9 Biodiversity on the Great Barrier Reef: Large-Scale Patterns and Turbidity-Related Local Loss of Soft Coral Taxa

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INTRODUCTION

Indo-Pacific coral reefs contain globally the highest level of biodiversity of any marine ecosystem, with the centre of this biodiversity located around the archipelago of Malaysia, Indonesia, and the Philippines. The Great Barrier Reef (GBR) is part of the Indo-Pacific biogeographic region, and contains a subset of the Indo-Pacific taxa found in the most species-rich areas farther north, as well as species that are not found anywhere else but on the GBR (Veron, 1995). Around 2800 coral reefs, extensive seagrass areas, species-rich soft- and hard-bottom inter-reefal and lagoonal ecosystems,

continental slopes, and pelagic ecosystems are all represented within the Great Barrier Reef Marine Park, which is the world's largest World Heritage Area (Wachenfeld et al., 1998).

Because of its vast size (348,000 km² area, stretching over 2000 km or 14° of latitude) and its high biodiversity, surveys and species inventories have been carried out only on a few taxonomic groups in small proportions of the marine park. Some areas are still uncharted even for shipping purposes. Large-scale systematic mapping of the major biotic groups such as scleractinian corals and fishes only began on a large scale in the 1990s. Other groups which are extremely species-rich, such as sponges, crustaceans, echinoderms, or molluscs, remain largely unmapped, although some of these taxa are likely to hold key positions in the ecosystem.

In this chapter we summarise the patterns in biodiversity for an abundant and species-rich group of organisms, commonly known as soft corals and sea fans, or octocorals (class: Octocorallia, Order Alcyonacea). Soft corals are sessile, perennial, and often long-lived corals. In contrast to the hard corals, they do not possess a massive external skeleton made of calcium carbonate; instead their colonies are supported by small calcareous needles or a hydroskeleton. Most "true" soft corals are phototrophic, i.e., they contain symbiotic algae (zooxanthellae) in their tissue which, depending on light, convert carbon dioxide into sugars, and thus supply the soft corals with energy. Most "sea fans" do not host zooxanthellae, thus their food depends entirely on material suspended in the water, a strategy called heterotrophy. Soft corals occur in high abundances on many types of coral reefs. They may numerically dominate reefs in turbid in-shore regions, as well as clear water reefs away from coastal influences (Benayahu & Loya, 1981; Tursch & Tursch, 1982; Dinesen, 1983; Dai, 1990; Fabricius, 1997).

Soft coral abundances and the number of soft coral taxa found at any location (richness) are subject to relatively strong physical control (Fabricius & De'ath, 1997). Like plants, they are inescapably subject to the light, wave, water quality, and sedimentary environment where they settled as larvae. Biotic controls, such as predation, or overgrowth by neighbours appear to be relatively ineffective for soft coral abundances. In contrast to the mass predation of hard corals by *Acanthaster planci* (De'ath & Moran, 1998), or mass "predation" of bêche-de-mer, trochus, giant clams, lobster, mud crabs, sharks, predatory fishes, turtles, and dugong (to name just some) by *Homo sapiens,* no large-scale mass mortalities are know for soft corals. The reasons for low biotic control are their high concentrations of toxic or feeding-deterrent metabolites (e.g., Coll et al., 1983; Sammarco et al., 1985; Maida et al., 1995) and low commercial value.

On the GBR, several hundred soft coral species coexist with around 350 species of hard corals (Cnidaria: Scleractinia; Veron, 1995). Space competition between the two groups may be important in areas of high densities but appears inconsequential in regulating abundances before crowding sets in (Bak et al., 1982; Fabricius, 1997). Competition is reduced because both groups occupy different trophic and physical niches. Differences between the trophic niches of hard and soft corals are related to two important morphological characteristics: First, efficient stinging cells allow hard corals to actively capture zooplankton as food. In contrast, the stinging cells of soft corals are poorly developed, hence their diet consists of predominantly small

suspended particulate matter and picoplankton (Fabricius et al., 1995a and b; Ribes et al., 1998; Fabricius & Dommisse, 2000). Second, the light-reflecting massive skeleton in hard corals is covered only by a thin layer of zooxanthellae-loaded tissue, providing for a high surface-area/volume ratio and hence very efficient photosynthesis in hard corals. In contrast, the photosynthetic efficiency of the phototrophic soft corals is low, due to the lack of a light-reflecting massive internal skeleton, and an unfavourably low surface-area volume ratio (Fabricius & Klumpp, 1995).

This chapter presents the large-scale patterns of biodiversity in soft corals (here used synonymously with taxonomic richness), and total hard and soft coral cover. Both abundances (cover) and biodiversity are being used to assess the state of ecosystems: low biodiversity and cover are both direct results of severe environmental conditions, and low cover also indicates a recent disturbance (Done et al., 1996). Low biodiversity can be the result of a high, or very low, frequency of episodic disturbance. In a frequently disturbed environment, speed of recolonisation determines whether a taxon survives or not, as slow-colonising or slow-maturing taxa will be unable to persist (Done, 1997). Under such circumstance, communities are characterised by low biodiversity and low cover, with an overrepresentation of young, fast colonising but competitively weak taxa. Occasionally, extended periods without disturbance allow competitively strong taxa to monopolise areas by slowly outcompeting and replacing the less defensive neighbouring taxa. Under such rare circumstance, the communities are characterised by low biodiversity but a high level of space occupancy, generally by large, old, and competitively strong individuals. The maintenance of a high level of biodiversity of tropical coral reefs is often attributed to an "intermediate" exposure to natural disturbances such as cyclones, floods, predators, or extreme temperatures, which relieve competition for space and facilitate the coexistence of a high number of species (Connell, 1976).

Water pollution and overfishing are the two major types of chronic man-made disturbance in coral reefs. Chronically, increased levels of runoff of sediments, nutrients, and pesticides impinge on coastal reefs, with wide-ranging effects on corals and other reef organisms (reviews in Pastorok & Bilyard, 1985; Rogers, 1990; Gabic & Bell, 1993; Wilkinson, 1999). Sometimes responses to these chronic disturbances are not obvious for several decades; however, a single severe disturbance event in a chronically disturbed area can trigger a phase shift from reef-building hard corals to non-reef-building taxa such as macro algae (Hughes, 1994; Done, 1992). Soft corals also established and monopolised space on some reefs after disturbance of hard corals, but such space monopolisation is restricted to a few taxa and a distinct type of reef habitat (shallow in-shore fringing reefs in moderately clear water: reviewed in Fabricius, 1998; Fabricius & Dommisse, 2000). It appears intuitive that chronic disturbance reduces diversity, because only few taxa will be robust enough to persist. The present study demonstrates that indeed the generic richness both of zooxanthellate and azooxanthellate soft corals is depressed in areas of reduced water clarity, one of the consequences of terrestrial runoff of nutrients and soils (Rogers 1990; Wolanski & Spagnol, in press). Such reduction in biodiversity will have to be considered in the debate of effects of chronic nutrient enrichment of in-shore reefs in regions of intense land use.

METHODS

FIELD METHODS

A large-scale biodiversity survey and species inventory program were carried out on the GBR between latitude 10 and 25°S. The surveys were designed to characterise patterns of biodiversity and physical conditions within the GBR, as a baseline for determining future trends and as a basis for identification of areas of highest protection value. The soft coral surveys were conducted on 161 reefs (~6% of the 2800 GBR reefs; Figure 1). On each reef, generally one to three sites (each in a different location, depending on time and accessibility) were inspected. Up to five transects were surveyed per site, each at a pre-defined depth-range (18 to 13 m, 13 to 8 m, 8 to 3 m, 3 to 1 m, and reef flat). All surveys were conducted by the first author, by scuba diving over a transect typically 200 to 300 m long and 1 to 3 m wide, for 10 to 15 min, or until no new taxa were encountered for several minutes. Longer transects were surveyed in areas of low visibility to compensate for a narrower field of view. A total of 1346 transects at 361 sites were investigated.

The surveys were carried out using a rapid ecological assessment technique (REA), based on abundance ratings of estimates of substratum cover in six ranked categories (initially developed for vegetation analyses by Braun-Blanquet (1964). REA was chosen rather than the more conventional belt and line transects because of its advantages in terms of area surveyed, time requirements, and the superior representation of rare and heterogeneously distributed taxa (the majority of taxa are rare in highly diverse communities). A wide variety of REA methods have been developed, assessed, and successfully applied to coral reef benthos surveys since the 1970s (e.g., Kenchington, 1978; Done, 1982; Dinesen, 1983; Miller & De'ath, 1995; Devantier et al., 1998); we followed a protocol similar to that of Devantier et al. (1998).

During the survey and after completion of each transect, the following data were recorded:

1. Relative abundances of taxa: 0 = absent; 1 = one or few colonies; 2 = uncommon; 3 = common; 4 = abundant; and 5 = dominant. Soft corals were surveyed mostly at generic rather than species level because a substantial proportion of species are still undescribed, and species identification requires a microscopic examination, which is unsuitable for large-scale field surveys. Samples of unknown or uncertain colonies were collected and later identified. Of the 61 genera recorded on the GBR, only the 40 most common taxa were recorded in the early phase of the surveys, and for consistency only these 40 taxa were included in the present analyses.
2. Visual estimates of overall abundance (percent total cover) of soft corals and hard corals. Cover was estimated in 2.5% increments from 1 to 10%, in 5% increments from 10 to 30%, and in 10% increments for >30% cover. An assessment of the precision of visual estimates of life coral cover indicated that differences between experienced observers were not significant (Miller & De'ath, 1996).

3. The following abiotic variables were estimated at all sites:
   a. Sediment deposit on the reef substratum (particle sizes ranging from very fine to moderately coarse), rated on a 4-point scale: 0 = none, 1 = thin layer, 2 = considerable amount of sediment which could be completely resuspended by fanning, and 3 = thick, deep layer of sediment.
   b. Turbidity (measured as visibility, in meters). The method was a modified Secchi disc technique, in that the maximum visible distance of a bright object was estimated horizontally at each survey site. A horizontal distance was preferred over the traditional vertical Secchi distance, as the former is not affected by shallow depths (on outer-shelf reefs, the bottom is often visible from the surface), and by surface refraction (thus estimates are less affected by the azimuth of the sun, cloud cover, and wave height).

ANALYTICAL METHODS

The first set of analyses was carried out on reef-averaged data, which is the relevant scale for management and conservation of biodiversity. We modelled spatial variation in richness, soft and hard coral cover, and physical variables using generalised additive models (Hastie & Tibshirani, 1990). Loess smoothers (Hastie & Tibshirani, 1990) were used to fit smoothed effects of both spatial and physical variables. The degree of smoothness was minimised but sufficient to account for both spatial effects and spatial correlation. The statistical software S-PLUS was used for all data analyses (Statistical Sciences, 1995).

Latitude and longitude would normally be used for the spatial component of such models. However, the GBR runs from ~SE to NW, and physical and ecological gradients, which run typically across and (to a lesser degree) along the shelf, are therefore tilted 45° to the geodesic system. To improve the analysis and graphical representation of the spatial patterns, the latitude/longitude data were converted into relative distance across and along the GBR (Figure 2). Relative distance across the GBR (henceforth: "across") is defined as the distance of a site to the coast, divided by the sum of distances to the coast and to the outer edge of the GBR. Relative distance along the GBR (henceforth: "along") is similarly defined as the distance to the northern end of the GBR divided by the sum of distances to the northern and southern ends of the GBR. This has the effect of mapping the GBRMP to a rectangle, or unit square if we assume that units across equate to units along (Figure 2). The coordinates of the across–along system are locally orthogonal and run at right angles and parallel to the coast, taking advantage of the fact that many processes are affected by the natural geometry of the GBR. Such presentation gives better resolution particularly of the steep gradients across the narrow shelf of the northern GBR.

Depth-related patterns were investigated at transect level, after dividing the data into groups representing six GBR regions (Figure 1): the northern and southern reefs, and three cross-shelf categories. The along-shore split was set at 19.5° latitude a zone of transition for soft coral communities (unpublished data). The northern 55% along included 901 transects, and the more homogenous southern 45% contained 445

transects. Splits across the shelf were set at 38 and 85% of across, with those reefs <38% representing the in-shore reefs, 38 to 85% representing the mid-shelf, and those >0.85% across classified as outer-shelf reefs.

RESULTS

SPATIAL PATTERNS IN SOFT CORAL RICHNESS, AND THE INFLUENCE OF TURBIDITY AND SEDIMENTATION

Total soft coral richness was consistently highest on mid-shelf reefs, and declined steeply toward the in-shore, and to a lesser extent toward the outer-shelf reefs (Figure 3). Along the shelf, richness was highest between 14 and 18°S, and declined slightly toward the north, and more strongly toward the south. The north-to-south decline was most pronounced on mid- and outer-shelf reefs (reduction from 25 to 15, and 22 to 13, respectively), and less so on near-shore reefs (reduction from ~12 genera in the north to ~8 in the south). The "hotspot" of soft coral biodiversity on the GBR was north of Cairns on the mid-shelf reefs, where up to 27 of the genera were recorded on individual reefs. Richness was lowest (~8 genera per reef) on the southern in-shore sites. Richness was well explained spatially, with 59.6% of variation explained by the smooth surface (df = 14.4).

Both water turbidity (visibility) and sediment deposits showed significant relationships with total richness when added to the spatial model. The required degree of spatial smoothing decreased substantially (from 14.4 to 8.4 df), suggesting the physical variables accounted for local variation previously unexplained by the more flexible spatial smoother. Visibility affected soft coral richness particularly strongly. Richness was highest in areas where visibility was 10 m or greater, and declined sharply in areas of <10 m visibility (Figure 3). The relationship of total richness to visibility was non-linear and negligible in areas of >10 m visibility. In all other areas, richness declined by ~1 taxon for each meter reduction in visibility. For example, two reefs in the same region (i.e., similar across and along location), with visibilities of 10 and 5 m, would be likely to differ in richness by five genera. Visibility on its own explained ~22% of the total variation in richness (Figure 4). Sedimentation also affected generic richness, although to a weaker extent than visibility (Figure 3). Richness increased linearly with increasing sedimentation, with an increase in sediment deposits of 1 rating increasing richness by 1.5 genera (4.3% of variation was explained by sedimentation alone; Figure 4).

The pattern in richness of zooxanthellate taxa largely matched that of the richness of all taxa (Figure 5), as was expected since 28 of 40 taxa were zooxanthellate. Richness of zooxanthellate taxa was greatest on the mid-shelf north of Cairns, and depressed on in-shore reefs north of Townsville (relative distance along = 0.45 to 0.8). Richness of the zooxanthellate taxa was affected by turbidity, similar to the effect on the total richness: richness declined by ~0.7 taxa m^{-1} at a visibility <10 m (Figure 5). Again, effects were negligible at levels of >10 m visibility. However, sediment had no effect on the richness of zooxanthellate taxa.

There were pronounced spatial differences in richness of the light-dependent zooxanthellate taxa and the light-independent zooxanthellae-free taxa. Richness of

zooxanthellae-free taxa almost continuously declined from north to south (Figure 6). Cross-shelf patterns were weak, but richness was slightly higher on the mid- and inner-shelf than on the outer-shelf. The in-shore area north of Townsville (poor in zooxanthellate taxa) was particularly rich in zooxanthellae-free taxa. Very few zooxanthellae-free taxa were recorded in the southern mid- and outer-shelf reefs. Effects of visibility on richness of the zooxanthellae-free taxa were again similar to those on the total richness, being negligible at levels of >10 m. Richness of zooxanthellae-free taxa declined by ~0.2 taxa m^{-1} decrease in visibility (Figure 6). Sediment again had no effect on richness. Of a total of 54% variation of richness of the zooxanthellae-free taxa explained by a combined spatial and physical model, 9% were explained by visibility on its own (Figure 7). In contrast, visibility explained 33% of variation in richness of the zooxanthellate taxa (total variation explained by the combined model: 63%).

SPATIAL DISTRIBUTION OF TURBIDITY AND SEDIMENTATION

Visibility was strongly related to relative distance across the shelf (Figure 8). This pattern was stable and emerged despite the noise of natural seasonal and wind-related variability. Lowest visibility (~4 m) was recorded on the innermost part of the shelf between Townsville and Cape Flattery (0.45 to 0.75 along, 0 to 0.2 across). Visibility was also low across the inner 40% of the wide shelf of the Broad Sound/Keppel Island region (~0.1 to 0.25 along, 0 to 0.4 across), where tidal ranges exceed 5 m. Both on mid- and outer-shelf reefs, the southern reefs tended to be more turbid than those farther north. Along-shore differences were most pronounced on the outer-shelf reefs: in the north, outer-shelf reefs had visibility of ~30 m, compared with only ~10 m in the south. Visibility was also related to the amount of sediment deposited on a reef. While the combined spatial and sediment model explained 85% of the variation in visibility, the spatial model on its own accounted for 83%, and sediment on its own for 57% of the variation (Figure 9).

Sediment deposits showed somewhat complementary cross-shelf patterns to that of visibility, with highest values along the coast between Bowen and the Daintree River, and lowest values on the outer-shelf reefs of the northern half of the GBR (Figure 8). The spatial model explained 66% of variation in the data (Figure 9).

PATTERNS IN SOFT AND HARD CORAL COVER

Soft coral cover was greatest (~30%) in the area covering the Whitsunday to Palm Islands groups (Figure 10). It was low in-shore in the area extending from south of Townsville to the Daintree River in the north. It was also low on the outermost reefs in the southern corner (Pompeys and Swains), and on the northern mid- and outer-shelf reefs. The spatial model explained 46% of variation in soft coral cover. Soft coral cover was unrelated to sedimentation and visibility.

Hard coral cover tended to increase with increasing distance from the coast (Figure 10). It was highest (mean: 35%) on outer-shelfs between Townsville and Cape Tribulation (0.5 to 0.7 along). The area of lowest cover was between the Whitsundays and the Broad Sound (0.3 to 0.4 along). Hard coral cover averaged <5% on 11 of the 161 surveyed reefs. The contribution of soft corals to the total

coral cover was high in the central GBR on reefs located 30 to 40% across the shelf. The spatial model explained only 21% of the variation in hard coral cover, and sedimentation and visibility did not explain additional variation (Figure 11). The proportion of soft coral cover to total cover followed from the patterns of soft and hard coral cover; it was again unrelated to sedimentation and visibility (Figures 10 and 11).

The relationship between site-specific soft coral richness and soft and hard coral cover within individual transects is shown in Figure 12. This analysis was done on transect level, since biotic variables are expected to interact locally. Soft coral richness increased with soft coral cover in areas <8% soft coral cover, but remained at ~10 genera per transect, independently of soft coral cover, where soft coral cover exceeded 8%. Soft coral richness was highest in areas of ~10 to 20% hard coral cover, and gradually declined toward 50% lower values in areas with very low or very high hard coral cover.

DEPTH-RELATED PATTERNS

Soft coral richness, defined here as the number of soft coral genera found at a site (depth zone), varied to a greater extent within the upper 18 m of depth, than within the 40- to 200-km distance across, and 2500 km along the shelf (Figure 13). Variation (22%) was explained by depth on its own, whereas across and along together explained 15%. Site-specific soft coral richness increased with depth at all shelf positions both in the north and the south (Figure 14).

Visibility was purely a function of shelf position and was independent of depth (Figure 14). On in-shore reefs both in the north and the south, visibility averaged 7 m (range: 0.5 to 18 m). Visibility on the northern mid-shelf and the southern mid- and outer-shelf was about twice those of the in-shore, and on northern outer-shelf reefs, visibility averaged 26 m.

The amount of sediment deposited on a reef site increased with depth and with decreasing distance to the shore (Figure 14). The thickest sediment deposits were found at or below 10 m depth on inner-shelf reefs. Sediment on deeper (10 to 15 m) mid- and outer-shelf sites was similar (mean of 0.8 to 1.2) to those of very shallow in-shore sites (0.8 to 1.2). The outer-shelf sites in the north had very low sediment levels at any depth, and in the southern half there was no difference in sediment deposits between mid- and outer-shelf reefs.

Mean total cover of soft corals and hard corals was strongly related to depth (Figure 15). On the northern GBR, the depth of greatest mean soft coral cover moved down-slope with increasing distance from the coast: on inner-shelf reefs, cover was greatest at 2 to 5 m depth (20% cover), on mid-shelf reef at 10 m (12%), and on outer-shelf reefs at ~15 m depth (17%). On the southern GBR, this pattern was maintained, except for inshore-sites at 15 m with high cover, attributable to dense soft coral stands at many sites on the Whitsunday Islands group.

Hard coral cover was a function of depth at any location across and along the shelf (Figure 15). Differences between the northern and southern sector were small. At all locations, hard coral cover was highest on the reef crests, dropping to lower values on the reef flat, and decreasing continuously with increasing depth on the outer reef slopes. Highest values were 43 and 38% on crests of outer-shelf of the northern and the southern reefs, respectively.

The contribution of soft coral cover to total coral cover (soft corals plus hard corals) increased with depth (Figure 15). It varied from around 40% to over 60% on the inner-shelf, between 15 and 43% on mid-shelfs, and 10 to 40% on the outer-shelf reefs. On mid- and outer-shelf reefs, it tended to be higher in the northern than in the southern part of the GBR.

DISCUSSION

The generic richness of soft corals changed over three spatial dimensions: down the reef slopes, across the continental shelf, and along the GBR. Additional differences in richness between neighbouring reefs were explained by water turbidity, and to a weaker extent by sediment deposition on the reef. Within any given area, more turbid reefs had lower soft coral richness than reefs closeby in clearer water. Similarly, reefs with higher sediment deposits were associated with slightly higher soft coral richness. The richness of both zooxanthellate and zooxanthellae-free taxa was affected by turbidity, indicating that effects were not only related to reduced light exposure (the larvae of zooxanthellae-free taxa often settle in low-light environments).

On coral reefs of the GBR, two well-described patterns in the distribution and abundance of biota are (1) depth zonations and (2) zonations across the shelf according to distance to the land and the edge of the continental shelf (Done, 1982; Williams, 1982; Dinesen, 1983). Depth and distance to the land are in themselves not causal but act as proxies for a range of co-varying abiotic and biotic environmental variables such as turbidity, sedimentation, light, and wave exposure. The complex interactions between such variables are not easily separated.

Patterns parallel to the coast and along the GBR are less understood than depth zonations and cross-shelf differences, as few consistent and spatially comprehensive data sets exist to date. A general decline in biodiversity on coral reefs away from the equator has long been recognised. Gradients in sea surface temperature and associated seawater chemistry, restricted larval transport through ocean currents after the ice age, and variations in rates of recruitment have been discussed as underlying mechanisms (Veron, 1995). In the soft corals, three taxa (Clavularia, Pachyclavularia, and Heliopora) were not recorded south of ~20° latitude, however another three taxa (Pinnigorgia flava, Plumigorgia, and Isis hippuris) were common in the south but rarely encountered north of 16° latitude (Fabricius & De'ath, 2000). Therefore, the decline in soft coral richness toward the south was not generally due to the complete absence of particular genera, but due to less frequent encounters of a wide range of taxa. The centre of richness of zooxanthellate soft corals coincided with the area of the GBR where a branch of the South Equatorial Current brings tropical water from the Solomon Islands and Vanuatu across the eastern Coral Sea. The current splits and bifurcates between 14 and 18° latitude (depending on season), and water (and larval) movement is unidirectional toward both the north and the south from the point of bifurcation (reviewed in Wolanski, 1994). It is unknown how these currents affect dispersal and richness, but interestingly, species richness in hard corals on the GBR is also highest in the same region, declining slightly toward the north and steeply toward the south (Veron, 1995). The issue is complicated by the fact