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Coral Reefs

Patterns in the distribution of sponge populations across the central Great Barrier Reef*

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Abstract. Coral reef sponge populations were surveyed at two spatial scales: different depths and different reef locations across the continental shelf of the central Great Barrier Reef. The surveys were conducted on the fore-reef slopes of 12 reefs from land-influenced, inner-shelf reefs to those in the oligotrophic waters of the Coral Sea. Few sponges occur in shallow waters and the largest populations are found between 10 and 30 m depth. Sponges are apparently excluded from shallow waters because of excessive turbulence and possibly by high levels of damaging light. Sponge biomass is highest on the inner-shelf reefs and decreases away from the coast, whereas abundance is generally higher on middle-shelf reefs. There are considerable overlaps in the species composition on middle-, outer-shelf and Coral Sea reefs, but those on inner-shelf reefs are significantly different. The nature and size of sponge populations reflect environmental conditions across the continental shelf. The larger inner-shelf populations probably reflect higher levels of organic and inorganic nutrients and reduced amounts of physical turbulence, whereas sponges on reefs further from shore may be able to resist greater turbulence but appear more sensitive to the effects of fine sediments. These latter populations are smaller, reflecting the reduced availability of organic matter, however, many of these sponges rely on cyanobacterial symbionts to augment nutrition in these clearer, more oligotrophic waters.

Introduction

Recent research has shown that populations of coral reef animals can vary considerably across longitudinal gradients that include broad continental shelves. The best published examples of these differences are reported for a transect from the coast across 120 km of the continental shelf on the central Great Barrier Reef and out to reefs on the Queensland Plateau, 220 km offshore in the Coral Sea (Wilkinson and Cheshire 1988). The differences in the populations of some reef animals are greater along this 120 km transect containing inner-, middle- and outer-shelf reefs than are observed on reefs of similar shelf location spread over 2000 km (Williams 1983).

Marked cross-shelf differences are reported in the populations of predominantly phototrophic animals such as hard corals (Done 1982) and soft corals (Dinesen 1983), and totally heterotrophic animals such as fishes (Williams 1982; Williams and Hatcher 1983; Russ 1984) and holothuroids (Hammond et al. 1985). The differences were attributed primarily to variations in physical factors and nutrient environments of the reefs across the shelf, from land-derived influences nearshore to oceanic conditions on the edge of the shelf and out into the Coral Sea.

Coral reef sponge species on the Great Barrier Reef include animals which are either predominantly phototrophic, mixed phototrophic and heterotrophic or totally heterotrophic (Wilkinson 1983). Therefore, variations in the amount of light transmittance is a physical factor that is likely to influence the distribution of sponges. The structure of the sponge community changes according to light along this cross-shelf transect with the growth of predominantly heterotrophic sponges inshore and a large proportion of phototrophic sponges offshore (Wilkinson and Trott 1985; Wilkinson 1987a). Similar marked differences have been observed in the trophic structure of fish communities with the major trophic group on outer-shelf reefs deriving their nutrition directly from benthic algae, whereas plankton eating fishes are prominent on middle-shelf reefs and omnivorous and carnivorous fishes are more prevalent on inner-shelf reefs (Williams 1982; Williams and Hatcher 1983; Russ 1984).

Variations in such physical factors as light, depth and turbulence were attributed as major factors influencing the distribution of sponges across one middle-shelf reef (Davies) of the central Great Barrier Reef (Wilkinson and Evans 1989). This paper reports surveys of sponge

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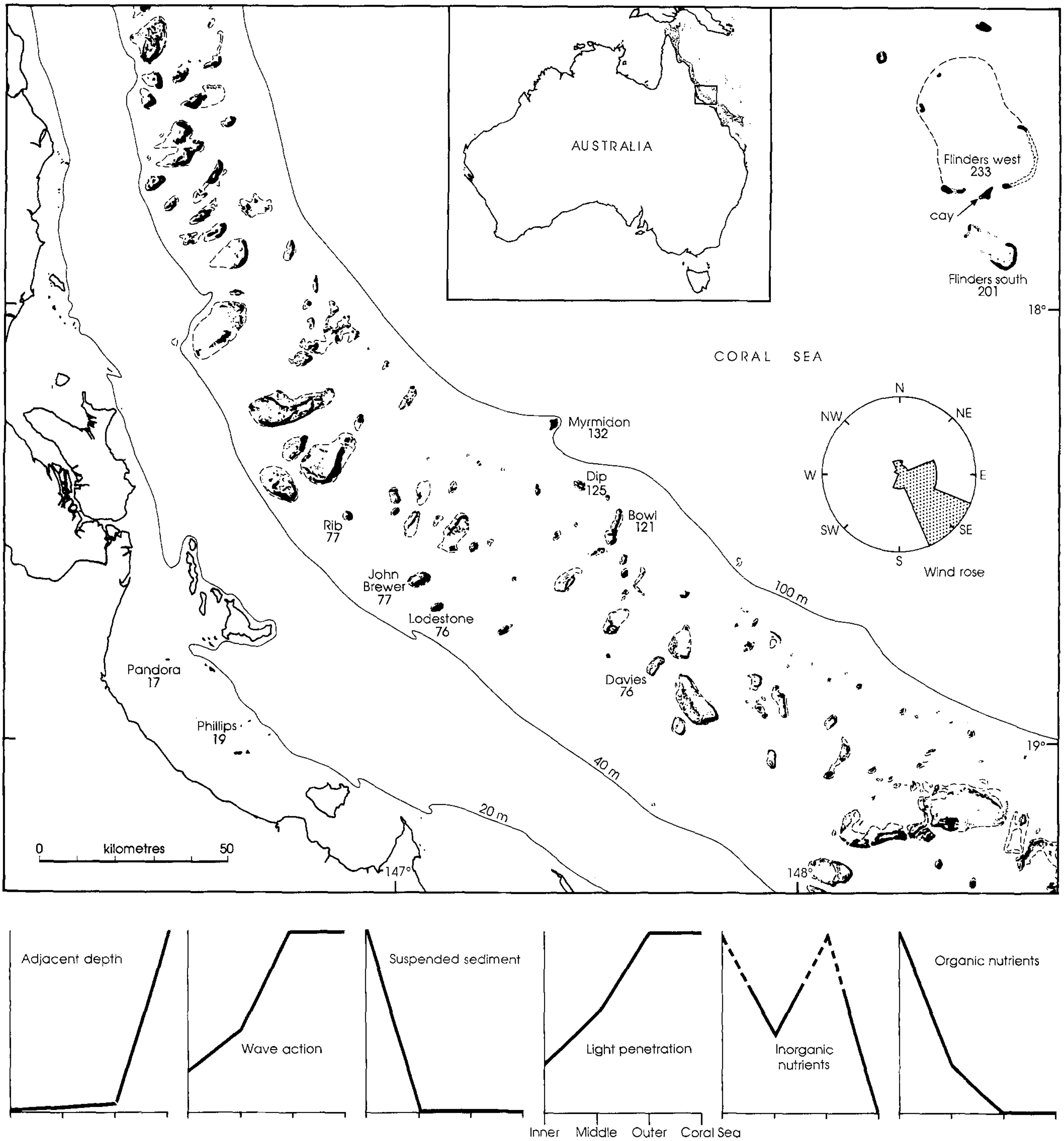

Fig. 1. Location of the survey sites of sponge populations on coral reefs across the central Great Barrier Reef with the 20, 40 and 100 m contour lines indicated. The distance from shore is marked alongside each reef and the wind rose showing the predominance of south east winds at John Brewer Reef is from Wilkinson and Evans (1989). Below are figurative indications of the environmental parameters from the following: wave action, Done (1982); sediments, Johnson et al. (1986); light penetration at 10 m depth, Wilkinson and Trott (1985); inorganic nutrients, Andrews (1983), Furnas and Mitchell (1986), Walker and O'Donnell (1981), Wilkinson et al. (1984); organic nutrients, Furnas and Mitchell (1986), Ullman and Sandstrom (1987)

populations on the fore-reef slopes of 8 reefs across the continental shelf and on 3 reefs in the Coral Sea, with the inclusion of the data from the fore-reef of Davies as an additional comparison. The aim of this research was to determine the variations in sponge community structure over broad spatial scales and identify those parameters of the population that can be used to characterize different reef systems or habitats. Depth and shelf location are the major spatial parameters used in the comparisons of sponge populations. These comparisons are concentrated at the species and ordinal levels including both biomass and abundance and constitute the most detailed published surveys of sponge populations across such broad spatial scales.

Materials and methods

Surveys of sponge populations were conducted in the following locations (Fig. 1): the south-east faces (proximal to the major wind and wave inputs) of two inner-shelf reefs (Pandora and Phillips), four middle-shelf reefs (Rib, John Brewer, Lodestone and Davies), two outer-shelf reefs (Dip, Bowl) and one Coral Sea reef (Flinders South). Some reefs were surveyed at other locations because of unfavourable weather (Myrmidon, north-east slope; Flinders Cay, south-west slope) or because no south-east side existed (Flinders West, a near vertical, south-west slope). All obvious sponges in triplicate 40 m^2 transects at 2.5, 5, 7.5, 10, 15 and 20 m were collected and weighed aboard ship as detailed previously (Wilkinson 1982). Cryptic, boring and very thin encrusting sponges were not collected.

Emphasis was placed on identifying the most prominent sponges through the assistance of P. R. Bergquist, J. Fromont, J. N. Hooper, J. A. Stoddart and J. Vacelet. All sponges were given unique species codes, checked against reference specimens and identified to at least Ordinal level. A further definition was made by dividing all sponges into the following categories (Wilkinson and Trott 1985): phototrophic (Ph), with large populations of cyanobacterial symbionts such that $Pg/R > 1.5$ for at least 8 h per day; mixed (Mi) with fewer photosynthetic symbionts usually as a thin layer on the outside such that $Pg/R < 1.5$; and heterotrophic (He) with no photosynthetic symbionts (Pg = gross photosynthetic oxygen production; R = respiration – method and data in Wilkinson and Trott 1985).

Data were assessed in three ways: (i) descriptive analysis of variations in sponge biomass, abundance and species structure over depth and shelf location scales; (ii) analysis of community structure (sensu Krebs 1978; e.g. Done 1982) in which sites are grouped on the basis of the similarity of species composition; (iii) discriminant analysis to quantify the similarities and differences between sites.

Communities were defined using an agglomerative hierarchical grouping procedure (HGROUP; Veldman 1967) on the first ten eigen vectors derived from a principal coordinate analysis (Gower 1966). The principle coordinate analysis (P-CORD) was used to reduce the dimensionality of the data matrix (the similarity matrix for the P-CORD analysis was derived using the Canberra metric coefficient on Gower-adjusted data).

Discrimination of the population assemblages at each site was achieved using univariate and multivariate analyses to test the significance of differences. One way ANOVA's were used to define the significance of the changes in "key" marker species or Ordinal/trophic (Ph, Mi or He) groups. A stepwise discriminant procedure was used to define the functions which best describe the Ordinal/trophic level differences between sites on the 12 reefs at the four cross-shelf locations.

Results

There are two marked trends in the data on fore-reef slope sponges from reefs across the central Great Barrier Reef: biomass, abundance and species richness all increase significantly with depth on all reefs to 15 or 20 m (the limits of these surveys), and there is an overall decrease in biomass and species richness with increasing distance from shore (Fig. 2). These trends are statistically significant (Table 1).

Sponge biomass is consistently low in all shallow fore-reef sites (< 10 m) across the continental shelf (Fig. 2a). Generally there are few sponges within the first 10 m depth and biomass increases from 10 to 20 m, with maxima around 20 m or deeper. The limit of the surveys on the inner-shelf reefs was 15 m, where the reef slopes

Table 1. Levels of significance for 2 way ANOVA tests for variations in sponge population parameters against *depth* to 20 m and cross-*shelf location* of the fore-reef sites on reefs across the continental shelf of the central Great Barrier Reef and into the Coral Sea; I = inner-shelf reefs; M = middle-shelf reefs; O = outer-shelf reefs; C = Coral Sea reefs

Dependent variable	Independent variable	
	Depth	Shelf location
Biomass	$F=13.02$ $P<0.005$ $7\,m<10\,m<15\,m<20\,m$	$F=12.75$ $P<0.005$ $I>M=O>C$
Abundance	$F=14.69$ $P<0.005$ $7\,m<10\,m<15\,m<20\,m$	$F=0.46$ $P=0.71$ $I=M=O=C$
Species richness	$F=42.98$ $P<0.005$ $7\,m<10\,m<15\,m<20\,m$	$F=12.77$ $P<0.005$ $I>M=O>C$

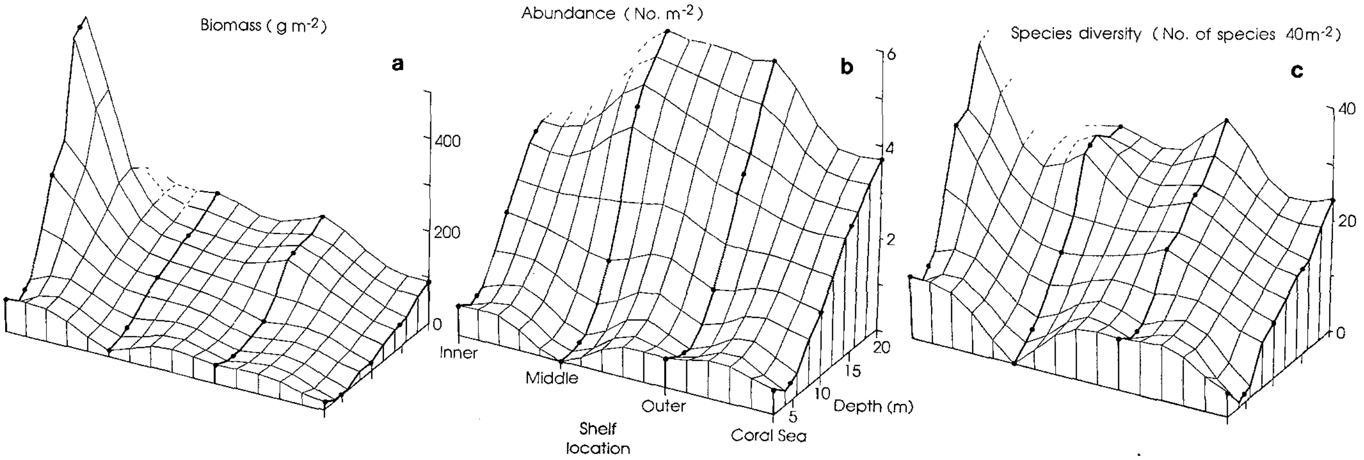

Fig. 2 a–c. Three dimensional surface plots illustrating both depth and cross-shelf variations in sponge populations on fore-reef slopes of reefs across the central Great Barrier Reef. The data (from Wilkinson and Trott 1985; Wilkinson 1988) for each depth are pooled means of 3 transects of 40 m^2 for all reefs from each shelf location in Fig. 1 and have been smoothed by computer to illustrate major trends: **a** wet biomass of sponges; **b** abundance of individual sponges; **c** species richness as a mean of the number of species per 40 m^2 transect terminate in mud; other surveys were limited to 20 m because of diving time limitations. When reconnoitring dives were made beyond 20 m depth, there were no noticeable changes in the species present or the abundance until depths beyond 30 to 35 m where there were considerably fewer sponges e.g. on Davies Reef (Wilkinson and Evans 1989).

Sponge abundance shows a similar pattern with depth (Table 1). Few sponges occur in shallow waters with populations increasing markedly at or below 10 m depth irrespective of location on the shelf (Fig. 2 b). Contrary to the biomass pattern, there is no significant difference in sponge abundance across the continental shelf (Table 1; Fig. 2 b).

The average weight (biomass divided by abundance) of individual sponges is significantly greater on inner-shelf reefs compared to reefs further from shore (note patterns in Fig. 2 a and b). This trend was most marked on the deeper sites of Flinders South where the average wet weight of individual sponges was 8.7 g, consisting almost entirely of a flattened, phototrophic dictyoceratid species (*Phyllospongia lamellosa*). In contrast, the average sponge weight at 15 m on the two inner-shelf reefs was 133.5 g. In general, shallow water sponges were larger than those in deeper waters.

Sponge species richness shows similar trends to biomass with more species on inner- and middle-shelf reefs (total of 88 and 90 species respectively; Table 2) compared to the outer-shelf and Coral Sea reefs (75 and 65 species; Fig. 2 c). Species richness also increased with depth to 15 or 20 m at all cross-shelf locations.

The sponge populations on the inner-shelf reefs showed little similarity with the other locations, with approximately 20% of inner-shelf sponge species occurring on the middle and outer-shelf reefs (Table 2). The degree of overlap of species between middle- and outer-shelf reefs is considerably higher (50 to 60%). Approximately a third of Coral Sea species occur on reefs within the main tract of the Great Barrier Reef.

Seven sponge species assemblages have been identified on the basis of species distribution patterns. These assemblages correspond to different locational or environmental factors (Fig. 3). All shallow sites (10 m or less) are similar due to low sponge abundance and few species. Because these shallow sites are spread across all cross-shelf locations, it is not meaningful to assign a characteristic species assemblage. All Myrmidon Reef deeper sites contained a number of species that were not found on the adjacent outer-shelf reefs. These sites are similar to the shallow sites because of low sponge abundance. The most abundant (with high biomass) are *Ircinia* sp. IE, *Pseudoceratina* spp. and *Dysidea* spp. The characteristic (unique) species of the site are *Dysidea* sp. DA, *Pseudoceratina* sp. VS, and *Psammocinia* cf *microconulosa* IH, but these are not abundant. Sponge communities from deeper water (15–20 m) on the Coral Sea reefs showed similarities to the shallow sites only because the populations consisted of few species and a low biomass (Fig. 4). *Callyspongia* sp. CL, *Dysidea* cf *silicata* AL and *Callyspongia* sp. MA were both characteristic and abundant on these reefs.

Table 2. Comparison matrix of the number of distinct species and higher order/trophic groups found in each cross-shelf location showing the number of taxa which are common to different locations

Location	Total	Co-occurrence on			
		Inner-	Middle-	Outer-	Coral Sea
Species					
Inner-	88	(88)	19	16	13
Middle-	90	19	(90)	45	21
Outer-	75	16	45	(75)	21
Coral Sea	65	13	21	21	(65)
Ordinal/trophic groups					
Inner-	18	(18)	15	15	14
Middle-	23	15	(23)	20	16
Outer-	23	15	20	(23)	17
Coral Sea	17	14	16	17	(17)

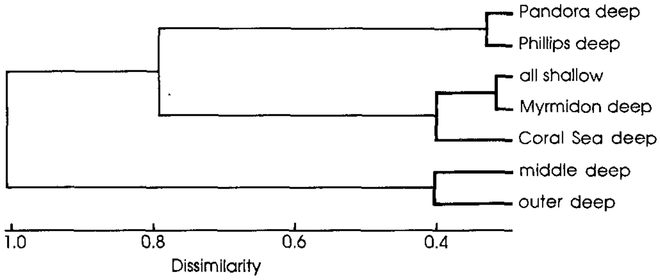

Fig. 3. Dendrogram showing the results of a hierarchical classification of all cross-shelf sites for the species assemblage of sponge populations. The major groupings are shown, each of which contains two or more depth groupings

The two deeper, inner-shelf sites have diverse sponge populations with high biomass, containing many species in common which are not evident on reefs further from shore (e.g. *Halichondria* sp. EP, *Xestospongia testudinaria* and sp. TL, *Ircinia* HW). The sites are, however, distinct because there are a number of species that are either unique to Pandora (Pa) or Phillips (Ph) or abundant on one and rare on the other (e.g. on Pa – *Dysidea* sp. DY, *Hyatella intestinalis*, *Chondrilla* sp. TR; on Ph – *Callyspongia* sp. AZ, *Iotrochota* sp. RE, *Jaspis* sp. YK). Deeper sites on the middle- and outer-shelf also contain large populations with relatively high biomass. The most abundant sponges on these reefs are foliose dictyoceratids (Wilkinson 1988) whereas the characteristic sponges on middle-shelf deep sites are *Haliclona* sp. BT, *Dysidea* sp. WF, and *Amphimedon* sp. BA and those on outer-shelf deep sites are species of the genus *Ircinia* spp. ID IT IU. The most abundant and characteristic species at all sites are represented in Fig. 4.

Classification of sponge populations at the ordinal/trophic level reveals several distinct patterns (Fig. 5). Dictyoceratids are the most prevalent sponges on the cross-shelf transect with a large proportion of heterotrophs (including the “mixed” category) on inner-, middle- and

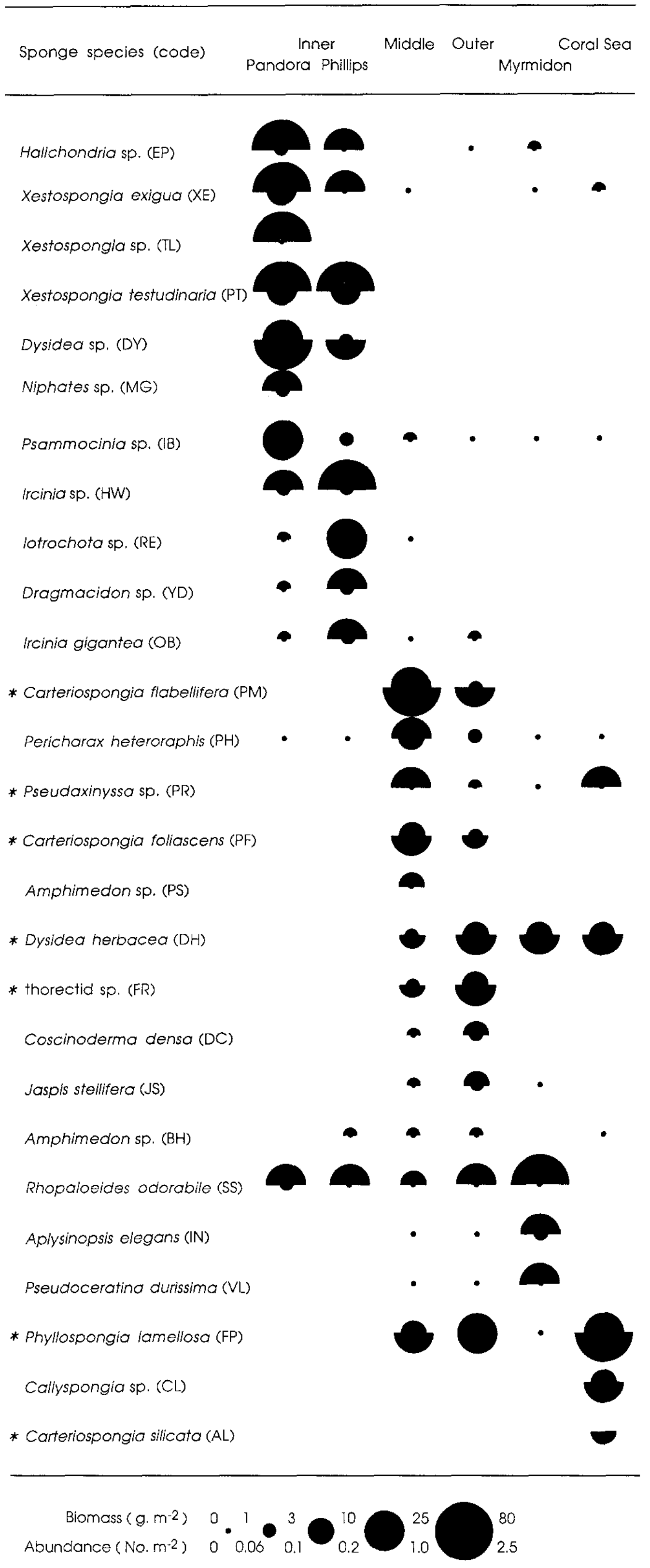

Fig. 4. Distribution patterns of the more prominent sponges on the fore reef slopes of reefs in the central Great Barrier Reef. Individual abundance (lower) and biomass (upper) data are presented proportionally from a mean of the major groupings represented in Fig. 3. Species marked * are those with predominantly phototrophic nutrition (Wilkinson 1983). The letters after each name refer to the authors' data base code

outer-shelf reefs and many phototrophs on all reefs except those of the inner-shelf. This trend reaches a maximum on the Flinders Reefs where phototrophic dictyoceratids comprise approximately 98% of the total sponge biomass at 15 and 20 m on the south east slope of Flinders South. On inner-shelf reefs there is also a predominance of heterotrophic Haplosclerida, Halichondrida and Poecilosclerida, whereas the only prevalent heterotrophs on the other reefs are dictyoceratids. Phototrophic axinellids (*Pseudaxinyssa* spp.) contribute significantly to the species assemblages in deeper water on middle-shelf and Coral Sea reefs.

Discriminant analysis of the sponge populations (with the species assigned to an Ordinal-trophic classification; Fig. 5) shows a distinct separation of sites into the

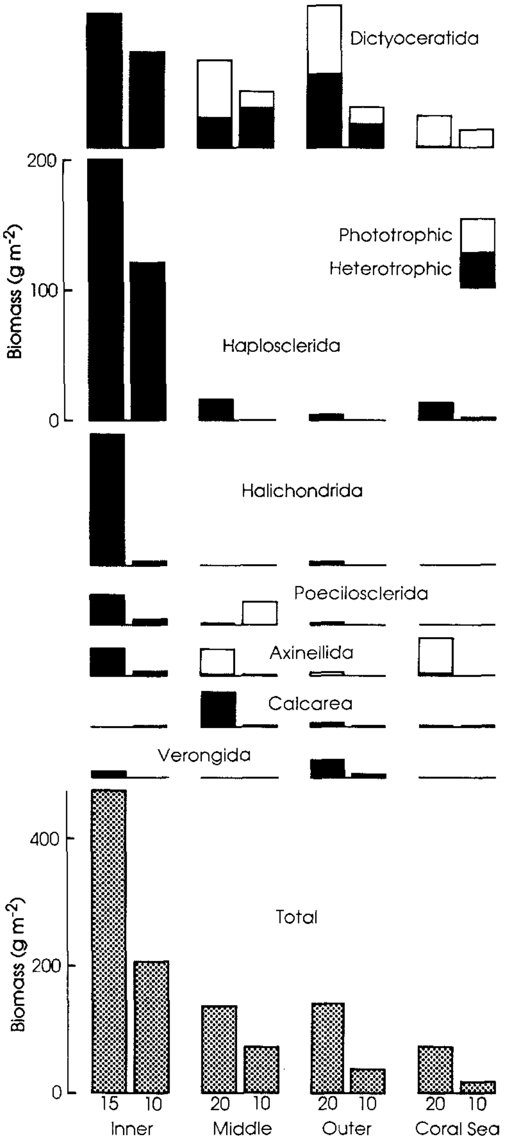

Fig. 5. Ordinal/trophic classification of biomass of sponge populations at 10 and 15 or 20 m depth on reefs (pooled) across the central Great Barrier Reef. All species were divided into two trophic groupings (phototrophic or heterotrophic plus mixed, in the sense of Wilkinson 1983) within sponge Orders using the taxonomic designations of Bergquist (1978). The total biomass (stippled) is included for comparison

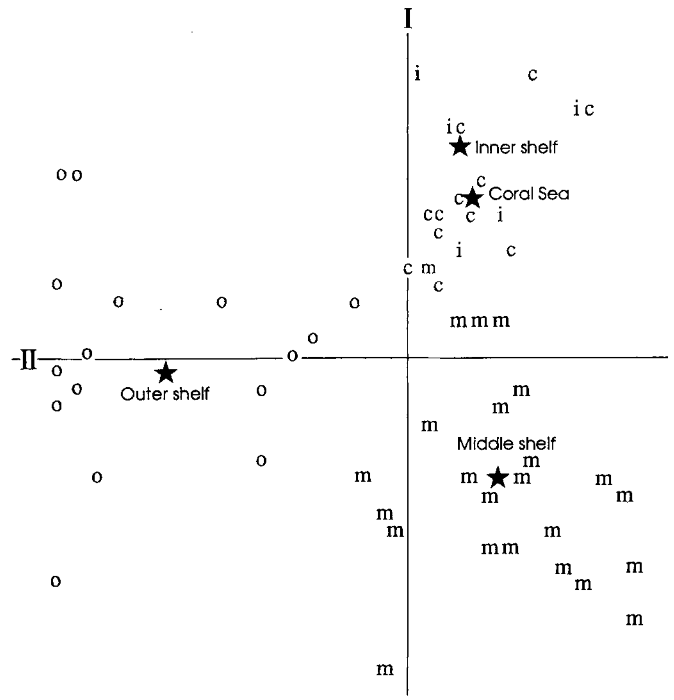

Fig. 6. A plot illustrating the differences in sponge community structure between sites across the central Great Barrier Reef. Sites have been plotted in multivariate space based on a discriminant analysis of community composition using the total biomass of each ordinal/trophic classification as represented in Fig. 5. Each depth site is represented by a code letter (i = inner-, m = middle-, o = outer-shelf, c = Coral Sea) with the stars representing the mean for each group. The third axis (III) is perpendicular to axes I and II but is not represented in the figure

Table 3. Results of the discriminant analysis represented graphically in Fig. 6. Actual Group represents the location at which population were surveyed; Predicted Group defines the site from which populations are predicted to have come on the basis of the ordinal/trophic classification. The incorrectly classified sites are Phillips 2 m (inner- as Coral Sea), John Brewer 15 m and Lodestone 5 m (middle- as Coral Sea), and Flinders West 15 m (Coral Sea as inner-); all based on low abundance data

Actual group	Correctly classified (%)	Predicted group membership			
		Inner-	Middle-	Outer-	Coral Sea
Inner-	85.7	6	0	0	1
Middle-	91.7	0	22	0	2
Outer-	100.0	0	0	14	0
Coral Sea	91.7	1	0	0	11
Total	93.0	7	22	14	14

four cross-shelf groupings (Fig. 6). This classification of sponge populations from all the reef sites resulted in the bulk of these sites classifying within the predicted groups (shelf location) with few exceptions (Table 3). The sponge populations from shallow water sites at the "hub of the wheel" (nearer the intersection of I and II) with the deeper sites clustering in groups along "spokes of the wheel" forming a "spiral" in space. The I and II canonical axes represent groupings of those sponge orders which result in the separation of the middle- and outer-shelf sites, whereas the III axis (vertical to I and II but not shown in Fig. 6) illustrates the variation along the full extent of the cross-shelf transect and shows a separation between inner-shelf and Coral Sea sites. The implied similarity of inner-shelf sponge populations and those of the Coral Sea (in the plane of I and II axes) is due primarily to a reduction in ordinal diversity at these locations as compared to middle- and outer-shelf locations.

Discussion

The biomass, abundance and species richness of sponges differ markedly with depth on reefs across the continental shelf of the central Great Barrier Reef. These quantitative parameters of sponge populations are related directly to depth with all increasing until approximately 20 m. Sponge biomass and species richness also show an apparent inverse relationship to the distance from land. These latter variations may be more appropriately expressed as direct proportional relationships to terrestrial influences from the Australian mainland *and/or* as inverse relationships to the influence of oligotrophic waters from the Coral Sea. These patterns, however, only apply for the obvious sponges with the small encrusting, cryptic and boring species being excluded. These exclusions would not affect the biomass patterns to any extent, but may affect the patterns of abundance and species richness.

The variation in sponge populations with depth on the cross shelf reefs is comparable with the pattern observed by Wilkinson and Evans (1989) on a middle-shelf reef in this region (Davies Reef). Here sponge populations increased from very few in shallow water to a maximum at approximately 20 m and then decreased in deeper water. There are few sponges within the first 10 m on any of the fore-reef slopes of the reefs examined. This resulted in these shallow water sites being distinguished from all the others during cluster analyses, but being grouped together because of the similarities of sparse populations (Figs. 3 and 6). Sponge populations were larger beyond 10 m depth at all locations across the continental shelf. This pattern is comparable with that shown for soft corals, with the largest populations occurring in deeper water as an apparent inverse correlation with hard coral abundance (Dinesen 1983).

Physical turbulence and, possibly, high levels of ultraviolet light are considered to be the major factors limiting sponge growth in shallow waters (Wilkinson and Evans 1989). Physical turbulence was considered to be the major factor limiting sponge populations in shallow temperature waters (Palumbi 1984) and also the factor for limiting soft coral growth in shallow zones of coral reefs (Dinesen 1983). Ultraviolet light may act to exclude some sponge species in shallow water as it has been shown that UV radiation adversely effects shallow water animals that are not protected by UV blocking compounds (Jokiel 1980). There are, however, extensive populations of sponges, particularly foliose dictyoceratids, growing in 1 to 3 m on parts of the reef flats protected from wave turbulence, immediately adjacent to the Flinders Reef sites (Wilkinson 1987 b). Therefore it is apparent that UV radiation does not exclude the most prevalent sponges, the foliose dictyoceratids (Wilkinson 1988), from the shallow parts of the fore-reef slopes of clean water reefs.

Sponges are larger, and more diverse on inner-shelf reefs than on reefs further from shore (Fig. 2). Furthermore, these inner-shelf sponges are taxonomically very different from those on the other reefs (Figs. 4 and 5) with the sponge nutrition being predominantly heterotrophic (Wilkinson and Trott 1985; Wilkinson 1987 a). These major differences coincide with two terrestrial influences not present on the outer reefs: land derived nutrient matter and terrigenous sediments. The two inner-shelf reefs are less than 20 km from shore and lie within the influences of a number of coastal rivers which periodically pour large amounts of land-derived organic and inorganic nutrients into the surrounding waters (Wolanski and Jones 1981). These nutrients are frequently resuspended back into the water column when moderate to strong winds result in sufficient turbulence to disturb the fine sediments in the shallow (<20 m) waters around these reefs (Walker and O'Donnell 1981; Ullman and Sandstrom 1987). The increased supplies of nutrient matter are the probable reason for the larger sponge populations on reefs close to shore. This is similar to the situation observed around large land masses in the Caribbean where there is extensive organic discharge (Wilkinson 1987 a).

There are significant variations in the deeper water (15–20 m) sponge populations between middle-shelf, outer-shelf and Coral Sea reefs (Table 1; Fig. 3) but these differences are less marked than those between inner-shelf reefs and the others. Sponge biomass and species richness decrease across the shelf in parallel with changes in the physical environments of those reefs (Fig. 1). Light transmittance and the degree of physical turbulence increase with increasing distance from shore (Done 1982; Wilkinson and Trott 1985) whereas the content of suspended sediments shows a reverse trend (Johnson et al. 1986). The most important change, however, is in the trophic structure of the populations. On the "clean" water reefs (middle-shelf to Coral Sea) approximately 50% or more of the sponges are phototrophic with much of their energy requirements derived from cyanobacterial symbionts (Wilkinson and Trott 1985). Such sponges are not evident on inner-shelf reefs where light penetration is markedly restricted. Thus, the incidence of phototrophic sponges is positively correlated with clean, oceanic-type waters with the highest proportion of phototrophic sponges occurring on the exposed slopes of the Flinders reefs, which are directly influenced by the oligotrophic waters of the Coral Sea (Wilkinson and Trott 1985; Wilkinson 1988).

The reduction in biomass and the change to populations characterized by large numbers of phototrophs on "clean" water reefs are attributed to two environmental factors. The amount of transmitted light to depths below 10 m is crucial to those sponges reliant on photosynthesis from symbionts (Wilkinson and Trott 1985). The overall reduction in biomass correlates with reductions in the amount of available organic matter in the seawater along the transect. Phytoplankton biomass is generally higher on inner- and middle-shelf reefs than those further from shore (Sammarco and Crenshaw 1984; Furnas and Mitchell 1986) and currents are stronger on average on outer-shelf and even higher on Coral Sea reefs (Andrews 1983) such that the excess primary productivity generated in the shallow waters on and around the reefs would be washed away with oligotrophic Coral Sea waters.

While the major differences in the nature and size of deep water sponge populations on reefs are determined by depth and factors acting at the scale of location on the continental shelf, there are significant differences between adjacent reefs within the same shelf location. These differences are most apparent between the two inner-shelf reefs and secondarily between Myrmidon and adjacent outer-shelf reefs. On the inner-shelf reefs, these differences are characterized by the prominence of several species on one of the reefs or markedly different amounts of some of the prominent sponges (Fig. 4). On Myrmidon Reef, many sponges that are prevalent on the other outer- and middle-shelf reefs are rare or absent e.g. the flattened, phototrophic dictyoceratids are particularly rare on Myrmidon Reef (Wilkinson 1988). Conversely, several species are prevalent that are rarely found elsewhere e.g. *Pseudoceratina* spp. The within-region differences may be due to variations in critical physical parameters (e.g. variations in the relative amounts of terrestrial vs oceanic influences) or to differences in water currents resulting in variations in larval recruitment and supplies of nutrient matter. The latter may apply for Myrmidon Reef which is situated on an extension of the continental shelf that projects out into the Coral Sea and into the East Australia Current (Fig. 1). Hence, Myrmidon Reef may not receive larvae of many sponge species because of this isolation.

Alternatively, the reasons for these differences between adjacent reefs may be due to stochastic developmental and temporal variations which can occur within populations which appear to be genetically similar (Lerner and Dempster 1962). Competitive interactions involving sponges are rarely observed and do not appear to be major influences determining the composition of the community, however, if such interactions interfere with life history parameters such as reproduction, the results can far outweigh the effects of major physical factors (the Montgomery Effect in White 1985). This study examined sponge populations at only one time, therefore it is essential to perform long term studies to determine whether the observed patterns are stable.

These marked differences in sponge populations across the continental shelf are comparable to other marked differences in the populations of hard corals

(Done 1982), soft corals (Dinesen 1983), and fishes (Williams 1982; Williams and Hatcher 1983) which are summarized in Wilkinson and Cheshire (1988).

Fish populations show significant cross-shelf variations with respect to species composition and nutrition. The largest populations of algal grazing fishes (30% of fish biomass) occur on outer-shelf reefs where algal productivity is highest, whereas the grazing fish population decreases (<10% of fish biomass) towards the coast where algal productivity is lowest (Williams and Hatcher 1983; Russ 1984; Williams et al. 1986). Algal biomass, however, shows an inverse pattern with highest biomass on inner-shelf reefs and lowest on the outer-shelf reefs (Wilkinson et al. 1984). Therefore, outer-shelf fish populations have a greater direct dependence on primary production than those on the inner-shelf. There is a direct parallel in sponges on clean-water reefs, where a greater proportion of the population is directly dependent on primary productivity from cyanobacterial symbionts (Wilkinson 1986).

Sponge populations vary considerably on reefs across the continental shelf of the central Great Barrier Reef with distinct changes in species composition, biomass, individual size and nutrition. These changes correspond to similarly marked changes in environmental parameters on and around the coral reefs. These changes reflect the strong influences of the land on inner-shelf reefs e.g. increased nutrients and sediments and lower levels of light penetration and physical turbulence, and the comparably strong influences of the Coral Sea at the edge of the continental shelf with lower levels of nutrients and sediments but increased light penetration and turbulence. Because sponges are relatively slow growing, the size and nature of the populations may be useful indicators of changes in environmental conditions acting over years to tens of years. This is apparently the case on some reefs in the Caribbean, where the size of sponge populations shows a direct relationship with increased input of organic pollution from human activities (Wilkinson 1987a).

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