

Ecology of sponges (Porifera) in the Wakatobi region, south-eastern Sulawesi, Indonesia: richness and abundance

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The influence of sedimentation, depth and substratum angle on sponge assemblages in the Wakatobi region, south-eastern Sulawesi, Indonesia was considered. Sponge assemblages were sampled from two reef localities. The first reef (Sampela) was highly impacted by high sedimentation rates with fine sediment particles that settle slowly, while the second (Hoga) experienced only fast settling coarse sediment with lower overall sedimentation rates. Sponge assemblages were sampled (area occupied and numbers) on the reef flat (0 m) and at 5 (reef crest), 10 and 15 m (15 m at Hoga only). Some significant ($P < 0.001$) differences were observed in the area occupied and the number of sponge patches between surface angles and sites. Significantly lower ($t > 4.61$, $df = 9$, $P < 0.001$) sponge numbers, percentage cover and richness were associated with the reef flat at both sites compared with all other depths at each site, with the exception of abundance of sponges on the reef flat at Sampela, which was much greater than at any other depth sampled. Species richness increased with depth at both sites but differences between surface angles were only recorded at Sampela, with higher species richness being found on vertical, inclined and horizontal surfaces respectively. A total of 100 sponge species (total area sampled 52.5 m²) were reported from the two sites, with 58 species found at Sampela and 71 species at Hoga (41% of species shared). Multi-dimensional scaling (MDS) indicated differences in assemblage structure between sites and most depth intervals, but not substratum angles. A number of biological (e.g. competition and predation) and physical (e.g. sedimentation and aerial exposure) factors were considered to control sponge abundance and richness. Unexpectedly a significant ($F_{1,169} = 148.98$, $P < 0.001$) positive linear relationship was found between sponge density and area occupied. In areas of high sponge coverage, the number of patches was also high, possibly due to fragmentation of large sponges produced as a result of predation and physical disturbance. MDS results were also the same whether sponge numbers or percentage cover estimates were used, suggesting that although these different approaches yield different sorts of information, the same assemblage structure can be identified.

INTRODUCTION

If changes in biodiversity are to be monitored in the future then baseline abundance and distribution data for specific localities and assemblages must be collected. Sponges are one group potentially suitable for biodiversity monitoring since not only are they abundant in temperate (Hiscock et al., 1983; Picton, 1990), polar (Dayton et al., 1974) and tropical benthic marine habitats (Rützler, 1970; Alvarez et al., 1990; Diaz et al., 1990), but they also have the ability to significantly influence other benthic community members. This is because they are one of the top spatial competitors (Bell & Barnes, 2003), they filter large quantities of water (Pile et al., 1997) and because some morphologies may influence near-boundary flow regimes (Hiscock, 1983). Finally, sponges may contain a number of potentially useful bioactive compounds (Erickson et al., 1997). Unfortunately, sponges are often ignored within large-scale surveys due to problems associated with the availability of taxonomic expertise, although recent texts are addressing these problems (e.g. Hooper & van Soest, 2002).

The Indian Ocean is considered to have the highest concentration of marine biodiversity (Stehli et al., 1967; Briggs, 1987; Hooper & Lévi, 1994; van Soest, 1994). However, even given the importance of sponges and the expected high biodiversity in the Indian Ocean few studies have quantified sponge richness, with limited taxonomic and ecological information being available compared with other tropical regions such as the Caribbean (but see van Soest 1990; 1994; Hooper & Lévi, 1994). Some earlier descriptions of the sponge fauna of this region are available (e.g. Topsent, 1897; Kieschnick, 1896, 1900; Thiele, 1899, 1903; Hentschel, 1912), but generally little quantitative ecological information is available. Sponge richness has been quantified in the west Indian Ocean where richness is high compared with other temperate, tropical and polar localities for which figures are available (Barnes & Bell, 2002). Although sponge species richness is generally considered to be high in tropical regions (e.g. Bell & Barnes, 2000a), area effects and habitat differences within such studies often prevent direct comparison between localities, regions and on global scales. From those tropical studies which are roughly

comparable (with an area sampled of between 40–50 m² on hard substrata), sponge species richness values range from between 40 and 80 species for coral reefs (Bell & Barnes, 2000a). Also, of the studies completed in tropical habitats few provide baseline survey data suitable for inclusion in biodiversity monitoring programmes or future assessment of assemblage change since only broad qualitative data are available.

Environmental parameters are well known to influence local sponge distributions, more so than biological factors (e.g., Wilkinson & Cheshire, 1989; Alcolado, 1990; Alvarez et al., 1990; Diaz et al., 1990; Schmahl, 1990; Witman & Sebens, 1990). However, within most habitats a suite of biological and physical factors are likely to be responsible for any individual species abundance and distribution pattern, rather than any particular variable. Sedimentation and water flow rates have been considered major factors controlling local sponge populations in temperate regions (Könnecker, 1973; Storr, 1976; Bell & Barnes, 2000a), with less specific small-scale information from tropical regions (Barnes, 1999; Barnes & Bell, 2002). One mechanism allowing sponges to survive in extremes of sedimentation and water flow is through macro and micro morphological adaptation (Palumbi, 1986; Manconi & Pronzato, 1991; Bell et al., 2002) with microhabitat exploitation also playing a significant role. For example, some sponge species in highly sedimented habitats may be found only on vertical cliffs, thus avoiding settling sediment on their surfaces (Bell & Barnes, 2000b,c), some may exhibit arborescent body forms decreasing the amount of settling sediment per unit area (Bell & Barnes, 2002). Substratum angle has rarely been considered when quantifying species distributions and abundance even though it is well known that species exploit microhabitats and that environmental characteristics (e.g. light and sedimentation regimes) can vary considerably between horizontal, inclined, vertical and overhanging surfaces. Tropical coral reef ecosystems are topographically complex with a range of surface angles, crevices and caves often being found in close proximity. These microhabitats will differ in environmental characteristics of which light and sedimentation are particularly important since they control the abundance of corals and macroalgae (Rogers, 1990), important spatial competitors of sponges on coral reefs (Aerts, 1998, 2000). Light is also an important factor in directly influencing the distribution of photophilous sponges (Sarà et al., 1979; Wilkinson, 1987).

A number of approaches exist in the quantification of sponges including numbers of sponges/patches (e.g. Bell & Barnes, 2000a–c), percentage cover (e.g. Alvarez et al., 1990; Corriero et al., 2000) and volume (e.g. Wilkinson 1987). Although a combination of these three methods represent the best approach to quantify sponge abundance, this is not always possible for practical and conservation reasons. Estimation of sponge abundance using numbers of sponges/patches may lead to an underestimation of the contribution of sponges to the community given their spreading nature. However, information on the number of sponges is important since if only an area-occupied approach is used there is no appreciation of the number of distinct sponges (i.e. 50% area occupied may represent 1 or 50 separate sponges). Although sponges may show seasonal fragmentation leading to the production of a

number of clonal patches, this may not always be the case. Since local (scale of metres or cms) sponge patches may be genetically distinct (and even if they are not) and influenced by local, micro-scale environmental characteristics, they should be recognized as being distinct. Percentage cover estimates of sponges are usually made using photographic methods (e.g. Corriero et al., 2000). This method has the potential for missing very small/juvenile sponges and it is also unreliable in identifying sponges to species level since tissues samples are required. This problem can be minimized by producing *in situ* quadrat maps and taking voucher specimens. For essentially three-dimensional species (e.g. arborescent forms) neither percentage cover nor numbers present are particularly suitable for sponge quantification and biomass estimates may be more appropriate. However, in most cases this is a destructive sampling method and is impractical for very large sponges (e.g. *Xestospongia*) or encrusting species that might be difficult to remove from the substratum (for definitions of morphologies see Boury-Esnaught & Rützler, 2000).

This study is intended to act as a preliminary investigation into the sponge assemblages in the Wakatobi region, Indonesia, and will address the following aims: (1) to provide an estimate of sponge species richness comparable to other world-wide figures from tropical, polar and temperate hard substratum habitats; (2) to provide a baseline survey of the abundance and species richness at two sites within the Wakatobi region experiencing different sedimentation regimes; (3) to consider the influence of a second gradient, that of depth (light and sedimentation), on sponge abundance and richness; (4) to determine if microhabitat scale differences occur in sponge assemblages between different reef surface types (vertical, inclined and horizontal surfaces) consistent with differences found for sponges in temperate ecosystems; (5) to consider the influence of sampling numbers of sponges compared with the percentage cover of sponges on aims 1–4; and (6) to compare the overall community structure between sites experiencing different sedimentation regimes since the presence of other taxonomic groups may influence community structure.

MATERIALS AND METHODS

Study site

The Wakatobi Marine National Park is located off the southeast coast of Sulawesi (Figure 1), Indonesia and is the second biggest marine park in Indonesia. It comprises four main islands and numerous smaller islands. Located off the coast of Kaladupa (Figure 1), in the northwest of the park, are two reef sites (Sampela and Hoga), which are subjected to quite different environmental conditions and represent different habitat quality (see Crabbe & Smith, 2002). Sampela reef has been described as a degraded and light-limited reef system (see Crabbe & Smith, 2002, 2003). This reef is located approximately 400 m away from the Bajau village of Sampela, which has been built on the extensive reef flats and is home to approximately 1300 people. Due to the past and continued exploitation of the reef (e.g. mining and fishing) and associated habitats (e.g. gleaning activities) by local

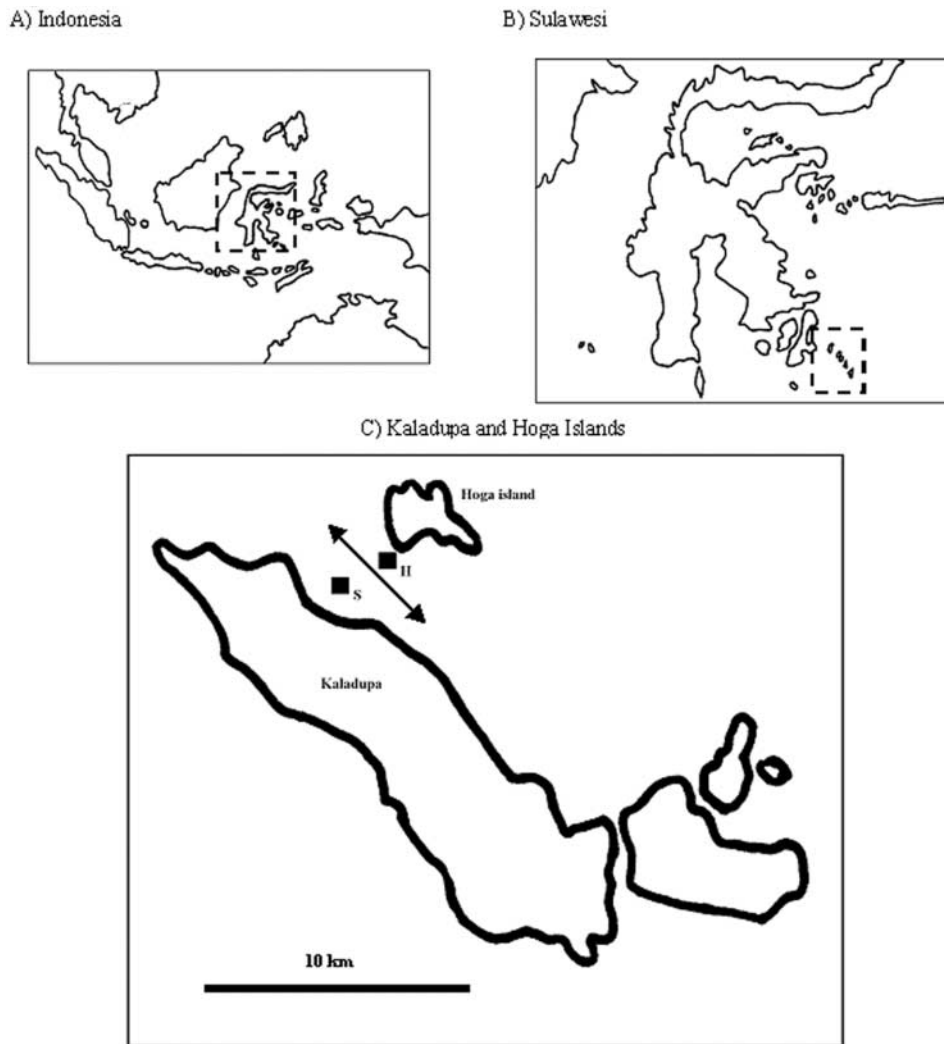


Figure 1. The area where sponge assemblages were sampled: (A) in Indonesia; (B) Sulawesi; and (C) at Kaladupa. Specific reef sites sampled at Hoga Island (H) and Sampela (S) are shown as solid squares. The Hoga-Kaladupa channel is shown by the double-headed arrow.

communities, the waters adjacent to the Sampela reef are characterized by high sediment loading. Sampela and Hoga also have different gross sediment deposition rates with $7.54 \pm 0.76 \text{ g.d.wt. m}^{-2} \text{ d}^{-1}$ being recorded at Hoga and $20.16 \pm 1.76 \text{ g.d.wt. m}^{-2} \text{ d}^{-1}$ at Sampela (Crabbe & Smith, 2002). Particles collected in sediment traps at Sampela were also much finer (smaller) than those at Hoga Island, where the sediment is mainly composed of sand particles.

The Sampela reef is a typical shallow fringing reef with a developed reef crest at 35 m depth and a fairly steep reef slope to a depth of between 1114 m after which a flat to gently sloping sandy habitat dominates. Throughout the reef wall are large areas of mass reef erosion characterized by unstable coral slips. The Sampela reef represents a degraded reef system characterized by low light availability below 5 m depth and high rates of sediment sedimentation. The second site (Hoga) is situated approximately 1.5 km from Sampela, immediately opposite the Sampela reef site but separated by a deep channel. Hoga is protected by park authorities as is Sampela reef, however, the Hoga site has recently been designated a local community supportive experimental

'No Take Area' and is therefore afforded a greater degree of protection (although it has been exploited in the past). Water quality is good and the site is not impacted by sediment load or deposition rates since it is not situated adjacent to a large reef dependent community. The Hoga site is a typical fringing reef with a well developed and diverse reef flat (between 0–4 m) and reef crest (between 4–6 m), with the reef slope extending to below 50 m in places. The reef is topographically diverse being characterized by vertical and steep walls, large overhangs and caves. Extensive reef monitoring (Smith et al. unpublished data) suggests that habitat quality of the Hoga reef is amongst the highest in the northern part of the marine park. As settling sediment particle size is much smaller at Sampela, sediment particles tend to remain in the water column much longer increasing turbidity and hence reducing light penetration. The larger sand particles at Hoga settle from suspension quickly. This occurrence is related to local hydrology as the Hoga site is mostly influenced by the Hoga-Kaladupa channel, whilst Sampela is in an enclosed lagoon and is buffered from the fast channel waters by an outer reef wall.

Protocol

Sponge assemblages

Ten 0.5m×0.5m random (within surface types available) quadrats were taken on vertical (90), inclined (45) and horizontal (0) reef surfaces at each site. Sampling was undertaken on the reef flat (0 m), 5 m, 10 m and 15 m (Hoga site only since the reef at Sampela only extends to 11–14m). Within each quadrat the number of each species (number of patches) was recorded along with the total area occupied by each species. Area occupied was calculated by photographing each quadrat (using Nikonos V, 28 mm lens and Aqua Flash II strobe at 1m from the substratum). Photographs were projected onto a screen of 400 dots and the sponge species beneath each dot noted and percentage cover calculated. A small tissue sample (5 mm³) was taken from each sponge species and an approximate plan was drawn of the location of sponges within each quadrat to enable individual sponges to be matched and identified within each photograph. Sponge tissue samples were then dissolved in bleach (on site) to remove all organic material, washed with freshwater and used to produce crude spicule preparations. Drawings were made from spicule preparations on site to allow identification to family/genus/species level on return to the UK. Since only spicule drawings were made on site (no sections), most species were only identified to family/genus level.

Sponge assemblage data from each site was log (x+1) transformed to reduce the importance of extreme values (rare species) prior to ordination by non-metric multi-dimensional scaling (MDS in Plymouth Routines in Multivariate Ecological Research [PRIMER]). This analysis was undertaken on a similarity matrix created from Bray–Curtis similarity analysis to ascertain any similarity or differences between sites, depth and surface angles (if any). Sponge abundance (percentage cover and numbers of sponges) was compared between sites, depth and surface angles using two-way analysis of variance (ANOVA) and *t*-tests. Generalized linear modelling (GLM) ANOVA was used to compare the linear relationships between sponge numbers and percentage cover at the two sites.

Overall community structure

The relative abundance of live hermatypic coral (mainly scleractinian but also including *Millepora* sp.), dead hermatypic coral, soft coral and macroalgae were assessed by the use of randomly placed 50 m continuous line intercept transects (see English et al. 1997). Sampling was undertaken across all habitats (while sponges were only sampled on hard/cliff/coral substratum) to give an indication of changes in major faunal groups between sites and with depth. Three replicates were assessed on the reef flat, at 5 m and 10 m (± 0.5 m in all cases) at each site and therefore 18 transects were studied as part of this investigation. Differences between cover of these different groups at the two sites and depths were examined using a two-way ANOVA (data was log x+1 transformed). The abundance of Scaridae (Parrot fish) was determined by a time and distance belt transect technique, ensuring a constant sampling effort. The abundance of this group

was determined since they were seen feeding on the reef directly and were considered important in the creation of new space and in fragmenting large sponges. Transects were 50 m long by 5 m wide and were examined over a 20 minute period. Triplicate transects were conducted (each transect was at least 50 m from each other) on the reef flat, reef crest (5 m) and upper reef slope (10 m) between 9 and 10 am on consecutive days.

RESULTS

Species richness

A total of 100 sponge species, comprising 38 families were reported from Sampela and Hoga Island reefs, with lower overall species richness being found at Sampela (58 and 74 species at Sampela and Hoga Island respectively) with 41% of species being shared (total area sampled=52.5 m²) between sites. However, one extra depth was sampled at Hoga. Differences in species richness were seen between different depths at the both sites (Figure 2). Low species richness was found on the reef flat at both sites (5 and 8 species at Sampela and Hoga respectively). Species richness increased with depth reaching a maximum of 25 and 33 species at 10 m and 15 m depths on vertical surfaces at Sampela and Hoga respectively. Differences between surface angles were only apparent at Sampela with the highest species richness at

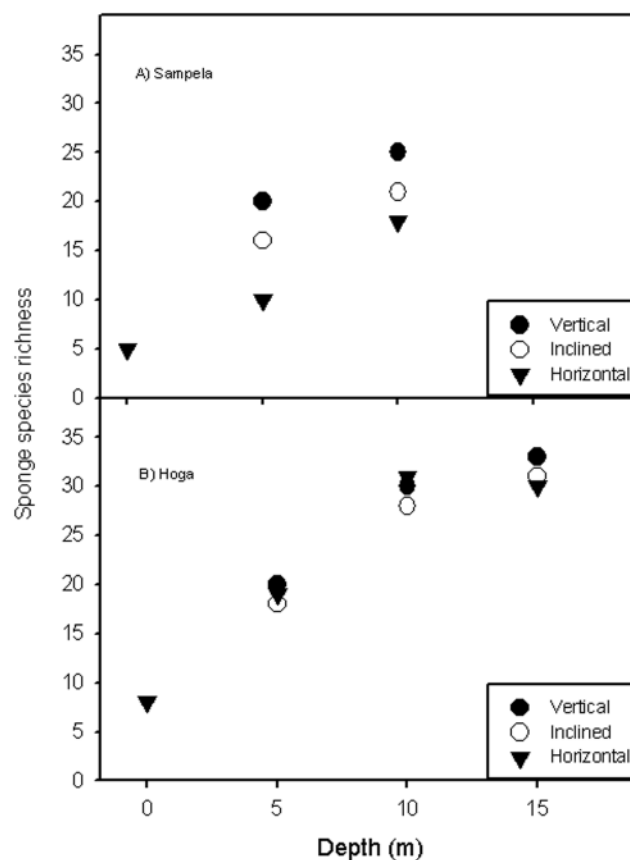


Figure 2. Sponge species richness at two coral reef sites (Sampela and Hoga) on the reef flat, 5 m, 10 m and 15 m (Hoga only) on vertical ($\sim 90^\circ$), inclined ($\sim 45^\circ$) and horizontal reef surfaces ($\sim 0^\circ$). Values given are for a total area sampled of 2.5 m².

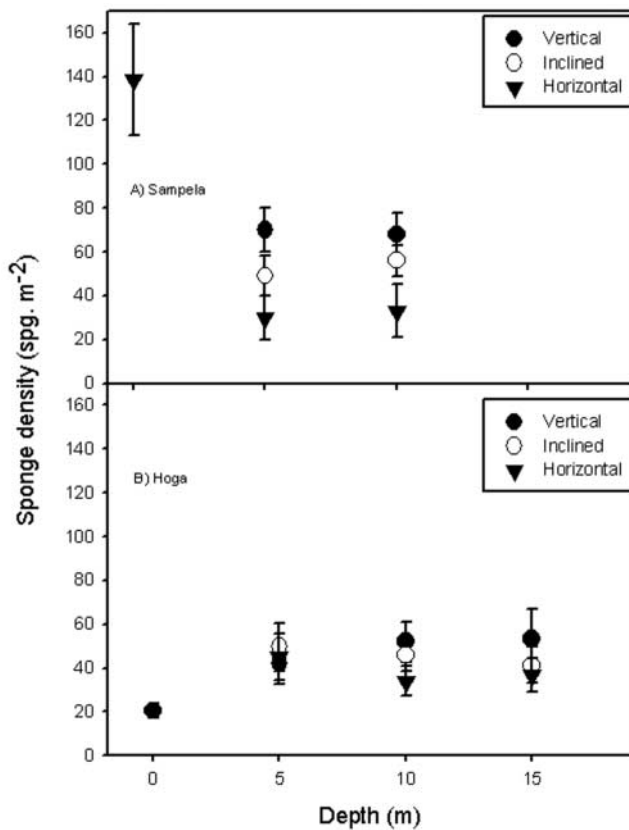


Figure 3. The number of sponges (sponges/patches m^{-2}) at two coral reef sites (Sampela and Hoga) on the reef flat, 5 m, 10 m and 15 m (Hoga only) on vertical ($\sim 90^\circ$), inclined ($\sim 45^\circ$) and horizontal reef surfaces ($\sim 0^\circ$). Mean values are from ten $0.5 m^2$ quadrats.

each depth being found on horizontal, inclined and vertical surfaces respectively. No differences were seen in sponge species richness between different surface angles at Hoga. Comparisons between sites showed higher species richness occurred at all depths and surface angles at Hoga compared with Sampela. On the reef flat only slightly higher species richness was found at Hoga (8 compared with 5). Between 5 and 10 m species richness increased by approximately 10 species on all surface types at both sites, although actual richness was lower at Sampela. Species richness only increased slightly between 10 and 15 m at Hoga (23 species dependent on surface angle).

Sponge numbers and percentage cover

Sponge numbers (spg.) and percentage cover varied between the two sites and in some cases between surface angles (Figure 3 & 4). A significantly higher ($t > 4.61$, $df=9$, $P < 0.001$) sponge density and percentage cover was observed at Sampela compared to Hoga Island on the reef flat. When sponge abundance data (percentage cover and numbers) was compared from all sites, depths and surface angles, significant differences were apparent ($F_{1,159} > 89.7$, $P < 0.001$). The differences can be attributed to depth and surface angle from Sampela since no significant ($P < 0.001$) differences were observed between any of the depth/surface angle combinations at Hoga. Therefore at Hoga the mean sponge density and percentage cover

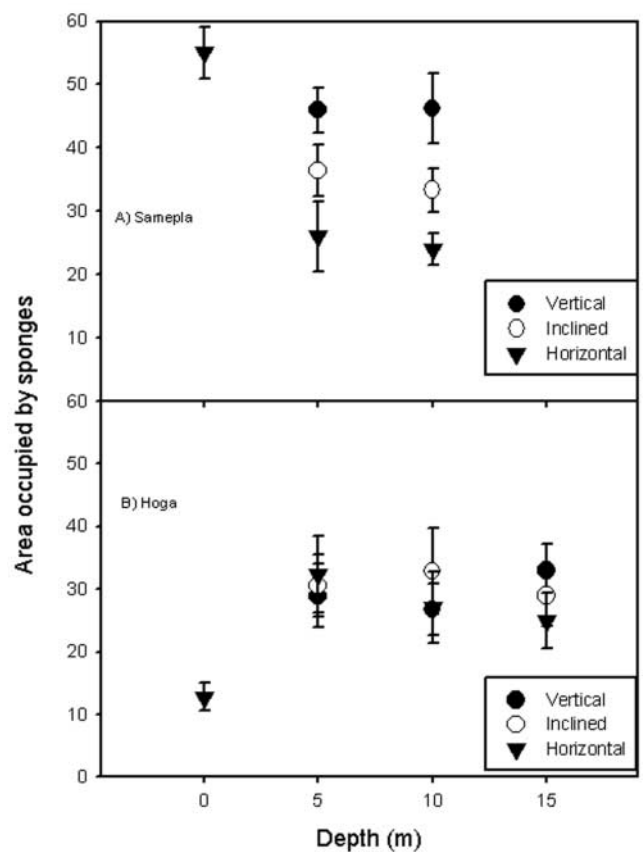


Figure 4. The percentage cover of sponges at two coral reef sites (Sampela and Hoga) on the reef flat, 5 m, 10 m and 15 m (Hoga only) on vertical ($\sim 90^\circ$), inclined ($\sim 45^\circ$) and horizontal reef surfaces ($\sim 0^\circ$). Mean values are from ten $0.5 m^2$ quadrats.

($\pm SE$) of $49 (\pm 10)$ spg. m^{-2} and $29.5 (\pm 7)\%$ respectively were recorded across all depths and surface types (except on the reef slope). At Sampela a significantly higher ($F_{1,59} > 48.7$, $P < 0.001$) abundance of sponges (numbers and percentage cover) were found on vertical, than inclined, than on horizontal surfaces. However, no significant differences were seen between different surface angles at the two depth intervals. Because of the variability between quadrats no significant difference in the abundance of sponges was seen between the two sites, with the exception of vertical surfaces at Sampela. Higher numbers (70 ± 11 spg. m^{-2} compared with 49 ± 10 spg. m^{-2}) and percentage cover ($45 \pm 7\%$ compared with $29.5 \pm 7\%$) of sponges were reported from vertical surfaces at Sampela compared to Hoga.

Sponge numbers were significantly correlated (Pearson's correlation coefficient = > 0.43 , $df=169$, $P < 0.001$) with percentage cover estimates at each site and a GLM ANOVA was used to compare the linear relationships between the two sites. The results showed no significant difference between the linear relationships at the two sites ($F_{1,169}=0.40$, $P=0.526$) and therefore the data was combined (Figure 5). Therefore, across all habitat areas of low sponge numbers corresponded with low percentage cover. Linear regression analysis of this relationship indicated the slope to be significantly different to zero ($t=12.2$, $df=169$, $P < 0.001$), while the intercept was not significantly different to zero ($t=0.57$, $df=169$, $P=0.56$).

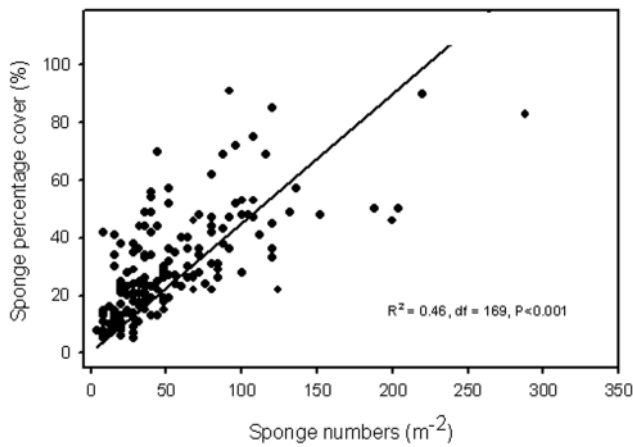


Figure 5. The relationship between numbers (sponges m^{-2}) and percentage cover (%) of sponges measured in quadrats combined from two reef sites in south-eastern Sulawesi. The fitted regression line: Sponge numbers (per $0.25m^2$) = $0.71 (\pm 1.2) + 0.42 (0.03) \times$ percentage cover.

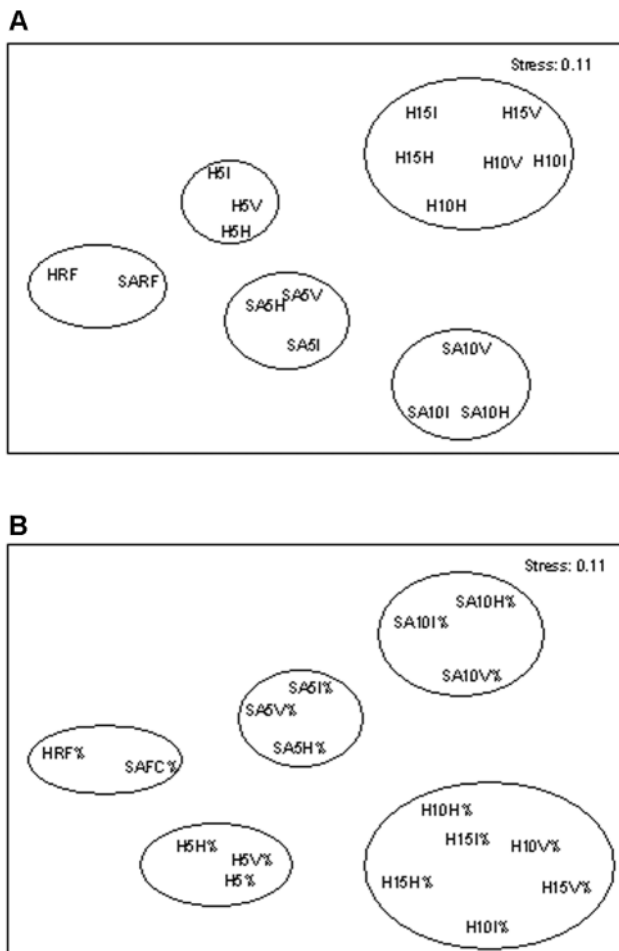


Figure 6. Multi-dimensional scaling plots (MDS in PRIMER) of the sponge assemblages based on the numbers (A) and percentage cover (B) of sponges at Sampela (SA) and Hoga (H) reefs, south-eastern Sulawesi on the reef flat (RF – 0 m), at 5 m (reef crest), 10 m and 15 m (Hoga only) on vertical ($\sim 90^\circ$), inclined ($\sim 45^\circ$) and horizontal reef surfaces ($\sim 0^\circ$).



Figure 7. The area occupied (percentage cover) by live coral, dead coral, soft coral and algae at two sites in south-eastern Sulawesi, Indonesia on the reef flat (0 m), 5 m and 10 m.

The ANOVA from regression analysis indicated sponge numbers to be significantly associated with sponge percentage cover ($F_{1,169} = 148.98, P < 0.001$).

Assemblage composition based on sponge numbers and percentage cover

The results of MDS indicated clear differences between sponge assemblages at Sampela and Hoga Island (Figures 5 & 6). The exception to this occurred on the reef flat where both sites appeared to have similar assemblages. There was also evidence of differences in assemblages with increasing depth at both Sampela and Hoga Island. Different assemblages could be seen at 0 m (reef flat), 5 m and 10 m at Sampela. However, at Hoga Island differences were seen between 0 m (reef flat) and 5 m, but the assemblages at 10 and 15 m showed no apparent differences, yet they were different to those at found at 0 m and 5 m depth. Little difference was observed in assemblage structure between vertical, inclined or horizontal surfaces at either site or at any of the depths studied. Therefore depth and site rather than surface angle structured the sponge assemblages.

Although the majority of specimens were not identified to the species level due to only preliminary and limited examination of tissue material on site, some characteristic species/genre were identified on the basis of morphological characteristics and spicule evaluation. *Xestospongia testudinaria* (Lamarck, 1815) was found on the reefs at Hoga and Sampela. However, the number of individuals was low (approximately 15 sponges seen at Hoga and 5 at Sampela), but most

Table 1. Sponge families reported from two sites in southeast Sulawesi, Indonesia. The number of species found at each site is shown.

Family	Sampela	Hoga
Ancorinidae	1	3
Agelasidae	2	2
Aplysinidae	1	2
Axinellidae	1	2
Callyspongiidae	0	3
Chalinidae	2	1
Chondrillidae	2	2
Ciocalyptidae	1	0
Clathrinida	0	2
Clionaidae	0	1
Coelosphaeridae	0	2
Desmacellidae	3	4
Dictyonellidae	4	2
Dysideidae	3	4
Geodiidae	1	0
Halichondriidae	2	2
Hymedesmiidae	3	1
Hymeniacionidae	1	2
Ianthellidae	2	2
Irciniidae	2	3
Isodictyidae	1	1
Microcionidae	4	6
Mycalidae	1	1
Neopeltidae	1	1
Niphatidae	3	3
Petrodiidae	1	1
Placospongiidae	1	0
Plakinidae	2	2
Phloeodictyidae	1	1
Raspailiidae	1	3
Spirastrellidae	2	2
Spongiidae	1	1
Suberitidae	4	3
Tedaniidae	0	2
Tethyidae	1	2
Tetillidae	0	1
Thorectidae	2	2
Timeidae	1	1

specimens were more than 1.5 m in diameter. On subsequent deeper dives in the region (up to 30 m), the numbers of this species appeared to increase and even larger individuals were observed (up to 2 m in diameter). At least one other *Xestospongia* sp. was observed. *Kallypilidion* sp. and *Amphimedon* sp. were also observed at both sites, although they appeared restricted to between 5 and 10 m in depth. Several sponge species that were found at Hoga, but not at Sampela included *Cinachyra* sp. *Callyspongia* spp, *Axinellid* sp. and *Gelloides* spp. However, even though these sponges were found within sampling areas, they were much more abundant locally in overhanging cave environments. The most conspicuous sponge species common at Sampela, but absent from Hoga, was *Liosina granularis* Borges & Bergquist, 1988 which was found covered in a fine layer of silt.

Overall community structure and parrot fish abundance

Total live hermatypic coral cover was significantly higher at Hoga compared with Sampela ($F_{1,17}=123.91$,

$P<0.001$) and hermatypic coral cover also differed significantly with depth at the two sites ($F_{2,17}=15.38$, $P<0.001$). This was largely due to increased cover at the 5 m contour (reef crest) whereas no significant differences were found in cover between the reef flats and reef slopes (10 m) at either site. The influence of depth on the percentage cover of corals was not site dependent. Dead coral cover differed significantly between Hoga and Sampela reefs ($F_{1,17}=5.17$, $P<0.05$) due to higher percentage cover at Sampela ($10.04 \pm 1.00\%$) than at Hoga ($4.26 \pm 0.72\%$). The percentage cover of dead coral did not differ between the three depth contours and there was no significant interaction between depth and site. Macroalgae was significantly ($F_{1,17}=39.63$, $P<0.001$) more abundant at Sampela ($11.72 \pm 1.55\%$) compared with Hoga ($7.67 \pm 2.01\%$) but did not vary with depth. The effect of depth on algal abundance was not significantly influenced by site. Soft corals were significantly ($F_{1,17}=4.73$, $P<0.05$) more abundant at Sampela ($29.12 \pm 0.84\%$) than at Hoga ($12.31 \pm 3.11\%$), but there was no significant difference between depth contours and site did not significantly effect how the abundance of soft coral varied with depth. Scaridae (Parrot fish) abundance data varied between sites and depths. Values of 3.3 ± 1.7 per 250 m^2 , 3.0 ± 1.5 per 250 m^2 and 5.7 ± 0.3 per 250 m^2 were record on the reef slope, crest and flat respectively at Sampela. Although little difference was seen between the abundance of Parrot fish on the reef slope, higher abundance was recorded at Hoga on the reef flat. Abundance values were 3.0 ± 2.1 per 250 m^2 , 1.7 ± 1.7 per $250 \text{ m}^2=10.7 \pm 4.3$ per 250 m^2 for the reef slope, crest and flat respectively.

DISCUSSION

Reef flat sponge assemblages

The most important environmental factor that differed between the two sites was sedimentation rate, which appeared to significantly influence reef crest and slope sponge assemblages (see below), but had little effect on reef flat assemblages since they were essentially the same at the two sites. Even though reef structure, complexity, sedimentation rate and coral cover varied between Sampela and Hoga, two environmental factors that are consistent between the reef flats are aerial exposure at low water spring tides and wave action. Sponges are generally intolerant of aerial exposure due to the drying of their soft tissues and the ultraviolet damage they may sustain. The periodic exposure of the reef flats at both sites may account for the similar sponge assemblages. There is also the possibility that reef flat assemblages may be negatively impacted by temperature increases in shallow water during low tide periods, although little is known about the thermal tolerance of sponges. The second important factor that may be similar between the two reef flats is wave exposure, which is higher on the reef flat than on reef crest and slope environments. Although detailed patterns of the variation in sponge morphologies between sites and depths was not described, notable was the domination of encrusting species (>95% of sponges) on the reef flat, which is typical of high-energy environments since these species reduce drag (Bell & Barnes, 2000a). However, desiccation (since reef flats are uncovered by

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the tide) may occur more quickly for encrusting species with a large surface area to volume ratio. Since these encrusting species were found most abundantly on the reef flat they may be phototrophic with distribution limited by light (Wilkinson, 1987), in this case an encrusting morphology may enhance photosynthetic efficiency.

Although a similar community structure was found on the reef flat between sites, sponge abundance was greater at Sampela, which may be explained by biological differences between the two sites. On the reef flat live hard coral cover was much lower at Sampela than at Hoga. This may be as a result of past human activities (e.g. coral mining) or increased sediment loading in the water column which could be negatively influencing coral recruitment (Crabbe & Smith, 2003). It appears the reef flat coral cover has little direct influence on sponge assemblage structure, although the abundance of the sponges found was greater at Sampela presumably because of reduced coral cover. Competitive processes, particularly those with corals, are likely to be very important in governing the abundance of sponges. Although sponges have been considered superior competitors against corals in some studies (Vicente, 1978; 1990), corals may be released from competition with sponges through predation pressures by spongivorous fish (Hill, 1998). As well as decreased live coral cover on the reef flat at Sampela, Parrot fish abundance was also reduced, presumably because of reduced reef complexity and food availability. This is important since this reduction may also account for the greater sponge abundance at Sampela because Parrot fish were commonly seen feeding on the reef and sponges. The low number of sponge species found on the reef flat is likely a result of physical processes, while the increased abundance of species found at Sampela is probably due to reduced competition with corals and reduced fish predation. More recent studies indicate the overgrowth of corals by sponges may not be that widespread (Aerts, 2000). Care should be taken when considering the interactions of sponges with corals since the majority of the information available is from studies in the Caribbean (e.g. Jackson & Buss, 1975; Vicente, 1978, 1990; Aerts, 1998, 2000) and such interactions may be different for Indian Ocean coral reef ecosystems.

Reef crest and slope sponge assemblages

On descending the reef slopes, sponge assemblages were much more diverse than those on the reef flats and differences in assemblage structure were noted in response to depth and between sites. That sponge numbers varied little between depths at Hoga was not surprising considering how little variation was seen in the abundance of the other dominant animal and plant groups. However, sponge abundance has been shown to increase with depth for a number of other tropical reefs, but most of this information is again available from Caribbean reef systems where gradual increases in depth are not always apparent (e.g. Alcolado, 1990). Non-hard coral species richness and abundance may be expected to increase in abundance with increasing depth, as coral species decline in response to reduced light levels (Porter, 1972). However, it is likely this situation may not occur until greater depths than

sampled within the present study, since corals may show morphological (Chappell, 1980) and physiological adaptation (Falkowski & Dubinsky, 1981; Porter et al., 1984). A decrease was seen in the abundance of non-sponge groups at Sampela, so an increase in sponge abundance might have been expected. Corals at Sampela also show a greater degree of vertical growth compared with Hoga (Crabbe & Smith unpublished) potentially increasing available space. However, increased sponge abundance may be prevented because of the higher rates of fine sediment settlement, offsetting the increase in available space.

Sedimentation has been shown to influence sponge assemblages in temperate regions (Könnecker, 1973; Bell & Barnes, 2000a), but less information is available for tropical sponge assemblages. Coral diversity is usually considered to decrease in response to increased sedimentation due to smothering and the reduction of light-dependent processes such as growth and calcification (Rogers, 1990). Sedimentation has also been considered to result in reduced pumping rates of the tropical sponge *Verongia lacunosa* (Gerrodette & Flechsig, 1979), but information on the effects of sedimentation on tropical sponge assemblages has not been well documented. The majority of sponges at Sampela had some fine sediment on their surfaces. Sponges can show considerable phenotypic plasticity (Boury-Esnault & Rützler, 1997) with specific morphologies often predominating in certain habitats (Bell & Barnes, 2000d) enabling the possibility for adaptation to local environmental conditions. For example, arborescent sponges may be more suited to sedimented environments as they reduce the amount of sediment settling on surfaces per unit volume compared with encrusting or irregular massive forms (Chappell, 1980; Bell & Barnes, 2000d). This is also true for *Acropora* species at Sampela (Crabbe & Smith, 2002). Sponge morphology was not recorded within each habitat because of the complexity and diversity of the body forms exhibited and subsequent difficulty in generalizing body forms, even under the scheme proposed by Boury-Esnault & Rützler (1997). Bell & Barnes (2001) described a method for estimating sponge species diversity based upon morphological diversity. The complexity of sponge morphologies found within Indonesian sponge assemblages requires this method to be revised to include a greater number of morpho-types.

Differences between surface types was only associated with the sedimented reef habitat at Sampela that is consistent with studies of temperate hard substratum reefs (see Bell & Barnes, 2000b,c). This may not be surprising since environmental characteristics between surface types in sedimented tropical and temperate habitats are likely to be the same. The dominant phyletic groups composing the overall community obviously differ between tropical and temperate regions since both hard and soft corals generally do not dominate the latter. Since hard corals might be expected to prefer horizontal and inclined surfaces in their need for light, soft corals and sponges might be more abundant on vertical surfaces. However, total coral abundance did not decrease significantly with depth, accounting for the similarity in sponge abundance and such a decrease in coral abundance may not occur until greater depths. At Sampela the different surface

angles will experience different sedimentation regimes, with less settlement being expected on vertical compared with inclined and horizontal surfaces (Bell & Barnes, 2000b,c). Higher sponge abundance and richness on vertical surfaces compared with other surfaces at Sampela may be due to the inability of sponges to tolerate sediment settlement on their surfaces, as they lack active sediment removal mechanisms. However, the abundance of sponges on inclined and horizontal surfaces was not significantly reduced at Sampela compared with Hoga, suggesting more favourable conditions for growth at Sampela on vertical surfaces compared with both Hoga and other surface angles at Sampela. Sponges inhabiting these vertical surfaces may be able to benefit from the increased material in the water column without the problem of material settling on sponge surfaces, while also benefiting from reduced competition with corals due to limited light availability. That no difference in assemblage structure (using MDS) was seen between different surface angles is perhaps surprising given the differences in species richness and abundance at Sampela. This can only be accounted for by a large number of rare species and similar proportions of the most abundant species.

The study of Bell & Barnes (2000a) described sponge species richness from a number of polar, temperate and tropical regions, where approximately similar sized sampling areas were considered ($\sim 100 \text{ m}^2$). The present study only sampled approximately half the area of those described by Bell & Barnes (2000a), yet species richness was still higher than for those values documented for other tropical localities. This is consistent with the view that the Indian Ocean represents the highest global concentration of biodiversity (Stehli et al., 1967; Briggs, 1987; Hooper & Lévi, 1994; van Soest, 1994).

Assessment of sponge abundance

The linear relationship between sponge density (numbers) and area occupied is not intuitive, since high percentage cover of sponges may result from the presence of several large sponges or many smaller ones. Fragmentation of sponges is well documented with small clonal patches being formed during seasonal regression of tissues when conditions are unfavourable for growth (Sarà, 1970; Stone, 1970; Elvin, 1976; Barthel, 1989). However, these studies are for temperate and Mediterranean species and no documented evidence exists to support tissue regression and subsequent regeneration in tropical sponges. Also, since this process is thought to be due to seasonal variation in food availability in temperate regions, the absence of this driving factor in tropical systems probably limits the extent to which this process occurs (Parsons et al., 1984). Another process that may be operating to cause the formation of multiple patches from a single large sponge in tropical environments is fish activity. Although a number of fish species are known to feed directly on sponges (Wulff, 1994), most sponges are considered to be well defended from predators through physical and chemical mechanisms (Randall & Hartman, 1968). During the course of this study Parrot fish (family Scaridae) were commonly seen inadvertently damaging sponges while feeding on the reef and also directly consuming sponge material. As the same sponge assemblages were identified

using MDS for sponge numbers and percentage cover it appears (at least in this reef system) that whether sponge abundance is sampled by counting the number of patches for each sponge, or area occupied, makes little difference to measuring differences in assemblage structure.

Conclusions

This study is the first to provide quantitative estimates for sponge richness within Indonesian waters. Richness and abundance has been shown to be high with sedimentation and depth affecting assemblage structure and abundance. Competitive interactions have been used to explain several of the patterns described, but it is apparent that further work is required as most of the information is from Caribbean reef systems. Also few studies have considered the overall community within studies of competition for space in benthic environments. More often competition between specific assemblages, species or pairs of phyla are used (e.g. Lang, 1973; Pansini & Pronzato, 1990; Tanaka & Nandakumar, 1994; Barnes & Dick, 2000; Maughan & Barnes, 2000). Generalizations about sponges being the top spatial competitors in coral reef (and other ecosystems) are difficult to accept since few studies have considered large numbers of species. Species identity may be one of the most important factors in competitive ability. In a recent study of temperate reef sponge interactions different sponge species varied in their competitive abilities with other sponges and non-sponge groups (Bell & Barnes, 2003). It seems more detailed studies on a larger range of sponge species and their interactions with non-sponge groups are required since much of our current understanding of tropical sponge distributions is based on competitive ability, although we only have data for a limited number of species. In the past sponge assemblages have been considered impoverished in sedimented conditions. However, information from this study and from temperate regions suggest species richness to be nearly as high as in non-sedimented environments, though the mechanisms controlling this are unclear, but may include physiological and morphological adaptation. Finally, the assessment of sponge abundance as either percentage cover or numbers of sponges was insensitive to identifying sponge assemblage structure.

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