that the richness of zooxanthellae-free taxa showed a clear north–south gradient, unrelated to that of the zooxanthellate hard and soft corals.

The total cover of soft and hard corals on the GBR remained uninfluenced by turbidity and sedimentation. This finding indicates the potential for species replacements: in certain circumstances, turbidity-tolerant taxa fill in the space for less tolerant taxa, so cover remains the same but diversity declines. It also highlights the need for detailed taxonomic inventories when conditions of coral reefs are to be assessed. Total cover, which is the only parameter assessed in some environmental studies, appears unsuitable for indicating changes such as increasing turbidity in the reef environment until high very levels are reached (e.g., Devantier et al., 1998; Morton, 1994). This is an important finding to consider when environmental impact studies or reef monitoring data are interpreted.

Water quality is a key parameter in the ecology of reef benthos and may account for differences in distribution and abundance of filter feeders such as soft corals. Annual mean concentrations of particulate nutrients and chlorophyll increase toward the shore (Furnas & Mitchell, 1986; Liston et al., 1992; Revelante & Gilmartin, 1982) and toward the more temperate southern parts of the GBR (Furnas, in preparation). Many octocorals are relatively inefficient in photosynthesis and depend on high levels of irradiance and additional food intake to cover their carbon demand (Fabricius & Klumpp, 1995). Turbidity negatively affects light availability but may represent a gain of suspended particulate food for organisms which are able to use it (Anthony & Fabricius, in press). The relationship with sedimentation is more complex: reefs completely free of sediment are generally also particularly wave-exposed or have steep slopes so sediment accumulation is reduced (Fabricius & De'ath, in press), which could contribute to the lower richness found on low-sediment reefs than neighbouring reefs with the same visibility but more sediment.

The question whether increased runoff affects turbidity on the GBR is still controversial. Larcombe and Woolfe (1999) suggest that turbidity and rates of sedimentation do not increase with runoff, because rates are driven by the physical environment (wave-related resuspension) and are limited by the surface area of deposition. On the other hand, water clarity in a flood plume is severely reduced, although the suspended material adds relatively little to the overall sediment weight (a "visually spectacular" plume often contains only a few mg l^{-1} suspended solids at greater distance from the river mouth; discussed in Larcombe and Woolfe, 1999, based on data from Taylor, 1996). While the coarse fraction settles out close to the river mouth, the muddy, light, and nutrient-enriched sediment fraction may remain in the system for months after discharge, where it will go through many cycles of deposition and resuspension before being metabolised or trapped in a north-facing embayment. Enhanced phytoplankton production due to the release of nutrients contributes further to increase turbidity.

Wolanski and Spagnol (in press) reported of the declining visibility on Low Isles, a coastal reef off Cairns (~16° 23′ S, 145° 34′ E). This island was investigated in detail in 1927/1928, and a mean visibility of ~11 m was recorded over a 6-month observation time. Today, maximum visibility rarely exceeds 8 m, and the mean is estimated to be around 6 m (Wolanski & Spagnol, in press; Bell & Elmetri, 1995; and our own observation over 10 days in three visits). Such change in visibility equals a loss of ~5 soft coral genera (Figure 4). We produced a simple and tentatively soft coral biodiversity response model to visualise the long-term effects of this change in water clarity on the generic diversity of reefs around Low Isles (Animation 1). The model was based on the following assumptions: pollution originated at the wet tropics coast at 0.6 along-shore distance, events were discrete pulse discharges of suspended particles, which were diluted with distance from the source while spreading radially. The response was modelled based on the non-linear relationship depicted in Figure 4. Wave- and depth-dependent settlement/resuspension cycles were ignored for simplicity. We started at the status of present-day visibility using our recorded visibility and richness data, and created a scenario in which coastal visibility dropped progressively to <3 m. Reduction in richness was noticeable well into the mid-shelf region. The present-day centre of soft coral diversity, located on the mid-shelf north off Cairns, diminished progressively, and disappeared except on the far northern edge of the GBR at increasing levels of turbidity. Although such decrease in visibility is hypothetical, the model nevertheless points at the importance of protecting the water quality in the wet tropics for a long-term preservation of biodiversity on the GBR.

The world presently faces a global biodiversity crisis, with highest levels of species extinctions recorded at least since the Cretaceous period. An estimated 100 species of animals and plants are being eradicated every day in terrestrial systems. Next to nothing is known about species extinctions in marine realms, and the understanding of patterns in biodiversity of coral reefs is rudimentary at best. Coral reefs are under increasing pressure worldwide, with a large proportion of coral reefs being already severely degraded, or at risk of degradation (Wilkinson, 1999). Three types of human activities are principal causes for reef degradation: Firstly, extensive land clearing, sewage discharge, and agricultural runoff affect coastal reefs by means of increased sediment and nutrient loads. Secondly, fishing is so intense and destructive in more densely populated regions that recruitment overfishing and downstream effects on abundances of macroalgae and corals have been recorded (Hughes, 1994; McClanahan et al., 1996). Thirdly, the frequency of bleaching and often death in all zooxanthellate organisms, including hard and soft corals, is currently increasing due to increasing maximum summer sea surface temperatures as a result of greenhouse gas emissions (Hoegh-Guldberg, 1999). Many taxa have pelagic larvae, thus reefs of the GBR which are numerous and connected by ocean currents may be replenished by larvae from undisturbed areas farther upstream. More isolated reefs are not as likely to experience recolonisation by pelagic larvae, and local extinctions in such oceanic atolls are likely (Wilkinson, 1999). The establishment of protected areas, which act as sources of larvae for exploited or disturbed areas, is the most promising approach for the local protection of coral reef biodiversity. At the same time, the health of coastal reefs is intricately linked with land management, and protected areas can only fulfil their role if deterioration of water quality is avoided by appropriate coastal zone and catchment management.

We do not know whether any keystone taxa are represented among the soft corals which are missing in areas of high turbidity (these are, in particular, members of the family Xeniidae). We also do not know how key functional processes (e.g., the chemical micro-environment on the reef, as soft corals constantly release anti-fouling substances [Maida et al., 1995], or competition with other benthos groups) are affected by the presence or absence of certain soft coral taxa. The study may serve as an example of the complexity of responses and relationships in coral reefs. In the presence of such sparse knowledge the precautionary principle in managing the adjacent land and preventing influx of nutrients and soils should prevail.

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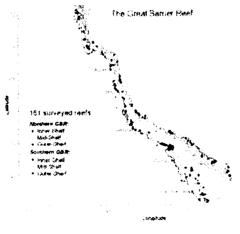


FIGURE 1 Map of the GBR indicating the locations of the sampled reefs. Colour codes define the position of the sampling points on the continental shelf: inner-shelf reefs are located on the innermost 38% of the shelf width, mid-shelf reefs are at 38 to 85%, and outer-shelf reefs are >85% across the shelf. Southern reefs are all reefs <45% along the shelf, with the northern reefs representing the remaining 55%.

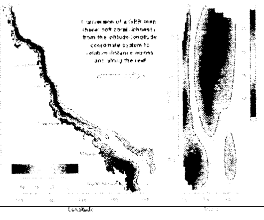


FIGURE 2 A spatial plot of soft coral richness, using the traditional geodesic coordinate system (latitude–longitude), and for easier viewing, in the coordinate system based on relative distance of a reef across and along the GBR shelf (right). A local regression spatial smoother was used to model richness, and the fitted surface was then mapped back to latitude–longitude coordinates.

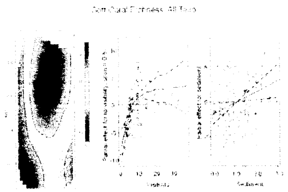


FIGURE 3 Left: Spatial plot of soft coral richness (number of genera encountered per reef). Local regression spatial smoothers were used for the spatial plots. Middle and right: Partial effects of visibility and sedimentation on soft coral richness. The red line is the partial effect (i.e., the effect of the explanatory variable holding all other explanatory variables constant), estimated by a local regression smoother (loess, span of 0.5) (left panel), or by a linear model (right panel). The blue dashed lines represent 95% confidence intervals, and the orange dashed line indicates the no-effects level. The points represent the residuals.

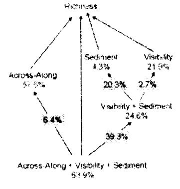


FIGURE 4 Proportion of variation in total soft coral richness explained by spatial (left arrows), physical (right arrows), and a combination of spatial and physical variables (central arrow).

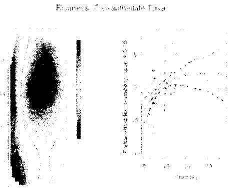


FIGURE 5 Left: Spatial plot of richness of zooxanthellate soft coral taxa. Local regression spatial smoothers were used for the spatial plots. Right: Partial effects of visibility on soft coral richness. For detailed legend see Figure 3.

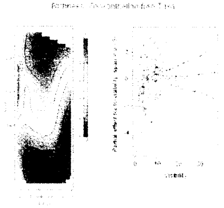


FIGURE 6 Left: Spatial plot of richness of zooxanthellae-free soft coral taxa. Local regression spatial smoothers were used for the spatial plots. Right: Partial effects of visibility on soft coral richness. For detailed legend see Figure 3.

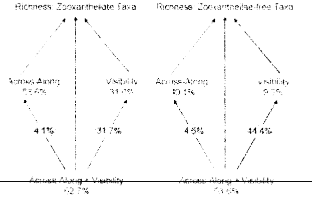


FIGURE 7 Proportion of variation in generic richness of zooxanthellate (left) and zooxanthellate-free (right) soft corals explained by the spatial variables and visibility.

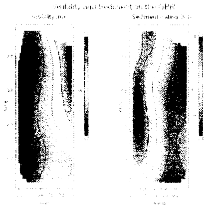


FIGURE 8 Spatial plot of turbidity (measured as Secchi visibility) and of sediment deposits on the reefs.

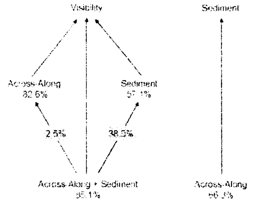


FIGURE 9 Proportion of variation in visibility and sedimentation explained. Variation in visibility was related to spatial variables (left arrows) and sedimentation (right arrows). Variation in sediment was explained by only spatial variables.

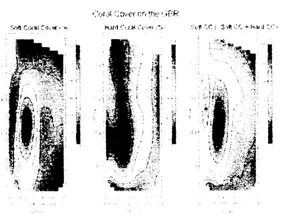


FIGURE 10 Spatial plot of soft coral cover, hard coral cover, and the proportion of soft corals of the total coral cover (soft coral plus hard coral cover).

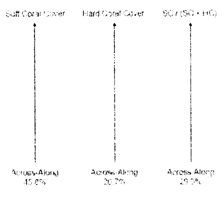


FIGURE 11 Soft coral cover, hard coral cover, and the proportion of soft corals to total cover explained by spatial variables. Physical variables had no effect on cover.

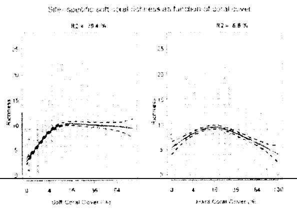


FIGURE 12 Relationship between site-specific soft coral richness, and soft coral cover (right) or hard coral cover (left). The solid line represents smooth fit (df = 4, $R^2 = 28.9$). Dashed lines are 95% confidence intervals.

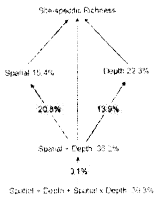


FIGURE 13 Proportion of variation in site-specific soft coral richness explained by spatial (left arrows), depth (right arrows), and a combination of spatial and physical variables (central arrow).

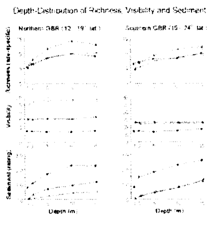


FIGURE 14 Mean levels of site-specific soft coral richness (number of genera per site), turbidity (visibility, in metres), and sediment (rated on a 4-point scale) as a function of depth and shelf position. Values are means, error bars represent 1 standard error. Orange line, filled squares = inner-shelf; green line, filled triangles = mid-shelf; and blue line, open circles = outer-shelf reefs.

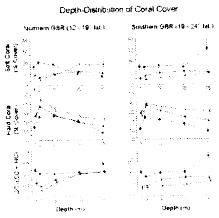
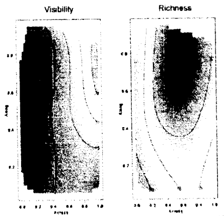


FIGURE 15 Mean levels of soft coral cover, hard coral cover, and the ratio between soft coral cover and total coral cover (hard corals plus soft corals) as a function of depth and shelf position. Values are means, error bars represent 1 standard error. Orange line, filled squares = inner-shelf; green line, filled triangles = mid-shelf; and blue line, open circles = outer-shelf reefs.



ANIMATION 1 Model of response in soft coral richness (number of genera per reef; right panel) to progressively decreasing water clarity (left panel). The green dot indicates the location of Low Isles.