

Phase shifts in coral reef communities and their ecological significance

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Abstract

Many coral reefs around the world have degraded to a degree that their present intrinsic value and utility are greatly reduced: (mass coral mortality followed by algal invasions; local depletions of reef fisheries; deficit of reef accretion compared to physical and biological erosion). Though we can sometimes identify proximal causes (outbreaks of coral predators and eroders; over-fishing; habitat destruction), we do not have a good understanding of how population, community and ecosystem structure and function differ in degraded from un-degraded reefs. The deficiencies in our understanding limit our ability to interpret the long-term significance of reef degradation, and therefore to develop scientifically based plans for conservation and management of reefs.

A particular course of action, or lack of action, based on uncritical acceptance of any of the various views of temporal variability can lead to further deterioration of specific reefs. None of these views – that reefs are either inherently robust, inherently fragile, or inherently resilient – is true over all time-space scales. This presentation reviews various models and case studies which suggest that reefs can be knocked precipitously or move slowly from one phase (coral-dominated) to another (coral-depleted and/or algal dominated). Transitions in the other direction ('recovery') involve changes (e.g. succession) in populations and communities (of all reef-associated biota, not just sessile benthos), and in reef function (e.g. community metabolism, trophodynamics) which are of great intrinsic interest but only poorly understood.

Introduction

We often hear coral reefs described in words something like these: oases of high diversity and productivity in oceanic deserts; builders of their own habitat; objects of great beauty. And yet just as frequently, it seems, we hear of yet another reef which has become 'degraded' in some way (e.g. Brown, 1987; Salvat, 1987). Reef degradation has many causes, both episodic disturbances of short duration (e.g. storms, outbreaks of coral predators; brief exposure to toxic pollutants; siltation caused by dredging), and chronic disturbances of

long duration, frequently anthropogenic. Hatcher *et al.* (1989) reviewed anthropogenic effects on coral reefs under 9 categories: sedimentation; sewage pollution, thermal pollution, radioactive pollution; hydrodynamic influences; physical disturbance; extractive activities; introductions; tourism. The scale of reef degradation ranges from the immediate vicinity of a marina development or sewage outfall, to a significant proportion of the reefs within large systems such as the Great Barrier Reef (GBR) or the Florida Keys. For example, populations of the coral eating crown-of-thorns starfish *Acanthaster planci* seeded suc-

cessive reefs in a north/south sequence over the decade 1980–90, causing serious damage to 65% of reefs surveyed in a 500 km section of the 2000 km long GBR (Moran *et al.*, 1988). By the time those in the south were attacked, there had been substantial coral recovery in the north (Done *et al.*, in prep.).

In this presentation, I discuss what degradation means. What are its symptoms and what is its significance in relation to ‘normal’ temporal variability in coral reef ecosystems?

The one universal symptom of coral reef degradation is mass coral mortality followed by an invasion of coral skeletons by algae. This is the ‘phase shift’ referred to in the title of this presentation. Associated with such a change, there may be significant depletions of reef fisheries, and a deficit of reef accretion compared to physical and biological erosion. Thus the reef is degraded in terms of its physical attractiveness, its fisheries yield and its ability to retain its integrity as a breakwater protecting adjacent shorelines. Clearly, the potential social and economic implications of reef degradation will depend on how long the reef remains degraded.

The following two quotations define some of the important ecological issues and points of disagreement about the significance of phase shifts in coral reefs. Referring to the entire Great Barrier Reef system (some 2900 reefs stretched over 2000 km), Davies (1988) says:

‘Its uniqueness is related to its robustness and its ability *always* to regenerate after catastrophes’ (italics added).

Referring to algal invasions of previously coral dominated areas of individual reefs, Hatcher *et al.* (1989) state:

‘Evidence is accumulating that coral reef benthic community structure can assume at least two stable forms: one coral-dominated and one macroalgae-dominated’.

A switch to macroalgal dominance which lasts years to decades constitutes a fundamental change in the benthic community structure of the reef with implications for the trophic structure of

the reef and its resource value to human populations (Dahl, 1974). A more protracted switch (decades to centuries) has major implications for reef maintenance and growth, whenever calcium carbonate losses to physical and biological erosion are not replaced by calcifying organisms such as corals and coralline algae.

Ecological and human consequences of phase change

The implications that extensive changes from coral to algal dominance have for the reef’s trophic structure and resource value to human populations have received little systematic study. Most or all the increased algal production may be dislodged by storms, thence being exported from the reef (Carpenter, 1990a) or entering benthic microbial communities on the reef (Moriarty *et al.*, 1985; Hansen *et al.*, 1987). In poorly flushed areas, accumulation of algal detritus could lead to excess biological oxygen demand and anoxic conditions inimical to survival of some higher reef biota (Johannes & Betzer, 1975). Not surprisingly, the worst reported community calcification rates on reef flats were recorded on coral/algal reef flats dominated by macroalgae – viz. at Tulear, Madagascar, and Moorea (Pichon & Morrissey, 1985; Sournia, 1976; both cited in Kinsey, 1985).

Increased macroalgal production may affect harvestable secondary production of herbivorous fish and invertebrates, and their fish predators. Fish production can be increased, either as an increase in population size (Carpenter, 1990b) or fish growth rates, in situations where food was previously limiting. However it may be unaffected in at least two circumstances: first, where food chains are based much more on turfs and/or pelagic zooplankton washed onto the reef’s windward margin (Hamner *et al.*, 1988), than on macroalgae; and second, where fish community structure is strongly determined by recruitment and comparatively weakly determined by food availability (Doherty & Williams, 1989). In either case, the significance of the loss of live coral may

relate much more to changes in habitat structure (Bell & Galzin, 1984) than to trophodynamic considerations. Effects on motile reef invertebrates may be equally unpredictable, and for the same sorts of reasons.

Time scales of decades to centuries are crucial in the context of a reef's ability to maintain its structural and biological integrity over geological time (Buddemeier & Hopley, 1988). It is true that coral reefs around the world have developed as and where they are, not despite, but because of, what Davies (*op. cit.*) refers to as catastrophes: i.e. continental drift, subsidence and sea-level change. It is impossible not to be impressed with these facts, and it is tempting to believe that coral reefs will persist despite anything human-kind may do to tropical seas. However our opinions – whether optimistic or pessimistic – should not be based only on the past 'track-record' of coral reefs. They should be based on an understanding of the ecological processes which determine whether in fact coral reefs, rather than algal-covered carbonate deposits derived from 'ex-reefs', can exist in environments created by an exponentially increasing human population.

In the remainder of this presentation, I refer to commonly used ecological 'models' relevant to the determination of benthic community structure on coral reefs. I then present some case studies which show how local ecological idiosyncracies of particular reefs – physical; nutritional; biological – can influence the course of benthic community development.

Models for community structure in reef corals and algae

Some characteristics of minimally disturbed coral communities on coral reefs are illustrated in Fig. 1. As time passes, the largest corals get larger; coral cover increases; β species diversity (scale of hectares) rises and asymptotes. These net increases occur despite localised colony mortality and recolonisation, which cause fluctuations in percent coral cover and α diversity (scale of square metres to decametres). The reviews of Connell

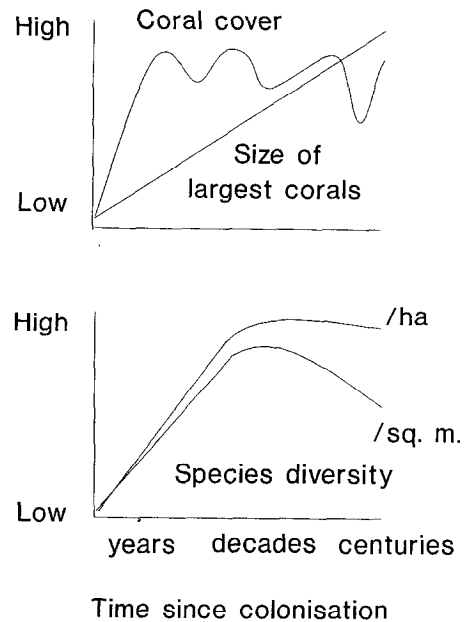


Fig. 1. Changes in some coral community attributes over whole reef scale versus increasing time since colonisation and without major disturbance. Partly after Connell (1978).

(1978) and Connell & Keogh (1985) discuss the implications of differences in scale, intensity and frequency of disturbance in relation to different life history strategies of corals.

Useful models for algal production and community structure on coral reefs have been provided by Littler & Littler (1985) and Steneck (1988). Spatial patterns of algal composition and production are strongly influenced by patterns of grazing, disturbance, and competition with corals, the potential upper levels of production being determined by ambient nutrient levels (Littler and Littler, *op. cit.*). There appears to be a systematic causative relationship between the intensity of grazing from scraping and denuding herbivores, and the structure of algal assemblages (Hixon, 1983; see also Fig. 2). It follows from Fig. 2 that if pressure of fishing substantially changes grazing intensity, a consequence of that fishing may be changes in biomass and community composition of the algal assemblage.

The types of changes which have been observed in coral reef benthic communities are shown in Fig. 3 (after Bazzaz, 1983). Reefs can be knocked

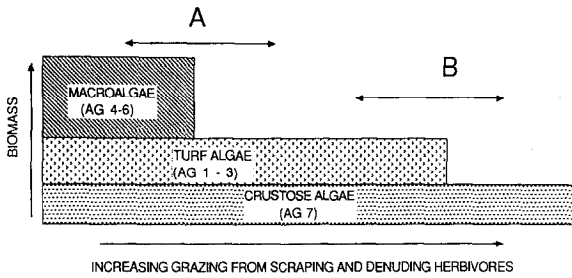


Fig. 2. Herbivore-induced changes in algal community structure, deduced from exclusion studies and natural herbivore mortalities. 'AG' refers to algal functional groups defined by Steneck (1988) as follows: 1 microalgae; 2 filamentous (simple); 3 foliose or sheet; 4 corticated or coarsely branched; 5 leathery; 6 articulated or jointed calcareous; 7 crustose. The most common herbivore-mediated shifts are between macroalgae and turfs (marked 'A') and between turfs and crusts (marked 'B'). Reproduced from Steneck (1988) with permission of the organizing committee of the Sixth International Coral Reef Symposium.

precipitously or move slowly from one phase (coral-dominated) to another (coral-depleted and/or algal dominated). For a period of time, algae become the dominant form of benthic cover. Disturbed areas can recolonise without passing through a macroalgal phase, or they may enter a macroalgal phase which they retain indefinitely, either because ongoing conditions favour algal growth over coral growth (Lighty, 1982; Lapointe, 1989) or because of a relatively brief period in which algal growth is enhanced, and is then sustained long after any measurable change in environment exists (Dollar & Grigg, 1981; Hatcher, 1984). Hatcher (*op. cit.*) lists the following examples of algal enhancing circumstances: (1) exclusion of grazers; (2) increases in availability of potentially limiting nutrients; (3) reduction of

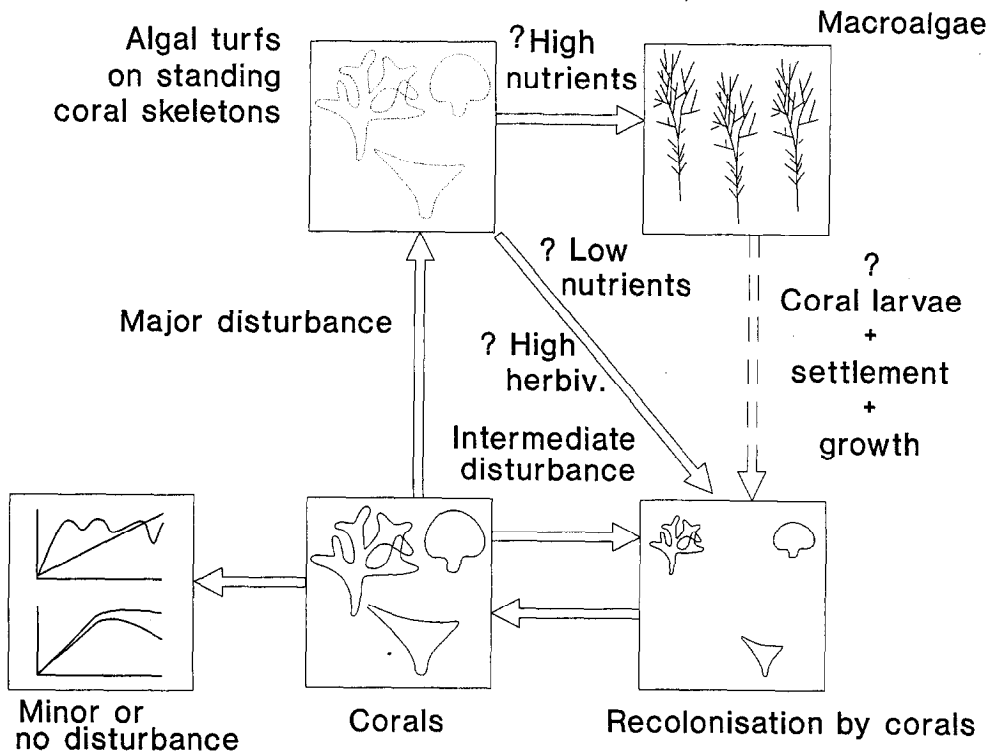


Fig. 3. Effects of different intensities of disturbance on coral reef benthic community structure (after Bazzaz, 1983). Coral communities which are undisturbed or subjected to minor disturbance (bottom left) undergo types of changes indicated in Fig. 1. After intermediate disturbance, the coral community nevertheless retains coral dominance, whereas major disturbance, by definition, causes a 'phase-shift' from coral dominance to algal dominance. The broken arrow indicates that reversion to coral dominance will not necessarily take place, and the question marks indicate location-dependant variables which will influence the trajectory of the benthic community.

competition with other benthic organisms (e.g. corals) by inhibiting their growth or killing them; (4) clearing or modification of large areas of substratum in a manner, or at a time which favoured colonisation by a formerly rare alga. Humans may be directly involved, either by affecting ambient nutrient or sediment loads, or by changing fish and invertebrate community structure by fishing.

Coral to algal phase transitions and the extent of coral recovery

The following six examples describe coral-algal(-coral) phase changes in Hawaii, Jamaica, Reunion, Moorea, and Australia. In some, the causes of the coral to algal shift are clear while in others, they are more conjectural. The examples show that there are no *a priori* reasons to expect that corals will necessarily re-establish populations in areas they dominated previously. Recovery of coral dominance requires a substantial supply of propagules (larvae, fragments), followed by prolific settlement and growth. Any given reef or part of a reef may be 'starved' of water-borne propagules as a consequence of a general scarcity of larvae in the water column (say as a result of isolation from source reefs – e.g. Glynn, 1985) or of topographic reef features which make it unlikely that larvae will be carried to the site in any given year (e.g. Black, 1988). Moreover, even when physical and nutritional conditions (including irradiance) are optimal for coral growth, the establishment of populations of corals may be essentially dictated by the presence, absence or abundance of 'other organisms', for example sea urchins and/or fish (see below).

Kaneohe Bay, Hawaii

In Kaneohe Bay, Hawaii, particularly in its poorly flushed southern basin, cause and effect have been clearly established. Several decades of siltation (due to dredging and land clearing) and eutrophication (due to sewage pollution) killed off most of the coral by the early 1970s (Smith *et al.*, 1981).

The reefs became colonised by a non-reef-building assemblage dominated by macroalgae (*Dictyosphaeria cavernosa*) and a variety of suspension and filter feeding organisms (Smith *et al.*, *op. cit.*). In 1977–78, the sewage was diverted away from the bay and by 1982 there was some decline in *Dictyosphaeria* and some increase both in numbers of colonies and percent cover of corals (Maragos *et al.*, 1985). This example demonstrates the capacity of corals to re-establish populations once a major perturbation is removed.

Discovery Bay, Jamaica

At Discovery Bay, Jamaica, a shift from coral to algal dominance has been well documented. The transitions which have taken place reflect both the nature and the chronology of recent disturbances, and an effect of over-fishing. In 1981, Hurricane Allen stripped off and smashed down most branching and much encrusting coral (Woodley *et al.*, 1981). Turf algae biomass was kept low by a dense population of the omnivorous sea urchin *Diadema antillarum* on the reef, and some recruitment of corals took place in 1980–83 (Hughes *et al.*, 1987). However, in 1982 there was mass mortality among the *D. antillarum* (Hughes *et al.*, *op. cit.*), and a dense carpet of macroalgae dominated by *Dictyota*, *Padina* and *Halimeda* species established itself, smothering the recruits and other small corals. Up to 1990, this algal carpet effectively excluded further coral settlement (Hughes, 1989 and pers. comm.).

The urchin density may have been high, and thus prone to the disease which finally decimated their populations (Carpenter, 1990a), because of overfishing of the fish predators and/or competitors of the urchins (Woodley, 1979). This hypothesis has been supported by work on Kenyan reefs, where urchin (*Echinometra mathaei*) densities are lowest in marine reserves protected from fishing for the last 2 decades (Muthiga & McClanahan, 1987). Fish predation rates upon the urchin are highest (McClanahan & Muthiga, 1989) in marine parks. However Samoilys (1988) considered that siltation and dynamite fishing also

directly affected the reefs and their fish populations.

There is still much to be learnt about the degree to which overfishing can change the abundance and composition of herbivorous fish, predators of herbivorous fish or invertebrates, let alone downstream effects on benthic community structure (Hay, 1984; McClanahan & Muthiga, 1989). Munro & Smith (1984) attributed major changes in total fish catch and composition in the Caribbean, including changes in the proportion of herbivorous fish, to sustained, intense and relatively indiscriminate fishing. In principle, fishing-induced changes in fish community structure may be expected to have significant effects on benthic communities. However fishing pressure is thought unlikely to affect reef fish community structure in systems with strong recruitment limitation of fish populations (Munro & Williams, 1985; Doherty & Williams, 1989).

La Saline Reef, Reunion

Overfishing is also thought to have played a part in the degradation of the reef at La Saline in Reunion. At that reef, chronic pollution and overfishing have been blamed for a marked coral-algal shift. There has been a proliferation of filamentous and fleshy algae *Vaughaniella* and *Gracilaria crassa* and the bioeroding sponge *Cliona inconstans* in previously coral-dominated areas (Cuet *et al.*, 1988). The shift to algal dominance is believed to result partly from chronic nutrient pollution of groundwater, but also from undergrazing by urchins, which were rare, and by fish, also rare as a result of daily netting of the reef. The algae killed corals by overgrowth, and it was predicted that it would also inhibit settlement of coral larvae.

Moorea, French Polynesia

At Moorea (French Polynesia), nutrients and overfishing have again been implicated in reef degradation. In addition, the importance to coral

recovery of hydrodynamics and of other populations (*viz.* urchins and damselfish) have also been recognised. In the period 1971–1981, the macroalgae *Boodlea siamensis* (Chlorophyta), *Sargassum* sp. and *Turbinaria ornata* (Phaeophyta) expanded their ranges from the fringing reef to the coral dominated inner and outer barrier reef (Payri & Naim, 1982). This took place during a period of dredging of the coral reef for building material (Gabrie *et al.*, 1985) and rapid development of agriculture and tourist accommodation adjacent to the shore (Salvat, 1987). It had persisted until 1989 (Done *et al.*, 1991) at which time much of the substratum occupied by macroalgae comprised standing skeletons of corals killed by *Acanthaster planci* around 1982 (Bouchon, 1985; Faure, 1989).

It is very easy to point the finger of blame at the coastal development and dredging, but difficult to prove the connections. There was no detectable elevation of nutrient levels in the strongly flushed lagoonal and inner barrier reef waters in a set of samples collected in 1976 (Ricard, 1982). Levels of nitrate + nitrite and reactive phosphate were much less than occur in moderately flushed lagoons of some GBR reefs 50 km and more from shore (Furnas *et al.*, 1990). This suggests that if nutrient enhancement is necessary to sustain the algal biomass at Moorea, it may occur in pulses, such as during dredging of storms (resuspension of reef sediments, perhaps enriched by septic tank runoff and groundwater), and wet season runoff of silt-laden water, (which retains its integrity to the outer reef passes (R. Steger, pers. comm.)). Alternatively, or in addition, there may be high nutrient fluxes, despite low ambient concentrations, as a result of very rapid uptake by benthic algae and phytoplankton (Atkinson, 1988).

Coral recolonisation at Moorea was very patchy by 1987–1989 (Done *et al.*, 1991). It was high on the outside of the northern barrier reef and low on the inner barrier reef. In order to understand coral recovery on the inner barrier reef, one needs to understand something of the hydrodynamics of the area and the natural history and population dynamics of some key species, notably sea urchins and damselfish. On some

areas of the reef platform, sand abrasion is a major problem for small corals. Only massive *Porites* corals were abundant in 1987–9, both because they were not eaten by the starfish, and because they can colonise the sand-blasted areas by fragmentation (Highsmith, 1980).

Poor coral settlement and survival were also noted in patches with dense urchin populations (especially *Diadema setosum* and *Echinometra mathaei*). However there are refuges from urchin grazing. These are damselfish (*Stegastes nigricans*) territories which cover about 40% of the habitat. Corals (notably *Acropora* and *Pocillopora* spp.) were much more abundant and diverse inside than outside the territories, probably in large part due to *S. nigricans*' active exclusion of urchins and herbivorous fish likely to graze off small corals. This finding is precisely the opposite to the observations on other damselfish species (e.g. Potts, 1977; Lobel, 1980; Kaufman, 1977), where there is a net detrimental effect on coral survival inside territories.

Nearshore and fringing reefs, Great Barrier Reef

Nearshore and island fringing reefs on the Great Barrier Reef (GBR) are dominated over much of their shallow, wave-swept slopes and flats by brown macroalgae, mainly *Sargassum* spp. The significance of this prolific growth is unclear. In the Caribbean, where *Sargassum*-dominated assemblages occupy a similar habitat, heavy wave-action is thought to favour *Sargassum* through exclusion of grazing sea urchins and fish (Adey *et al.*, 1977). Within recent years to decades, *Sargassum* dominated algal assemblages have both invaded large areas (hectares) of Great Barrier Reef fringing reefs previously occupied by living coral, and have themselves been displaced by corals in other areas (T. J. Done & K. F. Navin, unpubl.). The annual life cycle of *Sargassum* gives it an advantage in the wave-swept rubble banks, but puts it at a disadvantage when the alga is in direct competition for space against corals. Fast lateral growth of encrusting *Montipora* and tabulate *Acropora* corals enable them to overgrow *Sar-*

gassum holdfasts during their seasonal (summer) decline (Done & Navin, *op. cit.*).

High macroalgal biomass on GBR nearshore reefs may be indicative of high ambient nutrient concentrations and/or low levels of herbivory (Russ, 1984; Williams & Hatcher, 1983). A case has been made for eutrophication of GBR lagoon waters (Bell *et al.*, 1989), but it is also possible that current standing crops of macroalgae may not require an anthropogenic subsidy of nutrients. In a shallow (< 10 m) nearshore GBR station, soluble nutrients (nitrate + nitrite, reactive phosphate) were strongly correlated with previous day's wind speed, suggesting the nutrients were released from bottom sediments disturbed by waves (Walker & O'Donnell, 1981). However the degree to which runoff and sewage outfalls have enriched the sediment pore-water has not been investigated, even though Walker and O'Donnell's station is within a few kilometres of the sewage outfall of the largest city adjacent to the Great Barrier Reef.

Offshore reefs, Great Barrier Reef

On the Great Barrier Reef, coral to macroalgal phase shifts have been caused by major episodic disturbances such as *Acanthaster planci* and cyclones. *A. planci* infestations killed close to 100% of a high cover of corals over large areas early in the 1980s (Endean & Cameron, 1985; Done, 1985). Algal biomass per hectare increased greatly as a result of increased area for settlement (*viz.* skeletons of dead corals). Unfortunately, there has been no large scale systematic study of algal community dynamics following *A. planci* damage. However it appears that fish grazing, which usually keeps algal biomass low on these reefs (Russ, 1984; Williams & Hatcher, 1983) was no longer able to do so, and that there was an increase in abundance of fleshy macrophytes following the outbreak (Done, pers. obs.).

Nevertheless, there has been significant reversion towards coral dominance in the 6–10 years since the outbreak. Percent coral cover and colony size frequency distributions determined in

1990 (Done *et al.*, in prep.) are consistent with good settlement and growth of corals each year since the *A. planci* outbreak, and a high coral cover is predicted by the year 2000 (Done *et al.*, 1988). However on the inner lagoon of one reef (only 200–300 m from the well colonised outer slope), there had been a very poor recovery (Done *et al.*, in prep.), possibly due to low densities of planulae arriving in the lagoon, poor settlement, and/or post-settlement survival (see Babcock, 1988).

Summary of examples

Of all the examples, the outer slopes of offshore GBR reefs may provide the best ecological circumstances for coral recovery. There is an adequate supply of planktonic larvae from upstream reefs and communities (Oliver & Willis, 1987; Williams *et al.*, 1984), and sufficiently good early coral growth and survival throughout the first 6–10 years following the disturbance. By contrast, some reefs or sections of reefs may rarely be reached by dispersive coral larvae due to their remoteness from source reefs (Glynn, 1985), or unfavourable reef-scale circulation patterns (Black, 1988; cf. Sammarco & Andrews, 1988). In several other examples (e.g. Discovery Bay; Moorea) it was shown that it may be necessary to understand something of the natural history and population dynamics of other reef biota (e.g. urchins and damselfish), the direct effect of fishing on fish community structure, and indirect effects on benthic community structure.

Temporal perspectives on phase change

While degradation may seriously affect the immediate amenity of a coral reef, it may not be significant when viewed from a geological perspective.

‘Events that loom large in the eyes of contemporary observers....may be undetectable in the reef’s sedimentary record and trivial in the

reef’s geological history if the killed areas are promptly recolonised’ (Buddemeier & Hopley, 1988).

This is a perceptive statement, both acknowledging that ‘prompt recolonisation’ will not necessarily follow disturbance, and at the same time counselling conservationists, biologists and managers to seek a longer-term view of the implications of reef change. In some circumstances, corals of any type are very slow to recolonise damaged areas, there being little recovery after a decade or more, e.g. following coral mining at Maldives (Brown & Dunne, 1988), and following coral death at Moorea (Done *et al.*, 1991). However there are other examples where damaged areas have been promptly recolonised by reef building corals (Pearson, 1981; Colgan, 1987; Done *et al.*, 1988), and it is apparently on the basis of the latter type of example that some authors have been lured to suggest that corals are most likely to quickly (decades) establish dominance in any suitable surface which becomes available (e.g. Hopley & Kinsey, 1988 – writing in reference to inundation of coral reef tops with rising sea level).

However, the definition of that point in time when recovery may be regarded as ‘complete’ varies. Restitution of pre-disturbance percent coral cover is the most cited (see Pearson, 1981) but least stringent criterion of recovery. The most stringent – ‘total recovery’ by both ecological and geological standards – would be the restitution of prior diversity, mix of colony growth forms (if not species), colony size frequency distributions and structural extent and complexity of reef framework (after Johannes, 1975). These can take considerably longer to recover than percent coral coverage (see Fig. 1). For example, Done (1988a) and Endean *et al.* (1988) suggest that recovery of size-frequency distributions is partially killed and injured populations of slow growing corals (genus *Porites* and other massive corals) can take a century or more in the same habitats in which percent coral cover has recovered in the first 1–2 decades (Done *et al.*, 1988).

Problems and scale of management

One management option which is widely acceptable is the creation of marine preservation areas including coral reefs. Areas which are protected from human exploitation can act as reservoirs for unprotected reefs downstream, where species are depleted by fishing, collecting etc. However the same current systems which carry the larvae of corals and fish also carry pollutants, sediments, and the larvae of destructive organisms such as *Acanthaster planci* and *Drupella* spp. (coral-eating gastropods). It is therefore prudent from a reef conservation perspective to create as many reserves as possible, and to make them as large as possible. Experience on the Great Barrier Reef is that major coral kills can take place on reefs scattered over hundreds of kilometres of the reef tract, equivalent to the length of the entire Kenyan coast.

Conclusions

While the symptoms of widespread coral death and algal invasion are usually obvious, the causes are frequently more a matter for conjecture than direct observation. Where a cause is definitely identified – say, overfishing, siltation caused by dredging or land clearing, sewage pollution, toxic wastes – it may be in a country's best immediate economic interests to prevent that impact. As one example, Hodgson & Dixon (1988) found the revenue loss to dive tourism caused by siltation of a Philippine reef area would be greater than revenue gained by the logging watersheds which would cause the siltation in the first place. As a second example, Done (1988b) suggested in relation to Mauritian fringing reefs, that one must weigh the cost of protective management against the potential for reef erosion and damage to the shore and structures.

A scientist offering advice to government on the best course of action in relation to coral reef management walks a precarious path. Knowledge of general reef character, history, structure and processes – as can be gleaned from personal ex-

perience and from the literature – is just the beginning. The uncertainties associated with interpreting what has happened to a specific reef in the past, and predicting how it will behave in the future, must also be confronted. On the time and space scales relevant to coral reef management, it is not appropriate to make decisions based on a presumption that a specific reef or system of reefs has 'ability always to regenerate after catastrophes' (Davies, 1988). Neither is it correct to assume that a degraded reef will remain so forever, or that those reefs which do regenerate will do so in time scales which are convenient to human users of the reef.

This presentation has touched lightly on the many issues – physical, chemical and biological – which must be addressed in trying to understand the causes and consequences of coral to algal phase shifts in coral reefs. Clearly, a multidisciplinary approach is desirable for in-depth understanding of all complex natural systems. The initiatives of UNESCO – COMARAF in creating 'The Regional Project for Training and Research on African Coastal Systems', and the University of Nairobi in organizing this Symposium are both welcome and timely.

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