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Coral Reefs in the Anthropocene

Charles Birkeland

Abstract

Although coral reefs cover only 0.00063 of the surface of Earth, they have had important effects on the atmosphere, ocean chemistry, the shape of the surface of Earth, the diversity of life, the biogeographic distribution of life, and they provide hundreds of billions of dollars in value per year in goods and services to tens of millions of humans. All the continents, islands and freshwater habitats of Earth together occupy more than 460 times the total surface area of coral reefs, yet host only 19 phyla while coral reefs host at least 30 phyla of animals. The per square meter value of coral reefs in goods and services has substantially increased since estimated in 1997, but the total value has decreased from loss of coral-reef habitat and stock of large fishes. Coral reef ecosystems in natural undisturbed states can be inverted trophic biomass pyramids with especially high primary production, but meagre yield or net production. Extractive commercial fishing is potentially sustainable if medium-sized individuals and not large individuals are taken. The net yield for human consumption can be increased by removing the upper trophic levels, but the system is more sustainable and beneficial for humans when managed as a service-based economy rather than an extraction-based economy. The present interglacial period (the Anthropocene) has been exceptionally favorable to coral reefs for thousands of years until the recent three or four decades, in which the living coral cover has abruptly declined about 53% in the western Atlantic, about 40% in the general Indo-Pacific, and about 50% on the Great Barrier Reef. Reefs are presently threatened by increasing CO_2. Although there have been few, if any, extinctions, reefs are declining in topographic complexity and ecosystem services. This is most likely the trajectory for future decades and reflects the norm for much of the geologic history of coral reefs.

Keywords

Pyramid • Biosphere • Economy • Services • Productivity

1.1 Coral-Reef Ecosystems Have Low Sustainable Yields Because Diverse and Intense Interactions Consume the Production

As a foundation for managing reef resources, we should outline the reasons why coral-reef systems cannot maintain their basic structure while supporting an extractive economy. In their natural state, coral-reef communities are

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typically inverted trophic biomass pyramids with a greater biomass of consumers (invertebrates and fishes) than primary producers (cyanobacteria, dinoflagellates and other photosynthetic protists and various phyla of algae). Although coral-reef systems maintain tremendous primary production with rapid turnover and energy flow of producers, nearly all the net production is consumed within a system of approximately six trophic levels. It has been recognized by both scientists (e.g., Grigg et al. 1984) and fishers (testimony at UNEP conferences) that in order to increase net yield and sustain an economy based on extracting and selling biomass, it is necessary to diminish or remove the upper trophic levels. Alternatively, some islanders have found that system integrity can be maintained with subsistence fisheries and service-based economies by taking middle-sized fishes from species populations and extracting the interest rather than the capital from the population (Sect. 12.6).

Coral-reef ecosystems are among the most productive ecosystems in the world in terms of gross primary productivity, yet the net productivity (biomass yield or potential export) per unit area is only about a tenth of that from upwelling systems even though the upwelling areas have only about a ninth as much primary productivity per unit area as coral reefs (Fig. 1.1). The processes of predation and competition by a diverse array of consumers among six trophic levels on coral reefs leads to a substantial consumption of resources and reduction of the potential export from coral-reef systems. Hatcher (1997) found that the relatively small net (excess) community productivity sets an upper limit to sustainable yield (export from the reef) of about 2–3% of the gross productivity. Of this 2–3%, only about 10% is in a form usable for consumption by humans. This is well under 1% of the gross primary production by coral-reef ecosystems. Kinsey (1983) reviewed the literature on the metabolic performances of typical undisturbed reefs and found that biotically heterogeneous reef flats exhibited a remarkably narrow range in standard of performance. The community gross diel primary productivity (P) or photosynthesis closely matched the gross diel respiration (R) or community metabolism. Kinsey (1983) compiled most of the published information at the time on P and R from coral reefs around the world (mostly from the Pacific) and calculated that for the standard reef flat coral community, the ratio of community gross primary productivity to community gross respiration is usually very close to 1 (P/R = 1+/−0.1). This corroborates Nixon's (Fig. 1.1) and Hatcher's (1997) findings that most of what is produced on coral reefs is consumed on coral reefs and little is left for yield. Metabolic and stored energy are mainly recycled within the system and used in growth and maintenance of standing stock consumed locally.

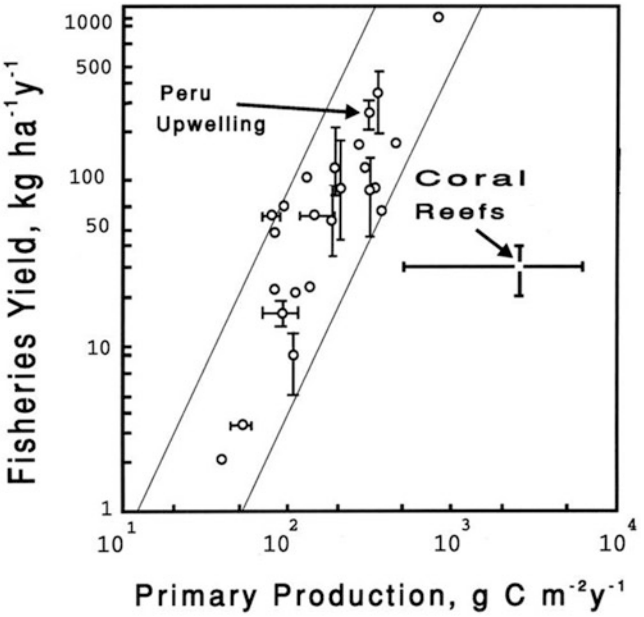


Fig. 1.1 Differences between coral reefs and other marine ecosystems in the relationships of fisheries yield to gross primary production. The non-coral-reef relationship is based on 49 studies at 25 sites (Redrawn from Nixon 1982)

Sargent and Austin (1949, 1954) and Odum and Odum (1955) had previously concluded that the coral-reef ecosystem is basically self-sufficient in primary production, with nearly all production provided by benthic algae (including algae from within the coral skeletons) and symbionts (zooxanthellae, cyanobacteria, *Prochloron*), with phytoplankton contributing little. The zooplankton is largely demersal, i.e., resident on the reef, dwelling within or near the substratum during the day and rising into the water column at night (Emery 1968; Porter and Porter 1977; Alldredge and King 1977, 1980; Hamner and Carleton 1979; Birkeland and Smalley 1981). Odum and Odum (1955) and Gerber and Marshall (1974) documented that the zooplankton and the rest of the suspension-feeders in the reef community consume "pseudoplankton", derived mostly from within the reef ecosystem. The photosynthetic pigments in the stomachs of zooplankton were mostly microscopic fragments from benthic algae. Phytoplankton from external sources made up almost none of the production.

The low export of coral reefs might also be attributed in part to the diverse array of animal/microbe photosynthetic symbioses that capture the solar energy but recycle and thereby retain nutrients within the system. The dinoflagellates *Symbiodinium* spp. provide caloric intake to some foraminiferans, scyphozoans, hydrocorals, octocorals, zoanthids, sea anemones, scleractinians, and bivalves, and are hosted by some ciliates, flatworms, and nudibranchs, while cyanobacteria provide photosynthetic intake to some sponges and the specific cyanobacterium *Prochloron didemni* provides calories for some ascidians.

Kinsey (1983) suggested that the “standard” P/R = 1 provides a basis for measuring the effects of stresses and perturbations in the altered environments. It would be instructive to determine if any of the widely distributed locations of measures of P and R ratios (mainly in the 1970s) have changed in the past 30–40 years. For example, for those sites at which herbivores have since been overfished, the reefs might experience an overall increased cover of algae. If this is the situation, we might predict the P/R > 1. Conversely, when there is substantial nutrient input from external sources, the trophic characteristics of the system can change drastically (Birkeland 1988a, b; Fabricius 2005). If the eutrophication of the coral-reef ecosystem results in a shift from benthic algae and zooxanthellae being the foundation of primary productivity to phytoplankton, it is usual that heterotrophic suspension-feeders occupy much of the substratum and the system could shift to P/R < 1 (Chap. 9).

This thorough use of available energy by the coral community might be attributed also to the diverse and abundant standing stocks of consumers. Mixed benthos assemblages on reef crests and flats constitute an effective filter that depletes the water of most suspended particulates including bacteria, cyanobacteria, phytoplankton, and zooplankton (Glynn 1973; Ayukai 1995; Fabricius and Dommisse 2000). Even dissolved organic carbon is substantially consumed (Reiswig 1981), making up 90% of the diet of some sponges (De Goeij et al. 2009). During the day, the planktivorous fishes form a “wall of mouths” that remove larvae (Hamner et al. 1988) and at night, the scleractinians and zoanthids form a “wall of mouths” (Fabricius and Metzner 2004) making it hazardous for larvae to recruit to coral reefs (Sect. 12.2). In addition, parrotfishes alone can subject a reef surface to over 150,000 bites per m^2 per day (Carpenter 1986) which can incidentally add to the dangers of recruiting coral spat. There is a diverse array of predators of scleractinian corals that includes 314 species of invertebrates from 5 phyla or 24 families (Stella et al. 2011) and 128 species of fishes from 11 families (Cole et al. 2008) that collectively prey on 28 genera of corals. In contrast to nutrient-rich pelagic areas of upwelling that have only 1½ trophic levels (Ryther 1969) and tremendous potential for yield, coral-reef ecosystems have relatively little nutrient input with six trophic levels (Grigg et al. 1984) through which much of the caloric and nutrient material is recycled and kept within the system and not exported. Much of the consumed and assimilated energy is expended as respiration at each trophic level, so more of the gross production is lost as respiration in a system with six trophic levels than in a system with two or three.

There is a greater diversity and abundance of vertebrates per m^2 on coral reefs than in any other ecosystem (Chap. 10). Vertebrates are all consumers. Even among the trophic levels of consumers, unexploited coral reefs can give the appearance of inverted trophic biomass pyramids with 80% of the biomass being the upper trophic level, the piscivores, and all the lower trophic levels of fishes lumped together being 20% of the vertebrates (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008; Fenner 2014). Although the findings of these surveys may be robust (Rizzari et al. 2014) insofar as relatively unexploited populations of piscivores on coral reefs far from human populations have a greater biomass of larger individuals compared to populations near human populations, Ward-Paige et al. (2010), Nadon et al. (2012), and Trebilco et al. (2013) provide arguments that the abundances of apex predators can be overestimated because of behavioral characteristics of fishes. Trebilco et al. (2013) also admonished that the coral-reef ecosystem was not an inverted trophic pyramid because of subsidies from external sources. Indeed, nutrient input from external sources can drastically affect the trophic structure of coral-reef communities (Chap. 9; Birkeland 1988a, b; Fabricius 2005; Fabricius et al. 2010).

Energy flow and turnover are greater at lower trophic levels, but can this actually produce inverted trophic biomass pyramids in natural undisturbed coral reefs in locations without substantial nutrient input from external sources? Odum and Odum (1955) found the biomass of zooxanthellae to be only about 15% of the animal tissue. Recent studies have indicated the biomass of zooxanthellae may be <5% of the coral animal tissue (Thornhill et al. 2011). This suggests a coral polyp could be an inverted trophic biomass holobiont in itself. Muscatine and Porter (1977) and Muscatine et al. (1981) have indicated it is possible that zooxanthellae could provide nearly all the caloric requirements of the animal tissue in corals, although external sources of food are required for particular elements such as nitrogen and phosphorus. Even though corals must obtain subsidies for particular nutrients, the energy flow through a particular biomass of zooxanthellae (producers) is potentially enough to support 6–20 times its biomass in animal tissue (consumers). However, corals also take up some nutrients from a variety of external sources such as dissolved organic matter, particulate organic matter, bacterioplankton, fecal material, and zooplankton, thereby indirectly feeding on byproducts of the benthic algal web. The degree to which individual corals depend upon zooxanthellae, zooplankton, or other materials for energy varies substantially with coral species, habitat depth, and other factors. Polyp size is no longer considered a reliable indicator of the proportion of energy provided by zooxanthellae or zooplankton (Sebens 1997). So for the discussion of inverted biomass trophic pyramids, the coral animal tissue needs to be lumped with other animals as consumers and the zooxanthellae need to be lumped with benthic algae as primary producers.

All animals are consumers, so the trophic pyramid based on benthic algae includes invertebrates with the fishes. A relatively undisturbed reef hosts about 200 g m^{-2} of fish in both the Atlantic and Pacific (Goldman and Talbot 1976; Williams and Hatcher 1983), with some locations hosting up to 800 g m^{-2} (Jarvis Island, Sandin et al. 2008). Even substantially overharvested fish associations such as Tabuaeran and Kirimati still host 170 and 130 g m^{-2} of fish respectively (Sandin et al. 2008). For consideration of whether an inverted trophic biomass exists, we will be very conservative by taking 150 g m^{-2} for fish, the average of the severely overfished Tabuaeran and Kirimati, in order to avoid the issue of fish behavior. Coral tissue is typically in the range of 40 g m^{-2} (Thornhill et al. 2011; Schoepf et al. 2013) if living coral cover is assumed to be about 60% on an undisturbed reef. Brock and Brock (1977) found the biomass of invertebrates in endolithic coral rock at six sites to range from 97 to 796 g m^{-2}, with an average of 317 g m^{-2}, but this does not include invertebrates living on the reef surface. Therefore, since consumer biomass combines the biomass of fishes (150 g m^{-2}, potentially up to 800 g m^{-2}) with the animal tissue of corals (40 g m^{-2}) and other invertebrates (317 g m^{-2}, in addition to invertebrates on the surface of the substrata), the consumer biomass on severely overfished coral reefs would be at least 500 g m^{-2}, not including invertebrates living on the surface.

For the producers, Bruno et al. (2014) found that macroalgal cover on "quasi-pristine reefs" generally ranged between 10% and 30% cover, averaging 22%. Klumpp and McKinnon (1992) found an overall average production of 150 g C m^{-2} $year^{-1}$ from a number of reefs on the Great Barrier Reef (GBR). The epilithic algal communities on reef slopes of the north, central and southern GBR ranged between 30 and 70% cover, or with a median algal cover on the GBR being roughly 2½ times the cover on "quasi-pristine reefs". Therefore, $150/2.5 = 60$ g C m^{-2} $year^{-1}$. Since biomass is generally composed of R-CHO (molecular weights of $C = 12$, $O = 16$ and $H = 1$), $29/12 = 2.4 \times 60$ g C m^{-2} $year^{-1}$ $= 144$ g epilithic algal biomass produced m^{-2} $year^{-1}$. Coral tissue is 40 g m^{-2} and 5–15% (Odum and Odum 1955; Thornhill et al. 2011) is zooxanthellae, so if we take the median ratio of zooxanthellae to coral tissue as 10%, the algal biomass would be 144 g C m^{-2} $year^{-1}$ plus 4 g m^{-2} or 148 g m^{-2}. This is substantially less than the 500 g m^{-2} consumer biomass.

However, the algal biomass was measured as the annual biomass production while the biomass of animals was assessed for a given moment. Many of the animals at upper trophic levels live for decades and take several years to mature (Sect. 13.5.3) while the net turnover of epilithic algal turf biomass is more rapid. Klumpp et al. (1987) found the net turnover of epilithic algal turf on two reefs in the Great Barrier Reef and one reef in Papua New Guinea (outside damselfish territories where the turnover was higher than the usual rate on a reef) to average about 4% day^{-1}, a complete turnover every 25 days or 14.6 times per year. If the algal turf biomass turns over more often than once a month, and the consumer biomass turns over less than once per year on the average, then the actual producer biomass at any one moment may be as much as an order of magnitude less than that of the consumers. This may remind us of the 1960s and 1970s when the spectacularly diverse and abundant array of animals (consumers) on coral reefs was in contrast to the relatively inconspicuous algae (Figs. 1.2 and 1.3). Macroalgae, however, usually have slower turnover than turf algae and contribute largely to the detrital foodweb.

Odum and Odum (1955) found that when boring algae are included with the epilithic algae, the primary producers average 703 g m^{-2}. This is greater than their findings for the biomass of epilithic algae. They concluded that "boring algae" (of which much is *Ostreobium*) in the coral skeleton beneath the polyp had about 16 times the biomass of the zooxanthellae in the polyp immediately above and made "it possible to explain the great preponderance of organisms classed as animals", i.e., if we include the boring algae, the producers have greater biomass at a given moment than the consumers. Tribollet et al. (2006) measured 40% of the total primary productivity in 3-m depth in Kaneohe Bay, Hawaii, as coming from endolithic algae. Bruggemann et al. (1994a, b) found that a major portion of the diet of parrotfishes, especially the large ones, was endolithic algae beneath sparse turf. *Sparisoma viride* obtained more energy from endolithic algae than from large turfs, macroalgae or crustose coralline algae (Bruggemann et al. 1994a). The larger parrotfishes can have a positive feedback with their major prey, endolithic algae, by grazing away the epilithic algae and thereby reducing the shade and allowing the endolithic algae to expand its range deeper into the reef framework (Tribollet and Golubic 2005). If endolithic algae are substantially greater in biomass than the epilithic algae, and if turnover is on the scale of animals, then it is possible that an inverted pyramid does not occur in coral reef communities. However, if the average turnover in endolithic algae is more rapid than the average turnover in animals, inverted

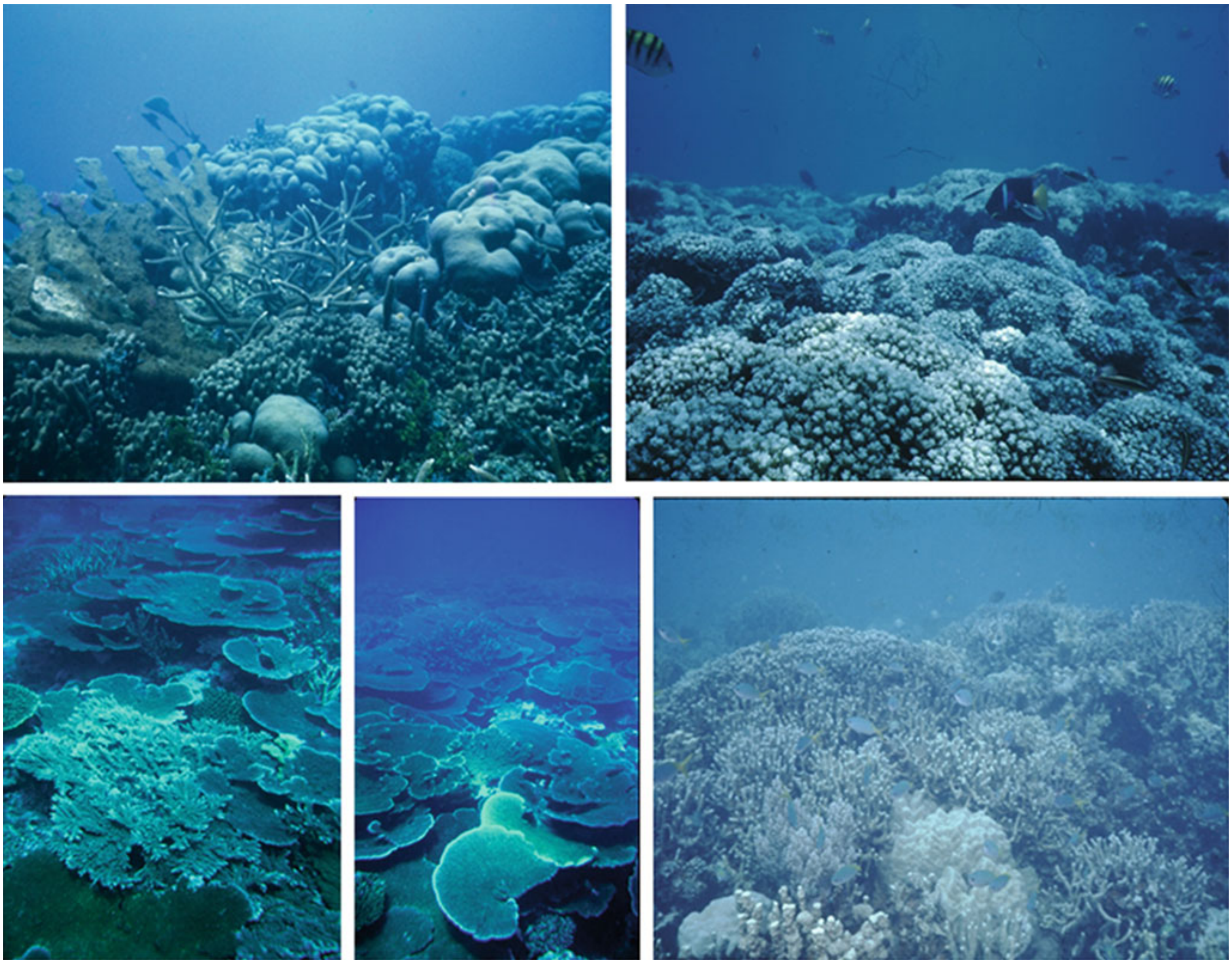


Fig. 1.2 Coral-reef scenes in the mid-1970s. As quoted in Jackson (2014), Sylvia Earle noted in 1972 that "…tropical reefs, notable for their dazzling profusion of animal life, are almost devoid of conspicuous plants". Bruno et al. (2014) found that in natural undisturbed baseline conditions, benthic algae is patchily distributed and can occupy up to 10–30% of the substratum, averaging 22%. Clockwise from *upper left*: Ucubsui Reef, San Blas Islands, Caribbean Panama; Islas Secas, Pacific Panama; Arekabesan Island, Palau; Aunu'u Island, American Samoa; also Aunu'u. These are not a random selection of photographs, but were selected to show how easy it was to be impressed with the prevalence of animal tissue in the 1970s. Odum and Odum (1955) argued that many, if not most, of the algae were endolithic and out of sight

pyramids on relatively natural unfished coral reefs is most likely the norm.

Whether or not undisturbed natural reefs can actually form inverted biomass trophic pyramids, there is intense predation by a diverse and abundant array of consumers. This makes recruitment a risky process for most species of corals and fishes, which selects life-history characteristics such as relative longevity for repeated attempts at reproduction (Sect. 12.2). It also explains the mediocre net production from very high gross primary production (Fig. 1.1). If either the larger individual predators or grazers are taken, the coral-reef community will usually undergo some fundamental changes. By reducing the number of trophic levels and diversity of consumers, the net productivity of the system can be increased and the processes of harvesting and marketing can be more efficient. However, the greatest values of coral reefs lie in their ecosystem services (Costanza et al. 2014) and coral-reef ecosystems have much more economic potential for service-based economies than extractive economies (Sect. 12.6.2). For isolated human populations that need to harvest coral reefs for protein and maintain the integrity of their food supply, they must exploit their stocks with two forms of moderation: using slot limits to take the intermediate size classes of each species taken and focusing on harvesting the interest or yield, not the capital (Sect. 12.6.1).

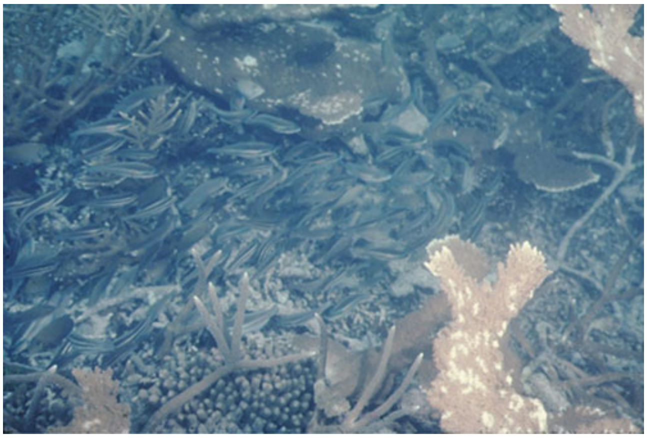


Fig. 1.3 Abundant *Scarus iserti* grazing turf algae among corals that take up most of the space. With little algal availability, the grazers keep the algae in the early stages of succession with rapid turnover and high net productivity (Klumpp et al. 1987), promoting the potential for an inverted trophic pyramid. If the coral is disturbed and the algae expand their spatial coverage and availability, the grazers can become more selective and avoid macroalgae with anti-herbivore defenses, facilitating the takeover of much space by macroalgae (Birkeland et al. 1985) with less turnover and net production, reducing the tendency towards an inverted trophic pyramid

1.2 Coral Reefs Affect the Global Biosphere

Living coral is a thin veneer, measured in millimeters. Yet this thin film of living tissue has shaped the face of Earth more than any other organisms, including humans, by creating limestone structures sometimes over 1,300 m (e.g., Enewetak Atoll) from its surface down to its base on volcanic rock, or over 2,000 km long (Great Barrier Reef). About half the world's coastlines are in the tropics and about a third of the tropical coastlines are made of coral reef. About 400 atolls can be found among archipelagoes such as the Tuamotus, Marshalls, Maldives, Laccadives, Chagos, most of the Carolines and Kiribati, and some of the Coral Sea islands and Seychelles, and these atolls have been formed by coral. In addition to enlarging high islands (such as the entire northern half of Guam) and extending and protecting coastlines, ancient biogenic reefs have coated some areas on continents.

Coral reefs are dynamic systems that influence the chemistry of the oceans and atmosphere. It has been calculated that roughly half the calcium that enters the sea each year around the world, from the north to south poles, is taken up and temporarily bound into coral reefs (Smith 1978). With each atom of calcium, a molecule of CO_2 is also deposited, with gross CO_2 fixation estimated on the order of 700 billion kg carbon per year. Coral reefs can produce limestone at the rate of 400–2,000 tons per hectare per year (Chave et al. 1972), but the rate of calcium carbonate production or deposition is not necessarily the main factor in calcium carbonate accretion or accumulation. Healthy coral communities that are functioning well as coral-reef ecosystems might not be performing well as reef builders. Although the rate of limestone production is high, the rate of reef growth can be low (Kleypas et al. 2001). If the $CaCO_3$ is created, whether as reef accretion or sediment, it is nevertheless removing CO_2 from the atmosphere. Although in the short term, the process of reef accretion releases CO_2 in minuscule amounts in comparison to the amount released by human activities, the amount of CO_2 accumulated and stored in reef structure over the past 200 million years has added up to a substantial portion of Earth's CO_2 and this has made living conditions more favorable for humans and other eukaryotes (Chap. 2).

Although corals have changed the shape of the surface of Earth, living coral reefs are estimated to presently cover only 284,300 km^2 (Spalding et al. 2001), only 0.00089 of the area of the oceans and 0.012 of the areas of the continental shelves. More importantly, while providing three-dimensional structures in shallow water where there would otherwise be only open water, coral reefs have also become "hotspots" for biodiversity. Coral reefs host 30 animal phyla (Paulay 1997), while all the terrestrial and freshwater habitats host only 19 phyla. A single 5 m^2 area of reef sampled in the Caribbean provided 534 species from 27 phyla and 44 classes (Small et al. 1998). The terrestrial and freshwater habitats cover 29% of the surface of Earth, yet the number of phyla in one 5 m^2 quadrat on a coral reefs in the Atlantic is substantially greater than all the terrestrial and freshwater habitats (rain forests, savannah, temperate forests, tropical rainforests, tundra, rivers, lakes, bogs) of the world. Coral reefs in the western Pacific host much greater diversity than reefs in the Atlantic.

Coral reefs have increased the diversity and affected the biogeography of marine life on Earth. By creating hundreds of atolls, reefs produce solid shallow-water substrata in the middle of the tropical oceans, providing stepping stones for dispersion that allowed the distribution of species across extensive spatial barriers that would not have otherwise occurred after volcanic islands sank (Grigg and Hey 1992). For example, there would have been no coral reefs or coral reef fauna in the Eastern Tropical Pacific (one of the four tropical marine faunal provinces of Earth) without the small reefs on Palmyra Atoll and Kingman Reef moving by plate tectonics into positions upstream from the Eastern Tropical Pacific in the North Equatorial Countercurrent (Dana 1975).

Coral reefs are among most biologically productive ecosystems in the world (Fig. 1.1). The global potential for coral-reef fisheries has been estimated at 9 million tons per year, which is impressive in view of the relatively small area of coral reefs compared to the world ocean, and to the total marine fisheries of the world being about 75–100 million tons per year (Smith 1978; Munro 1984). Coral reefs, on the other hand, are vulnerable to overexploitation if harvested repeatedly (Sect. 12.5.1).

So these are paradoxes. Although coral reefs are the most productive ecosystems in the sea, the fisheries of coral reefs are among the most vulnerable to overexploitation (Sect. 12.5). Despite having the power to create the most massive structures in the world made by living creatures (including man), the thin film of living tissue of coral reef is particularly vulnerable to natural disturbances and effects of human activities (Chap. 11). Coral reefs and other animal-algal reefs are the first to go during periods of climate change, but they have always come back. This combination of attributes – creative power and fragility, resilience and susceptibility, productivity and vulnerability to overexploitation – makes management of coral-reef systems a particular challenge to science.

1.3 The Economic Goods and Service Values of Reefs

In 1997, the value of annual production of coral reefs in both goods and services was calculated to average \$6,075 ha^{-1} $year^{-1}$ for a global total at \$375 billion per year (Costanza et al. 1997). By 2014, the average per hectare value of coral reefs in adequate condition has increased tremendously to about \$352,000 ha^{-1} $year^{-1}$, 32% by inflation of the dollar and 5,762% by additional considerations of services such as storm protection, erosion protection and revenue from tourism (Costanza et al. 2014). For coral reefs, the assessment by Costanza et al. (2014) was not based strongly on extractive economies, but rather on ecosystem services. They emphasized that expressing the ecosystem services in terms of dollar value "does not mean they should be treated as private commodities that can be traded in private markets. Many ecosystem services are public goods or the product of common assets that cannot (or should not) be privatized".

Although the calculated value of each hectare of healthy reef has increased, the global total value of coral-reef goods and services has dropped (Costanza et al. 2014) because of the percent area of reefs having been degraded (53% in the greater Caribbean, Jackson 2014), 19% on average for the world (Wilkinson 2008). A major factor in calculations is that the estimation of total shallow living coral cover worldwide in 1978 was over 600,000 km^2 (Smith 1978), while it is now 284,300 km^2 (Spalding et al. 2001). However, the widespread increase in overharvesting of reef fishes may be an additional factor lowering the quality and value of goods and services. Overharvesting comes both from increased populations in less developed countries and from a "gold rush" by developed countries (Anonymous 2000 in The Economist).

Coral reefs are found in over 100 countries, mostly in the less economically developed tropical regions. People depending on coral reefs for part of their livelihood and for obtaining part of the protein in their diet are estimated to number in the tens of millions (Salvat 1992). Despite the vulnerability of reefs to overharvesting for export, reef fisheries had served for hundreds and, in some locations, thousands of years as major sources of food for subsistence. This is certainly a major value of coral reefs. Unfortunately, the number of people exploiting reefs for protein in impoverished communities increases when the human population grows more rapidly than the availability of employment opportunities. The feasibility of fishing reefs near shore without substantial investment in equipment makes reef-fishing the only source of food in countries without substantive welfare.

Fishermen might be aware that they could catch larger fish with less effort if they restrained from fishing for a year or two, but they have families to feed now. It becomes a positive feedback process. The large fish are the first to be caught (Fenner 2014). As the fishes get smaller, it takes a greater number to feed the families. In order to catch enough smaller fishes, it becomes necessary to use methods such as gill nets, traps, muro-ami, and explosives (widely available as munitions left over from World War II, but easily made elsewhere from herbicides and sugar). For example, a quarter of the population of the Caribbean resides in Haiti and it population is growing at 2.5% annually. When Reef Check surveyed 120 km of Haitian coast in 2011, the largest fish they observed was 15 cm (6 in.) in length (Anonymous 2011). There is exponentially greater fecundity in the larger fishes (Sect. 12.5.3) so when relentless fishing pressure brought about by the need for protein for local people with low-incomes removes the larger fishes, there is less chance for the fish population to recover. Even with rich coral growth, the total value may have decreased in recent decades because of fewer large fish.

The diverse stocks of fishes on coral reefs are impressive, especially the stocks in relatively untouched areas with inverted trophic structure. This unfortunately encourages the investment into fishery-based economies. An article in The Economist likened commercial trade in large coral-reef fish to a "gold rush. . .an extractive industry that eventually exhausts the resource it exploits" (Anonymous 2000). Even exploited stocks on coral reefs can be at 200 tons km^{-2}, but the population is especially vulnerable if larger individuals are taken (Sect. 12.5). Since the 1970s, the catch-per-unit-effort (CPUE) in a number of fish stocks exposed to extractive fisheries has been reduced by about 80% and has not recovered for decades (Sect. 12.5.1). Coral reefs have perpetually sustained coastal populations in some areas, perhaps for centuries, because people would catch only what they needed for the immediate future. But with the development of refrigeration, long-distance shipping became possible and opened the world as a potential market. This removed limits on need, so the development of commercial fisheries became a gold rush.

Coral reefs indirectly benefit pelagic fisheries by supplying food for more wide-ranging coral-reef or inshore pelagic fishes. Sudekum et al. (1991) calculated that just two of the species of jacks, *Caranx ignobilis* and *C. melampygus*, together eat 30,600 metric tons per year of benthic fauna from French Frigate Shoals, an atoll in the northwestern Hawaiian Islands.

Introducing alien species to coral reefs for future harvest is generally not a good idea for fish or algae, but I have not heard of any problems, only benefits, from the introduction of large herbivorous gastropods. The herbivorous "topshell" *Trochus niloticus* was introduced widely in the North Pacific (Chuuk, Pohnpei, Marshall Islands, and dozens of atolls in the Caroline Islands) in the 1920s and 1930s and Guam and Saipan in the 1950s. In the 1950s, 1980s and 1990s, it was also introduced widely in the South Pacific including American and Independent Samoas, Tonga, Cook Islands, French Polynesia (Tahiti and the Tuamotus), and Loyalty Islands (Eldredge 1994). By 1980, there was an annual global harvest of about 6,000 tonnes (Bouchet and Bour 1980). The herbivorous "green snail" *Turbo marmoratus* was also introduced to the Society Islands and Samoa, but was not as productive, providing a global harvest of 800 tonnes in 1986 and 1,000 tonnes in 1987 and 1988. These gastropods are harvested for local subsistence protein and commercially for the high quality mother-of-pearl in their shells used in ornamental and curio trade.

Giant clams (Tridacnidae) have also been introduced to new locations and also reintroduced to locations where they had previously been overfished to extinction. Transfers have been performed widely in the Pacific. *Tridacna gigas*, *T. derasa*, and *Hippopus hippopus* were all introduced to Independent Samoa, Fiji, Cook Islands, Saipan, Kosrae, Chuuk and Yap. *Tridacna gigas* and *T. derasa* were also introduced at American Samoa, Tuvalu, Pohnpei, Majuro, and Guam and *T. gigas* and *H. hippopus* at Tonga. I have not heard of them causing any ecological problems. However, wild populations of tridacnids are hard to sustain because they are conspicuous, easy to collect, and must live about 15 or 20 years before they become effectively fecund. Viet Nam exported 29,000 kg of *T. gigas* shells in 2000. They were taken in abundance in Indonesia for a while (1,160 tons of giant clam shells were taken from outer islands to market in Jepara, north-central Java, in 1982), but the two largest species (*Tridacna gigas* and *T. derasa*) are suspected to now be extinct around Java and Bali. Overharvest had also apparently brought *Tridacna gigas* to extinction in Fiji, New Caledonia, Vanuatu, Kosrae, Pohnpei, Chuuk, Yap, Guam, Saipan, Northern Marianas, Taiwan, and the Ryukyu Islands. *Tridacna derasa* seemed to be harvested to extinction at Vanuatu, Guam, Northern Marianas, and Federated States of Micronesia (Kosrae, Pohnpei, Chuuk, Yap). *Hippopus hippopus* was brought to extinction at Fiji, Tonga, both Independent and American Samoa, Guam, the Northern Mariana Islands, and Taiwan (Eldredge 1994). Some of these extinct populations have been reestablished by the introductions listed above. Giant clams have also been shipped to the Caribbean where tridacnids from Palau have been cultured in Bonaire, Guadeloupe, and south Florida (Eldredge 1994).

Unlike gastropods which may be able to provide sustainable fisheries on the reef, the giant clams seem to be too easy to find and collect and have too long a generation time for field populations to sustain harvest. The Government of Palau established the Marine Protection Act of 1994 that prohibited the export of invertebrates from the coral reef, but allowed export of specimens derived by aquaculture. The Belau Mariculture Demonstration Center in Palau has shown that aquaculture and export of giant clams is feasible (Heslinga et al. 1984).

As with giant clams, an advantage towards sustainability of the aquarium-fish trade is the potential for aquaculture, rather than collection from the wild. At least 269 species of coral-reef fishes can be successfully bred by hobbyists (Murray and Watson 2014) and there should be economic incentive to further develop the capabilities for breeding ornamentals, considering the marine ornamental trade already amounted to as much as $330 million over a decade ago (Wabnitz et al. 2003). Harvesting from the wild can have serious damaging effects to the structure of coral reefs. For example, the collection of sabellid feather-duster worms involves digging and dislodging corals, so each one collected is damaging to the reef structure. The average number of *Sabellastarte* collected each year for the aquarium trade in Kaneohe Bay, Hawaii, has been 43,143 (Friedlander et al. 2008), so that meant the same number of holes and dislodged chunks were placed in the coral reef substrata each year. The detaching of corals for the aquarium trade also fractures the reef substratum, and attaching and retrieving gill-nets for collecting fishes breaks coral branches and abrades living coral tissue. Cyanide and Clorox are incidentally toxic to corals and other reef animals not targeted.

It would seem that the aquarium trade would be a more stable source of income than fish for food because of the tremendously greater value per gram of product, because of the spread of the harvest among more than 1,802 species, and because of the more limited demand in total biomass. However, there is a positive feedback process such that when a species becomes rare, it becomes more valuable (Courchamp et al. 2006). A rare fish can cost as much as

$20,000 (Rhyne et al. 2012b). This is destabilizing because the demand on common fishes diminishes and the demand of rare species intensifies.

The marine aquarium trade is a rapidly growing business, with 871 live coral imported into the United States in 1984, 40,000 in 1988, about 250,000 in 1991, and 1.5 million by 2010 (Derr 1992; Wells and Hanna 1992; Tissot et al. 2010). Indonesia exports about 900,000 scleractinian colonies per year and Fiji exports about 600 metric tons of "live rock" per year (Bruckner 2002). Aquarists in the United States purchase 68% of all live corals and 95% of the "live rock" from Fiji on the market (Bruckner 2002). Now it is estimated that on the global scale at least 50 million coral-reef animals are sold annually in the aquarium trade (Rhyne et al. 2012a). The number of species of reef fishes that were imported into the US in 2005 was 1,802 from 50 families (Rhyne et al. 2012b). The number of individuals imported to the US each year is about 11 million. These values are low because they are not including Hawaiian endemic species and other species not counted because they were not recorded as imports (Rhyne et al. 2012b). Between 10 and 30 million reef fishes worth up to $750 million are exported from Southeast Asia annually (Bruckner 2002). About 1,500 people make a living collecting live aquarium fishes in the Philippines, from which 5,774,579 are imported to the US (Rhyne et al. 2012b). The export of aquarium fishes from the Philippines brought in nearly US$ 2.5 million in 1978 and US$ 2.75 million in 1979 (Salm 1984). About 50,000 persons are employed in the aquarium trade in Sri Lanka (Craik et al. 1990), the source of 3,288, 434 imports to the US. The coral-reef aquarium trade operates in the hundreds of millions of dollars annually, and is growing very rapidly (Wabnitz et al. 2003).

The number of aquarium fishes taken from the kona (leeward) coast of the island of Hawaii was about 90,000 in 1973 and 422,823 in 1995 (Tissot and Hallacher 2003). In 2000, fish replenishment areas (FRAs) were established, taking up 35.2% of the coastline. With the establishment of these FRAs in 2000, and possibly because of harvesting the middle-sized individuals, leaving the exponentially more fecund breeding stock and allowing the juveniles to grow rapidly (Sect. 12.6.1), the collection stabilized at a reliable 300,000–450,000. This practice of moderation by leaving areas for replenishment and leaving the larger individuals provided a secure 2,400–3,600 fish per km of coastline per year.

A variety of seaweeds are also collected from coral reefs and used for food, folk medicine, and fertilizer, and sold for agar and carrageenan. In 1989 alone, the Philippines produced 65,600 metric tons of algae of the genus *Eucheuma*, worth tens of millions of dollars (South 1993).

Corals deposit tremendous quantities of limestone. Large amounts of the coral limestone also contributes to coral rubble and sand. Blocks of living or dead coral are used for building materials, breakwaters, and cement. In Sri Lanka in the 1980s, over 2,000 metric tons of live coral skeletons, 7,000 metric tons of coral rubble, and 34,000 m^3 of sand were removed from the coast each year (Wells and Hanna 1992). However, the economic value in many of the resources are far less when extracted than when left in place. In favorable environmental conditions, the living reef can be a self-repairing and self-augmenting breakwater with rising sea level.

Coral reefs can produce substantial revenue from jewelry and curios. Jewelry is potentially sustainable because a very few grams of physical material is exported for a substantial income. On lagoonal reefs of 19 of the islands (raised atolls) of the Tuamotus in the late 1980s, high-priced black pearls from the culture of the coral-reef oyster *Pinctada margaritifera* brought $25 million in 1988 and $37 million in 1990. However, there should be concern that the culture of dense populations on coral reefs in enclosed lagoons can facilitate disease. In 1985, a disease affecting *P. margaritifera* was first observed in the Gambier Islands and then in the Tuamotus. By 1988 50–80% of the cultured stock died of the disease.

In contrast to jewelry, the export of curios can be devastating. Curios and souvenirs made from black corals, gorgonaceans (especially sea fans), seashells, giant clams, dried fishes and echinoderms support a multimillion-dollar international business. During the mid 1980s, 4,500 metric tons of shellcraft per year (not including mother-of-pearl) was being exported from the Philippines (Wells and Hanna 1992). In 1988, 1,456 metric tons of ornamental corals were imported into the USA (Wells and Hanna 1992). The curio trade has leveled off about 1990 when the live trade for ornamental aquarium animals began to expand rapidly (Bruckner 2002).

There are important alternative nonextractive productions of corals that are useful for humans (Sect. 1.1). Coral reefs function as protection against waves for other coastal habitats, sources of food for pelagic fishes, sources of genetic diversity for aquaculture and pharmaceuticals, and as sources of income from tourism and recreation. Scuba-diving on coral reefs forms the main base of the economies of a number of tropical developing countries. Tourism of coral reefs brings in about $85 million a year to the national economy of Palau, a Pacific country with a population of about 21 thousand. Scuba-related tourism brings in about $23 million annually to Bonaire, about half its gross domestic product in 2002. The total annual value of coral reefs to Guam is 139 million US$ per year (mpy), of which 114 mpy is coral-reef tourism and recreation and 4 mpy is commercial fishery (Brander and van Beukering 2013). The rest was for environmental services such as protection against storm waves. Of the total 1,747 mpy value of coral reefs to Hawaii, 356 mpy is from reef-related tourism and recreation, while 3 mpy is from commercial fishery. Puerto Rico showed 192 mpy from recreation and tourism and 1 mpy for small-scale fishing. In developed countries like the U.S. and Australia, the economic value of coral reefs for tourism is also large. Reef tourism is estimated to be worth about $1.6 billion a year for Florida's economy, with over two million tourists visiting John Pennecamp Coral Reef State Park and Key Largo National Marine Sanctuary alone (Wells and Hanna 1992). Attributes of the coral-reef ecosystem (Sect. 1.1) and of its fishes (Sects. 12.5 and 12.6) explain why coral reefs can support a dependable service-based economy, but not an export economy.

The potential for pharmaceuticals from natural products from coral reefs would seem to be greater than from other systems because biodiversity and ecosystem complexity of coral reefs is on a higher scale than in other ecosystems (Sect. 1.1). Rainforests are considered to have a greater biodiversity at the species level because of insects and flowering plants. However, coral reef communities have the greater diversity in terms of prevalent phyla and kingdoms, a greater diversity of basic animal body plans, symbiotic relationships, and natural products chemistry. Of 34 animal phyla, 30 are found on coral reefs, while only 19 are found in all the terrestrial and freshwater habitats on Earth. The potential of coral reefs as a source of new chemicals for pharmaceuticals compelled the National Institutes of Health (including the National Cancer Institute and the National Institute of General Medical Sciences) to fund the establishment of a laboratory in Micronesia. The marine laboratory on Chuuk and then Palau was contracted to provide specimens of at least 5,000 different species of coral-reef organisms as material for chemical exploration.

Some natural-product chemicals have undergone clinical analysis. A number of prostaglandins were discovered in large quantities in the common gorgonacean *Plexaura homomalla* (Bayer 1974). Prostaglandin is a potent pharmaceutical that affects a wide range of clinical applications in humans including assisting the process of childbirth, terminating pregnancies, and treatment of cardiovascular disease, asthma, and gastric ulcers. A chemical from the red alga *Portieria hornemannii* has shown antitumor activity for a variety of human tumors (Fuller et al. 1992). Didemnin B from the coral-reef ascidian *Trididemnum solidum* has demonstrated activity against leukemia, a variety of human tumors, viruses, carcinomas (including melanoma) in clinical trials. The purity of $CaCO_3$ produced by corals makes it valuable for use in bone-marrow transplants.

Reefs serve as protection against wave action. During typhoons, the damage from wave action to coastal communities is much less where there are reefs. On Guam, the damage from wave action in areas protected by extensive reef flats was minor, but in areas around the villages of Inarajan and Merizo, where the fringing reefs are narrow, wave action damaged homes, removed buried caskets from cemeteries, moved automobiles, carried a refrigerator away from inside a home, and caused wave-damage as far as a kilometer inland. In addition, coral reefs protect mangroves and seagrass beds in some localities, and thus they provide protection for nurseries of commercially important fishes. Coral reefs are self-repairing, and the cost of building and maintaining equivalent breakwaters are nearly always omitted in the consideration of the commercial value of coral reefs.

As the value of reefs to the economic and social well-being of human communities in coastal regions becomes apparent, the cost assessments of damages to coral reefs become large. The Government of Egypt claimed US$ 30 million for damage to 340 m^2 of coral reef in the Strait of Tiran, although the final settlement was out-of-court for US$ 600,000, or US$ 1,765 m^{-2} (Spurgeon 1992). This was considerably less than the cost calculated for reef damage in Florida. Assuming the minimum nonmarket value for live coral, assuming the reef would recover naturally rather quickly, and assuming financial rate of return for lost revenue from tourism of only 3%, the calculations presented in a legal journal for the minimum damage to the local economy caused by the grounding of the M/V WELLWOOD on Molasses Reef off the Florida Keys was $2,833 m^{-2} (Mattson and DeFoor 1985). By these calculations, Molasses Reef, just one of many reefs off the Florida Keys, is worth about US$ 400 million. In December 2003, the cruise ship MV Island Explorer ran aground on Apo Reef in the Philippines. The ship's company paid $700,000 for 2,750 m^2 of damaged reef. In February 2009, the USS Port Royal (a navy ship) ran aground on a reef on the south shore of Oahu. A total of 15 million US$ (8.5 million for loss of natural resources and 6.5 million for restoration costs) was paid, which comes to $16,854 m^{-2}.

The economy of atolls is nearly completely dependent upon the coral reefs, whether the economy is based on fisheries, aquaculture, or tourism. Because of these goods and services, President Clinton's Executive Order 13089 established the US Coral Reef Task Force and from 1999 to 2011, to which Congress appropriated approximately $169 million for the protection of coral reefs. The Australian Government has spent on average about $32.4 million per year since 1996 for maintaining the Great Barrier Reef. There are approximately 686 organizations dedicated to reversing the decline of coral reefs (International Directory of Coral Reef Organizations, www.coralreef.org, 27 January 2013). Yet, despite all this effort and investment, there is no evidence that the rate of reef degradation has begun to decrease (Sect. 1.4).

Perhaps the most important role of coral reefs in the lives of local people is usually not recognized by outsiders. This is the stabilizing effect of reefs on social structure. Fishing is often a cooperative activity in which each of the family members has a clearly recognized role. It has been discerned from interviews of fishermen in Palau that fishing activities help solidify the roles and importance of members of the family. It was stated that reefs may be more important in providing the opportunity for fishing activities than in providing the catch. Fishing and reef-gleaning is often perceived as fun and wholesome. In cases where large developments such as resorts or military bases obstruct access of local people to traditional fishing or reef-gleaning areas, the effects cannot be overcome simply with jobs providing wages by which foods can be purchased. As social structure deteriorates, the numbers of suicides and criminal acts increase. The economic costs of such societal maladies are rarely taken into account in the evaluation of coral reefs, but nevertheless, these costs of the deterioration of coral reefs are ultimately paid by all of us.

1.4 Present Situation of Coral Reefs

> With all due respect to those contributing effort and funding towards protecting coral reefs, the millions of dollars that are being spent will be of no avail unless there is a concentrated effort to obtain explicit progress in reducing CO_2 emissions. (Ove Hoegh-Guldberg)

Although some human resources associated with coral reefs are recognized as having been overharvested for hundreds of years (Jackson 1997; Wing and Wing 2001), coral reef ecosystems usually recovered rapidly from injuries and therefore appeared to be in good condition until the mid-1970s (Fig. 1.2). The general belief was that although coral reefs were often damaged by local factors such as hurricanes, crown-of-thorns predation, sedimentation, sewage, chemical pollution, and so forth (Johannes 1975), disturbance and recovery were important in maintaining coral-reef diversity (Connell 1978). The diverse mosaic of corals (Fig. 1.2) were considered to be an array of patches in various stages of recovery.

Coral reefs were remarkably resilient in that they were able to recover rapidly, even after relatively large-scale severe disturbances. For example, only 5 years after a volcanic eruption provided a 70,000 m^2 sheet of basalt in the shallow waters of an Indonesian island, the hardened lava had been colonized by 124 species of coral and 61.6% +/− 7.5% of the surface was living coral cover (Tomascik et al. 1996). Predation by *Acanthaster planci* on reefs of Guam devastated the coral communities along 38 km of coast (Chesher 1969), but living coral cover on a submarine terrace increased from <0.9% cover in 1970 to 65% in 1981 (Colgan 1987). Sano (2000) reported recovery of living coral cover from 0.0 to 100% from 1987 to 1997 at Iriomote Island in the Ryukyus south of Okinawa. Recovery from extensive devastation of coral in American Samoa took 15 years (McArdle 2003). The numerous disturbances of reef communities from *A. planci* outbreaks in Micronesia occurred over a large geographic area nearly the size of the conterminous United States in 1969. Most recovered by 1978–1981 (Birkeland and Lucas 1990). Although there are sometimes reports of recoveries in less than 10 years (e.g., Johns et al. 2014), the mode of time needed for coral-community recovery from substantial damage was 10–15 years.

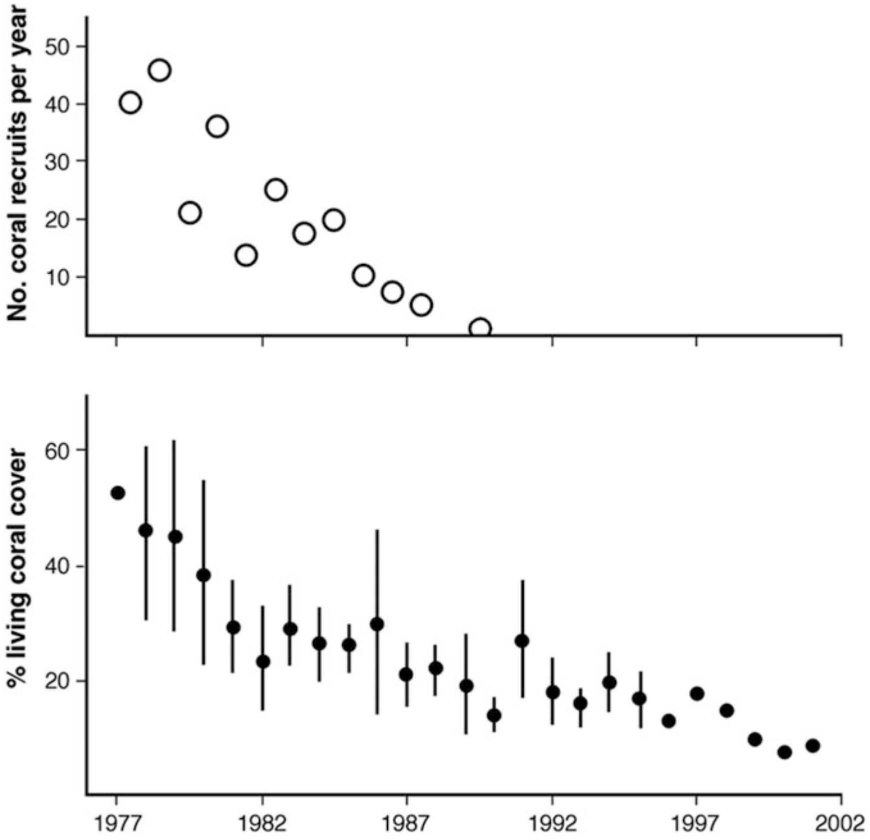
It should be clarified that “recovery” in 10–15 years is here considered in terms of extrinsic (collective) variables such as living coral cover and species richness. When considering intrinsic (individual colony) variables such as colony size and three-dimensional structure, “recovery” may take centuries (Fig. 12.1).

Prior to the 1970s, coral communities generally responded with resilience to event-driven acute disturbances. By the mid-1970s, coral communities started demonstrating positive-feedback responses in negative directions to trend-driven chronic disturbances (Fig. 1.4; Chap. 11). New disturbances began to create conditions that opened new self-reinforcing processes or conditions that changed the trajectory towards further deterioration. In 1982, Bill Gladfelter called attention to the spread of the white-band disease that began in the mid-1970s, affecting *Acropora palmata* across the greater Caribbean. He foresaw that this killing of a large portion of a dominant three-dimensional coral framework-builder would have continuing effects on ecology of Caribbean coral reefs. The 1982–1983 El Niño caused extensive coral bleaching throughout the eastern tropical Pacific, but its effects continued for at least 6 years through 1989 by opening paths of influence previously unavailable to *Acanthaster planci*, *Diadema* and *Eucidaris*, and *Stegastes* (Glynn 1990). In 1983, 2 years after a disease spread through the main Hawaiian Islands killing diadematid echinoids (Birkeland 1989), a very similar diadematid disease spread across the greater Caribbean, from Panama to Bermuda, within a year (Lessios et al. 1984). The demise of this dominant herbivore *Diadema antillarum* had compounding effects on the ecology of Caribbean coral reefs (Hughes 1994).

During the record-breaking 1997–1998 El Niño, the shallow seawater temperatures were especially warm. Extensive coral bleaching occurred circumtropically, degrading coral reef communities especially in the Indian Ocean and in the western Pacific Ocean where approximately 16% of the living coral cover of the world was killed. Then in an especially warm 2005, there was a major bleaching event in Caribbean corals even though it was not an El Niño year (Wilkinson and Souter 2008).

In the past, corals have typically recovered promptly after large-scale mortality from outbreaks of crown-of-thorns, hurricanes, lava flows, and other events. The drop in coral

Fig. 1.4 Decline in living coral cover across the greater Caribbean from 1977 to 2001 (From Gardner et al. 2003) and decline in coral recruitment in 12 1-m^2 plots near Discovery Bay, Jamaica, 1977–1993 (From Hughes and Tanner 2000)



community resilience may be based on a lack of replenishment more than coral mortality (Fig. 12.1). There may have been a substantial decline in coral recruitment from 1977 to 1993 in Jamaica (Hughes and Tanner 2000) and from 1979 to 2004 in Curaçao (Bak et al. 2005). The general decline in coral recruitment in the past decades has been associated with the lower abundance of reproductive adult colonies (Fig. 1.4) and the resulting lower fecundity of the population as a whole (Brainard et al. 2011; Birkeland et al. 2013). However, Hughes et al. (2000) found that the amount of recruitment to coral populations on the Great Barrier Reef was not significantly correlated with the number of adult colonies (living coral cover), but with fecundity. In corals, fecundity decreases as the colony is stressed (Sect. 12.2.2). Despite common successes in ameliorating local factors that would have degraded coral-reef communities, the global changes brought about by increases in CO_2 may be chronically stressing corals and thereby reducing fecundity (Sect. 12.2.2).

During the past decade, the governments of Australia, Queensland, and the United States have invested hundreds of millions of dollars into the processes of protecting and restoring coral reefs. There are hundreds of NGOs committed to protecting coral reefs (www.coralreef.org). These efforts have produced many local successes, but corroborating the concerns expressed by Ove Hoegh-Gildberg at the beginning of this section, local successes have failed to prevent the global decline of coral reefs. The Great Barrier Reef (De'ath et al. 2012), the wider Caribbean (Gardner et al. 2003), and the Indo- Pacific Ocean (Bruno and Selig 2007) have all had significant losses in coral cover over decadal scales, and even no take reserves (Huntington et al. 2011) and national parks (Rogers and Muller 2012) have experienced mass mortality events and coral declines.

Corals in the 360,000 km^2 Papahānaumokuākea Marine National Monument have experienced episodes of bleaching and disease (Kenyon and Brainard 2006) despite being geographically remote, far from human development, and protected from direct human disturbances. The Great Barrier Reef is possibly the best-managed large-scale (345,400 km^2) coral-reef reserve, with about 30% of its area protected against any fishing or resource removal, but it has lost 50.7% of living coral cover since 1985 (De'ath et al. 2012). De'ath et al. calculated that the outlook for the GBR could be favored with the control of crown-of-thorns seastar outbreaks and improvement of water quality, but the final sentence in the abstract was "Such strategies can, however, only be successful if climatic conditions are stabilized, as losses due to bleachings and cyclones will otherwise increase." Although there are about 500 marine reserves in the wider Caribbean, this area has lost 80% of its living coral cover during the same period that the GBR lost over 50%

(Gardner et al. 2003). The Indo-Pacific has generally lost about 40% of coral cover between 1968 and 2003 (Bruno and Selig 2007). For the world as a whole as of 2008, 19% of coral reefs have been lost and about 35% are seriously under local threats, leaving about 46% that are mainly under threat from CO_2, despite over 660 marine reserves that include coral reefs (Spalding et al. 2001).

Prior to the 1970s, coral communities generally responded to acute (event-driven) disturbances with resilience. But the massive reef-building scleractinians were selected for survival over fecundity (Sect. 12.2.2), so by the mid-1970s, coral communities started demonstrating positive-feedback responses in a negative direction to chronic (trend-driven) disturbances (Chap. 11). Stress from changes in ocean temperature and chemistry possibly costs corals lower fecundity and diminished recruitment (Chap. 11; Sect. 12.2.2). This is driving coral communities towards the norm of the 140 million years before the present Neogene (the more recent 23.8 million years), the norm in which scleractinian reef-building corals were diverse, but reef-building was minimal. We may not lose a diverse array of scleractinian corals (Sect. 12.4.1), but we are likely to experience substantial reef deterioration (Sect. 12.4.2) unless we can reduce CO_2 emissions to the natural state.

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