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# 15 Biodiversity and Ecosystem Function of Coral Reefs

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Working Group – listed at the end of the chapter)

## 15.1 INTRODUCTION

The world has many thousands of living coral reefs, located in the tropics and sub-tropics between approximately 30° N and 30° S, where the minimum sea surface temperature rarely falls below 18°C (Figure 15.1). Collectively, they cover an area in excess of  $6 \times 10^5 \text{ km}^2$  (Smith 1978) and encompass a wide range of forms, biological composition, diversity and structural organization. This reflects disparate bio-geological origins, ages, biogeographic settings and environments (Figure 15.2). The largest coral reefs are oceanic atolls on top of submerged volcanoes, often measuring up to tens of kilometers across (Figure 15.2). The largest *continuous tracts* of coral reefs occur on shallow (<100 m deep) continental shelves (Figure 15.2a). Reef forms include both coastal and island fringing reefs, and autonomous platforms located from a few to tens of kilometers from the nearest land, and hundreds of meters to tens of kilometres from each other. For example, in eastern Australia, the Great Barrier Reef occupies a region approximately 2000 km long and 50–150 km wide, and contains almost 3000 fringing and platform reefs ranging in length from less than 1 km to about 30 km (Hopley 1982). Continental shelf reef systems with similar diversity of form can be found along the eastern coasts of Africa, Asia and Central America.

Biodiversity and the products of ecosystem function are both very apparent on coral reefs. Through geological time scales, their ecosystem processes produce, accumulate and cement limestone skeletons of a diversity of taxa into wave-resistant structures which can dwarf the tallest forests. Through evolutionary, ecological and human time scales, they provide foci for speciation and habitats for a spectacular variety and a substantial biomass of other biota. Today, they provide important ecosystem services to



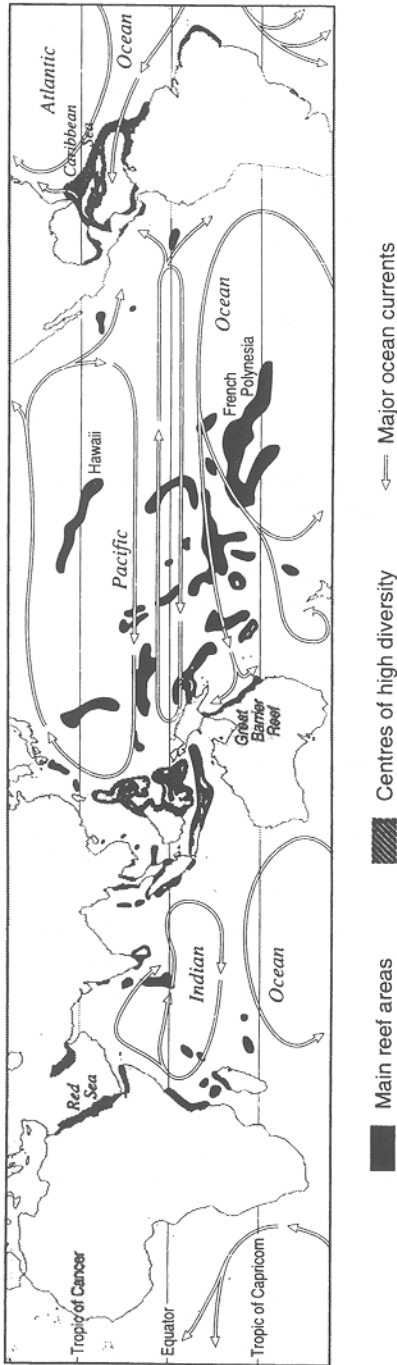
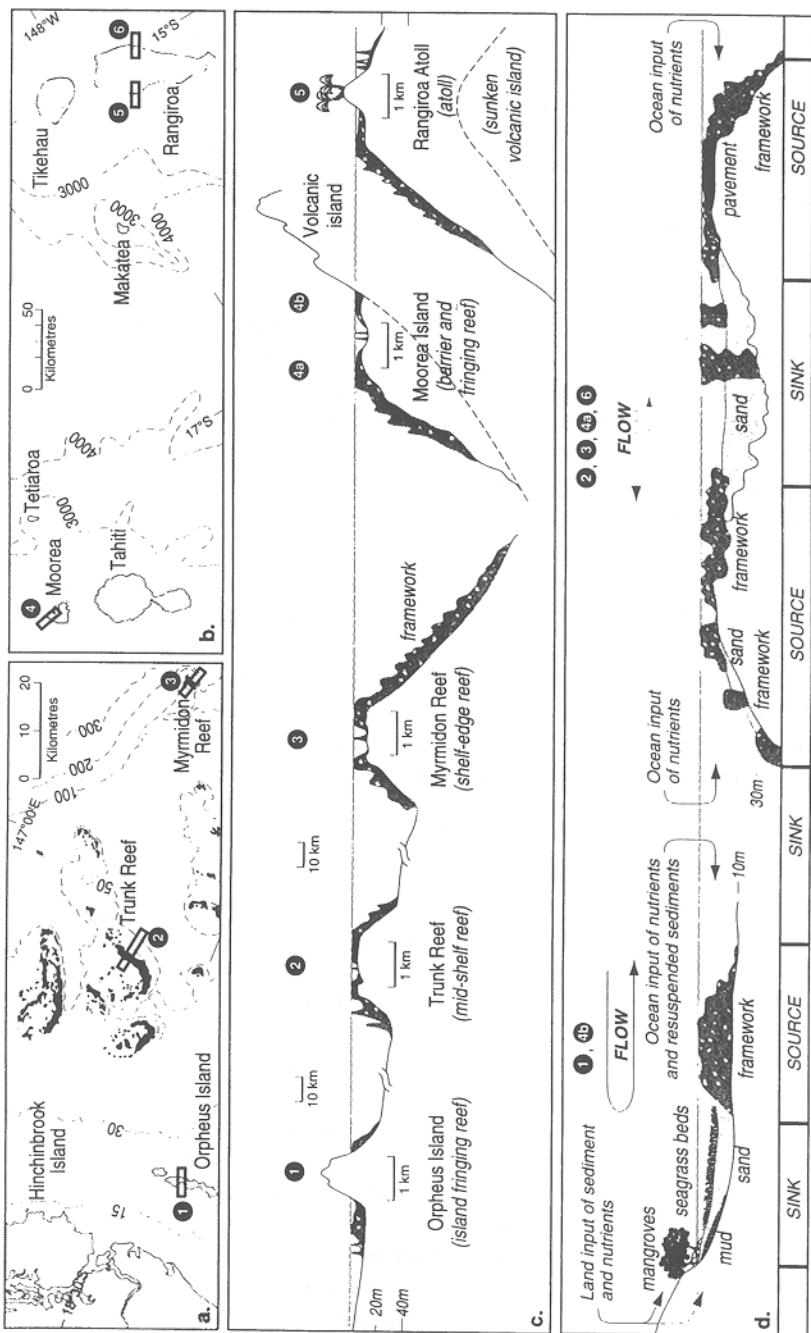


Figure 15.1 Worldwide distribution of coral reefs showing centers of high species diversity in the Indo-Pacific province (Western Pacific Arc) and the Western Atlantic (Caribbean)



**Figure 15.2** Diversity of coral reefs and shared functional characteristics in terms of sources and sinks of trophic and biocostructional outputs. (a) Reef shapes and bathymetric setting on a continental shelf (Great Barrier Reef, Australia). (b) Profiles showing some of the variety in types, sizes and geomorphological antecedents of coral reefs. (c) Stylized cross-sections of generalised fringing reef (left) and reef not closely associated with land (right). Many nearshore reefs are "buffered" from terrestrial inputs of sediment-laden nutrients by mangroves and/or seagrasses near to, or intimately associated with, the reefs. Margins of reefs and zones within reefs tend to be sites of greatest accumulation of reef framework and production of organic matter (see text). Materials produced in these "source" zones are transported by gravity, biota and currents to adjacent "sink" zones.

humans, ranging from the material needs of tropical populations who exploit their carbohydrate, protein and limestone resources, to recreation for millions of tourists, and a contribution to biogeochemical cycling. Although they transform  $\text{CO}_2$  to  $\text{CaCO}_3$ , the process actually contributes to atmospheric  $\text{CO}_2$  (Smith and Buddemeier 1992). However, the relatively small global area of reefs makes their contribution to the global carbon cycle small compared with that of other sources and sinks (Smith 1978).

Coral reefs have more species and co-evolved relationships per unit area than any other marine ecosystem but, with the exception of a few groups such as fishes and corals, most taxa are poorly known (Böhkle and Chaplin 1968; Springer 1982; Achituv and Dubinsky 1990; Butman and Carlton 1993). Reefs have fewer species than tropical forests, with which they are often compared, but a much higher phyletic diversity (Ray and Grassle 1991; Briggs, 1994). In both systems, disturbance plays a major role in the maintenance of diversity (Connell 1978) and rare species, which have either very clumped and localized or overdispersed distributions, are collectively important (Grassle 1973; Connell 1978). Rare species are also, by virtue of small population sizes, the most vulnerable to local extinction.

High species and genetic diversity are defining characteristics of coral reefs, but there are huge differences in species composition and diversity among reefs on biogeographic scales (Potts and Garthwaite 1991; Pandolfi 1992; Jablonski 1993; Knowlton and Jackson 1994, Vernon 1995). Collectively, coral reefs are rich in phyla and diversity within phyla, and uniform taxonomically down to the level of Order. Individual reefs vary greatly in their composition and diversity at the levels of Family, Genus and Species. Distinctively different coral reef biota occupy the western Atlantic and the Indo-Pacific Oceans, and within each province, there is a center of high biological diversity: the Caribbean Sea and the Western Pacific Arc, respectively (Figure 15.1). Even the most depauperate coral reef is likely to be more diverse and structurally complex than any adjoining benthic community. However, coral-reef scientists have not often addressed whether reefs having naturally low biodiversity differ in ecosystem function from more diverse reefs, or from those which have had their biodiversity lowered by humans.

In recent years, molecular studies have demonstrated a strong genetic basis for much of the morphological and distributional variation seen within coral reef species (Knowlton *et al.* 1992; Miller 1994). For purposes of this synopsis, however, the numbers of species refer to the conventional taxonomy, while recognizing that the formal species delineations are currently subject to debate Veron (1995).

Different coral reef locations (regions, positions on continental shelves, positions on reefs) are characterized by differences in water quality (Birkeland 1987, 1988) and in the frequency and intensity of natural stressors and disturbances. Examples are exposure to hurricane waves (Scoffin 1993), flood

plumes and lethal temperature excursions associated with El Niño Southern Oscillation (ENSO) events (Glynn 1990) or other regional or global climatic fluctuations. Whole human generations can pass without any Papuan or Maldivian reef being disturbed by hurricane-generated waves, or any Red Sea or Western Australian reef coming under the influence of flood waters. By contrast, it is to be expected that sometime before one's children finish their schooling, their favorite snorkel site in Puerto Rico or the central Great Barrier Reef will be damaged by hurricane waves, fresh water or both.

### 15.1.1 Use, abuse and management of coral reefs

Coral reefs provide essential services to humans (UNEP/IUCN 1988). Large human populations live on islands built solely by coral reefs (e.g. atoll nations of the Indian and Pacific oceans) or by coral reefs in conjunction with other marine sediments (e.g. the Florida Keys). To many coastal and island communities, particularly in the developing countries of central America, the Caribbean, Africa and Asia, coral reef biota are important sources of food and of reef limestone, sands, rubble and blocks for use as building materials. The physical barriers provided by coral reefs protect coasts from erosion by storm waves. Tourism associated with coral reefs provides many countries with significant foreign exchange earnings. For example, in Queensland, Australia, tourism associated with the Great Barrier Reef is the State's second largest industry sector and valued at around \$1.5 billion per annum. Beyond these perhaps obvious benefits, coral reef plants, animals and microbes are rich in unusual organic compounds, including antitumor compounds whose potential is just now beginning to be defined (Guan *et al.* 1993)

However, coral reefs in many parts of the world are degraded or at risk through over-exploitation and abuse (Brown 1987; Salvat 1987; D'Elia *et al.* 1991; Wilkinson 1993). Active management of the use of coral reefs (Kenchington and Agardy 1989; Kelleher 1994) and research in support of issues defined by users and managers (Crossland 1994) are now well established in various parts of the world.

### 15.1.2 Chapter goals and some definitions

Our intent is to provide an overview of *the influences of biological diversity on ecosystem function* and to suggest research that will contribute to our long-term understanding of biodiversity and the management of reefs for sustainable use. We define "biodiversity" as the diversity of genotypes, species, communities, habitats, whole reefs and regions. In all cases, to adequately link biodiversity with ecosystem function, the term "biodiversity" must embrace both the elements of richness and evenness (e.g. as in the species diversity concept), and some notion of *abundance per unit area*. For

example, two reef zones may have identical species richness and relative abundances, but the one with the greater total biomass will contribute more to limestone and/or protein accumulation. Below, we show that the links between "biodiversity" thus defined and scaled, and the function or dysfunction of coral reefs, are complex and poorly understood.

At all scales, biodiversity and ecosystem function are emergent properties of population and community dynamics of plants and animals: temporal fluctuations in the abundance of populations will be reflected in aspects of ecosystem function. Although traditionally characterized as "a well-ordered, climax system" in which predator population explosions do not occur (Odum 1971), coral reefs are extremely dynamic at the level of populations and communities. Current coral-reef paradigms, particularly since the seminal work of Connell (1978), tend to give a greater emphasis to chance, disturbance and cyclicity than those of earlier decades. Coral-reef environments are not always benign, and population explosions and crashes, notably involving reef-building corals, echinoderms and algae, occur commonly on contemporary coral reefs (see references below).

How much of this temporal variability is "natural" and how much a symptom of human influences is the central focus of much current research. Strong arguments have been made (e.g. Endean and Cameron 1990a,b; Done 1992a, and see below) that reductions in coral-reef biodiversity caused by human activities have amplified, and that such activities have possibly even been the primary cause of these fluctuations. Therefore our chapter also considers the system properties of "resistance" ("the opposition offered") and the "resilience" ("ability to return to original form") of coral reefs subject to natural and anthropogenic stress and disturbance.

## 15.2 A CONCEPTUAL FRAMEWORK

### 15.2.1 Carbon pathways, reef function and reef degradation

The essential functional characteristics that distinguish coral reefs from other ecosystems are illustrated in Figure 15.3a. (A representation of the enormous network complexity, not represented here, is provided by Johnson *et al.* 1995.) Photosynthesis by diverse plant forms (from unicellular dinoflagellates to fleshy macro-algae and coralline crusts) fixes carbon into compounds which are directed into pathways that are primarily *bioconstructional* (arrows 1 and 2) or *trophic* (arrow 3) in output. Total photosynthetic output per unit area depends on total solar energy and its reduction in intensity and changes in spectral composition as it passes down through the water column. The former is a function of geographic location, and the latter of water transparency, which is affected by human activities on and among the reefs, proximity

to sources of terrestrial runoff, and land use. The total carbon fixed also depends on other water quality characteristics (such as nutrient concentrations, pH, dissolved CO<sub>2</sub>, O<sub>2</sub>, HCO<sub>3</sub>, temperature and salinity).

The partitioning of fixed carbon between the *bioconstructional* and the *trophic* pathways (Figure 15.3a) depends on the composition and relative abundance of benthic biota. The *bioconstructional* pathways refer to the accumulation of limestone building blocks, the cements which bind them together into reef *framework*, the sediments derived from both the physical and biological erosion of blocks and framework, and the sand-sized skeletal elements of a variety of plants and animals. The *trophic* pathway refers to the food web, including plant–herbivore–predator links accumulating harvestable protein resources, and “losses” (arrow 5) to a microbial-processed detrital compartment.

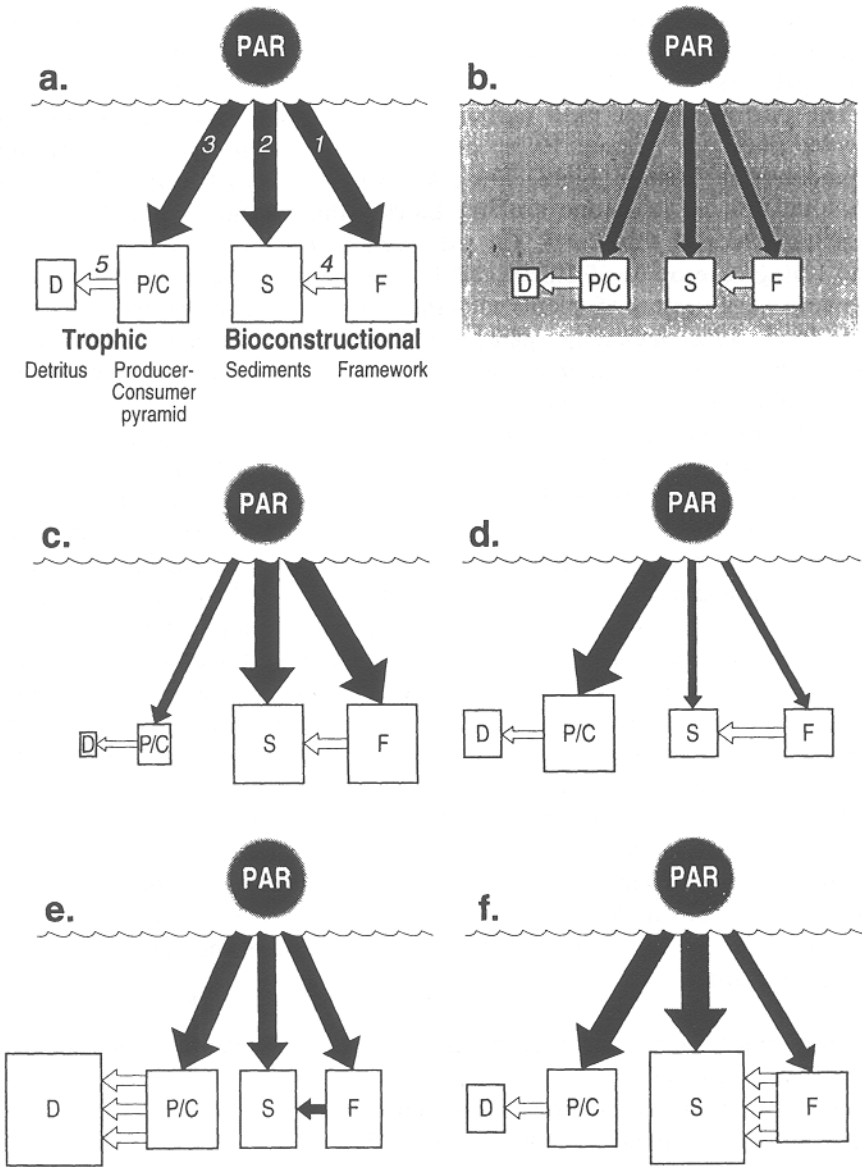
Consumer and decomposer elements of the trophic pathway are supplemented to a greater or lesser degree by imported organic matter (not shown in Figure 15.3) comprising detritus, phytoplankton, zooplankton and vertebrates. Wilkinson (1986) and Birkeland (1987) identified a “nutritional spectrum” of coral reefs and reef benthic communities, ranging from those which are predominantly autotrophic (as in Figure 15.3), to those which are highly reliant on imported organic matter (see also Section 15.3).

The trophic characteristic that humans value most highly in any reef is a maximum sustainable yield of protein (e.g. as fishes, crustaceans, mollusks and echinoderms). The bioconstructional characteristic most valued by humans, *and essential for the long-term structural integrity of a reef*, is the net accumulation of framework.

Reef scientists, users and managers often describe coral reefs as “*degraded*” when they fail to match the presumed (but rarely documented), sustained protein yields, structural integrity or aesthetic qualities of earlier times. Assuming, for the sake of illustration, that the arrow thicknesses and box sizes in Figure 15.3a represent this preferred state, the degradation may take several forms:

- when total fixed carbon is depressed, leading to low yields of protein and/or limestone (Figure 15.3b);
- when an imbalance between *trophic* and *bioconstructional* pathways leads to low yields of either protein (Figure 15.3c) or limestone (Figure 15.3d);
- when the apportionment of carbon within the *trophic* pathway favors detritus over food webs sustaining protein production (Figure 15.3e);
- when the apportionment of limestone within the *bioconstructional* pathway leads to prolonged transformation of material from framework into rubble, sands and silts (Figure 15.3f).

Within this conceptual framework, reef ecosystem function is driven by



**Figure 15.3** (a) Pathways of fixed carbon leading to *trophic* and *bioconstructive* outputs of framework, sediments, fleshy plants, consumers and organic detritus. PAR signifies “photosynthetically active radiation”. Arrows (see also Figure 15.4) signify biological groups and processes as follows: 1, carbon fixed by symbiotic zooxanthellae and coralline algae; 2, carbon fixed as small skeletal elements of foraminifera, calcareous algae and other non-framework builders; 3, carbon fixed as edible plants; 4, limestone fragmented to sands and silts by bio-eroders; 5, losses of

those events, factors or processes that determine the pathways and fates of carbon within a reef and among its various habitats and zones. *Biodiversity loss* has functional consequences if it contributes to any of the manifestations of degradation listed above.

### 15.2.2 Trophic roles

The *primary producers* of coral reefs are extremely diverse. Like most shallow hard and sandy substrata throughout both tropical and temperate seas, they are inhabited by all the major algal groups (benthic micro- and macro-algae, coralline algae), and commonly by seagrasses. What sets coral reefs apart are the symbiotic *zooxanthellae*, the single-celled, dinoflagellate algae of many species (Trench 1987; Rowan and Powers 1991) which live within the cells of many animal calcifiers (notably corals, foraminifera and mollusks) and are the powerhouses of coral reefs (see Section 15.2.3). Planktonic primary production (phytoplankton) is sometimes important in lagoons (Charpy-Roubard *et al.* 1988), but usually minor compared with overall benthic production on hard substrata and sands. The relative amounts of carbon going into the trophic as opposed to the bioconstructional pathway depends on the apportionment of plant standing crop between calcifiers and all other algae.

Primary producer populations (density and biomass per hectare) vary greatly within and among reefs as a function of ambient nutrient regime, successional status, wave energy and grazing pressure (Littler and Littler 1985; Birkeland 1987, 1988). A diverse and abundant array of vertebrate and invertebrate *grazers* scrape, browse, crop and suck this plant production (Hatcher 1983), often inadvertently ingesting varying amounts of detritus, limestone and living material (e.g. coral tissue, epiphytic micro-invertebrates)

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plant and animal biomass to detrital pathways. Arrow thicknesses and box sizes have no absolute quantitative meaning other than to signify that (a) is a "normal" reef with the "proper balance" between bioconstruction and protein production. Panels (b)–(f) exemplify the types of changes in ecosystem configuration which may signify degradation of the reef (i.e. relative sizes of arrows and boxes compared to (a)), as follows: (b) total fixed carbon depressed due to rapid attenuation of photosynthetically active radiation caused by turbid water (shading); (c) excess carbon fixed as limestone rather than edible plants; (d) excess carbon fixed as edible plants rather than limestone; (e) excess edible plants "lost" as detritus rather than contributing to higher trophic levels; (f) excess of carbonate fixed as small skeletal elements in non-framework builders (shaded arrow) and/or excess framework transformed to sediments by bio-eroders. Causes of transitions among these various states are discussed in the text. Some of these configurations representing "degradation" at the scale of a whole reef represent "normal function" in specific zones within a reef (Section 15.3)

in the process. Coprophagy is common among certain reef fishes, and is believed to be of major importance in sustaining fish biomass in areas in which other food sources are intermittently limited (Robertson 1982). Where high daily plant production sustains high grazing rates, the standing crop of benthic algae is commonly very low, and export of plant material, either into the open sea or to *detrital-based* sites in sheltered sand accumulations such as lagoons, is minimal. By contrast, some high-latitude and disturbed reef systems support dense beds of annual macrophytic algae (Carpenter 1986; Crossland 1988).

Corals are food for many types of fish and invertebrates. A variety of fishes nip, crunch or scrape corals (Bellwood and Choat 1990; Bellwood 1994), leaving localized injuries which heal rapidly. Others kill entire colonies. In low abundances, coral predators such as crown-of-thorns starfish (*Acanthaster planci*), gastropods (*Drupella* spp. and *Coralliophila* spp.) and bristleworms (Polychaeta, Amphinomididae), harvest coral soft tissue at rates that are sustainable within local communities and promote diversity by opening substrata for colonization (Glynn 1982). There are also secondary predators on the adults and juveniles of the coral predators (e.g. fish, gastropods, shrimps for *A. planci*; fish for *Drupella* and *Coralliophila*), although their efficacy in regulating local abundances of these corallivores has been difficult to demonstrate (Endean and Cameron 1990b; Ormond *et al.* 1990)

The marine trophic pyramid beginning with phytoplankton and benthic algae and culminating in the large predatory sharks and teleost fishes is multi-layered (Grigg *et al.* 1984) and each layer is diverse (Sale 1991). *Benthic carnivores* and *mid-water carnivores* (reflecting the sources of their prey) can comprise >60% of species (Sutton 1983), whereas the relative importance of *herbivores* and *planktivores* varies in different settings, presumably reflecting differences in the importance of benthic plants and plankton in reef trophodynamics (Williams 1982; Russ 1984a, b). Estimates of sustainable harvest of secondary production, mostly in the form of fishes, mollusks, echinoderms and crustacea, are up to 15 t wet weight ha<sup>-1</sup> on reefs fished according to customary practices (Munro and Williams 1985).

### 15.2.3 Bioconstructional roles

*Bioconstructors* *Bioconstructors* (Figure 15.4) are the sessile benthic organisms that produce skeletons of aragonite and calcite, minerals based on calcium carbonate CaCO<sub>3</sub> with traces of Mg and Sr (Chalker 1983; Smith 1983). They comprise two broad categories: framework builders and non-framework builders.

*Framework builders*, notably corals and encrusting coralline algae, accrete a framework of dense intergrowths of rigid skeletons and encrustations (Scoffin

1987). *Primary framework-builders* consist of massive and robustly branching or platy coral colonies (decimeters to metres across) which are analogous to the structural components of a building (Ginsburg and Lowenstam 1958), and various encrusting coralline algae, analogous to the cement, mortar, glues and plaster that hold the components of a building together. *Secondary framework-builders* are smaller (centimetres to decimeters) colonies of the same groups and other attached organisms such as bryozoans and bivalve mollusks. These add small-scale topographic complexity to the framework.

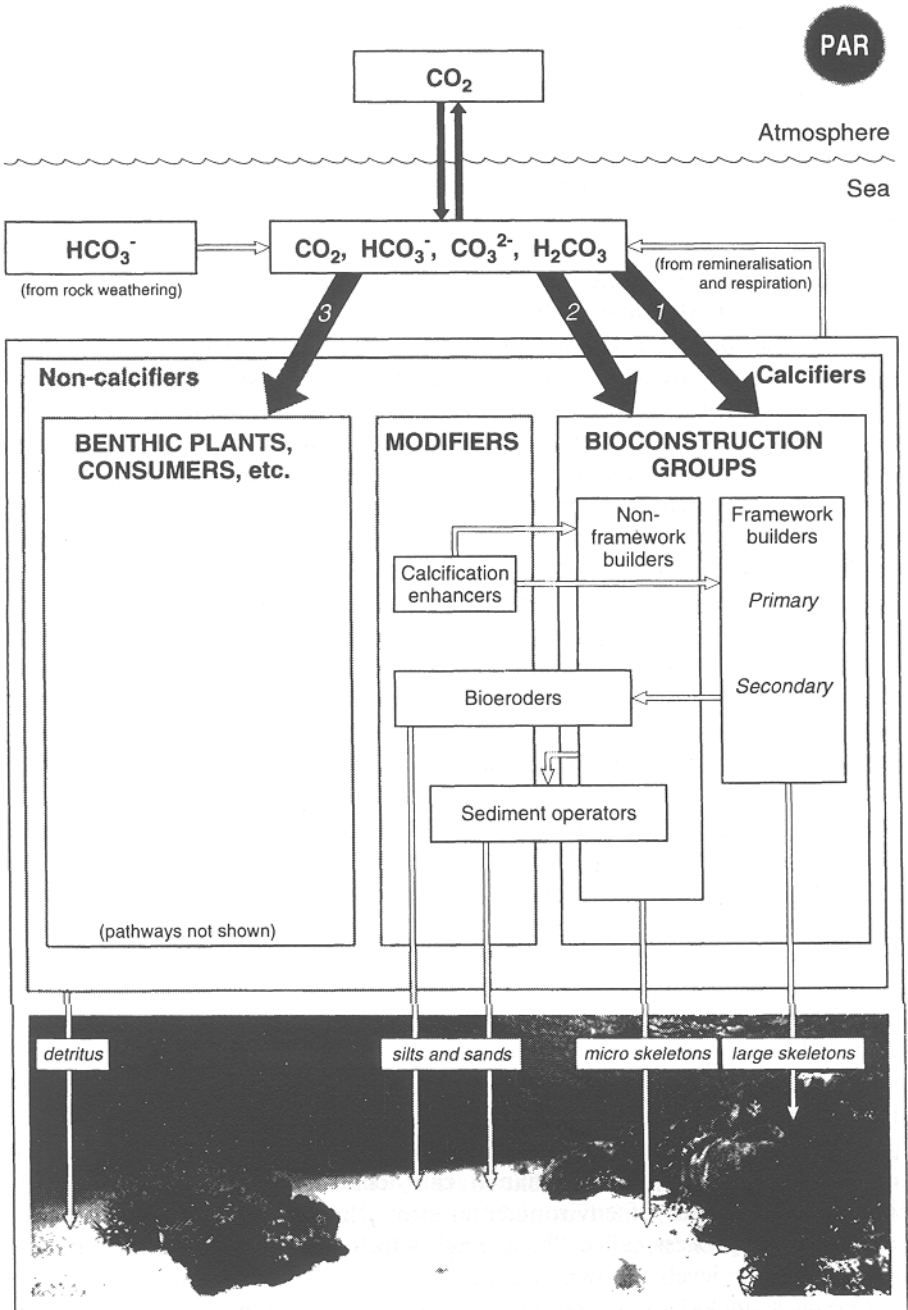
Framework and infilled sediments are also bound by submarine lithification, a process involving chemical transformation and micro-organisms (Macintyre and Marshall 1988). The development and strength of marine cements that bind the framework together is much greater on reefs with high water transparency and wave action than on those in turbid, sheltered waters (Marshall 1985). The life expectancy of a coral-derived framework depends on the strength of cementation, and also on species composition and diversity and the ambient wave regime (Done 1992b; Massel and Done 1993). In the absence of physical disturbance accretion can continue for centuries, but with episodic physical destruction, coral-dominated substrata are from time to time transformed to bare pavement, rubble and/or algal-covered framework, and a "recovery" period is initiated (see below).

A second important group of bioconstructors are the *non-framework builders*. These include foraminifera, erect coralline algae (notably the genus *Halimeda*) and most mollusks, which contribute loose shells and skeletal fragments to the extensive sedimentary deposits associated with coral reefs, and to the framework itself, as trapped sands, silts and gravels (Hopley 1982).

*Modifiers* *Modifiers* (see Figure 15.4) include three functional groups which act at the levels of individuals and populations to affect benthic community performance and bioconstruction – *calcification enhancers*, *bioeroders* and *sediment operators*.

*Calcification enhancers* are the symbiotic, unicellular dinoflagellate algae, or "zooxanthellae", which occur by the thousands within cells of most corals and many other calcifying organisms on reefs (from microscopic foraminifera to giant clams). They are the reef's powerhouse, because the products of their metabolism "power" the critical reef process of calcification in the host. During sunny days, the host uses photosynthate and O<sub>2</sub> as quickly as they are generated by the zooxanthellae, increasing its calcification rates many times faster than it can achieve at night (Chalker 1983). However, in periods of environmental stress, host and symbiont may part company in a process called "bleaching" which reduces calcification rates to their night-time levels (Brown and Ogden 1992).

*Bioeroders* include a diverse array of fish, invertebrates (notably sponges, bivalve mollusks, sipunculans, echinoids and polychaete worms) and filamen-



tous algae that bore into living or dead framework or etch, scrape or nip into its surface (Hutchings 1986). Grazers assume major importance as incidental bioeroders as they remove skeletal matter in the process of extracting the nutritional soft tissues. Echinoids commonly erode channels and depressions in the bases of living corals and the reef framework. This action simply adds to habitat complexity when echinoderm abundances are low ( $\leq 1 \text{ m}^{-2}$ ). However, it can reduce coral framework to rubble and sand over vast areas when abundances are high ( $10\text{--}100 \text{ m}^{-2}$ ), which can be a result of overfishing of the fish predators of urchins (McClanahan and Muthiga 1988).

*Sediment operators* are the animals which mobilise or immobilise sediments. Diverse mollusks, polychaete worms, holothurians and fish pass sand through their alimentary canals in order to assimilate diatomaceous algal films covering the sands. The fish may defecate considerable distances from where they ingested the sand. Tube worms bind sand grains and shells into their tubes. The coral framework itself can baffle sands against entrainment by passing currents.

#### 15.2.4 Facilitating roles

In the long term, the persistence of a coral reef requires that its overall rate of mass and volumetric growth of framework equals or exceeds losses to biological and physical erosion and transport of sediment away from the framework zones. Persistence is thus a function of benthic community structure as well as the vitality of associations between zooxanthellae and individual hosts. Mass bleaching can facilitate the switch between net accretion and net decay. This switch may also be mediated by a biotic functional group called the *facilitators*.

*Facilitators* are biota whose actions directly affect benthic community structure, and hence the apportionment of carbon between and within pathways with bioconstructional outputs, and those without (e.g. the various configurations of Figure 15.3). Grazing herbivores, for example, facilitate coral growth by preventing algal overgrowth of newly settled and small corals (Hatcher 1983). However, excessively high densities of urchin grazers can lead to destruction of corals (Sammarco 1982, and above), and exces-

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**Figure 15.4** (*opposite*) Functional groups having bioconstructional roles on coral reefs. Reef construction is a result of the activities of stony coral framework builders which are influenced by "modifier groups" such as calcification enhancers, eroders and sediment operators (see text). Arrows (see also Figure 15.3) signify biological groups and processes as follows: 1, carbon fixed by symbiotic zooxanthellae and coralline algae, 2, carbon fixed into small skeletal elements of foraminifera, calcareous algae and other non-framework builders; 3, carbon fixed in fleshy plants

sively low densities can lead to undergrazing and overgrowth of corals by algae (Cuet *et al.* 1988; Hughes 1989). Certain species of abundant territorial damselfish are also important facilitators of benthic community structure. These fish maintain algal "gardens" (Kaufman 1977; Lobel 1980) that can cover a significant fraction of some reef zones (Klumpp *et al.* 1987; Done *et al.* 1991), sometimes to the detriment of framework builders. Some facilitator abundances are prone to extraordinarily large fluctuations. Examples (discussed in more detail below) are the sea urchins mentioned above, and the sea-star predator on Indo-Pacific corals (the crown-of-thorns starfish *Acanthaster planci*), which transforms vast areas from coral to algal dominance, and thus has lasting effects on the rates and nature of framework accretion.

### 15.3 ECOSYSTEM PROCESSES AT SCALES OF WHOLE REEFS AND ZONES

#### 15.3.1 Whole reefs

Forty years ago, Odum and Odum (1955) proposed that the high accumulation of biomass on coral atolls compared with the surrounding oceans depended on two factors: (a) effective use of a non-limiting supply of solar energy, and (b) tight recycling of potentially limiting nutrients. Solar energy is fixed by the zooxanthellae within coral cells, by micro-algae covering virtually every non-living surface, and by abundant macro-algae, turfs and corallines. By contrast, planktonic production is close to zero. Recycling is accomplished at two levels: as exchange in metabolic products between host and zooxanthellae within the coral cells and as the transfer of plant and animal production within complex and many layered food-webs on the reef.

Subsequent work, which has embraced a greater variety of reef types, notably those on continental shelves, has modified some aspects of this view of reef function (Pomeroy *et al.* 1974; Hatcher 1988; D'Elia and Wiebe 1990; Rougherie and Wauthy 1993). Rougherie and Wauthy (1993) proposed that atolls receive a major input of nutrient-rich water from the deep ocean. Geothermal heating reduces the density of deep, nutrient-rich water, causing it to percolate to the surface of the atoll, where the nutrients are incorporated into microbial systems, plankton and higher food chains. This hypothesis provides a mechanism for sequestering a major exogenous supply of nutrients.

Other work suggests that most reefs occupy waters that are in no sense "deserts" (D'Elia and Wiebe 1990). Although P and N in reef waters normally occur at concentrations not much above limits of detection (Furnas *et al.* 1990), the supply is continuous (in dissolved forms, suspended detritus, phytoplankton and zooplankton). Moreover, N is fixed from dissolved N<sub>2</sub> by

a number of groups, notably cyanobacteria (Order Cyanophyta), and much N and P are remineralized within detrital systems, primarily by invertebrates and microbes within lagoonal sands (Hansen *et al.* 1987). The main limiting nutrient in oligotrophic coral reef waters may be Fe (needed for chlorophyll – Entsch *et al.* 1983), suggesting that tight recycling may be very important for this element at least.

### 15.3.2 Zones

The reef's effectiveness in "harvesting" nutrients and organic matter from the passing flow is assumed to be related to biodiversity at the levels of feeding guilds and reef zones. "Zones" are belts of reef, usually a few metres to tens of metres wide and having characteristic combinations of substratum, benthic assemblage and fish assemblage. They occur down the sides of reefs (reflecting gradients in wave action, light and sediment stress) and horizontally, across their tops (reflecting differences in exposure to waves, currents, water quality and air (Figure 15.2d; Geister 1977; Done 1983). These "reefscape"-scale expressions of biodiversity are both reflected in, and a product of, local differences in bioconstruction, transport and cycling of materials and in community metabolism.

If a guild of planktivorous fishes inhabits the reef's seaward slopes, it transfers nutrients and organic matter from plankton to the front of the reef (Glynn 1973, 1989; Hamner *et al.* 1988). Benthic planktivores and filter feeders (e.g. corals, gorgonians, crinoids, antipatharians) similarly affect transfers from the water column to the reef (Sebens and Johnson 1991). The quantitative importance of transfer through these upstream "walls of mouths" should depend on the composition and abundance of the zooplankton, the planktivorous fish and the benthic planktivores (Johannes *et al.* 1972). Subsequent zones across the reef flat receive "used" water, whose nutrient, organic and dissolved gas concentrations are determined by the amounts added and subtracted by the communities of all upstream zones (Crossland and Barnes 1983). There is thus an alternation of production and consumption within different zones ("sources" and "sinks" in Figure 15.2d) that is a key characteristic of coral reefs; downstream zones consume some of what those upstream produce (Crossland and Barnes 1983). The absolute and relative magnitudes of production and consumption of the zones determine the performance and "health" of the whole reef (see below).

However, the composition of zones varies among oceans, regions and environmental gradients (Done 1982; Wilkinson and Cheshire 1989). In clear, oligotrophic waters in the tropics, zones within a reef are most easily distinguished by differences in the distribution and abundance of coral species, while on sub-tropical coral reefs (Crossland 1988), and in more turbid tropical reefs (Birkeland 1989a), fleshy macro-algae often dominate the reef

crest and shallow slopes. In highly eutrophic areas, hard substrates in nutrient-enriched waters may be totally dominated by benthic filter feeders such as sponges, oysters and tube worms, sometimes to the exclusion of corals (Birkeland 1988). Major anthropogenic and natural impacts on biodiversity (see below) commonly cause phase shifts from coral to macro-algal dominance on the scales of zone and reef (Done 1992a; Hughes 1994), and changes in the spatial mosaic within zones (viz. fragmentation, richness, grain and pattern) owing to patchy mortality, invasions and physical redistribution of biogenic sediments (Scoffin 1993).

Similar within- and among-region differences are also seen in other groups. Western Atlantic coral reefs have a relatively small number of fish species with less specialized feeding requirements than those on Indo-Pacific reefs (Bellwood 1994), where species richness is about six times as great (Thresher 1991). Within the Great Barrier Reef, herbivores are more diverse and abundant on windward slopes of more offshore reefs, and planktivores are more diverse and abundant on mid-shelf reefs (Williams 1982; Williams and Hatcher 1983; Russ 1984a,b). Feather stars (Echinodermata; Crinoidea), that are a diverse and important component of the "wall of mouths" on western Pacific reefs, are entirely absent from central and eastern Pacific reefs (Birkeland 1989). Here the transfer of nutrients and organics is effected without them, the role presumably being taken up entirely by other benthic filter feeders and planktivorous fishes.

### 15.3.3 Ecosystem processes and "reef health"

Kinsey (1988) categorised the substrata of coral reefs into three all-inclusive types: "continuous framework", "algal pavement" and "sand/rubble" (see Figure 15.2d). Metabolically, these substrata have been shown to perform within narrow ranges, and to exhibit up to a 20-fold difference in their rates of calcification and photosynthesis (Table 15.1). These patterns are widespread across a wide range of reefs around the world (Kinsey 1985). In coral framework areas, and on "healthy" reefs at the "whole reef" scale, production and respiration are approximately balanced (i.e.  $P/R \approx 1$ ). By contrast, algal pavements produce more than is consumed ( $P/R > 1.0$ ) and the biota of sand/rubble areas consume imported detritus ( $P/R < 1$ ).

Likewise, the "proper" configuration for the apportionment of carbon among pathways and compartments at the scale of a whole coral reef (Figure 15.3a) reflects contrasting configurations at the scale of its individual zones (i.e. Figure 15.3b represents a deep zone where low light levels limit both plant and limestone production; Figure 15.3c represents a zone of vigorous framework accumulation; Figure 15.3d represents a zone where there is a high transfer of plant matter into animal protein; Figure 15.3e represents a zone of unpalatable macrophytes; Figure 15.3f represents a zone which is a

**Table 15.1** "Standards of metabolic performance" for three main types of benthic substratum. Source: Kinsey (1991)

Biogenic substratum <sup>1</sup>	Photosynthesis (gC m <sup>-2</sup> day <sup>-1</sup> )	P/R	Calcification (kg CaCO <sub>3</sub> m <sup>-2</sup> y <sup>-1</sup> )
"Continuous coral"	20	1	10
Algal pavement	5	> 1	4
Sand and rubble	1	< 1	0.5

<sup>1</sup>These three categories are the dominant substrata in the "framework", "pavement" and "sand" zones, respectively, of Figure 15.2 and Section 15.2.3. Varying proportions of one or both of the other two categories may be present.

major source of limestone sediments). In other words, carbon fluxes, sources, sinks and links, which if measured at the scale of a whole reef would be deemed to signify "degradation", often reflect "healthy" ecosystem function at the scale of individual zones.

The passage of time is often accompanied by changes in the relative abundance of the different patch types, and the absolute abundance of calcifying versus non-calcifying biota within patches (Hughes 1989; Done 1992a,c). On the one hand, a long period of uninterrupted increase in the cover and biomass of corals and coralline algae can increase metabolic performance in the direction of "continuous coral" (Table 15.1). On the other hand, a period in which mortality and injury of corals and coralline algae exceeds growth and repair can "turn off" the reef's framework building performance altogether, transforming whole reefs or even reef tracts into a state where net physical and biological erosion exceeds net construction (Buddemeier and Hopley 1988). "Turn-on" requires a restoration of coral area, volume, mass and vigor to a level of calcification not less than around 4 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup>, which is slightly under half the rate of "continuous coral". Attainment of this level of metabolic performance requires a substantial assemblage of corals and coralline algae, but in the short time scales so far studied, seems to be largely independent of their composition and species diversity.

## 15.4 BIODIVERSITY LOSS AND ECOSYSTEM DYSFUNCTION

### 15.4.1 Facilitators as links between humans, biodiversity and ecosystem function

Three case studies illustrate reef turn-off caused by population fluctuations in echinoderm *facilitator* species. In the first, the turn-off appears to be rapidly reversible without human intervention in human time scales; in the

latter two, the situation appears to be irreversible, or at least much slower than expected.

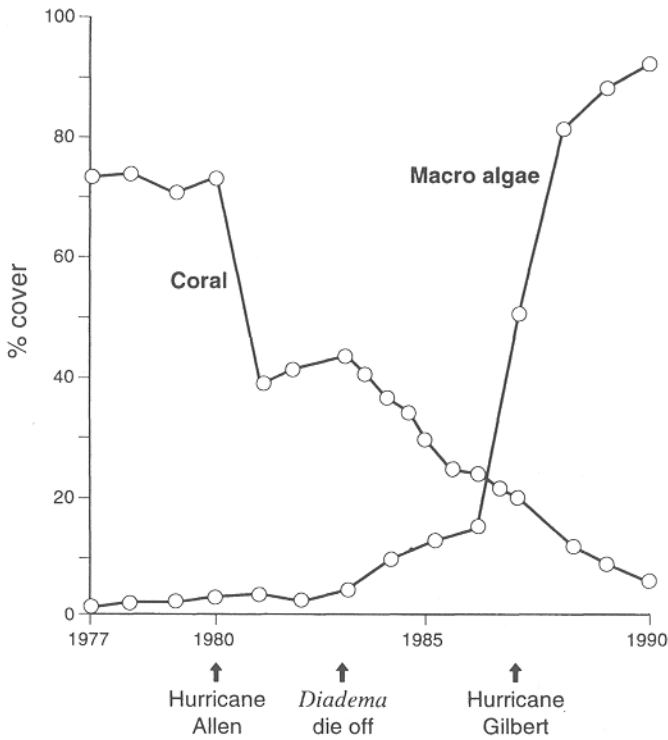
*Crown-of-thorns starfish* In the 1960s and 1980s, populations of the crown-of-thorns starfish *Acanthaster planci*, for reasons unknown, increased by several orders of magnitude and killed much of the coral over large areas throughout the central portion of the Great Barrier Reef (Moran 1986) and elsewhere in the Indo-Pacific. On each occasion, one or more good years for the starfish recruitment combined with abundant palatable coral to allow local starfish populations to explode (Antonelli *et al.* 1990). Complete consumption of all available coral tissue caused the highly aggregated starfish populations to emigrate to and feed in contiguous areas of high coral cover. Algal turfs and fleshy macro-algae colonised the dead coral skeletons and became the dominant benthic biota. Over a period of a decade or so, corals and coralline algae gradually reestablished their dominance in many shallow reef areas (Done 1992c).

Functionally, the initial change from coral to algal dominance represents a shift from the Figure 15.3a configuration to that of Figure 15.3d, and the recolonisation by coral represents the reverse transition. There was no apparent increase in the abundance of grazing fishes in response to the increased algal biomass (Williams 1986). Thus, the outbreak more likely initiated an increase in the detritus compartment (Figure 15.3e) than in usable protein.

Biodiversity has been implicated in hypotheses about both the cause of the outbreak and the system response. Ormond *et al.* (1990) proposed that a reduction in fish predation rates on juvenile starfish, caused by intensification of fishing-pressure since the 1960s, could have led to increased juvenile survival and thus to adult outbreaks. Keesing and Lucas (1992) showed how the level of total coral cover (and hence, presumably, community calcification rate) could be a function of coral biodiversity; viz. the relative abundance of highly palatable versus less-palatable coral species.

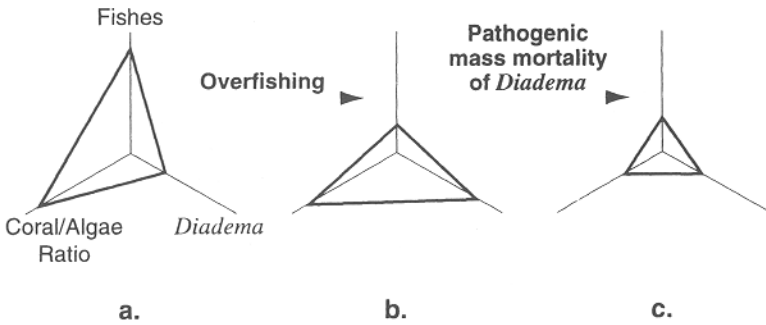
*Caribbean sea urchin* In the Caribbean, dense populations of the herbivorous sea urchin *Diadema antillarum* collapsed throughout the Caribbean in 1983 (Lessios 1988). Dramatic changes on some Jamaican reefs subsequent to the collapse have been documented by Hughes (1989, 1994; Figure 15.5). Reef slopes formerly covered by dense coral assemblages became covered by dense beds of benthic algae (Carpenter 1990), and remain in this state today (Hughes 1994).

Like *Acanthaster planci* outbreaks, the high-density populations of *D. antillarum* are also believed to be anomalous and related to biodiversity loss (Figure 15.6) Jackson (1994) suggested that in pristine, pre-Columbian times, *D. antillarum* competed for its share of benthic algae against a diverse assemblage of fish and invertebrates. Corals were beneficiaries, because the



**Figure 15.5** Changes in the abundance of corals and algae at Discovery Bay, Jamaica, indicating the timing of Hurricanes Allen and Gilbert, and the mortality in *Diadema antillarum* (redrawn from an unpublished figure with permission of T.P. Hughes)

grazers prevented the algae from overgrowing them. Since Columbus, a relentless increase and diversification in fishing effort and catch has dramatically reduced populations of *D. antillarum*'s competitors and its predators. The release from both competition and predation allowed *D. antillarum* populations to increase dramatically (Ogden *et al.* 1973; Hughes 1994; Jackson 1994), and it alone became responsible for grazing benthic algae down to levels at which they were not major competitors of hard corals. However, *D. antillarum*'s high densities, while allowing it to "do the job" of the missing grazers, also made its populations vulnerable to disease. In 1983, perhaps inevitably, a lethal pathogen decimated *D. antillarum* populations throughout the Caribbean (Lessios 1988). We may surmise that the pristine situation of smaller, multi-taxa populations of grazers would not have been subject to such an event. Moreover, declines in one grazer population may have been more readily compensated for by increases in others.



**Figure 15.6** Changes in relative abundance of Caribbean corals as a response to overfishing and mass-mortality in *Diadema antillarum* (a) Pristine situation prior to overfishing, with grazing role shared among diverse fish and invertebrates; (b) *Diadema* populations elevated due to overfishing of its competitors and predators; (c) coral to algae ratio depressed due to release of all grazing pressure and death of corals due to algal overgrowth and other causes (after Jackson 1994)

Widely throughout the Caribbean basin, a number of circumstances have acted in synergy with the absence of the urchin to favor the dominance of fleshy benthic macro-algae over corals (Knowlton 1992); the increased availability of nutrients (Hallock 1987), the increased sedimentation associated with deforestation (Cortés and Risk 1985), the physical destruction of large areas of coral by hurricanes (Woodley *et al.* 1981; Hughes 1989), oils spills (Jackson *et al.* 1989), and mass bleaching of corals (Williams and Bunkley-Williams 1990). Functionally, the changes appear to be equivalent to those caused by *A. planci* outbreaks – viz. predominance of the trophic pathway over the bioconstructional, and a predominance within the trophic pathway of the detrital branch (Figure 15.3d,e).

*East African sea urchin* A third variation on the theme has been described in Kenya, East Africa. The density of the herbivorous sea urchin *Echinometra matthai* is 100 times greater on reefs unprotected from fishing than it is on protected reefs (McClanahan and Muthiga 1988, 1989). The difference is correlated with differences in fish predation on the urchin, which is four times greater within than outside protected areas. *E. matthai* grazes algal turfs, but is also an incidental bio-eroder of reef framework (Figure 15.3f). The reefs with high urchin populations are totally devoid of visible macro-algae (it is grazed before biomass accumulates to any appreciable degree) and the coral framework appears to be undermined faster than it can be replaced by the coral growth (T.J. Done, personal observations, 1990). There are poor prospects for coral recolonization, because each square centimetre is grazed too frequently for newly settled corals to survive and grow

(microscopic corals and grazed indiscriminately along with the algal turfs and skeletons).

As with *A. planci* and *D. antillarum*, the inference is that human reduction of fish biomass and diversity is a causal link with the abundance of *E. matthai*. At optimal densities *E. matthai* facilitates coral recruitment and growth at rates that more than compensate for bioerosion incidental to its grazing. However, like *D. antillarum*, its dense populations may also be vulnerable to pathogenic disease. Should that happen, and the urchin populations crash, coral to algal transitions similar to those in the Caribbean may follow (see also Done 1992a).

#### 15.4.2 Water quality and land runoff effects on biodiversity and ecosystem function

The water flowing onto a coral reef acts as a transport medium for materials (organic matter, nutrients, sediments, propagules – see Section 15.3) which are beneficial when delivered at appropriate concentrations and frequencies, but may be deleterious when delivered in excess.

*Mechanisms for nutrient impacts on coral reefs* Four mechanisms for nutrient impact on reefs are recognised, although cause and effect have been difficult to establish unequivocally (Bell 1992). Should they reach a reef in solution, nutrients can affect reefs by (1) weakening coral skeletons (Hallock and Schlager 1986), and (2) fertilizing benthic algae on the reefs so that they smother living corals (Smith *et al.* 1981; Lapointe 1989). Nutrients may also act to the detriment of coral reefs because of the phytoplankton blooms initiated by elevated nutrient levels. These blooms may (3) reduce water transparency (Lapointe and O'Connell 1989) and hence the vigor of coral growth, and (4) if they die on the reef *en masse*, starve reef animal communities of oxygen (Johannes 1975).

*Symbiont diversity as a basis for adaptation?* Within rather narrow limits, individual corals can “photoadapt” to gradual changes in available light by regulating photosynthetic pigments and zooxanthellae densities (Dustan 1979; Battley and Porter 1988). Diversity in photoadaptability is an important hedge against minor environmental deterioration, be it based in corals or zooxanthellae, or at the level of species or genotype (Buddemeier and Fautin 1993). A single species of coral can host several distinct taxa of zooxanthellae, with the dominant zooxanthella being correlated with the amount of available light (Rowan and Knowlton 1996). Different coral/symbiont combinations may act to maximise calcification under particular light regimes, thus allowing the critical ecosystem outcome of accumulation of framework to be maintained over a wider depth range than would be possible if such a diversity of combinations did not exist.

*Landscape/seascape diversity as buffers protecting coral reefs* Coral reefs depend to a large extent on the existence of "properly functioning" adjacent habitats for their own well-being. This is an important aspect of biodiversity at the landscape/seascape scale. The concentrations and frequencies of water-borne materials carried to reefs are determined by events and processes occurring at a distance from the reef (e.g. in terrestrial catchments, rivers, estuaries, the open sea). For example, high flows of freshwater into reef waters can cause high rates of coral injury and mortality (Sakai and Nishihira 1991), whereas riparian and strand vegetation can restrain soil and freshwater runoff into coral reef waters (Kuhlmann 1988). Mangroves and seagrasses trap and utilize river-borne, nutrient-laden silts, thereby buffering coral reefs from potentially damaging excesses of nutrients or sediments (Ogden and Gladfelter 1983; Birkeland 1985).

In extreme cases of poor land use adjacent to reefs in poorly flushed embayments, land runoff of sediments and nutrients can lead to the transformation of coral reefs to piles of coral rubble dominated by microbes, worms and sponges (Smith *et al.* 1981). Even on some open coasts, where terrestrial discharges are carried along a reef-fringed shore, impacts may be major and widespread (Tomascik and Sander 1985, 1987a,b; Cortés 1990). On other open coasts, by contrast, direct impacts of even very nutrient-rich outfalls may be minor and localized (Grigg 1994), and those impacts, potentially mediated by the planktonic system, are advected away from reefs.

## 15.5 BIODIVERSITY AND RESILIENCE

### 15.5.1 Replenishment of populations

Resilience is the ability of populations to replenish losses incurred as part of normal population fluctuations or as a result of exploitation or other human impact. Given the key functional roles of many coral reef populations in bioconstruction and protein production, resilience benefits not only the individual populations concerned, but also the maintenance of key ecosystem outputs of framework and protein.

However, resilience in a coral reef population is as much a function of the location of the coral reef in relation to other reefs as a property of the population itself (Johnson and Preece 1993). Individuals usually exist in partially isolated sub-populations linked by pelagic dispersal of larvae (Hughes *et al.* 1992; Knowlton and Jackson 1994). Both year-to-year population replenishment, and genetic diversity within and among the local sub-populations, depend on the strength of these links. Within large and dense archipelagos arranged along major current systems (e.g. the Great Barrier Reef), most reefs are assailed regularly by dense aggregations of the

larvae of fish, corals and other invertebrates released from upstream reefs (Oliver and Willis 1987; Doherty and Williams 1988). In this setting, high degrees of gene flow have been demonstrated in a number of invertebrate taxa (Benzie 1993, 1994; Benzie *et al.* 1995). There is, however, enormous interannual variation in larvae supply and recruitment success, over scales from patch reefs to regions (Doherty and Williams 1988), and unexpected restrictions to gene flow can occur (Benzie 1993, 1994; Benzie *et al.* 1995).

At reefs separated from their neighbors by great distances, unfavorable currents, or both (e.g. French Polynesia), larvae from other reefs are more likely to arrive as a dribble than as a torrent, and at intervals of many years, decades or even longer. For their year-to-year replenishment, populations on isolated reefs must depend much less on larvae from other reefs and much more on retention of their own reproductive output (Planes 1993). This includes locally settling larvae (e.g. Stoddart 1983), and asexually produced buds (e.g. Sammarco 1981) and fragments (e.g. Done and Potts 1992). Both larval-retention rates and conditions for survival are a function of the reef's shape and hydrodynamic setting. The residence times of water and the rates of delivery for water-borne materials (larvae, nutrients, suspended sediments) depend on the presence or absence of features such as a lagoon, its depth, the number and width of passages, the continuity and height of the reef rim, tidal characteristics, and so on (Black 1993, Wolanski 1994). Such considerations affect both the probability that larvae will be carried to a particular part of a reef, and the likelihood that it will survive and grow once there.

### 15.5.2 Life history strategies, resilience and resistance

In corals, diversity of coral growth form, life-history strategies, demographic performance, palatability, protective symbionts and strength of attachment have both phenotypic and genotypic bases (Veron 1986, 1995; Knowlton and Jackson 1994). Such diversity maximizes the chance that long-term accretion of framework will be achieved in the face of periodic disturbance (Connell 1978; Rogers 1993). The "intermediate disturbance hypothesis" (Connell 1978) holds that a low rate of disturbance allows competitively dominant corals to monopolize areas, a high rate allows only the most rapid colonizers to dominate, and an intermediate rate favors coexistence of many species. At the population level, the resilience of massive corals killed or injured by crown-of-thorns starfish (Done 1987) or hurricane waves (Massel and Done 1993) is largely a function of the relationship between intensity and frequency characteristics of the disturbance and key life-history parameters of the corals.

Depauperate coral communities at reefs with weak or infrequent connections to source areas may lack both resistance and resilience (Preece and

Johnson 1993; Johnson and Preece 1993). For example, a combination of catastrophic events at very depauperate eastern Pacific Reefs decimated their two main framework builders (Glynn and de Weerd 1991). The coral community lacked resistance because these corals happened to be vulnerable to high temperature associated with the 1982 El Niño (Glynn 1988, 1990), and to storm waves, which easily dislodged the decaying skeletons. It lacked short-term resilience because there were insufficient larvae of any coral species establishing colonies at the site. Restoration of its functionality in terms of framework accretion awaits a chance colonisation event by the reef-building biota, an event which may be extremely rare in human time scales.

## 15.6 SUMMARY, RECOMMENDATIONS AND CONCLUSIONS

### 15.6.1 Summary

The coral reef has traditionally been portrayed as an oasis of diversity and biomass in the oceanic desert. This chapter emphasizes that there is also a great diversity among coral reefs, due to differences in their biogeographic and environmental settings, and their geological histories. Nevertheless, all build and maintain substantial wave-resistant structures and accumulate biomass per hectare well above that of the surrounding ocean. It has been proposed that if they are "healthy", they perform the critical ecosystem-level functions of photosynthesis, respiration and calcification within predictable bounds (Kinsey 1988, 1991), regardless of the specific details of biological composition and diversity. Reefs performing up to these standards (Table 15.1) possess a capacity for net accretion of limestone which is an essential, but not sufficient, condition for maintenance of the coral reef as an entity.

Net limestone accretion could conceivably be achieved solely by encrusting and erect coralline algae, foraminifera, mollusks and echinoderms. However, in the absence of a framework, these groups are incapable of building the porous, three dimensional, wave-resisting reef structures that provide habitats for a myriad other forms. Reef-building corals provide that dimensionality.

Corals can be severely depleted or entirely destroyed over large areas by any number of natural and anthropogenic disturbances, events which in many circumstances lead to an undergrazed reef covered by macroalgae, or a bare, overgrazed reef being actively eroded. Diversity of growth form, palatability, tenacity and physiological tolerances – at the levels of genotypes and species – provide corals collectively with the capacity to occupy gaps and resist disturbance in a wide range of environments. Diversity of life-history strategies and abundant parental stocks in strategic places provide coral communities with a capacity for resilience. Reefs or

patches of reef may rely mostly on their near neighbours for year-to-year recruitment, but the global distribution of coral reefs also reflects a remarkable capacity for reef species to disperse across oceans. Managers and commercial users of coral reef resources need to be mindful of the connectivities among reef populations and of the range of time and space scales over which they operate, and scientists need to provide managers with a more quantitative understanding of these issues (Done 1994).

### 15.6.2 Recommendations

*Scientific research needs* The scope of work needed to address the issue of ecosystem consequences of biodiversity in coral reefs is, in broad terms, similar to that identified for other marine ecosystems (Butman and Carlton 1993): (1) research on the determinants of species distribution and abundance, and (2) biology and ecology of species that play a pivotal role in the maintenance and generation of diversity as it relates to community and ecosystem function and stability.

As in other ecosystems, the success of crucial aspects of this work will rely on improvement and expansion in several related areas which are currently deficient. For example, there are still many reef groups and locations for which taxonomic treatises are unavailable or sub-standard, and there remain fundamental questions regarding the distinctions between species. These questions – which are germane to the assessment and monitoring of *species* diversity and the analysis of its origins, as well as its implications for ecosystem function – can now be approached using genetic probes unavailable only a few years ago. All are aspects which are integral to the DIVERSITAS program concerned with the broader issues of biodiversity throughout the biosphere (Grassle *et al.* 1990; di Castri and Younès 1996).

Coral reefs provide a number of challenges and opportunities in addressing this scope of research. For both individuals and for multidisciplinary collaborations within and among institutions and countries, they include a combination of comparative and experimental approaches:

- experimental reduction of diversity of some reef areas over a period of time while monitoring structure, dynamics and ecosystem processes of the simplified and control (unmodified) systems;
- comparative studies of these types on “pristine” reefs and reefs of the same type in the same region which have already been subjected to natural or unplanned perturbations which have resulted in reduced diversity;
- comparative studies on reefs with strong natural differences in biodiversity due to their geographic locations and environmental settings;

- “a cross-biome experiment” in which, in the manner of the Hubbard Brook experiment (Borman and Likens 1979), terrestrial scientists investigate various aspects of catchment transformation under management, and marine scientists investigate the consequences for populations, communities and processes in adjacent estuaries, coastal waters and reefs.

*Applications to management of coral reefs* The basic issue for management is to discriminate between human impact, which can be managed, and the natural variation of ecosystems. The ecological structure and function of a coral reef in any particular location will be the result of the long-term (over geologic time) interplay between natural factors upon which (in recent time) human impact has been superimposed. Inter-disciplinary studies conducted over the full range of regional development of reefs and encompassing the time scale of ocean processes will provide the best opportunity to identify thresholds and rates of responses of reefs to global change, and to evaluate the success of our attempts to manage them for sustainable use. Study of the Quaternary history of fossil coral reefs, like those undertaken on Quaternary vegetation patterns, may also shed light on the natural responses of reef ecosystems to perturbations at local (tectonic) and global (sea level and climate fluctuation) scales.

Application of research findings to management objectives aimed at sustaining proper ecosystem function and services will require a quantitative and predictive understanding of many of the issues raised in this chapter. Quantitative studies are needed to understand: the real threats posed by terrestrial input in specific contexts (e.g. the extent of the influence of Hallock and Schlager's (1986) “nutrient halo” at river mouths under conditions of flood and low flow); mechanisms and thresholds leading to state changes and wide population fluctuations in “facilitator” populations (Done 1992a; Knowlton 1992); the domains of water quality, hydrodynamics and grazing pressure that maintain certain reef states, and the areas over which such domains exist. Additional efforts should also be directed toward elucidating patterns of hydrodynamic closure, reef interconnectedness and population replenishment. Ecological models are needed to predict the responses of coral reefs under different scenarios of growth in human populations, urbanization, industry and agriculture, and under different regimes of management.

*The need for international collaboration* There are strong practical arguments for strengthening international collaboration and communication among reef scientists, oceanographers and terrestrial researchers. Extreme pressure on coral reef biodiversity and function already exists on coral reefs in many parts of the world. However, the natural replenishment of the depleted reef resources in one country may rely on the reproductive output of reefs in

another, and the conditions for maintenance of biodiversity and ecosystem function may be strongly influenced by land use practices and runoff. Thus individual reefs cannot be either managed or understood in isolation from other reefs, or from adjacent marine or terrestrial habitats. For these reasons, existing intergovernmental arrangements, including those among developing tropical countries where most coral reefs occur, and between developing and developed nations should be supported and strengthened. Networks of marine laboratories are a readily available infrastructure to carry out synoptic, standardized protocols of observations on the structure and function of coral reefs within coastal zones. The network is a powerful tool for the development of meso-scale remote sensing of the coastal zone, particularly land-sea interactions, interplay of coastal and oceanic processes, and regional patterns of marine biological diversity. The CARICOMP network of Caribbean marine research laboratories, parks and reserves (Ogden 1987) is one such arrangement which links nations bordering the Caribbean sea. This network provides a useful model for information sharing, cooperation and coordination among coral-reef scientists.

### **15.6.3 Conclusion – biodiversity and ecosystem function, from genes to regions**

To conclude, we have identified how biodiversity, from genes to regions, may affect ecosystem function in coral reefs. At a single reef, diversity in the life-history characteristics of reef biota, both within and among species, provides the basis for occupancy and survival in the broad range of environments that the reef provides. The diversity of a reef's zones is essential to the maintenance and accretion of the overall structure itself, and of its protein resources. Each zone's characteristic abiotic substrates and communities provide it with particular capabilities of processing inputs and producing outputs of framework, sediments and organic matter.

At a regional scale, part of the enormous genetic and species diversity of coral reef biota allows framework-building communities to occupy turbid nearshore environments as well as the transparent oceanic waters of the popularly-conceived "typical" coral reef. A second region scale element of biodiversity is the topology of the hydrodynamic inter-connectivities which carry reproductive outputs among reefs. Diversity in the dispersing capabilities of coral-reef species allows region-scale topologies to be matched by species capable of exploiting them. The siting of marine protected areas as effective replenishment refuges for a region's coral-reef resources needs to be guided not only by the status of the protected and exploited populations, but also by their connections with other reefs.

The broad scope of this chapter has led us to make many generalities, based on selective use of the literature, and often to develop ideas beyond

the available data. We hope that this approach stimulates reef scientists to refine our good ideas and to refute our bad ones.

## ACKNOWLEDGEMENTS

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