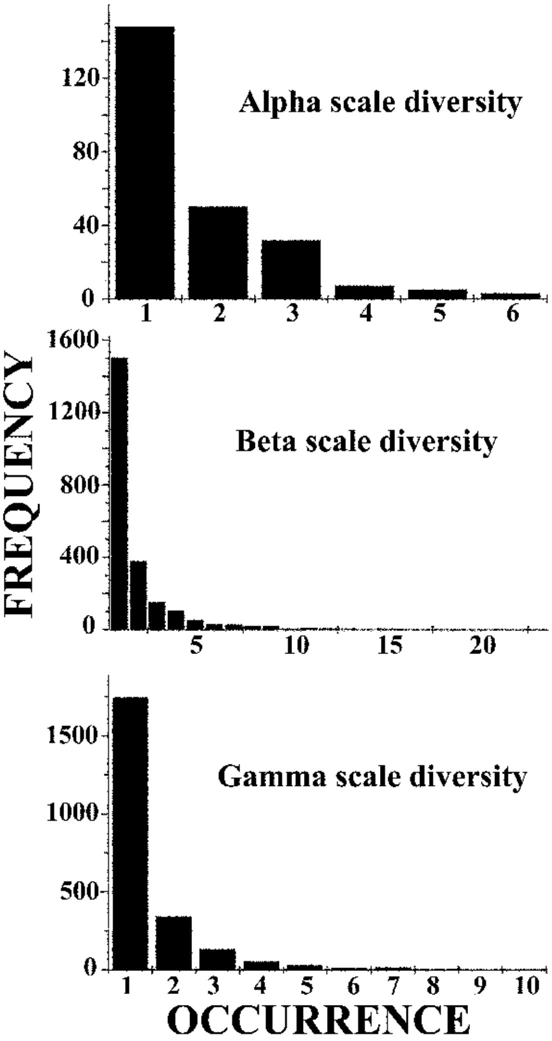

Figure 5. Frequency distribution of sponge species at α, β and γ scales of diversity, showing frequency of occurrence (number of species) in one or more localities. α Scale = 226 spp (Kennedy and Hooper, unpublished data); β and γ scales = 2324 spp.

Sahul Shelf carbonate platform reefs, intermediate between groups A and C (possibly reflecting the equal influence of geographic position (connectivity) and environmental factors).

Results of cluster analyses (Figure 7) and MDS ordination (Figure 8) considered together confirmed four major groups of faunas. (1) Cluster group 1 (Figure 7), including MDS groups A and B (Figure 8). Within the WA, NT and Gulf of Carpentaria group three distinct subgroups were delineated (with moderate bootstrap support of 63–74%). Their differentiation appears to correspond to environ-

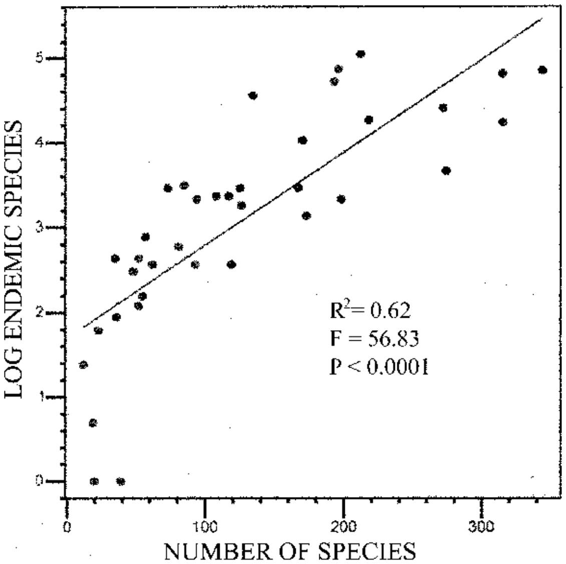

Figure 6. Regression analysis comparing (log) number of endemic species and species richness for 37 faunas at the β scale of diversity.

mental factors: (1.1) inshore highly turbid sandy or muddy sand communities with very large tidal regimes (Broome, Dampier, Port Hedland, Darwin, Wessel Islands, Gove; supported by high bootstrap values of 84–100%); (1.2) highly turbid muddy or muddy sand substrata (Torres Strait, and the three Gulf of Carpentaria regions; with bootstrap support of 71–86%); and (1.3) inshore southwestern and northwestern community living on a range of substrata (terrigenous sand to muddy substrata), in moderate to high tidal regimes, and consequently with only low bootstrap support of 56% to support their alleged affinities (Joseph Bonaparte Gulf and Archipelago, Exmouth Gulf, Shark Bay and Houtman Abrolhos).

(2) Cluster group 2 (Figure 7), including MDS groups C and E (Figure 8). The Australian carbonate platforms are clustered into a single major group, with subsequent differentiation into eastern Indian Ocean and western Pacific faunas. Four distinct subgroup assemblages are apparent, where affinities between these faunas appear to correspond to their geographic proximity more than to any obvious physical differences between them. (2.1) Sahul Shelf reefs (Rowley Shoals, Ashmore, Cartier and Hibernia Reefs) are emergent reefs subjected to high tidal regimes lying on the edge of the continental shelf, the most northerly being about 100 km from Roti, Indonesia. The low bootstrap support (58%) uniting this group probably reflects the considerable heterogeneity between faunas of each of these reefs, as previously reported by Hooper (1994), irrespective of the relatively close proximity of some reefs (<20 km apart). These northwestern shelf reef faunas are also more similar to the Gulf of Thailand–Andaman Sea sponge faunas than to some other regions within Australia (Figure 7). (2.2) The Queensland Plateau carbonate

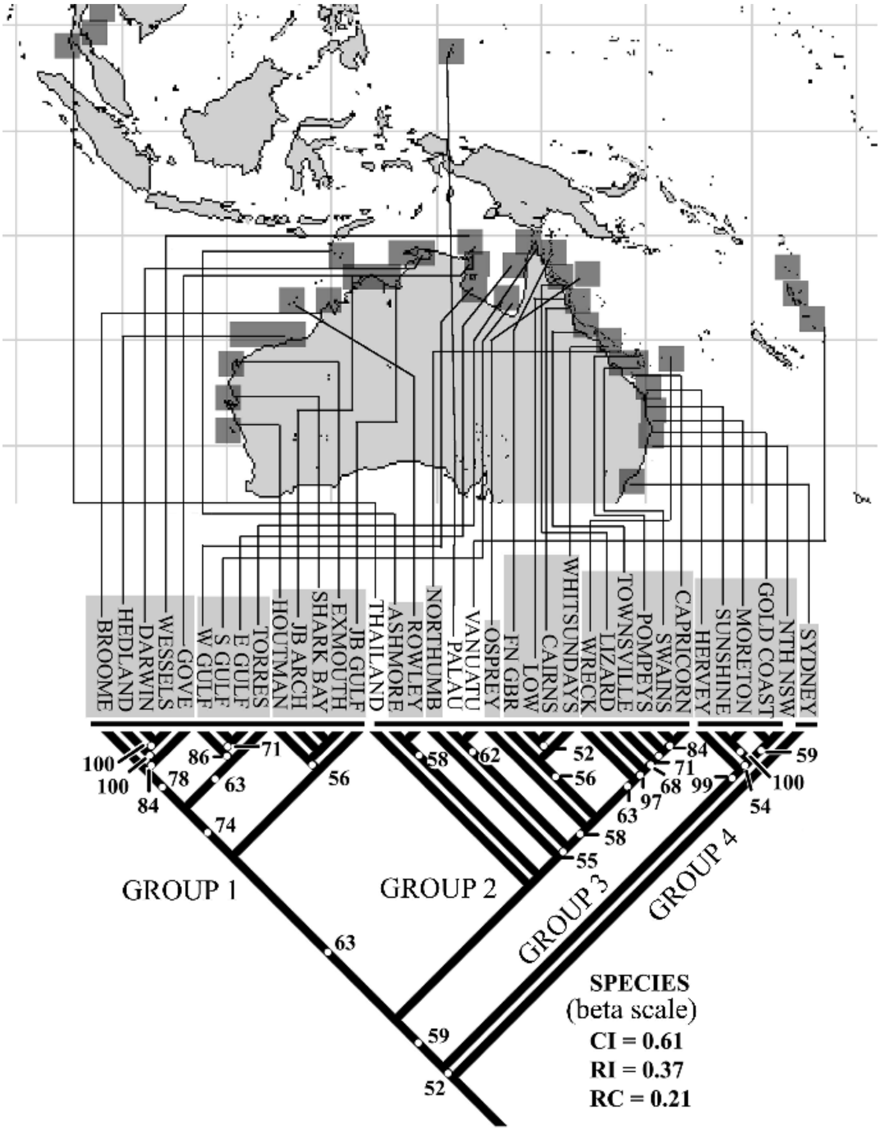

Figure 7. Hierarchic classification of taxonomic affinities between sponge faunas at the β scale of diversity, based on species composition using similarity distance matrix (Paup version 4.0b4a; Swofford 2000). Bootstrap values (Hillis and Bull 1993) of >85% are apparently equivalent to 95% confidence limits. Only consensus values of >50% were considered. Key to abbreviations and symbols: CI – consistency index; RI – retention index; RC – rescaled retention index (Swofford 2000); FN – far northern; horizontal bars over crown groups represent major clusters, groups 1–4.

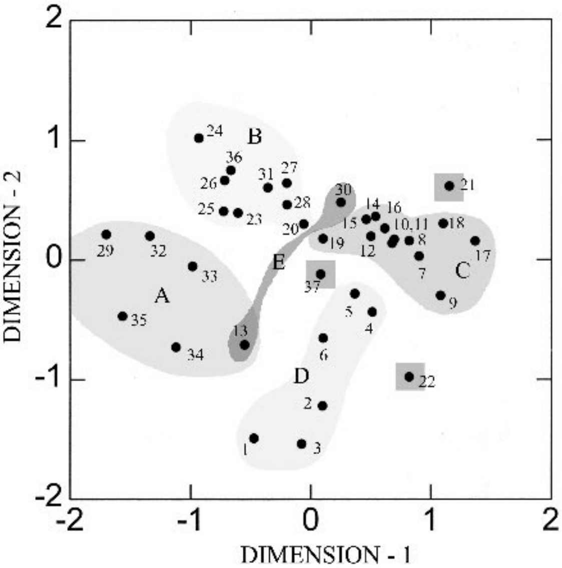

Figure 8. Non-metric 2D MDS based on the Jaccard dissimilarity matrix analysing affinities between species in the 37 faunas at the β scale of diversity. Refer to Table 1 for key to faunas. Key to highlighted clusters: A – western and southwestern WA; B – northwestern WA, northern NT, northeastern Gulf of Carpentaria and Torres Strait Qld; C – northeast Qld and the Coral Sea carbonate platforms; D – mid- and southeastern Australia (Qld and NSW); E – Sahul Shelf carbonate platform reefs off the northwestern coast of WA.

platform fauna (Osprey and Bougainville Reefs; united by only 58% bootstrap support) is also more closely related to the remote Vanuatu/Palauan faunas than to any other Australian regions (although again with only 55% bootstrap support). The Great Barrier Reef appears to be divided into two faunas (supported by 58% bootstrap): (2.3) inner reefs (Whitsunday Is, Cairns region reefs of Batt, Oyster, Sudbury and Opal Reefs, the Low Isles, inner far-northern reefs including Cockburn, Flinders, Howick and Turtle Island groups, and embayments such as Shelburne Bay; but also with low bootstrap support of 52–56%), and (2.4) mid- and outer-Great Barrier Reefs (GBR) (Lizard, Direction Islands, Ribbon, Noname, Yonge Reefs, mid- and outer-reefs of the Townsville region such as Palm Is, Slashers, Broadhurst, Hook, Old, Stanley, Myrmedon Reefs, southern outer reefs of the Pompey and Swains groups, and Capricorn-Bunker Group) and more southern oceanic reefs of Wreck and Cato, and Saumerez Reefs on the Marion Plateau (with more substantial bootstrap support of 68–97% uniting these faunas). This latter high bootstrap support may be indicative of greater relative homogeneity between these individual reef faunas, as compared to other regions at least. The Northumberland Group (off Mackay, Qld) is anomalous and disregarded from these analyses since only a single locality was sampled (yet contained about 20% of apparently endemic species).

(3) Cluster group 3 (Figure 7), including MDS group D (Figure 8). Within the

southern Qld–NSW fauna three regional subgroups are differentiated. (3.1) Hervey Bay is a unique embayment dominated by mud, sandy mud and seagrass habitats without emergent reef systems, and as such its sponge fauna differs significantly from adjacent coastal reefs and other embayments (with 54% bootstrap support). (3.2) Moreton Bay and Sunshine Coast regions (extending from Noosa to South Stradbroke Island) contain a large embayment with emergent coral reefs, fringing rock and coral reefs as well as soft sediments (100% bootstrap support). (3.3) Gold Coast to Byron Bay (59% bootstrap support).

(4) Cluster group 4 (Figure 7), including MDS analysis (isolated point 1, Figure 8). The Sydney–Newcastle–Illawarra region differs substantially from the others at the base of the cluster (although with only 52% bootstrap support to support these differences) and probably warrants recognition as its own province relative to others recognised here.

Sponge faunas of the more southern reefs in the Coral Sea – Saumarez Reef (Marion Plateau) and the isolated oceanic Wreck and Cato Reefs – are more closely related to the mid- and outer-GBR faunas than they are to reefs on the more northerly Queensland Plateau (Osprey and Bougainville Reefs, with bootstrap support of 63%), probably reflecting their closer proximity to the GBR reefs than to the Queensland Plateau (Figure 6). Analyses of γ scale diversity – in which the 37 β scale faunas were amalgamated into 13 γ scale faunas based on taxonomic affinities (Figure 9), and MDS analysis of these data (Figure 10) – demonstrated stronger affinities between the Vanuatu and Queensland Plateau, and the Thailand and Sahul Shelf faunas, respectively (Figure 10, stress of configuration = 0.1589), than with more closely adjacent regions.

Biodiversity at the genus level

Genus richness

Biodiversity of sponge genera, at both β and γ scales of diversity, does not differ substantially from species data. ‘Hotspots’ of genus richness at the β scale (compare Figures 11 and 12 with Figures 2 and 4, respectively) are found at the Capricorn-Bunker Group (118 genera), Lizard and Direction Islands (104), Wessel Islands (116), Darwin and Cobourg Peninsula (111) and Dampier–Port Hedland regions (129) (Figure 11). At the γ scale of diversity two faunas are richest in their genus diversity: mid- and outer-GBR (154 genera), the ‘Top End’, NT, and the mid-northwest coast of WA (168) – the latter defined as a single faunistic region based on genus richness (Table 2).

Genus endemism

At the β scale the highest levels of apparently endemic genera (i.e., genera found in only one of the regions surveyed, but not necessarily endemic to Australia or other localities in the Indo-west Pacific) occur in the Dampier–Port Hedland regions (WA) (6 genera), Capricorn-Bunker Group (GBR) and Vanuatu (5), Sydney (NSW) and Thailand (4), and Moreton Bay, Cairns region (Qld), Wessel Islands (NT), Shark Bay and Broome (WA) (3) (Table 1), with an average of 2.4% apparently endemic

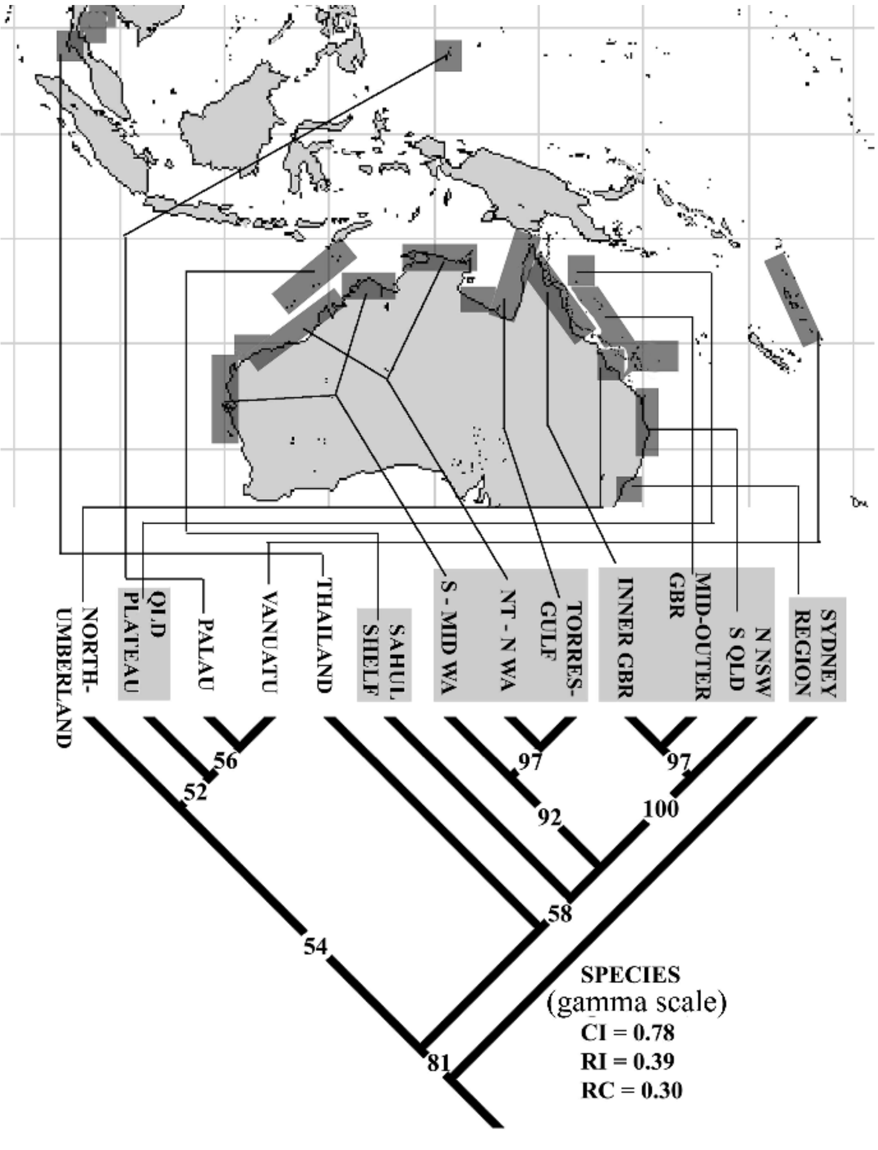

Figure 9. Hierarchic classification of taxonomic affinities between sponge faunas at the γ scale of diversity, based on species composition. Refer to Figure 7 for explanation. Shaded provinces refer to in-groups; unshaded provinces refer to outgroup faunas (except Northumberland Islands fauna which is discarded from analyses due to low collection effort; refer to text).

genera per region. At the γ scale most regions contain at least a few endemic genera, with the Top End having the highest number (23 apparently endemic genera); the mid- to outer-GBR has 10, and northern NSW and southern Qld has 8 (Table 2), with an average of 4.6% apparent endemism.

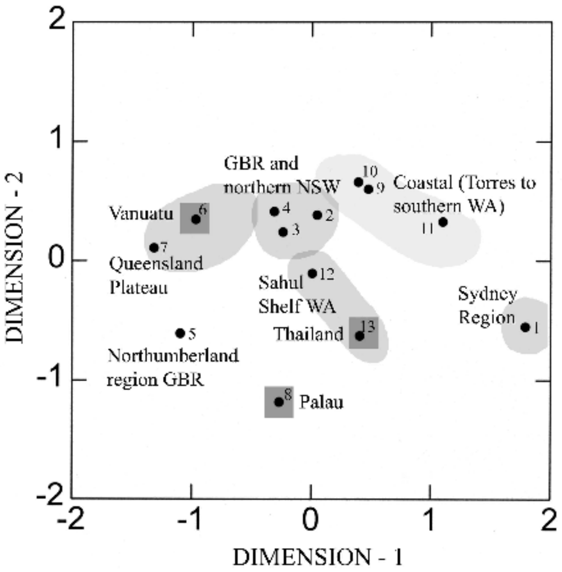

Figure 10. MDS ordination of affinities in species composition between faunas at the γ scale of diversity. Refer to Table 1 for key to faunas.

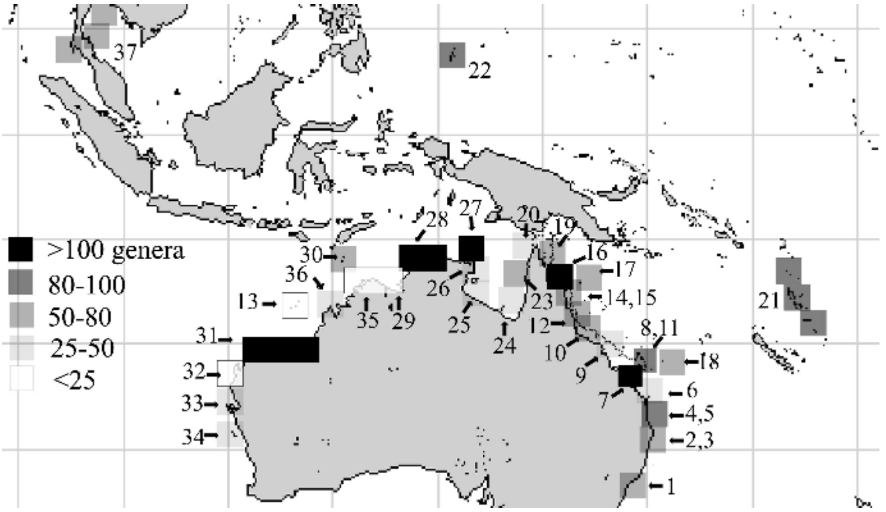

Figure 11. Genus richness for sponge faunas at the β scale of diversity. Refer to Figure 2 for explanation.

Faunal affinities

Patterns of genus-level similarity at the β scale were not well resolved using any of the analytical tools (additive trees, cluster trees (not shown), or distance matrix classifications; Figure 13), with several unresolved polychotomies not supported by

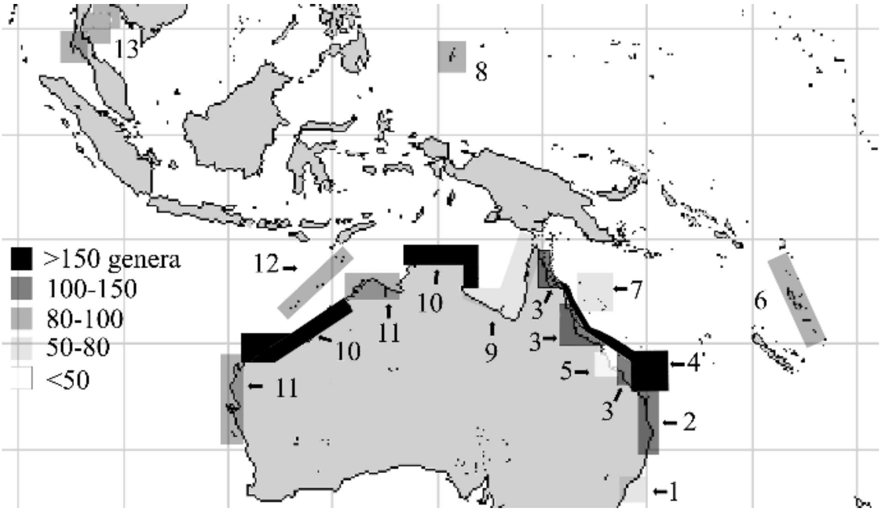

Figure 12. Genus richness for sponge faunas at the γ scale of diversity. Refer to Figure 4 for explanation.

bootstrapping (i.e., <50% bootstrap support). Furthermore, only one branch of the tree – viz. the eastern Australian carbonate platform reefs, with coral reef associated genera extending from the Sunshine coast (southern Qld) northwards, and including most of the GBR (Figure 13, group 2) – corresponds in general to species-level data (compare with Figure 7, group 2). Even this group, however, is not well resolved, containing a discrete cluster of regions including the outgroups of Palau and Thailand, and several west coast regions.

Further comparison between genus- and species-level data (Figures 13 and 7) reveals several marked differences in their inferred marine area relationships, although interpretation of the tree based on generic affinities must be done cautiously given its partially unresolved polychotomies (bootstrapping >50%). In particular, the Moreton Bay region, southern Qld, is most similar to other Queensland localities based on species-level data (Figure 7, group 3), but very different from all other regions based on genus-level data (Figure 13, ungrouped). This particular difference may be due to the presence of several species-rich genera unique to the Moreton Bay region, such as many species of Microcionidae and Raspailiidae already known to be endemic to this region (Hooper 1991, 1996), as well as many other species so far undescribed (Queensland Museum database). The Moreton Bay region also has a greater diversity of habitats than either northern (GBR) or southern (temperate) regions, and contains both tropical species at their southern-most limits and temperate species at their northern-most limits of distribution. This region, therefore, has an increased potential for hybridisation between these faunas (Davies 1994; Veron 1995), thus increasing the potential for species-level but not genus-level diversity.

Table 2. List of regional sponge faunas at the γ scale of diversity.

Region (γ scale)	Region name	No. of localities sampled	No. of species	No. of endemic species	Endemic species %	No. of genera	No. of endemic genera	Endemic genera %
1	Sydney region	42	134	95	71	66	4	6
2	Northern NSW–southern Qld	104	393	188	48	131	8	6
3	Inner GBR reefs	154	338	103	30	124	5	4
4	Mid-outer GBR and Marion Plateau reefs	242	710	391	55	154	10	6
5	Northumberland Group	1	36	7	19	29	0	0
6	Vanuatu	53	193	112	58	91	5	5
7	Queensland Plateau	16	85	33	39	51	0	0
8	Palau	24	212	155	73	86	2	2
9	Torres Straits–Gulf of Carpentaria	143	183	62	34	76	1	1
10	Top End (NT) and mid-northern WA	411	646	364	56	168	23	14
11	Mid-south and Kimberley coast WA	50	154	62	40	81	5	6
12	Sahul Shelf and Banks	62	139	39	28	81	4	5
13	Thailand	141	196	130	66	73	4	5

Faunas were differentiated by computer similarity analysis, including the number of collections, numbers of species/genera, and number and proportions of apparently endemic taxa.

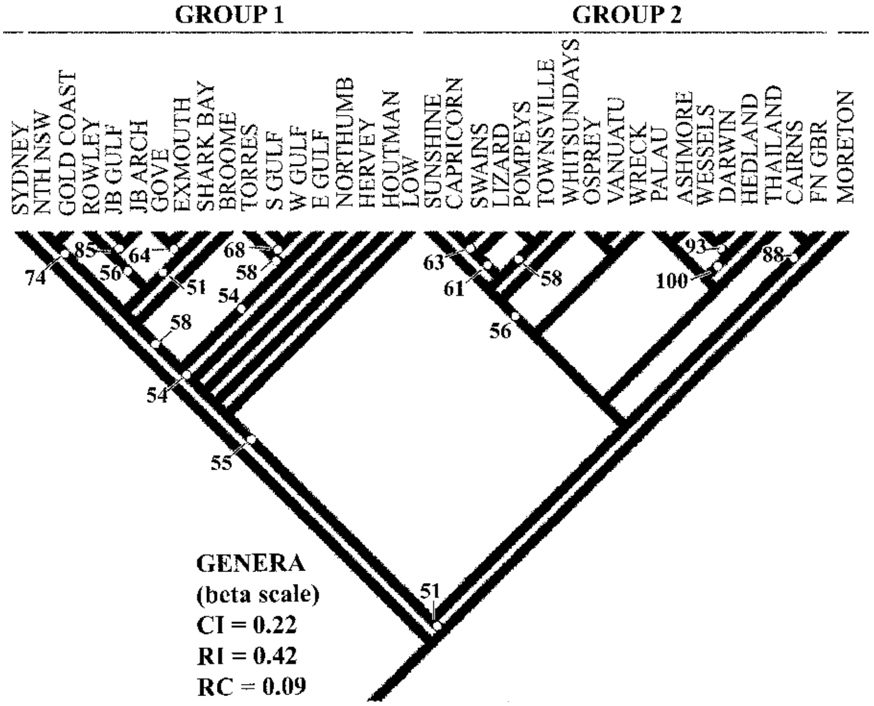

Figure 13. Hierarchic classification of taxonomic affinities between sponge faunas at the β scale of diversity based on genus-level taxonomic composition. Refer to Figure 7 for explanation.

At the γ scale of diversity data are superficially more informative (Figure 14), although again not widely supported by bootstrapping. There are two major faunas containing more similar genera, and two other single-member groups apparently unresolved and without significant bootstrap support. One group contains Australian continental faunas, east, north and west coasts (Figure 14, group 1). The other contains the offshore faunas of the Queensland Plateau, Sahul Shelf and the outgroups of Vanuatu, Thailand and Palau (Figure 14, group 2), discounting the Northumberland region, inner GBR as anomolous (as noted above). The Torres Strait and the Gulf of Carpentaria, Qld, NT (region 9), the Sydney–Newcastle–Illawarra, NSW (region 1), and the mid-south–Kimberley coast region, WA (region 11) are isolated either side of these two main groups (Table 2, Figure 14). This is more clearly demonstrated in the MDS analysis (Figure 15) (stress of configuration = 0.1159).

Thus, there are differences in outcomes based on taxonomic affinities, at both β and γ scales of diversity, depending on whether species or genus data are used in analyses. These patterns contrast to genus richness data, which correspond very closely to species-level data, with a strong correlation at both β ($R^2 = 0.949$, $P < 0.0001$) and γ scales of diversity ($R^2 = 0.901$, $P < 0.0001$) (Figure 16, Table 2).

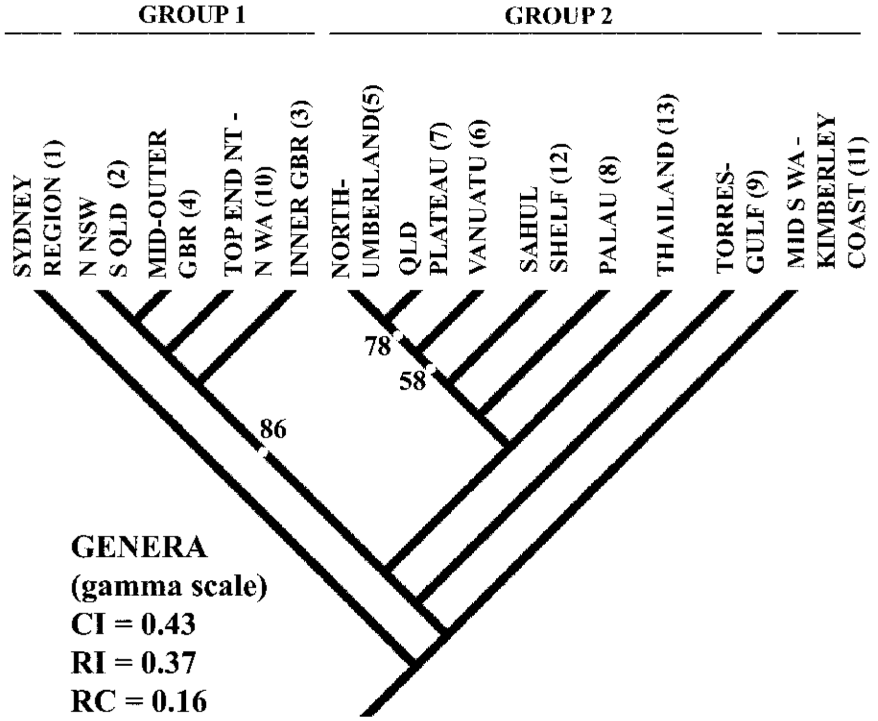

Figure 14. Hierarchic classification of taxonomic affinities between sponge faunas at the γ scale of diversity based on genus-level taxonomic composition. Refer to Figure 7 for key to abbreviations. Numbers correspond to regions defined in Table 1 and Figure 15.

Discussion

Gradients in sponge biodiversity

The high diversity of marine invertebrates in the tropical Indo-Pacific has been attributed to a long history of evolutionary stability, fluctuating isolation and consequent reunification of island and archipelago faunas, producing cycles of allopatric and sympatric speciation (Gray 1997). It has often been assumed that many of these faunas have very broad Indo-Pacific distributions, with fairly uniform or stable rates of speciation and evolutionary change across the broad range of environmental and ecological areas in the Indo-Pacific (Taylor 1997). These general assumptions are partly based on the misconception that the tropical Indo-Pacific contains a universally highly diverse, genetically connected and uniform ecosystem (reviews in Veron 1995; Taylor 1997).

Increasingly, however, genetic evidence supports what has been long suspected but rarely proven (e.g., for sponges, Klautau et al. 1999), that many marine invertebrate faunas are highly heterogeneous in their diversity and species composition (Kohn 1997). This has produced a mosaic of diversity gradients which are

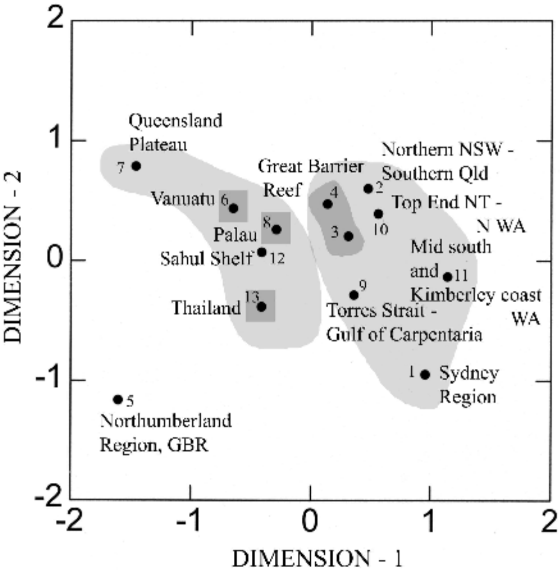

Figure 15. MDS ordination of affinities in genus-level composition between faunas at the γ scale of diversity. Refer to Table 2 for key to faunas.

legacies of large scale (continental scale) historical events, smaller scale (α, β and γ scale) fluctuations in rates of speciation and extinction (Crame and Clarke 1997; Hoeksema 2000; Meyer and Paulay 2000), as well as many local environmental factors such as influences of topographic heterogeneity at all scales (Taylor 1997; Guichard and Bourget 1998). Gradients discussed most frequently include latitude and depth (e.g., pertaining to mollusc faunas, Crame and Clarke 1997; Kohn 1997) and nutrients, light and turbidity (e.g., reef sponge faunas, Wilkinson and Cheshire 1989). However, these are not necessarily the most significant, nor do they operate at all spatial scales. Fluctuations in sea levels during the Pleistocene dramatically influenced connectivity and the evolution of east–west species pairs (e.g., crustaceans, Poore 1995; corals, Veron 1995; cowries, Meyer and Paulay 2000), and other forms of isolation, evolution of species, and proliferation of 'hotspots' that do not generally correspond to marine gradients (e.g., seamount faunas, Richer de Forges et al. 2000).

For marine sponges we found that gradients in diversity, endemism and taxonomic relationships varied across all tropical and warm temperate Australian marine faunas. These patterns, evaluated at small or α scale (Kennedy and Hooper, unpublished data), medium or β scale (Hooper et al. 1999; present study), and larger or γ scales (present study), generally deviated from biodiversity models derived from analyses of other marine taxa.

Morphometric analyses of preserved taxonomic collections indicate that there may be a small but significant proportion of sponge (morpho)species that are truly widely distributed, extending from the Red Sea to Tahiti [with estimates ranging

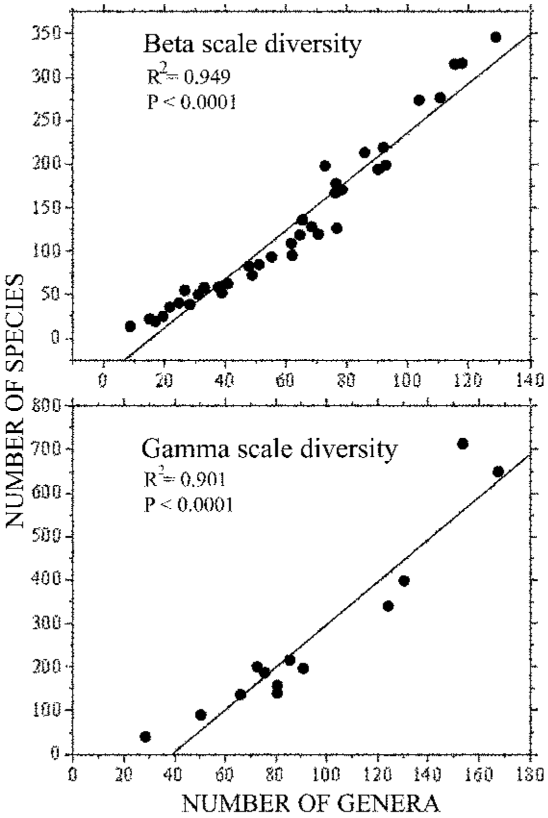

Figure 16. Regression analysis of relationship between species- and genus-level diversity (richness) for 37 β and 13 γ scale sponge faunas.

from 5% (Hooper 1994) to 15% of Indo-Pacific species (Hooper and Lévi 1994)]. The alleged existence of these cosmopolitan morphospecies implies wide connectivity across this vast region. However, conspecificity between these widely dispersed, and often disjunct faunas has rarely been tested using non-morphological data (e.g., allozymes, ITS sequences, etc.). Conversely, there is an increasing body of evidence to show that allopatric populations of sponges consist of complexes of genetically distinct sibling species (e.g., Solé-Cava et al. 1992), as found increasingly for other phyla (e.g., Meyer and Paulay 2000). To date there has been only one such study of a widely distributed Indo-Pacific morphospecies (*Astrosclera willeyana*) (Woerheide 1998), showing (albeit so far inconclusively) that genetic differences between populations correlated with subtle but persistent morphological differences (i.e., a series of regional cryptic sibling species). Sponges appear to be ultraconservative, whereby genetic differences are not always manifested at the morphological level (Klautau et al. 1994), and moreover, the poriferan taxonomic framework is mostly founded on highly variable morphometric data that are open to widely different subjective interpretation (e.g., Klautau et al. 1999). These problems challenge our abilities to define true sponge biodiversity, with estimates likely to vary between the various spatial scales of investigation. Consequently, estimates of sponge biodiversity at larger scales (γ and continental scales) are possibly much higher than reported here.

Scales of biodiversity assessment

At the small (α) scale of diversity cross-shelf patterns in sponge distributions were the only obvious detectable gradient in diversity. From one example presented here mid-shelf reefs contained the richest sponge faunas and also had the greatest number of unique ('apparently endemic') species compared to both the inner and more outer reefs (Kennedy and Hooper, unpublished data). A similar trend was noted for sponge faunas of the Spermonde Archipelago, southwest Sulawesi, Indonesia (De Voogd et al. 1999). However, both these studies examined faunas living on fringing coral reefs that lacked any large lagoon or outer barrier reef system. By comparison, the Wilkinson and Cheshire (1989) cross-shelf study of central GBR sponge faunas found that inner (lagoonal) reefs contained highest species richness, with diversity diminishing seawards.

These comparisons highlight the importance of local environmental factors, particularly specific reef geomorphology, water turbidity, nutrients etc. (review in Veron 1995) for local diversity gradients. These factors have been widely used to explain the distributions of many other marine invertebrates (e.g., review in Taylor 1997). Wilkinson and Cheshire (1989) suggested that differences in the composition and organisation of sponge communities across the GBR shelf reefs were largely due to differential nutrient, turbidity and light regimes. Consequently, inshore waters that have the highest levels of nutrient input may also have the highest primary production via the phytoplankton, such that the bottom community is dominated by suspension feeders (Taylor 1997).

Wilkinson and Cheshire (1989) also noted that outer reefs with oligotrophic conditions are dominated by phototrophic species, whereas mid- and inner-reefs contain more heterotrophic species. These findings, however, were largely derived from studies of the larger, more conspicuous species that Wilkinson and Cheshire (1989) suggest form the reef's major living biomass. Conversely, it is now clear that phototrophic sponges comprise only a small proportion of any Indo-west Pacific coral reef sponge diversity. Moreover, phototrophic species are restricted to the reef flats and shallow waters, whereas there are a myriad of other heterotrophic species living within all reef communities, at all depths, and it is this community that contains the greatest proportion of endemic taxa (Hooper 1994; Hooper et al. 1999; present data). An even far greater diversity of species is found in the smaller, cryptic habitats (e.g., sciaphilous, encrusting, plaque-forming taxa), although this fauna has barely been sampled to date. Consequently, nutrient levels (and related factors) may account for only small-scale gradients in cross-shelf distributions of the larger, highly productive phototrophic sponge communities, whereas other factors (such as local recruitment and connectivity, local geomorphology associated with niche specialisation) have an equal or probably greater importance in biodiversity gradients at the small scale.

At larger (β) scale biodiversity 'hotspots' did not generally correspond to latitudinal gradients (endemism, richness, taxonomic relationships between faunas), whereas biogeographic and environmental influences (especially sediments and tidal regimes) appear to be more prominent. β Scale regions containing the richest species diversity (>250 species) included the extreme southern and northern reef systems of the GBR, the Wessel Islands and the Darwin region (NT), and the diverse sponge faunas on the central western coast, off Dampier and Port Hedland (WA). Many of these regions also contained the highest levels of regional species endemism. At the γ scale of diversity species richness and endemism were highest (>600 species, >50% endemic species) in the mid- to outer-reefs of the GBR, the 'Top End' (NT), and the mid-west coastal faunas (WA). These 'hotspots' were also evident at the genus level, each containing >100 and >150 genera for β and γ diversity, respectively. In this context these data support the contentious use of higher order taxa as 'surrogates' for species-level biodiversity, based on richness and endemism data at least (e.g., Kerr 1997; Maddock and Du Plessis 1999). Conversely, taxonomic affinities (relatedness) amongst faunas at both β and γ scales of diversity produced different patterns, varying according to whether species or genera were used in analyses. Genus-level data consistently underestimated sponge marine area relationships, differentiating only two γ scale faunas (with two unresolved single-member faunas on either side of these groups), versus four based on species-level data. In this respect genus-level data are unsuitable 'surrogates' for species-level biodiversity. On this basis we suggest that species richness and endemism data are only two aspects of biodiversity analysis, and their apparent value as pivotal indicators of biodiversity has been over-emphasised in the literature. We contend that taxonomic relationships (faunal affinities) between adjacent marine areas are equally important in assessing biodiversity 'hotspots', at all spatial scales. In other words, taxa that are shared between marine areas provide more informative data on marine area relationships, more accurately reflecting the processes operating in those areas.

Delineating marine areas within tropical and warm temperate Australia

A consensus of several datasets (species richness, species endemism, numerical similarity analysis of species composition) delineated four major groups of sponge faunas. Within each of these groups several smaller faunas were also apparent, each containing species with greater similarity than to adjacent faunas (refer to Figures 7–10).

(1) The southwestern, western and northwestern inner continental reefs, islands, embayments, shelf faunas and coastal communities of WA, northwestern WA, northern NT, and Gulf of Carpentaria (NT, Qld) faunas. Within this group three distinct faunas were apparent, with their affinities corresponding closely to differences in environmental factors (sediment type, turbidity, tidal regimes).

(2) The carbonate platform reefs of both western and eastern tropical Australia,

with four subgroups differentiated, including two GBR provinces (inner reefs, and mid- and outer-reefs, the latter including the more southern oceanic reefs), Queensland Plateau (Coral Sea) and the Sahul Shelf of WA. The affinities of these subgroup faunas appear to correspond more to their geographic proximity than to any obvious environmental differences between them. The Sahul Shelf fauna was least similar to the other Australian carbonate platform faunas, showing greater affinities to the Thai fauna, and thus supporting the contention that connectivity (recruitment) of western reefs occurs from the Indo-Malay Archipelago (facilitated by the Leeuwin Current) and not from the Coral Sea (via Torres Strait) (Veron 1995).

Similarly, the Queensland Plateau sponge fauna was more similar to Vanuatu than to the adjacent two GBR faunas, undoubtedly related to prevailing westerly ocean currents (Vanney 1991). This conflicts with evidence from corals. Davies (1994) suggested that coral recruitment to the GBR was largely exogenous, with the vital gene pool located on reefs on the Queensland Plateau. Although there is obviously some level of connectivity between sponge faunas on the Queensland Plateau and those on the GBR reefs (as demonstrated by the co-occurrence of many species in each of these faunas), our data suggest that affinities between these regions may not be as substantial as they are for corals. It is highly probable that recruitment patterns for sponges differ substantially from those of corals, and also that these patterns vary between the inner GBR reefs, the mid- and outer-GBR reefs, the Queensland Plateau reefs, and those of Vanuatu. These patterns now have some further empirical support from molecular data on calcarean sponges from each of these regions (Woerheide et al. 2000).

(3,4) Mid-southeastern coastal reefs and embayments (Qld, NSW); and the non-reefal fauna of southeastern Australia (NSW), with four faunal assemblages recognised in this area, correlated partially to the possession of special habitats (e.g., seagrass beds, embayments etc.), but also obviously largely influenced by biogeographic factors. In this group the most southern fauna (the Sydney region) has the highest levels of species apparent endemism (i.e., relative to the other regions studied here) and clearly represents a distinctive provincial fauna in its own right (Hooper et al. 1999).

Significantly, in this area occurs a sharp transition zone between two eastern biogeographic provinces, the tropical (Solanderian) and temperate (Peronian) faunas (Bunt 1987). Sponge faunas changed substantially between Moreton Bay (Qld) and Byron Bay (NSW) (a distance of approximately 110 km) such that tropical species live on the northern sides and in the more shallow parts of reefs whereas temperate species occur on the southern sides and in deeper channels on these reefs (Davie and Hooper 1998). This zone is an area where gradualism plays an important evolutionary role in marine biodiversity (Davies 1994), with the mixing of tropical and temperate faunas historically producing unique taxa, and with many truly endemic species of sponges already described from this region (Hooper 1996) and many more awaiting description (Queensland Museum database). There is no equivalent sharp transition zone on the western coast, where tropical species extend further into higher latitudes via the Leeuwin Current. Consequently, this mid-eastern biogeographic transition zone is a pivotal region for future biodiversity research.

Possible causal mechanisms (and biases in data)

Factors important to sponge biodiversity obviously differ between the various faunas, especially at different spatial scales of assessment. The example presented for α scale diversity found an average of 34% of species apparently endemic to these reefs. By comparison, at the β scale of diversity 37 regional faunas contained an average of 27% of species apparently endemic to only one region, whereas at the γ scale the 13 faunas showed much higher apparent endemism (mean of 47%). This latter figure is undoubtedly a product of averaging the effects of β scale spatial heterogeneity in species composition amongst adjacent faunas over a larger (γ scale) region. This supports earlier contentions (Hooper 1994; Hooper et al. 1999) that Indo-west Pacific individual reefs and reef systems have highly heterogeneous sponge faunas, irrespective of their proximity to each other, and each containing approximately 30% of unique species [with environmental gradients, such as topography, predominant; as also suggested for corals by Veron (1995)]. The implication of these data is that larger-scale preservation zones (at β and γ scales of diversity) are far more effective as conservation strategies because they contain both richer and more endemic taxonomic resources, whereas smaller (e.g., α scale) reserves are unlikely to contain sufficient genetic resources to be truly representative of any particular bioregion.

For various marine taxa there is a growing realisation that modern patterns of biodiversity are products of a substantial historical legacy (Crame and Clarke 1997; Kohn 1997). This is clearly evident for sponge distributions at the γ scale, where biogeographic factors are more obvious in their influence on biodiversity. For example, Sydney (NSW) and Houtman Abrolhos (WA) contain many unique species (71 and 44% apparent endemism, respectively), with faunas possibly of Gondwanan origin, and certainly showing greater differences in their taxonomic relatedness from the tropical (allegedly Tethyan) faunas. However, at this larger scale some physical gradients are also evident, such as significant differences in geomorphology and sediments, circulation patterns and geographic proximity (connectivity). For example, three adjacent faunas at similar latitudes – Gove and the Wessel Islands region (NT) (with terrigenous sandy sediments), the Gulf of Carpentaria and Torres Strait (NT and Qld) (with ‘blue mud’ and muddy sand) and the northern GBR (carbonate platform) – had very little overlap in their species composition, despite their close and contiguous proximity.

At the α scale biodiversity estimates are clearly biased by high species heterogeneity, where the contribution of unique or rare species to biodiversity estimates is considerable (Kennedy and Hooper, unpublished data), such that only about 40% of the fauna contributes information on inter-reef relationships. At the α scale higher levels of endemism reduce the effectiveness and predictive value of presence/absence data to biodiversity indices, whereas these estimates become more accurate and useful at the β and γ scales. At these larger scales rare species are more likely to be contained within investigated faunas, and affinities between these faunas are more likely to be determined by biogeographic factors than by small-scale taxonomic heterogeneity (e.g., local topographic differences). We suggest that medium scale (β diversity) faunas contained the greatest proportion of biological information of all spatial scales because they have a significantly larger pool of species to assess inter-regional taxonomic affinities while also having a similar proportion of unique species (64%) as α scale diversity faunas (60%). In contrast, larger scale (γ) faunas have more unique species (74% apparent endemism) but also contained a smaller pool of shared species to assess marine area relationships.

Biodiversity indicators

Our finding of a strong correlation between endemism and richness, for both species and genera, at α, β and γ scales of diversity, supports similar data from terrestrial sources (e.g., Kerr 1997). The issue of which dataset (endemism vs. richness) contributes most effectively as an index of biodiversity 'hotspots' is still contentious. For a single taxon analysis, as presented here for Porifera, a conservation strategy designed to protect centres of species richness would also include adequate protection for unique (endemic) taxa. This finding, however, does not address the question of whether sponge biodiversity 'hotspots' correspond to those of other taxa (Kerr 1997 and references therein). For the marine biome this information is still clearly contradictory, with different taxa showing different gradients in biodiversity. Development of a consensus model, if at all possible, is vital to the design of effective conservation strategies and marine protected areas that protect/contain truly representative biodiversity. This is contrasted with models based on umbrella taxa, such as large charismatic species, often used inappropriately as surrogates for real species diversity (e.g., Mace et al. 2000) and which produce unsubstantiated estimates and 'hotspots' of marine biodiversity.

Scales of predictability

High variations in taxonomic richness, endemism and community relationships amongst study sites, at all spatial scales, are indicative of a mosaic of sponge biodiversity gradients existing throughout tropical Australia. For sponges, this mosaic appears to be largely influenced by differences in local physical and environmental features (e.g., topography at the α scale, geomorphology, sediment type, nutrients, turbidity and tidal regimes at the β scale), with biogeographic factors increasingly influential at larger (γ and continental scales of diversity). High heterogeneity of sponge faunas significantly reduces the effectiveness of spatial and numerical models to predict biodiversity without substantial *a priori* knowledge of the diversity of habitats contained within small scale study sites. Thus, predictive models are ineffective for sponge faunas at the α scale, where taxonomic heterogeneity enables only major community patterns to be differentiated (e.g., near-shore vs. off-shore faunas). The impact of heterogeneity on these biodiversity models decreases at larger spatial scales, increasing their accuracy and value (although they are perhaps less relevant as practical tools for marine resource management and marine area conservation at these scales).

Acknowledgements

We gratefully acknowledge continued financial support from industry and other sources to undertake fundamental biodiversity studies on this important but still largely neglected phylum of sessile marine invertebrates, in particular, AstraZeneca Australia, ORSTOM Noumea, US National Cancer Institute (Washington), the Coral Reef Research Foundation (Palau and Los Angeles), Australian Biological Resources Study (Environment Australia, Canberra), and CSIRO Marine Research (Cleveland, Brisbane). We also gratefully acknowledge the positive comments of two anonymous reviewers who improved this manuscript.

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