Coral Community Adaptability to Environmental Change at the Scales of Regions, Reefs and Reef Zones

ABSTRACT
Projected global increases in temperature, sea level, storminess and atmospheric carbon dioxide (CO$_2$) are likely to cause changes in reef coral communities which the present human generation will view as deleterious. It is likely coral community trajectories will be influenced as much by the reduction in intervals between extreme events as the projected increases in means of environmental parameters such as temperature, atmospheric CO$_2$, and sea-level. Depressed calcification rates in corals caused by reduced aragonite saturation state of water may increase vulnerability of corals to storms. Moreover, reduction in intervals between storms and other extreme events causing mass mortality in corals (coral predators, diseases, bleaching) are likely to more frequently "set back" reef coral communities to early successional stages or alternate states characterized by non-calcifying benthos (plants, soft corals, sponges). The greater the area and the longer the duration of dominance of putative "coral/coralline algae" zones of coral reefs by non-calcifying stages, the less will be the reef's capacity to accrete limestone bulk locked up in the big skeletal units of late successional stages (i.e., very large old corals). Averaged over decades to centuries, the effects of such changes on the coral community's carrying capacity for other biota such as fish are unpredictable. A "shifting steady-state mosaic" null model may provide a useful conceptual tool for defining a baseline and tracking changes from that baseline through time.

INTRODUCTION
I use the term "coral community" to describe the local assemblage of stony coral and other conspicuous benthic populations which can co-habit with them (e.g., algae, soft corals, zooanthids) on reefal or non-reefal substrates (Done, 1992, Devantier et al., 1998). By "local" coral community I refer to the places that people anchor their boats at and swim around in. On coral reefs, coral communities dominated by stony corals and encrusting coralline algae are best developed on seaward slopes, and on the margins of shallow subtidal reef flats. Coral communities are the aesthetic face of coral reefs, and this, along with their major role as reef builders and complex three dimensional habitats for other reef organisms, is good reason to consider the environmental changes they will face over coming decades, and how they may respond. At the local scale, the environment endured and exploited by the coral community is defined by a long list of variables, many of which may change under global change scenarios (Brown, 1997a): the prevailing day to day and season to season regime of waves, light, nutritional input and aragonite saturation state of the water; the regime of natural catastrophic disturbances, be they decadal or less frequent; the rates and interannual variability in supply of larvae and spores of benthic biota capable of settling and surviving at that place; the incidence of pathogens which are fatal for key groups such as corals; the local ecological determinants of space occupancy by competing benthic groups, such as physical interactions between them, and the daily rate of scraping of the substratum by fishes and invertebrates (e.g., Sammarco et al., 1974; Hatcher 1993; McCook, 1996). Changes in coral communities attributable to global environmental change per se may be difficult to recognise because coral communities are highly
dynamic on ecological time scales (Fig. 1), and their dynamic properties vary substantially among regions and habitats (e.g., Scoffin, 1993; Dollar and Tribble, 1993; Done and Potts, 1992). They exhibit changes in cover, vertical relief, biomass, relative abundance of species and diversity over time scales of years to decades, slowly increasing in undisturbed periods, and often crashing following catastrophic disturbances (e.g., Dollar and Tribble, 1993). In those areas where global change is manifest as a reduction in the return interval between highly destructive events such as cyclones, floods (Pittock, 1999) and outbreaks of coral predators (e.g., Done, 1988), one might predict that the stage, age and size frequency distributions of coral populations and communities across regional seascapes will be skewed more to earlier successional stages (Fig. 1b) than is presently observed. Such changes, though perhaps mere noise in the context of the global scene and of geological and evolutionary time (e.g., Grigg and Dollar, 1990; Done, 1997), are major determinants of how reefs are perceived and managed.

There is a long list of direct human impacts on coral reefs that act locally but are globally widespread and ubiquitous (Brown, 1987; Ginsburg, 1994): sedimentation, overfishing and destructive fishing; pollution, to name just a few. In this paper, it is useful to view global changes as an overlay on both the natural spatial and temporal variability in coral communities, plus the localised human impacts. At the organizational level of communities and populations, net outcomes of all these three sources of change may most strongly be manifest in community succession and population dynamics viewed over local to regional space scales, and decadal time scales.

One measure of the reef-building potential of coral-dominated zones and other reef zones is their community calcification rate. Reef zones dominated by corals and/or coralline algae calcify at rates up to 10 kg-CaCO$_3$ m$^{-2}$ y$^{-1}$ (Kinsey, 1991). The rate appears to be largely independent of the precise taxonomic composition and relative abundance of the calcifying species present (Kinsey, 1991). However community calcifying rate can presumably be reduced to lower (including negative) levels where disturbances or other ecological or environmental changes cause calcifying corals and coralline algae to be replaced by fleshy algae, bioeroders, filter feeders and other non-calcifying or slowly calcifying organisms (Kinsey, 1988). The possibility of such transitions are thus of more than academic interest, affecting not only reef aesthetics, habitat amenity, and biodiversity issues, but also the maintenance of reef mass and volume.

**NICHES AND ENVIRONMENTAL CHANGE**

The environmental niches for coral communities are defined by a wide range of physical, chemical and ecological variables (Brown, 1997a). Key parameters include prevailing waves forces, temperature, aragonite saturation state, turbidity and supply of organic and inorganic nutrients, and planktonic productivity. The extent to which a potential habitat satisfying the physical/nutritional niche is actually occupied by a coral dominated community is strongly predicated on demographic and ecological considerations, especially the rate and reliability of supply of viable propagules, and on rates of scraping of the substratum for epilithic algae by herbivorous fishes and invertebrates (Hatcher, 1983 and see "phase shift" below). Many environmental variables are projected to substantially change over the next 50 to 100 years. Contrasting changes in light penetration and wave exposure on steep and flat topographies are predicted as a result of rising sea level per se (Fig. 2). Hopley and Kinsey (1988) have pointed out that on reef flats, it is likely corals will flourish in some previously high intertidal areas from which they were formerly excluded or limited by excessive exposure to the air, while on deeper slopes, phototrophic corals may need to become increasingly heterotrophic to survive in a regime of reduced light. However, of the climate change factors projected for the next century, those
that may have the greatest implications for coral communities and reef growth are not so intuitively obvious. They are the combined effects of projected decreases in aragonite saturation state of surface waters (Opdyke and Kleypas, 1999) and increases in storminess (Pittock, 1999). It has been suggested that by 2070, coral calcification rates may have fallen by as much as 9-30% as a direct physiological consequence of the projected reduction in aragonite saturation of tropical waters arising from increased atmospheric CO\(_2\) concentration (Gattuso et al., 1999b). If this reduction is manifest at the community and reef zone level, it may be due, in addition to changes in calcification in individual organisms, to changes in demographic parameters of reef-building populations under the new conditions (settlement density, recruitment and survivorship rates per unit area).

One aspect of environmental change discussed below is the possible effect of a reduced calcification rate on coral vulnerability to storms. Depending on the nature of the physiological response of individual organisms, there are quite different implications for their life expectancies, for the lengths of successional series, for the rate and the mode of reef accretion, and thus for the nature of coral reefs as biogenic wave-resisting structures.

POTENTIAL RESPONSES TO GLOBAL ENVIRONMENTAL CHANGE

A. DIRECT CLIMATIC INFLUENCES ON CORAL COMMUNITIES

Sea level rise of the order predicted in the next century (20-95 cm) is occurring at a rate which are relatively slow (<1 cm\(\cdot\)y\(^{-1}\)) compared to coral vertical extension rates of corals (up to 20 cm\(\cdot\)y\(^{-1}\)). In coral communities, consequences will most likely vary greatly between regions (e.g., doldrum versus cyclone latitudes), within regions (e.g., across broad continental shelves--Fig. 2), and within reefs. At the local community level, outcomes will reflect habitat-specific differences in physiological capacities of extant individuals, as well as events and processes operating at the scales of local sub-populations, and regional meta-populations. For example, on many shallow and gentle reef slopes and sheltered reef flats, individual acclimatization and local sexual or asexual propagation may be of paramount importance in enabling the local community to accommodate sea level changes. However these highly localized strategies may be less effective in maintaining a community where the suitable envelope of substrate, light, water motion and nutrition moves rapidly across near horizontal areas, such as coastal areas with highly mobile deposits of terrigenous sediments (Fig. 2; Kleypas, 1996; Larcombe and Woolfe, 1996). In such cases, coral community establishment on newly exposed substrata may rely much more on long distance dispersal and colonization.

B. ENVIRONMENTAL TRACKING WITHIN A REGION

In the past, the same coral taxa and growth forms have tended to develop in the same geomorphological zones of coral reefs, be they replicated through time at the one place (Pandolfi, 1996), or throughout a region at the one time (Geister, 1977; Done, 1982; Pandolfi, 1996), i.e., given many opportunities, the same species inventory tends to assemble in similar places. Local assemblages can undergo cycles of disturbance and recovery over scales of whole reefs, reef zones and patches within zones, and time scales of decades to centuries (Fig. 1; Fig. 3; Dollar and Tribble, 1993; Done 1992, 1997). At regional scales (100s of square kilometers and up) and, over sufficiently long time scales, coral communities have a history of tracking their preferred environmental niche which may suggest that as an entity, they will be predisposed to "adapt" to prospective changes in environment over the next century (Fig. 2). Thus, precedents
suggest that coral communities have historically had a good capacity to track their re-distributed preferred physical niches.

**C. LOCAL RESPONSES TO ENVIRONMENTAL CHANGE**

Table 1 shows ways that local coral communities might respond to environments which gradually become increasingly stressful and/or more frequently disturbed under global climate change scenarios. They range from (Table 1a), physiological tolerance by current occupants of specific places; (b) faster turnover (decline in the longevity of the same species), to (c) strategy shifts (shifts in species composition to a hard coral community which occupies the place by increasing relative abundance of r-selected hard coral species compared to K-selected hard coral species) and (d) phase shift (transition to a well adapted but functionally different group--e.g., from hard coral dominated to soft coral or macro-algae dominated). Note, however, that "phase shifts" can also occur in circumstances where there is a temporary perturbation but no lasting environmental change (see below).

**D. POPULATION AND COMMUNITY IMPLICATIONS OF ADAPTIVE MODES IN TABLE 1**

a) Tolerance.--In this response, there would be no change to the longevity of individual corals, nor novel changes in rate of nature of successional changes taking place at that site, i.e., it could be thought of as the "business as usual" outcome at the level of local populations and communities. However in changed environmental circumstances, that outcome may have required adjustments at the level of individual benthic organisms (Brown, 1997a) and symbiotic partnerships (Rowan and Knowlton, 1991). From a community perspective, it is clear that individual corals can survive decades to centuries, during which time they tolerate environmental fluctuations which are sometimes stressful (Barnes and Lough, 1996). Tolerance of stressful environmental conditions may sometimes be accompanied by sub-lethal bleaching (Brown, 1997b)--i.e., major changes in cell densities and/or strains of symbiotic zooxanthellae (Rowan and Knowlton, 1991; Buddemeier and Fautin, 1993; Fitt and Warner, 1995). In principle, the considerable genetic diversity within both coral species and zooxanthellae partners (Rowan and Knowlton, 1991) suggests potential for a greater breadth of physiological tolerance than might previously been expected.

b) Faster turnover of populations of same species.--Global environmental change may be manifest as changes at one place of a similar order to existing difference between regions. On the Great Barrier Reef, population dynamics of massive Porites-populations are influenced by locally and regionally varying frequencies and intensities of castastrophic disturbances, namely cyclone-generated waves (Massel and Done, 1993) (Fig. 4) and predation by crown-of-thorns starfish (Done, 1988) (Fig. 5). Both disturbances have major latitudinal and among and within-reef differences in frequency and intensity. These influence survivorship schedules and stable and transient size and age frequency distributions in Porites. Population modeling suggests that increase in frequency and/or intensity of either or both disturbances should tend to skew size frequency distributions towards smaller size classes (Done, 1987; Massel and Done, 1993), with or without exogenous recruitment to the local Porites population. In terms of rates of coral community turnover, there should, under accepted greenhouse scenarios (Pittock, 1999), be more "21°S-like" and fewer "16°S-like" reefs (Fig. 4); more "Green Island--like" reefs and fewer "John Brewer--like" reefs (Fig. 5).

A 9-30% reduction in colony calcification rate would affect the resilience (sensu speed of recovery of hard coral populations and cover) of areas affected by increased frequencies both
storm (Fig. 4) and starfish (Fig. 5) impacts. Maintaining skeletal density at the cost of a reduction in lateral extension rate would slow down growth and repair between impacts, thus tending to increase the time it would take for restoration of coral cover to levels vulnerable to further outbreak populations of the starfish. It would also take longer for corals to grow to sizes most vulnerable to dislodgment by storm waves, and for communities to reach cover levels vulnerable to starfish outbreaks. By contrast, maintaining extension rates would maintain rates of recovery of total hard coral cover, but the colonies and the community would be more vulnerable to storm waves of a given strength (due to lower skeletal density).

c) Strategy shift—a move to more ephemeral reef builders. In a "strategy shift," a change takes place between contrasting coral states (ephemeral versus perennial) that contribute in different ways to reef growth. For example, a currently widespread transition in Belizean reefs is from staghorn coral (living Acropora cervicornis on stacks of their own rubble several meters thick) to the thin bladed anastomosing coral Agaricia tenuifolia (Aronson and Precht, 1997). This transition may reflect a combination of 1) Caribbean-wide, synchronous mortality among A. cervicornis populations caused by various 'band' disease (cyanophytes and fungi that infect and kill coral tissue); 2) the resulting severe limitation in the number of viable A. cervicornis larvae reaching affected reefs, and 3); an opportunistic response by Agaricia tenuifolia, a Belizean endemic coral that is relatively unaffected by the band diseases, and which has capacity to reproduce both asexually (through fragmentation) and sexually. The chain of events that lead to this fundamental structural change was initiated by a regional phenomenon (the fatal band diseases). There is a disturbing possibility that, as a result of land clearing for forestry and agriculture, there may have been a dramatic increase in the incidence of the band diseases, as terrestrial pathogens are washed from disturbed soils into the sea and complete vegetative stages of their life cycle on the medium provided by coral tissue (C. D. Harvell, personal communication). As land clearing and other disturbance of soil continue globally, consequent coral mortality may become even more widespread (Littler and Littler, 1996; Miller, 1996). As in the case of crown-of-thorns starfish discussed below, there is a need to understand the extent and significance of the transition at the regional scale.

In the Indo-Pacific, crown-of-thorns starfish can kill fields of very large massive Porites corals (life expectancies to several centuries--Done and Potts, 1982) to be quickly replaced (a decade or so) by fast growing table Acropora and other ephemeral corals with life expectancies measured in only years to decades (Done and Devantier, 1990). The transition has occurred at a number of locations in recent decades (Cameron and Endean, 1985; Done, 1987, 1988) and its significance needs to be assessed over regions and over decades to century time scales (Bradbury and Seymour, 1997; Done, 1997). An increase in disturbance frequencies may be viewed as an element of global change, albeit possibly caused by cumulative local human influences on starfish abundance (Cameron and Endean, 1985). The consequences of such an increase would be expected to manifest as a qualitative shift in stage frequency distribution from Fig. 1b to Fig. 1d (Done, 1987, 1988).

Should the frequency of such perennial to ephemeral coral transitions increase throughout a region and over coming decades, there would be an increase in the proportion of reef areas accreting through the sedimentary, compared to the framework mode of construction (Davies, 1983). Any change in the relativity between the two construction modes could thus have implications for ongoing stability of the reef structure in increasingly stormy seas.

d) Phase shift. In a "phase" shift (Done, 1992), a transition takes place from a community dominated numerically and functionally by reef building organisms (e.g., corals and
coralline algae) to one dominated by non reef building organisms (e.g., most soft corals; fleshy algae e.g., Fig. 6a). Birkeland's (1987) eutrophication model (Fig. 7a) emphasizes nutritional control of such a phase shift (Hallock and Schlager, 1986, Hallock, 1987). Hence, a flourishing algal community cohabiting with a coral community, and possibly out-competing it for limited space, may be symptomatic of increased nutrient loadings, and a cause for action to reduce the source of the pollution. However it is also important to note that "phase shifts" can be easily misinterpreted because they can take place in the absence of change in the local nutritional environment. For example, Hatcher (1984, 1990), and Knowlton (1992) show how intrinsic life history characteristics of component species can predispose radical changes in community composition and relative abundance without change in environmental conditions. Other authors (e.g., Jackson, 1994, 1997, Fig. 7b; Hughes, 1994; Dayton et al., 1995; Roberts 1995, McManus, 1997) have pointed out the synergies between natural disturbance and over-fishing can radically affect benthic community composition. They point out how increases or decreases in the abundance of substratum-scraping fish or urchins can have profound and contrasting effects on benthic community structure (see also Fig. 6). Scraping on the one hand keeps substratum free of fouling benthos, providing opportunity for settlement of new benthic organisms, including corals, and reducing direct competition between algae and corals (Hughes, 1994). On the other hand, it destroys newly settled corals, and so the balance between rates of scraping and rates of coral settlement may be critical in determining when and where coral communities can be initiated (e.g., Sammarco et al., 1974; McCook, 1996; McCook et al., 1997).

DISCUSSION

As has been suggested for ecological systems generally (e.g., Jones and Pittock, 1997), the trajectories of sessile communities on coral reefs will be influenced as much or more by the reduction in intervals between extreme events as the projected increases in means of environmental parameters such as temperature, atmospheric CO[sub2] and sea-level. There are projected direct effects of increased atmospheric CO[sub2] on the critical process of calcification (Gattuso et al., 1999a). There are also the projected changes in the frequency and intensity of extreme events (Figs. 1, 4, 5). By affecting parameters such as percent coral cover, size frequency distribution, and/or abundance of calcifying versus non calcifying organisms, such frequency and intensity changes may cause measurable changes in populations and communities that will have deleterious ramifications for calcification rates at the scale of whole reef zones. Put another way, the greater the area and the longer the duration of dominance of the putative "coral/coralline algae" zones of coral reefs by noncalcifying organisms, the less will be the reef's capacity to accrete limestone bulk locked up in the big skeletal units of "old growth" formations, as opposed to non-calcifying pioneer benthos (plants, soft corals, sponges) or to hard coral species with shorter life expectancies. Such a statement is not meant to deny that cyclical and successional characteristics must always have been present in reef coral communities (Davies, 1983; Grigg and Dollar, 1990). It is merely to emphasize that more parts of more reefs will spend more of their existence in earlier successional stages than would be the case in the absence of projected changes in mean environmental conditions and increases in frequency and intensity of extreme events, and moreover, that such changes will certainly change the surface architecture, and very likely change the mode and rate of accretion, and the relative rates of erosion and accretion.

THE "STEADY STATE SHIFTING MOSAIC" AS NULL HYPOTHESIS
Observers who look at the same small patches of reef over a period of years to decades (e.g., Hughes, 1994; Connell et al., 1997; Oliver et al., 1995; Done, 1997), observe ongoing changes in percent cover and biomass of coral communities. Given this small scale dynamism, an important question becomes, what are the appropriate spatial scales, and what are reasonable periods of observation over which change should be assessed? Even currently growing coral reefs represent the results of periods of vigorous growth interspersed with periods of destruction and re-distribution of sediments (Davies, 1983), and there are naturally senescent reefs, colonized by reef-building corals and coralline algae, but in which net accretion over decades and hectares are long gone (Hopley, 1982).

In the context of global environmental change, observers of coral communities need to recognise the circumstances under which we might expect slow net changes (such as net accretion or net erosion of reef structure) as opposed to cyclic revolutions (growth, destruction and redistribution of coral biodiversity and biomass without net accretion). Perhaps we can learn from similar process and scaling difficulties encountered in interpreting patchiness and change in forest ecosystems, where the "steady state shifting mosaic" paradigm of Bormann and Likens (1979) has proven useful. They define a Steady State in terms of biomass and species composition and biogeochemical function. "For the ecosystem as a whole, over a reasonable period of time, gross primary production equals total ecosystem respiration, and there is no net change in total standing crop of living and dead biomass. Species composition and relative importance of species are fairly constant. However any point within the ecosystem is constantly cycling through changes in both biomass and species composition and function. We use the word steady state with some trepidation, since ample evidence suggests that the condition we define above is at very best one of slow net changes or possibly a period of quiet antecedent to a cyclic revolution ... from this holistic foundation, ecologically sound programs of landscape management can be developed" (Bormann and Likens, 1979, p. 4).

Bormann and Likens were referring to northern hardwood forests of the USA, but they did express the hope that some of the principles they espouse might be "extrapolated or modified for other ecosystems." Much of what they say does seem remarkably applicable to coral reefs, in particular, the balance between production and respiration (Kinsey, 1988), the shifting mosaic of sessile community structure and composition (Done, 1997), and the tensions between notions of steady state, slow change, and catastrophic change (Grigg and Dollar, 1990). The "steady-state" model provides a workable null hypothesis against which we may evaluate net change in a spatially and temporally variable system.

There is growing evidence that human impacts have already fundamentally altered many coral reef areas in ways which will compromise their ability to adapt to the purely physical and chemical aspects of global change (Brown, 1987; Ginsburg, 1994). To assess it, we will need to develop better baseline expectations (Eakin et al., 1997), which will depend on us learning to know where the local patch on the local reef fits into the regional picture and in the natural and human-affected environment. In coral reef regions in which episodic severe disturbance is the norm, distinguishing impacts of global changes from background patterns of change may be facilitated by adoption of the "shifting steady state mosaic" view, in which regional change is measured as departure from an expected distribution of states and successional stages (Fig. 1a).

Concerns about coral communities as the aesthetic face of coral reefs and their roles as complex three dimensional habitats for other reef biodiversity are already major incentives for policy and management (Dight and Scherl, 1997). At local and regional scales worldwide, there are major actual and potential threats to coral community persistence and reef accretion that
result from cascading effects of human over-exploitation of coral reef resources compounded by
effects of runoff from disturbed coastal areas and catchments (Dayton et al., 1995; Brodie, 1995;
Done et al., 1996; Roberts, 1996; McManus, 1997; Jackson, 1997; McClanahan and Obura,
1997).

Now, we also need to learn to recognise where global environmental changes and human
population pressures synergistically threaten to directly bring about net CaCO$_3$ loss per
hectare per decade. Having done that, we need to distinguish between 1) those places where the
decline is strictly a consequence of water column physics and chemistry (i.e., reduced aragonite
saturation state; increase in mean temperature; increased storminess), and 2) those places where,
in spite of suitable water column properties, there is net CaCO$_3$ loss because the reef-
building community is too sparse as a result of diminution or failure of ecological processes.
These processes include recruitment of key functional groups like corals, other invertebrates and
fish; dampening by predators of outbreaks of destructive species like crown of thorns starfish;
prevention of build up of algal biomass by a sufficient abundance of herbivorous fishes and/or
invertebrates. In as much as humans contribute to both causes, both need to be addressed. The
former needs to be addressed at the level of global atmospheric CO$_2$ through international
conventions which go beyond measures agreed in the Kyoto protocol of 1997, the latter through
renewed policy and management initiatives at local and regional scales.

ADDED MATERIAL

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TABLE 1. Continuum of responses proposed for reef coral community subject to
changed environmental conditions, including increased disturbance regime. (FN*)

<table>
<thead>
<tr>
<th>Change</th>
<th>Adaptive mode</th>
<th>Outcome of</th>
<th>environmental change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minor</td>
<td>a) Tolerance</td>
<td>No change in composition or demography</td>
<td></td>
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<tr>
<td></td>
<td>Organism level acclimatization</td>
<td>Matching new circumstances by increased turnover of same species</td>
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<td></td>
<td>to new circumstances</td>
<td>Reduced life expectancies</td>
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(Acknowledgments continued...)
<table>
<thead>
<tr>
<th>Functional group</th>
<th>Reef-building corals and coralline algae</th>
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<tr>
<td>Change</td>
<td>Major environmental change</td>
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<tr>
<td>Adaptive mode</td>
<td>c) Strategy shift MATCHING NEW CIRCUMSTANCES by species replacement</td>
</tr>
<tr>
<td></td>
<td>d) Phase shift NEW ENVIRONMENT INIMICAL with former functional group</td>
</tr>
<tr>
<td>Outcome</td>
<td>Replacement by more ephemeral species in same functional group</td>
</tr>
<tr>
<td></td>
<td>Replacement by different functional group</td>
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<tr>
<td>Functional group</td>
<td>Non reef-building benthos</td>
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**FOOTNOTE**
* Modes a), b) and c) represent three ways of remaining a coral community, and hence in some sense, "adapting." Mode d), the phase shift, is a change to something other than a coral community, and hence indicates "failure to adapt." Note that "phase shifts" can also occur in circumstances where there is a temporary perturbation but no lasting environmental change (see text).

**FIG. 1.** Possible consequences for "coral communities" of increased frequency and intensity of disturbance predicted in global climate change scenarios. The symbols and corresponding histograms categories represent the successional stage and the mean age of the dominant conspicuous sessile benthic organisms, be they primarily fleshy algae (left symbol) or corals/coralline algae (all other symbols). (a) In a low disturbance regime (curved arrows), the succession from bare substratum to fleshy algae to coral/coralline algae may proceed uninterrupted for decades to centuries at many local sites. At regional scales (b), the consequent stable stage distribution would tend to be dominated by old growth stages. (c) In a high disturbance regime, few sites could proceed uninterrupted through to old growth stages, and the regional landscape would be dominated by earlier successional stages. The completion of the fleshy algae to coral/coralline algae transition can be a major bottleneck either caused or exacerbated by human activity (see text).

**FIG. 2.** Contrasting ecological processes and coral reef outcomes of sea level rise of ? 1 m over a century in turbid nearshore and clear offshore waters on a continental shelf such as the central Great Barrier Reef. Boxes indicate different relative importance of vertical and lateral adjustments that reefs need to make to track suitable environments. Offshore reefs "keep up" through growth and local dispersal, while coastal shoals, incapable of building true reefs, and are buried. Creation of new shoals relies on broad scale dispersal to occupy newly suitable habitat.

**FIG. 3.** Illustration of ecological resilience in an ephemeral coral community in an optimal setting following almost total coral death caused by crown-of-thorns starfish Acanthaster planci L. a) Means of index of hard coral cover in 4 m segments along three contiguous 32 m belt transects at 3 m depth on Rib Reef, Great Barrier Reef. b) Trend lines for the diameter of the upper quartile of table Acropora plotted against years since disturbance at depths of ? 1 m (dots and upper line), ? 3 m (squares and curved line) and ? 5 m (triangles and lower straight line). (Source: T. J. Done and others, in preparation).

**FIG. 4.** Possible consequences of projected increase in physical disturbance regime on local community succession illustrated by existing regional variation. Expected longevity of unattached massive corals in the Great Barrier Reef shown here (Massel and Done, 1993) may also be thought of as a surrogate for the longevity of uninterrupted succession of the total coral community. Projected increases in storminess would tend to transform coral longevity profiles.
like (a) to the more ephemeral type (b). The figures here assume identical skeletal densities and linear extension rates. In reality, these already vary regionally, and may change further under global change scenarios, with consequences for longevity probability curves.

FIG. 5. Consequences of increased frequency and/or intensity of predator or disease-induced coral mortality. For 'crown-of-thorns' starfish predation on Porites corals in the Great Barrier Reef (Done, 1988), field data and transition-matrix simulation modeling suggest a 15 year interval may be sustainable at John Brewer Reef (19°S), but that the same interval would decimate the coral population at Green Island (17°S). The interval between these episodic mortality events that is necessary to allow "complete recovery" (criterion-restore abundance of 1 m + size class) is a function of the pre-existing structure of the target coral population, the size-specific damage regime, and inter-episode rates of coral recruitment, survivorship, growth and repair. All of these parameters, as well as outbreak intervals of the starfish, may change under global change scenarios.

FIG. 6. Contrasting role of fleshy algae and grazing/scraping in coral communities. (a) High seasonal abundance of Sargassum sp. in area of low live coral, and high coral rubble. (b) Dead patches on a 3 m diameter Porites colony kept free of large benthos by daily grazing and scraping of algal turfs by scarid and acanthurid fishes.

FIG. 7. Mechanisms for human-mediated phase changes from coral dominance to dominance by fleshy algae or filter feeders. (a) Highly oligotrophic waters favour 'classic' communities dominated by corals and coralline algae, while natural gradients or human induced shifts in water quality towards increasing dissolved nutrients and particulate organic matter (plankton and detritus) favour fleshy algae and filter feeders, respectively (Birkeland, 1987). (b) The coral to fleshy algae transition may also occur, possibly without changes in water quality, in response to removal of grazing/scraping pressure (Jackson, 1994). In Discovery, Bay Jamaica, the well documented synergisms between hurricanes, Malthusian overfishing (McManus, 1997) and the collapse of populations of the urchin Diadema antillarum are collectively thought to be sufficient to account for high biomass of prostrate fleshy algae without invoking elevated nutrient levels. The algal mat both reduces opportunities for coral settlement and overgrows small corals (Hughes, 1994.)

REFERENCES


