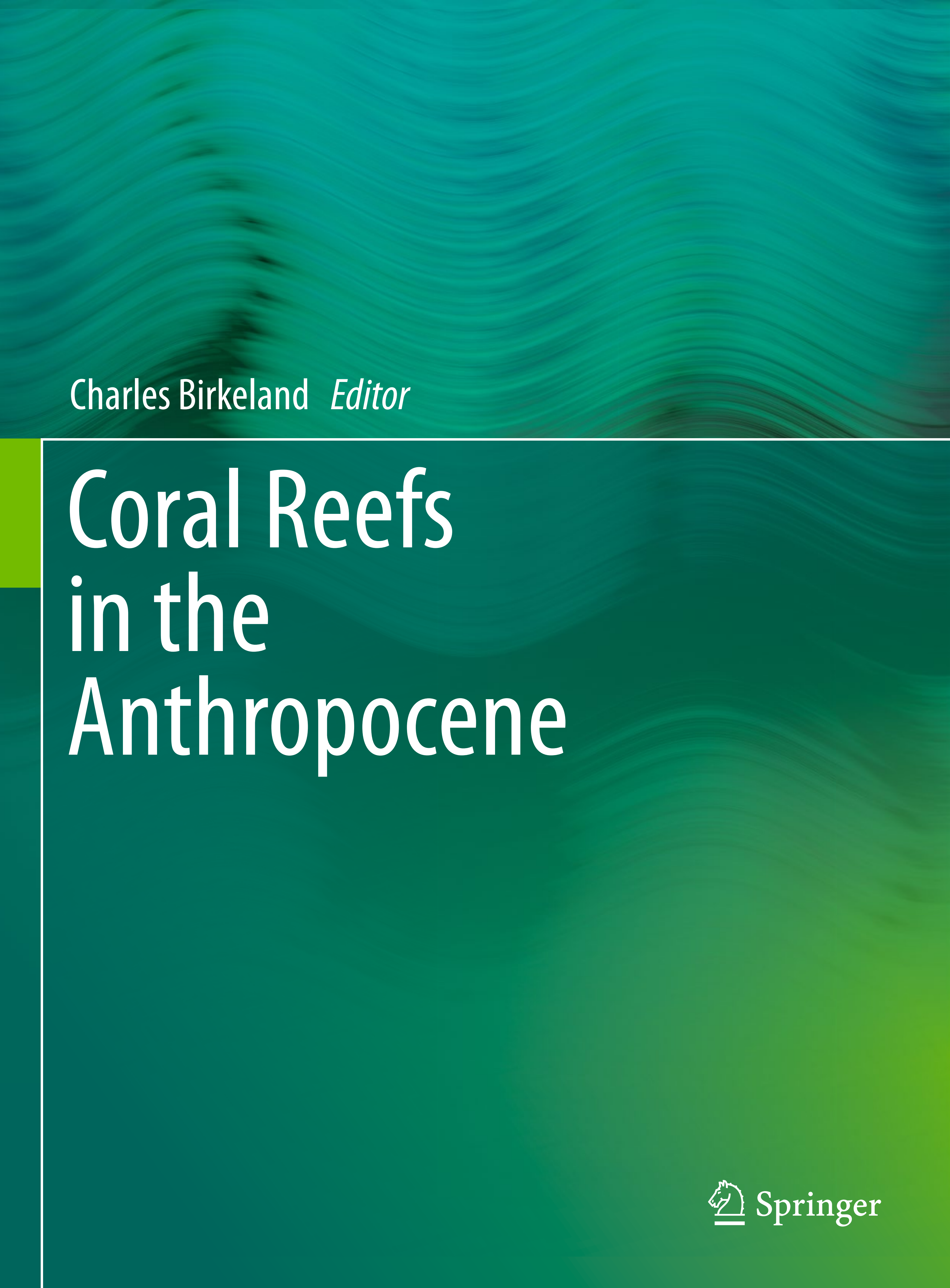

Charles Birkeland *Editor*

Coral Reefs in the Anthropocene

Springer

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The cover photograph is courtesy of Jacob Asher, NOAA, Coral Reef Ecosystem Division. The photograph is from Jarvis Island.

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Coral Reefs in the Anthropocene

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Robert Earl Johannes
26 September 1936–4 September 2002

The book is dedicated to Bob Johannes who continuously opened new doors to the understanding and management of coral reefs. His pioneering work was exceptionally original and influential because he followed his own insight into truly important processes and was not constrained by mainstream paradigms and by the perspectives of his peers and administrators. He was able to perceive the value of knowledge of peoples of other cultures and training. He recognized that Pacific islanders sometimes knew the biology and life histories of coral reef fishes better than did the scientists and that many of *their management practices were more effective. He was able to listen to the local fishermen, placing their knowledge as complementary to science.*

Bob was a real pioneer because he was true to himself. As he developed a previously unrecognized field of study and became a leader in this new field, he would ponder what was important to the world, and then on several occasions, he would make seemingly abrupt and dangerous changes in direction of his career. His dissertation at the University of Hawaii was involved with the processes that control coastal and oceanic productivity. During his postdoc at the University of Georgia, his host Lawrence R. Pomeroy noted that "Bob was one of the true pioneers of marine microbial ecology – before there was a recognized field of marine microbial ecology. His work is still cited as landmark stuff." Bob then focused on the ecology of coral reefs. He coedited books on tropical marine pollution in 1975 and on coral reef research methods in 1978. His first student Chris D'Elia said "While Bob is appropriately remembered as a prolific author and researcher, he had strong leadership skills as well. For example, he did an exceptional job as chief scientist on the 1971 Symbios Expedition."

Bob Johannes was also one of the first to recognize and act on the importance of having the general public be aware of the implications of new findings in coral reef ecology. In 1972, he produced a movie "Cloud Over a Coral Reef" on reef degradation in Kaneohe Bay, Hawaii, resulting from substantial nutrient input from a sewer outflow and urban runoff. The movie was made with the hope that it could help provoke some public action to correct the problem. Some of his colleagues gave him a bit of flak for this because in the early 1970s there was a prevalent opinion that scientists should practice pure science and leave communicating with the public for someone else to do.

Bob Johannes was always ahead of his time. In closing his 1975 review of pollution and degradation of coral reef communities, he concluded that "environmental crises develop faster than they can be completely assessed. In this context it is more important to make interim decisions in time than to make scientifically satisfying decisions later. Pollution biologists sometimes inject too much traditional laboratory caution into matters of immediate practical concern. They hesitate because their information is not final… environmental post mortems become their stock and trade. 'They measure and we weep.'"

In Palau during the mid-1970s, Bob Johannes discovered the value of traditional community-based resource management systems and began to develop the concept of integrating indigenous knowledge with Western science. His method of living in Palau and learning by discussing fishing practices with the elder fishermen was so outlandish at the time; some of his colleagues had concluded he had "dropped out." The book he produced in 1981 on his findings, Words of the Lagoon, has become a classic on community-based resource management. In 1978, Bob wrote a review of the traditional marine conservation methods in Oceania and their demise. In 2002, he wrote a more hopeful review of the renaissance of community-based marine resource management in Oceania. Tom Graham wrote that

"Although Bob took no credit for these positive changes, they can easily be traced in large part to his efforts during the last 25 years to reveal the value of customary models of resource management, as well as his success at inspiring others to help salvage what was left of them."

Johannes respected the importance of rigorous science in testing hypotheses, but he stressed that also taking a less constrained multicultural perspective can allow us to have a better chance of having the right hypotheses to test. In The Plight of the Osfish, or Why Quantitative Sophistication Is No Substitute for Asking the Right Questions, he told of how a fisheries agency used a rigorously designed survey of fishermen to approach the mystery of why the bonefish populations were declining through the years. The fishermen were selected randomly for the review and were asked to check which of the alternative answers to questions seemed correct. An independent investigator named "Bert" made a point of asking the older men, some so old they no longer did much fishing (a biased, non-random selection), and interviewed them with an open flexible discussion (not easily analyzed quantitatively like the forms with checked alternatives), allowing the older men to simply express their opinions rather than choosing among a well-organized series of alternatives. The interviews with the elders provided the correct insight into what was happening with the bonefish because the quantitative forms were not asking the right questions.

Toward the end of his life, with the support of a Pew Fellowship and leveraged funds from the Nature Conservancy and the South Pacific Forum Fisheries Agency, Bob Johannes undertook extensive investigations of the ecological, economic, and social effects of the suddenly arising billion-dollar-per-year live reef food fishery and destructive fishing practices such as fishing with cyanide and explosives.

Bob Johannes taught us that we must respond to environmental or managerial crises in time with the best available information, we should keep a multicultural perspective on problems so we have a better chance of asking the right questions, and we should integrate indigenous knowledge with Western science, but his most important contribution was his discovery that the diverse and unpredictably variable multispecies reef fisheries are too complex to manage with rigorous scientific algorithms for optimal or sustainable yield, and so he made a compelling case for adaptive data-less management. Attempts to manage coastal finfisheries to achieve optimal yields have been dismal, but Bob reported examples of successful indigenous adaptive data-less management. To establish a priori regulations based on quantitative assessments is comparable to attempting the programming of an automobile to go between home and the office downtown using data on distances, speeds, timings of stoplights, etc. The conditions of such trips are just too variable for this to work. The more successful approach is to use a driver to flexibly adjust to unexpected numbers of pedestrians, behaviors of motorists, and unexpected events such as jaywalkers, ambulances, and fender benders. However, by "data-less," Bob did not mean we should do away with quantitative research *(which would be "dataless"). Quantitative research is still important, but it must be complementary to a flexible adaptive management based on indigenous knowledge. If we demand quantitative research for the management of each coastal marine system, it would not be cost-effective even if it were theoretically possible.*

The Authors

Preface

When *Life and Death of Coral Reefs* came out in 1997, it was just before the 1997–1998 circumtropical warming and bleaching event, an event that awakened us to the realization that processes affecting coral reefs were expanding to a global scale. Our basic perspectives on coral reefs have been changing at an accelerating pace, so each new book is produced with a whole new paradigm. This book is new, not an update or revision. Even in some chapters covering the same subject in the two books, a change in perspective is required by the unfolding of our perception of the nature of forces affecting coral reef systems. For example, in *Life and Death of Coral Reefs*, Barbara Brown provided an excellent timeless review of the conceptual framework of disturbances, organizing her chapter around different scales of tolerances and on the different kinds of natural and human disturbances. In this book, Margaret Miller shifted the focus from disturbance as events to disturbance as continuing trends. The fact that coral disturbance regimes are continuing to worsen while recovery capacities are waning compels us to accept that management strategies must focus on both of these processes.

New perspectives are also being provided by new tools. Nancy Knowlton and Matthieu Leray give a tour through the disparate ways the techniques of molecular genetics have caused major changes in our understanding of the evolutionary history of corals and have transformed our understanding of ecological and biological processes of coral reefs. Molecular biology opens more doors to coral reef science than the telescope did to astronomy because molecular genetics leads us through more dimensions. Dan Barshis follows this with an explanation of the genomic potential for coral survival of global changes in ocean chemistry and climate. The new perspectives of each chapter in this book are important for efforts in conservation, not just science.

Peter Glynn and Derek Manzello explain that while the effects of ocean acidification on the metabolic expense of calcification may vary among genera of corals, the acceleration of bioerosion by lower pH is general and critical. Adapting to ocean acidification by itself is facing an indifferent nonresponsive physical factor, but adapting to bioeroders is coevolving in an arms race. Dennis Hubbard takes us through how changes in seawater temperature, storm intensity, aragonite saturation state, and pH bring major shifts in the balance between carbonate production, destruction, and export. From a global perspective, Pamela Hallock spells out how the production and preservation of reef limestones is intimately connected to the Earth's biogeochemical cycles, especially of carbon, oxygen, nitrogen, and phosphorus. She elucidates how records preserved in limestones provide scientists and policy makers with insights into likely consequences of human activities for the future, not only of reefs but of the diversity of ecosystems on Earth.

Gisèle Muller-Parker, Chris D'Elia, and Clay Cook tell how cost-benefit analysis is a useful approach to examine symbioses in the context of environmental change and human impacts upon corals and coral reefs. By using new tools developed to assess the stability of the symbiosis, we may be better able to understand and predict the effects of future stressors and perturbations that threaten reef ecosystems.

Esther Peters explains how the multitude of stressors affecting reef organisms, particularly along heavily urbanized coastlines, and the introduction of species to distant reefs by global transport are contributing to disease in coral reefs. She presents new developments in disease diagnoses, an overview of diseases of reef organisms, and how diseases have adversely affected coral reefs. The application of concepts from the field of conservation medicine aids our understanding of diseases and their influence on organisms of reef ecosystems

Mark Hixon tells how the coral-seaweed-herbivore triangle is an accepted generalization embedded within a complex web of biotic interactions and abiotic conditions that bring exceptions. He provides rules of thumb for management that are essential for fostering the ecological resilience of coral reefs.

The introductory chapter reveals how the trophic structure of the coral reef ecosystem provides the greatest difference between gross productivity and net productivity, perhaps of any marine system. To export a substantial supply of food for humans, the net production might be enhanced by reducing the upper trophic levels, and this has generally been happening nearly globally before coral reef science became active. The final chapter tells how some islanders harvest reef resources for subsistence and local market yet maintain the integrity of the coral reef system by harvesting the intermediate-sized individuals from fish populations and taking the interest rather than the capital. The Palauans have exemplified the globalization of their economy while maintaining the integrity of their coral reef systems by keeping resource consumption local and having their international economy service-based rather than export-based.

Until recent decades, the conditions during the present Neogene Period were the best experienced for reef building by scleractinian corals since the Middle Jurassic. Although the hermatypic scleractinia were diverse through 130 million years previous to the Neogene, the shallow ocean waters were low in magnesium, low in pH, and high in temperature, so reef construction was meager. The Anthropocene may be returning corals from temporarily magnificent reef accretion to the “norm.” We may keep the corals, but lose the ecosystem services of reefs.

Honolulu, HI, USA Charles Birkeland

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1 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.

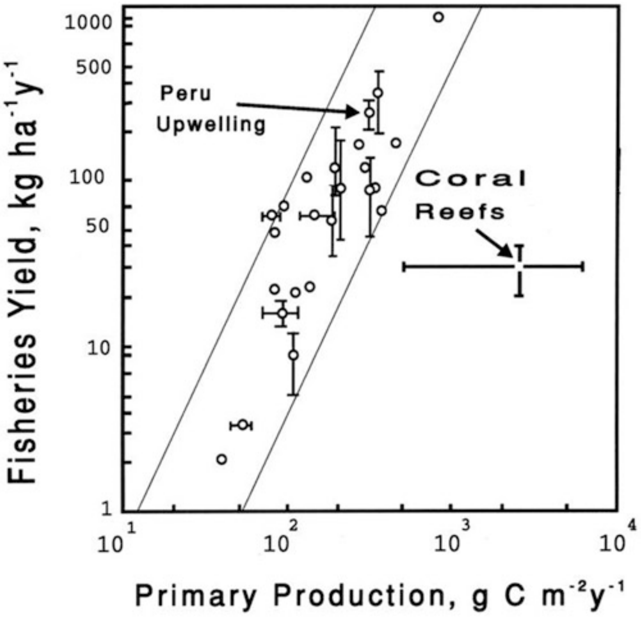


Fig. 1.1 Differences between coral reefs and other marine ecosystems in the relationships of fisheries yield to gross primary production. The non-coral-reef relationship is based on 49 studies at 25 sites (Redrawn from Nixon 1982)

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

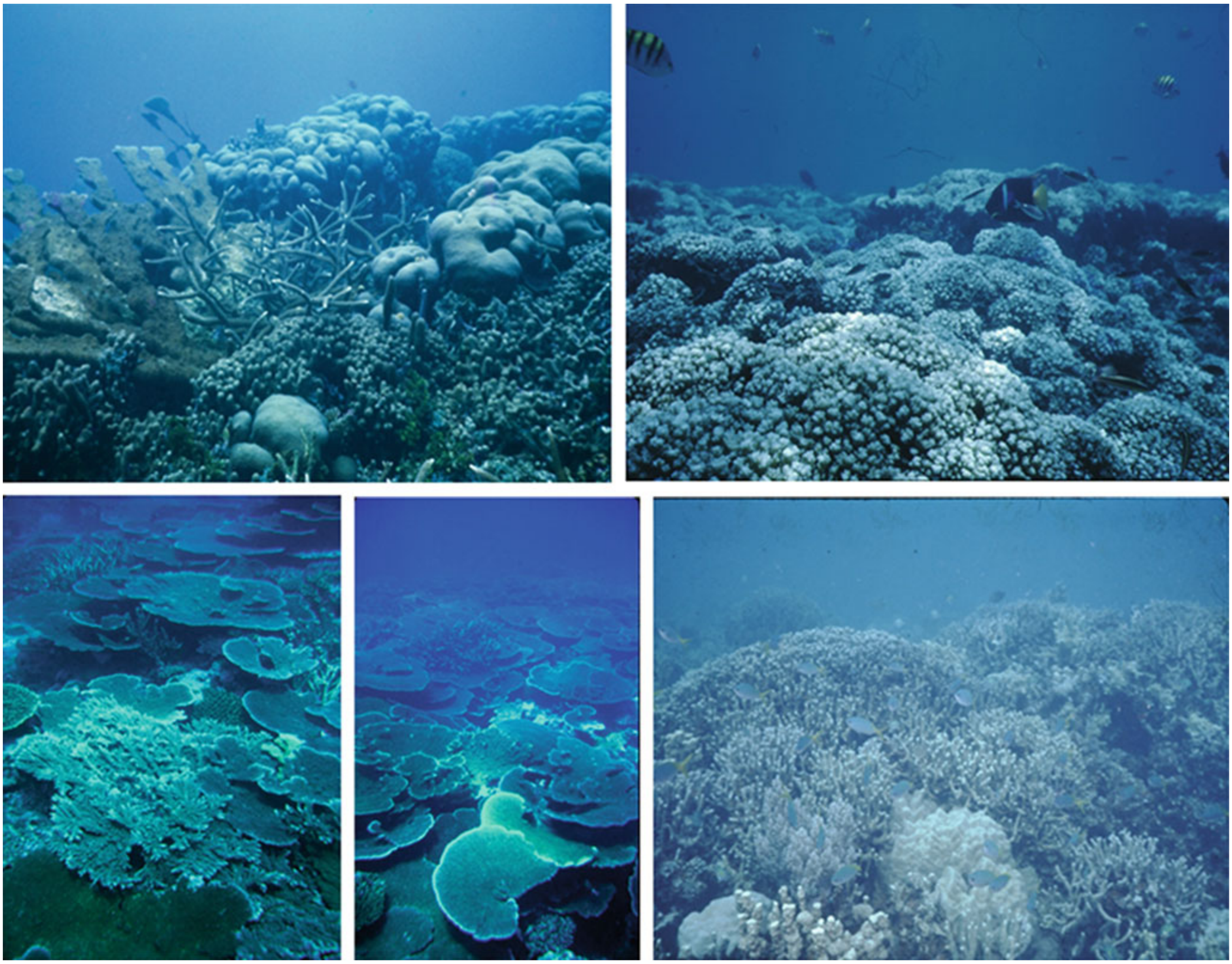


Fig. 1.2 Coral-reef scenes in the mid-1970s. As quoted in Jackson (2014), Sylvia Earle noted in 1972 that "…tropical reefs, notable for their dazzling profusion of animal life, are almost devoid of conspicuous plants". Bruno et al. (2014) found that in natural undisturbed baseline conditions, benthic 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).

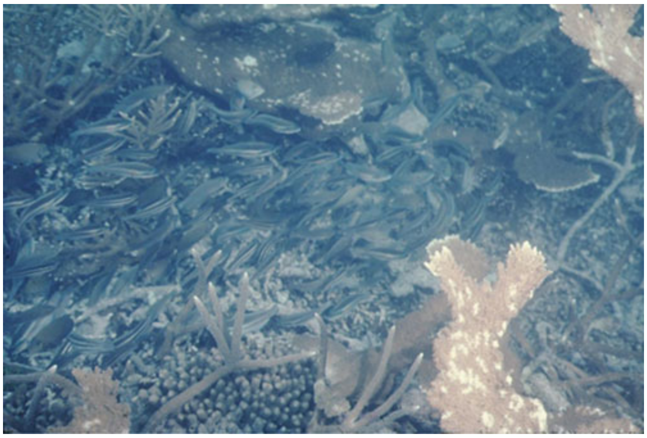


Fig. 1.3 Abundant *Scarus iserti* grazing turf algae among corals that take up most of the space. With little algal availability, the grazers keep the algae in the early stages of succession with rapid turnover and high net productivity (Klumpp et al. 1987), promoting the potential for an inverted trophic 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.

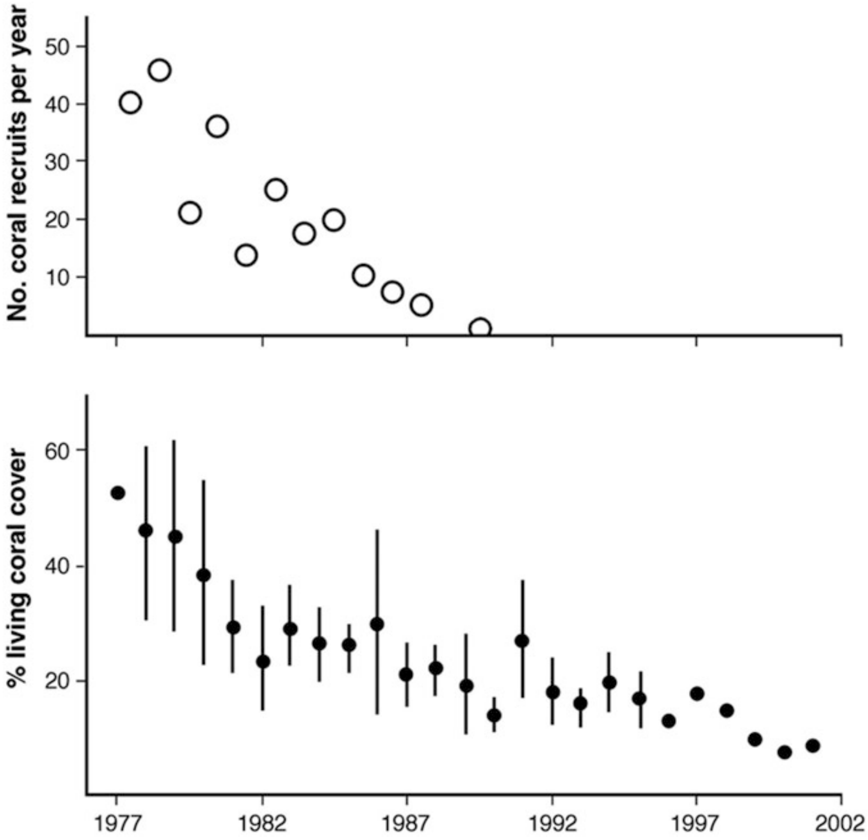
It should be clarified that "recovery" in 10–15 years is here considered in terms of extrinsic (collective) variables such as living coral cover and species richness. When considering intrinsic (individual colony) variables such as colony size and three-dimensional structure, "recovery" may take centuries (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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Changing Influences Between Life and Limestones in Earth History

2

Pamela Hallock

Extinction is forever.

(Anonymous)

Abstract

Coral reefs are among the most beautiful, diverse and fascinating ecosystems in the modern oceans. For anyone intrigued by reefs, their geologic history is a never-ending mystery series, complete with paradoxes to unravel and mass “murders” to solve given only partial texts and enigmatic clues. Limestones not only record much of the history of life on Earth, they are a major reason why life occurs on Earth! Moreover, they “go missing” at catastrophic events that, on several occasions, caused extinctions of more than half of all multicellular species. The production and preservation of reef limestones is intimately connected to the Earth’s biogeochemical cycles, especially of carbon, oxygen, nitrogen and phosphorus. Continental collisions, changes in sea-floor spreading rates, massive meteor impacts, and glacial-interglacial cycles with resulting changes in sea level, are all subplots in the history of reefs. The evolution of photosynthesis that triggered the first global “pollution” event, the escalation of predation as indicated by increasing prevalence of shells, and the ubiquitous and repeated development of mutualistic symbioses, provide analogies to modern environmental challenges. The Earth’s biogeochemical cycles, which have evolved over more than 4,000 million years, have been profoundly disrupted by human activities. Carbon dioxide in the atmosphere, for example, has increased more over the past 200 years than it did between glacial advances and retreats. Within this century, atmospheric CO_2 concentrations will rise to levels comparable to those 40–50 million years ago. The records preserved in limestones can provide scientists and policy makers with insights into likely consequences of human activities for the future not only of reefs, but of the diversity of ecosystems on Earth.

Keywords

Carbonate • Tectonics • Calcification • Biogeochemical • Carbon cycle

2.1 Reefs, Limestones, and Human History

Limestones and coral reefs have been used by human populations for most of human history. Not surprisingly, the features that made them useful are characteristics inherent to the environments in which reef creatures lived and the minerals from which they made their shells and skeletons. Reef ecosystems provided food to coastal populations, and where there were uplifted reefs near the shorelines, those

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humans utilized caves and springs for shelter and fresh water. Ancient limestones, moreover, are not restricted to coastlines. As limestones are everywhere prone to dissolution, cave formation, and freshwater springs, evidence of early human habitation can be found in limestone caves nearly everywhere they occur on land. Another characteristic of limestone, which early humans probably discovered when they lived in caves, is that it is softer than most other rocks and can be readily carved. In their caves they made holes for storage or hanging items; they also made implements, building material, decorative items and statues.

With the Industrial Revolution, limestones gained much additional economic value because many ancient underground reef provinces are major oil and gas reservoirs; those shallower are often important aquifers. Those same characteristics noted above, solubility and relative softness compared with many other kinds of rocks, are again key features. The porous to cavernous nature of many limestones make them exceptional hydrocarbon reservoirs. And their relative softness made drilling very feasible using early technology. As a result, the literature on ancient reefs and lesser carbonate buildups is vast. A few of the multitude of useful compilations include Milliman (1974), Wilson (1975), Bathurst (1976), Toomey (1981), Scholle et al. (1983), Fagerstrom (1987), Crevello et al. (1989), Riding (1991), James and Clarke (1997), Camoin and Davies (1998), Wood (1999), Stanley (2001), Kiessling et al. (2002), Pomar and Hallock (2008), and Swart et al. (2009). This chapter cannot provide the details available in these books. Instead it summarizes the significance of biogenic reefs and limestones within the context of environmental conditions through Earth history.

2.2 Biogenic Sediments and Reefs

Coral, oyster, and other biogenic reefs are produced by the combination of biological, chemical, physical and geological processes. Ideally, a biogenic reef is a significant, rigid skeletal framework that influences deposition of sediments in its vicinity and that is topographically higher than surrounding sediments. For example, a coral reef is a rigid skeletal structure in which stony corals are major framework constituents. Another term for a limestone structure or buildup produced by biological activity is **bioherm**. Less rigid accumulations of biologically produced sediments are often referred to as reef mounds (James 1997; Schlager 2003).

Calcareous shells and skeletons produced by a wide variety of protists, algae and animals become biogenic sediments upon the death of those organisms. The metabolic activities of some kinds of bacteria and microalgae also contribute to the biogeochemical precipitation of calcareous minerals, producing microbolites, stromatolites, and ooids in the benthos, and lime muds (whitings) in seawater overlying shallow banks and shelves. While biogenic carbonate sediments can occur with siliciclastic sediments, carbonates are most prevalent in marine environments that are separated by distance or physical barrier from substantial influx of sediments from land.

Nearly 50 % of the modern ocean floor is covered by pelagic carbonate ooze, which includes minute calcareous plates produced by coccolithophorids (microalgae) and shells of planktic foraminifers (protists), both of which live primarily in the surface waters of the open ocean (Kennett 1982; Seibold and Berger 2010). Shells and skeletons of benthic organisms, as well as microbially produced particles, also are important sediment constituents, especially on continental shelves, in some coastal areas, and on oceanic banks and shoals. Although the area over which pelagic carbonates accumulate is many times greater than the total area of neritic accumulation, Morse and Mackenzie (1990) estimated that ~16 % of annual global carbonate production in modern oceans occurs on reefs, shelves and banks. Moreover, they estimated that more than 80 % of the pelagic production dissolves in the water column or on the sea floor, while only about 40 % of neritic production is lost to dissolution. Thus, neritic carbonates account for roughly a third of the annual carbonate sedimentation globally.

Whether biogenic constituents make up most of the bottom sediments or whether they are only minor contributors depends upon several factors. One factor is the rate at which sediments from land enter the marine environment via runoff from rivers and streams, thereby diluting the biogenic contribution. Another factor is the rate at which shells and skeletons are produced by biotic communities living in the marine environment. A third factor is the rate at which sediments, both terrigenous and biogenic, are removed from that environment by transport or dissolution. The biotic community not only produces sediments, it also affects rates of dissolution, physical breakdown and transport of sediments.

Lees (1975) recognized three classes of shallow-water carbonate sediments, based upon their major constituents. He called the simplest group "**foramol**" sediments after two of the most important constituents: benthic foraminifers and molluscs, especially fragments of snail and bivalve shells. Lees noted that foramol sediments are characteristic of temperate shelves, but sometimes dominate in tropical areas where reefs do not occur. Other common constituents of foramol sediments are fragments of coralline red algae, sea urchin spines and plates, bryozoans, barnacles, and worm tubes. James (1997) recommended using the term "heterozoan" to describe such assemblages because constituents other than foraminifers and mollusks commonly dominate. Lees' (1975) second category is called "**chloralgal**" for its dominant constituent, the remains of calcareous green algae such as *Halimeda*; foramol constituents are secondary components. Chloralgal sediments are prevalent in expansive shallows like Florida Bay and the Bahama Banks, and in **mesophotic** (=low light) settings including the lagoon behind the Ribbon Reefs of the northern Australian Great Barrier Reef. Lees' (1975) third sediment category is "**chlorozoan**", which is the typical sediment around coral reefs. Coral, along with coralline and calcareous algal remains, are the characteristic constituents, with the shells of larger benthic foraminifers, as well as molluscan and urchin shells or fragments, as secondary components. Larger benthic foraminifers, which depend on algal symbionts in a relationship very similar to that of corals and their zooxanthellae, may locally dominate sand-sized sediments. Bryozoan, barnacle, and worm shell debris are typically scarce in chlorozoan sediments because these organisms thrive in waters with richer food supplies than do corals. James (1997) combined the chlorozoan and chloralgal assemblages into the "**photozoan**" assemblage to reflect the dependence of both associations on photosynthesis.

Whether biogenic sediments accumulate in place or are transported elsewhere for deposition depends upon bottom topography, the strengths of waves and currents, and the ability of the benthic community to reduce sediment transport. Fagerstrom (1987) proposed "**guild**" terminology to characterize benthic organisms by their geological roles in reef communities (Table 2.1). He used the term "**bafflers**" for organisms that project upwards from the sediment, slowing water motion and providing quieter places for sediments to settle. Organisms that live in or directly on the sediment, holding or encrusting it in place, can be considered "**binders**". Microalgae and bacteria grow and develop mats directly upon sediments, accumulating where wave and current motion is limited or intermittent. Bacterial filaments provide strength to these mats, which can resist as much as ten times more wave or current energy than is required to move similar unbound sediments (Grant and Gust 1987). **Stromatolites** are biogenic structures consisting of layered accumulations of microbolites, which include trapped or secreted sediment in algal or bacterial mats (Grotzinger and Knoll 1999; Reid et al. 2000). Ancient stromatolites produced the first bioherms in the fossil record. The best known modern stromatolites occur in Shark's Bay and elsewhere in West Australia (Logan et al. 1974; Reid et al. 2003), as well as several localities on the Bahama Banks (Dill et al. 1986; Reid et al. 1995) and elsewhere.

A variety of elongate, upward-projecting plants and animals can baffle water motion and trap sediments. On modern shallow shelves, seagrass beds effectively stabilize sediment over vast areas (Agawin and Duarte 2002). Seagrass blades slow water flow, allowing suspended sediments to settle out. Sediments are then held in place by extensive seagrass root and rhizome systems, as well as by the holdfasts of algae living within the seagrass bed. Sediment-dwelling macroalgae are also effective bafflers and binders, as are sponges, soft corals, sea whips and sea fans. In fossil reefs, a variety of less familiar organisms performed similar roles (Fagerstrom 1987; Wood 1999; Keissling et al. 2002).

The ultimate bafflers are the biogenic framework constructors, which in modern tropical shallow-water environments are primarily stony corals. These organisms grow upward or outward in branching, massive or platy morphologies, secreting substantial quantities of calcium carbonate, while trapping even greater quantities of sediment within and in the lee of the reef framework. Encrusting coralline algae bind the reef framework and enclose sediments in massive, wave-resistant structures recognized as coral reefs.

The three-dimensional topography of the reef provides abundant habitats for the diverse array of organisms that dwell within the reef structure. Some of these organisms are encrusters, including coralline algae, many kinds of sponges and some kinds of sessile foraminifers and mollusks. Many produce shells or skeletons that contribute to reef sediments. Thousands of species are wholly soft bodied and have little direct influence on the reef structure. All contribute to the diversity and energy flow within the community.

A variety of organisms also contribute to the breakdown of the reef structure by boring into it or scraping away at it as they graze. Such organisms are known collectively as "**bioeroders**" (Neumann 1966) or "**destroyers**" (Fagerstrom 1987). Bioeroding organisms are a diverse and important component of the reef community (Chap. 4). Organisms that bore or etch their way into the reef include bacteria, fungi, several varieties of sponges, worms, clams, and urchins. Organisms that scrape away limestone as they graze algae include urchins, chitons, snails and fish. Many reef fish feed by biting off bits of coral or coralline algae, subsequently defecating sand. In a healthy, actively accreting reef, bioeroders contribute to the diversity of microhabitats within the massive reef structure. However, if reef growth slows in response to natural or anthropogenic environmental stresses, the rates of destruction can exceed rates of accretion (Glynn 1988; Hallock 2001).

2.3 Basic Carbonate Chemistry

The major chemical constituent of calcareous sediments and limestones is calcium carbonate ($CaCO_3$). Organisms secrete $CaCO_3$ typically either as calcite or aragonite (Morse and Mackenzie 1990; Hallock 2011). The obvious difference between these minerals is their crystal structure;

Table 2.1 Important roles (guilds) taxa play in carbonate buildups

	Framework builders	Encrusters	Binders	Bafflers	Sediment producers	Bioeroders	Dwellers
Stony corals	XXXXXXXXXX	XXXXXXXX	XXXXXXXX	XXXXXXXXXX	XXXXXXXXX		
Coralline red algae	XXXXXXXX	XXXXXXXXXX	XXXXXX	XXXXXX	XXXXXXXXX		
Calcareous green algae			XXXX	XXXXXX	XXXXXXXXXX		
Seagrass			XXXXXXXXX	XXXXXXXXX			
Cyanobacteria	XXXX**		XXXXXXXXX	XXXX	XXXXXXXX**	XXXX	XXXX
Non-calcareous algae			XXXX	XXXX			XXXXXXXXX
Octocorals			XXXX	XXXXXXXXX	XXXX		
Sponges	XXXX**	XXXX**	XXXX**	XXXX	XXXX	XXXXXXXXX	XXXX
Foraminifers		XXXX			XXXXXXXXX		
Echinoids					XXX	XXXXXXXXX	
Crinoids				XXXX**	XXXX**		
Bivalves	XXXX**	XXXX	XXXX**	XXXX**	XXXX**	XXXX	
Gastropods		XXXX	XXXX	XXXX	XXXX	XXXXXX	XXXX
Other mollusks						XXXXXX	XXXX
Bryozoans		XXXX**	XX	XXXX**	XXXX**		
Brachiopods	*******	*******	*******	*******	X*******		
Barnacles					XX	XXXX	
Annelids						XXXX	XXXXXX
Fish					By bioerosion	XXXXXXXXXX	XXXXXXXXXX

XXXX indicates relative importance in modern shallow-water reefs, XXXX** indicates that the group was more important in fossil buildups, and ****** indicates primarily important in fossil reefs

Table 2.2 Characteristics of the principle calcium carbonate minerals

Mineral name	Aragonite	Calcite	Mg-Calcite
Chemical composition	$CaCO_3$	$CaCO_3$	$(Ca, Mg)(CO_3)_2$
Crystal system	Orthorhombic	Rhombohedral	Randomly substituted $MgCO_3$ in a disordered calcite lattice
Habit	Columnar or fibrous	Coarsely crystalline to massive	Coarsely crystalline
Fracture	Subconcoidal	Concoidal	Disordered
Hardness	3.5–4	3	3 or less
Solubility	~1.5× more soluble than calcite	Least soluble, most stable form	At 25° C, <8.5 mol% $MgCO_3$ is less soluble than aragonite
Other	Stronger than calcite per unit Ca^{2+}	More brittle than aragonite	At 25° C, >8.5 mol% $MgCO_3$ is more soluble than aragonite
Biological advantages	For branching morphologies, muscle attachments	Requires less energy to precipitate and maintain under lower saturation states	Does not require genetic capability to exclude Mg; advantageous where strength is less important
Environmental advantages	Warm, supersaturated seawater with high Mg: Ca ratio	Most stable at lower carbonate saturation states–cooler waters, higher pressure, low Mg:Ca ratios	Thermodynamically controlled; chemistry varies with environmental conditions
Disadvantages under specific conditions	Metastable, soluble	Excluding Mg requires energy and genetic capability	Solubility, structural limitations

calcite forms rhombohedral crystals while aragonite forms orthorhombic crystals (Table 2.2). Crystal structure is biologically significant because aragonite is structurally stronger than calcite, which is important for organisms with upright or branching morphologies. Another difference is in the chemical stability of the minerals at temperatures and pressures found on land and in the oceans. Aragonite more readily precipitates in warm seawaters that are supersaturated with $CaCO_3$, but it is less stable in cooler seawaters and in freshwater.

In warm environments, calcite precipitation tends to be inhibited by Mg^{2+} dissolved in seawater. Thus, organisms must either expend energy to remove Mg^{2+} from the calcifying fluids or incorporate it into the calcite crystal structure, thereby producing Mg-calcite shells or skeletons (Hallock 2011). Mg-calcite is energetically advantageous in terms of calcification, but the resulting calcite is structurally weaker. The Mg^{2+}/Ca^{2+} ratio in seawater, along with temperature, determines how much Mg^{2+} is incorporated in Mg-calcite shells. Over time, most aragonite and Mg-calcite either dissolve or recrystallize, so calcite predominates in ancient limestones.

The solubility of $CaCO_3$ is easily misunderstood if one expects this substance to behave like other familiar solids. For example, table salt and sugar both dissolve faster in hot water than in cold. $CaCO_3$ is more soluble in cold water. The key to this intuitive discrepancy is in the reaction of carbon dioxide with water:

$$CO_2 + H_2O <==> H_2CO_3 <==> H^+ + HCO_3{}^- <==> 2H^+ + CO_3{}^{2-} \tag{2.1}$$

That is, carbon dioxide (CO_2) and water (H_2O) combine to form carbonic acid (H_2CO_3), which can then dissociate to hydrogen ions (H^+) and bicarbonate ($HCO_3{}^-$) or carbonate ($CO_3{}^{2-}$) ions. The two-headed arrows indicate that the reaction can go either direction depending upon environmental conditions. The dissolved inorganic carbon concentration of a sample of seawater is the sum of the carbon in these four states. In surface seawaters, CO_2 is only a small fraction of the total carbon, often less than 1 %, while $HCO_3{}^-$ typically dominates (Morse and Mackenzie 1990).

How much CO_2 can be dissolved in water and which state predominates depends primarily upon temperature, pressure, and concentrations of other dissolved materials (Morse and Mackenzie 1990). Cold water can hold far more CO_2 in solution than warm water; an example is a cold carbonated beverage, which loses CO_2 as it warms. Similarly, water under pressure can hold more CO_2 in solution. Addition of dissolved salts (i.e., increasing salinity) decreases the ability of water to dissolve CO_2. Surface waters of the ocean can hold less CO_2 in solution than deeper waters, and tropical waters hold less than temperate or polar waters.

Carbon dioxide and water react with $CaCO_3$ in the following way:

$$CO_2 + H_2O + CaCO_3 <==> Ca^{2+} + 2HCO_3{}^- \tag{2.2}$$

The more CO_2 that is dissolved in water, the more readily the water can dissolve $CaCO_3$. Conversely, any process that removes CO_2 from solution promotes the precipitation of $CaCO_3$. Since calcium ion (Ca^{2+}) and bicarbonate ion ($HCO_3{}^-$) are both abundant in seawater, modern tropical ocean-surface waters are most conducive to the precipitation of $CaCO_3$, while deeper and colder ocean waters are more apt to dissolve $CaCO_3$.

2.4 Limestones and Earth History

Limestones and dolostones are a major reason that life exists on Earth. Since limestones are $CaCO_3$ and dolostones are $Ca,Mg(CO_3)_2$, they store immense quantities of CO_2 in the Earth's crustal rocks. Without limestones, the concentration of CO_2 in the Earth's atmosphere would be about 100 times higher, similar to that of Venus, and the surface of the Earth would be nearly as hot as that of Venus (425 °C) (Condie 1989).

Carbon dioxide is referred to as a greenhouse gas because it absorbs heat energy. Most of the energy reaching a planet's surface from the Sun is visible light. The planet's surface absorbs that radiation, is warmed by it, and reradiates heat (infrared radiation) back into space. Carbon dioxide in the atmosphere acts as an insulating blanket by trapping part of the infrared radiation the planet would otherwise lose into space.

Venus and Earth are quite similar planets. A major factor in their histories, which culminated in life on Earth but not on Venus, is distance from the Sun. This determines the intensity of solar radiation falling on the planet's surface. Based on distance from the sun and without considering atmospheric effects, the average surface temperature of primordial Venus is estimated as 60 °C and of primordial Earth as -30 °C. Volcanic eruptions released water vapor, hydrogen sulfide, methane, ammonia, carbon dioxide, and other gases from these planets' interiors, producing atmospheres. Approximately 10 % of the gaseous volcanic emission was CO_2. So both planets had insulating atmospheres and likely were somewhat warmer than estimates based only on distance.

Carbon dioxide is removed from the atmosphere during weathering of rocks (Berner 2006). Rainwater, in which carbon dioxide is dissolved, falls on rock (represented here by basalt – $CaSiO_3$), slowly weathering it away to dissolved silica (H_4SiO_4), calcium ions, and bicarbonate ions:

$$3H_2O + 2CO_2 + CaSiO_3 ==> H_4SiO_4 + Ca^{2+} + 2HCO_3^- \qquad (2.3)$$

In lakes or oceans, dissolved silica precipitates out to form opal ($SiO_2 \cdot nH_2O$):

$$H_4SiO_4 + (n-2)H_2O <==> SiO_2 \cdot nH_2O \qquad (2.4)$$

while Ca^{2+} and HCO_3^- react to form $CaCO_3$ (Eq. 2.2 read right to left). Through geologic time, the opal crystallizes to quartz and the $CaCO_3$ accumulations become limestone, dolostone or marble.

The solubility of CO_2 is strongly temperature dependent, as is the weathering reaction (Eq. 2.3), which further explains why Earth supports life while Venus does not. On primitive Venus, an average surface temperature in excess of 60 °C inhibited dissolution of CO_2. Weathering of crustal rocks was minimal and CO_2 rapidly accumulated in the atmosphere. Today the atmosphere of Venus is 95 % CO_2 and life is precluded by a runaway greenhouse effect (e.g., Rosenquist and Chassefiere 1995). In contrast, with a primordial atmosphere, daytime temperatures on much of the Earth's surface probably supported liquid water at temperatures of 0–25 °C, which was optimal for CO_2 dissolution and weathering of basalt. As a result, CO_2 was removed from Earth's atmosphere and accumulated in crustal rocks. Today only about 0.04 % of the Earth's atmosphere is CO_2 and the average surface temperature of approximately 14 °C (Axelrod 1992) readily supports life.

2.5 The Atmosphere and the Evolution of Life

During the first 1,000 Myr of Earth's history, most precipitation of $CaCO_3$ likely occurred spontaneously (abiotically) when concentrations of Ca^{2+} and HCO_3^- supersaturated warm waters. The evolution of life on Earth profoundly altered this relationship (Fig. 2.1). Microbes evolved the ability to utilize energy from chemical bonds or sunlight to produce organic matter (abbreviated below as CH_2O) from CO_2 (Canfield and Raiswell 1999; Riding 2000), using either hydrogen sulfide (H_2S) or water (H_2O) as the hydrogen donor:

$$H_2S + CO_2 <==> CH_2O + S_2 \qquad (2.5)$$

$$H_2O + CO_2 <==> CH_2O + O_2 \qquad (2.6)$$

If diffusion and mixing processes in seawater are limited relative to the rate of photosynthesis, removal of CO_2 from solution by photosynthesis can promote $CaCO_3$ precipitation (see Eq. 2.2). For example, on a warm, shallow, subtidal flat where cyanobacterial mats cover the bottom, $CaCO_3$ crystals may form in the water or within the mats (Pentecost 1991; Reid et al. 2003). The result can be the formation of stromatolites. By this mechanism, tremendous volumes of limestone were deposited in shallow shelf seas from about 2,800 to 600 million years ago (Ma) (Grotzinger 1989; Riding 2000). During this time, photosynthesis forever changed the Earth's atmosphere by removing CO_2 and producing free oxygen, resulting in oxygenated oceans and atmosphere essential for the evolution and survival of

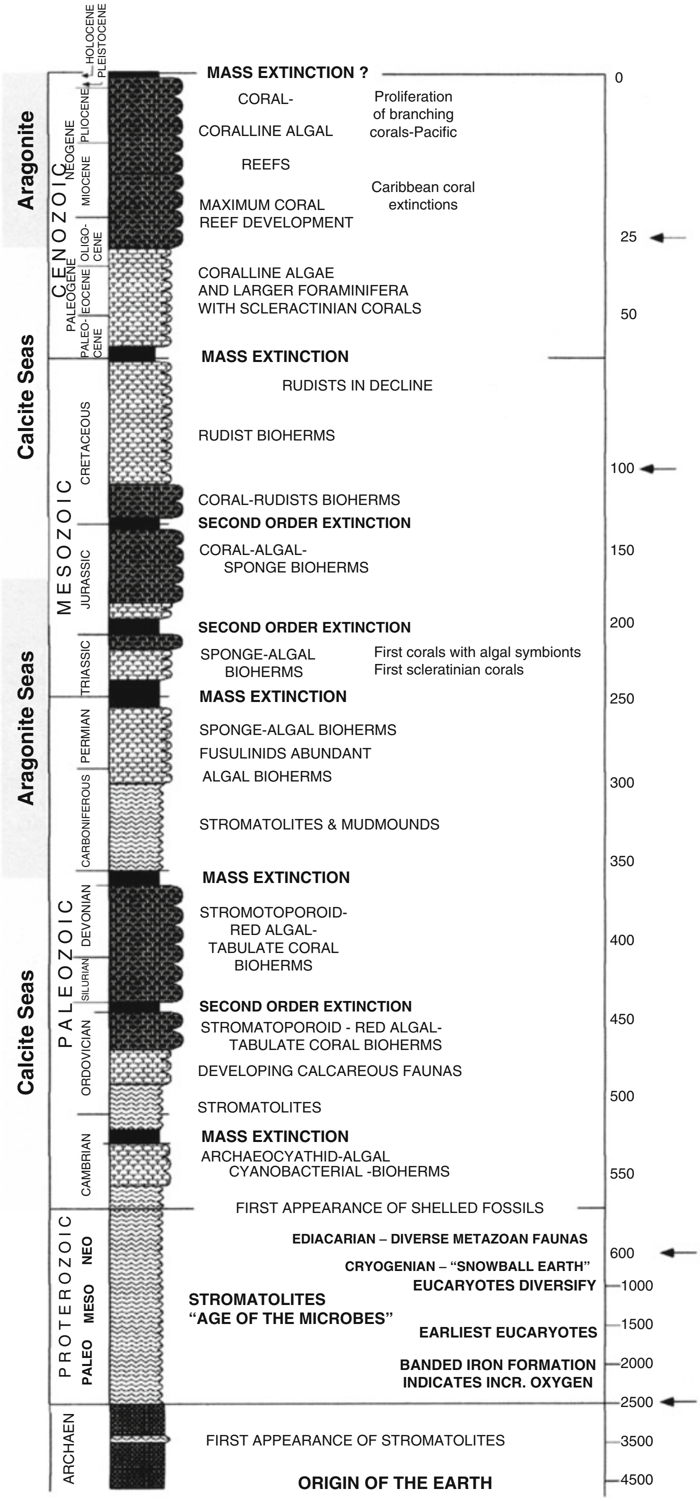


Fig. 2.1 The geological time scale illustrating major reef-related events. The *arrows* along the right side of the figure note scale changes, with the scale greatly expanded over the past 100 million years, especially the past 25 million years

multicellular life forms (Lovelock 2000; Och and Shields-Zhou 2012).

During the ~4,600 Myr lifetime of the Sun, its luminosity has increased roughly 40 % as a part of the natural aging process of a star (Gilliland 1989). If the process of carbon dioxide removal from the Earth's atmosphere was purely geochemical, the rate of removal would have declined as solar radiation intensified, and the Earth would have become warmer. But since the evolution of photosynthesis, life forms have influenced the concentrations of CO_2 and O_2 in the atmosphere. As solar radiation has intensified, rates of photosynthesis have likely increased (Lovelock 2000). The long-term increase in rates of photosynthesis can partly account for the overall decline in CO_2 concentrations through geologic history of the Earth (Berner 2006).

However, the decline in CO_2 concentrations in the atmosphere has been neither uniform nor continuous. Global tectonic activity, which has not been constant through geologic time, is a major influence on input and withdrawal of CO_2 in the atmosphere (Eyles 1993). Over Earth history, volcanic rates have generally declined as the Earth's interior has progressively cooled (Drake 2000). Over the time scales of large-scale plate tectonic processes (10s–100s of Myr), volcanic rates have varied, slowing as large continental masses collided and speeding up as they rifted apart. For example, during the Cretaceous Period (the Age of the Dinosaurs), 150–65 Ma, the rates of oceanic rifting and subduction were substantially faster than modern rates. Atmospheric CO_2 concentrations, which were as much as five to ten times higher than present, produced greenhouse conditions in which high latitudes enjoyed temperate climates and polar regions were ice free (Mackenzie and Anderssen 2013). Thus, during intervals such as the Cretaceous, the long-term decline in atmospheric CO_2 concentrations temporarily reversed.

A critical driver of CO_2 decline has been the successive evolution of groups of photosynthetic protists and plants with new and more efficient pigments and enzyme systems. Proliferation of new organisms likely contributed to second-order declines in atmospheric CO_2 concentrations that triggered global cooling and culminated in major episodes of high-latitude glaciation. Prior to the Neoproterozoic, which began roughly 1,000 Ma (Fig. 2.1), bacteria were the major photosynthesizers. The evolution of the nucleated cell from the symbiosis of three or four different kinds of bacteria provided the evolutionary breakthrough that later made multicellular life possible (Margulis 1993). The evolution of green and red algae and of the primitive phytoplankton known as acritarchs ~1,200 Ma increased the efficiency of photosynthesis and therefore rates of CO_2 extraction. A major glacial event occurred in the Cryogenian Period of the Late Proterozoic, starting about 850 and ending approximately 635 Ma (Pierrehumbert et al. 2011). Global cooling associated with this extensive glacial episode slowed rates of extraction of atmospheric CO_2 by the biotic community.

The proliferation of multicellular life following the Cryogenian has been attributed to suitable atmospheric oxygen concentrations (Och and Shields-Zhou 2012). Shelled organisms first appeared ~570 Ma (Conway Morris 1993). Atmospheric oxygen concentrations also supported primitive land colonizers such as lichens and cyanobacteria (Yuan et al. 2005). The resulting organic acids and primitive soils increased rates of rock weathering, thereby increasing rates of CO_2 removal from the atmosphere. Diversification and proliferation of marine life were occurring by the Ordovician Period, which culminated in another major glacial episode 458–428 Ma (Frakes and Francis 1988).

The evolution and diversification of land plants more than 350 Ma resulted in worldwide accumulation of vast quantities of coals in the Carboniferous Period (Fig. 2.1). Burial of these coals removed tremendous quantities of CO_2 from the atmosphere, contributing to Late Carboniferous glaciation. The evolution of advanced land plants with complex root systems also increased intensity of rock weathering and development of soils (Mackenzie and Anderssen 2013).

In the Mesozoic, many new taxa evolved with the potential to influence the distribution of CO_2 and HCO_3^- in the atmosphere, oceans, and sediments (Beerling and Berner 2005). During the middle Triassic to early Jurassic, several new groups of biogenic-sediment producers evolved and diversified, profoundly changing oceanic sedimentation and sequestration of organic matter. Planktic foraminifers and coccolithophorids, which represented new plankton lineages, began producing calcite shells and plates in the surface waters of the open ocean, so that their calcareous sediments today cover half the ocean floor (Kennett 1982). On shallow shelves, scleractinian corals and a variety of larger foraminifers developed symbioses with microalgae, greatly increasing their potential for carbonate production (Stanley 2003). High rates of CO_2 emission associated with rapid rates of seafloor spreading (i.e., volcanism) during the Cretaceous more than compensated for carbonate production by these new groups of organisms. And along with the new calcareous organisms, the proliferation of flowering plants on land and of extremely fast-growing diatoms in aquatic environments during the late Cretaceous and early Paleogene likely played a role in the global cooling that has occurred over the past 50 million years, culminating in the glacial advances and retreats of the Pleistocene over the past 2–3 Myr (Pagani et al. 2009).

Atmospheric CO_2 concentrations also vary on much shorter time scales. Concentrations were about 180–200 ppm during glacial advances and about 280 ppm during interglacials (Delmas 1992). These differences, their causes, and their significance is at the heart of modern studies of global climate change. Seasonal vegetation has such a strong influence on modern atmospheric CO_2 concentrations that differences between spring and autumn are routinely recorded at the Mauna Loa Observatory in Hawaii (Yajnik and Swathi 2012).

2.6 CO_2 and Time Scales

One of the key paradoxes of carbonates is that how rock weathering and limestone accumulation influence atmospheric CO_2 concentrations depends upon the time scale being considered (Kinsey and Hopley 1991). On the scale

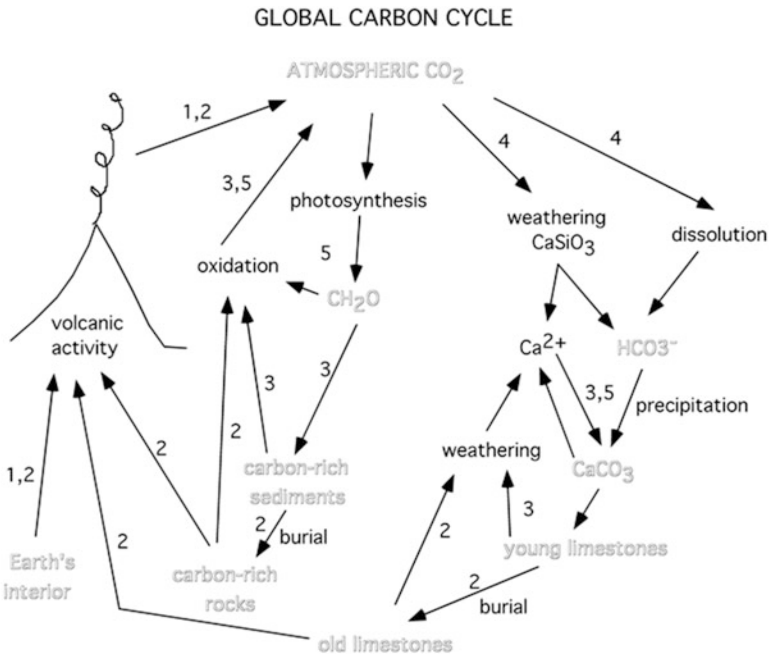


Fig. 2.2 Simplified representation of the global carbon cycle over time. *1* Rates have slowed through Earth history. *2* Rates controlled by plate tectonics. *3* Rates change with sea-level fluctuations. *4* All of these processes influence rates. *5* Biological-scale processes

of Earth history, limestones are clearly important reservoirs of CO_2. This process can be summarized by the simplified expression:

$$CO_2 + CaSiO_3 ==> SiO_2 + CaCO_3 \qquad (2.7)$$

Yet on time scales relevant to humans, Vescei and Berger (2004) and others have argued that production of limestones is a net producer of CO_2, based on the relationship shown in Eq. 2.2 (right to left), i.e., for each $CaCO_3$ precipitated from seawater, one HCO_3^- is converted to CO_2.

The key to understanding this paradox is recognizing that carbon exists in a variety of forms (Fig. 2.2). The ultimate source of carbon is from within the Earth. Volcanic activity delivers carbon to the atmosphere, where it primarily occurs as CO_2, or to the ocean, where it primarily occurs as HCO_3^-. Organic carbon, produced mostly by photosynthesis (Eq. 2.6), occurs in short-term forms in living organisms, wood, soils, peat, water and sediments. Long-term storage of organic carbon occurs in hydrocarbon deposits and carbon-rich rocks such as coal and oil shales. Carbon in $CaCO_3$ sediments is recycled back into dissolved form when aragonitic lime muds from carbonate platforms such as the Bahama Banks are carried by currents into the deep ocean. Aragonite in limestone is also recycled during glacial advances when sea level can fall 100 m or more so that reef limestones are exposed to the air where they are recrystallized or eroded. $CaCO_3$ can be stored as limestones and dolostones within the Earth for millions to thousands of millions of years, until plate tectonic activity uplifts the rocks and exposes them to erosion, or until they are melted or metamorphosed by volcanic activity.

Figure 2.2 is a simplified representation of the CO_2 cycle, which is characterized by processes operating on four major time scales:

1. On the scale of Earth history and the evolution of life (10^9 years–billions of years), CO_2 concentrations have been declining in the atmosphere to compensate for increasing solar output. Carbon has been stored in the Earth's crust as limestone and carbon-rich materials such as coal, oil shale, oil and gas.
2. On tectonic time scales (10^6–10^8 years–millions to hundreds of millions of years), atmospheric CO_2 has varied in response to changes in rates of volcanic activity, which are determined by rates of formation and subduction of the Earth's crust. Limestones and other carbon-rich rocks can be melted or metamorphosed by volcanic activity, recycling stored CO_2 back to the atmosphere-ocean pool.
3. On glacial/interglacial time scales (10^4–10^5 years–tens to hundreds of thousands of years), CO_2 in carbon-rich sediments is recycled when shallow-marine sediments are alternately deposited and eroded in response to sea-level rise and fall. During interglacial times when reefs are most actively accreting, the global oceanic HCO_3^- pool is more rapidly converted to CO_2 and $CaCO_3$, so atmospheric CO_2 concentrations rise somewhat. During glacial events, when sea level is low and reef limestones are actively eroded by CO_2 dissolved in freshwater, atmospheric CO_2 decreases and oceanic HCO_3^- increases.
4. Organisms typically act on biological time scales, which range from nannoseconds for enzymatic processes up to hundreds of years ($<10^3$ years) for long-lived plants or fungi.

Humans, however, have perturbed long-term carbon cycles by extracting fossil fuels, which accumulated over hundreds of millions of years. Burning of fossil hydrocarbons has released huge quantities of CO_2 into the atmosphere. This process has shifted carbon from long-term storage in the Earth's crustal rocks to CO_2 in the atmosphere and oceans. At the same time, humans have tilled organic-rich soils, drained wetlands, and burned forests, thereby releasing carbon from shorter-term storage in soils and vegetation to CO_2 in the atmosphere. Deforestation, oxidation of organic matter in soils and wetlands, and widespread use of herbicides has also reduced rates of CO_2 removal from the atmosphere to short-term storage. Meanwhile, the decline in populations of reef-building corals has reduced calcification rates by these organisms. By disrupting both long and short-term carbon storage, human activities over the past 100 years have increased CO_2 concentrations in the atmosphere more than reef growth influenced CO_2 in the past 15,000 years. Within the twenty-first century atmospheric CO_2 concentrations are predicted to rise to concentrations comparable to those that occurred during the Eocene, 40–50 Ma, when the polar regions were nearly ice free (Feely et al. 2009).

2.7 Evolution and Carbonate Mineralogy

A geochemical paradox of declining concentrations of atmospheric CO_2 through time is that $CaCO_3$ has become increasingly easier for organisms to precipitate. Proterozoic oceans, responding to a more CO_2-rich atmosphere, were able to hold in solution comparably high concentrations of Ca^{2+} and HCO_3^-, even in shallow water. Shallow-water $CaCO_3$ precipitation was probably a "daylight" activity, where photosynthesis within dense mats of cyanobacteria rapidly removed CO_2, creating local supersaturation of seawater with respect to $CaCO_3$. At night and possibly seasonally, seawater equilibrated with the atmosphere and became less supersaturated when photosynthetic rates slowed or stopped.

Approximately 570 Ma, a critical point was reached in the atmospheric-oceanic chemical system; shells evolved in several different groups of organisms. This event indicates that a geochemical threshold was reached; quite possibly atmospheric CO_2 concentrations dropped sufficiently so that low-latitude, shallow-water systems were consistently saturated with $CaCO_3$. Energetically, the protective and supportive advantages of a mineralized shell or skeleton finally exceeded the costs of shell precipitation and maintenance. Biomineralized organisms have since flourished in marine environments, secreting predominantly $CaCO_3$ or calcium phosphate shells or skeletons.

The succession of carbonate minerals through the geologic record, both biogenic and inorganic, also indicates geochemical influence (Sandberg 1983; Stanley and Hardie 1998; Hallock 2011). Although some of the earliest animals secreted calcium phosphate shells, calcite rapidly became the dominant shell material. Aragonite also appeared in shells in the early Paleozoic, though aragonitic algae did not produce significant bioherms until the Carboniferous. Aragonitic scleractinian corals did not evolve and construct reefs until the Triassic, only about 230 Ma (Stanley 2003). This trend reversed as aragonite production declined and calcite production increased during the Cretaceous Period, when atmospheric CO_2 concentrations rose as rates of volcanic activity increased at mid-ocean ridges and subduction zones. At the same time, rates of removal of CO_2 from the atmosphere by terrestrial weathering were relatively low because tectonic highlands were limited in extent (Eyles 1993). Aragonite-producing corals did not fully regain a dominant position until about 40 Ma, with the beginning of global cooling that led to the Neogene world of waxing and waning continental glaciers (Pomar and Hallock 2008).

Another critical factor controlling carbonate mineralogy is the Mg/Ca ratio in seawater, which is largely influenced by ion exchange at ocean-ridge systems (Hardie 1996). The alteration of new basalt at the seafloor removes Mg^{2+} from seawater and releases Ca^{2+}; the rate of this exchange is dependent upon the rate of ocean crust formation. Thus, times of rapid seafloor spreading result not only in elevated concentrations of CO_2 in the atmosphere and HCO_3^- in seawater, but also higher Ca^{2+} concentrations in seawater. Such conditions are energetically more favorable for organisms that secrete calcite than those that produce aragonite. Conversely, when seafloor spreading rates slow, rates of Mg^{2+} removal from, and Ca^{2+} release into, seawater decline. The result is higher Mg/Ca ratios in seawater, which favors aragonite or Mg-calcite precipitation. Thus, tectonically-forced changes in seawater chemistry have influenced evolution and reef-building capacity of calcareous biotas, as well as the composition of carbonate cements (Stanley and Hardie 1998).

A second implication of the reduction of CO_2 in the atmosphere, and therefore the partial pressure of CO_2 in surface waters of the ocean, is the possibility that shortage of CO_2 can limit photosynthesis (Pomar and Hallock 2008). In shallow, warm, brightly illuminated waters, HCO_3^- is abundant and dissolved CO_2 is scarce. By using energy from photosynthesis to actively uptake Ca^{2+} ions from seawater, cells can use the calcification process to convert bicarbonate ions (HCO_3^-) to CO_2 needed for photosynthesis (Cohen and McConnaughey 2003). Calcareous algae, which may have been the first multicellular organisms to utilize calcification this way, first appeared in the Cambrian. The Mesozoic diversifications of modern calcifying algae, including coccolithophorids in the plankton and melobesian green and coralline red algae in the benthos, along with the

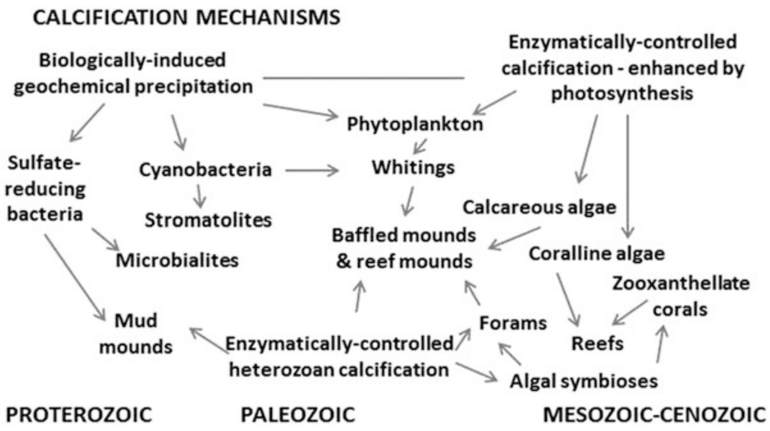


Fig. 2.3 Calcification mechanisms and when they first were important in construction of biogenic reefs

proliferation of algal symbiosis in foraminifers, corals, and some bivalves, provide further evidence of biotic response to declining CO_2 concentrations in the atmosphere (Pomar and Hallock 2008).

Webb (2001) subdivided biomineralization into biologically-induced precipitation that is the by-product of metabolic activity, and biologically-controlled skeletogenesis that is enzymatically controlled. The first mechanism, which includes geochemical precipitation of $CaCO_3$ in response to CO_2 uptake by photosynthesis, was particularly effective in the Proterozoic under relatively high atmospheric pressures of CO_2. The second mechanism, enzymatically controlled biomineralization, appeared in the Cambrian, probably when CO_2 concentrations declined sufficiently that the expenditure of energy for shell construction and maintenance became less than loss to predation without skeletal protection, at least in warm, shallow water (Fig. 2.3).

Precipitation of $CaCO_3$ induced by sulfate-reducing microbes is a type of biologically-induced calcification whose role in carbonate buildups has become increasingly recognized in recent years. Schlager (2000) referred to such carbonate textures in mud mounds at platform margin and upper slope depths as **automicrite**, in which microbial activity and decaying organic matter were key components (Monty 1995; Schlager 2000), and with marine cements as important secondary components. Pomar and Hallock (2008) suggested that automicritic boundstones represent a particular type of carbonate facies that predominated at times in Earth history when metazoan consumers were absent (e.g., Pre-Phanerozoic) or reduced in abundance (e.g., following mass extinction events). With few consumers, excess primary production in overlying waters allows organic matter to accumulate on the seafloor where it can be metabolized by microbial activity. For every two organic carbon atoms consumed during sulfate reduction, one of those carbons can be incorporated as $CaCO_3$ (Baumgartner et al. 2006), providing tremendous potential for calcium carbonate precipitation where sufficient organic carbon substrate meets sufficient rates of exchange of seawater. Shelf edge and upper slope locations provide potential for organic accumulation, oxygen-minimum conditions, and water movement associated with internal waves (Pomar et al. 2012) or contour currents that provide necessary seawater exchange.

Enzymatically-controlled biomineralization mechanisms include (a) biomineralization by heterotrophic protists and metazoans, in which the energy source is ingested food; (b) biomineralization by mixotrophic protists and metazoans, in which photosynthetically derived energy significantly enhances calcification rates; and (c) biomineralization by photosynthetic protists (red and green algae, also coccolithophorids), in which photosynthesis provides energy for calcification and, at the same time, calcification can provide CO_2 for photosynthesis (Cohen and McConnaughey 2003; Pomar and Hallock 2008). The potential for calcification to provide CO_2 for photosynthesis became particularly advantageous when reduced atmospheric CO_2 concentrations began to limit aquatic photosynthesis in warm, shallow seas.

The strategies whereby photosynthesis provides energy for enzymatically-controlled biomineralization arose independently in several lineages of Foraminifera, Porifera, Cnideria, and Mollusca, as well as in at least three divisions of algae. This mechanism has profound and almost paradoxical implications for atmospheric CO_2 concentrations. The very process that makes CO_2 instantaneously available for photosynthesis can be responsible for the long-term removal and burial of CO_2 as $CaCO_3$.

Global cooling, on the other hand, reduces the rate of CO_2 burial by calcification. If organisms draw too much CO_2 out of the atmosphere, onset of glaciation lowers sea levels and reduces the habitats of warm-water calcifying organisms, as well as that of terrestrial plants. Lowered sea level also prevents burial of some limestones, instead exposing them to erosion and returning the HCO_3^- to the hydrosphere.

Paradoxically, as atmospheric CO_2 concentrations decline, aragonite, which is more rapidly recycled by freshwater weathering during glacial advances, becomes easier to precipitate in warm waters.

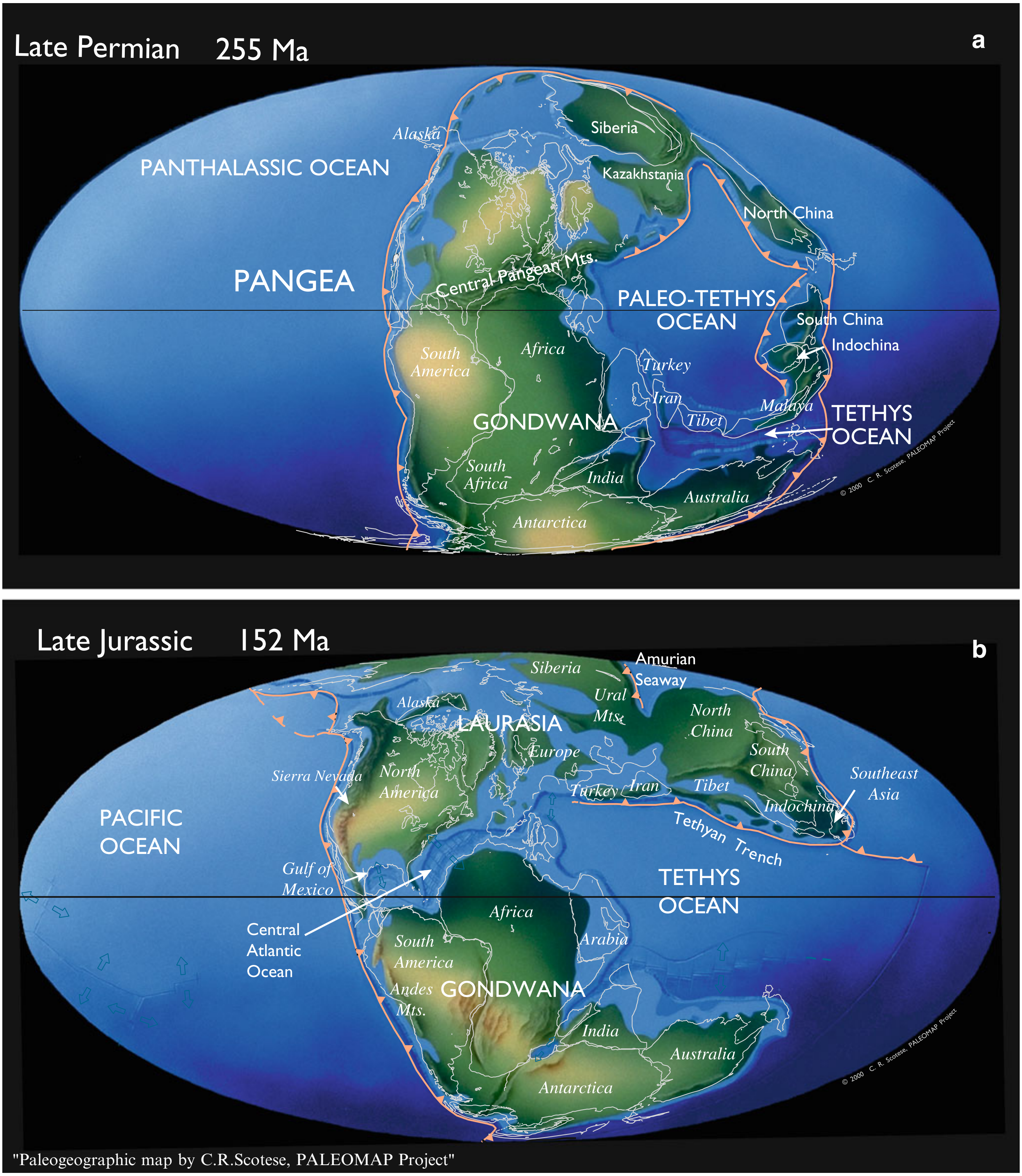
2.8 What Is Required to Accumulate $CaCO_3$

Although calcium carbonate sediments have been produced and limestones have been accumulating for more than 3,500 Myr of Earth history (e.g., Grotzinger 1989), major accumulations of limestone represent deposition during relatively small proportions of geologic time (Schlager 1981). Times and places for substantial sedimentary carbonate accumulation require an array of appropriate environmental conditions, as well as appropriate suites of carbonate-producing biotas. The classes of carbonate sediments (Lees 1975; James 1997), combined with the guilds of Fagerstrom (1987), can be merged into the concept of "carbonate factories" (Schlager 2000), including the tropical shallow-water factory, dominated by photoautotrophic, biotically-controlled skeletal production and abiotic precipitates; the cool-water factory, dominated by heterotrophic skeletal production; and the mud-mound factory, dominated by biotically-induced production (predominantly microbial) and abiotic precipitates that formed at or near the sea floor. Two additional factories involve production of carbonates within the water column: the neritic carbonate factory (whitings), which are biotically-induced by photosynthetic microbes and microalgae in highly supersaturated waters (Robbins and Blackwelder 1992), and the pelagic carbonate factory of biotically-controlled skeletal production, either directly associated with photosynthesis (coccolithophorids) or by planktic foraminifers, many of which host algal symbionts.

A major limiting environmental factor is that shallow, euphotic shelf areas suitable for prolific production and accumulation of reefal carbonates represent less than 2 % of either the Earth's surface or the ocean volume. Furthermore, preservation of $CaCO_3$ is as important as production for accumulation and persistence in the rock record. Several factors influence both production and preservation potential within the limited available environments. One very important condition is the persistence or repeated submergence of substantial areas of shallow shelf at mid to low latitudes over sufficient time intervals so that limestones can accumulate, i.e., the presence of accommodation space (Pomar 2001). A second condition is relatively low input of terrigenous sediments and inorganic nutrients, especially nitrogen and phosphorus (Hallock 2001, 2011). A third condition is the presence of biota that can precipitate or enhance the precipitation of $CaCO_3$.

The persistence or repeated submergence of substantial areas of shallow shelf at mid to low latitudes is controlled by plate tectonics and climate, which together control sea level. Rates of sea-floor spreading influence the average depth of the ocean. When sea-floor spreading rates are high, the average depth of the ocean basins is shallower, pushing water higher onto the continental shelves (Kennett 1982). The relative proportions of continents that are colliding or overlying rifting centers also influences global and local sea level. For example, all of the major continents came together in the late Paleozoic to form the supercontinent of Pangea (Fig. 2.4). This can be compared to India colliding with Asia to form the Himalayas, but on a much larger scale. As the continents merged, spreading rates slowed, sea level relative to the continents receded, and there were few shallow-shelf areas; most that occurred were inundated by terrigenous sediments eroded from the highlands. Through the latest Paleozoic and into the early Mesozoic, Pangea remained as one supercontinent. Heat from the Earth's interior accumulated beneath Pangea, thermally uplifting and rifting it apart. The supercontinent at this stage was somewhat analogous to Africa today, which has very narrow continental shelves and where eroding highlands plunge into deep rift valleys. As the continents rifted apart and moved away from one another during the Cretaceous (Fig. 2.5), they slowly subsided. Australia today is probably the closest analogue for continents in the Cretaceous, with generally low relief, passive margins on three sides, and a broad, shallow sea to the north between the continent and tectonically active Indonesia and New Guinea. In the Cretaceous, higher elevations were primarily in island arcs analogous to the Marianas Islands or Japan.

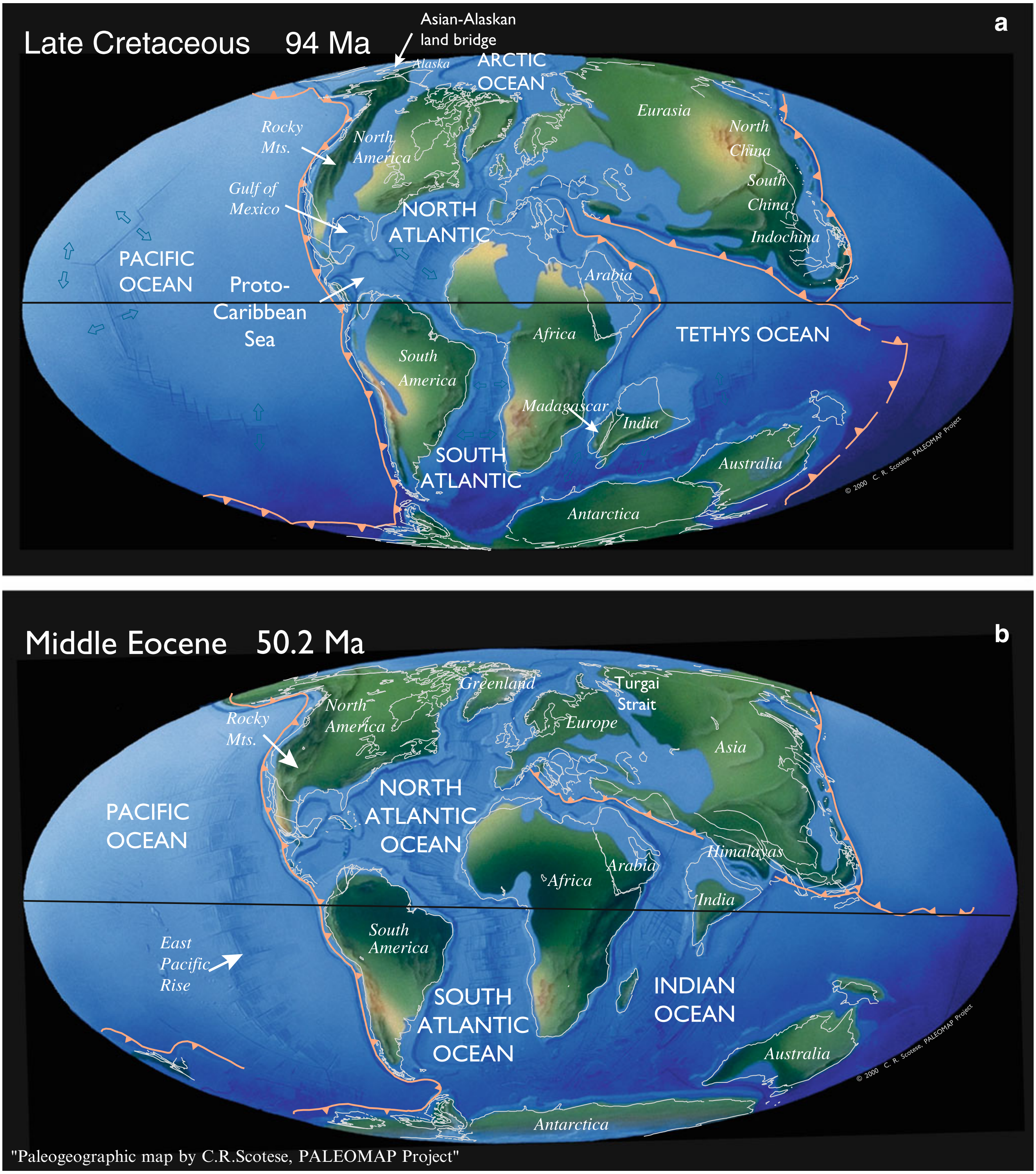
Sea-floor spreading rates and climate interact through a variety of feedback mechanisms to further influence sea level (Worsley et al. 1986). As the continents ground together to form Pangea, sea-floor spreading and overall volcanic rates slowed, further lowering sea level. Reduced volcanism resulted in reduced emissions of volcanic gases, including CO_2. As a result, the Earth's climate was cooler. Conversely, as continents moved apart, sea-floor spreading rates increased, volcanic rates increased, and CO_2 emissions increased, triggering global warming in the Jurassic and Cretaceous. Relative sea level influences global climate because it alters the reflectivity (albedo) of the Earth; land is more reflective than water, while ice is more reflective than land. The higher the sea level, the more solar energy the Earth can capture and so the warmer the climate. Globally warm climates, known as greenhouse conditions, promote even higher sea level, because polar ice is minimal to nonexistent. Finally, without polar ice, deep waters in the oceans are much warmer, so thermal expansion of the water further raises sea level.



"Paleogeographic map by C.R.Scotese, PALEOMAP Project"

Fig. 2.4 Plate reconstructions for (**a**) the Permian Period, illustrating the supercontinent Pangea that formed during the late Paleozoic and (**b**) the Late Jurassic Period (Middle Mesozoic), illustrating the opening of the North Atlantic (From Scotese 2002)

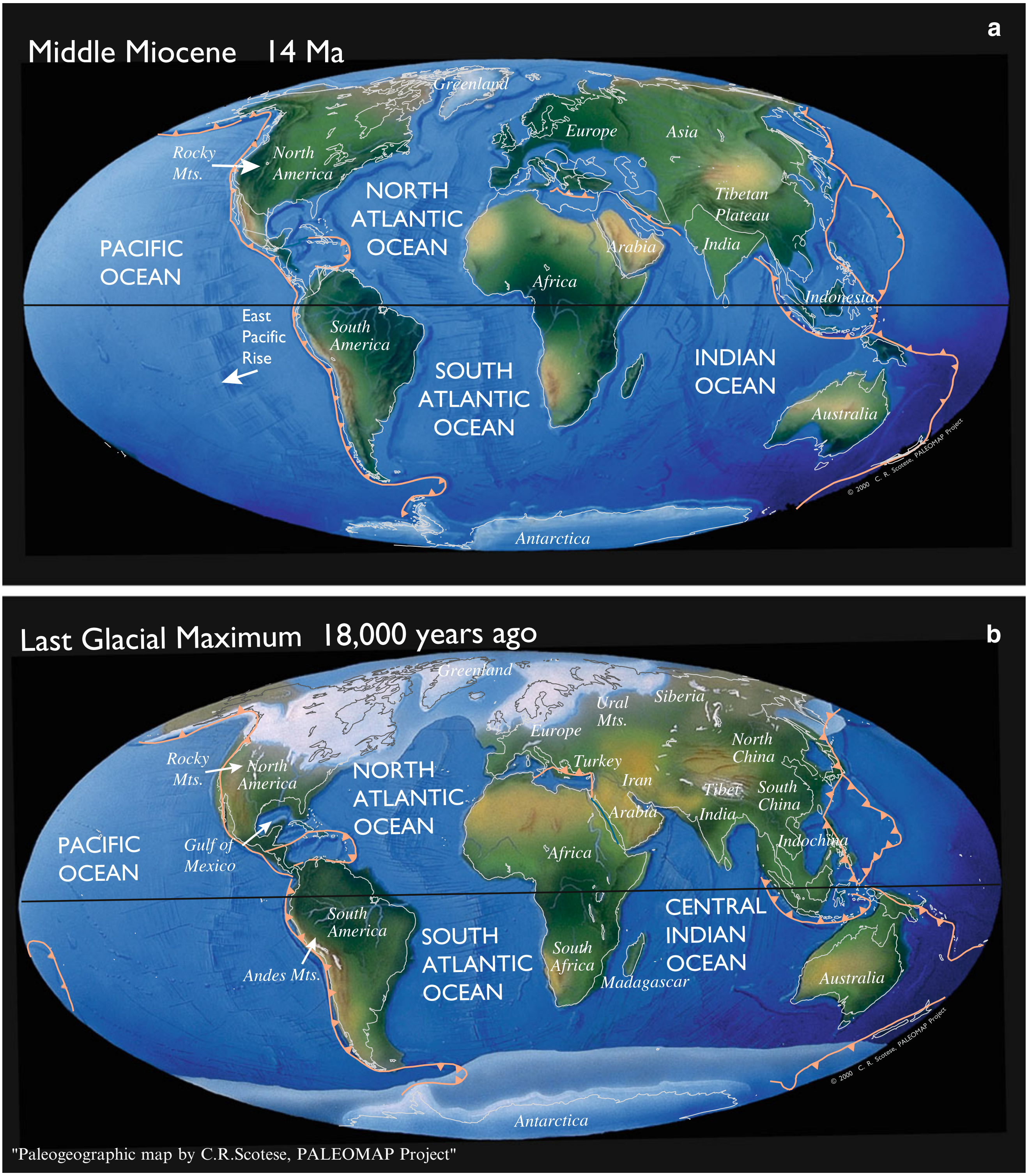
The differential heating of the equator relative to the poles drives atmospheric and oceanic circulation. Plate tectonics control the positions and elevations of land masses relative to the oceans and so further influences atmospheric and ocean circulation by providing passageways and barriers (Eyles 1993). For example, separation of Antarctica and Australia in the late Eocene and the opening of the Drake Passage between Antarctica and South America in the



"Paleogeographic map by C.R.Scotese, PALEOMAP Project"

Fig. 2.5 Plate reconstructions for (**a**) the Late Cretaceous, after the breakup of Pangea, when circumtropical circulation was well developed and (**b**) the middle Eocene, illustrating somewhat restricted circumtropical circulation and hints of future south circumpolar circulation (From Scotese 2002)

Oligocene (Figs. 2.5 and 2.6), enabled the development of the circumpolar current in the Southern Ocean (Flower 1999). This caused the climatic isolation of Antarctica and polar cooling. Closure of the Panamanian Seaway over the past few Myr restricted and ultimately terminated flow of the Caribbean Current into the Pacific, diverting the current northward to accelerate the Gulf Stream (Lutz 2010). Delivery of warmer water to high northern latitudes increased snowfall, contributing to glaciation (Raymo 1994).



"Paleogeographic map by C.R.Scotese, PALEOMAP Project"

Fig. 2.6 Plate reconstructions for (**a**) the middle Miocene, when the Central American Seaway was still open but circumtropical circulation diminished as India and the Middle East collided with Asia, while south circumpolar circulation was complete and (**b**) the Pleistocene – the last glacial maximum, when sea level was about 130 m lower than at present (From Scotese 2002)

Global climate is strongly influenced by CO_2 concentrations in the atmosphere (Pearson and Palmer 2000), and therein lies yet another paradox of limestones and coral reefs. Times of global warming (Fig. 2.1) were times of widespread limestone deposition, but not of coral-reef development (Stanley and Hardie 1998; Hallock 2011).

For example, paleo-isotopic evidence indicates that tropical sea-surface temperatures during the Cretaceous and early Paleogene were at least 28–32 °C (Pearson et al. 2001), while seawater in the polar regions and deep seas was 10–15 °C warmer than today (Flower 1999). Yet coral reefs did not widely flourish until the Oligocene Epoch, with the onset of global cooling under declining atmospheric CO_2 concentrations.

2.9 History of Biogenic Reefs Through Time

The Geologic Time Scale (Fig. 2.1) has five major divisions called Eons, each of which is characterized by the appearance of major groups of organisms that proliferated and profoundly influenced the subsequent Eon. The earliest history of the Earth is referred to as the Hadean Eon, which lasted ~600 Myr during which time the newly formed planet was cooling. The Archean Eon, ~1,500 Myr long, was the time when prokaryotic microbial life appeared, proliferated and diversified, leaving the earliest evidence for stromatolites, for photosynthesis, and ultimately, for the first free oxygen (Dobretsov et al. 2008).

The Proterozoic Eon was truly the "Age of the Microbes", but it was also a time of profound environmental change. Many microbes were driven to extinction or "underground". Some adapted by developing symbioses with other microbes (producing nucleated, eukaryotic cells) that allowed them to survive the Earth's first "pollution" event – the Great Oxygenation Event (Holland 2006) of shallow aquatic systems, which occurred between ~2,400 and 2,000 Ma (Paleoproterozoic). The first evidence for eukaryotic organisms has been found in some of the youngest rocks that are considered Paleoproterozoic. Oxygen is toxic to all cells to some degree, which is why eukaryotic cells have anti-oxidant defense mechanisms. Once cyanobacteria developed photosynthesis, using sunlight to fix water and carbon dioxide into organic matter, their proliferation was assured. At the same time, anaerobic bacteria became restricted to anaerobic environments, were forced to adapt, or perished.

Evidence for very early oxygenation of shallow aquatic environments is found in banded iron deposits, which occur on the ancient cores of all the continents and have been utilized as iron ores by human populations for thousands of years (Cloud 1973). Iron (Fe) comes in two forms, reduced Fe^{2+} and oxidized Fe^{3+}. Igneous rocks are rich in Fe^{2+}, which is quite soluble in water. However, if there is free oxygen in the atmosphere or dissolved in water, the Fe^{2+} oxidizes to Fe^{3+}, which is very insoluble. The most likely way that immense quantities of iron could accumulate with alternating layers of chert was when the atmosphere still lacked oxygen. As water weathered rocks on land, Fe^{2+} readily dissolved, along with H_4SiO_4. The Fe^{2+} laden rivers and streams flowed into lakes, lagoons or shallow-shelf areas, where cyanobacteria were actively photosynthesizing and oxygenating the waters. The iron oxidized, producing iron oxides that accumulated as sediments.

Calcium is also very abundant in volcanic rocks, and is readily dissolved out of those rocks by CO_2-rich rainwater, resulting in fresh waters laden with Ca^{2+} and HCO_3^- flowing into shallow waters where active photosynthesis induced precipitation of $CaCO_3$, resulting in stromatolites or whiting-type muds. Mesoproterozoic age stromatolitic limestones also occurred nearly worldwide, sometimes alternating with shales that alternate green and red because they were deposited under either anoxic (green shales) or oxygenated (red shales) conditions.

Eukaryotic protists that emerged in the Mesoproterozoic included the red and green algae. Other eukaryotic innovations, including evidence for sexual reproduction and multicellularity, first appeared in the Mesoproterozoic, fully developing in the final Era of the Proterozoic. The Neoproterozoic Oxygenation Event (Och and Shields-Zhou 2012), during which multicellular organisms began to proliferate, partly coincided with extensive glaciation during what is known as the Cryogenian Period. The final period of the Neoproterozoic, the Ediacaran, is known for its diversity of novel fossils of soft-bodied organisms that represent most known animal phyla, as well as several enigmatic ones (Knoll et al. 2006). Stromatolites and other microbolites remained the dominant reef structures through this final Era before the emergence of shelled metazoans that heralded the Phanerozoic Eon (Grotzinger and Knoll 1999).

Whether Proterozoic or Phanerozoic, microbes have been producing microbolites and stromatolites for more than 3,400 Myr; shell-forming animals for just 570 Myr (Fig. 2.1). Factors that have controlled the formation of biogenic reefs through time include climate, ocean chemistry and circulation, availability of habitat, and existence of reef-forming biotas. The history of reef development and reef-building biotas has not been continuous. Instead, it has been characterized by long periods of persistence of simple mud-mound or reef-mound communities, followed by episodes of development of complex baffler and framework-building communities, then termination of the complex communities by major extinction events. The compendium edited by Kiessling et al. (2002) provides a comprehensive view of distributions, biotas, and dynamics of Phanerozoic reefs; the summary below provides only a brief glimpse of reef history.

Kiessling (2001) defined four basic reef types: (a) true reefs constructed largely by a framework of skeletal remains of reef-building organisms; (b) reef mounds, where the remains of skeletal reef-building organisms and mud matrix are about equally important; (c) mud mounds, which have only minor skeletal components; and (d) biostromes, which have abundant skeletal components but minimal depositional relief. These categories, as well as other ways that reefs have been classified, are more convenient than mutually exclusive. Even within individual reef structures, there may be a colonizing stage by a binder community, a diversification stage by a baffling and binding community, and a climax stage of framework builders, binders, dwellers, and destroyers (Fagerstrom 1987).

From 3,400 to 540 Ma, prior to the appearance of shelled animals, whether stromatolitic buildups developed was controlled primarily by suitability of physical and chemical environments. Stomatolitic limestones and dolostones accumulated where seawater was warm enough and shallow enough for photosynthesis by cyanobacteria to promote $CaCO_3$ precipitation over sufficient area and time to be preserved, or where organic matter accumulated on the sea floor under conditions that sustained carbonate precipitation in conjunction with sulfate reduction or other microbial processes. With the evolution of the Foraminifera, as well as multicellular life such as worms and trilobites, that bulldozed through the algal mats, eating and disrupting them, stromatolite preservation potential declined (Conway Morris 1993; Bernhard et al. 2013). Kiessling (2001) noted that microbial activity has become less prominent in reefs over time, though stromatolites remain "uncommonly common" even in Holocene sediments (Reid et al. 1995, 2003).

2.9.1 Paleozoic Era: Time of Ancient Animal Life

The first biomineralized animal communities to act as significant bafflers appeared in the lower Cambrian Period, from about 550 Ma (Wood 1999). The archaeocyathids or "ancient cups" are thought to have been calcified sponges; their erect skeletons trapped calcareous muds, which may have been chemically precipitated in response to photosynthesis in cyanobacterial mats or in the plankton. Calcified cyanobacterial/algal mats and encrusters formed major components of the archaeocyathid reef mounds. Trilobites and sponges were among the inhabitants. "Reef tracts" produced by these communities were extensive in Siberia, southern Australia, and Antarctica, which lay in low latitudes at that time (Copper 1994). By the Middle Cambrian these primitive sponges were mostly extinct, so microbial processes again largely produced the reef mounds that have been preserved (Rowland and Shapiro 2002).

The second major diversification of calcified algae and animals capable of producing, trapping and binding large volumes of calcareous sediments began in the Ordovician Period (~500 Ma). Sponges and the earliest corals played major baffler roles, cyanobacteria persisted as binders, while trilobites and primitive snails grazed the algae or fed upon microbe- and algae-rich muds (Webby 2002). By the Middle Ordovician, a greater diversity of calcified animals had evolved. These organisms were more prolific sediment producers, more effective sediment bafflers, and included taxa with the potential to construct framework. Important contributors included bryozoans; stromatoporoids (calcareous sponges); and Solenopora, which have long been considered calcareous red algae, though Riding (2004) argued that they were chaetetid sponges. The early reef mounds provided a multitude of niches for trilobites, brachiopods, snails, cephalopods (including ancestors of the chambered *Nautilus*), other animals that fossilized, and probably many soft-bodied organisms that left little or no fossil record.

By the Late Ordovician, tabulate and rugose (horn) corals had become important components of the reef community (Webby 2002). A typical succession (e.g., James 1983; Copper 2002) consisted of a baffler-colonizer community of stalked crinoids and bryozoans that trapped muds and began to accumulate a structure. Soon this habitat was invaded by sponges, solitary horn corals, small tabulate corals, and massive stromatoporoids, which together constructed larger skeletal structures and trapped calcareous muds and sands. Algae, smaller corals, bryozoa, brachiopods, clams, snails, trilobites and other arthropods found shelter or food within the reef. Encrusting stromatoporoids bound the skeletal elements together, and typically overgrew and eventually dominated the whole structure. In this climax phase, which may have been very wave resistant like a modern coralline algal ridge, the diversity of species was low.

Interesting comparisons can be made between the Middle Paleozoic (Ordovician to Devonian) bioherms and modern coral reefs. The shells and skeletons were predominantly constructed of calcite, whereas modern corals and calcareous algae secrete aragonite skeletons (Stanley and Hardie 1998). Individual structures in the Paleozoic were often similar in size to small patch reefs, connected by expanses of calcareous sands or muds, so regional accumulations of limestone were comparable in scale to modern reef tracts (Webby 2002). However, there was no strong evidence for algal symbiosis in the calcifying animals and calcareous algae were of limited importance. Thus, primary calcification mechanisms responsible for precipitation of most of the early to middle Paleozoic limestones were likely biologically-enhanced geochemical precipitation, with microbes continuing to play major roles, and biomineralization by animals. Extensive Devonian reef complexes along the northern margin of the Canning Basin, Western Australia, as well as others found in Alberta, Canada, Belgium and Germany, are comparable in size to, or even larger than, modern western Atlantic reef systems like the Florida Keys reef tract (Stanley 1992; Webb 2002).

In the Late Devonian (~360 Ma) a major extinction event eliminated most of the reef-building coral-stromotoporoid communities. Subsequently, carbonate production was predominantly microbial, including automicrites in deeper-water mounds and stromatolites and calcimicrobolites in shallower water. Corals and stromatoporoids continued their presence in some Canadian reef mounds. Early Carboniferous buildups scattered around the world were mud mounds containing mostly automicrites and cements, sometimes associated with crinoids and bryozoans. Rugose corals, chaetitids, and brachiopods were among the metazoan taxa that diversified the mud mounds as carbonate-producing metazoan communities recovered (Webb 2002).

Late Carboniferous biotas contain many unusual and taxonomically problematic groups that mostly represent binder and baffler communities. Wahlman (2002) recognized several types of buildups along a spectrum, depending upon whether major components were algal, sponge or bryozoan, and whether environmental controls were temperature, water depth, light penetration, etc. A prominent feature was the prevalence of aragonite-producing phylloid algae and problematic aragonite-producers identified as *Paleoaplysina*, that may have been codiacean algae or possibly hydrozoans. The evolution and diversification of large, structurally complex fusulinid foraminifers represent the strongest evidence for algal symbiosis in important calcareous-sediment producing taxa in the Paleozoic. These two groups, the phylloid algae and the fusulinids, may represent the first major proliferation of organisms calcifying to enhance photosynthesis. On a global scale, the continents were colliding to form Pangea. Glaciation was occurring; reduced atmospheric CO_2 concentrations (Sandberg 1983) and higher Mg/Ca ratios in seawater reflected reduced seafloor spreading rates (Stanley and Hardie 1998). Both factors were conducive to aragonite precipitation and to calcification to enhance photosynthesis (McConnaughey and Whelan 1997; Pomar and Hallock 2008). Moreover, interglacial sea-level rise provided accommodation space for carbonate buildups, while subaerial dissolution and cementation during sea-level regression promoted lithification of carbonate sediments, increasing their preservation potential.

The Permian, which was the last period of the Paleozoic, was characterized by tectonic and volcanic activity as the assembly of Pangea came to its climax (Fig. 2.4). Numerous shallow seas and basins developed and were destroyed during this period (Weidlich 2002). A combination of the variety of regional environmental conditions during deposition, and the economic resources that resulted, have contributed to the diversity of biotas and interpretations of Permian reefs and limestones.

Among the most studied buildups are those of the Permian Basin in west Texas and southeastern New Mexico, USA (Weidlich 2002). The long-lasting but discontinuous accumulation of the Capitan reef complex has revealed that macrofauna were not essential to the buildup. According to Weidlich (2002), the most important constituents of the Capitan Reef limestones include micro-framework produced by diverse assemblages of low-growing algae and microbes. These rocks are also notable for extensive geochemically precipitated cements, to the extent that more than three-quarters of the limestone can be micro-framework of low-growing producers and carbonate cements that precipitated in seawater, especially under hypersaline conditions. A diverse community of bafflers and binders included sponges, bryozoans, crinoids, and brachiopods that trapped and bound muds and coarser sediments produced by the community (Wood 1999). An immensely diverse sediment-producing dweller group, such as foraminifers (including fusulinids), snails, clams, small corals, brachiopods, cephalopods, and arthropods, thrived in these buildups.

Further demonstrating the diversity of Permian carbonate factories, the succession of buildups in the Permian Basin are quite different from three other carbonate factories that Weidlich (2002) described from the Middle and Late Permian elsewhere. The Tethyan carbonate factories, preserved in limestones deposited on the shelves, basins and terrains to the east of Pangea, were characterized by a diversity of reef types and macro-reef builders with high percentages of carbonate mud. Other oceanic (island-arc) terrains lacked macro-reef builders, instead were characterized by calcimicrobes and carbonate muds. The fourth carbonate factory, with abundant bryozoans, brachiopods and crinoids, was a cool-water facies.

2.9.2 The End-Permian Mass Extinction

The Permian-Triassic boundary (PTB) was characterized by the most extreme mass extinctions of the Phanerozoic. Barash (2012) reviewed the extinctions, geochemical signals, and discussed the series of events that likely contributed to the severity and timing. Estimates of extinction of 96 % of marine invertebrates and 70 % of terrestrial vertebrates are common in the literature. The first major extinction event occurred in the mid to late Permian (260 Mya), primarily affecting marine benthic organisms. Subsequently, the events of the PTB at 251–252 Mya also impacted the plankton, with near complete collapse of marine ecosystems.

The assembly of Pangea, which ended in the mid/late Permian, resulted in a land mass that stretched pole to pole. The Panthalassa Superocean covered roughly two-thirds of the Earth's surface. The Tethyan Sea was bordered on the west by Pangea and was partly separated from Panthalassa by smaller land masses to the east.

The PTB events apparently involved successive environmental changes that became increasingly inhospitable to protists and metazoans (Barash 2012). Extensive, explosive volcanism spewed ash, aerosols, and gases such as CO_2 and H_2S, chlorine and fluorine into the atmosphere in multiple locations. The eruptions that produced the Siberian Traps represent one of the largest volcanic outpourings in Earth history, certainly in the Phanerozoic. Moreover, the magma passed through and burned vast coal beds, releasing much more CO_2. And the eruptions occurred in exactly the time interval, 250–252 Mya, as the PTB mass extinctions. Global warming likely was interrupted by episodes of "volcanic winters", when ash and aerosols reduced light reaching the Earth's surface, thereby reducing photosynthesis and primary productivity. Conversely, when atmospheric conditions allowed sufficient sunlight to reach the sea surface, volcanic ash likely fertilized high rates of primary productivity by cyanobacteria. Warming of deeper ocean waters, combined with excess sinking of organic matter, promoted superanoxia, which ultimately spread to shelf environments. Further global warming likely resulted from the release of methane from gas hydrates in marine sediments. Sulfur and halogen-rich volcanic aerosols eroded the stratospheric ozone, further impacting organisms, while allowing high-energy, short wavelength (ultraviolet) solar radiation to reach the Earth's surface and further contribute to global warming. Certainly all of these factors would have devasted marine and terrestrial protists and metazoans. Moreover, Barash (2012) further discusses multiple meteor impacts that have been documented within the same time interval, proposing that they further contributed to the collapse of eukaryotic organisms and communities.

2.9.3 Mesozoic Era: Time of Intermediate Animal Life

The PTB was followed by a prolonged episode (at least 6–8 Myr) in which bioherms produced by metazoan communities are absent in the rock record (Flügel 2002). The few, small, Early Triassic buildups that have been recorded were produced by microbial processes, especially associated with low oxygen conditions. When substantial carbonate buildups reappeared in the Middle Triassic, microbial contributions continued to be primary or at least secondary components.

Because rates of sea-floor spreading continued to be low, Mg/Ca ratios in seawater were conducive to "Aragonite Seas" (Fig. 2.1) from the late Paleozoic through the Triassic Period (Stanley and Hardie 1998). In the Middle Triassic, sponge-algal communities gradually resumed production of reef mounds and included among their subsidiary fauna the first scleractinian corals, which produced aragonite skeletons (Stanley 2003). According to Flügel (2002), coralline sponges were the major baffler and frame-building organisms in many Triassic reefs; among the very diverse sponge biota were Mg-calcite and aragonite producing taxa. By the late Triassic, the scleractinian corals had diversified and new forms restricted to shallow, brightly illuminated waters very likely hosted zooxanthellae (Stanley 2003). Corals and coralline sponges produced framework, while other sponges, as well as bryozoans, bivalves and serpulid worms, were more minor constructors. Calcareous green algae (producing aragonite) and coralline red algae (Mg-calcite) contributed significantly to Middle and Late Triassic reefs (Flügel 2002). Associated fossilized taxa were a diverse group of ammonites, brachiopods, bivalves, snails, echinoderms, foraminifers, and worms.

The story of Triassic reef development at first glance looks like a progression from microbial to sponge-algal to coral-sponge (metazoan-dominated) reefs. In reality, the global-environmental instability that peaked with the PTB continued, with relatively short pulses of reef blooms, setbacks, and episodes of diversification (Flügel 2002). Yet the importance of photosynthesis in reef construction was evident, both in the significant contributions of calcified algae and the emergence of zooxanthellate corals.

The end-Triassic mass extinction abruptly terminated reef-building assemblages. Estimates of the percentages of surviving taxa differ among published reports. For example, Wells (1957) estimated that ten scleractinian genera survived into the Jurassic, while Flügel (2002) suggested as few as 3 of 77 Triassic coral genera survived into the Jurassic, with only slightly higher survival in key reef-associated sponge genera. More recently, Lathuiliere and Marchal (2009) reported at least 20 surviving genera. Moreover, the causes of the extinction event are not well constrained, though ocean acidification associated with emplacement of the Central Atlantic Magmatic Province is a primary suspect (Martindale et al. 2012). As discussed earlier for the PTB, massive volcanic events can produce a cascade of detrimental environmental conditions. The lack of preservation potential associated with ocean acidification also can amplify the apparent abruptness of an extinction event.

Following extinctions at the end of the Triassic, Jurassic reef-building communities slowly reestablished, requiring about 8 Myr to produce significant buildups. The breakup of Pangea and associated acceleration of sea-floor spreading rates resulted in generally rising sea level, increasing atmospheric CO_2, and declining Mg/Ca ratios in seawater. Several evolutionary events, as well as environmental trends, emerged in the Jurassic that fully developed in the Cretaceous Period, with profound influence on global carbonate production and accumulation, and upon global carbon cycles. The appearance of calcareous nanoplankton including coccolithophorids in the Early Jurassic, and of the planktic foraminifers in the Middle Jurassic, provided the potential for carbonate production throughout the surface oceans and accumulation of pelagic carbonates in deep-sea settings (depending upon ocean chemistry). On the shallow shelves, large bivalve species proliferated as carbonate producers, and trapping carbonate muds produced by the neritic whiting factory. By the Cretaceous, bivalves dominated shelves and platforms, especially in tropical seas (Höfling and Scott 2002; Johnson et al. 2002).

Leinfelder et al. (2002) grouped Jurassic reefs into three basic types: coral, siliceous sponge, and pure microbolite, with coral-microbolite intergrades among the most prominent. These authors also noted that buildups produced largely by bivalves also were relatively common. The breakup of Pangea provided extensive "trailing-margin" continental shelves where mixed terrigenous and carbonate sedimentation was prevalent. Nutrients carried into the shelf environments by terrestrial runoff likely promoted plankton densities and accompanying whitings that favored filter-feeding sponge and bivalve assemblages over zooxanthellate corals (Leinfelder et al. 2002). Pomar and Hallock (2008) also noted that microbolite buildups were associated with excess organic matter, low oxygen, and sulfate reduction in outer shelf/slope settings.

The 80 Myr Cretaceous Period is characterized by widespread carbonate depositional systems, including reefs, platforms and pelagic carbonates. The term "Cretace" refers to chalk (pelagic-carbonate) terrains that are widespread in northern Europe (Harbaugh 1974). Two global "crises" resulted in extinctions and association changes that influenced both benthic and planktic biotas, one crisis in the mid-Early Cretaceous and the other in the early-Late Cretaceous (Höfling and Scott 2002).

The most important metazoans in Cretaceous buildups were the rudistid bivalves. There is little evidence that rudists had algal symbionts; the prevalence of carbonate muds in most rudist buildups indicates that water transparency may have been poor. Skelton et al. (1992) interpreted rudists as having been super bafflers, trapping huge quantities of mud and actually growing upward supported in mud. Characteristically, rudist thickets and buildups have relatively few species and few associated organisms. Banktop habitats occupied by rudist taxa may have been somewhat analogous to those of modern seagrass beds; rudist thickets trapped sediments carried in by the currents as well as sediments produced in situ by the breakdown and bioerosion of the rudists themselves. Because exceptional high-latitude warming occurred in the Cretaceous, the low latitude banktop habitats were consistently very warm and often hypersaline. The more biologically complex bivalves may have been better able to survive these extremes than zooxanthellate corals (Johnson et al. 2002), whose symbiotic relationship is particularly sensitive to temperatures above 30 °C (Wooldridge 2013).

Geochemical conditions also favored rudists over corals (Stanley and Hardie 1998; Pomar and Hallock 2008). The rudists secreted outer shells of calcite, with an inner layer and muscle insertion sites of aragonite (Skelton 1976). Proportions of aragonite to calcite varied in different lineages of rudists; some secreted shells were as much as 60 % aragonite, though many were less than 30 % (Kauffman and Johnson 1988; Skelton and Gili 2012). Whatever the proportions, the predominance of rudists over wholly aragonitic corals represented a decline in aragonite production associated with photosynthesis. Rapid sea-floor spreading enhanced removal of Mg^{2+} from seawater at mid-ocean ridges, thereby promoting calcite precipitation (Stanley and Hardie 1998). Volcanic emissions associated with rapid spreading rates also elevated CO_2 in the Cretaceous atmosphere, making aragonite more soluble and therefore less energetically advantageous to produce (Hallock 2011). As noted by Pomar and Hallock (2008), tropical environmental conditions during the Cretaceous favored biologically controlled metazoan calcification combined with neritic production of biologically-induced whiting-type calcitic muds. Photosynthetically-enhanced calcification by scleractinian corals with zooxanthellae was largely restricted to higher latitude and mesophotic (low-light, deeper) shelf margins.

2.9.4 Cretaceous Boundary Extinctions

A major biotic crisis ended the Cretaceous Period. While this mass extinction event is best known for the demise of the dinosaurs, rudist bivalves also became extinct (Johnson et al. 2002), as did most shallow-water, tropical carbonate-producing protists and animals (MacLeod and Keller 1996). Few calcareous tropical species survived the terminal Cretaceous extinction event.

During the Cretaceous many scleractinian corals occupied deeper shelf and upper slope environments, perhaps to escape warm, saline waters or direct competition with rudists (Johnson et al. 2002). As a result, at least nine genera (Rosen 1998) and possibly 26 genera (Fig. 13.9) survived the extinction. The terminal Cretaceous event was similar to those of the early Cambrian, late Ordovician, late Devonian, and late Permian in that reefs generally vanished a million years or more before the final extinction events (Copper 1994). Thus, episodes of environmental perturbation or climatic deterioration that caused collapse of reef ecosystems preceded the terminal extinction events, which geologists have used to define significant boundaries in geologic time.

Two major competing explanations for mass extinctions, including the Cretaceous-Paleogene (K-P) boundary extinctions, are bolide (meteor or comet) impacts and extensive volcanic episodes (Alvarez 2003). Because bolide impacts are instantaneous events, while extensive volcanism can take place over 100,000 to a million years or more, scientists with evidence for more gradual events at the Cretaceous/Paleogene boundary have tended to favor volcanism as the cause (Officer and Drake 1985). There is now conclusive evidence, including the Chixculub crater on the Yucatan Peninsula in Mexico, for a massive bolide impact at the K-P boundary (Alvarez 2003). However, there is also ample evidence for copious and rapid eruptive volcanic activity over a wide area in India prior to the K-P boundary (Bhattacharji et al. 1996). Most importantly, the mechanisms are not mutually exclusive as a cause of mass extinctions. On the contrary, if a bolide impact occurred during a period of environmental deterioration resulting from volcanism, already stressed ecosystems would more likely have been pushed to collapse.

Either bolide impact or massive, long-term eruption of flood basalts would have catastrophically impacted shallow-water, photosynthetic, carbonate-producing reef organisms. Either process would have profoundly influenced ocean chemistry in ways detrimental to $CaCO_3$ production. The energy of a meteor passing through the atmosphere would have oxidized nitrogen in the atmosphere, resulting in global acid rain that would have acidified shallow oceanic waters, dissolving $CaCO_3$. Volcanism emits large quantities of hydrogen sulfide (H_2S), which would have oxidized to sulfur dioxide (SO_2) and hydrated to sulfuric acid (H_2SO_4), resulting in global acid rain. Furthermore, the earthquake caused by a 10 km diameter bolide hitting the Earth could have eliminated all nutrient-depleted shallow-water environments worldwide, just by stirring the oceans (Hallock 1987). Deeper oceanic waters, where there is insufficient light for photosynthesis, are substantially richer in inorganic dissolved nitrogenous and phosphatic compounds that are needed by plants to photosynthesize, than most photic surface waters. These nutrient-rich waters represent approximately 98 % of the total ocean volume (Hallock et al. 1991). Such a tremendous shock would have generated tsunamis and internal waves, rapidly mixing deeper waters into shallow waters and stimulating red-tide-like blooms of a few, fast-growing species of phytoplankton (disaster species – Fischer and Arthur 1977; Copper 1994).

Whatever occurred, among the lessons to be learned from end-Cretaceous and other major extinction events are that the most prolific carbonate-producing protists and metazoans are particularly sensitive to environmental perturbations because they thrive within relatively narrow environmental limits. Waters in which they proliferate must be warm but not too warm, clear and well illuminated but with not too much biologically damaging ultraviolet radiation, nutrient-depleted, and highly supersaturated with respect to Ca^{2+} and HCO_3^-. Most reef-building organisms live at low latitudes on shelves and banks in the shallowest 100 m (330 ft), and thrive at depths less than 20 m (66 ft), in an ocean that averages 3,800 m (12,500 ft) in depth (Kennett 1982). Waters suitable for shallow-water reef development make up less than 1 % of the ocean volume under optimum conditions; suitable benthic habitat is far less. Thus, regional or global events that eliminate habitat for reef-building and reef-dwelling plants and animals can eliminate huge numbers of species and are recorded in the rock record as mass extinction events (Hallock 1987). Because reef species are often highly specialized to their environment, many specializations are lost in these events, while less specialized, more opportunistic species typically survive.

2.9.5 Cenozoic: Time of Recent Animal Life

Paleocene and Eocene shallow-water limestones tend to be dominated by the fossil remains of bryozoans, coralline algae, sponges, and foraminifers (Hallock et al. 1991; Copper 1994). High atmospheric CO_2 concentrations and greenhouse climate, which reached an apex during the Cretaceous, continued for another 20 Myr into the Cenozoic (Berner 2004). Diversification of coral assemblages occurred much earlier than extensive reef construction (Frost 1977). Pochon et al. (2006) postulated that *Symbiodinium* zooxanthellae in corals originated in Early Eocene, with subsequent episodes of divergence during times of global cooling. Nearly all the major circumtropical frame-building genera of scleractinian corals had evolved by the latest Eocene (Veron 2000). Thus, the Eocene, like the Cretaceous, was a time of diverse coral assemblages and widespread occurrences of carbonate-producing biotas with limited coral-reef construction. Frost (1977) suggested that the capacity to construct massive wave-resistant reef structures developed long before such structures were widely produced, suggesting geochemical control, as further discussed by Pomar and Hallock (2008).

Consistent with high atmospheric CO_2 concentrations and low Mg/Ca ratios in seawater (Stanley and Hardie 1998), prolific calcification by calcitic larger foraminifers and coralline red algae (e.g., Plaziat and Perrin 1992) recovered faster than comparable aragonite production by corals and calcareous green algae. The best known larger foraminiferal limestones are the Eocene Nummulitic Limestones of Egypt, from which the Pyramids were built. Shallow-water limestones of Eocene age that are rich in fossils of larger foraminifers are widespread in mid to low latitudes (Beavington-Penney and Racey 2004). Larger foraminiferal fossils can be found in Oregon, southern England and other localities as high as 51° N latitude

(Adams et al. 1991; Perrin 2002). Their complex shells, by analogy with modern larger foraminifers, appear to have been highly adapted to house algal symbionts. Shallow-water limestones dominated by coralline-red algal nodules were also common (Bryan 1991). Paleocene-Eocene limestones dominated by coralline algae or larger foraminifers are common hydrocarbon reservoirs where deeper in the subsurface and major aquifers where they are nearer the surface.

High-latitude cooling began in the middle Eocene, with widespread Antarctic glaciation at the Eocene-Oligocene boundary, which DeConto and Pollard (2003) attributed to declining atmospheric CO_2 concentrations. Reefal buildups were similar to those of the earlier Eocene both in relative scarcity and composition (Perrin 2002). As the Atlantic Basin expanded, the Caribbean province became more isolated from the Tethyan/Indo-Pacific realm. Based on morphologies, coral families were traditionally assumed to have arisen in the Indo-Pacific. However, Fukami et al. (2004), based on molecular genetics, showed that several Atlantic coral taxa are genetically distinct and represent endemic taxa. Those authors suggested that the divergence occurred near the Eocene-Oligocene boundary.

Coral communities flourished circumtropically beginning in the late Oligocene. By the early Miocene, reefs and reef-associated biotas worldwide had expanded their latitudinal distributions by more than 10° north and south (Adams et al. 1991), reaching their acme in the mid Miocene (Perrin 2002). The expansion in reef-building capacity corresponded to increasing Mg/Ca ratios in seawater (Stanley and Hardie 1998) and falling atmospheric CO_2 concentrations (Pearson and Palmer 2000), both of which promoted aragonite precipitation in warm, tropical waters.

Paradoxically, many coral and larger foraminiferal species were lost from Caribbean faunas at the end of the Oligocene, and many more became extinct during the Miocene (Edinger and Risk 1994). There were also extinctions of Indo-Pacific corals, but far fewer (Veron 2000). Closure of the Tethys Seaway further isolated the Atlantic/Caribbean reef biotas (Pomar and Hallock 2008). Progressive blockage of the Central American Seaway (Fig. 2.6) probably accounted for environmental changes that resulted in many Caribbean extinctions (Edinger and Risk 1994). Throughout the Paleogene, flow through the Central American seaway was bi-directional (Nisancioglu et al. 2003). Because the Atlantic has higher evaporation rates compared with rainfall rates than the Pacific, sea level in the Pacific is slightly higher than in the Atlantic. As a consequence, when the Central America seaway was open, water had to flow from the eastern Pacific into the Caribbean (Haug et al. 2001). However, the easterly trade winds forced surface waters to flow westward from the Caribbean to the eastern Pacific. As long as the Central American passageway was wide and deep, two-way flow was accommodated by westward surface flow and eastward subsurface flow, probably at depths in excess of 50–100 m (Maier-Reimer et al. 1990). However, as the Isthmus emerged, flow was constricted and surface flow likely reversed during calm weather. As a consequence, nutrient-laden eastern tropical Pacific waters were more frequently and consistently introduced into Caribbean surface waters.

Edinger and Risk (1994) observed that shelf-edge and slope-dwelling coral genera were nearly eliminated in the Atlantic in the early Miocene. The corals that survived were mostly banktop species capable of tolerating higher nutrients and higher sedimentation rates, as well as higher bioerosion rates (e.g., Hallock 1988). Larger foraminifers revealed the same trends. Slope-dwelling taxa were nearly eliminated, while shallower-dwelling taxa of bank tops and restricted environments thrived (Hallock and Peebles 1993). Other banktop biota, including octocorals and calcareous algae, became more important components of the Caribbean benthos than on comparable Pacific reefs.

Since the middle Miocene, there has been progressive high-latitude cooling, compression of tropical habitats, and increasing temperature gradients between high and low latitudes (Lear et al. 2003). Pochon et al. (2006) noted that the majority of extant *Symbiodinium* lineages have diversified since Middle Miocene. Some global cooling likely benefited the coral-*Symbiodinium* symbiosis, which is sensitive to high light under elevated temperatures (Wooldrige 2013). Pomar and Hallock (2008) further postulated that Neogene cooling supported the co-evolution of zooxanthellate corals and coralline algae into shallow, high-energy waters, where their carbonate production potential is highest.

2.10 Pleistocene and Holocene Reefs

Northern hemisphere climatic deterioration accelerated ~2.6 Ma with the onset of the Pleistocene Epoch (Fig. 2.1). The climatic fluctuations strongly influenced tropical reef-associated biotas in a variety of ways. Some taxa became extinct. Others, like the fast-growing *Acropora* and *Montipora*, diversified and now account for ~25 % of modern Indo-Pacific coral species (Veron 2000). Successive isolation and mixing of populations, which typically accompanies fluctuations in sea level, have long been recognized as mechanisms promoting evolutionary diversifications (Hallam 1985). Veron (2000) further proposed the process of reticulate evolution whereby populations were separated by changes in sea level and surface currents, and when reconnected, allopatric speciation had occurred, but some closely related taxa then hybridized, increasing the genetic diversity of resultant reconnected taxa. Pleistocene glacial advances and retreats induced such successive isolation and mixing events, which likely contributed to the very high extant species diversities of *Acropora* and *Montipora*.

A fascinating paradox of limestones and climate is that active reef building and coral evolution occurred during the Pleistocene, despite high-latitude climatic deterioration that resulted in as many as 21 glacial advances and retreats (Delmas 1992). Sea-level fluctuations of as much as 140 m (450 ft), caused by repeated accumulation and melting of Northern Hemisphere and Antarctic continental glaciers, accompanied cyclic reduction and expansion in the areas of warm, tropical seas. The solution to this paradox may be that tropical climatic, geochemical, and topographic conditions during interglacials were nearly optimal for reef-building. Atmospheric CO_2 concentrations were relatively low (though not as low as during glacial advances) and subtropical/tropical sea surface temperatures were nearly ideal. Both factors promoted aragonite calcification by corals and calcareous green algae, which in turn enhanced their rates of photosynthesis and biological productivity.

Times of rising sea level are also favorable for reef building, providing space for accumulation of substantial thicknesses of reef limestone, which have high probability of preservation in the rock record. Except for active tectonic areas, most shallow shelves on trailing continental margins subside at rates of a few centimeters per 1,000 years (Schlager 1981). In contrast, the most actively accreting portion of a reef system can grow upward at rates of at least 4 m/1,000 years, and under exceptional conditions as much as 20 m/1,000 years (Hubbard, this volume). But reefs most rapidly accrete when growing in water depths of less than 20 m, where there is plenty of sunlight for photosynthesis. The only circumstances in which reefs can accrete upward at high rates for more than about 5,000 years, and produce more than 20–30 m thicknesses of limestone, are if the shelf rapidly subsides or sea-level rises. Thus, during times of interglacial sea-level rise, the margins of continental shelves, limestone banks, and volcanic islands provided ideal locations for thick sequences of reef-associated limestones to accumulate (Pomar 2001).

2.11 Conclusions

The history of reefs is like a fascinating and ongoing novel, full of paradoxes and unexpected feedback mechanisms. One of the most difficult concepts to understand is that limestones are both storehouses and sources of CO_2, depending upon the times scale being considered. Through geologic time, limestones have stored CO_2 and are therefore responsible for a livable planet. Yet on the shorter time scales of glacial cycles, interglacial reef building may move as much as 100 ppm of HCO_3^- from the bicarbonate pool in the oceans to CO_2 in the atmosphere. Erosion of young, predominantly aragonitic-coral limestones and sediments occurs when sea level falls, sequestering CO_2 from the atmosphere to HCO_3^- in the oceans. On human time scales, reefs are relatively minor players in the CO_2 story. Fossil fuels, like ancient limestones, represent long-term storage of CO_2 in the Earth's crust. Human activities, especially the burning of fossil fuels, have added more CO_2 to the atmosphere in 100 years than reef building did in 15,000 years.

The major lesson to be learned from the history of reefs is that they are constructed by complex and specialized biological communities. Because these systems are highly adapted to a limited range of environmental conditions, they are extremely sensitive to local, regional and global environmental perturbations. Environmental crises, culminating in global mass-extinction events, have repeatedly caused the demise of whole communities of reef-building organisms and the myriad of organisms that depended upon reef structures for habitat. Subsequent recovery of reef-building communities required millions of years.

Some individuals argue that humans are simply part of nature; that exploding human populations are naturally generating the present episode of mass extinction from which the Earth will recover in 10 or 20 million years. But from a human perspective there is a difference between a mass extinction event caused by a meteor impact and the ongoing one being caused by human activities. Human intelligence has reduced biological limitations on both the growth rate of human populations and the environmental damage that any individual human can cause. Is it too much to hope that human intelligence can be utilized to bring an end to the current human-generated mass-extinction event before the most specialized and diverse biological communities, like coral reefs and rain forests, are lost to future human generations? A few human cultures, notably Micronesian inhabitants of atolls and coral pinnacles, are known to have developed sustainable societies in resource-limited habitats. Can "modern" humans develop a sustainable global society based on recognition of globally-limited resources? Or do humans simply represent another of the "disaster" species that proliferate globally at mass-extinction events; in this case, the Anthropocene Mass Extinction?

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Reef Biology and Geology – Not Just a Matter of Scale

3

Dennis K. Hubbard

Nature is what nature is. . ... science is what we think nature is on a given day.

(A. Conrad Neumann)

Abstract

The geological distribution and developmental history of coral reefs have been largely controlled by physical factors such as plate tectonics, sea-level changes, wave energy, salinity, light, temperature, nutrients, sediment, and antecedent topography. Although the geological and biological patterns have generally been consistent over the past 12,000 years, sub-millennial intervals of variation remind us that long-term patterns provide only part of the picture. Looking forward, changes in seawater temperature, storm intensity, aragonite saturation state and pH may bring a major shift in the balance between carbonate production, destruction and export. While rising sea level alone will probably not significantly change reef communities or over-top low reef islands, even small increases of water depth will have disproportionate effects on the wave energy passing over the reef crest. Moreover, the impacts of increasing storminess will rival declining coral cover as a major control over the carbonate budget of coral reefs in the coming century. Understanding what is to come will require a perspective that is impossible from any single discipline.

Keywords

Carbonate budget • Development • Holocene • Accretion • Zonation

3.1 Introduction

By the 1990s, the decline of "reef health" was already a focal point in both the popular and scientific literature. Outbreaks of the crown-of-thorns seastar *Acanthaster planci* had devastated large sections of the northern Great Barrier Reef (Endean 1973; Moran 1986). In the Caribbean, overfishing (McClanahan and Shafir 1990), followed by the sudden and still largely unexplained population crash of the long-spined sea urchin *Diadema antillarum* (Lessios et al. 1984) resulted in a shift from reefs dominated by corals to those on which macroalgae were the principal component (Hughes 1994; Jackson et al. 2014). In the years immediately following its original description (Gladfelter 1982), White Band Disease (WBD) had been largely ignored. However, the subsequent decimation of the *Acropora palmata* community throughout the Caribbean and western Atlantic by WBD (Aronson and Precht 2001b) put it at the center of the debate on community stability and its relationship to reef development. Harvell et al. (1999) described a host of new diseases and the list continues to grow. A scientific focus on increasing coral bleaching and disease triggered U.S. congressional hearings in 1992 and a greater popular awareness of the declining state of the world's coral reefs.

None of these issues have gone away since "Life and Death in Coral Reefs" first appeared in 1997. Overall reef decline continues (Gardner et al. 2003; Hughes et al. 2003;

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Carpenter et al. 2008; Burke et al. 2011; De'ath et al. 2012). In the Caribbean, White Band Disease has been joined by others that have attacked the genus *Orbicella* in particular (Bruckner and Hill 2009). While the region is home to only 8 % of the world's coral reefs, it has been the focus of over half of the world's disease reports (Harvell et al. 2004). Looking ahead, we anticipate increased pressure by combined bleaching and disease (Miller et al. 2009), lower pH (Zeebe and Wolf-Gladrow 2001; Hoegh-Guldberg et al. 2007), accelerating sea-level rise (Church and White 2011) and increasing storm intensity (Webster et al. 2005).

Reef decline is nothing new, not historically and certainly not geologically. Caribbean coral diversity has been declining for at least the past 30 million years in response to a gradual restriction of what was once a great circum-equatorial Tethys Sea some 200 million years ago (Frost 1977). The final door was slammed shut on Atlantic-Pacific larval exchange with the formation of the Isthmus of Panama over the past few million years (Murdock et al. 1997; Vermeij 1978, 1993). More recently, *Homo sapiens* has exerted ever-greater control on reef development as population has increased and, with it, human exploitation of critical habitats and resources in tropical coastal areas. Changes in tropical wetness over the past 12,000 years (Hodell et al. 1991; Thompson et al. 1995; Gasse 2000) have facilitated an agrarian society and the more intense resource utilization that accompanies it. Jackson (1997) proposed that the reefs we all consider "pristine" in our recent discussions had already suffered significant decline long before ecologists started looking carefully at coral reefs, and certainly before serious monitoring efforts began.

In the 1980s the emphasis was more on site-specific and seemingly isolated decline related to nearby centers of human exploitation. Gradients of increased impact in the direction of cities, coastal development projects or other intensive anthropogenic activities drove research toward understanding the links between stress and coral decline on the scale of single reefs. Management strategies were largely focused on identifying problems that could be tied to a specific cause and then mediating that perceived source of stress by legal regulation. Inherent in this strategy was the pragmatic concept of establishing thresholds below which development could continue with "acceptable" levels of local decline.

More recent changes in how we think about reef decline have been driven by a growing awareness of the interconnectedness of global systems. It has become increasingly apparent that changes on "our" reef may be as much a result of distant forces as those we can measure locally. As our focus shifts more toward global controls, factors like intensification of atmospheric instability due to rising global temperatures, faster sea-level rise, and the potential for facilitating pathogenic stressors have expanded. As a result, our management perspective has broadened to include factors that are not specific to a single reef or even a single region. With this redirection has come a heightened awareness that we need to think about coral reefs at a variety of spatial and temporal scales: from genetic shifts at the cellular level to the response to pollution at the organism level and vertical accretion across entire reefs – all in light of recent climatic shifts occurring at local, regional and even global scales. Equally important is temporal scale – from the duration of individual studies where processes can be observed and measured up through time spans greater than the lives of individual researchers or even the disciplines of ecology or geology.

3.2 The Importance of Perspective

This chapter considers the processes that control the "look" of modern coral reefs and their fossil forebears. The scale on which these processes occur is discussed along with the varying perspectives of researchers from different disciplines. Biologists have the advantage of being able to directly observe and measure changes in both processes and the organisms that they control. The accuracy of their characterizations is limited only by their originality and the sensitivity of the methods and instruments that they use. However, this ability to directly observe comes at a price. The intensity and resulting costs associated with such detailed measurements make it difficult to conduct studies over larger areas. As a result, "typical" areas are often described as proxies for much larger pieces of real estate. Also, the lifetime of individual researchers and the short attention span of funding agencies severely limit the temporal perspective of even the best site-specific investigations. Mapping provides a detailed snapshot of what a reef looks like, the myriad interactions on that landscape and the processes that mediate either change or stability. Monitoring records provide a short "newsreel" of change over a funding cycle or, at best, the career of an individual researcher. Most recently the "headlines" have focused on decline. What is missing is the context of the longer-term record within which these brief events have occurred. To illustrate this one need only consider that the duration of a National Science Foundation Long-Term Ecological Monitoring program is typically a few decades at best.

In contrast, geologists must deal with a fickle record that has been ravaged by **taphonomy** (the selective and taxonomically biased preservation of different organisms in different physical settings), **diagenesis** (the chemical changes that obliterate or obscure details after burial) and **erosion** (the wholesale removal of entire, and often extensive intervals of time). What is left are the tattered remains of a full-length motion picture with pieces of film marred by countless splices, seemingly endless scratches that obscure fine detail, and even changes in the starring actors midway through the film. Evolutionary changes make comparison with modern scleractinians difficult at best, and the blurring of the record by unknown physical and chemical forces since original deposition only make things worse. The perspective of great space and time offers countless advantages over shorter-term studies. What is often missing, however, are the details that characterize modern biological investigation.

The challenge is to take the best of both and combine that into an integrated view that gives us our best chance of accurately separating natural from anthropogenic change. What can we take from modern biological studies to help us understand the distant past and the vagaries of reef evolution? What can we learn from the longer but poorer geologic record that might help us to put the recent decline revealed by monitoring studies into a longer-term natural context? While fraught with peril, this integrated approach should be the holy grail of management. However difficult the task, effectively integrating and comparing geological and biological data is what presently stands between effective management strategy and the misdirection of already limited environmental capital to things that are either beyond our control or “aren’t really broken”.

The initial version of this chapter that appeared in 1997 focused primarily on scale as a way to explain how biologists and geologists see reefs differently. While that is still a central theme, challenges related to climate change have added different dimensions that cannot be explained by simple scaling. Even biologists are thinking more about larger-scale carbonate cycling as carbonate producers are being lost, ocean chemistry has made it more difficult to maintain a skeleton and changing nutrient regimes are fundamentally changing the balance between carbonate producers and organisms that destroy substrate. However, this view still remains fundamentally biological in nature.

It is becoming increasingly obvious that physical factors are playing an expanding role that cannot be adequately addressed by even the best short-term study that focuses solely on biotic interactions. The contributions of diversity to the complex structure that we call a reef come full circle when we recognize that this heterogeneity, in turn, controls the organisms that it can support. Bioerosion is flattening reefs, changing both their physical and biological structures. The fate of bioeroded sediment within the system is changing drastically as larger storms appear to be more commonplace. Thus, the shift toward greater physical control may suggest that our different perspectives of “change” are more than just looking at the same suite of biologically dominated processes through different lenses. The fate of low-lying islands will be defined as much by physical factors like sediment transport, the increasing loss of protection by lagging reefs and the greater loss of detritus as storms become more violent as it will be by declining abundance and diversity.

This chapter is divided into three parts. The first outlines the dominant factors controlling the location and character of coral reefs today and, by extension, in the geologic record. Having established these basic controls, we will turn briefly to how corals have built the massive structures beneath them. Finally, we attempt to integrate all this information into a consideration of reefs under the influence of global change. For obvious reasons, the latter will carry an admittedly geologic bias, in large part due to the training of the author. However, it is also somewhat purposeful inasmuch as the biological perspective has historically dominated the discussion of reef decline. The greatest possibility for a new contribution to the dialog would, therefore, perhaps lie outside that area.

3.3 Processes That Control Reef Development

The following pages discuss the factors that are generally thought to be critical in determining where reefs occur today and what they look like. To facilitate the presentation, these have been broken down into three groups, based on the scale at which they are most important. However, some can operate at different scales and boundaries often overlap. Macro-scale processes are those that exert control either globally or over very large distances (i.e., thousands of kilometers) and over longer periods of time. Primary among these are worldwide changes in sea level and large-scale movements of the Earth’s crust. Meso-scale processes are generally physical-oceanographic in nature and operate within individual oceans or basins (e.g., latitudinal changes in mean water temperature, variations in wave energy across an ocean basin) and over historical time scales. Micro-scale processes are those that affect organisms at the spatial scale of individual reefs and over a time scale from individual studies to the career of a researcher. Purposefully absent from this discussion, although no less important, are even shorter-term (e.g., minutes to days), organism-level processes that are detailed in other chapters within this volume. The miniscule attention span of politicians is below the threshold of this discussion.

3.3.1 Macro-scale Controls

3.3.1.1 Tectonics

Our earliest reef studies focused on the role of major crustal shifts in preserving fossil reefs. Workers in the Italian Alps and elsewhere during the nineteenth and early twentieth centuries (e.g., Darwin 1842, 1913; Mojsisovics 1879) concluded that great upheavals of the Earth’s surface must have been responsible for fossil reefs that occurred so far

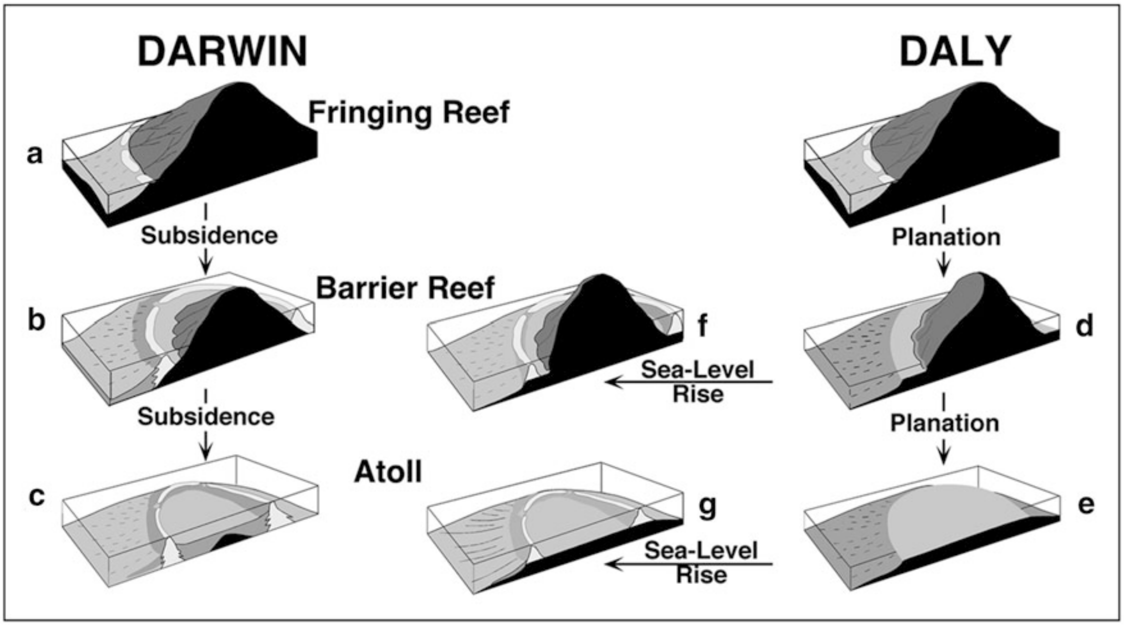


Fig. 3.1 Two theories on the origin of fringing reefs, barrier reefs and atolls. Darwin felt that the spatial patterns he observed from the H.M.S. Beagle reflected an evolutionary sequence. As a volcano subsides, the reef accretes vertically to stay near sea level and the fringing reef (**a**) evolves into a barrier reef (**b**) and, eventually, an atoll (**c**). In contrast, Daly (*right*) envisioned changing sea level as the sole determinant of reef character. During a lowstand, waves plane off a platform (**d**, **e**). During the ensuing sea-level rise, reefs form near the edge of the new shelf. Whether a barrier reef (**f**) or an atoll (**g**) will form depends on the extent of the island's removal. Deep cores through Eniwetak and Bikini Atolls eventually vindicated Darwin's hypothesis

above sea level. It was already known that, while modern shallow-water corals do not generally exist at depths greater than 100 m, many fossil reefs attained a thickness of hundreds or even thousands of meters. It was correctly posited that this reflected the upward building of the reef by organisms within the photic zone as the foundation beneath them sank gradually – the process of **subsidence** (Darwin 1842).

Throughout the 1800s, the geological community debated over how subsidence related to reef development. In 1832, Charles Lyell suggested that modern atolls might be thin calcareous crusts atop submerged crater rims with upward coral growth offsetting subsidence:

> . . . we might imagine, that if Java and Sumatra were submerged, they would give rise to a somewhat similar shape in the bottom of the sea; for the volcanos of those islands observe a linear direction, and are often separated from each other by intervals, corresponding to the atolls of the Maldivas; and, they might leave an unfathomable ocean in the intermediate spaces. p. 286

Lyell's early discussion of the continuum of process through geological time had a profound influence on a young Charles Darwin. Based on observations in Pacific and Indian Ocean atolls, Darwin (1842) similarly argued that the worldwide distribution of reefs could be explained by underlying geologic processes. He proposed that fringing reefs, barrier reefs, and atolls represented an evolutionary continuum from the former to the latter (Fig. 3.1). Like Lyell, he envisioned a volcanic island slowly sinking, but did not tie reef building to the crater rim; atolls formed only after full submergence of the volcanic cone, but fringing and barrier reefs formed as soon as volcanic processes abated to the point where reef building could begin.

In Darwin's model, **fringing reefs** initially built on the volcano slope – close to shore, owing to the steep flanks of the underlying cone (Fig. 3.1a). As the volcano sank, the reef close to shore built vertically into the growing **accommodation space**. As the island progressively disappeared and the reef built vertically, the expanse of water between the reef and shore grew wider and deeper; the reef would thus evolve into a **barrier reef** separated from the island by a broad lagoon (Fig. 3.1b) and eventually an **atoll** with no central island at all (Fig. 3.1c).

As evidence, Darwin cited a gradual shift in island/reef morphology from high volcanic peaks fringed by reefs at one end of an archipelago to barrier reefs and lower islands in the central reaches and finally to atolls at the other end. These ideas were published in "The Structure and Distribution of Coral Reefs" in 1842, 17 years before his better-known "The Origin of Species". Darwin's proposal that systematic spatial change was a proxy for temporal progression was a brilliant one but, without an underlying mechanism to drive the phenomenon, his ideas were not widely accepted until deep cores through Enewetak and Bikini atolls more than a century hence revealed the sunken volcanoes underpinning those reefs and Darwin's theory (Ladd and Schlanger 1960).

The relatively recent recognition of plate tectonics has provided a unifying theory to help explain the large-scale distribution of reefs on a global scale. The constant motion of giant fragments of oceanic and continental crust creates dynamic zones of seafloor spreading and crustal collision. Although the rates of movement that are involved will never affect transoceanic airfares, predictable patterns of uplift, subsidence, or stability have emerged as important, long-term controls of reef development. While his ideas about subsidence as a universal control of reef type were flawed, the works of Darwin and his contemporaries still provide many of the fundamental truths about reefs that are at the foundation of reef science today.

3.3.1.2 Sea Level

Periodic changes in the spatial relationship between Earth and the Sun have resulted in predictable and recurring changes in global climate (Milankovitch 1930) and, therefore, sea-level rise and fall. Changes in Earth's tilt and wobble, the shape of its orbit and the proximity of the planet to the sun during northern summer and winter all affect changes in the global heat budget. In warmer times, the ocean expands, freshwater is added from melting terrestrial glaciers, and sea level rises. During cooler periods, water contracts, continental glaciers grow larger and sea level falls. Climate-driven fluctuations in sea level have occurred throughout geological time, but appear to have become more pronounced after the breakup of the single supercontinent, Pangaea, 250–200 million years ago. The 40,000 and ca. 100,000-year glacial cycles predicted by Milankovitch have now been confirmed by isotopic data (e.g., Emiliani 1966) and have increased in their importance since the onset of icehouse conditions in the mid-Pleistocene.

With each waxing and waning of sea level, reefs that lived near the upper limit of each cycle have been alternately flooded and exposed. The result is a series of reefs, each built upon the remains of its predecessor, much like ancient cities stacked one upon another as favorable trade conditions remained constant each time territory was abandoned and then resettled. Present-day reefs, which have formed over the past 10,000–12,000 years, are simply the latest participants in this cycle of colonization and abandonment and sit atop their Pleistocene forebears.

In 1915, Reginald Daly proposed an alternative to Darwin's subsidence theory. It involved the formation of a wave-cut bench during each drop in sea level, followed by a subsequent sea-level rise and reef colonization on top of the resulting terrace (Fig. 3.1d–g). This idea was born from his observations that the depths of lagoons he examined tended to be similar. He argued that this reflected wave-cut platforms at similar depths from site to site, and proposed that the only plausible mechanism to explain this was a worldwide drop in sea level. The main blow to Daly's ideas came when Davis (1923) pointed out the lack of cliffed shorelines that should be commonplace behind the barrier reefs of Pacific islands were Daly's hypothesis correct. Without these logical remnants of the wave-planation process, the sea-level hypothesis of Daly became untenable.

As is often the case in great debates, the truth lay in the middle and involves both sea level and tectonics, although not in the precise ways envisioned by either Daly or Darwin. The rise and fall of sea level sets a global tempo for highstand reef exposure during lows and reoccupation during highs. Equally important, however, are the interactions with local tectonic motions that exert a complex control over the long-term development of reef communities as well as the character and history of the structures that they build. By identifying the patterns common to depositional sequences from many different ocean basins, seismic stratigraphy has been used to construct records of worldwide sea-level change through time (Vail et al. 1977; Haq et al. 1987). The commonality of these patterns from site to site argues for a global control (i.e., glacial eustasy). However, careful analyses of variations from this pattern at some sites have allowed us to understand the superimposed effects of local tectonics on global changes in sea level. The term **relative sea-level change** refers to variations in sea level at any one locality resulting from the combined effect of glacio-eustatic sea-level rise and fall (that related to changing climate) and local or regional tectonic motions.

3.3.1.3 Reef Accretion Under the Influence of Relative Sea-Level Change

Each time sea level rises over the edge of a tropical carbonate platform, reefs will usually form. The site of colonization will be dictated by factors discussed later in this chapter, but is often atop the previous generation of reefs. The fate of the reef will depend on the rate of relative sea-level rise compared to the rate of calcium carbonate production on the reef (Fig. 3.2). Under conditions of near balance, the carbonate produced in the reef just offsets sea-level rise, and reef accretion is vertical. In areas where sea level is rising slowly compared to the rate of carbonate production, the excess material will cause the reef to expand laterally. In the Caribbean, sea level has gradually slowed since ca. 7,000 calibrated years before present and the forereef is steep. This has resulted in seaward progradation (e.g., Buck Island in the U.S. Virgin Islands: Fig. 3.3). In many Indo-Pacific sites and along the Great Barrier Reef, sea level reached its maximum 6–8,000 years ago and little or no accommodation space was created after that. These reefs have been sites of ever-widening reef flats. When carbonate production cannot keep pace with rising sea level, the reef will either i) retreat

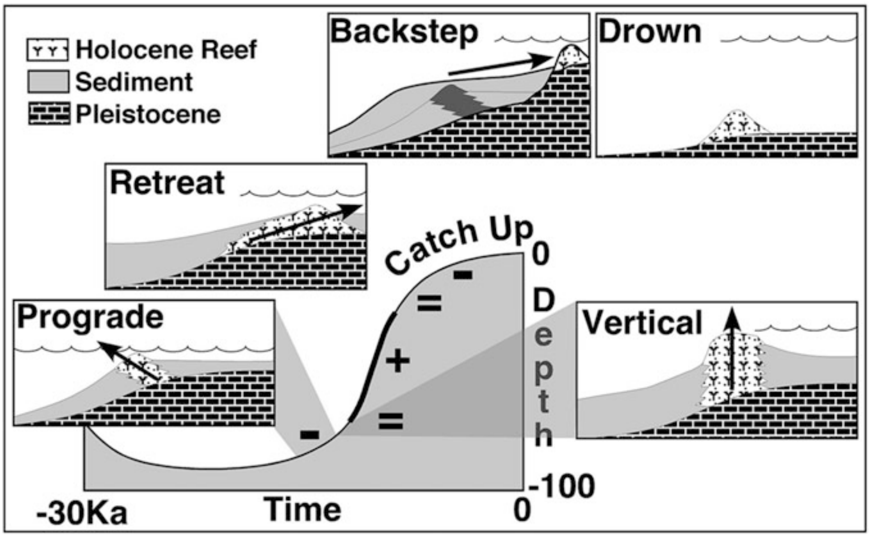
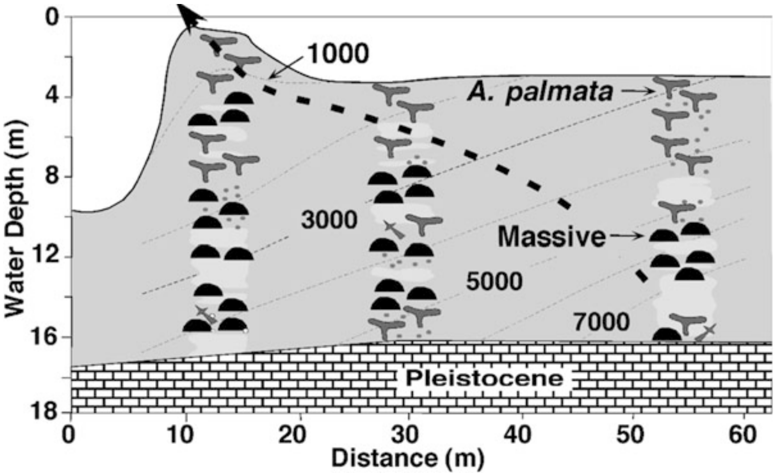


Fig. 3.2 Sea-level rise vs. reef accretion. The simplified sea-level curve represents a 100-m change in sea level over ca. 30,000 years. When sea level is rising slowly relative to the reef's ability to produce carbonate (−) the reef will prograde as it builds upward. A near balance between the accommodation space created by rising sea level and carbonate being produced by the reef (=) will result in vertical accretion. As rising sea level outpaces production (+, shown by *thicker line*), the reef will either retreat upslope (e.g., the Dominican Republic), backstep to higher ground (e.g., Puerto Rico) or "drown", depending on the severity and duration of the inequity. As sea level starts to slow down near the *top* of the curve, any reefs still within the photic zone will gradually "catch up". A drop in sea level will expose the reef until the ocean floods it again during the next glacio-eustatic cycle (After Hubbard 2011)

Fig. 3.3 Cross section through Buck Island reef. The upward transition from massive to branching corals and the sloping isochrons reflect both upward and seaward reef building (*arrow*) as carbonate production exceeded the space created by sea-level rise (After Hubbard et al. 2005)



upslope, ii) backstep to a landward and shallower site that is conducive to reef initiation (Blanchon 2011), or iii) drown. Hubbard et al. (1997) documented backstepping of Holocene reefs off Puerto Rico (Fig. 3.4) and showed a similarity of pattern and scale with Devonian examples from Australia (Playford 1980) and Canada (Viau 1988).

In 1985, Neumann and Macintyre proposed a tripartite classification for Holocene reefs viewed in cores or outcrop; reefs are inclined to either "keep up," "catch up," or "give up" (Fig. 3.5). "Keep-up" reefs were able to maintain their crests at or near sea level throughout their history. As such, the preserved corals (or other carbonate producers) exhibit growth forms typically found in shallow water (e.g., branching acroporids in the Caribbean). "Catch-up" reefs started in deeper water (ca. 10–20 m) but later caught up, usually after the rate of sea-level rise slowed. Such reefs are characterized by a lower (older) section dominated by deeper-water organisms that are overlain by younger biota formed in progressively shallower water as the reef "caught up." "Give-up" reefs are those that, for whatever reason, could not keep pace with sea level and simply stopped accreting.

A common misconception in the older literature is that reef building rates of 10–15 mm/year are commonplace. As

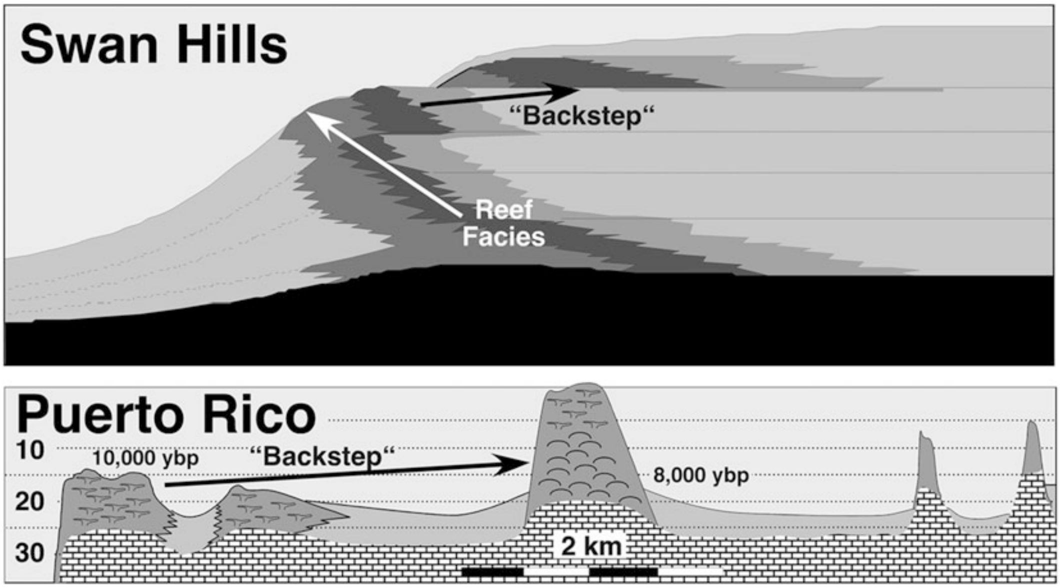
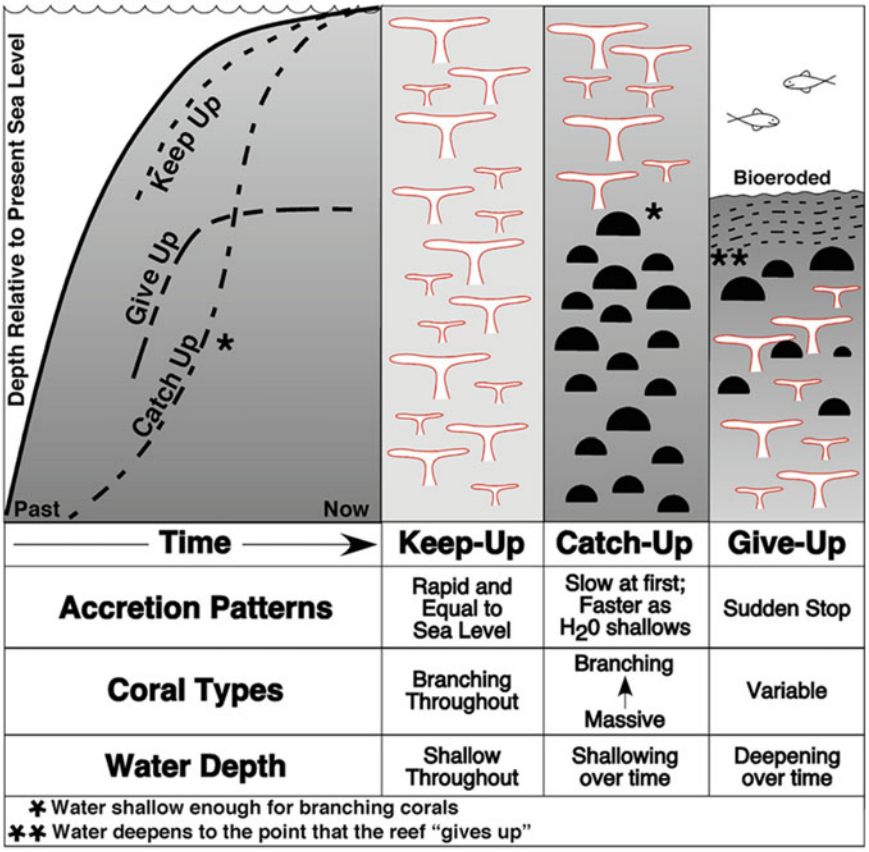


Fig. 3.4 Backstepping in Devonian reefs of Canada (*upper*) and Holocene reefs off Puerto Rico (*lower* – plotted at the same scale) (After Viau 1988). The Devonian reefs initially built up and out (like Buck Island: Fig. 3.3), but suddenly backstepped landward i.e., moved right) as sea level presumably sped up. Off Puerto Rico, shelf-edge reefs dominated by branching corals "gave up" as massive-coral reefs formed further landward. Note the similarity in reef thickness and the scale of backstepping in the two examples (After Hubbard et al. 1997)



Time →	Keep-Up	Catch-Up	Give-Up
Accretion Patterns	Rapid and Equal to Sea Level	Slow at first; Faster as $H_2$0 shallows	Sudden Stop
Coral Types	Branching Throughout	Branching ↑ Massive	Variable
Water Depth	Shallow Throughout	Shallowing over time	Deepening over time

* Water shallow enough for branching corals
** Water deepens to the point that the reef "gives up"

Fig. 3.5 Reef sequences as indicators of sea-level rise. A "keep-up" reef is capable of matching the rate of sea-level rise and will be comprised almost exclusively of shallow-water corals. "Catch-up" reefs generally started in deeper water e.g., massive corals) and gradually built closer to sea level (branching corals), usually after sea level slowed. "Give-up" reefs can be highly variable because their character will reflect the conditions before they gave up as well as those responsible for their demise. Reefs will generally give up if: (**a**) sea level is rising too fast, or (**b**) something compromises the ability of the reefs to keep up (After Neumann and Macintyre 1985) such, “give-up” reefs would predominantly reflect sudden jumps of sea level, e.g., the meltwater pulses of Fairbanks (1989) or dramatic declines in water quality (Adey et al. 1977; Schlager 1981; Blanchon 2011). However, more recent summaries of reef-accretion (Davies and Hopley 1983; Montaggioni 2005; Dullo 2005; Hubbard 2014) show that Holocene reefs built at rates closer to 3–4 mm/year and that rates above 10 mm/year are rare. Thus sea-level rise exceeded the accretionary capacity of most reefs throughout all but the latest Holocene, and drowning was as much “business as usual” as a reflection of extreme events as had been widely presumed.

This realization has important implications for our models of reef-building in response to sea-level rise in the twenty-first century. Coral reefs may soon be incapable of keeping pace with rising sea level, due to both accelerating sea-level rise (Grauss and Macintyre 1998; Church and White 2011) and perhaps slower rates of calcification in response to elevated CO_2 (Kleypass et al. 1999). This is not to say that they will soon be drowned or even that community structure will be significantly altered owing to greater water depth alone. However, even small increases in water depth over the reef crest can have disproportionate effects on wave energy passing over the reef and striking the shoreline behind it (Ogston and Field 2010). Combined with “flatter” reefs (Alvarez-Filip et al. 2009) that will provide less frictional attenuation of incoming waves and a higher frequency of intense tropical storms and hurricanes (Webster et al. 2005), this could increase beach erosion, accelerate ground-water salinization and generally render low-lying islands uninhabitable long before waves actually overtop their higher elevations (Hubbard et al. 2014).

3.3.2 Meso-scale Controls

3.3.2.1 Temperature

Coral reefs are generally restricted to water between 18° and 36 °C, with an optimal range of 26–28 °C. Today, this generally restricts coral reefs to latitudes between 20° and 25° north and south (Fig. 3.6). Exceptions do occur however. Abundant but low-diversity coral cover exists around Easter Island despite temperatures below 18 °C and a position at 27° S (Hubbard and Garcia 2003).

Within the normal range, certain corals will grow faster or slower, depending on temperature (Weber and White 1974; Glynn and Stewart 1973). Drastic thermal shifts can result in reduced coral vitality (e.g. bleaching, reproductive inhibition) or, in extreme instances, total destruction of entire reef systems. Glynn (1984) emphasized the importance of unusually high water temperatures in the widespread mortality of corals along the western coast of Panama. It is now generally accepted that recent episodes of coral bleaching, where corals expel their zooxanthellae (Chap. 5), are related to higher-than-normal maximum temperatures over the past several decades. At the other end of the scale, Walker et al. (1982) proposed that well-developed massive-coral communities in the northern Florida Keys were limited to areas shielded from the periodic influx of cold water pushed out from Florida Bay during the passage of major cold fronts.

It is important to note that most corals exist near their upper thermal limits. Therefore, even a slight increase in tropical temperatures in the future could have significant impact on the distribution of corals in the tropics. It is also important to realize that bleaching need not be related to an

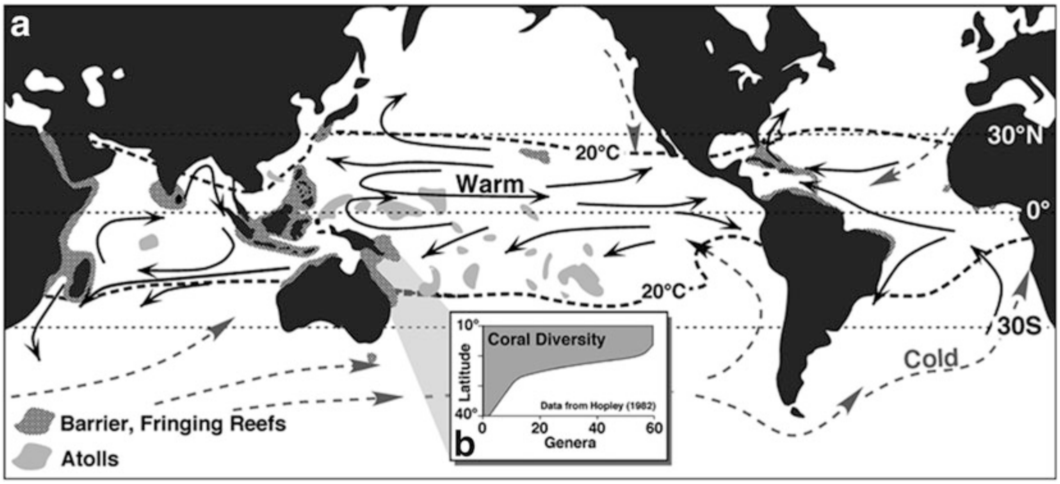


Fig. 3.6 **a** Worldwide distribution of reefs. Reefs are confined to areas bathed by warm currents (>20 °C). Reef locations are from Darwin (1842). (**b** – *inset*) Latitudinal variation in species diversity along the Great Barrier Reef. Note the increase in the number of genera toward the equator

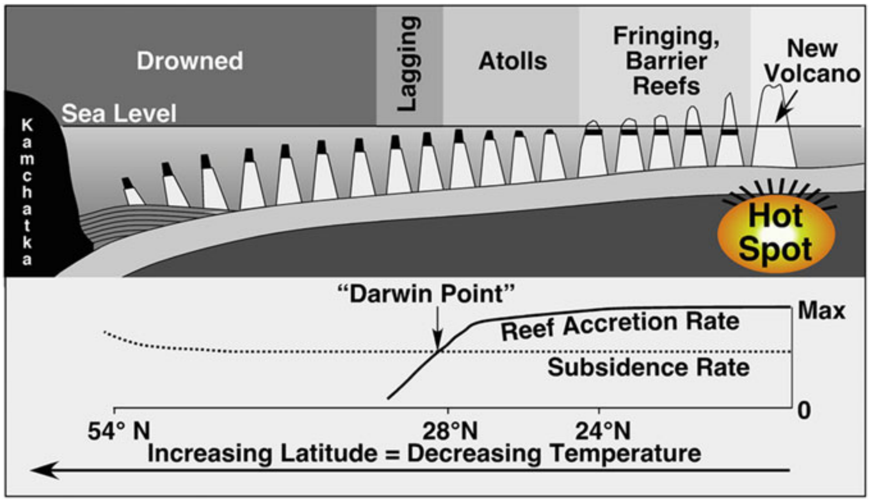


Fig. 3.7 The combined effects of subsidence and temperature on reef development in the Hawaiian Archipelago. As the Pacific crust beneath the Hawaiian islands moves to the northwest, it cools and subsides. South of roughly 29°N, the reefs can produce carbonate at a rate fast enough to offset subsidence. North of this, however, cooler water inhibits coral growth to the point that the reefs can no longer keep up. As a result, they are gradually drowned (After Grigg 1982)

absolute threshold above which corals will succumb. Many western Pacific corals (e.g., Indonesia) regularly experience temperatures that would induce bleaching in the Caribbean Sea. Conversely, scleractineans in the cold waters off Easter Island bleached at temperatures well below what is normal in the Caribbean (Wellington et al. 2000; Hubbard and Garcia 2003). If there is good news in any of this, recent studies have suggested that species within some back-reef areas where temperatures fluctuate significantly may offer a pool of more thermally resistant species (Oliver and Palumbi 2011).

On a geological scale, patterns of Pacific atoll development have been explained as a response to temperature changes in conjunction with tectonic effects. Grigg (1982) proposed that north of roughly 29°N in the Hawaiian Archipelago, lower temperatures have depressed carbonate production to the point where reefs cannot keep up with subsidence (Fig. 3.7). South of this "Darwin Point," barrier reefs and atolls are maintained. To the north, reefs are in various stages of "giving up." Similarly, cores through the Great Barrier Reef of Australia record a gradual shift from subtropical seas to a more tropical climate over the past 30 million years as the Australasian plate slowly moved toward the equator (Davies et al. 1987, 1991).

3.3.2.2 Salinity

Coral reefs are limited to areas of reasonably normal marine salinity (3.3–3.6 %). Below these levels, carbonate buildups are progressively dominated by vermetids, oysters, serpulids, and blue-green algae (Teichert 1958; Heckel 1974). Coral reefs do not generally occur above this range. Low salinity (along with high turbidity) is a primary reason why extensive coral reefs do not occur opposite the mouths of major rivers (e.g., the Amazon and Orinoco rivers of northern South America empty into seas that are otherwise suitable for reef development). On a smaller scale, the passes through many nearshore reefs can be controlled by present or past stream locations.

3.3.2.3 Wave Energy

The oceanographic regime in which a reef occurs is among the most important determinants of its character. Breaking waves generate currents that bring in large volumes of low-nutrient ocean water and remove waste products from the system. Benthic zonation within a single reef is to a large extent determined by the relative abilities of various organisms to either survive turbulent conditions or to take advantage of the vigorous water motion caused by passing waves. In shallow water, *Acropora palmata* grows quickly, and can grow rapidly above the traction carpet of sediment that is mobilized each time storm waves strike the reef crest. In deeper water, fragile platy corals are not negatively impacted because of the greatly attenuated surge at depth.

Regional variations in wave climate have been shown to exert a primary control on the character of the shallow-water reef crest and the zonation along the front of Caribbean reefs (Adey and Burke 1977; Geister 1977; Fig. 3.8). In addition, storms can play an important role in determining reef character. In the Caribbean, three primary hurricane tracks emerge from data compiled by Neumann et al. (1981) over the past century, and reef type is quite sensitive to this pattern (Hubbard 2011, 2014). Reefs along the most exposed Windward Islands are dominated by a high return frequency of storms that break up branching corals plus a high prevailing wave energy level that discourages grazing even in calmer times (Fig. 3.9). This encourages the formation of thick algal crusts and ridges in shallow water. In the Pacific, the location of Guam in the western monsoon trough correlates highly with the "topographically dull" reefs offshore and the architectural preponderance of "square cement bunkers with small windows and large shutters" on land (C. Birkeland, pers. commun.). Weaker but still frequent

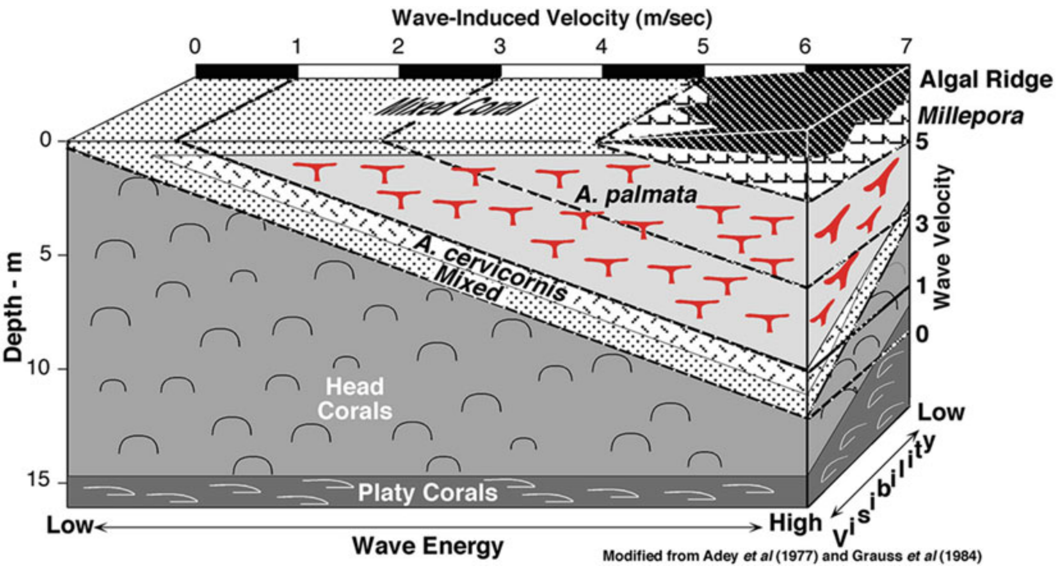


Fig. 3.8 Diagram summarizing the effects of wave energy and water clarity on the zonation of Caribbean reefs (After Adey and Burke 1977). With increasing wave energy, the boundaries between the *A. palmata*, the *A. cervicornis*, and the head-coral zones are progressively deepened. This is closely tied to magnitude of the wave-induced velocity that increases with larger waves (boundaries from Grauss et al. 1984). Turbidity and nutrient levels, which are often tied to one another (Hallock 1988), can also affect coral zonation. Increased sediment and nutrients in the water drive corals into ever-shallower water, seeking light. The shallowest zones (e.g., algal ridges, *Millepora*) are less affected by sediment as they occur in such shallow water that light attenuation is not a factor.

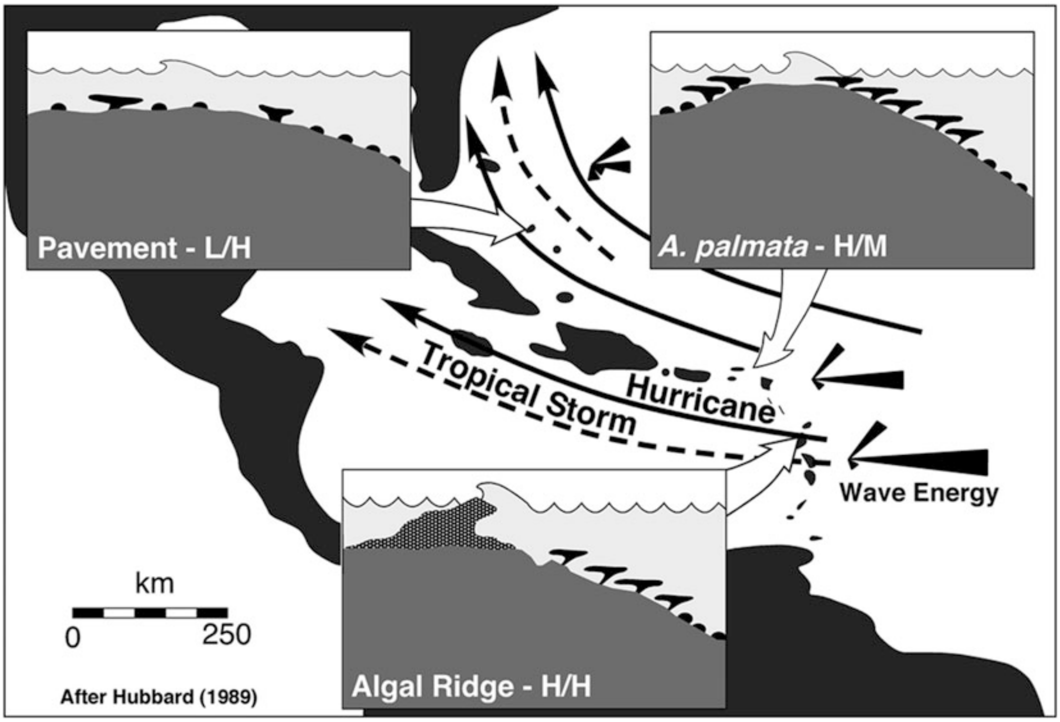


Fig. 3.9 Wave energy as a control of Caribbean reef type. Major storm tracks are shown by the *solid* and *dashed arrows*. Prevailing wave energy is shown graphically by the rose diagrams at individual sites and is based on synoptic wave observations for the region (U.S. Naval Weather Service Command 1979). The importance of ambient wave energy and major storm (e.g., L/H = **L**ow ambient wave conditions/**H**igh hurricane frequency) and the resulting reef types are shown in the *insets*. Where both ambient wave energy and hurricane frequency are high, the reef crest is characterized by algal ridges (e.g., Windward Islands). Where day-to-day wave energy is still moderately high but hurricane frequency and intensity is somewhat less, well-zoned reefs occur (e.g., St. Croix). Areas that are generally less energetic except for the passage of major storms (e.g., the Bahamas) are typically broad, wave-swept pavements (Walter Adey's “false reefs”). (After Hubbard 2011, 2014)

storms in the western Atlantic, combined with much lower prevailing wave energy tend to encourage wave-swept pavements with poorer development of branching acroporids. Lower day-to-day wave energy makes it easier for grazers to operate anywhere on the reef. Intermediate wave energy and hurricane frequency in the northeastern Caribbean encourage varied coral-community relationships and some of the best-developed reef-front zonation seen in the region. In a sense, this regional pattern follows Connell's Intermediate Disturbance Hypothesis, although at a scale different from that of species diversity.

3.3.3 Micro-scale Controls

3.3.3.1 Light

The influence of light intensity and spectral character has been generally understood since the pioneering work of Quoy and Gaimard (1825). Darwin (1842) clearly recognized light's importance in controlling the maximum depths to which he observed corals throughout the Pacific. More recent studies have further quantified this long-recognized pattern although the general relationships remain unchanged. In clear water, light intensity decreases exponentially with water depth and the light spectrum shifts rapidly toward the blue end. As a result, photosynthesis and $CaCO_3$ production drop off with depth.

In addition to changes in growth rate, reduced light at greater depths can cause polymorphic corals to change their shape from domes in shallow water to plate-like morphologies at greater depths. The latter is more efficient for light gathering as it places all the photoreceptors (in this case, symbiotic organisms within the coral tissue) along upward horizontal surfaces where light intensity is greatest – effectively a self-orienting "photocell"). Some of the best understood corals in this respect belong to the *Orbicella* complex from the Caribbean. (This was formerly called the *Montastraea* complex, but it is now known that *Orbicella* and *Montastraea* are in different families that diverged millions of years ago.) Coral-growth rate within most massive species drops from nearly a centimeter per year in shallow water (0–10 m) to a millimeter or less in deeper water (>12–15 m: Dustan 1975; Hubbard and Scaturo 1985). This is accompanied by a change in morphology from heads to plates. Similar patterns also occur for *Porites lutea* and *P. lobata* in the Pacific (Buddemeier et al. 1974; Isdale 1984).

Knowlton (1993) demonstrated genetic differences associated with the different morphotypes and, based on this information, *Orbicella annularis* was subsequently subdivided to include *O. franksii* and *O. faveolata*. It is worth remembering, however, that the experimentally induced changes in colony shape documented by Grauss and Macintyre (1982) occurred on individual colonies transplanted to different depths. Therefore, while genetic character may go hand-in-hand with species-related shape preferences at a given depth, individual colonies can still take on the shapes of their sibling species when light availability is varied.

3.3.3.2 Nutrients

Until the latter twentieth century, abundant nutrients were generally considered beneficial to reefs. Early references to reefs preferring areas of upwelling or other sources of nutrients underscore this misconception. More recently, it has been recognized that high nutrient levels are actually detrimental to "reef health" (Kinsey and Davies 1979). At the organism level, it has been proposed that high phosphate levels in the water may shut down the calcification mechanism (e.g., phosphate "poisoning" of Simkiss 1964). At the community scale, autotrophs within the reef (primarily zooxanthellae and algal turfs) are well suited to a steady stream of water with low nutrient levels. Higher nutrient levels tend to favor sponges (Wilkinson 1987) and macroalgae (Steneck 1988), which can outcompete corals and turf for space and prevent larval settling. Macroalgae may provide lower nutrient values than turfs, thus reducing the availability of useful biomass for grazers. Once the coral dies, higher levels of nutrient availability can support heavy infestation by infaunal borers (Hallock 1988), and in particular, sponges (e.g., *Cliona* spp.: Moore and Shedd 1977) that will progressively destroy the remaining skeleton and can remove any record of its existence (Chap. 4). Estep et al. (2008) documented a strong shift in dominant bioeroders from sponges in oligotrophic Caribbean fore-reef environments to molluscs (especially *Lithophaga* sp.) in the more restricted Holocene reefs of the Enriquillo Valley of the western Dominican Republic.

3.3.3.3 Sediment

Despite an impressive body of literature (for reviews, see Hubbard and Pocock 1974; Hubbard 1987), only limited quantitative information exists on the specific responses of reef organisms to sediment loading. Controlled experiments have documented surprising tolerance by corals to high doses of sediment over short periods of time (Taylor and Saloman 1978; Rogers 1983). Nevertheless, the literature is replete with postmortem autopsies of reefs killed by sediment. The obvious factor here is time. Although corals can survive acute loading at high levels, even lower-level stress can gradually wear down the reef's defenses and result in severe, and perhaps irreversible, degradation.

The most important effects of sediment stress include (1) smothering, (2) abrasion and (3) shading, all of which result in an inhibition of coral recruitment. Of the three, smothering is the easiest to visualize. Under natural conditions, reefs on the downwind flank of large carbonate platforms can be buried by sediment washed off the bank as it is flooded by rising sea level (Hine and Neumann 1977). During storms or, more recently, dredging of nearby areas, the levels of suspended sediment can increase markedly, resulting in extensive damage to reef corals and other sediment-sensitive biota. Such problems have been described in Australia (Fairbridge and Teichert 1948), Hawaii (Johannes 1975; Maragos 1972), Puerto Rico (Kaye 1959), and the U.S. Virgin Islands (van Eepol and Grigg 1970; Dubois and Towle 1985), among others.

During storms, physical abrasion by moving sediment can cause substantial damage to coral tissue (Hubbard 1992). Even under less energetic conditions sediment scour can play a role in limiting the types of corals that can thrive along the shallow reef crest. *A. palmata* grows quickly after settlement and is, therefore, less likely to be killed before it can build above the level of natural "sandblasting" associated with even small storms. Its success in times past was a balance between the destructive effects of high waves and wave-mediated removal of sediment from a coral that cannot perform that function itself.

While more subtle in its effects than abrasion or smothering, shading is probably the most important of all the sediment-related effects. Reduced levels of light due to suspended sediment in the water column can retard coral growth (Hubbard and Scaturo 1985; Hubbard et al. 1986), impact natural zonation patterns (Fig. 3.8; Morelock et al. 1979; Hubbard et al. 1986), and induce wholesale mortality if allowed to persist for an extended period of time.

All of these effects act together to exert a significant natural control on the distribution of coral reefs (Roy and Smith 1971; Morelock et al. 1979; Cortes and Risk 1985; Hubbard 1986). More recently, the dominant sources of increasing sediment loading have been related to land clearing for development and agriculture (McCulloch et al. 2003).

3.3.3.4 Antecedent Topography

Because of the fierce competition for space and the necessity for reefs to rid themselves of excess sediment produced by bioerosion, topographically elevated areas offer significant benefits to larval recruits and well-developed reefs alike. Roberts et al. (1977) showed that breaks in slope, especially at the platform margin, are focal points for wave and current energy and offer enhanced transfer of nutrients, sediment and metabolic waste. The constant input of carbonate ions also results in enhanced cementation and the generation of hard bottoms better suited for larval recruitment. Thus, bio-physically mediated topography is a primary influence on where corals can recruit and flourish.

Like ancient cities, reefs tend to be built upon the ruins of their predecessors (Fig. 3.10). As sea level falls and rises again, the remnants of the last generation of reefs serve as

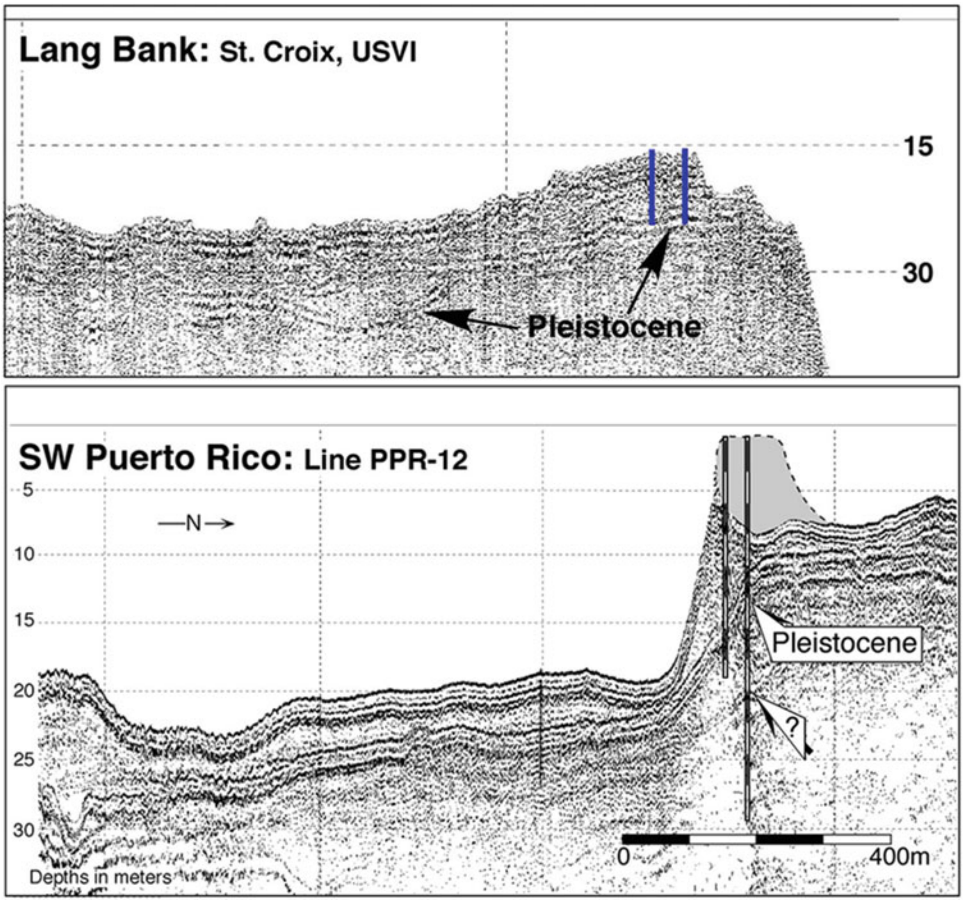


Fig. 3.10 Antecedent control of present-day reefs. The *upper panel* shows a seismic line across the southern margin of Lang Bank on eastern St. Croix (USVI) (After Hubbard et al. 2013). The seismic line in the *lower panel* is from the southwestern insular shelf of Puerto Rico. The underlying Pleistocene surface was verified by cores. Note how the Holocene build-ups sit atop highs on the underlying Pleistocene surface (Seismic data courtesy of U.S. Geological Survey)

areas of preferential coral recruitment. Reefs will tend to re-establish on previous reefs because they are hard and topographically elevated. Also, the conditions that favored the previous reefs likely return with re-flooding of the area by the next rise in sea level. In particular, elevation offers significant advantages during early shelf flooding when sediment that was created by weathering during previous exposure is stirred up by waves, increasing natural turbidity levels. Thus, reef sequences that are recognized in the fossil record are often not single depositional units, but rather a complex of several generations of reefs, each localized atop the remains of an earlier one. Many present-day reefs sit astride their Pleistocene ancestors that formed 120,000 years earlier.

One process that creates antecedent topography is **karst dissolution**. During episodes of lowered sea level, biologically produced and reactive limestone strata are dissolved by rainwater. Carbonate ions are transported down through the permeable strata until their concentration in the ground water is high enough to induce re-precipitation, usually as calcite. Thus, exposure to under-saturated rain and surface waters induces wholesale removal of carbonate at the surface. Citing both experimental studies and field examples, Purdy (1974) proposed limestone dissolution as a primary mechanism for creating antecedent topography. While reefs are forming, they are usually reinforced by aragonite and magnesium calcite cements that form within their interstices. The resulting mass is more resistant to dissolution than are the muddier and un-cemented sediments of the adjacent platform or lagoon. Thus the topography left by the reef system can be enhanced during exposure.

3.4 Reef Building

3.4.1 What Is a Reef?

To the earliest mariners, "reefs" were anything that might damage their keels (from the Nordic "rif"). These included biologically produced structures, the subject of this book, as well as piles of rocks left in shallow water by the last glaciation or the U.S. Army Corps of Engineers. Biologists are more concerned with the slate of organisms and the ecological interactions among them. In contrast, geologists focus more on the structures that they build – hence differences in definitions. The latter largely characterize reefs based on their shape in cross section and their relation to surrounding strata.

For purposes of our discussion, the following are considered to be critical factors or characteristics related to reefs. First, the features discussed here ultimately owe their origin to biological production. Even the cements that fill voids and were once thought to be the product of physiochemical precipitation are now understood to be universally mediated or created by micro-organisms. Second, reefs are rigid structures that stand topographically above their surroundings and, therefore, exert some degree of physical control over the oceanographic processes in their vicinity. For the geologist, topography is perhaps the most important trait that sets "true reefs" (**bioherms**) aside from flat hard-bottom communities (**biostromes** or "coral carpets": cf. Dunham 1970) that do not offer the spatial heterogeneity that is so important to the diversity on modern coral reefs.

Structural complexity is what the geologist is left with in the fossil record and this explains our fixation on this characteristic. However, large-scale topographic expression and more-local spatial heterogeneity are equally important to the modern ecologist; they help determine what organisms live on a particular piece of submarine real estate and how they interact with their peers. A suite of sessile organisms sitting atop a feature rising above its surroundings will function in fundamentally different ways than a similar community on a flat bottom. In fact, topography (or its absence) will in many cases preclude particular communities from occurring at all due to important differences in physical processes that are induced by abrupt topographic change (Roberts et al. 1977). Swimming over a modern reef, the associations with underlying structure are more obvious but still may be overlooked as researchers focus on smaller-scale species interactions. To the geologist, the presence or absence of this topographic relationship lay at the very heart of what is and is not a reef.

Traditionally, geological discussions have focused on what is responsible for creating topographic complexity and the rigidity that maintains it in the face of wave attack. Early workers stressed the obvious role of organisms in providing rigidity (Lowenstam 1950; Newell 1955; Heckel 1974). As a result, in-place and interlocking framework was traditionally seen as a prerequisite for the high-diversity geologic assemblage of calcifying organisms considered to be a "true reef" by most geologists. Conversely, anything not containing a preponderance of organisms in life position did not qualify (Fagerstrom 1987; Stanley and Fagerstrom 1988).

The popularity of this view is understandable. A paleontologist swimming across the surface of a modern reef 50 years ago saw a seemingly endless and topographically complex seascape of upright, living corals. The ecological literature of the day stressed the fierce competition for space and the superiority of certain species over others in light of their ability to occupy and defend this space. So, geologists visiting a modern reef usually came away with impressions that focused more on corals and calcification than biological erosion (Chap. 4) and the physical redistribution of detritus by waves and currents. The fish swimming across the reef taking the occasional, gentle nibble on the bottom was viewed as a process of perhaps academic interest but, at best, of secondary importance to the “real” reef story – calcification. Likewise, the myriad processes going on within the upper reaches of the reef substrate were out of sight. Thus “corals growing on the backs of other corals” was seen as the most logical way to build a rigid and topographically elevated structure.

However, applying this “framework model” to ancient reefs met with little success. In contrast to the dominance of in-place calcifying organisms envisioned in traditional models of modern reefs, researchers often found fossil reefs comprised of recognizable clasts “floating” in a matrix of sediment, skeletal debris and cement. Rather than questioning the prevailing model, researchers focused on why ancient reefs were so different from what modern reefs “must” look like inside… hence, Mike Lloyd’s quip “The present is the key to the late Pleistocene… perhaps” (email to Bill Precht shared with the author).

The introduction of the submersible rock drill by Ian Macintyre in 1975 gave geologists a cost-effective way to access to the interiors of modern reefs. Although some reefs contained measurable proportions of what was interpreted as in-place “framework” (e.g., Macintyre and Glynn 1976), most revealed what was arguably toppled coral skeletons mixed in with a high proportion of loose sediment and smaller coral debris (Hubbard et al. 1990). Based on an analysis of cores collected from a variety of reef environments all across the Caribbean (Fig. 3.11), Hubbard et al. (1998) proposed that the interiors of many, if not most, modern reefs were dominated by a mix of in-place and toppled corals set in a matrix of sediment, smaller skeletal fragments and open voids – a fabric similar to ancient reef-related deposits.

The importance of this is twofold. First, if so many modern coral reefs are not dominated by in-place and interlocking corals, then it should no longer be the primary criterion by which ancient reefs are judged. Second, while in-place and interlocking framework is a perfectly good way to create a rigid and topographically elevated structure, it is not the only pathway to that end. Further, given the dominance of sediment and rubble over corals in life position, it is difficult to build a wave-resistant structure by coral-growth alone given the importance of physical and biological erosion that we have taken for granted.

What emerges is a picture that acknowledges the importance of bioerosion that breaks down primary structure and marine cementation and encrustation that “glue” everything back into a more solid reef mass. Thus, bioerosion, cementation and encrustation are elevated from bit players to co-stars in Bob Ginsburg’s hypothetical long-running geologic play in which the plot stays the same even though the actors change over evolutionary time.

Most of the building blocks of a modern coral reef started as scleractinians, but they have been, to varying degrees, toppled and then modified by multiple generations of boring, sedimentary infill, encrustation and cementation (Schroeder and Zankl 1974; Schroeder and Purser 1986). The ultimate reef fabric is determined by the relative importance of (1) initial carbonate production, (2) physical and biological breakdown of this primary framework (3) the patterns of sediment storage within or removal from the reef, and (4) the levels of secondary cementation and encrustation.

This is not to say that reefs largely comprised of in-place organisms do not exist. To the contrary, the massive reef ridges of the Pacific and eastern Caribbean are dominated by layer upon layer of undisturbed massive coralline algae. These owe their existence to high waves that exclude grazers. Conversely, where wave energy is low enough to preclude extensive storm damage, in-place corals can dominate. A Holocene reef in the Enriquillo Valley of the Dominican Republic is largely comprised of in-place and well

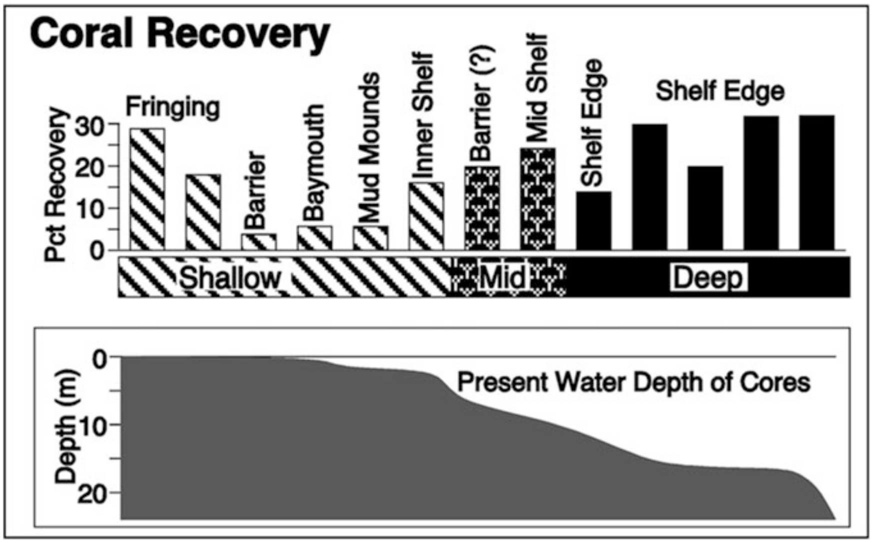


Fig 3.11 Core recovery (percent) from several Caribbean reefs. The composite profile shows the approximate depth from which each set of cores was recovered (i.e., cores are not from a single site). Note that recovery is less than 35 % overall and the highest is generally found in deeper reefs that are dominated by more resistant massive corals that grow more slowly but are harder to move. The majority of the reef fabric in all cores consists of open voids and sediment produced by bioerosion and not in-place and interlocking framework (After Hubbard et al. 1998)

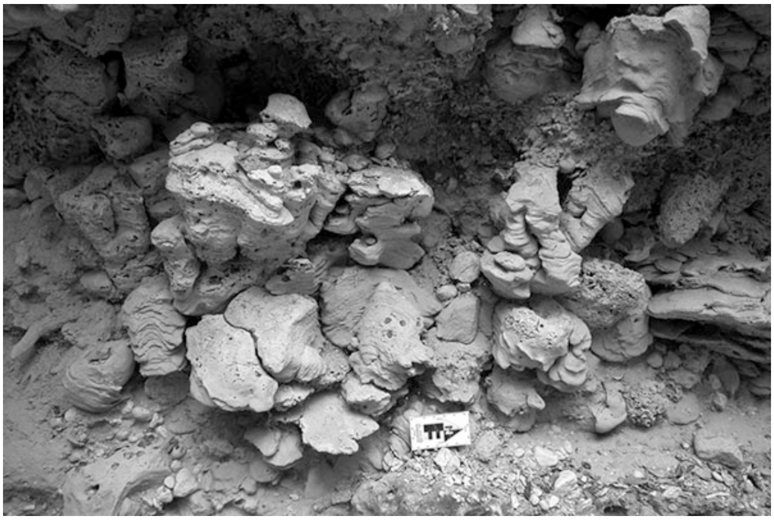


Fig. 3.12 Photograph of in-place, massive corals in Cañada Honda, Dominican Republic. The facies is interpreted as a moderate depth (ca. 20 m) fore reef in a regime of higher-than-normal sedimentation rates. Elevated sedimentation is responsible for both the limited species diversity (mostly *Siderastrea siderea*, *Orbicella faveolata* and *Agaricia* spp.) and the excellent preservation. The more bioeroded colonies (mostly *S. siderea*) probably grew at rates faster than local sedimentation. Less bioeroded colonies grew at rates approximately equal to the rate of sediment build-up. The scale *arrow* is 10 cm in length

zoned corals (Fig. 3.12) as are some of the protected *A. palmata* reefs on the leeward side of Curacao (Pandolfi and Jackson 2001). Nevertheless, there are countless other examples that we all agree are "reefs" as we swim over them but which are dominated inside by both in-place and toppled calcifying organisms in a sediment and rubble matrix that is volumetrically more important than corals, in place or otherwise. To use a dominance of in-place and interlocking primary organisms as the sole yardstick against which ancient reefs are measured is no longer appropriate.

Thus, our definition of a "true reef" must be expanded to include topographically elevated and rigid structures, built of organically derived materials that have to varying degrees been broken down and redistributed over both short distances (i.e., a toppled coral will usually remain in or near the community where it lived) and bound into the overall fabric by encrustation and cementation (Fig. 3.13).

3.4.2 Corals Grow: Reefs Build

We now understand that coral growth is only one part of reef building. Once a corals dies, it is subjected to both physical and biological breakdown. Algae that overgrow the dead substrate are a preferred diet of many fishes, echinoids, and other marine grazers. In the process of scraping or biting these algae, grazers remove bits of carbonate substrate. Alongside the grazers, countless other organisms bore into the reef, seeking shelter. The reader is referred to Chap. 4 which provides a more complete discussion of this important suite of processes.

Recent suggestions that coral reefs are "flattening" (Alvarex-Filip et al. (2009) have led us to revisit the important relationship between substrate production and destruction initially considered nearly 50 years ago by Scoffin et al. (1980) and Stearn et al. (1977). More recently, Perry et al. (2008, 2012) have developed protocols that resemble coral-monitoring but quantify both the organisms that create carbonate and those that break it down.

However, even this more holistic view still minimizes important physical processes that contribute to reef building. Land (1979) argued that carbonate found within the reef falls mainly into two categories: original coral skeletons and sediment derived from their physical and biological breakdown. The total volume of carbonate initially produced by a known distribution of organisms on the reef surface was termed **Gross Carbonate Production** (P_g). The net amount carbonate remaining within the reef (P_n) should consist of recognizable coral (both toppled and in life position) and sediment that has been incorporated into the reef edifice. The difference would be a measure of the amount of material that has been exported from the reef and permanently lost (SED_e). Stated mathematically:

$$P_g - P_n = SED_e : \tag{3.1}$$

The most detailed carbonate budget to date is from a reef along the north coast of St. Croix (Hubbard et al. 1990). Using quantitative data on reef cover, coral growth rates, cores that document long-term reef accretion, and sediment export data, all from the same locale, they concluded that nearly 60 % of the carbonate that was produced within the reef was reduced to sediment by bioerosion. Nearly half of

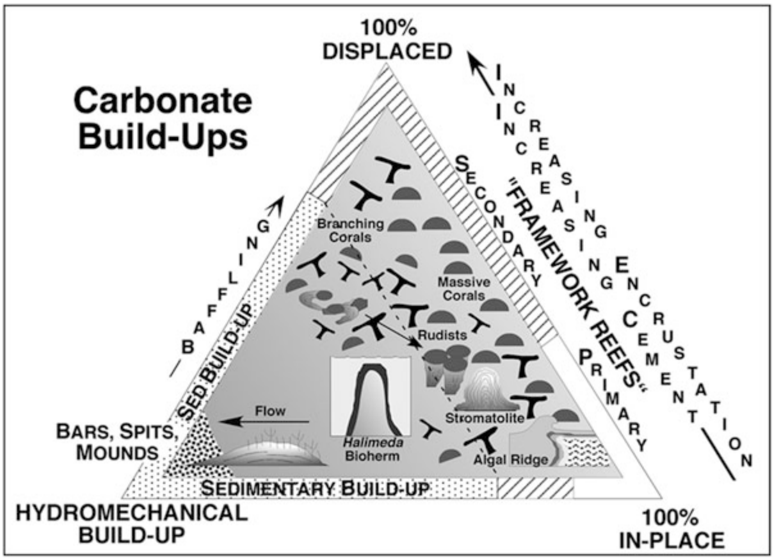


Fig. 3.13 Reef-classification based on the relative importance of skeletal elements that are (**a**) in growth position (in-place as primary framework), (**b**) displaced (i.e., toppled but close to where they lived – secondary framework) or (**c**) transported out of their original reef zone or the reef altogether – hydromechanical build-ups. The *dashed line* shows the approximate boundary between "reefs" and hydromechanical buildups (After Hubbard et al. 1998)

that was exported from the reef, primarily during storms (Hubbard 1992); the remainder was reincorporated within the reef interior. From this study, three important points emerged. First, recognizable coral (41 %) was less important in the reef than sediment (45 %) and open void space (14 %). Second, it was difficult to demonstrate that the majority of the remaining coral was in place while some pieces had been demonstrably moved or toppled. Finally, a reef that contains more loose detritus than in-place framework will probably not be a rigid structure. Thus, the stabilization of detritus by cementation and encrustation is an essential part of reef building that has been widely ignored. From these observations and measurements, they argued that in-place and interlocking framework is not necessarily an integral characteristic of all "true reefs" – and may exist in few. If we reconsider reef building to be the sum of all the processes discussed above, then the fate of all that bioeroded sediment is critical if we are to fully understand the vertical accretion of coral reefs in both the past and the future.

Total reef-carbonate production has been dropping dramatically due to the lower abundance of live corals. In addition, increasing calcification will reduce the capacity for each reef organism to create skeletal material (Hoegh-Guldberg et al. 2007; Doney et al. 2009). The growing interest in bioerosion provides important information on the destructive side of Land's simple equation. However, it does little to address the fate of the material produced by these destructive processes. If sediment is reincorporated back into the reef, then it adds to the edifice on which future coral recruitment and growth will occur. To the extent that it is stabilized by encrustation and cementation, it also contributes to the rigidity of the reef. However, this is only part of the story.

We know that carbonate production is significantly lower than it was five decades ago. . . and it is likely to continue to decline. The changing balance of bioerosion is more difficult to quantify. Fewer grazing organisms may equate to lower substrate loss and less sediment production. However, changing nutrient dynamics may shift that side of the equation more toward infaunal bioeroders. Whatever this balance looks like, we must also understand the fate of all that sediment if we are going to fully characterize the reef-building process.

3.4.3 A New Reef-Building Model

Numerous summaries have demonstrated the strong relationship between water depth and coral-growth rate. Boscher and Schlager (1992) developed a calcification model based on an exponential drop in light intensity and, therefore, photosynthesis. Using this model, they reproduced depth-related growth patterns for *M. annularis* (the taxonomy has since changed) derived from direct field measurements. They surmised that, while reef accretion would be slower than coral growth, it must follow a similar depth-related pattern, an assumption that prevails in recent models of coral reefs in the twenty-first century and beyond (DiCaprio et al. 2010; Toomey et al. 2013).

A recent summary of Caribbean reef accretion raises the likelihood that this fundamental assumption is flawed and that reef building is more than a collection of biological processes. Based on 151 reef-core intervals from 12 Caribbean sites, Hubbard (2009) found no correlation whatsoever between the rate of reef building and paleo-water depth. Moreover, the coral type (branching vs massive) preserved in the reefs had little effect on their rate of vertical accretion. Gischler (2008) came to the same conclusion based on reef cores from Belize and noted that reefs dominated by massive species built faster than those dominated by branching A. *palmata*.

Ultimately, this probably reflectes differences in the durability and transportability associated with different colony morphologies.

Clearly, these and similar summaries indicate that a reef-building model tied primarily to individual depth-related processes is critically flawed. The challenge is to figure out what might be missing. One possibility is that light may be affecting both photosynthetically driven calcification and the density of algae that are consumed by grazers in similar ways. In this scenario, carbonate production and bioerosion would co-vary with depth, resulting in a balance between the two over at least the depth range in which shallow reefs occur (Hubbard 2009). However, Weinstein et al. (2014) reported no differences in the loss from experimental substrates to a water depth of 30 m off the south side of St. Thomas in the US Virgin Islands. Similarly, a study from two reefs off nearby St. John showed no depth-related decline in bioerosion (Whitcher 2011; Whitcher et al. 2012). If these results are widely applicable, then the depth-related bioerosion patterns that have emerged when greater depths are considered may not apply to the upper photic zone inhabited by shallow-water reef corals.

Any attempt to explain the apparent lack of depth control in shallow-water reef building must take the following into account:

- Light, photosynthesis and coral-growth rates decrease with water depth
- Vertical reef accretion does not decrease with water depth (down to at least 23 m)
- Bioerosion apparently does not decrease with water depth (down to at least 30 m)
- Depth-related reef zonation generally persists in both outcrops and cores
- Sediment will preferentially move downslope, especially during storms

Resolving these observations requires a closer look at the behavior of the different types of carbonate material within the reef. Massive corals are less resistant to breakage than faster-growing shallow-water species and they will be less affected by wave action due to their position further down the forereef. If they do move, they are less likely to be transported as easily or as far as sediment. In contrast, sand and mud created by bioerosion will be easily transported unless it is sequestered well within the reef. It will move primarily during storms and the processes associated with such events tend to move sediment landward into the lagoon or downslope and out of the reef edifice altogether.

Given that there is more sediment than corals preserved in most reefs, its fate cannot be ignored in the accretionary balance. A model where detrital sediment is transported into deeper reef zones while the larger coral blocks stay closer to the sites from which they were toppled satisfies the constraints listed above and would blur depth-related accretionary patterns while still maintaining reef zonation. This infers that changes in carbonate budgeting in future reefs could be as much about changing patterns of sediment redistribution and export as it is about lowered carbonate production. Regardless of what the mix of processes looks like quantitatively, the fact that sediment transport is totally ignored in our present models argues that we need to rethink them – especially in the face of increased storminess in years to come.

3.5 Future Reefs and *Homo stupidus*

Having discussed the factors that control reef formation and the ways they accrete, the discussion returns to where it started – the changing reef seascape in recent years. Are reefs “declining”? If so, what is driving these changes? How do they fit into the known mechanisms of climate modulation? How might remaining reefs respond to the dramatic changes in sea level that have been proposed for the coming decades? And finally, what can.... and what should we be trying to “fix” – and how?

3.5.1 Reefs in Flux

It is inescapable that the world’s reefs are changing dramatically – and it seems to be for the worse. However, most of the study sites on which we base these ideas were chosen because they were, for example, the “best developed,” or the “most diverse” of the reefs that could be found at the time. Thus our starting points for earlier comparisons were to some extent skewed. Equally important, our anthropocentric perspective focuses on changes in our lifetime and the attendant assumption that the reef we saw on our first visit was “normal”. A survey of the coral communities around Easter Island found a luxuriant, albeit low-diversity, coral community all around the island – except for on the windward side (Hubbard and Garcia 2003), where conventional wisdom would tell us to look for the “best” reefs. The shallow community consisted of an assemblage of abundant corals (up to 100 % over large areas; avg. ca. 50 %). However, video from the 1970s show that the shallow insular shelf had been dominated by *Sargassum*. After the near extirpation of macroalgae following a severe El Niño, corals dominated by *Pocillopora* spp. gradually moved into the newly created space in shallow water. So, which was the “better” or “healthier” community, the algae that were compromised by climate change or the corals that replaced them? And, how does this tie into the complex story of colonization on Easter Island? It is perhaps ironic that the rapid takeover by coral was lamented by locals as a shift away from the “normal” and “healthy” community dominated by algae –

an argument that we are not used to hearing in the reef community.

To further complicate the picture, subsequent bleaching associated with La Niña warming devastated the shallow-water coral community that had dominated for over a decade (Wellington et al. 2000; Hubbard and Garcia 2003). Were algae or coral the "normal" shallow marine community around Easter Island? Which was "better"? What will replace the recently killed *Pocillopora*? Are the patterns of rapid change in this remote area new or just part of a longer "boom-and-bust cycle? What role, if any, did either the low diversity or the particular members of the community have to do with this unusual history? And finally, because Easter Island is farther from major land masses than just about anywhere on Earth, is there any area that is totally outside anthropogenic influence if we are at the heart of the problem?

The story from Easter Island might be cast off as interesting but not relevant to the larger global situation. Nevertheless, Jackson (1997) cautioned that historical evidence shows that many of the patterns we see as unusual today were already occurring at the time of Columbus. Thus, the reefs that we first studied in the 1950s were probably not "pristine" and some of the degradation that we have more recently documented had already begun. Rudimann (2005) argues that the shift in humans from hunter-gatherers to agrarians may have begun the present climate decline as early as 8,000 years ago.

None of this presumes that recent changes in coral reefs are not "real" or that increased human exploitation is not tied up in the story. However, if we are going to effectively use our limited environmental capital, then we need to take a hard look at our personal and often anthropocentric perspectives with respect to "good" and "healthy". The fundamental challenge is to separate natural from anthropogenic change and to come up with practical strategies based on that differentiation. To apply this to the fate of reef building in the near future, we need to make sure that we fully understand the processes that contribute to this venture in a wholly natural scenario.

3.5.1.1 Is the Past the Key to the Present?

Studies of Quaternary reefs provide an important longer-term look at patterns of reef development against which we might compare recent change. Paldolfi (2002) remarked that the Pleistocene reefs exposed in the cliffs around Curacao "show strikingly clear and repeatable differences in coral species abundance patterns among reef environments, similar to zonation patterns previously described for living reefs at Curacao and elsewhere in the Caribbean prior to the 1980s." Jackson (1992) similarly proposed that Pleistocene reefs were more stable in the long term and that the presence or absence of the classic reef-zonation pattern might be used to distinguish between "normal" versus "unhealthy" Caribbean reefs. However, they both cautioned that, while long-term stability may be the hallmark of large-scale Pleistocene reef development, variability and even anarchy may be the natural picture at smaller spatial and temporal scales (Jackson 1991; Pandolfi and Jackson 1997).

A number of recent studies have built on this theme of long-term stability and have proposed that the events associated with recent coral-reef decline are not the norm. Comparing Pleistocene and modern reefs on San Salvador, Greenstein (1999) proposed that, "the current and rapid decline of *A. cervicornis* observed on Bahamian patch reefs may be a unique perturbation that contrasts with the long-term persistence of this coral species during Pleistocene and Holocene time." Aronson and Precht (2001b) similarly noted a recent community change from *A. cervicornis* to *Agaricia tenufolia* on Belize patch reefs. Cores through the upper part of the reefs revealed no such widespread community change between the two species over the past few thousand years. Based in large part on these findings, they wrote, "paleontological data suggest that the regional *Acropora* kill is without precedent in the late Holocene" (Aronson and Precht 2001a). These statements infer that the recent geologic record is unambiguous and that short-term changes documented by reef monitoring over the past two to four decades are in fundamental contrast to stability before humans came to be an important factor in the coral reef equation.

3.5.1.2 Buck Island: A Tale of Two Analyses

One of the longer coral-reef monitoring records comes from Buck Island Underwater National Monument in the eastern Caribbean. Surveys were initiated in the late 1970s, before the onset of coral diseases and other changes we have documented in reefs. The successive surveys chronicle decline related to disease, hurricanes and a variety of other factors in an area administratively protected from direct human impact – especially nutrients and over-fishing. This was the site of the first described incidence of White Band Disease (WBD) by Gladfelter (1982). As part of the effort to understand reef development within the park, seven reef cores were drilled along two of the long-term monitoring transects. The goal was to interpret the geological history of the reefs and to relate that to community structure within the present-day reef system.

Figure 3.14 compares the relative abundance of corals in the seven cores to the changing composition of the recent reef community since 1970. The importance of *Acropora palmata* in the cores over the past 6,000 years closely matches the pre-WBD community (i.e., 1976), suggesting that a community absent *A. palmata* has not been the geologic norm in this area. It was initially suggested that, "this may indicate that 'White Band Disease' and similar

Fig. 3.14 Graph of coral abundance along the northern Buck Island monitoring transect versus what was found in cores from the same reef. Note the close agreement between the abundance of *A. palmata* in the cores (i.e., the longer-term "geological trend") and the monitoring transect in 1976, prior to the onset of White Band Disease. It might be concluded from this figure that the dramatic loss of *A. palmata* after 1976 was an event that was "unprecedented" over the 7,000 years represented by the Buck Island cores

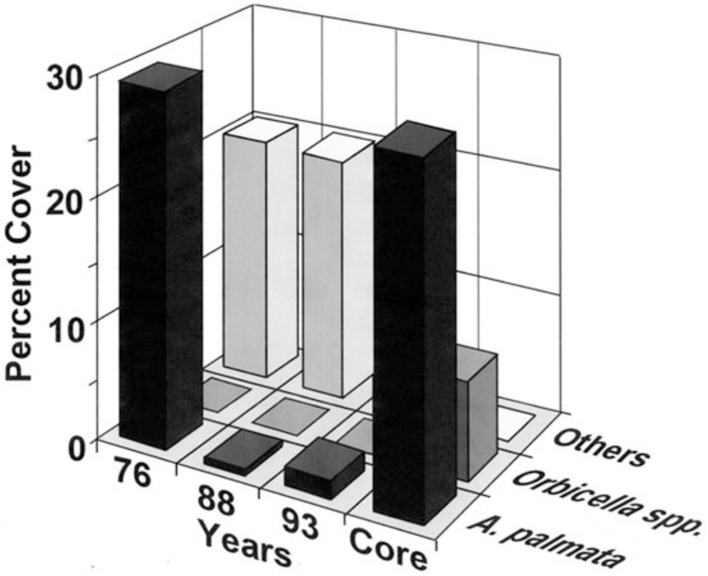
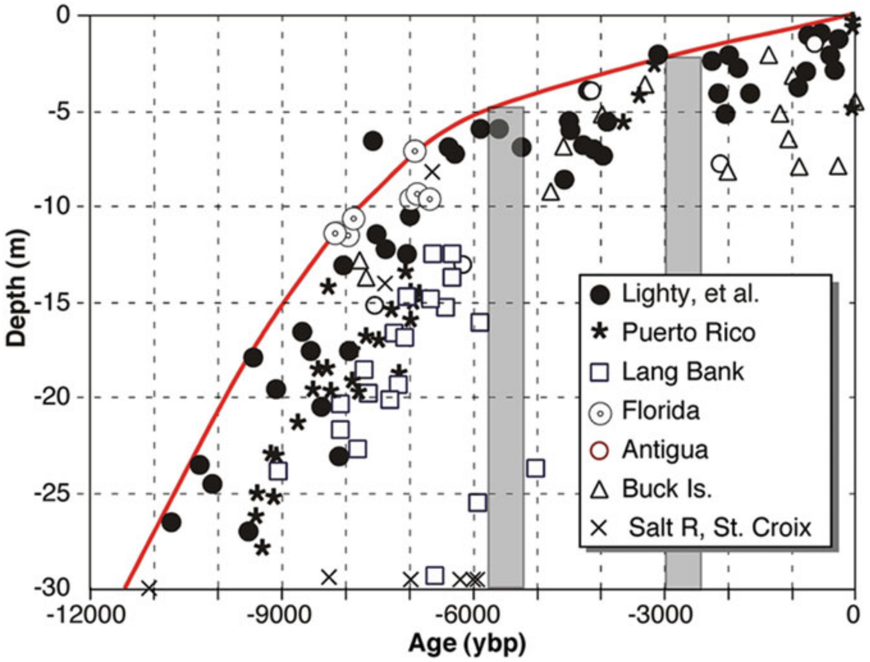


Fig. 3.15 Summary of the Caribbean record of *A. palmata* over the past 12,000 years. Two 500-year intervals of either greatly reduced abundance or absence of *A. palmata* (*gray shaded*) are in apparent contradiction to recent statements about the "unprecedented" nature of such events (After Hubbard et al. 2005)



afflictions have been less important in the geologic past" (Hubbard et al. 1994), a conclusion similar to those just described for other sites.

However, more detailed analyses of the cores identified two gaps in the record of *A. palmata* at Buck Island (Hubbard et al. 1998, 2000, 2005). A compilation of all radiometrically dated *A. palmata* samples found in the literature suggests that these gaps persist throughout the Caribbean and western Atlantic region (Hubbard 2014). The first gap, about 5,700 years ago (Fig. 3.15), was associated with regional abandonment of Caribbean shelf-edge reefs and an abrupt landward shift in reef position (i.e., backstepping). The second, about 3,000 years ago, is related to no such event and remains largely unexplained.

Each gap spans nearly a millennium and is followed by what appears to be full recovery of the *A. palmata* community.

Whatever happened at Buck Island, it appears to have been coincident with what was happening regionally. While a reef crest dominated by *A. palmata* was spatially dominant in the overall history of the reef, it was absent for nearly a third of the time. Thus, we need to be very careful to not equate spatial dominance to temporal persistence.

Earlier scientific wisdom held that reefs were inherently stable systems in which little changed from year to year.

With further study, we have come to realize that present-day reef equilibrium can be very dynamic, and that reefs are potentially capable of significant change over relatively short spans of time – even when "nothing is wrong". The question now before us is how the changes that we are seeing fit into the grand scheme of things over the longer haul.

The all-too-common decrease in coral cover and the attendant rise in macroalgae on so many of the world's coral reefs are the cumulative result of bleaching, disease, increased nutrients, sedimentation, and myriad other factors related to growing human population growth and ever-expanding exploitation. If we ignore these basic truths while we try to sort out other pressing but more complex and indirect global issues, we run the risk of exceeding an environmental "angle of repose" before our data are good enough to assess blame with certainty. On the other hand, we can little afford to "fix" everything that seems broken. It is difficult to decide which reflects greater hubris, our earlier sense that we could manipulate our environment without impact or our sense that we can now repair the damage caused by this misconception.

3.5.2 So, What Do We Do?

Bruce Hatcher posited that "paleontological and sclerochronological studies of corals and reef provinces provide the best available tools to expand the temporal horizons of observation" (from Pandolfi 2002). However, the shift from coral to macroalgal dominance is virtually impossible to detect in the fossil record because such algae do not preserve well, if at all. Also, important gaps in the fossil record can be missed if we use a visually discernable change in species composition as the sole way to detect them. How many of the gaps identified for *A. palmata* for the last 10,000 years exist in the spatially persistent Pleistocene records of Barbados, Curacao and other places cited as examples of pre-anthropogenic stability in Caribbean reefs? It may be premature to dismiss Grigg's (2000) concerns over the effects of temporal scale and measurement artifacts on comparisons of long-term geological and short-term biological data. Careful radiometric dating is the only obvious solution, but the cost of such an effort at a scale that will allow us to address regional or global phenomena is daunting. Nevertheless, it may remain as the only plausible approach to a real understanding of short-term change in reef-community structure over longer periods of time – short of centuries of monitoring.

Having said all this, whether or not past gaps in the *Acropora* record exist or not, and who has the better understanding of community stasis is no longer the main issue. Even if such gaps are commonplace, the stress levels that accompanied subsequent recovery in the past were less intense and undoubtedly different than what is occurring today. While the resolution of such issues is of great importance to science and, once resolved, will have overwhelming bearing on conservation policy, the answers are not available now and will probably not be for some time to come.

In the meantime, we may be left with something no more complex than "Pascal's Wager" in the seventeenth century relating to the existence of God. What we are in effect doing today, as was Pascal centuries ago, is weighing the relative consequences of acting on a premise that might eventually be proven wrong. Pascal argued that if we presumed God's existence and were wrong, the world would simply be left with "an excess of virtue", certainly preferable to the "eternal damnation" that would follow incorrectly denying God's existence. Applying this to the present environmental situation (Hajek 2001), a policy that moves toward sustainability even if no crisis actually exists, still results in "infinite utility" – we will have coral reefs to pass on to future generations.

So, is science irrelevant to the growing environmental debate? Absolutely not! Science has given us our present understanding of the issues; we have done our jobs well. There is still an important role for science as we continue to unravel the intricacies of community structure on a variety of scales and use that information to propose sound environmental and conservation policy, hopefully well into the future. Our continued participation is demanded. However, the time it will take to arrive at the level of scientific certainty that skeptics demand is a luxury that we no longer have. The pressing goal for now is to change public attitudes and create a consensus toward sustainability – and fast!

Consider for a moment the body of information that was provided to support the existence of Weapons of Mass Destruction in Iraq. We willingly embarked on a track that was infinitely costly in dollars, international good will and quality of life for countless groups; this was ultimately shown to have been based on seriously flawed information. By comparison, consider the quality of the information that points to elevated levels of carbon dioxide in our atmosphere, the adverse environmental and economic impacts of an economy totally dependent on fossil fuels, the increased degradation of coral reefs in proximity to centers of human population, and the spent biotic systems that we will be handing down to future generations. Yet, we refuse to act upon this infinitely better body of information because it is "too costly" to respond until we "know for sure".

This paradox will be solved only by a fundamental change in public perception and political will. While scientists must play a role in this process, the change will not be driven by good science alone – recent history has painfully demonstrated this. Perhaps it really is as simple as Pascal posited centuries ago. If we act on a presumed environmental crisis – one that is ultimately shown to be less severe than we presently think, we will have perhaps overspent dollars that some presume we can ill afford.

However, we will have a planet that is fundamentally better off and will have acted on behalf of those least represented in the recent debate – future generations, lost species and increasingly degraded habitats. If, on the other hand, we choose to deny what is ultimately proven to be a real crisis, we will be faced with a failed life-support system and a path that no amount of capital wealth can reverse. We need to replace the present economic mindset that our dollars need to be preserved until we can absolutely quantify the problem with one that places a much higher value on environmental capital that cannot be regained in the next rebound of the stock market.

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Bioerosion and Coral Reef Growth: A Dynamic Balance

4

Peter W. Glynn and Derek P. Manzello

> *The question at once arises, how is it that even the stoutest corals, resting with broad base upon the ground, and doubly secure from their spreading proportions, become so easily a prey to the action of the same sea which they met shortly before with such effectual resistance? The solution of this enigma is to be found in the mode of growth of the corals themselves. Living in communities, death begins first at the base or centre of the group, while the surface or tips still continue to grow, so that it resembles a dying centennial tree, rotten at the heart, but still apparently green and flourishing without, till the first heavy gale of wind snaps the hollow trunk, and betrays its decay. Again, innumerable boring animals establish themselves in the lifeless stem, piercing holes in all directions into its interior, like so many augurs, dissolving its solid connexion with the ground, and even penetrating far into the living portion of these compact communities.*
>
> *L. Agassiz (1852)*

Abstract

Bioerosion, involving the weakening and breakdown of calcareous coral reef structures, is due to the chemical and mechanical activities of numerous and diverse biotic agents. These range in size from minute, primarily intra-skeletal organisms, the microborers (e.g., algae, fungi, bacteria) to larger and often externally-visible macroboring invertebrate (e.g., sponges, polychaete worms, sipunculans, molluscs, crustaceans, echinoids) and fish (e.g., parrotfishes, acanthurids, pufferfishes) species. Constructive coral reef growth and destructive bioerosive processes are often in close balance. Dead corals are generally subject to higher rates of bioerosion than living corals, therefore, bioerosion and reef degradation can result from disturbances that cause coral mortality, such as sedimentation, eutrophication, pollution, temperature extremes, predation, and coral diseases. The effects of intensive coral reef bioerosion, involving El Niño-Southern Oscillation, *Acanthaster* predation, watershed alterations, and over-fishing, are re-examined after ~20 years (early 1990s–2010). We review the evidence showing that the biologically-mediated dissolution of calcium carbonate structures by endolithic algae and clionaid sponges will be accelerated with ocean acidification. The $CaCO_3$ budget dynamics of Caribbean and eastern tropical Pacific reefs is reviewed and provides sobering case studies on the current state of coral reefs and their future in a high-CO_2 world.

Keywords

Rates • Excavating • Degradation • Acidification • Microborer

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4.1 Introduction

Coral reefs are among the Earth's most biologically diverse ecosystems, and many of the organisms contributing to the high species diversity of reefs normally weaken them and convert massive reef structures to rubble, sand and silt. The various activities of those reef species that cause coral and coralline algal erosion are collectively termed **bioerosion**, a name coined by Neumann (1966). A **bioeroder** is any organism that, through its assorted activities, erodes and weakens the calcareous skeletons of reef-building species. Although an extensive terminology has been adopted only during the past three decades, bioerosion has been recognized as an important process in reef development and maturation for more than a century (e.g., Darwin 1842; Agassiz 1852). Traces of biologically-induced erosion in ancient reef structures indicate that bioerosion has probably had some effect on reef carbonate budgets since Precambrian and Cambrian times (Vogel 1993).

Most bioeroder species are both small in size and secretive in living habits. Although the majority of bioeroders and other cryptic organisms are not visible on coral reefs, it has been suggested that their numbers and combined mass equal or exceed that of the surface biota (Grassle 1973; Ginsburg 1983). Recent research supports this hypothesis (Enochs 2012). Ginsburg has coined the term **coelobite** to refer to the profusion of organisms inhabiting cavities on reefs. For convenience, bioeroders that are usually present and visible on reef surfaces are termed **external bioeroders** and those living within calcareous skeletons are termed **internal bioeroders** (Fig. 4.1a). The feeding scars produced by an external bioeroding pufferfish (*Arothron*) can become permanently incorporated in the skeleton of a massive coral (Fig. 4.2a). A heavily infested coral by internal bioeroders,

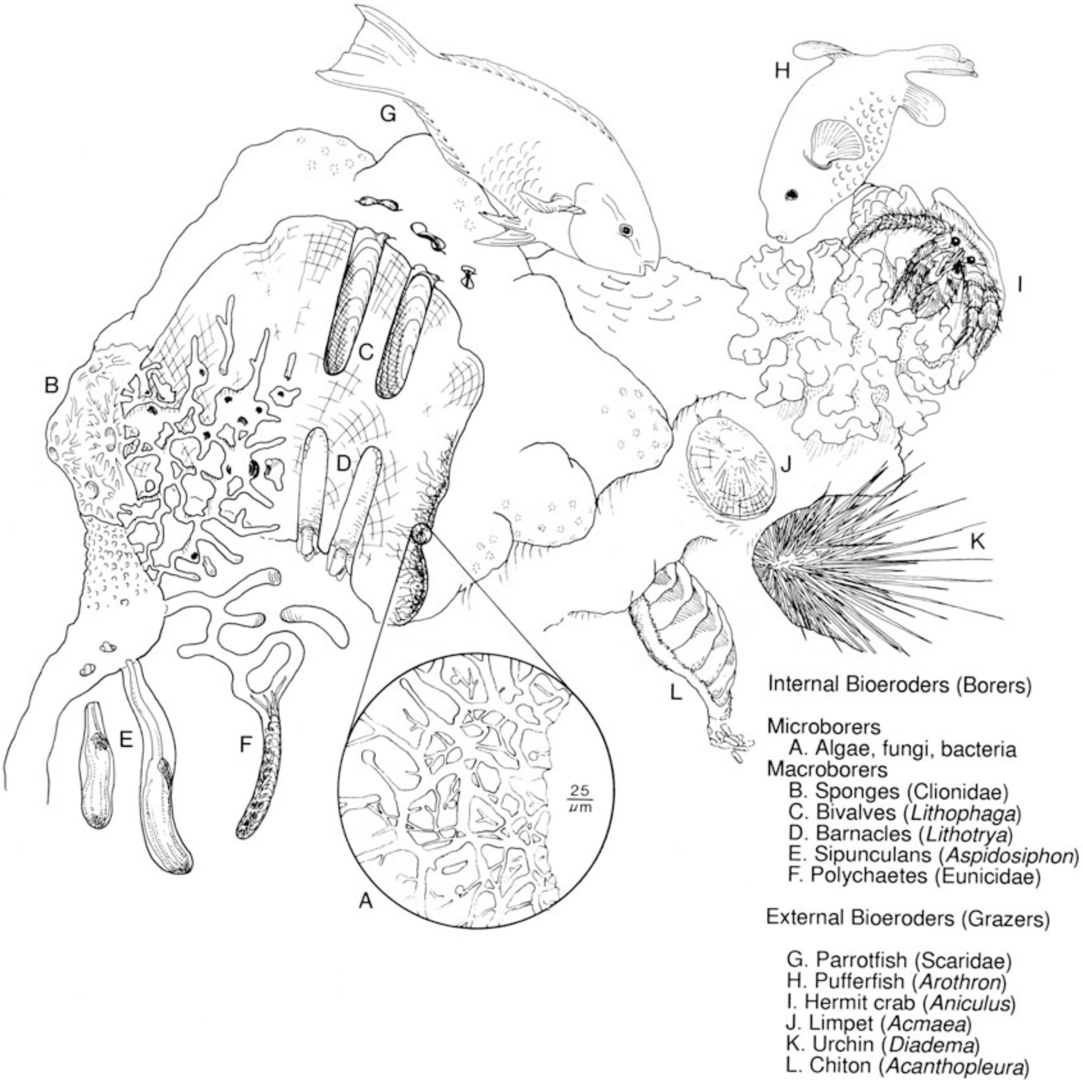

Fig. 4.1 Variety of external and internal bioeroders that commonly attack coral skeletons. A legend provides identification of the taxa illustrated

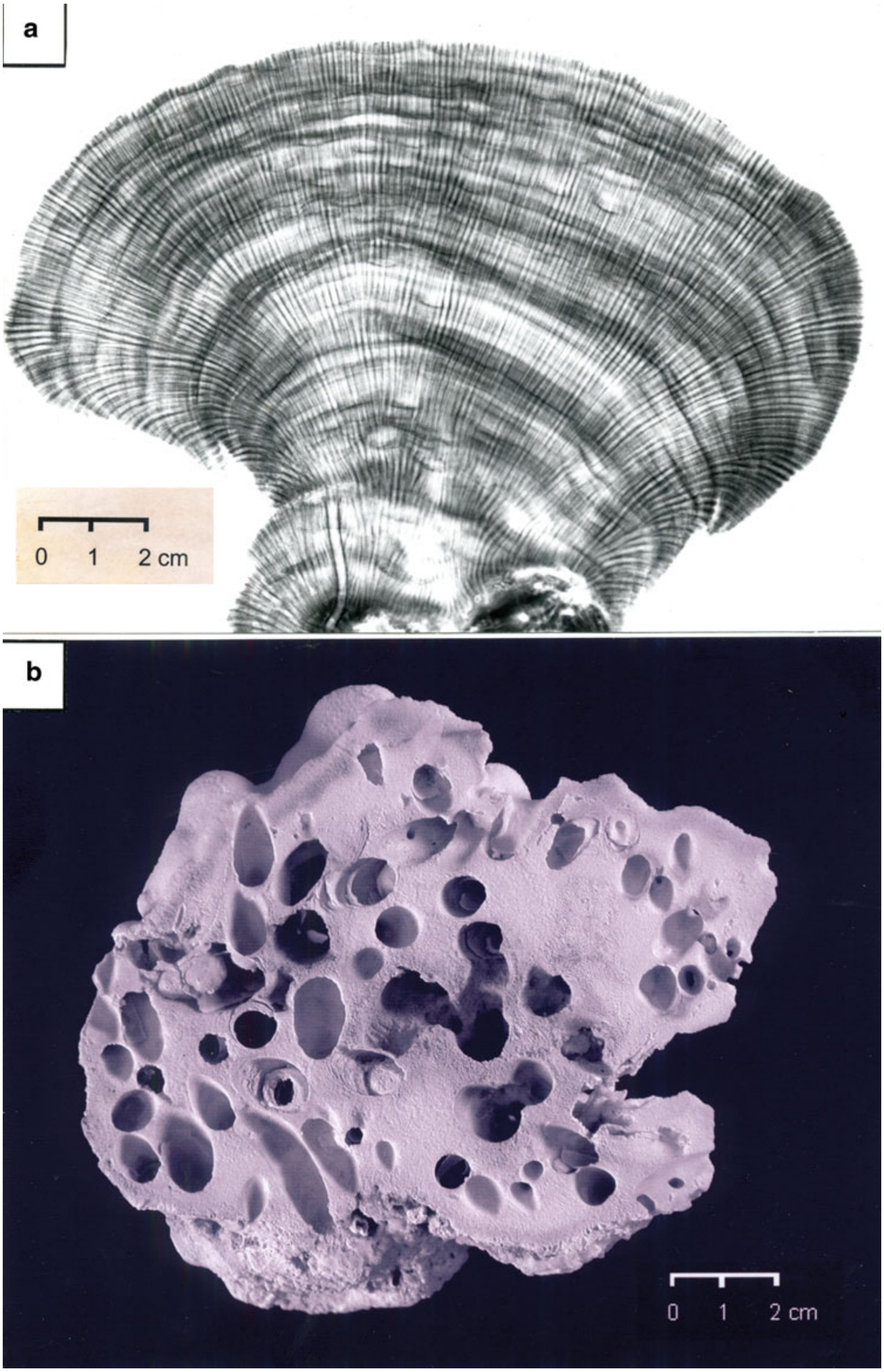

Fig. 4.2 (**a**) X-ray photograph of *Porites lobata* slab cut parallel to the skeletal growth axis. Lunate pufferfish feeding scars, produced externally, are now permanently embedded in the skeleton (6–8 m depth, Clipperton Atoll). (**b**) Cross section of *Porites panamensis* extensively bored by lithophagine bivalves (5 m depth, Pearl Islands, Panama)

e.g. lithophagine bivalves, can severely damage and weaken the colony skeleton (Fig. 4.2b).

Several studies have shown that bioeroders are important in sculpting coral reef growth and in producing the sediments (rubble, sand, silt and clay) that characterize coral reef environments. Indeed, carbonate budget studies have demonstrated that constructive and destructive processes are closely balanced on many reefs with net reef accumulation barely ahead of net reef loss (Scoffin et al. 1980; Glynn 1988; Fig. 4.3). Bioerosion proceeds at high rates in certain zones which have high living coral cover and high rates of accretion (Kiene 1988). Sometimes, however, an imbalance develops with erosional processes gaining the upper hand. When environmental conditions

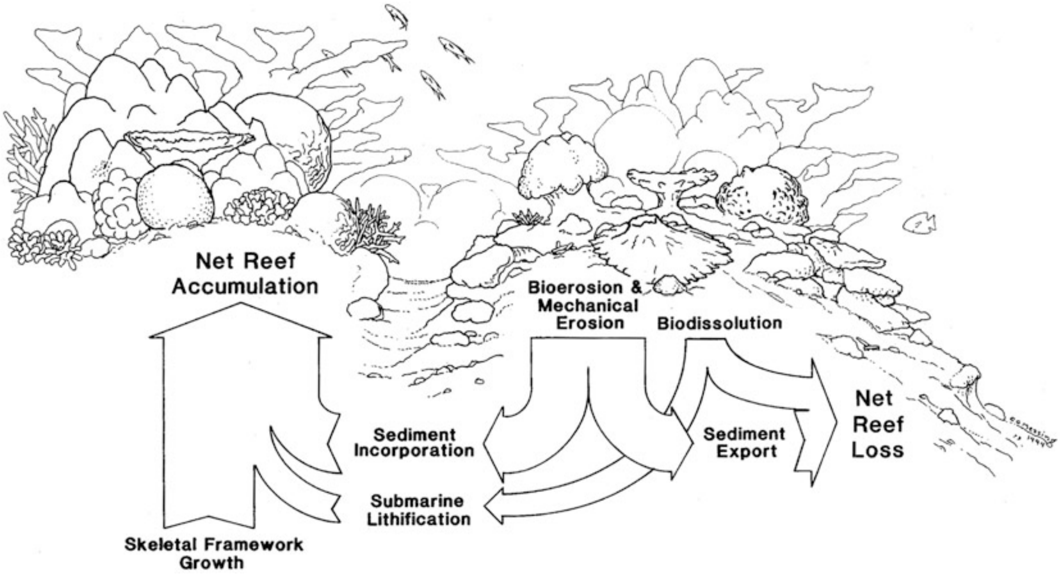

Fig. 4.3 A generalized scheme illustrating the principal components of coral-reef construction and destruction. In order for reef growth to occur, rates of bioerosion and mechanical erosion must not exceed the rate of net reef accumulation. The relative contribution of inorganic and biological dissolution (= biodissolution) to total reef dissolution is presently unknown. Both components are likely to increase with ocean acidification

decline abruptly, for example during a stressful thermal bleaching event, or over an extended period, such as years of increasing sedimentation or eutrophication, coral recruitment and growth decline or cease, limestone foundations are compromised and reef death ensues.

The aim of this chapter is to (a) illustrate the diversity of bioeroders on coral reefs, (b) identify the most destructive bioeroder groups, (c) describe the more prevalent modes of limestone destruction, and (d) highlight some case studies of intensified bioerosion on particular reef systems. In this updated review, with reference to the diversity of bioeroding taxa ‘(a)’, protistan foraminiferans are now included as agents of reef carbonate breakdown although it is not yet possible to assess their overall importance. Under case studies ‘(d)’, the effects of continuing, global-scale disturbances that impact coral communities and accelerate bioerosion, namely ENSO warming events and eutrophication, are re-examined in the light of recent findings. For example, the recovery of the Kān’eohe Bay *Porites* fringing reef, from 1993 to the present (2013), is examined. More recently attention has turned to ocean acidification and its effects on coral carbonate structures. This newly recognized factor, affecting calcification and cementation, can potentially exacerbate bioerosive processes and is also considered below.

In light of the many well documented studies of accelerating coral reef decline during the past decade, it is now all the more critical to understand the conditions that promote bioerosion, a pivotal process affecting the growth potential of coral reefs. For more technical information on this subject, the reader may consult the articles in Carriker et al. (1969) and Barnes (1983), and the reviews by Golubic et al. (1975, 2005), Warme (1975, 1977), Risk and MacGeachy (1978), Trudgill (1983), Macintyre (1984), Hutchings (1986, 2011), Perry and Hepburn (2008), Tribollet (2008), and Tribollet and Golubic (2011). An online bibliographic review of the bioerosion literature is provided by Wilson (2008).

4.2 Bioeroder Diversity

Bioeroders are abundant and diverse members of coral reef communities, belonging to four of the five kingdoms of life on earth, and to most animal phyla. Why have so many taxa become bioeroders? By far, the bioeroders hidden within coral skeletons, the **cryptic biota**, have the greatest taxonomic diversity. It is probable that intense competition and predation have led to the selection and evolution of cryptic life styles. Many of these secretive species are without toxins, armature, spines and thick shells, traits that are so common to their congeners living on reef surfaces and exposed to predators.

Depending upon their location on calcareous substrata, bioeroders can be classified as epiliths, chasmoliths and endoliths (Golubic et al. 1975). **Epilithic species** live on exposed surfaces, **chasmoliths** occupy cracks and holes, and **endoliths** are present within skeletons. Assignment to these categories is not always clear, however, for some bioeroders may belong to more than one microhabitat or change microhabitats during feeding, reproduction and development.

Bioeroders breakdown calcareous substrata in a variety of ways. The majority of epilithic bioeroders are herbivorous grazers that scrape and erode limestone rock while feeding on associated algae. In terms of eroding capabilities, grazers range from non-denuding and denuding herbivores that remove mainly algae and cause little or no damage to substrata to excavating species that remove relatively large amounts of algae, including calcareous algae, and the underlying limestone substrata (Steneck 1983a). Most endoliths are borers that erode limestone mechanically, chemically or by a combination of these processes. The important role of bioeroders can be appreciated when one realizes that coral reefs are predominantly sedimentary features made up of calcareous particles that are generated in large measure by the activities of bioeroders (Sects. 2.2 and 3.4).

Many species that bioerode calcareous skeletons are minute, requiring microscopical methods for study, and are referred to as **microborers** or endolithic microorganisms (Golubic et al. 1975; Macintyre 1984). To this group belong three kingdoms, namely bacteria and cyanobacteria (PROKARYOTAE), FUNGI, and eukaryotic microorganisms such as protozoans and algae (PROTOCTISTA). The **macroborers** are generally more conspicuous on coral reefs, and include numerous invertebrate and vertebrate taxa in the kingdom ANIMALIA. Most endolithic invertebrates are suspension feeders, gathering their food passively or actively from the water column.

Endolithic microborers, possibly Cyanobacteria, are among the first recognizable bioeroders in the fossil record, having left minute borings in late Precambrian ooids of Upper Riphean/Vendian age, 570–700 Myr (Campbell 1982). While endolithic borers increased steadily during the Paleozoic era, from five to nine classes, they comprised only a small part of hard-ground communities and penetrated structures superficially, i.e., to maximum depths of 2–3 cm (Vermeij 1987). A notable increase in endolithic taxa occurred during the Mesozoic era with the appearance of deep borers, such as pelecypods, gastropods and lithotryid barnacles, capable of penetrating substrates to depths of 15 cm. Excavating bioeroders, comprising mobile epifaunal invertebrates and herbivorous fishes, made their first appearance during the Late Mesozoic and Early Cenozoic (70–60 Myr) and have persisted until today. These animals – chitons, limpets and other gastropods, sea urchins and parrotfishes – are dominantly herbivores whose feeding activities incidentally produce large quantities of sediment. Herbivory and bioerosion by these groups are probably more intense now than at any time in the past (Steneck 1983b). Vermeij (1987) has argued that this Mesozoic increase in the size and extent of excavation among vagile bioeroders can be interpreted as an evolutionary response to escalating predation and competition on open rock surfaces.

4.2.1 Bacteria

Although our knowledge of the bioeroding potential of bacteria and the various taxa involved is very limited, preliminary observations suggest that these organisms may be important under certain conditions. A pilot study in Hawai'i indicated that brownish areas inside the skeletons of massive corals contained from 10^4 to 10^5 bacteria per gram dry weight (DiSalvo 1969). Boring sponges also were closely associated with bacteria, which could possibly have assisted the sponges' penetration into the coral. Different workers have shown that bacteria can etch the surface of limestone crystals and dissolve the organic matrix of coral skeletons, causing internal bioerosion (DiSalvo 1969; Risk and MacGeachy 1978).

Several species of Cyanobacteria, formerly known as blue-green algae, are capable of eroding reef rock from the splash zone to depths of at least 75 m. Species of *Hyella*, *Plectonema*, *Mastigocoleus*, and *Entophysalis*, for example, have been found on limestone surfaces, inside cavities, and penetrating reef rock (Fig. 4.4a, b). A close relative of *Hyella* has been found in Precambrian algal reefs that existed 1.7 billion years ago (Vogel 1993). The boring is a dissolution process accomplished by the terminal cells of specialized filaments. Cyanobacteria have been implicated in the erosion of lagoon floor sediments on the Great Barrier Reef, amounting to the dissolution of between 18 and 30 % of the sediment influx rate (Tudhope and Risk 1985) (Table 4.1). (It should be stressed that most of the rates of erosion listed in Tables 4.1 and 4.2 were obtained with different methods and therefore should be compared with due caution. See Kiene [1988] for an assessment of the strengths of the methods and some problems with the intercomparisons.)

4.2.2 Fungi

Boring fungi have been found in modern corals in the Caribbean, French Polynesia and on the Great Barrier Reef (Australia). Twelve genera belonging to the Deuteromycota or Fungi Imperfecti have been isolated from a variety of scleractinian corals and a hydrocoral (Kendrick et al. 1982). Fungi are capable of deep penetration into coral skeletons by chemical dissolution. The hyphae produce narrow borings and penetrate the deepest recesses of coral skeletons, probably because of their ability to utilize the organic matrix of coral skeletons (Fig. 4.4c, d). Endolithic fungi growth can cause unique skeletal protuberances in living corals due to the localized deposition of dense skeletal material, perhaps as defensive barrier (Le Campion-Alsumard et al. 1995). Fungi have also been implicated in the etching of calcareous surfaces, the weakening and dissolution of calcareous

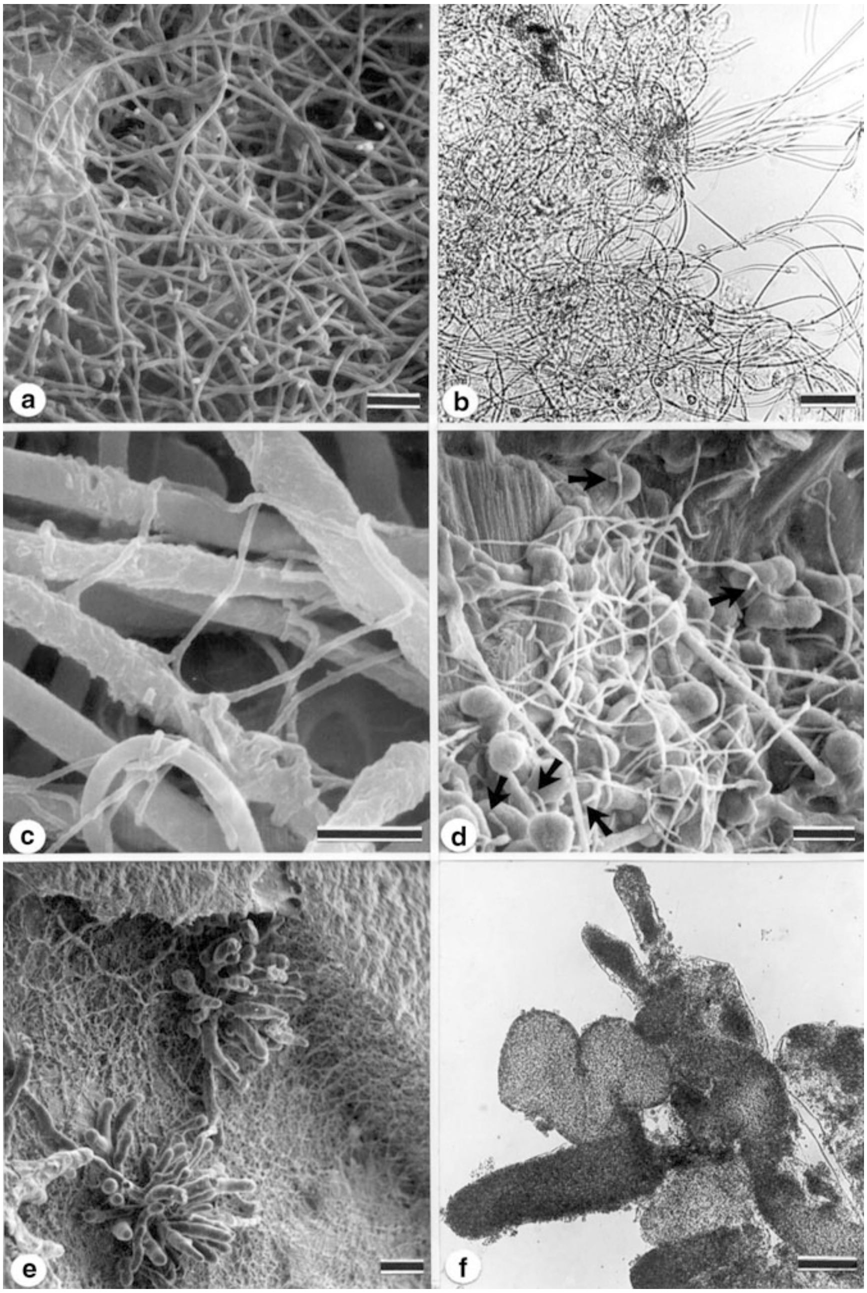

Fig. 4.4 Photomicrographs of endolithic microborers in limestone substrates. Cyanobacteria: (**a**) *Plectonema terebrans* Bornet and Flahault, scanning electron micrograph (*SEM*) of plastic casts of filaments in an acid-etched shell; (**b**) *P. terebrans*, transmitted light micrograph (*TLM*) of filaments isolated by dissolution. Fungi: (**c**) SEM of plastic casts of fine fungal hyphae intertwined with the larger filaments of *P. terebrans*; (**d**) SEM of fungal borings covering and possibly feeding (*arrows*) on the underlying cyanobacterium. Chlorophyta: (**e**) *Ostreobium brabantium* Weber Van-Bosse, SEM of plastic cast of large radiating growth form in an acid-etched shell fragment; (**f**) *O. brabantium*, TLM of filaments isolated by dissolution. Scale bars: **a** = 50 μm, **b** = 40 μm, **c** = 5 μm, **d** = 25 μm, **e** = 200 μm, **f** = 100 μm (From May et al. 1982)

sediments as well as the calcareous tube linings of various endoliths. Because of the difficulty of distinguishing between fungal and algal borings, estimates of dissolution rates due to boring fungi alone are not yet available.

4.2.3 Algae

Green (Chlorophyta) and red (Rhodophyta) algae have been implicated in the erosion of coral rock under various reef settings. Green and red algae occur on limestone surfaces, in cavities and within coral skeletons (Fig. 4.4e, f). Freshly fractured corals often reveal layers of green banding a few cm beneath the live coral surface. The green color is due to the presence of chlorophyll pigments, which intercept light passing through the coral's tissues and skeleton. This greenish layer is often referred to as the "*Ostreobium* band", named after a green alga that is commonly present in coral skeletons. However, the green band may also contain a variety of different kinds of algae, e.g., species of *Codiolum*, *Entocladia*, *Eugomontia*, and *Phaeophila*. The importance of boring algae as bioeroders is controversial; some workers claim that they are among the most destructive agents of reef erosion whereas others maintain that they cause only minimal damage (Sect. 1.1). Nonetheless, mixtures of internal bioeroder taxa – including green and red algae, bacteria, cyanobacteria, and fungi – can produce similar high-end erosion rates, ranging from 330 g $CaCO_3$ m^{-2} $year^{-1}$ on a Caribbean coral reef at Bonaire to 470 g $CaCO_3$ m^{-2} $year^{-1}$ on the Great Barrier Reef (Table 4.1).

Table 4.1 Rates of bioerosion by internal borers

Taxonomic group	Erosion rate (g $CaCO_3$/m^2/year)	Borer abundance	Particle size (µm)	Habitat	Locality	Source
Cyanobacteria						
Mostly cyanobacteria with some fungi	350	Microborings permeated sediment grains	2–6	Lagoon-floor carbonate sediments	Davies Reef, Great Barrier Reef (GBR), Australia	Tudhope and Risk (1985)
Cyanobacteria, algae, fungi	80	Chlorophyte and cyanobacteria predominant[a]	?	Inshore reef, eutrophic, turbid waters	Snapper Island, GBR	Tribollet and Golubic (2005)
	430			Offshore reef, oligotrophic, clear waters	Harrier Reef	
	470				Osprey Reef	
Cyanobacteria, chlorophytes, rhodophytes, fungi, bacteria	330 ± 50[b]	?	?	Leeward reef, high coral cover	Bonaire	Perry et al. (2012)
	290 ± 10[b]	?	?	Windward reef, low coral cover		
Porifera						
Clionaid sponges, *Pione lampa* Laubenfels predominant	23,000	Infested limestone substrates	30–80	Subtidal limestone notch, 1–3 m depth	Bermuda	Neumann (1966)
Cliona and *Siphonodictyon*	7000	Abundant in crustose coralline algae and in dead and live corals	30–80	Subtidal test blocks fringing reef	Bermuda	Rützler (1975)
	180[c]				Barbados	Scoffin et al. (1980)
Clionaid sponges	10 ± 2	*Cliona delitrix*	?	Leeward reefs, high coral cover	Bonaire	Perry et al. (2012)
	70 ± 20	*C. aprica*	?			
		C. caribbaea				
	2 ± 4	*Cliona delitrix*	?	Seaward reefs, low coral cover		
	5 ± 4					
Polychaeta						
Cirratulid, eunicid, sabellid, and spionid worms	690	13,000 ind. m^{-2}	10–30[d]	Forereef slope	Lizard Island, GBR	Davies and Hutchings (1983)
	840	24,000 ind. m^{-2}		Reef flat		
	1800	85,000 ind. m^{-2}		Lagoonal patch reef		
Crustacea						
Lithotrya ?dorsalis Sowerby	14[c]	Common	?	Fringing reef	Barbados	Scoffin et al. (1980)
Lithotrya sp.	0.8 cm^3 ind^{-1} year^{-1}	Common	2–4[e]	Intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)
Sipuncula						
Phascolosoma, 3 spp.		Uncommon in corals	<63	Fringing reef	Barbados	Scoffin et al. (1980)
Paraspidosiphon, 3 spp.	8[d]					
Lithacrosiphon gurjanovae Murina						
Mollusca						
Lithophaga nausta (Phillipi)	0.9 cm^3 ind^{-1} year^{-1}	Common	?	Intertidal limestone shore	Aldabra Atoll, Indian Ocean	Trudgill (1976)

(continued)

Table 4.1 (continued)

Taxonomic group	Erosion rate (g $CaCO_3/m^2$/year)	Borer abundance	Particle size (μm)	Habitat	Locality	Source
Lithophaga laevigata (Quoy and Gaimard)	9000	1,870 ind. m^{-2}	10–100	Largely dead patch reef, 6–10 m depth	Caño Island, Costa Rica	Scott et al. (1988)
Lithophaga aristata (Dillwyn)						
Invertebrata						
Sipunculans, Polychaete worms, Bivalve molluscs	50 ± 23^{f}	All taxa present	?	Inshore reef, eutrophic,	Low Isles	Tribollet and Golubic (2005)
			?	Turbid waters	Snapper Island, GBR	
	280^{g}	Increase in boring sponges	?	Inshore and offshore reefs	Snapper Island	
					Low Isles	
					Harrier Reef	
	80^{g}	Worms predominant (sipunculans, polychaetes)	?	Offshore reefs, oligotrophic	Lizard Island	
					Ribbon Reef	
					Osprey Reef	

[a] Predominant taxa present on exposed surfaces

[b] Mean rate (±1SD), low confidence in data

[c] Calculated from an overall borer bioerosion rate of 200 g m^{-2} $year^{-1}$, and assuming that sponges were responsible for 89 %, barnacles for 7 %, and sipunculans for 4 % of the total bioerosion (Scoffin et al. 1980)

[d] For an eunicid (Ebbs 1966), and from information supplied by P. Hutchings (pers. comm.)

[e] From Ahr and Stanton (1973)

[f] Mean rate (±1SD) for six sites, exposure time = 1 year

[g] Mean rate for three sites, exposure time = 3 years

4.2.4 Foraminifera

Some 20 species of bioeroding foraminiferans, belonging to 11 families, have been reported mainly from turbulent, tropical waters (Vénec-Peyré 1996). The majority of these mostly endolithic species occur in coral reef environments and have been found to excavate a variety of substrates, e.g. coralline algae, foraminifers, corals, bryozoans, molluscs, crustacean carapaces, wood and rocks. Only a single species from the Red Sea, *Cymbaloporella tabellaeformis* (Brady), has been reported to excavate coral skeletons. Most workers hypothesize that foraminifers penetrate hard substrates by chemical dissolution. Only a few quantitative studies on the abundances of bioeroding foraminifers are available. One such survey estimated population densities of between 150,000 and 250,000 individuals/m^2 in bioclasts present in sedimentary biotopes on a coral reef at Moorea, French Polynesia. No information is presently available on the rates of bioerosion by foraminiferans. In addition to the erosion caused directly by these protists, it is likely that the minute depressions excavated on substrates may also facilitate the recruitment of other bioeroding taxa. Clearly, much remains to be learned about the destructive capacity of these organisms.

4.2.5 Sponges

The most important genera of siliceous sponges known to bore into calcareous substrata are *Cliona*, *Anthosigmella* and *Spheciospongia*, order Hadromerida, and *Siphonodictyon*, order Haplosclerida (Wilkinson 1983). Clionaid sponges (Family Clionaidae) are among the most common and destructive endolithic borers on coral reefs worldwide. Zea and Weil (2003) have revealed that a formerly regarded single species of *Cliona* in the Caribbean consists of at least three distinct excavating sponge species. Upon splitting open infested corals, clionaid sponges are revealed as brown, yellow or orange patches lining the corroded interiors of the coral skeleton (Fig. 4.5a, d). Most boring sponges form 5–15 mm diameter chambers with smaller galleries branching off the main chambers. Their depth of penetration into the coral skeleton is usually no greater than about 2 cm. Some sponges (*Siphonodictyon*), however, can form chambers up to 100 mm in diameter that penetrate to 12 cm into coral colonies. Subsurface excavation by clionaid sponges removes the skeletal support of coral calyces, thus causing the collapse and death of polyps. In highly infested colonies, some boring sponges emerge from the skeleton, grow over and even kill live coral tissues on reef surfaces. On western Atlantic reefs,

Table 4.2 Rates of bioerosion by external grazers

Taxonomic group	Erosion rate (g $CaCO_3$ m^{-2} $year^{-1}$)	Grazer abundance (ind. m^{-2})	Particle size (mm)	Habitat	Locality	Source
Crustacea (hermit crabs)						
Trizopagurus magnificus (Bouvier)	103	27.5	0.12–0.5	Pocilloporid patch reef	Pearl Islands, Panama	Glynn et al. (1972)
Aniculus elegans Stimpson	8.5	0.02	0.25–3.0			
Mollusca						
Polyplacophora (chitons)						
Acanthopleura granulata Gmelin	227	5.5	0.03–1.0	Intertidal limestone rock	San Salvador Island, Bahamas	Rassmussen and Frankenberg (1990)
Chiton tuberculatus Linné	394	22	?	Lower intertidal coral rubble	La Parguera, Puerto Rico	Glynn (1970)
Gastropoda						
Acmaea sp.	19.2	8	0.03–1.0	Intertidal limestone rock	Andros Island, Bahamas	Donn and Boardman (1988)
Nerita tessellata Potiez and Michaud	154	220	0.03–1.0	Intertidal limestone rock	Andros Island, Bahamas	McLean (1967)
Echinodermata (sea urchins)						
Diadema antillarum Phillipi	4,600	9	?	Patch reef	St. Croix, U.S. Virgin Islands	Ogden (1977)
Diadema antillarum	5,300	23	0.05–0.5	Fringing reef	Barbados	Scoffin et al. (1980)
Diadema mexicanum A. Agassiz	139–277	2–4	0.5–2.0	Lower seaward slope	Gulf of Chiriquí, Panama	Glynn (1988)
	3,470–10,400	50–150				
Diadema savignyi Michelin	3,400	4.8	Sand	Reef lagoon	Moorea, French Polynesia	Bak (1990)
Echinometra lucunter (Linnaeus)	3,900	100	?	Algal ridge	St. Croix, U.S. Virgin Islands	Ogden (1977)
Echinometra mathaei (Blainville)	70–260	2–7	?	Limestone rock	Enewetak Atoll	Russo (1980)
Echinometra mathaei[a]	1,600	0.09	?	Outer reef flat	La Saline reef, Reunion Island	Chazottes et al. (2002)
	4,300	14.0				
Echinothrix diadema (Linnaeus)	803	0.6	Sand	Reef lagoon	Moorea, French Polynesia	Bak (1990)
Eucidaris galapagensis Döderlein	3,320	4.6	0.05–3.0	Reef flat, pre-1982	Floreana Island, Galápagos Islands	Glynn (1988)
	22,300	30.8		Reef flat, post-1983		
Diadema antillarum	10 ± 10	*D. antillarum*	?	Leeward reefs	Bonaire	Perry et al. (2012)
Echinometra viridis	10 ± 20	Predominant grazer		High coral cover		
	0			Windward reefs		
				Low coral cover		
Pisces						
Scarus iserti (Bloch)[b]	490	0.6	0.015–0.25	Patch reef	Panama	Ogden (1977)
Sparisoma viride (Bonnaterre)	61	0.01	Silt-sand	Fringing reef	Barbados	Frydl and Stearn (1978)

(continued)

Table 4.2 (continued)

Taxonomic group	Erosion rate (g $CaCO_3$ m^{-2} year^{-1})	Grazer abundance (ind. m^{-2})	Particle size (mm)	Habitat	Locality	Source
Scarus vetula (Bloch and Schneider)	140 ± 30^{c}	0.08	Silt-sand?	Reef slope	Bonaire,	Bruggemann et al. (1996)
	2,420 ± 190			Shallow reef	Netherlands Antilles	
Grazing and browsing fishes	110	0.01	?	Patch reef	Bermuda	Bardach (1959, 1961)
Chlorurus microrhinos^{d}	420–5,470	0.0007–0.009^{e}	Fine sand	Fringing reef	Lizard Island	Bellwood (1995)
	1,010–3,280	0.002–0.005^{f}	Fine sand	Fringing reef	Heron Island	Bellwood (1996)
	6,500	0.006		Shallow reef edge	Lizard Island, GBR	
Chlorurus sordidus (Forsskål)	110–500	0.02^{e}	Fine sand	Fringing reef	Lizard Island	Bellwood (1995)
	260–980	0.011–0.12^{f}		Fringing reef	Heron Island	
Parrotfishes (dominantly)	110–9,100	?	?	Reef flat, slope,	Llewellyn reef, Australia GBR	Kiene (1988)
	400–600	0.04–0.06	Fine sand-gravel	Lagoon habitats		
				patch reefs	Saipan, Mariana Islands	Cloud (1959)
Scaridae	7 ± 1	primary grazers	?	Inshore reefs, eutrophic, turbid waters	Snapper Island	Tribollet and Golubic (2005)
					Low Isles	
	320 ± 40	primary grazers	?	Offshore, oligotrophic, clear waters	GBR	
					Lizard Island	
	770 ± 220				Ribbon reef	
					GBR	
Sparisoma viride	2100 ± 1060	*S. viride* predominant	?	Leeward reefs	Bonaire	Perry et al. (2012)
	2750 ± 1390			High coral cover		
				Seaward reefs		
	950 ± 620			Low coral cover		
	1750 ± 810					
Pufferfish						
Arothron meleagris (Bloch and Schneider)	30	0.004	2–8	Pocilloporid reef	Pearl Islands, Panama	Glynn et al. (1972)

[a] Dominant echinoid affecting erosion; represented overall between 80 and 100 % of total sea urchin abundances

[b] A senior synonym of *Scarus croicensis*

[c] Mean ± standard deviation

[d] Formerly confused with *Chlorus gibbus* Rüppell, a closely related Red Sea species

[e] Abundance data are from Choat and Bellwood (1985)

[f] Abundance data are from Choat and Robertson (1975)

Cliona sp. is sometimes very abundant, forming dark brown patches several meters in extent that kill or overgrow dead surfaces and erode all calcifying organisms (Fig. 4.6). In a comparative study in Bonaire, of leeward and seaward reefs with high and low coral cover respectively, Perry et al. (2012) reported significantly higher clionaid bioerosion rates on the former than the latter (Table 4.1).

Sponge boring is accomplished by amoebocytes that etch and chip minute calcareous fragments from limestone substrata (Rützler and Rieger 1973; Pomponi 1979). The ends of etching amoebocytes flatten against the calcareous substratum and extend fine pseudopodial (filopodia) sheets into the limestone at the cell's periphery. The filopodia coalesce centrally, cutting out a hemispherical carbonate chip (Fig. 4.5e–g). This cutting is accomplished by enzymes that simultaneously dissolve calcium carbonate and the organic matter matrix of skeletons. At the end of this process, both the chip and the etching cell are transported away from the site of erosion and are expelled from the sponge. Based on careful microscopic examination, Rützler and Rieger (1973) estimated that only about 2–3 % of coral skeletons are dissolved with the remainder dispersed as

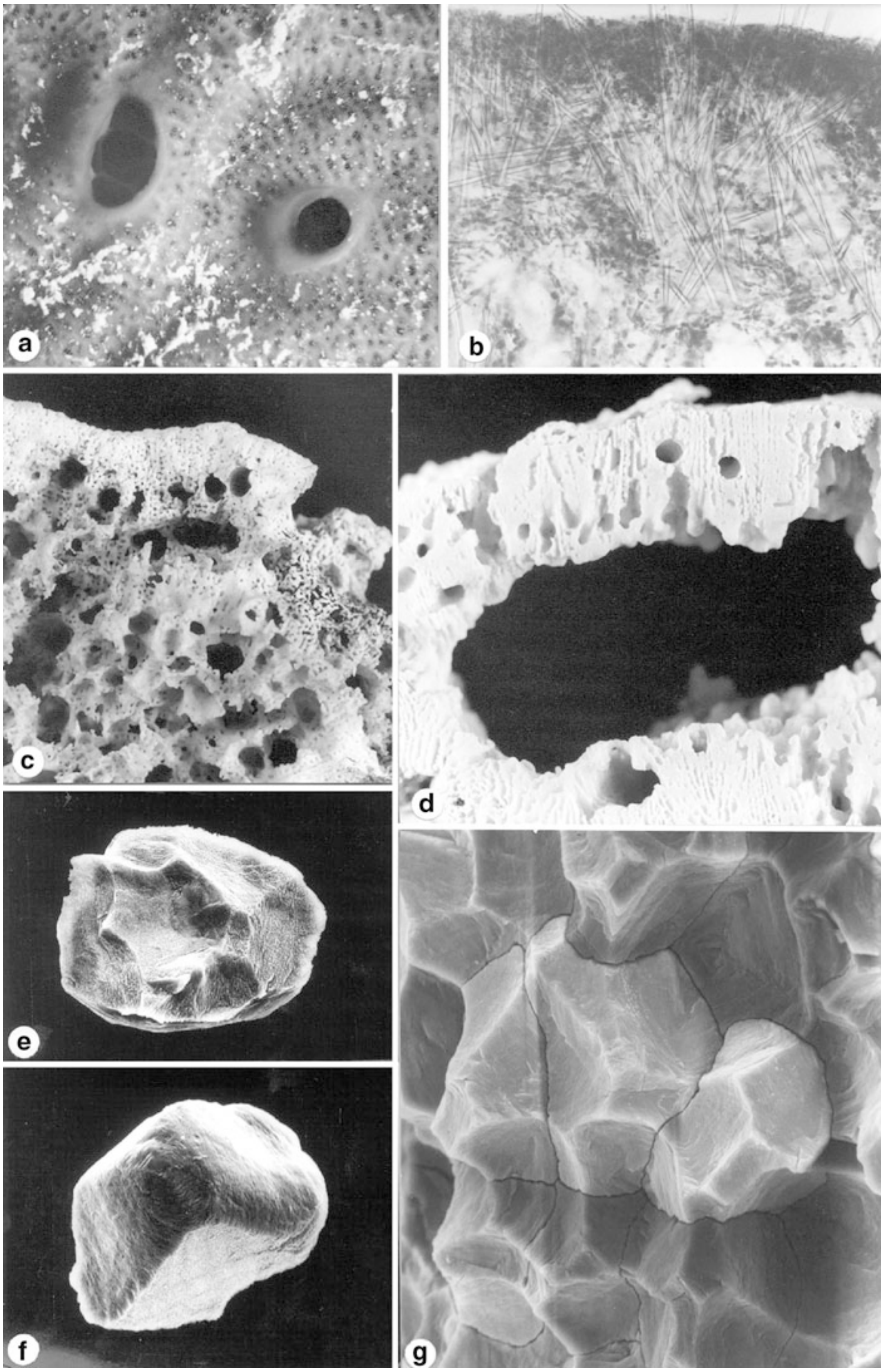

Fig. 4.5 Boring sponges in limestone substrates. (**a**) Two oscula of *Pione* (formerly *Cliona*) *lampa* (Laubenfels) visible on the surface of a massive coral (*Diploria*). (**b**) Vertical section through peripheral region of *Spheciospongia othella* Laubenfels revealing abundant spicules. (**c**) Chambers of *Cliona dioryssa* (Laubenfels) in porous coral rock. (**d**) A large tunnel running below the surface of coral rock excavated by *S. othella*. (**e**) Upper scalloped and (**f**) lower convex surfaces of isolated limestone chips discharged through the osculum of *P. lampa*. (**g**) Group of chips etched from substratum by *P. lampa* but still in place. Magnification: **a**, **c**, **d** ×3; **b** ×140; **e**, **f** ×1,500; **g** ×600 (**a**–**d** from Rützler 1974; **e**, **f**, **g** from Rützler and Rieger 1973)

silt-sized chips. These oval-shaped, faceted chips are easily recognized in sediments and can contribute up to 30–40 % numerically to the fine silt fraction of sediments on Pacific and Caribbean reefs. However, a recent study that simultaneously measured chemical and mechanical (chip production) bioerosion found that the rate of chemical dissolution was three times greater than the amount of $CaCO_3$ eroded via chip production (Zundelevich et al. 2007).

4.2.6 Polychaete Worms

Polychaete worms that bore into reef rock are enormously abundant in certain environments, prompting some workers to conclude that they are among the most important endolithic borers on coral reefs (Davies and Hutchings 1983). Various species in the following families typically form circular holes 0.5–2 mm in diameter that penetrate up to 10 cm into the interiors of coral skeletons: Cirratulidae,

Fig. 4.6 A Caribbean boring sponge (*Cliona* cf *caribbea*) covering and eroding several square meters of reef substrate, San Blas, Panama, 3 m depth (30 June 1993). *Arrows* denote perimeter of sponge patch

Eunicidae, Sabellidae and Spionidae. Eunicid holes often form a sinuous and anastomosing network (Fig. 4.1). The mechanism of boring has been reported for a few polychaete species. Some eunicids employ their mandibles to excavate. Spionids bore mainly by chemical dissolution with some removal probably due to mechanical abrasion by chaetae (Haigler 1969). Cirratulid and eunicid species are predominantly deposit-feeders whereas sabellids and spionids are mainly filter-feeders. The close physical association of eunicids and spionids with endolithic algae also has suggested the utilization of boring algae as a food source (Risk and MacGeachy 1978).

A quantitative study of boring polychaetes conducted at Lizard Island, Great Barrier Reef provides numerical abundances and bioerosion rates of a pioneer polychaete community. At various times during the study it was not uncommon to find between 27,000 and 80,000 boring polychaetes per m^2 in experimental coral blocks set out in three different reef environments (Davies and Hutchings 1983). These worms caused erosional losses of from 0.7 kg m^{-2} $year^{-1}$ on the reef front to 1.8 kg m^{-2} $year^{-1}$ on a leeward patch reef (Table 4.1).

4.2.7 Crustacea

Barnacles, shrimp, hermit crabs and other kinds of crustaceans can erode reef rock (Warme 1975). Barnacles and shrimp are endolithic borers, producing cylindrical chambers whereas hermit crabs are external bioeroders that abrade live coral surfaces.

Three groups of barnacles contain species that reside in the skeletons of dead corals, namely thoracicans, acrothoracicans and ascothoracicans. Members of the latter two taxa occupy small, mm-sized cavities that keep pace with the host coral's growth, i.e., they become embedded within the coral skeleton without causing extensive erosion. Species of *Lithotrya*, members of the thoracican barnacle taxon, erode 2–10 cm long oval-shaped cavities on the undersides of reef rock and beach rock in shallow, agitated waters (Fig. 4.1). The barnacle's basal plate is attached at the inner-most end of the cavity and the body hangs downward toward the opening with cirri exposed to food-bearing currents. The cavities are formed apparently by mechanical abrasion effected by calcified plates that cover the barnacle's body. Unlike other invertebrate endoliths, such as polychaete worms and gastropods, adjacent tubes of boring *Lithotrya* are commonly interconnected, and heavily infested limestones are thoroughly honeycombed and subject to frequent breakage. An average of one boring per cm^2 was observed on beach rock in Puerto Rico, and up to 30 % of the substratum had been removed from some of the samples examined (Ahr and Stanton 1973). Overall, however, results from studies in the Caribbean and Indian Ocean indicate that boring barnacles cause relatively little erosion compared with other internal borers (Table 4.1).

Alpheus simus Guerin-Meneville, a pistol shrimp, bores into coral rock on Caribbean reefs and causes considerable erosion on some Costa Rican reefs (Cortés 1985). Male/female pairs excavate 10–15 mm diameter chambers that penetrate as deep as 15 cm into dead coral rock. Microscopical study of the chamber walls suggests that this shrimp bores mainly by chemical means. Seven pairs of shrimp were found in one 1,500 cm^2 block, and each pair occupied an average chamber volume of 20 cm^3. This is equivalent to the removal of about 950 cm^3 of calcium carbonate m^{-2} . The life span of the shrimp is about 2 years, but since succeeding generations of shrimp probably occupy the same chambers it is not possible to calculate annual erosion rates.

Two species of hermit crabs that feed on live coral produce large amounts of calcareous sediment when they scrape corals to remove soft tissues (Fig. 4.1). The average mass of coral abraded by a small hermit crab [*Trizopagurus magnificus* (Bouvier)] was about 10 mg ind^{-1} day^{-1}, and for a large hermit crab (*Aniculus elegans* Stimpson) about 1 g ind^{-1} day^{-1} (Glynn et al. 1972). Relating hermit crab population densities and erosion rates, it was found that *Trizopagurus* and *Aniculus* respectively were responsible for the generation of about 1 and 0.1 metric tons of coral sediment ha^{-1} $year^{-1}$ on a fringing reef in Panamá (Table 4.2). Since this rate of coral abrasion by hermit crabs has not been reported elsewhere, it is possible that these high levels of erosion are unique to the eastern Pacific.

4.2.8 Sipuncula

Although it is well known that species in several genera of sipunculans (peanut worms) penetrate coral skeletons, there is no general agreement on the overall importance of this group in the bioerosion of coral reefs. Perhaps this is due to their great variation in abundance from reef to reef and across reef zones (Macintyre 1984).

Sipunculan borings are cylindrical and pencil-sized or slightly smaller, ranging from straight to sinuous and from near-surface to several cm deep in coral skeletons, depending on the species (Fig. 4.1). Sipunculans are abundant on some reefs: nearly 800 inds m^{-2} were present in reef crest substrata, and 1,200 inds m^{-2} in *Porites* coral skeletons in Belize (Rice and Macintyre 1982). Even at 30 m depth, 40 inds m^{-2} were found. While feeding, sipunculans extended their introverts outside of their cavities and appear to ingest debris, sand and algae. The exact manner of boring is not known, but may involve both chemical dissolution and mechanical abrasion (Rice and Macintyre 1972). An estimated sipunculan erosion rate on a Barbados reef indicated only minor carbonate loss (Table 4.1).

4.2.9 Mollusca

Most bioeroding molluscs are external grazers that abrade reef rock while feeding on algae and associated organisms residing on and within limestone substrata. The eroding capacity of surface enmeshed and endolithic algae, important components of the diet of grazing molluscs, also weakens the substratum and thus facilitates erosion during feeding. A group of mussel-like endolithic borers also is prominent on many reefs worldwide.

Molluscan bioeroders are generally most abundant in the intertidal zone with some species extending their ranges into supratidal and subtidal habitats (Fig. 4.7a). Species abundances also change horizontally with chitons often most plentiful in areas protected from strong wave assault and limpets, certain snails, and echinoids more common in wave swept habitats (Fig. 4.7b). Under quiet to rough water conditions, grazing molluscs are largely responsible for producing the notches and nicks on tropical limestone shores. Most early workers surmised that intertidal notches were formed through strictly physico-chemical processes (e.g., the localized lowering of pH and accompanying carbonate dissolution), which resulted in the erosion of the underlying rock. Under extremely rough conditions, many bioeroders either disappear or their activities are greatly reduced. Calcifying taxa, such as coralline algae and vermetid molluscs, increase in abundance with increasing exposure, probably because of ecologic requirements for high energy habitats and a lower abundance of fish consumers in rough water areas (Fig. 4.7c). Vermetid/coralline algal buildups help protect the underlying limestone, thus limiting bioerosion and the development of intertidal notches and nicks in such areas (Focke 1978).

Several species of chitons (Class Polyplacophora), e.g., members of *Acanthopleura* and *Chiton*, erode chiefly intertidal limestone substrata while grazing on algae. The grazing is achieved with a magnetite (Fe_3O_4) or other mineral-enriched radula, a tooth-bearing strap of chitinous material, that effectively abrades the substratum (Lowenstam and Weiner 1989). Some erosion also occurs at homing sites, rock depressions that are occupied by chitons when not foraging. As many as 50–100 sausage-shaped, 1–3 mm long fecal pellets are voided daily by individual chitons (Rasmussen and Frankenberg 1990). Erosion rates vary greatly among sites as they are influenced by local differences in rock type and condition, and ecological factors affecting chiton abundances and feeding activities (Table 4.2).

Limpets and snails (Class Gastropoda) often occur with chitons on intertidal carbonate substrata. *Acmaea*, *Cellana* and *Patelloida* are common limpet genera, and *Cittarium*, *Littorina*, *Nerita* and *Nodilittorina* are some common snail genera. Like chitons, limpets and snails utilize a radula to

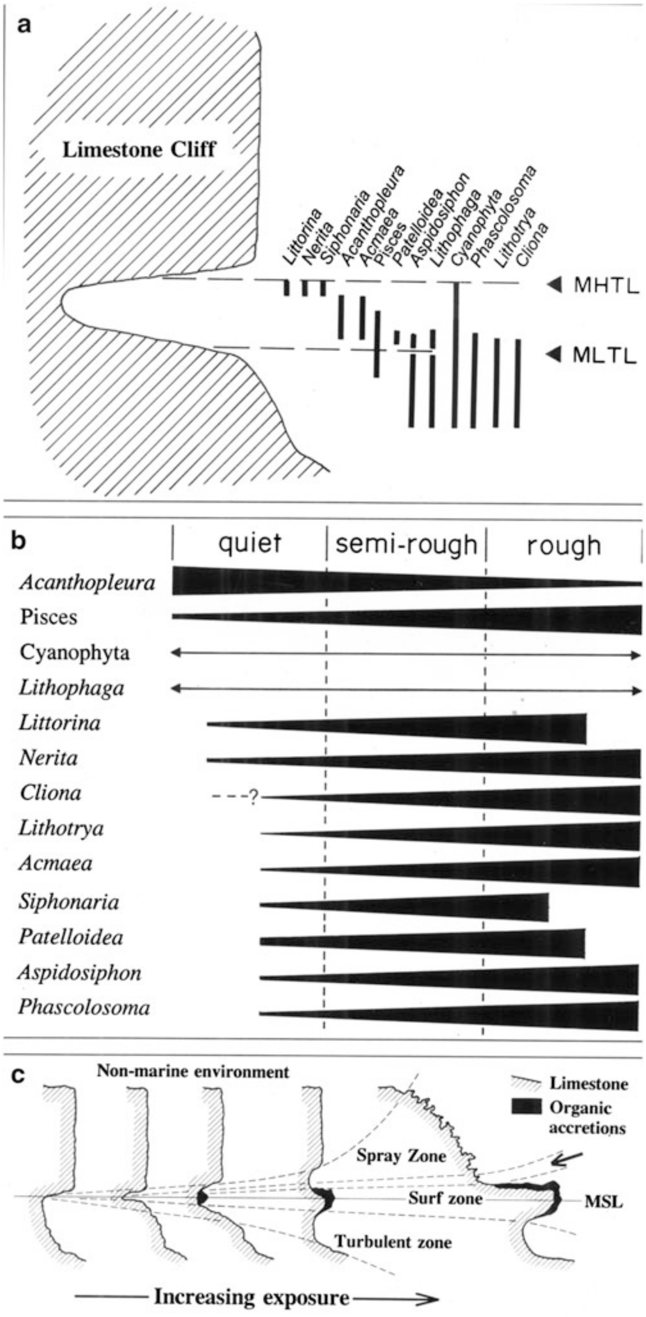

Fig. 4.7 Vertical (**a**) and horizontal (**b**) distributions of bioeroding molluscs and other bioeroder taxa on a limestone shore at Palau, Caroline Islands. Theoretical relationship (**c**) of coastal profile morphology to water turbulence at Curaçao, Netherlands Antilles. An *arrow* locates a "transition zone" between the "spray" and "surf zones" (**a** and **b** after Lowenstam 1974; **c** after Focke 1978)

scrape rock surfaces. The radula of patellacean limpets is an especially effective excavating organ with opal ($SiO_2.nH_2O$) or goethite ($HFeO_2$)-sheathed radular teeth (Lowenstam and Weiner 1989). The radula of snails contains proteinaceous teeth, but these grazers are still capable of erosion because of the often weakened condition of the rock substratum upon which they feed (Table 4.2). Some gastropods (muricaceans, naticids) and cephalopods (notably *Octopus* spp.) employ the radula as a drilling tool, producing circular holes in thick shells to help expose the soft tissues of their gastropod and bivalve prey (Ekdale et al. 1984). The contribution of the fine grains thus produced to reef sedimentation rates has not been reported, but drilled mollusc shells are commonly observed in reef sediments.

Species of *Lithophaga* and *Gastrochaena* (Class Pelecypoda) bore into dead and live corals, and are most abundant subtidally, with some of these bivalves attacking reef corals to their lower depth limits. *Fungiacava* spp. penetrate live mushroom corals, but their activities are relatively minor. The siphonal openings of *Lithophaga* typically have a keyhole-like appearance on coral surfaces and the circular holes penetrate vertically into the skeleton, from 1 to 10 cm deep depending upon the species (Figs. 4.1 and 4.2b). The lithophagines are deposit and suspension feeders, often most abundant in areas of high productivity. The mantle glands of *Lithophaga* secrete acid that dissolves and weakens the limestone substratum. The vertical and rotational movements of the shell also assist in boring, resulting in the production of silt/sand-sized sediment. Population densities in productive equatorial eastern Pacific waters range from 500 to 10,000 inds m^{-2} (Scott et al. 1988), which can lead to rapid reef erosion (Table 4.1).

4.2.10 Echinoidea

Sea urchins (Echinoidea) are the only echinoderms capable of significant bioerosion. Several species in the following genera abrade large amounts of reef rock while feeding and excavating burrows: *Diadema*, *Echinometra*, *Echinostrephus*, and *Eucidaris*. Sea urchins possess a highly evolved jaw apparatus (Aristotle's lantern), a flexible and protrusible mastigatory organ consisting of five radially arranged, calcified teeth. The teeth are mineralized, and must be harder than the corroded surfaces they scrape. Sea urchin spines also assist in bioerosion when they are employed in the enlargement of burrows. Sea urchins graze on algae growing on dead coral substrata, but in some areas also attack live coral. On seaward reef platforms where water flow is vigorous, sea urchins usually remain in their burrows and feed predominantly on drift algae. In the Bonaire study by Perry et al. (2012), high echinoid bioerosion occurred on leeward reefs with high coral cover, but none was reported on windward reefs, similar to the habitat differences noted for clionaid sponges (Table 4.2). Sea urchins can cause substantial erosion at low and moderate population densities; at high densities, their destruction of reef substrata rivals clionaid sponge erosion and can lead to rapid framework loss.

4.2.11 Fishes

Numerous fish species erode reef substrata while grazing on algae, and also fragment colonies while feeding on live coral tissues or when extracting invertebrates from coral colonies (Randall 1974). Surgeonfishes (Acanthuridae) and parrotfishes (Scaridae) are the principal grazing groups with some fishes in the latter family capable of scraping and extensive excavation. On western Pacific reefs, excavating parrotfishes primarily bite convex surfaces, thus reducing the topographic complexity of reefs (Bellwood and Choat 1990). Some Atlantic and Pacific parrotfishes occasionally scrape and ingest live coral tissues (Bellwood and Choat 1990; Glynn 1990a). Triggerfishes (Balistidae), filefishes (Monacanthidae) and puffers (Tetraodontidae, Canthigasteridae) are largely carnivorous in feeding habits and are responsible for fragmenting or grazing on live coral colonies (Fig. 4.2a). The jaw muscles and tooth armature are well developed in all of these families. Parrotfishes also have a pharyngeal mill, a gizzard-like organ that further reduces the size of ingested sediment. Fish teeth are composed of dahllite [$Ca_5(PO_4CO_3)_3(OH)$] or francolite (the fluorinated form), both apatite minerals that are harder than $CaCO_3$ (Lowenstam and Weiner 1989).

Parrotfish grazers can produce large amounts of sediment on reefs, especially when their population densities are high. For example, *Scarus iserti* generated nearly 0.5 kg $CaCO_3$ m^{-2} $year^{-1}$ on a Caribbean reef in Panamá with a high abundance of just under one fish per m^2. Entire grazing fish communities, comprised dominantly of parrotfishes, typically erode large amounts of reef substrata. One of the highest erosion rates reported for fishes, 9.1 kg $CaCO_3$ m^{-2} $year^{-1}$, occurred in the lagoon of an Australian reef (Table 4.2). It should be recognized, however, that relatively few scarid species in any given fish community are capable of excavating significant amounts of carbonate substrata. For example, Bellwood and Wainwright (2002) noted that only one of 18 scarid species at a Lizard Island site (Great Barrier Reef) effected high rates of erosion. Additionally, at a Red Sea site, three of ten scarids contributed importantly to bioerosion, and at a Caribbean site (Carrie Bow Cay, Belize) only one of six scarids excavated reef substrata. In this regional comparison, the highest rate of bioerosion was effected by the Australian scarid *Chlorurus microrhinos*, which excavated 6,500 g m^{-2} $year^{-1}$ (Table 4.2). Parrotfishes can exhibit interesting spatial differences vis-à-vis grazing activity and consequent erosion (Table 4.2). On the Great Barrier Reef, highest erosion was observed on offshore reefs in oligotrophic waters compared to inshore reefs in eutrophic environments (Tribollet and Golubic 2005). On reefs at Bonaire, parrotfish erosion rates were generally highest on leeward reefs with high coral cover compared to seaward reefs of low coral cover (Perry et al. 2012).

While carnivorous fishes can cause substantial damage locally, their reef-wide effects seem to be relatively minor. For example, a pufferfish (*Arothron*) that erodes about 20 g of coral per day results in a total reef loss of only 30 g $CaCO_3$ m^{-2} $year^{-1}$ (Glynn et al. 1972) because of a relatively low population size of 40 individuals per hectare (Table 4.2).

Several other bioeroders known to produce traces or otherwise damage reef rock, e.g. foraminifers, zoanthids, bryozoans and brachiopods (Warme 1975), may contribute to reef degradation under special conditions. To assess the relative importance of the various bioeroders considered in this survey, one may compare their rates of reef destruction with known carbonate production rates. Net carbonate production rates vary greatly among reefs and between reef zones, but 3,000–5,000 g $CaCO_3$ m^{-2} $year^{-1}$ have been reported for many of the world's coral reefs (Kinsey 1983). Among the internal borers, clionaid sponges and lithophagine bivalves can cause a comparable level of bioerosion, and of the external grazers sea urchins are equally destructive. Reef frameworks are generally reduced to silt and fine sand by internal borers and to fine and coarse sand by external grazers. The combined effects of other bioeroders may also contribute importantly to reef erosion in particular areas or zones and at different times.

4.3 Conditions Favoring Bioerosion

Bioerosion increases under a variety of circumstances that can be classified according to (a) conditions causing coral tissue death and (b) conditions that provide a growth advantage to bioeroder compared with calcifying species' populations. Some of the more important situations that can alter the course of bioerosion are noted here in general terms. Specific examples are considered below in the examination of case studies (Sect. 4.5).

Aside from a few species that invade coral rock directly through living tissues (e.g., some boring sponges, bivalves and barnacles), the great majority of endolithic borers attack dead skeletons (Fig. 4.8). In general, any condition that causes coral tissue death will increase the probability of invasion by borers and grazers. Thus, any natural or anthropogenic disturbances that lead to the loss of live coral tissues will ultimately increase the chances of bioeroder invasion and higher rates of limestone loss. Many disturbances leading to tissue loss are obvious, including storm-generated surge that dislodges and topples corals, sediment scour and burial, tidal exposures, sudden temperature changes, freshwater dilution, sewage and eutrophication, predation, and disease outbreaks (Endean 1976; Pearson 1981; Grigg and Dollar 1990).

While violent tropical storms are natural events that are known to seriously affect coral reefs, storm damage certainly must be exacerbated on reefs that have been heavily

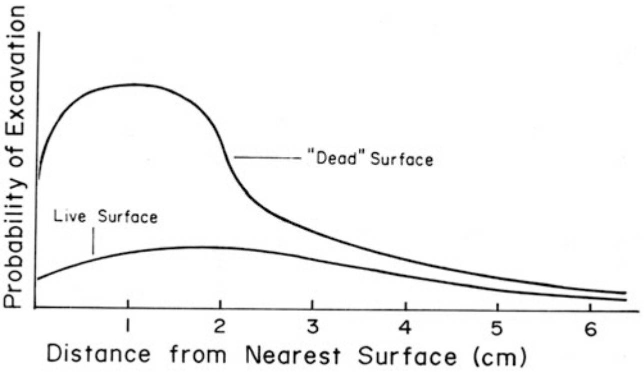

Fig. 4.8 Graphic model showing the probability of excavation of endolithic bioeroders as a function of distance from a coral's surface (Redrawn from Highsmith 1981a). *Curves* are illustrated for corals with dead and live surfaces

bioeroded beforehand. Sudden chilling episodes are also natural disturbances that can have devastating effects on tidally exposed or shallow coral assemblages, especially on high latitude reefs. Numerous incidences of coral bleaching (loss of zooxanthellae and/or pigmentation) and mortality were observed world-wide in the 1980s and 1990s, and many of these events occurred during periods of elevated sea temperatures coincident with El Niño-Southern Oscillation activity. Corals that were damaged or killed during these bleaching events have been subject to further damage by bioerosion. Rützler (2002) noted examples of accelerated boring sponge erosion on bleached Caribbean corals stressed by temperature extremes and other suboptimal conditions in recent years. In some parts of the eastern Pacific where coral mortality was high and community recovery slow, extensive damage by both internal and external bioeroders has been observed.

Increases in nutrient loading often cause coral tissue mortality, lowered reproductive success and lower rates of coral settlement and recruitment. Besides such direct negative effects on reef-building corals, nutrient inputs can also cause changes in the community structure of epilithic algae. On a La Saline Reef (Reunion Island), increased nutrification has been found to favor the replacement of algal turfs by encrusting calcareous algae and macroalgae (Chazottes et al. 2002). On the one hand, this qualitative change in algal cover can result in reduced bioerosion by external bioeroders and macroborers, but on the other hand it can elevate rates of bioerosion by microendolitic borers. External bioeroders (sea urchins and fishes) may feed less on calcareous algae and macroalgae than on turfs. This reduced grazing in turn allows the proliferation of endolithic borers, whose growth would otherwise be limited under intense grazing pressure. It is cautioned that this sequence of events is not invariant due to other factors that often accompany elevated nutrient conditions (see below).

Predator outbreaks leading to high coral mortality, such as by seastar (*Acanthaster*) and snail (*Drupella*) corallivores reported from various areas of the Indo-Pacific, can set the stage for rapid bioerosion. Territorial damselfish that colonize dead reef surfaces can cause complex responses that both increase and decrease bioerosion. Damselfish that invade dead coral patches typically kill nearby corals while enlarging their territories. Studies in Australia have shown that the algal turf communities maintained by damselfish favor the proliferation of internal bioeroders (Risk and Sammarco 1982). However, the territorial defensive behavior of damselfish also limits the bioerosive activities of external grazers such as parrotfishes and sea urchins (Glynn and Wellington 1983; Eakin 1993).

Coral tissue loss due to a variety of diseases can be substantial (Chap. 8; Peters 1984). For example, "black line disease" or "black band disease", the result of a cyanobacterial infection (Rützler et al. 1983), may consume one-half of the living tissues of a coral during a single warm season infestation. All live tissues may be sloughed from corals by "white band disease", "shut-down-reaction" or "stress-related-necrosis". Though the causative agents of such diseases often remain elusive, their occurrence seems to be influenced by elevated sea water temperature, increased sedimentation and turbidity.

Since the majority of endolith bioeroders are suspension or filter feeders in contrast to calcifying species, which are dominantly autotrophic, generally increases in nutrients, organic matter and plankton biomass tend to favor increases in bioeroder compared with calcifier populations (Fig. 4.9). Because land runoff usually augments siltation and nutrient loading simultaneously (and sometimes pollutant levels), it is often difficult to distinguish between these effects. Unlike La Saline Reef, Pari et al. (1998) found that a polluted reef in Tahiti (at Faaa) is subject to intense grazing by sea urchins. But this South Pacific site is influenced by elevated nutrients, and additionally by terrigenous sediments and chemical pollutants. Moreover, the Pacific reef also exhibits different algal assemblages. Thus, even though both reefs are subject to high nutrient regimes, it is not possible to predict changes in the rates of bioerosion because of potentially numerous confounding influences.

There are at least two ways in which bioerosion is self-reinforcing. The first of these is the weakening effect of bioeroders on reef structures and the skeletons of calcifying organisms. For example, as bioerosion increases the volume of internal spaces (porosity) of coral skeletons, less mechanical force is required for breakage, toppling and overturning (Fig. 4.10). Thus, heavily bioeroded reefs are more susceptible to damage by strong surge and projectiles accompanying violent storms. The second kind of positive feedback results from increasing levels of sediment production by bioeroders and its deleterious effects on calcifying populations.

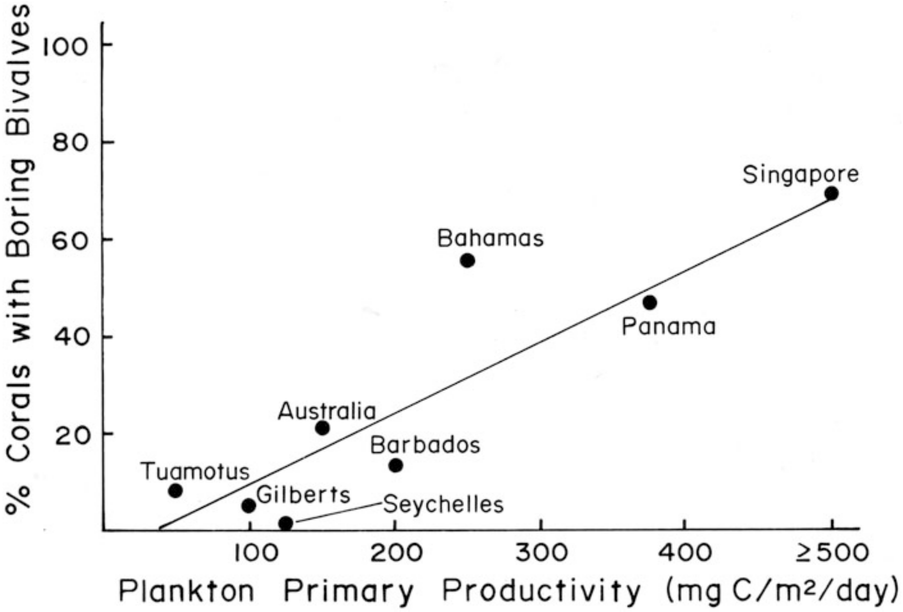

Fig. 4.9 Relationship between the percentage of massive corals infested with boring bivalves and levels of phytoplankton productivity at several geographic locations (Redrawn from Highsmith 1980). Selected areas with values close to the plotted means are indicated. Each mean consists of various sampling areas and colony numbers, respectively, as follows: Tuamotu Islands—6, 212; Gilbert Islands—2, 58; Seychelle Islands—2, 12; Australia—7, 135; Barbados—7, 55; Bahama Islands—2, 64; Panama—4, 70; Singapore—5, 144

Overfishing can also promote increased bioerosion on reefs. If natural fish predators of some bioeroder populations are eliminated, e.g. triggerfishes that prey on sea urchins, then it is possible for grazing sea urchin populations to increase in size with a devastating effect on reef limestones. Overfishing of parrotfishes causes declines in bioerosion, given their role as important bioeroding agents on reefs. However, the long-term effect of parrotfish exploitation is a depression in the overall carbonate budget because the absence of parrotfishes leads to a decline in coral cover and carbonate production from increases in algal abundance due to reduced grazing (Kennedy et al. 2013). Angelfish predation exerts a strong control on the abundances of clionaid sponges (Hill and Hill 2002), thus overfishing of these species might lead to increases in boring sponge population size.

Climate change, owing to anthropogenic CO_2 emissions since the industrial revolution, is a leading threat to the survival of coral reef ecosystems over the twenty-first Century (Hoegh-Guldberg et al. 2007). Elevated and increasing CO_2 concentration in the Earth's atmosphere is associated with global warming and an increase in extreme weather events and patterns (IPCC 2007). Warm water bleaching events have increased in severity and spatial scale, particularly over the past 30 years (Baker et al. 2008). Bleaching events reduce $CaCO_3$ production by corals, but also can be followed by increases in bioeroder abundances (Glynn 1988). After ENSO-related bleaching and mortality in the eastern tropical Pacific (ETP), echinoid abundances increased greatly, in part due to the resultant increase of algal food sources on dead coral skeletons, and caused significant bioerosion of reef framework structures (Glynn 1988; Eakin 2001). Clionaid sponges have also been reported to increase after bleaching events, perhaps due to the increase in available substrates following coral mortality (Rützler 2002; Schoenberg and Ortiz 2009). This is not limited to warm water bleaching, as clionaid sponge populations also exhibited large increases after cold-water bleaching in the Florida Keys (Manzello, pers. obs.) that caused mass coral mortality (Lirman et al. 2011). An increase in the frequency, severity, and/or duration of warm and cold-water events with climate change negatively impact the $CaCO_3$ budget of coral reefs via reductions in coral calcification and increases in bioerosion.

Anthropogenic CO_2 emissions are not only changing the climate of the planet, but they are also altering the chemistry of the world's oceans. About one-third of all the CO_2 released into the atmosphere since the industrial revolution has been taken up by the oceans (Sabine et al. 2004). This process, termed ocean acidification (OA), has caused a decline in oceanic pH of 0.1, and will likely cause a further decline of 0.3–0.4 pH units by the end of the twenty-first century (IPCC 2007). The anthropogenic acidification of the oceans is occurring at a rate that is unprecedented over at least the past 55-300 million years (Hönisch et al. 2012). OA results in a decrease in seawater $[CO_3{}^{2-}]$ and, consequently, a decrease in the saturation state of carbonate minerals ($\Omega = [CO_3{}^{2-}]\ [Ca^{2+}]/K'sp$, where $K'sp$ is the solubility product for a carbonate mineral). Declines in aragonite saturation state (Ω_{arag}, aragonite is the crystalline form of $CaCO_3$ precipitated by scleractinian corals) lead to reduced rates of coral calcification (Langdon and Atkinson 2005). In this review, we have emphasized that the rate of $CaCO_3$ production only slightly exceeds its rate of loss on healthy coral reefs, therefore any disturbance forcing global-scale declines in calcification, such as OA, is alarming (Kleypas et al. 1999a).

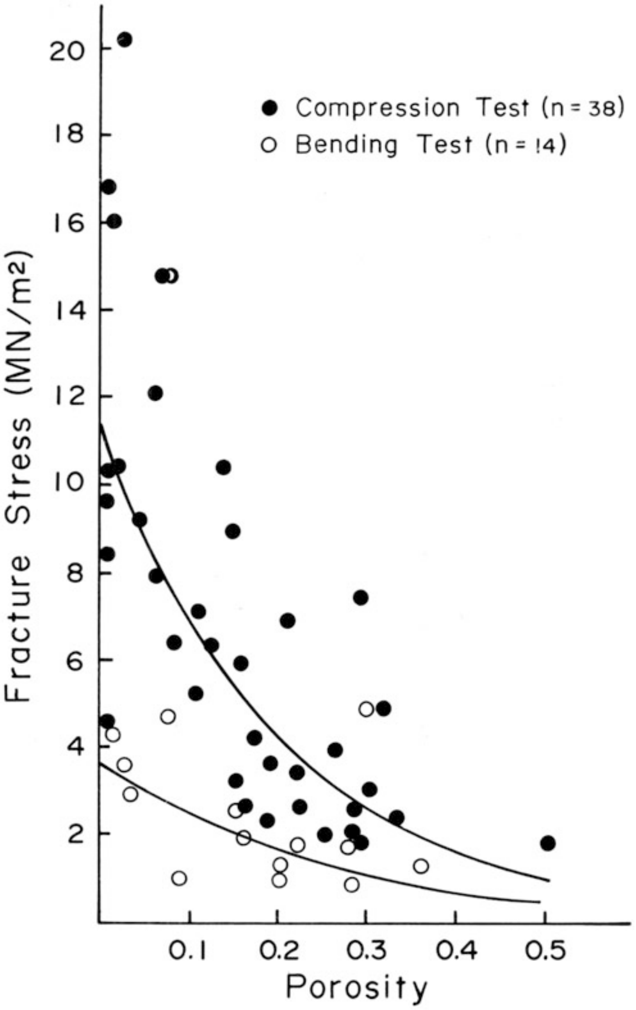

Fig. 4.10 Plot of coral strength to breaking versus amount of bioerosion by *Lithophaga* (Redrawn from Scott and Risk 1988). The compression and bending tests are two measures of a coral's strength. *N* = newton, a unit of force, *MN* 0.22481 × 10^6 lbf. Porosity indicates the percent of the skeleton removed

Recent experimental work has shown that high-CO_2 conditions lead to accelerated rates of bioerosion by endolithic algae and clionaid sponges. Tribollet et al. (2009) exposed coral blocks to 400 ppm and 750 ppm pCO_2 for three months following the recruitment of a natural epilithic and endolithic community over 8 months of field deployment in Hawai'i. The alga, *Ostreobium querkettii*, was the dominant agent of bioerosion and the depth to which its filaments penetrated the coral rock substrate increased significantly in the high-CO_2 treatment, leading to a 48 % increase in $CaCO_3$ dissolution. Reyes-Nivia et al. (2013) observed enhanced biologically-mediated dissolution associated with increases in endolith biomass and respiration during combined exposure to elevated CO_2 and temperature. These workers found a significant effect of substrate, as skeletons of the coral *Porites cylindrica* exhibited a higher increase in endolith bioerosion when compared to the more dense *Isopora cuneata*, as well as an increase in the relative abundance of *O. querkettii* within the endolithic community. This is intriguing as previous authors have suggested that internal bioerosion is highest in more dense coral skeletons (Highsmith 1981b; Schönberg 2002), yet the response due to high temperature and high-CO_2 may follow a reverse pattern.

Bioerosion by clionaid sponges will also intensify in a high-CO_2 world (Wisshak et al. 2012; Fang et al. 2013a, b; Enochs et al. 2015). Biologically-mediated chemical dissolution by the common Caribbean boring sponge *Pione lampa* (formerly *Cliona lampa*) is predicted to increase 99 % by the end of the twenty-first century as a result of OA, which is nearly double the expected decline in coral calcification (Enochs et al. 2015). Fang et al. (2013a) examined the combination of high-CO_2 and high-temperature and reported increases in both sponge biomass and bioerosion rate by the zooxanthellate Pacific boring sponge *Cliona orientalis*. However, these workers found that *Symbiodinium* population abundances within *C. orientalis* decreased with increasing CO_2 and bleached in their experimental treatment, mimicking elevated temperatures and CO_2 concentration expected by the end of the century under a business-as-usual emissions scenario. In spite of this, bioerosion rates were still highest in the bleached sponges at the highest exposures of CO_2 and temperature, even though biomass was reduced by bleaching and peaked at a lower CO_2 scenario. In a complementary study, it was suggested that the stimulation of bioerosion at high-CO_2 in *C. orientalis* may be tempered by high temperatures due to bleaching, reductions in biomass, and an overall negative energy balance, as more carbon is consumed than produced at high temperature (Fang et al. 2013b). This suggests that bioerosion rate could increase up to some thermal threshold and then decline due to bleaching, and potentially cease, if mortality occurs.

Enochs et al. (2015) observed a similar parabolic or asymptotic response in *Pione lampa* to high-CO_2, however this was independent of bleaching, as this species is azooxanthellate, and temperature was held constant at 25 °C. Further work is necessary to better understand the mechanism of CO_2 stimulation of biologically mediated chemical dissolution in clionaid sponges to determine if this similarity is a coincidence or represents an optimal pH range for clionaid physiological function.

4.4 Variety of Effects

The chief effect of bioerosion emphasized thus far is the mass of calcium carbonate that is reduced to sediments or is dissolved from reef substrata. The weakening of reef substrata by bioeroders that remove relatively little carbonate, but attack critical supporting structures, can be just as important in promoting reef erosion. Large massive corals may be easily toppled or overturned after their supporting bases have been weakened by endolithic borers such as *Cliona*, *Lithotrya* and *Lithophaga* or by grazers that attack bases and hollow out the interiors of colonies such as *Diadema* and *Eucidaris*. Many of the displaced corals on reefs, e.g., those making up emergent, rubble ramparts or deep, forereef talus accumulations, owe their new locations in large measure to bioerosion. Large stands of *Acropora* corals that collapsed after *Acanthaster* predation on reefs in Japan, Palau and Australia were presumably destabilized as a result of the weakening of dead skeletons by intensified bioerosion (Moran 1986; Birkeland and Lucas 1990).

Aside from weakening reef substrata, the cavities produced by bioeroders increase habitat complexity and thus the variety and biomass of reef associated organisms (Enochs and Manzello 2012a, b). Numerous reef species live permanently attached to cavity walls, pass particular stages of development in cavities, and reside in cavities by day or night. Reef cavities tend to collect sediments that are produced locally or are transported to reefs from more distant sources. The microenvironmental settings of cavities promote internal cementation and the strengthening of reef substrata. Cycles of internal bioerosion, infilling of cavities and cementation may be repeated so that eventually the reef rock appears quite different from its original condition.

The sediments generated by bioeroders accumulate around reefs and eventually infill and bury frame-building species (Fig. 4.11). This effect leads to the shoaling of reef waters and influences the development of reef zonation. Under moderate regimes of bioerosion, sediment accumulation does not overwhelm reef framework growth, however, excessive bioerosion can lead to premature burial and widespread coral death.

When bioerosion is excessive it can reduce the topographic complexity of reefs. The reefs noted above in the

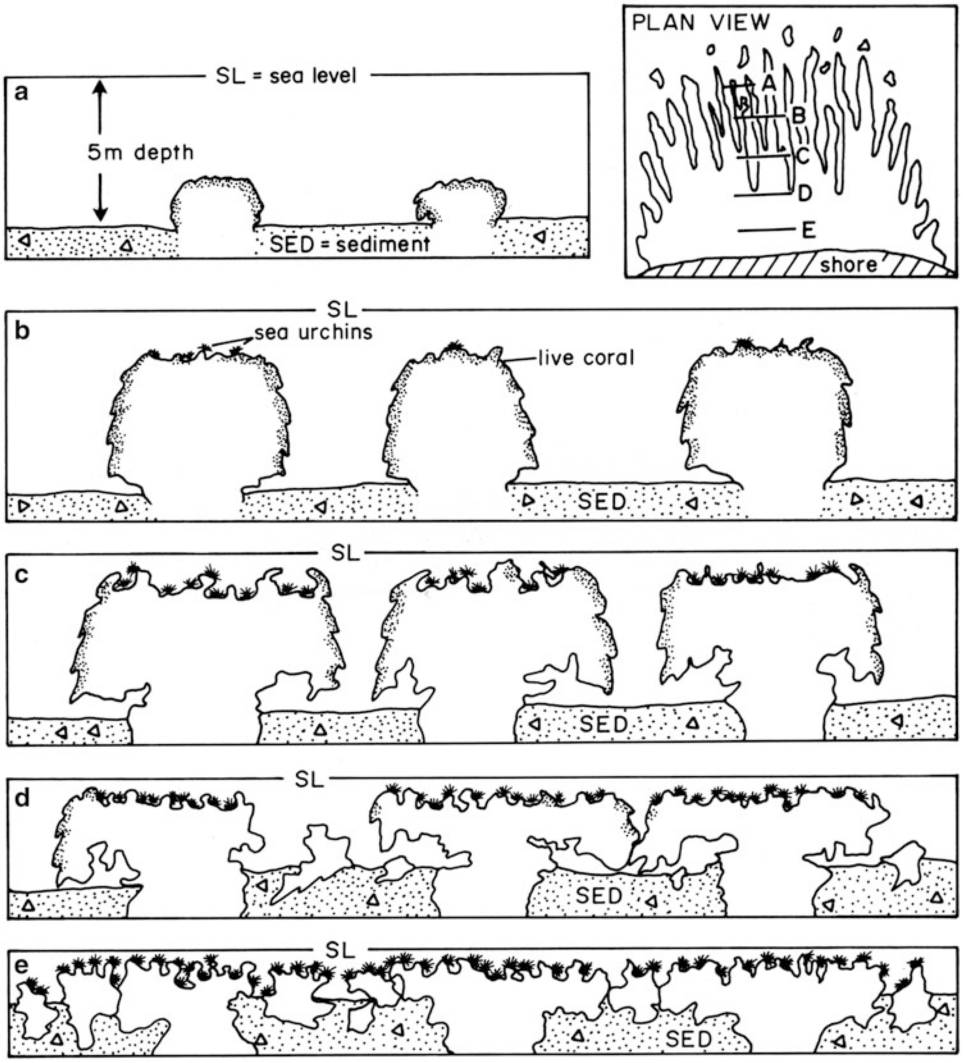

Fig. 4.11 Cross-section views of a fringing reef off the west coast of Barbados showing coral framework growth, bioerosion, and infilling by bioeroded sediments. Panels **a**–**e** illustrate seaward (*deep*) to shoreward (*shallow*) reef sections. The inset plan view shows the location of the panels (After Scoffin et al. 1980)

western Pacific that were subjected to intense predation by *Acanthaster* and then bioeroded, lost much of their three dimensional structure with the collapse of the *Acropora* canopies. The loss of these erect corals would eliminate important microhabitats for fishes. The topographic complexity of eastern Pacific reefs can also be reduced by echinoid bioerosion following El Niño disturbances. Coral reefs in the eastern Pacific, particularly in the Galápagos Islands, have been bioeroded to rubble and fine-grained sediments following high coral mortality and low recruitment, respectively, during and after the 1982–1983 El Niño event (Glynn 1994; Reaka-Kudla et al. 1996). Erect, branching coral frameworks have collapsed and massive corals have detached from the substratum and fragmented. Coral recruitment is now generally severely limited with macrobenthic communities composed dominantly of turf algae, gastropods, sea urchins and sea cucumbers.

Like many kinds of plants that spread from cuttings, it seems that some corals may actually benefit from increased breakage facilitated by bioerosion. A common mode of reproduction in many branching coral species is by asexual fragmentation (Tunnicliffe 1979; Highsmith 1982). It has been argued that propagation by this means, which usually results in local rather than distant dispersal, is advantageous to populations that are well adapted to particular environmental settings. Asexual reproduction occurs most commonly among branching, plate-like and other such colonies of delicate morphology with bioerosion aiding breakage by mechanical and biotic agents. Large clones of corals that dominate certain reef zones have arisen by this means (Highsmith 1982).

4.5 Case Studies

Six documented cases of environmental alterations that have affected or threaten reef-building corals are now examined. The first two examples, disturbances caused by El Niño-Southern Oscillation and predator outbreaks, are ostensibly natural events. Runoff and overfishing effects are then examined, representing two examples caused by humankind. In addition, we discuss how many Caribbean reefs are presently in a net erosional state and how they will further be affected by climate change. Lastly, we show how eastern tropical Pacific reefs represent a real-world climate change model, providing insight into how thermal stress and ocean acidification may affect coral reefs of the future.

4.5.1 El Niño-Southern Oscillation

Elevated seawater temperatures that accompanied the 1982–1983 El Niño-Southern Oscillation (ENSO) caused high coral mortality on reefs in the equatorial eastern Pacific. Mortality ranged from 50 to 99 %, resulting in the virtual elimination of coral cover on many reefs. Coral recruitment has been low to non-existent on many of the affected reefs, which had shown little signs of recovery after 10 years. A more recent analysis of coral reef recovery in the eastern tropical Pacific, including effects of both the 1982–1983 and 1997–1998 ENSO events, revealed no recovery at most monitored sites for periods of up to 20+ years (Wellington and Glynn 2007; Baker et al. 2008; Glynn et al. 2015).

Sea urchin abundances have increased dramatically on dead reef patches. In Panamá, *Diadema* population densities have increased from 3 inds m^{-2} before 1983 to 80 inds m^{-2} after 1983 (Glynn 1988). Similarly, in the Galápagos Islands *Eucidaris* population densities increased from 5 to 30 inds m^{-2} from before to after 1983. Probably contributing to this post-El Niño sea urchin increase were the high mortality of lithophagine molluscs (Scott et al. 1988) and the resulting large numbers of vacant bore holes that became available in massive *Porites* colonies. Numerous juvenile *Eucidaris* ($\leq$1 cm test diameter) recruited to these newly available shelter sites. The grazing activities of these sea urchins are very destructive (Table 4.2) and their sudden increases in population size, combined with low coral recruitment, have resulted in severe bioerosion of coral reef frameworks. Post El Niño bioerosion rates for *Diadema* in Panamá amounted to 10–30 g dry wt $CaCO_3$ m^{-2} day $^{-1}$, and for *Eucidaris* in the Galápagos 50–100 g dry wt $CaCO_3$ m^{-2} day $^{-1}$. Carbonate breakdown caused by other external and internal bioeroders was about equal to that caused by sea urchins in Panamá, but only about one-fifth of the erosion caused by sea urchins in the Galápagos Islands. Total bioerosion ranged from 10 to 20 kg $CaCO_3$ m^{-2} year^{-1} in Panamá and from 20 to 40 kg $CaCO_3$ m^{-2} year^{-1} in the Galápagos Islands. Both of these rates exceed net carbonate production of ~10 kg $CaCO_3$ m^{-2} year^{-1}, estimated for reefs in these areas before 1983. If bioerosion continues at this pace, without an increase in coral recruitment, it is highly likely that many reef formations in the eastern Pacific will disappear.

Studies in the Galápagos Islands and Panamá to the year 2000, demonstrated virtually total reef frame loss in the central and southern islands (Glynn 1994; Reaka-Kudla et al. 1996; Glynn et al. 2001) and substantial calcium carbonate declines in the latter region (Eakin 2001). *Eucidaris* population densities have remained high in the central and southern Galápagos Islands through 2012 with continuing bioerosion of any remaining limestone structures. Eakin's modeling results, incorporating post 1997–1998 data, indicated that the Uva Island reef in Panamá was still in an erosional state in the year 2000, ranging from around –3,000 to –18,000 kg $CaCO_3$ year^{-1} net. A current assessment of coral recovery on the Uva reef in Panama, up until

2010, has revealed a steady increase in live coral cover of ~35 %, and no increase in populations of echinoid bioeroders (Glynn et al. 2014).

While the coral mortality noted above had been caused primarily by elevated sea temperature extremes during El Niño events, it is necessary to recognize that sudden declines in temperature during La Niña events can also result in widespread and significant coral mortality. A sudden transition from a moderate El Niño warm event to a strong La Niña cold condition in 2007, from 26–28 °C to 16 °C over just 6 days, resulted in island-wide coral bleaching in the Galápagos Islands (Banks et al. 2009). Little recovery was observed after one year, which likely increased the vulnerability of corals to bioerosive processes.

4.5.2 Crown-of-Thorns Seastar (*Acanthaster*)

This example is instructive because it reveals some of the long-term consequences of coral death and bioerosion at the community level. Between 1981 and 1982, the corallivore *Acanthaster planci* increased greatly in abundance at Iriomote Island, southern Japan, and by the end of 1982 it had killed virtually all the corals on a large study reef (Sano et al. 1987). This sudden loss of live coral precipitated major changes in the physical and biological character of the coral reef.

About two years following the *Acanthaster* outbreak, most of the erect coral (*Acropora*) canopy had collapsed, a result of bioerosion and water movement. Compared with the live reef, the dead reef exhibited low structural complexity. By 1986 all of the corals were broken apart and the reef formation had been converted into a flat plain of unstructured coral rubble. The degradation of the reef was correlated with marked changes in the fish community. As the topographic complexity of the reef decreased, the numbers of associated fish species and their abundances also declined. Fishes that fed exclusively on live coral tissues disappeared completely from the dead reefs. The declines in fishes with other diets, e.g. planktivores, herbivores and omnivores, were believed due in large measure to the loss of living space and to overall declines in prey on the degraded reef.

More recent studies of large-scale coral predation by *Acanthaster*, followed by intense bioerosion with reductions in reef fish abundances and diversity, have followed in broad outline the course of events at the Iriomote reef described above. A follow-up study of the degraded Iriomote reef demonstrated rapid recovery under conditions of high coral recruitment and survivorship (Sano 2000). Arborescent *Acropora* spp. began recruiting in 1989, and by 1995 and following years coral cover had reached about 100 %, closely matching pre-*Acanthaster* live coral cover values. This buildup in coral cover was accompanied by increases in the species richness and density of adult fish assemblages, to predisturbance levels. It will be instructive to compare this example of rapid recovery, occurring over a period of only eight years, with data from other coral reef areas as they become available.

4.5.3 Runoff (Eutrophication, Sedimentation, Freshwater and Pollutants)

One of the best examples of reef degradation caused by runoff is that reported for the Kāne'ohe Bay, Hawai'i coral reef ecosystem (Banner 1974; Smith et al. 1981; Jokiel et al. 1993). Because the mismanagement of the Kāne'ohe Bay water shed has led to multiple effects, e.g., sewage pollution, agricultural runoff, increased sedimentation and freshwater dilution, it is not always possible to identify individual or combined stressors. However, the occurrence of coral reef mass mortalities during storm floods and a general decline in coral cover during a period of increasing sewage stress implicates these stressors in the degradation of Kāne'ohe Bay coral reefs over two decades (1960–1978).

During the first half of the Twentieth century the coral reefs of Kāne'ohe Bay were in a healthy state, supporting a local artisanal fisheries and offering one of the best underwater vistas of "coral gardens" in the Hawaiian Islands. In 1963, a large sewage outfall was installed in the bay, which had an increasing effect on corals until 1978 when the outfall was moved to the deep ocean outside the bay. The eutrophication caused by increasing sewage loads favored the growth of a bubble alga (*Dictyosphaeria cavernosa*) and suspension feeding and bioeroding species that combined to degrade the reef communities over a 15 year period (Fig. 4.12). Following the sewage diversion, clear signs of renewed coral growth, reduced bioerosion, and reef community recovery were evident by 1983. Severe storm flooding in 1987 caused extensive coral mortality, but surviving corals quickly resumed rapid growth and the condition of reef communities (as of 1993) had remained favorable.

Another 16 years have passed without a major disturbance event affecting corals, however, notable changes in several reef-associated benthic species have occurred. Thanks to the monitoring efforts of P Jokiel, J Stimson, and N Sukhraj, the recent status of the Coconut Island (= Moku o Loe Island) fringing poritid reef can be briefly reviewed. Since 2006, *Dictyosphaera* has decreased in abundance, and several species of red algae have become closely associated with *Porites compressa*, in some instances attached to the peripheral branches of corals (Stimson and Conklin 2008; N Sukhraj pers comm). In addition, a non-boring invasive sponge, *Mycale grandis*, is sometimes present adhering to the sides of coral branches (Coles

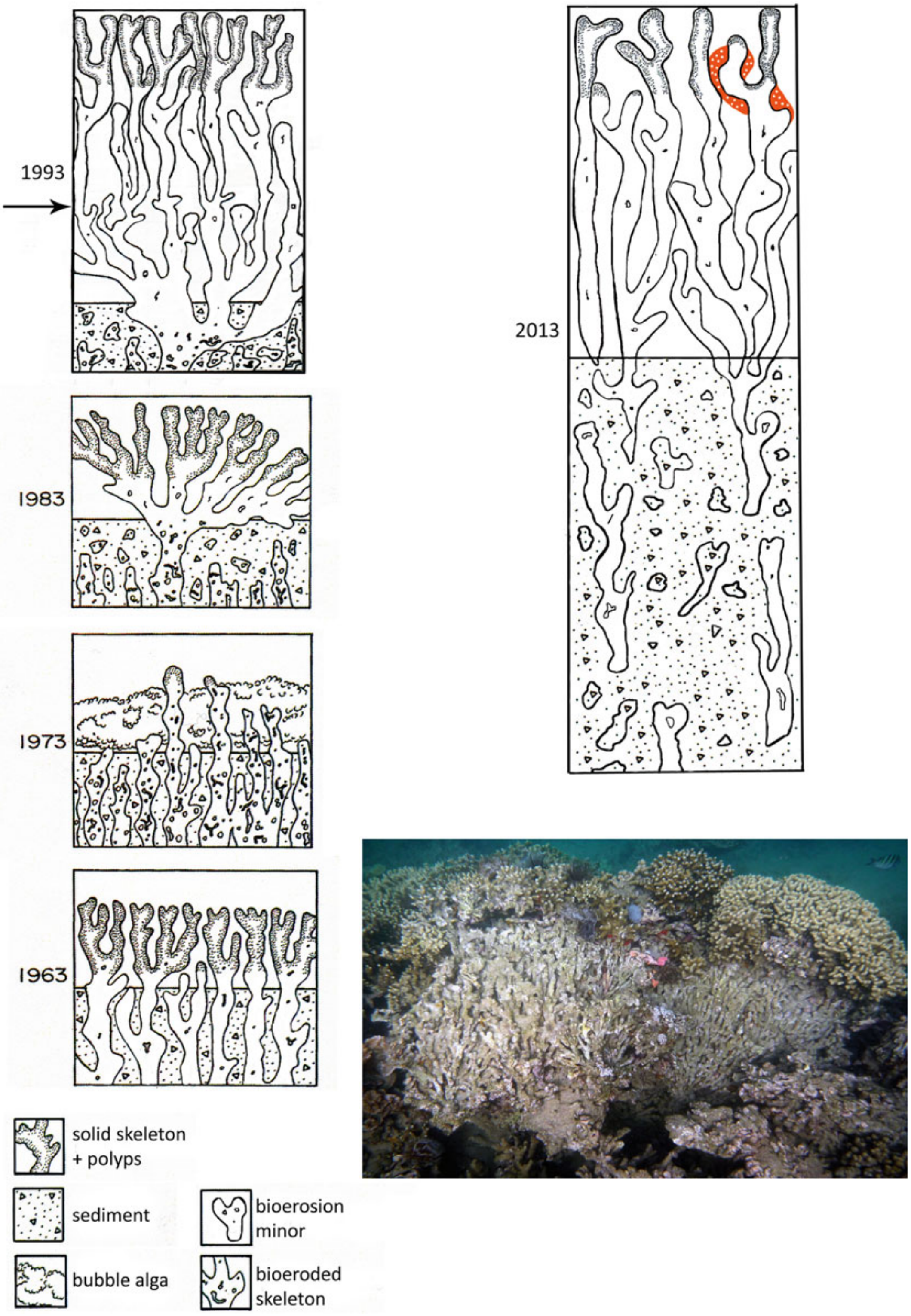

Fig. 4.12 Cross-section of *Porites compressa*, the predominant frame-building coral of the Coconut Island fringing reef. Prepollution (1963), pollution (1973), and postpollution (1983–2013). *Arrow* marks 1987 flooding event. Colored overgrowth denotes *Mycale grandis*

et al. 2007). It now appears that interphyletic competition is more prevalent, but rapid coral growth, with branch elongation rates of 2.4–3.5 cm year^{-1} in reef crest and slope zones (Jokiel 1986), is contributing to vigorous reef progradation. Rapid vertical coral growth at shallow crest depths leads to framework instability, fracturing, and downslope block transport, extending reef foundations seaward. This case history illustrates a degree of resiliency to a disturbance that might have led to reef community collapse in a sewage-stressed environment.

As the human population continues to increase along tropical and subtropical coastal areas, it should be no surprise that reports of associated pollution stress are also on the rise. Indeed, numerous recent studies have documented the deterioration of coral reefs worldwide with eutrophication, related to urbanization (sewage pollution), inappropriate agricultural practices and industrial pollution sources, being the root cause of this decline. It is cautioned that the entry of polluted freshwater into coastal zone communities is not always obvious as sources can include large volumes of groundwater discharge as well as surface effluents. Representative examples of coral reef bioerosion and deterioration under nutrient-rich conditions have been documented in studies in the Indian Ocean (Risk et al. 1993; Chazottes et al. 2002), Indonesia (Tomascik et al. 1997; Holmes et al. 2000), the Great Barrier Reef, Australia (Risk et al. 1995) and at several other Pacific Ocean sites (Hutchings 1994), off Brazil (Leão et al. 1993) and at several localities in the Caribbean Sea (Smith and Ogden 1993).

4.5.4 Overfishing

Several studies in the Caribbean and off the Kenyan coast in the Indian Ocean have presented evidence suggesting that sea urchin abundances are controlled by finfish predators. When fish predators of sea urchins are abundant, urchin abundances tend to be low, but when fishing pressure is high, leading to the disappearance of urchin predators, then urchins can become exceedingly abundant. A study of protected (non-fished) and overfished Kenyan coral reef lagoons indicates that the removal of top, invertebrate-eating, fish carnivores can have cascading effects on coral reef community structure and function (McClanahan and Shafir 1990).

Triggerfish predators of sea urchins were relatively abundant in protected coral reef lagoons, but rare in comparable unprotected environments. The removal of the natural predators of sea urchins by overfishing resulted in several direct effects on the urchin prey and several indirect effects on the condition of the coral reef community. Overfished reefs demonstrated high sea urchin abundances, high urchin survival, and high urchin diversity compared with non-fished reefs. Correlated with the dominance of sea urchins on overfished reefs were declines in (a) live coral cover, (b) calcareous and coralline algal cover, (c) substratum diversity, and (d) topographic complexity. These changes were caused by increased substratum bioerosion, especially by *Echinometra mathaei* (de Blainville), the competitively dominant sea urchin in unprotected Kenyan reef lagoons. The end result of overfishing is accelerated bioerosion, a reef surface dominated by algal turf, and likely a decline in the reef's fisheries productivity.

A convincing case of the over-harvesting of sea urchin predators (lobsters, fishes) in the Galápagos Islands, leading to increased external bioerosion, exemplifies the potential for secondary additive effects that could impede coral and reef recovery (Edgar et al. 2010). Low abundances of *Eucidaris galapagensis* were present in marine protected areas or far from fishing ports, sites supporting high natural abundances of urchin predators. These areas also demonstrated higher levels of coral cover and less disturbance to coral communities recovering from ENSO mortality events.

4.5.5 Caribbean Reef $CaCO_3$ Budgets: Current Status and Future Trends

Coral reefs are in decline globally and the state of Caribbean reefs is arguably the most alarming. Caribbean reefs have experienced multiple interacting disturbances that have driven or exacerbated large-scale coral mortality. In no particular order of importance, the loss of acroporids due to white-band disease, the basin-wide ecological extinction of the keystone sea urchin herbivore *Diadema antillarum* due to an unidentified pathogen, overfishing, coral bleaching, and land-based sources of pollution have all been linked to the collapse of Caribbean coral reefs (Hughes 1994; Aronson and Precht 2001; Jackson et al. 2001; Eakin et al. 2010). Live coral cover has declined by about 80 % since the 1970s, reefs are losing architectural complexity, $CaCO_3$ production has declined to 50 % below historical averages, and more than a third of sites recently surveyed (37 %) were already net erosional (Gardner et al. 2003; Alvarez-Filip et al. 2009; Perry et al. 2013). Many Caribbean reefs are at or close to $CaCO_3$ budget neutral, termed "accretionary stasis," leading to the concern that the persistence of architecturally complex reef framework structures is in doubt (Perry et al. 2013).

Two recent studies have forecasted future Caribbean reef $CaCO_3$ budgets using different approaches, yet both yielded similarly negative prognoses. Enochs et al. (2015) used the *reef budget* methodology of Perry et al. (2012) to estimate present day and future $CaCO_3$ budgets for 37 reefs across the Florida Reef Tract when projected atmospheric CO_2 levels reach 750 ppm, a conservative estimate for end of the twenty-first century conditions. These workers assessed three differing scenarios: (1) no change in coral cover, no change in coral and coralline algae calcification with OA, increase in bioerosion with OA; (2) no change in coral cover relative to present-day, expected declines in coral and coralline algae calcification due to OA, increase in bioerosion; and (3) 50 % decline in coral cover with expected declines in calcification and increases in bioerosion. The declines in calcification were estimated based on published rates, whereas changes in bioerosion were based on the rate of increase in chemical dissolution shown for the common Caribbean bioeroding sponge *P. lampa* with high-CO_2 (+99 %) in the same study, coupled with the predicted rate of dissolution increase by endolithic algae of 48 % (Tribollet et al. 2009). Under present-day conditions, 89 % of reefs on the Florida Reef Tract were already net erosional. For scenario 1, 92 % of reefs became net erosional, whereas all reefs considered were net erosional under scenarios 2 and 3. This modeling exercise illustrated the potential importance of endolithic algae bioerosion. Even though the rates of dissolution per area coverage and the expected stimulation of biersoion at high-CO_2 are both lower than what is expected for *P. lampa*, the dominance of bare substrate as a result of very low coral cover leads to a domineering role for endolithic algae in the reef $CaCO_3$ budget in a high-CO_2 world. These projections stress the likely importance of local management to safeguard reef ecosystem function in an era of global change. Overfishing of those species that control clionaid populations, such as angelfishes, as well as coastal eutrophication should be controlled and not allowed to exacerbate the expected increase in bioerosion (Rose and Risk 1985; Hill and Hill 2002; Ward-Paige et al. 2005).

Kennedy et al. (2013) combined ecological models with carbonate budgets and assessed the dynamics of simulated Caribbean coral reefs based on the latest climate projections. This study assessed the interacting role of local management of fisheries and land-based sources of pollution. The same trend towards net erosion was apparent under all climate scenarios of increased temperature and CO_2, but local management of fisheries, specifically protection of grazing parrtofishes, was found to delay reef loss by a decade. However, positive $CaCO_3$ budgets were only generated when local action was combined with aggressive emission reductions that would limit global warming to less than 2 °C. Changes in coral calcification due to warming and acidification were most important in their $CaCO_3$ budget simulations for healthy, coral-dominated reefs. The controls on bioerosion, such as sea urchin population sizes, sponge boring rates, and nutrification became the dominant drivers of the carbonate budget at low coral cover.

4.5.6 Eastern Tropical Pacific Coral Reefs: A Real-World Climate Change Model

Coral reefs of the eastern tropical Pacific (ETP) provide a real-world example of reef growth, development, structure and function under high-CO_2, low-Ω_{arag} conditions that encompass the range of expected changes for the entire tropical surface ocean with a doubling and tripling of atmospheric CO_2 (Manzello et al. 2008; Manzello 2009, 2010a). The naturally high-CO_2 of the ETP causes reefs in this region to persist near the Ω_{arag} distributional threshold for coral reefs (Kleypas et al. 1999b). Reef structural development is highly limited in the marginal low-Ω_{arag} environment of the ETP and reef structures are ephemeral on geological timescales (Manzello 2009). Calcium carbonate cements, which bind reef frameworks and sediments, do not precipitate above trace levels in the ETP and rates of bioerosion are the highest measured anywhere in the world (Manzello et al. 2008).

Eastern tropical Pacific reef response to ENSO warming varies regionally as a function of CO_2, providing possible insight into reef persistence vis-à-vis warming in a high-CO_2 world. Galápagos coral reef communities experienced a greater thermal stress (+2 to 3 °C for several months) during the 1982–1983 ENSO when compared to Panamá (+1 to 2 °C for two months) (Podestá and Glynn 2001). As a result, coral bleaching mortality was higher in Galápagos (97–99 %) compared to Panamá (75–85 %; Glynn 1990b). Following this mass mortality, reef framework structures in the southern Galápagos Islands were rapidly bioeroded to rubble and sand and are now non-existent (Glynn 1994; Reaka-Kudla et al. 1996). Conversely, reef framework structures have persisted in Panamá despite net erosion and the additional severe 1997–1998 ENSO event (Eakin 2001). Intriguingly, only one reef has persisted in the northern Galápagos Islands, where pH and Ω_{arag} are regionally elevated (Manzello et al. 2014). The impact of high-CO_2, low-Ω_{arag} seawater on carbonate cement precipitation and its apparent inverse relationship to bioerosion rate in the ETP adds a key piece to the puzzle as to why reefs throughout the ETP are poorly developed and ephemeral on geologic time-scales (Manzello et al. 2008).

The observation that the highest bioerosion rates ever documented on coral reefs are coincident with very low-Ω_{arag} and bioerosion rates across the ETP are inversely related to Ω_{arag} and $CaCO_3$ cement abundance (Manzello et al. 2008) has been criticized by Tribollet and Golubic (2011). Three specific criticisms were stated: (1) correlations of bioerosion rate with cement abundance and Ω_{arag} were considered "erroneous" because they were not supported experimentally, (2) the presentation of differing types of bioerosion (total, internal, external) were said to be incomparable, and (3) the increase in substrate available for colonization after the 1982–1983 ENSO coral bleaching mortality event was argued to be a more "probable" explanation for the high rates of bioerosion reported by Reaka-Kudla et al. (1996); and they also suggested the rates of bioerosion during the time of study were likely different. Only ETP bioerosion rates were compared and plotted alongside the measured cement abundances in our study because (a) these are where the Ω_{arag} and cement data were collected, and (b) these rates are in fact comparable. Bioerosion research in the ETP has a considerable history and was initiated more than 30 years ago by Glynn et al. (1979), who showed the characteristic very rapid rate of bioerosion by the echinoid *Eucidaris galapagensis* in the Galápagos Islands. The pioneering research by Glynn and colleagues was subsequently advanced by Scott et al. (1988) in Costa Rica, Eakin (1993, 2001) in Panamá and later by Reaka-Kudla et al. (1996) in the Galápagos Islands. The methodology employed by Glynn and Eakin was the same (Glynn et al. 1979; Glynn 1988; Eakin 1996). The work by Reaka-Kudla et al. (1996) did use different methods, but generated similar rates to those initially published by Glynn (1988). Rates of bioerosion were comparably high prior to the 1982–1983 ENSO (23.5 kg m^{-2} $year^{-1}$) in the southern Galápagos Islands (Glynn 1988) to the results reported nearly two decades later by Reaka-Kudla et al. (1996). The assertion that the rates reported by Reaka-Kudla et al. (1996) were most likely just an artifact of an increase in available substrate for colonization is uninformed. Three different studies have shown that bioerosion in the Galápagos is uncharacteristically high and this was known and published before the 1982–1983 ENSO bleaching/mortality disturbance (Glynn et al. 1979; Glynn 1988; Reaka-Kudla et al. 1996).

A comparison of published rates of bioerosion was explored by Manzello et al. (2008) because of the suggestion by pioneering coral reef geologist, Ian Macintyre, that submarine cementation is an important control on the construction and binding of reef framework structures (Macintyre 1997). With this in mind, and the finding that only trace amounts of cement precipitate in ETP reef structures, maximum published rates of bioerosion were compiled to determine if the rates of ETP bioerosion were unique. The ETP bioerosion rates mirrored coral reef cement abundances. The non-ETP maximum rates reported in the literature illustrate that ETP reefs are subject to unprecedented levels of rapid bioerosion, reconfirming that which was known for more than three decades (e.g., Glynn et al. 1979). Differing agents of bioerosion were indeed reported, but the chief objective was to show maximum mean recorded rates from the literature, regardless of bioerosion agent, to confirm the far greater magnitude of rates in the ETP. Bioerosion rates from outside the ETP were listed for qualitative comparison and were not used in the study.

This study was further misrepresented by Tribollet and Golubic (2011) when they claimed that the conclusion was drawn that bioerosion was negatively correlated with Ω_{arag} and cement abundance, when no such statistical test was conducted or reported. In fact, Manzello et al. (2008) solely stated "cement abundance was positively related to Ω_{arag}, but inversely related to bioerosion rate in the ETP." This statement only reported an apparent trend. The lack of cement in the ETP is later hypothesized to be a factor in the high bioerosion rates of this region, referencing the other published rates to show just how high rates in the ETP are relative to other locations. The publication concludes, "In summary, this study suggests a link between Ω_{arag}, inorganic reef cementation, and coral reef development in the ETP. . .The ETP examples suggest that coral reefs of the future could be more susceptible to erosion." Tribollet and Golubic (2011) misinterpreted the hypotheses, unnecessarily attacking claims that were not stated.

Recent research on Galápagos reefs and calcification dynamics provide new insights into reef structure and function in a high-CO_2 world. As previously mentioned, only one coral reef persists today within the entire Galápagos archipelago and this reef is located at the remote, northern-most Darwin Island (Glynn et al. 2009, 2015), where pH and Ω_{arag} are regionally elevated (Manzello et al. 2014). Conversely, coral reefs in the southern islands disappeared where pH < 8.0 and $\Omega_{arag} \leq 3.0$, and have not recovered. We found that high nutrients in the upwelled waters of the southern Galápagos Islands may enhance coral calcification under high-CO_2, but ultimately increase reef ecosystem sensitivity to ocean acidification. The warming and acidification that caused the functional collapse of Galápagos reefs is expected to occur world-wide by mid-century for most reefs based on current CO_2 trajectories (Frieler et al. 2013; van Hooidonk et al. 2014).

4.6 Conclusions

The fossil record demonstrates that bioerosion and reef growth have always been inseparable. Moderate levels of bioerosion may benefit coral reefs in at least four ways, by (1) creating sedimentary substrata that provide lebensraum for hosts of associated reef species, (2) providing cavities and contributing toward topographic complexity that serve to increase the biodiversity, biomass and productivity of reef communities, (3) structuring reef morphology and growth, and (4) promoting the regeneration and rejuvenation of senescent reef-building organisms.

Except for obvious reef destruction by large populations of sea urchins, bioerosion per se as a possible threat to coral reefs is seldom considered explicitly. This is probably because of the large amount of 'cryptic' bioerosion caused by endoliths and the often delayed effects of bioerosion on coral reef communities. For example, descriptions of reef damage caused by violent storms are numerous in the literature, but the contributory effects of bioerosion are seldom mentioned. The prior weakening of reef structures by bioerosion or the accumulation of sediments causing scour and burial during a storm are effects that may have been initiated years before an acute disturbance event resulting in reef devastation.

The existence of coral reefs beyond this century is in jeopardy. The concern has progressed from the dramatic losses of live coral (Gardner et al. 2003), to the likelihood that the underlying framework of coral reefs will erode away (Hoegh-Guldberg et al. 2007; Manzello et al. 2008; Perry et al. 2013). Coral cover has declined across broad geographic scales (Gardner et al. 2003; De'ath et al. 2012), leading to declines in $CaCO_3$ production. Furthermore, declines in coral growth and calcification have been documented in the Indian, Pacific, and North Atlantic Oceans over the past 30 years (Edmunds 2007; Cooper et al. 2008; Bak et al. 2009; De'ath et al. 2009; Tanzil et al. 2009; Manzello 2010b). The production of $CaCO_3$ on coral reefs is depressed at a seemingly global scale. This suggests that the future impacts of OA on the negative side of the coral reef carbonate budget, namely via stimulation of biologically-mediated dissolution, may be more detrimental than the decline of coral calcification. Indeed, Kennedy et al. (2013) explicitly demonstrated that changes to coral calcification are only reflected in the $CaCO_3$ budget when coral cover is high. When coral cover is low, bioerosion of the reef framework becomes the dominant process.

What are some of the measures that can be taken to limit bioerosion? The most obvious is to reduce coral mortality because numerous bioeroders increase their activities and abundances on dead reef substrata. Direct damage to calcifying organisms can be reduced significantly by several practices already adopted within protected coral reef parks. For example, the use of mooring buoys, navigational markers, the prohibition of destructive fishing techniques, and the banning of coral collecting or touching live corals have all alleviated damage to coral reefs in many areas. The possibility of indirect effects, such as overfishing causing increases in bioerosion, should also be considered in coral reef management plans.

Another method of limiting coral mortality after severe physical damage, e.g., by a ship grounding, involves restoration techniques to stabilize damaged corals and reef substrata (Hudson and Diaz 1988). Hard and soft corals may be transplanted and cemented to stable reef substrata, fractured frameworks may be secured, and the rebuilding of reef topography accomplished by replacing and cementing dislodged corals and sections of framework.

Numerous effects that can accelerate bioerosion are often far-removed from coral reefs and therefore sometimes difficult to link with reef decline. Deforestation, land-clearing and mining activities lead to increased sedimentation, freshwater dilution and nutrient loading around reefs that may be situated hundreds of kilometers from the affected sites. These sorts of activities may alter reef environments such that certain types of bioeroders could increase in number and possibly accelerate destructive processes. The potential damage of such anthropogenic stresses to coral reefs also may be augmented by natural disturbances such as violent storms, extreme temperature changes, diseases and predator outbreaks. For example, most corals may tolerate low salinities for a few hours or days, but salinity stress in combination with a pathogen could precipitate high coral mortality. Many kinds of runoff include combinations of several pollutants, e.g. sewage, detergents, heavy metals, fertilizers, pesticides, and oil, that may act synergistically to reduce live coral cover.

It is now generally understood that bioerosion will be accelerated in a high-CO_2 world via stimulation of biologically-mediated chemical dissolution in endolithic algae and clionaid sponges. It has been suggested that a similar amplification of erosive ability may occur in all bioeroding organisms that utilize chemical dissolution to excavate reef substrates (Enochs et al. 2015). This includes lithophagine bivalves, cirripedes, and various polychaete worms. Many of these bioeroders have greater tolerances to environmental perturbation than corals. In fact, clionaid sponges appear to gain a competitive advantage during thermal stress and coral bleaching events (Rützler 2002; Schönberg and Ortiz 2009). There is much to be learned about coral reef bioerosion, but one thing seems clear – research on bioerosion will most certainly increase over this century because the importance of this fundamental process in coral reef dynamics will likely become increasingly difficult to ignore. Local-scale management of fisheries and watershed pollution would not only benefit corals, but should help limit the proliferation of bioeroders in a high-CO_2 world.

In summary, the dynamic balance between reef growth and bioerosion depends on the vitality of numerous calcifying species. If humankind's activities can be limited to non-intrusive pursuits such as observing and filming reef organisms, and if reef water quality and natural circulation patterns can be safeguarded, then one of the world's most exquisite ecosystems can be enjoyed by posterity.

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Interactions Between Corals and Their Symbiotic Algae

5

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Abstract

The mutualistic relationship between corals and their dinoflagellate endosymbionts is a key factor in the evolutionary success of hermatypic (reef building) corals. The endosymbiotic algae benefit corals in numerous ways that have contributed to the long term persistence of coral reefs over geologic time. In this chapter we review ecological and physiological aspects of the interactions between corals and their symbiotic algae in light of recent advances in our knowledge of the diversity of these symbionts. While the role of symbiont diversity in promoting coral survival during environmental bleaching events has been a major focus of recent research, its importance in other physiological and ecological contexts such as inorganic nutrient dynamics and photosynthetic carbon fluxes has received much less attention. We suggest that cost-benefit analysis is a useful approach to examine these symbioses in the context of environmental change and human impacts upon corals and coral reefs. Weighing the costs versus the benefits of the symbiotic association under specific environmental perturbations has potential for use as an indicator of the health of not only corals but indeed the whole coral reef ecosystem. Drastic changes in the stability of the symbiosis, evidenced by changes in the ratio of zooxanthellae to animal biomass in corals, may turn out to be a useful diagnostic indicator of stresses to coral reefs. By using new tools developed to assess the stability of the symbiosis, we may be better able to understand and predict the effects of future stressors and perturbations that threaten these beautiful reef ecosystems.

Keywords

Cost-benefit • Stability • Holobiont • Bleaching • Calcification

5.1 Introduction

The mutualistic relationship between corals and their dinoflagellate endosymbionts is a key factor in the evolutionary success of **hermatypic** (reef-building) corals. In the two decades since the original publication of this chapter, there has been an explosion of research on *Symbiodinium*

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We dedicate this chapter to our late mentor and friend, Len Muscatine, who was a leading figure in research on algal-invertebrate symbiosis, and who played a major role in our professional development.

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(the genus of coral endosymbionts), fueled by advances in molecular genetics. These advances have the potential to better understand the adaptive capabilities of the symbiotic partners that contribute to this success. Different types or species of zooxanthellae are likely to have differing adaptive capabilities and tolerances to environmental extremes (Chap. 7) that will impact the survival of corals. Changes in the composition of symbiont populations may result in an increased ability to survive future environmental stresses. Although the increasing importance of other microbial associates in the coral **holobiont** (i.e., the coral host and all symbionts; Knowlton and Rohwer 2004) is recognized, our focus here is on corals and their dinoflagellate symbionts, generally referred to as **zooxanthellae**.

It has long been known that these endosymbiotic algae are beneficial to their coral hosts. These include faster rates of calcification, photoautotrophy as a source of nutrition, the ability to acquire inorganic nutrients, and many other attributes that are believed to contribute to the persistence of coral reefs in geologic time. Consequently, environmental and physiological conditions that result in changes in the relationship between the animal host and its symbiotic algae may have profound ecological effects. The genetic diversity of the endosymbionts that is now known to exist contributes to the coral holobiont's ability to cope with changing environmental conditions (Stat et al. 2006).

This chapter discusses the coral-zooxanthella symbiosis from the perspective of the nutrient dynamics and energetics of the association and in the context of the stability and adaptability of the symbiosis in the coral-reef ecosystem. We examine aspects of the structure and function of the symbiosis that contribute to the high rates of calcification and productivity exhibited by reef corals. We discuss some of the factors that influence the density of symbionts and hence the physiological balance between the symbiotic partners. We consider the effects of both natural and anthropogenic events on coral reef ecosystems with respect to how they might affect the stability and survival of the symbiosis. We also consider the possible costs and benefits associated with the symbiotic condition. While we refer to relevant advances in our understanding of the genetic diversity of the endosymbionts, a more detailed discussion is found in other chapters (Chap. 6). It is becoming increasingly clear that specific host-symbiont combinations play vital roles in the physiological and ecological fitness of corals. We conclude our discussion by speculating about the value of using the coral symbiotic association as a measure of the "health" of coral reef ecosystems. Other aspects of the symbiosis are reviewed elsewhere (cell biology: Davy et al. 2012; ecological diversity of *Symbiodinium*: Finney et al. 2010; infection by *Symbiodinium*: Fransolet et al. 2012).

5.2 Description of the Symbiosis

5.2.1 Coral Anatomy and Location of Zooxanthellae

For our purposes here, a brief review of coral morphological features will suffice; a more complete description of coral morphology can be found in other publications (e.g., Veron 2000; Borneman 2001). Scleractinian corals are typically colonies of polyps linked by a common gastrovascular system, although some solitary, single-polyped forms exist (e.g., *Fungia* spp.). Polyps are small, fleshy extensions of the live coral tissue covering a non-living calcareous structure of the colony, referred to as the **corallum**. Although the living tissue is normally a veneer of just a few millimeters in thickness, the calcium carbonate it has deposited over time can be meters in height or diameter (Fig. 5.1). Irrespective of the size colonies may attain, the thin layer of coral tissue itself is simply composed of two cell layers: the epidermis (sometimes referred to as ectodermis) and the gastrodermis (sometimes referred to as endodermis; Fig. 5.1). A thin connective-tissue layer, the **mesoglea**, composed of collagen, mucopolysaccharides, and some cells, separates these two cell layers. The lower epidermal layer, the **calicoblastic epidermis**, secretes the calcareous external skeleton. The upper layer of epidermis (oral, or free epidermis) is in contact with seawater (Fig. 5.1). The individual polyps form **corallites**, i.e., skeletal tubes of deposited calcium carbonate that may be connected and fused in brain corals or are interconnected by what is referred to as the **coenenchyme**. The tissues of **imperforate corals** are restricted to the surface of the skeleton. In **perforate corals**, the skeleton is penetrated by pores containing live coral tissue, but even in this case living tissues do not extend deeply into the corallum, and diffusive exchange of oxygen and other metabolites appears to occur quite readily, aided by many cilia in the coral's epidermal layers. Coral colonies grow by depositing new skeleton and budding additional polyps as the surface area of the tissues increases with size.

Many coral polyps are biradially symmetrical, with the central gut cavity lined by gastrodermis (Fig. 5.1). Tentacles, typically in multiples of six, surround the mouth and are used for capture of particulate food, including zooplankton. Food consumed by one polyp is shared with neighboring polyps via the gastrovascular system that functions in circulation and digestion of food particles. Polyp mouths also provide direct exchange of water and particulate food and wastes between the gastrovascular system and the external seawater.

The arrangement, density and size of polyps are characteristic for each coral species. However, coral species may

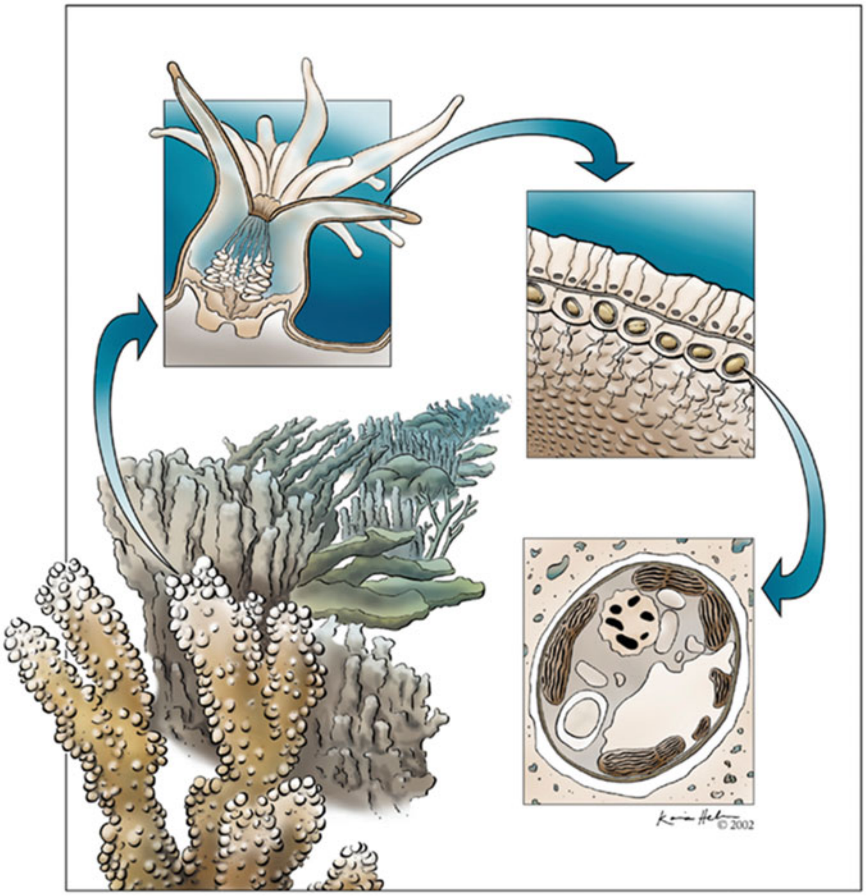

Fig. 5.1 The coral symbiosis. A cross-section of a single coral polyp from a coral colony is shown in the upper left-hand boxed *inset*. The *arrow* leading from the coral polyp points to a section through the two tissue layers of the oral surface of the polyp (see also Fig. 5.2). The epidermis is the upper tissue layer in contact with the seawater, and the gastrodermis is the lower tissue layer in contact with the gastrovascular cavity. The gastrodermis contains zooxanthellae. The *arrow* from a zooxanthella points to a cross-section of the alga. The alga is enclosed in a perivacuolar animal membrane. Internal features shown in the cross-section include the nucleus with its permanently condensed chromosomes, sections of the chloroplast with banded photosynthetic membranes, a large (*white*) vacuole, and starch and lipid inclusions

exhibit different morphologies depending on environmental conditions such as water motion and light, and this causes problems in taxonomy of corals (Veron and Pichon 1976; Veron 2000). Molecular approaches to coral taxonomy have been useful in circumventing these problems (Stat et al. 2012).

5.2.2 Zooxanthellae

“**Zooxanthella**” is a general descriptive term for all symbiotic golden-colored algae that live in animals, including corals, sea anemones, molluscs and other taxa. Although the term has no taxonomic meaning, “zooxanthellae” is used primarily to refer to dinoflagellate symbionts, a group of diverse algae. It continues to be a useful label, given the current state of uncertainty in the taxonomy of coral symbionts.

Zooxanthellae found in corals are typically 8–12 μm diameter cells that reside exclusively in membrane-bound vacuoles in the gastrodermal cells (Fig. 5.1). Their areal density normally ranges from 1×10^6 cm^{-2} to 6×10^6 cells cm^{-2} of coral surface, although this may be highly variable on both temporal and spatial scales (e.g., Fitt et al. 2000). Seasonal differences exist in the density of zooxanthellae in corals; tropical corals during low light (“winter”) months have greater numbers of zooxanthellae (Fagoonee et al. 1999; Fitt et al. 2000). More information about the variability of zooxanthellae densities within colonies and among coral species is needed, especially given the critical role of zooxanthellae in coral nutrition, and the underlying responses to coral bleaching, a phenomenon in which the host loses its symbionts under conditions of stress.

Based on early morphological studies, zooxanthellae in corals and other cnidarians were originally believed to belong to one cosmopolitan species, *Symbiodinium microadriaticum*. The genetic diversity of zooxanthellae was first discovered by comparing the morphology and growth of symbionts isolated from different hosts in culture, resulting in the formal description of four species and the realization that different zooxanthellae were found in different animal hosts (reviewed by Trench 1993; Rowan 1991; Rowan and Powers 1992). This led to the concept of symbiont specificity, with one host selecting and maintaining one type of zooxanthella (its specific symbiont) over all other zooxanthellae. This concept, too, has changed. Our ability to distinguish among zooxanthellae through genetic analyses of molecular sequences (Chap. 6) has resulted in an explosion of different zooxanthella "taxa" (with some named as species, LaJeunesse et al. 2012) and the discovery that different taxa may inhabit the same host species and even the same host organism. With the use of next-gen and other sequencing approaches, it is becoming increasingly apparent that individual hosts may harbor multiple genotypes, with some persisting at low frequencies (Fay and Weber 2012), indicating that the symbiotic relationship is much more flexible than previously thought (Baker 2003), including the possibility that a given coral may acquire different types under different conditions. As the potential diversity of symbionts within a species or individual coral is limited, the significance of symbiont specificity with respect to the stability and ecological persistence of the coral symbiosis is a major research question.

Based on their genetic relatedness, zooxanthellae of corals and other invertebrate hosts are currently placed in nine major groups (= clades; designated A through I), and others are likely to be identified. Although members of a clade are more closely related to each other than to members of other clades, individual taxa within each clade exhibit broad genetic diversity. Zooxanthellae belonging to five of the clades (A–D and G) occur in corals. The individual genotypes of most zooxanthellae identified by their DNA sequences have yet to be formally described as new species. Those coral symbionts that have been given species designations have been assigned to the genus *Symbiodinium*.

The biogeographic distribution of members of the different clades of zooxanthellae in corals indicates the diversity of zooxanthellae is higher in the Caribbean than in the Indo-Pacific, where the vast majority of corals contain only members of clades C and D. The reasons for these ocean-basin differences are, as yet, unresolved. In the Caribbean, clade A zooxanthellae are found in high light shallow water corals, and members of clade C are found in deeper corals (LaJeunesse 2002), in the same coral or among different species. However, interpretation of ecological distribution patterns is complicated by the observation that some zooxanthellae are specialists, maintaining specific associations with only one host, while other generalist zooxanthellae associate with many hosts and have a wide biogeographic distribution. No strong relationship is evident between the types of zooxanthellae in closely related hosts, nor among the types of hosts inhabited by closely related zooxanthellae (Baker 2003; LaJeunesse et al. 2010).

The dinoflagellates comprise a diverse group of mostly planktonic, free-swimming single-celled microscopic algae that exhibit a variety of feeding modes ranging from **photoautotrophy** (photosynthetic carbon fixation) to **heterotrophy** (dissolved organic carbon uptake or feeding on particulate food). Zooxanthellae are photosynthetic and contain characteristic dinoflagellate pigments (diadinoxanthin, peridinin) in addition to chlorophylls *a* and *c*. They are brown or yellow-brown in color. Although zooxanthellae may be heterotrophic in corals as they have been shown to take up and assimilate dissolved organic carbon from host sea anemones, their own photosynthesis seems to contribute most to their energetic needs.

Zooxanthellae can live independently of their animal host. Free-living zooxanthellae have been found in sediment and water column samples (Takabayashi et al. 2012). Many strains of *Symbiodinium* isolated from host tissues have been cultured in inorganic algal media, although the inability to culture some strains is of great potential interest. These uncultivable strains may have specific requirements for some set of as yet undefined host or other microbial symbiont conditions (including nutritional requirements) that warrant further study. Cultured zooxanthellae have been used to study growth rates and compare genetic and physiological characteristics of symbionts from different hosts. Zooxanthellae living in animal cells are usually found in the coccoid stage (non-motile, lacking flagella); this differs from the free-living motile (dinomastigote) stage that possesses two flagella (Fig. 5.2) and exhibits a characteristic swimming pattern. In culture, zooxanthellae alternate between the coccoid and dinomastigote stages, often on a diurnal pattern. The dominant dinoflagellate feature evident on the ultrastructural level is the nucleus with permanently condensed chromosomes (**dinokaryon**; Fig. 5.1).

Santos and Coffroth (2003) showed that the life cycle of zooxanthellae, like that of most dinoflagellates, is dominated by asexual reproduction of haploid vegetative cells. The high genetic diversity of zooxanthellae suggests extensive recombination, although sexual reproduction has not been documented for these algae. As these authors point out, "questions pertaining to recombination in these enigmatic dinoflagellates, such as the factors that induce it and whether it occurs inside or outside a host, remain to be answered" (Santos and Coffroth 2003).

5.2.3 Acquisition of Zooxanthellae by Corals

Young corals derived from both asexual and sexual reproduction typically contain zooxanthellae. In asexually produced (clonal) coral colonies, zooxanthellae are directly transmitted in the coral buds or fragments that form new colonies. In sexually produced corals, acquisition of zooxanthellae is either directly from the parent (vertical), or indirectly from the environment (horizontal). The method of symbiont acquisition and whether or not the eggs contain zooxanthellae are characteristics of each coral species. A confounding factor is the frequency of sexual versus asexual reproduction in each coral. A coral that relies almost exclusively on asexual reproduction (i.e., budding or

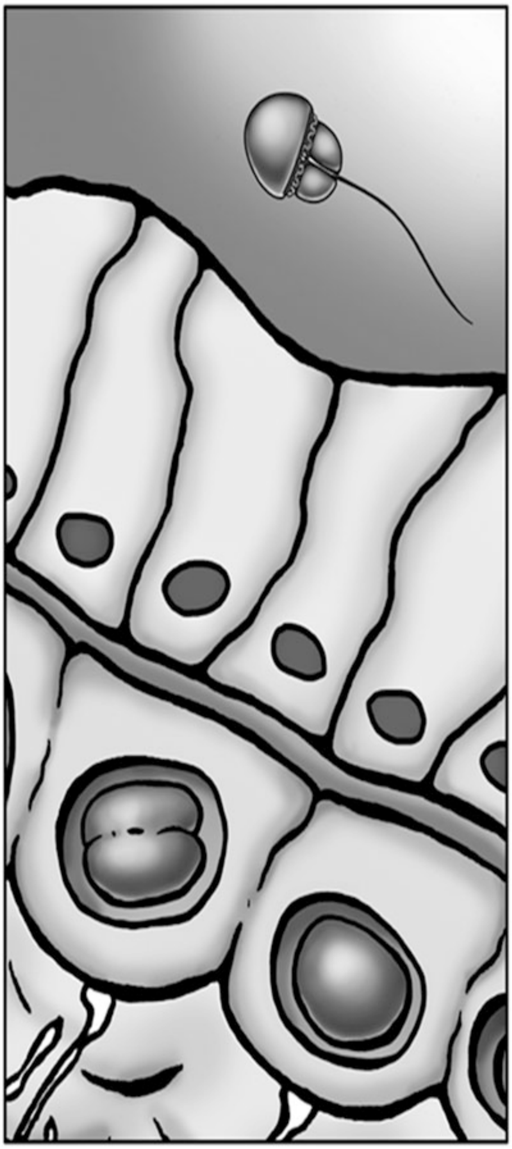

Fig. 5.2 A section through the two tissue layers of the oral surface of the polyp showing the different life forms of zooxanthellae. A free-living motile cell (dinomastigote) is shown swimming in the seawater above the layer of nucleated oral epidermal cells. The two gastrodermal cells each contain one coccoid zooxanthella; the cell on the left is in the process of dividing. The actual sizes of zooxanthellae range from 5 to 20 um, depending on species and life form

fragmentation) for propagation, where direct transmission of zooxanthellae is guaranteed, may not exhibit highly developed mechanisms for transmission of these algae during sexual reproduction.

During direct transmission via sexual reproduction, zooxanthellae are transferred to the eggs or to larvae brooded by the parent. The eggs of most species of corals do not contain zooxanthellae. For those that do, zooxanthellae free in the gastrovascular cavity may be ingested by gastrodermal follicle cells and expelled near the oocytes by passing through temporary gaps in the mesoglea, where they are phagocytosed by the mature oocyte (Hirose et al. 2001). Alternatively, cytoplasmic extensions of the gastrodermal cells that contain zooxanthellae may invade the egg plasm, as has been described for marine hydroids (Trench 1987). These eggs may be released and fertilized in the water, or the larvae may develop from eggs fertilized and retained within the parent coral. If fertilized eggs do not contain zooxanthellae, larvae brooded by the parent through the early stages of development may take up zooxanthellae at any time prior to release. The presence or absence of zooxanthellae in eggs and planula larvae may affect their ability to persist in the plankton, as the photoautotrophic contributions of the zooxanthellae are potentially important factors in explaining the large distance of dispersion of some species (Richmond and Hunter 1990).

Corals that do not inherit parental zooxanthellae must obtain them from seawater. The concentration of zooxanthellae in seawater over the reefs is likely to be quite low under normal conditions; free-living zooxanthellae also occur in sediments (Takabayashi et al. 2012). Positive chemotaxis of motile zooxanthellae towards the coral animal increases the probability of contact between appropriate partners (Fitt 1984; Hollingsworth et al. 2005). Free-living zooxanthellae may show preferential chemotaxis towards newly settled nonsymbiotic coral polyps. In experiments with the soft coral *Heteroxenia fuscescens*, motile zooxanthellae were attracted to animal extracts of juvenile nonsymbiotic polyps but not to extracts of adult symbiotic polyps and seawater controls (Pasternak et al. 2004). Zooxanthellae also may be supplied indirectly to the coral by ingestion of fecal material released by corallivores and of zooplankton prey containing zooxanthellae. Regardless of the mechanism, indirect acquisition of zooxanthellae provides the potential for colonization by zooxanthellae that are genetically distinct from parental symbionts. Whether or not this actually occurs depends on host coral recognition and acceptance of a symbiont, and the chance encounter of the appropriate partners. There is no indication that host corals with direct, vertically transmitted zooxanthellae contain fewer zooxanthellae types than corals that acquire their symbionts horizontally by open acquisition (Baker 2003). Together with recent evidence that newly settled polyps of some species contain different zooxanthellae than their respective adult colonies (Coffroth et al. 2001; Cumbo et al. 2013); corals are likely to be able to acquire different zooxanthellae throughout their lives.

Coral "bleaching" also provides the potential for establishment of a new population of zooxanthellae in adult corals. Buddemeier and Fautin (1993) originally proposed the "Adaptive Bleaching Hypothesis" as a possible explanation for the ability of corals to change the composition of their zooxanthellae symbionts from one clade to another.

Corals lose coloration (become bleached) when they lose most of their zooxanthellae or when stressed zooxanthellae lose their photosynthetic pigments. Corals that survive a bleaching event involving the loss of zooxanthellae eventually regain normal densities of zooxanthellae (they “re-brown”) when environmental conditions improve. The source of zooxanthellae for the recovery and re-browning of a bleached coral is unknown. Free-living zooxanthellae may invade corals after a bleaching event, residual zooxanthellae (of the former dominant type or of a cryptic resident type) may re-populate their bleached host coral, or both may occur.

Field studies have shown that the re-population of bleached tissues by free-living or residual zooxanthellae may change the genetic composition of the population of symbiotic algae within a coral (Baker et al. 2004; Kemp et al. 2014). Although changes in the composition of symbiont populations are hypothesized to result in an increased ability to survive future environmental stresses (Buddemeier and Fautin 1993), these changes may be temporary, with subsequent reversions to original symbiont complements (Thornhill et al. 2006). Some evidence indicates that resistance to bleaching increases after symbiont populations change (Baker et al. 2004), and that thermally resistant symbionts may represent a temporary stopgap solution to surviving periods of heat stress. However, these newly acquired symbiont strains may confer lowered fitness upon hosts compared to the normal symbiont complement (Little et al. 2004; Mieog et al. 2009), and may be opportunistic “weed” species that confer short term advantages only during stressful periods.

5.3 Nutrition and Adaptations to Environmental Factors

5.3.1 Coral Nutrition

The success of corals in low-nutrient tropical waters is due largely to the variety of modes that corals utilize to obtain nutrition (Fig. 5.3). The animal has two primary nutritional modes: capture of particulate food by polyps and input of translocated photosynthetic products from its zooxanthellae. The amount of photosynthetic carbon translocated to the animal host is often sufficient to meet its metabolic respiratory requirements. Corals may also take up dissolved organic compounds from seawater, a process that is aided by the extremely high surface area to tissue volume ratio of corals and the presence of cilia on their epidermal cells. However, the nutritional importance of this uptake, and of that of other food sources such as microplankton and bacteria (either free-living or associated with mucus and particulate debris) is uncertain. Animal metabolic waste products derived from feeding may be retained within the coral, as they are a source of the inorganic nutrient elements (e.g., N, P) required by the zooxanthellae.

Zooxanthellae are photoautotrophs and thus require only inorganic nutrients, carbon dioxide, and light for photosynthetic carbon fixation. Inorganic nutrients may be acquired from coral animal waste metabolites, or from seawater after passage through animal tissues, or from nitrogen fixation by symbiotic cyanobacteria. Host feeding is probably more important as a source of N for corals and zooxanthellae at depth (Muscatine and Kaplan 1994; Heikoop et al. 1998). Zooxanthellae may also obtain organic nutrients from the animal, although the extent to which this occurs, and its significance, is not well understood. The extent of symbiont heterotrophy may depend on environmental considerations (light, depth) and the particular strain of symbiont involved.

The variety of coral nutritional modes suggests that corals are adaptively polytrophic and opportunistic feeders. This polytrophism seems to account for corals’ ability to thrive in low-nutrient water (Muscatine and Porter 1977). However, environmental constraints and energetic costs associated with the maintenance of symbiotic algae, as discussed below, may under certain circumstances favor holozoic modes of nutrition, e.g., at depth (Muscatine et al. 1989) or following bleaching events (Grottoli et al. 2007).

Uptake of nutrient elements in an inorganic form from seawater by zooxanthellate corals was first observed by Yonge and Nicholls (1931) working with phosphate (PO_4^{3-}). Subsequently, such uptake has been observed by many authors for a variety of inorganic nutrient forms of nitrogen and phosphorus (PO_4^{3-}, NO_3^-, NH_4^+), and it has been firmly established that net uptake of inorganic nutrients occurs even at the characteristically low environmental concentrations observed in tropical seas. This mode of nutrient acquisition, once considered a curiosity, is now believed by many researchers to constitute a significant source of N and P to the symbiotic association (Fig. 5.3). However, the physiological mechanism by which this uptake occurs has been the subject of considerable debate.

Two alternatives exist to explain the uptake of dissolved inorganic nutrients even at low ambient concentrations, algal-mediated assimilation and host-mediated assimilation. This phenomenon has been investigated most extensively for ammonium. With respect to algal mediation of assimilation, D’Elia et al. (1983) proposed the “depletion-diffusion” hypothesis, suggesting that zooxanthellae reduce the coral intracellular concentration of inorganic metabolites such as NH_4^+ to such low levels that a concentration gradient is established resulting in an inward (perhaps enzymatically facilitated) diffusion of dissolved inorganic nutrient from the external seawater. In contrast, proponents of the host-mediated assimilation model (Rees 1987; Miller and Yellowlees 1989) suggest that the uptake of NH_4^+ (and by

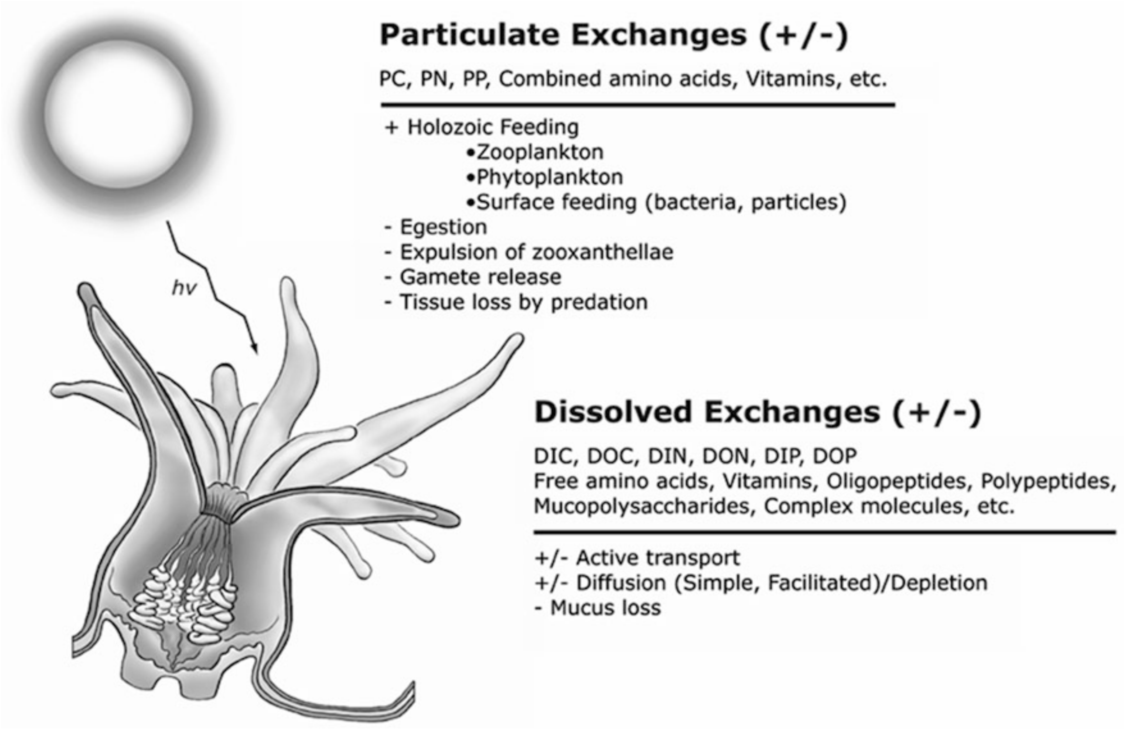

Fig. 5.3 Particulate (P) and dissolved (D) exchanges of inorganic (I) and organic (O) carbon (C), nitrogen (N), and phosphorus (P) between a coral polyp and the seawater environment. "+" exchanges represent inputs from the environment to the coral, and "−" exchanges represent losses from the coral to the environment. Internal exchanges (not shown) include uptake by symbiotic algae and translocation between the algae and the host

extension, other nutrient ions) is more likely mediated by assimilatory enzymes in animal tissues, and then transported in an organic form to the zooxanthellae.

For ammonium uptake and assimilation, at least, several strong lines of evidence suggest that the former mechanism is the more likely of the two alternatives. Kawaguti (1953) and Muscatine and D'Elia (1978) found that zooxanthellate, but not azooxanthellate corals take up ammonium. D'Elia et al. (1983) found that isolated zooxanthellae take up ammonium, and that uptake kinetics of isolated algae closely approximate those of intact symbioses. These authors found differences in uptake kinetics between isolates of zooxanthellae, but the genetic basis of these differences is not known. Given the genetic tools now available for *Symbiodinium*, this is a question that should be addressed.

D'Elia and Cook (1988) provided indirect evidence that ammonium concentrations in host cytoplasm are indeed low enough to create a concentration gradient from seawater to the cytoplasm, and Szmant et al. (1990) showed that corals conserve N, which is consistent with establishing a low internal ammonium concentration. Most significantly, ^{15}N studies show that ammonium is initially assimilated by the zooxanthellae, and that some of this assimilated N is transferred to the host (Swanson and Hoegh-Guldberg 1998; Kopp et al. 2013). However, there is some evidence that host tissue may also assimilate ammonium (Lipschultz and Cook 2002).

The ramifications of the algal-mediated nutrient uptake mechanism are significant: zooxanthellae **in hospite** (living within host cells) are likely to be nutrient-limited, as hypothesized by Cook and D'Elia (1987), who provided a list of criteria for establishing nutrient limitation. Accordingly, increases in nutrient concentrations in ambient seawater that corals are exposed to, should, in fact, enhance cell division, growth rates and biomass of zooxanthellae, as observed by numerous authors (e.g., Hoegh-Guldberg 1994), affecting the stability and physiological balance of the symbiotic association.

5.3.2 Productivity of Corals and Role of Zooxanthellae in Calcification

Photosynthetic carbon fixation by zooxanthellae ($P_{\mathbf{zx}}$) accounts for the high productivity of corals (Hatcher 1988, 1997). Any carbon fixed by zooxanthellae in excess of their own respiratory (R_{zx}) and growth requirements is potentially available to the host coral as a carbon and energy source. If the carbon fixed by zooxanthellae meets or exceeds the combined respiratory carbon requirement of the coral and zooxanthellae ($P_{zx} > R_{zx + animal}$; ratio of P:R > 1), the coral is potentially photoautotrophic with respect to carbon and does not require external carbon sources to obtain energy. When P:R is less than one, carbon must be supplied from other nutritional sources, either particulate or dissolved (Fig. 5.3) for the coral to satisfy energetic needs. P:R ratios derived from oxygen measurements generally show that shallow water corals have a P:R > 1, while the P:R of deep water corals is less than one. Therefore, deep water corals are more likely to require external subsidies of organic carbon for maintenance and growth than are shallow water corals.

Zooxanthellae enhance coral calcification and thus are responsible for much of the formation of the massive coral reef framework. The direct relationship between coral calcification rate and light indicates the fundamental importance of symbiont photosynthesis (Barnes and Chalker 1990), although how photosynthesis enhances calcification is still unresolved. Several models have been proposed for the mechanism of enhancement of calcification by zooxanthellae. One is the contribution photosynthetic products of zooxanthellae to the process of calcification. These products could enhance calcification by providing energy for aragonite deposition or for the active transport of calcium ions across the calicoblastic epidermis for calcification. These products could also provide precursors for the synthesis of the organic matrix upon which $CaCO_3$ is deposited. Another possibility is that symbiont photosynthesis alters the physico-chemical environment to provide favorable conditions for calcification (Gattuso et al. 1999). Photosynthesis removes CO_2, raising the pH and the aragonite saturation state, which favors carbonate deposition. In turn, calcification generates protons (H^+) that are transported back into the coral tissues. The decrease in pH from the extra protons results in an increase in carbon dioxide, supplying the primary substrate needed for photosynthesis by zooxanthellae in the light (Al-Horani et al. 2003). A third possibility is that the removal of phosphate by zooxanthellae enhances calcification since phosphate is an inhibitor of $CaCO_3$ crystal formation (Simkiss 1964). Despite the abundance of models, the significance of each one with respect to the link between calcification and symbiosis with zooxanthellae has not been determined.

The following section describes the factors that influence the productivity of zooxanthellae and hence the amount of carbon potentially available to the coral. The balance between primary production and respiration (P:R) for a coral with a stable population density of zooxanthellae depends on environmental factors that affect both photosynthesis of the zooxanthellae and respiration rates of both partners. The most important factors are light and temperature.

5.3.3 Effect of Light and Temperature on Productivity of Zooxanthellae

The reliance of corals on phototrophic nutrition and photosynthetically enhanced calcification favors the proliferation of corals in shallow, clear waters. Total daily production depends on the amount of light received by zooxanthellae, which is related to the light penetrating to the seawater depth where the coral is located and to the light transmitted through the coral animal tissues and reflected by the coral skeleton. Photosynthetic rates increase directly in response to increase in light intensity up to a certain light intensity, after which they are either independent of further increases in light or inhibited by high light (Hatcher 1988). Consequently, mechanisms for regulating light capture and penetration through the coral are advantageous and are evident in both the zooxanthellae and the host coral.

Some corals grow well in the presence of high levels of ultraviolet (UV) radiation, while others are killed by exposure to high UV. The former include corals that are normally found in high light (in shallow water), while the latter include corals that live at greater depths or that are “shade-loving” species. Corals have a suite of molecules that protect against UV-induced reactive oxygen species (Lesser 1997; Mazel et al. 2003) as well as UV-absorbing “sunscreen” compounds that protect against UV damage (Dunlap and Chalker 1986). The quantity of their UV-absorbing sunscreens is related to the incident UV energy, and declines in corals with depth. These sunscreens include mycosporine-like amino acids (MAAs), and appear to be located primarily in the animal tissues and afford protection to symbiotic zooxanthellae that do not make MAAs (e.g., members of Clade B; Banaszak et al. (2000)) or that have low concentrations of these compounds.

Animal tissue pigments, contributed by four or more groups of color types of GFP-like proteins (GFP, green fluorescent protein), may serve to regulate the light received by zooxanthellae. In high light-adapted corals, fluorescent proteins are concentrated in the epidermis above the algae and may serve as a protective screen to scatter the light and remove excess light energy by fluorescence; the same proteins located below the algae in the gastrodermis in shade-adapted corals might help collect light under low light conditions by back-scattering and transformation of light to photosynthetically-active wavelengths (Salih et al. 2000). However, Mazel et al. (2003) propose that the physical absorption, emission and reflection properties of GFPs do not function in optimizing light conditions for photosynthesis; instead, GFPs may help remove potentially damaging reactive oxygen species (ROS) produced during photosynthesis. Given the role of ROS in coral bleaching (Lesser 1997), GFPs may serve as a “bleaching monitor” (Roth and Deheyn 2013).

By their location in a thin layer of photoprotective living tissue, supported by a strong skeleton formed by their animal partner (Fig. 5.1), zooxanthellae maximize light capture and are highly productive. This light capture is enhanced by the physical properties of the skeleton (Enríguez et al. 2005). Although they are essentially "imprisoned phytoplankton," they enjoy many of the benefits of a macroscopic benthic lifestyle such as that of a seaweed. Such advantages include maintenance in the photic zone with good water exchange. In addition, individual polyps exhibit behaviors (contraction and expansion) that help regulate and optimize the light environment for their symbiotic algae. The coral also provides protection against herbivores that feed on planktonic algae. As in trees, upper layers of the coral canopy receive more light than the understory surfaces of coral branches, and zooxanthellae in shaded and unshaded portions of the colony may exhibit different degrees of photoadaptation and exist at different population densities in coral tissues.

Individual zooxanthellae acclimate to changes in light by changes in their photosynthetic systems, including the light-harvesting ability of photosynthetic units (amount of pigment) and the rate of carbon fixation (enzymatic adaptations). Zooxanthellae in corals from shaded habitats usually contain more chlorophyll and accessory light-harvesting pigments, held in larger chloroplasts with a greater number of chloroplast membranes, and thus are more efficient at light capture under low light conditions. The size of their light harvesting units is large. Zooxanthellae in corals in high light environments contain less photosynthetic pigment, in smaller light harvesting units in fewer chloroplast membranes, and sustain high rates of carbon fixation under high light conditions by containing more photosynthetic units. As light intensity also varies on a daily and seasonal basis, zooxanthellae are also likely to acclimate to these temporal changes in light conditions.

The differential ability of coral species to photoacclimate to prevailing light regimes via these mechanisms may limit their distribution in different light environments. Genetic differences in the photophysiology of different species or taxa of zooxanthellae are also likely to have a large effect on the optimal light regimes of individual coral species, and on the distribution and ecological role of these corals under changing environmental conditions. In some cases, a species may exhibit changes in symbiont composition with depth (Rowan and Knowlton 1995), while other coral species do not (Iglesias-Prieto et al. 2004). Clearly, proper quality and quantity of light are essential at the coral holobiont level for (1) the overall stability of the association; (2) the ability of the symbiosis to exhibit net production ($P > R$); (3) the expression of photosynthetic pigments and the density of the zooxanthellae; and (4) diel behavioral aspects such as polyp expansion and contraction.

Temperature also affects metabolic rates of corals and their symbionts. The influence of temperature on productivity depends on how photosynthesis of the algae and respiration of both the algae and coral animal respond to changes in temperature. In general, corals are adapted to their ambient temperature conditions. Shallow corals may tolerate a wider range of temperatures than deep water corals, and corals (and their zooxanthellae) may show latitudinal differences in their temperature responses. For example, P:R ratios for the same species of corals in Hawaii and Enewetak across a temperature range (18–31 °C) showed that Enewetak corals were adapted to their higher ambient temperatures (Coles and Jokiel 1977). As was discussed for light, temperature tolerances may depend on the individual coral species and the particular genetic strains of zooxanthellae involved. See Chap. 7 by Barshis for further discussion.

High temperature is known to cause coral bleaching, but there is no given temperature that causes coral bleaching. Instead, prolonged exposure to increases of 1–3 °C above long-term annual maximum temperatures (ranging from 25 to 35–36 °C) are likely to induce bleaching (Coles and Brown 2003). High light and ultraviolet light exposure may exacerbate the effects of high temperature, and other stressors may also initiate this phenomenon, which argues for caution in interpreting every bleaching event as the result of a temperature anomaly. Clearly, exposure to temperatures exceeding the tolerance range of the symbiosis affects its stability, generally resulting in the loss of zooxanthellae and possibly in the death of the host. The loss may be due to effects on the zooxanthellae (e.g. Tchernov et al. 2004), on the host (e.g. Fitt et al. 2009), or on both partners. Both the rate of the temperature change and the duration of the temperature anomaly can effect bleaching. As with changes in light, the ability of the coral to adapt to change in temperature or in other environmental factors depends on the acclimatory capability of one or more of the following: the animal, the zooxanthellae, and the symbiotic association as a whole.

5.3.4 Effect of Nutrient Supply on Zooxanthellae in Corals

Corals thrive in seawater where the concentrations (standing stock) of the major growth-limiting nutrient elements, nitrogen and phosphorus, are typically very low. A tenet of algal-animal symbiosis is that it evolved in response to relatively low ambient nutrient concentrations, and that accordingly, such conditions provide corals a competitive advantage over other benthic species. Corals conserve nitrogen by having low rates of protein catabolism and catabolizing translocated lipids and carbohydrates (Szmant et al. 1990).

Various sources of N and P exist for symbiotic zooxanthellae. The algae can obtain inorganic nutrients via recycling of waste products from their animal host, and "new" nutrients from the uptake of dissolved inorganic compounds from seawater and zooplankton capture by the coral (Fig. 5.3). In fact, early investigations of the role of symbiotic algae in corals suggested that they served as the kidneys for the animal (Yonge and Nicholls 1931), although this is now considered highly unnecessary because of the proximity of the tissues to seawater and the relatively small thickness of the coral tissue layer. Although dissolved concentrations of nutrients are very low in most tropical waters, mass transport of nutrients via diffusion or transport across coral surfaces may be sufficient, when assimilated, to supply the nutrient requirements of the algae and its host (Hoegh-Guldberg and Williamson 1999). Such transport is enhanced by water movement on reefs (Thomas and Atkinson 1997).

Although corals are adapted to waters containing very low levels of nutrients, corals can persist when nutrient levels around reefs become periodically elevated due to increased run-off from adjacent land, point source inputs (from sewage and industrial effluents), or periodic upwelling. Most corals are unable to adapt to acute, high level nutrient enrichments and generally compete poorly with benthic macroalgae under such conditions. Excess nutrients may decrease calcification rates, as described earlier phosphate interferes with aragonite crystal formation during calcification. Elevated nitrate inhibits coral calcification (Marubini and Davies 1996). However, given the differences in uptake kinetics between cultured isolates of zooxanthellae (D'Elia et al. 1983), it is possible that symbiont strain is important in those corals that exist in environments with reduced nutrients. For example, Godinot et al. (2013) found differences in alkaline phosphatase activity between zooxanthellae from different clades, although it is not clear how these differences relate to environmental concentrations.

Elevated phosphate levels (exceeding about 1 μM) and dissolved inorganic nitrogen levels (exceeding about 6 μM) destabilize the symbiosis by enhancing growth rates of the zooxanthellae, but it is unclear how often reef seawater concentrations exceed these values. Recent studies have shown that higher symbiont densities increase the likelihood that elevated temperatures will trigger bleaching events (Wooldridge 2009; Wiedenmann et al. 2012; Cunning and Baker 2013). Under less stressful conditions, elevated growth rates of the zooxanthellae relative to the host may simply result in the expulsion of extra algae, The expulsion of zooxanthellae may also represent a unique detoxification mechanism for the coral. For example, zooxanthellae have a high tolerance for heavy metals and accumulate them from seawater. Periodic expulsion of zooxanthellae could reduce the "body burden" of heavy metals (and nutrients) in the coral animal, as demonstrated for temperate sea anemones (Harland and Nganro 1990).

Corals that survive direct effects of added nutrients may succumb to indirect effects such as reduction of light by increased phytoplankton biomass in the water column and overgrowth by fleshy seaweeds.

5.4 Stability of the Symbiosis

A stable symbiosis is defined as one in which the density of zooxanthellae in corals remains relatively constant under a given set of environmental conditions and the symbiotic partners do not change over time. This constancy may be important in balancing the benefits and the costs of the symbiosis (Table 5.1). Thus, the growth of zooxanthellae in corals must be regulated somehow relative to the growth of the host. Either the growth rates of the zooxanthellae and the animal cells are comparable, or, if different, excess zooxanthellae are expelled from the coral.

Direct measurements of growth rates of zooxanthellae in coral tissue are difficult to make. Doubling times have been estimated from diel measurements of the mitotic index (= the percent of dividing cells, Fig. 5.2) of zooxanthellae. However, this approach makes assumptions about the duration and phasing of cell cycle stages that may be difficult to validate. Doubling times for symbiotic zooxanthellae calculated by this approach show them to be at least an order of magnitude lower than for cultured zooxanthellae maintained in nutrient-enriched seawater.

Zooxanthellae growth rates and densities may be regulated by the availability of nutrients. Resource limitation may help maintain the balance between zooxanthellae and animal biomass and growth rates. Upper density limits are likely controlled indirectly by the animal cell habitat, slowing zooxanthella division rates by limitations on space or diffusion of gases (CO_2, O_2) through animal tissue. It has been suggested that the host may produce a compound that inhibits algal growth once a certain density has been reached, but this has yet to be demonstrated. Corals are known to expel zooxanthellae, and this is believed to be an important mechanism for controlling densities. As discussed above, corals with elevated symbiont densities following elevated nutrients may be more susceptible to bleaching events. Furthermore, as numbers of zooxanthellae increase in coral tissue, self-shading of cells will reduce available light and there will be intense competition for limited resources, CO_2 and nutrients, potentially reducing net production and growth. In certain rapidly growing areas of the coral, animal growth rates may exceed those of the zooxanthellae, and populations of zooxanthellae are thus "diluted." For example, tips of branches of rapidly growing species often appear white due to reduced algal densities.

Table 5.1 Putative benefits and costs of the symbiotic relationship for the coral animal, for zooxanthellae, and for the holobiont

Benefits	Costs	Indirect (+/− effects)
A. Animal		
Supply of reduced carbon, offsetting respiration costs and conserving metabolic reserves	Regulation of algal growth and production of peri-algal vacuoles	High surface area-to-volume ratio favors both light capture and prey capture
Increased growth and reproduction	Defenses against high oxygen tension, high light, and UV	Restriction to the photic zone
Increased calcification rate	Mechanisms for rejection of non-beneficial types or excess algae	
Conservation of nutrients	Vulnerability to environmental stresses that affect plants	
Sequestration of toxic compounds by algae		
B. Zooxanthellae		
Supply of CO_2 and nutrients from host	Translocation of a significant fraction of photosynthetic carbon to animal; growth rate is regulated	Nutrient supply is regulated
Maintenance in photic zone	Regulation of growth rate; growth slower in coral than in free-living state	Protection from grazers
Protection from UV damage by animal tissues	Expulsion from host	Dispersal by predators on animal tissue
Maintenance of a high population density of a single or few genotypes by host under uniform environmental conditions	Supply of CO_2 and nutrients limited by host	
C. Coral symbiotic association		
Increased growth, more competitive for space on reef	Compounded sensitivity to environmental stresses that affect algae, animals, or both	
Increased ability to partition resources of food and space	Restricted tolerance range of light, temperature, and sedimentation conditions for growth	
Increased resistance to water motion due to high calcification		

Notes: Factors which are not direct benefits or costs are listed as indirect effects. The relative contribution of each factor to maintaining the balance between benefit and cost of the symbiotic association is unknown, as is the synergistic interaction among these factors. Also, not all of these putative benefits have been documented in corals, such as sequestration of toxic compounds by algae

Environmental factors that are likely to affect both animal and algal growth include physical conditions and the availability of prey. Light directly affects photosynthetic productivity, while prey capture directly affects animal tissue growth and indirectly affects growth of zooxanthellae by its potential supply of nutrients and creation of new animal tissues that provide habitat for more zooxanthellae. Although the intracellular habitat of zooxanthellae has been considered a nutrient-rich environment (Fig. 5.2), these algae display characteristics that suggest that their growth is normally nutrient-limited (Cook and D'Elia 1987). It has been frequently observed that the addition of dissolved inorganic nitrogen to seawater causes an increase in the growth rate of zooxanthellae (e.g., Hoegh-Guldberg 1994) and in their nitrogen to phosphorus ratio (Muller-Parker et al. 1994). The opposite trends occur when symbiotic associations are maintained with no particulate food resources in low nutrient seawater. It is unknown if the animal withholds nutrients from its algae, or if the supply is limited by the availability of nutrients (including animal prey and seawater as sources), or both. Nutrient limitation of the growth of zooxanthellae may favor the coral animal by creating an excess of photosynthetic carbon products that cannot be used for production of new cells and is therefore translocated to the animal host (Falkowski et al. 1993). Conversely, the addition of nutrients may trigger the diversion of photosynthate to fuel symbiont growth. Wooldridge (2010) has characterized the situation as one of "controlled parasitism", in which the host may regulate its symbionts via a number of mechanisms.

The review of Fay and Weber (2012) and more recent work on the diversity of zooxanthellae taxa in corals make it clear that apparently stable populations may exhibit profound changes in the genetic composition of the zooxanthellae inhabiting corals over time. We may expect more examples of this as more sensitive next-gen sequencing techniques are used to study these associations. As noted above, the extent of these changes depends on the specific combinations of host and symbiont. Furthermore, symbiont densities may follow predictable seasonal cycles, with highest densities of symbionts during low light winter months, highest animal tissue biomass in spring, and lowest population densities of zooxanthellae during late summer and fall months (Fitt et al. 2000). These seasonal cycles may represent fine-tuning of the symbiosis in response to seasonal changes in light and temperature, with resultant effects on coral growth. In some cases these seasonal patterns may include periodic changes in the relative frequencies of symbionts, with more heat-resistant strains becoming more frequent during warmer months (Chen et al. 2005). As opposed to these normal cycles in zooxanthellae population dynamics, symbiont population densities may be disrupted by stressors that result in the mass expulsion of zooxanthellae, resulting in visibly bleached corals. Environmental stresses such as extreme temperatures, high light, air exposure, or rapid change in salinity cause coral bleaching. These large-scale disruptions in the symbiosis may produce positive or negative shifts in the balance between benefits and costs of the symbiosis (Table 5.1). If the coral survives the stress and regains a normal population density of zooxanthellae, there may be a period during the re-population phase when algal growth rates exceed those of the animal tissue.

5.5 Cost-Benefit Analysis of the Symbiosis

Table 5.1 presents features that we consider to represent significant benefits and costs of the symbiotic relationship between zooxanthellae and their coral animal hosts. These features are presented from the perspectives of each partner and of the complete association. We suggest that this approach, albeit somewhat anthropomorphic, is a useful way to consider the symbiosis and may be helpful in framing future research directions. Other perspectives may be found in Wooldridge (2010) and Lesser et al. (2013).

From the animal's perspective, "sufficient" numbers of zooxanthellae (partially determined by strain or type of zooxanthella) must provide some input of energy towards offsetting its respiratory requirements. A balance must exist between photosynthetic production and the metabolic cost of maintaining the algae. The costs include mechanisms to cope with high oxygen tension (activation and increase in levels of antioxidant enzymes) and possible regulation of the growth rate of zooxanthellae (Table 5.1). Since most corals contain 1×10^6 cm^{-2} to 6×10^6 zooxanthellae cm^{-2}, it is likely that this range represents optimal algal densities that balance the benefits and costs of the symbiosis. Rapid changes in densities of zooxanthellae in corals due to environmental perturbations, for example coral bleaching in response to high temperature and algal growth in response to increase in seawater nutrients, will upset this balance and may stress the coral by uncoupling algal and animal growth. From the alga's perspective, the coral must provide a good habitat. The "economic" benefit of the partnership may be viewed as the net return based on the relative costs of the symbiosis between zooxanthellae and the coral animal (see also Wooldridge 2010).

Although it is often difficult to evaluate benefits and costs, obviously when benefits exceed costs there is a net benefit to sustaining the symbiosis, and the association might be expected to persist in a stable state. Conversely, when costs exceed benefits, the net costs could result in the end of the association. Thus, the persistence and stability of the symbiotic relationship at both ecological and evolutionary scales must depend on the net benefit of the symbiosis over relevant time scales with respect to its ability to withstand environmental stresses and to compete for space and other resources with other benthic organisms.

In some cases, benefits or costs of the partnership have been experimentally verified. For example, the enhancement of coral calcification by zooxanthellae is documented, both from comparison of calcification rates of symbiotic and non-zooxanthellate corals and by the light-enhanced calcification rates of symbiotic corals. In other cases, the relationships are less obvious. One must recognize that our knowledge of the costs and benefits of the relationship is limited. Subtle yet crucial benefits and costs may exist that we cannot yet identify or quantify: the use of transcriptomic, proteomic and metabolomic approaches will likely identify more of these in the future. Moreover, the cumulative effect of different costs and benefits may not be simply additive. The interactive and synergistic effects between factors are not likely to be easily quantified.

The diversity and number of the entries in Table 5.1 suggest that the balance between benefit and cost for the relationship is highly dynamic and varies according to both previous and current conditions, as well as the particular combinations of host and symbiont. Organisms have a physiological minimum and maximum tolerance to, and an optimum value for, any given factor. Within limits, such ranges of tolerance are useful constructs for the consideration of the environmental conditions both necessary and sufficient for survival. We can only speculate whether the susceptibility of a coral to given stressors will be increased, decreased or modulated when compared to the susceptibility of the individual partners to the same stressors.

When a coral is stressed to a point where the relationship is disrupted, the costs of maintaining a symbiosis have clearly exceeded the benefits. This may provide for the short-term survival of the coral and of the zooxanthellae, and involve changes in symbiont populations, as noted above during bleaching events. When favorable conditions return, the original symbiosis would be expected to be re-established because the benefits to the coral are required in the long-term.

Disruption of the association by stressors may, in turn, have major consequences not only for the individual corals but also for the coral reef ecosystem. A particularly good example of this can be seen in the effect of temperature-induced coral bleaching on community structure in the Eastern Tropical Pacific (Glynn 1991). In 1982–1983, a very strong El Nino-Southern Ocean oscillation (ENSO) event resulted in severe warming and severe bleaching of corals in Costa Rica, Panama, Colombia and Ecuador. Mass mortalities of corals occurred and reef structure changed substantially. The mass bleaching events of 1999 caused widespread mortality of corals in the Indo-Pacific, but many of these reefs have shown signs of recovery (Wilkinson 2008). Such severe effects notwithstanding, disruption of the symbiosis by stressors may also provide the opportunity not just to "weather a storm" but to "change partners" to other zooxanthella taxa or species that can provide better benefits and lower costs for particular environmental conditions (Buddemeier and Fautin 2004a). For example, if zooxanthellae with high thermal tolerance successfully populate bleached corals, the new combination may be more resistant to subsequent high temperature stresses.

As we consider the factors affecting the costs and benefits of maintaining the symbiosis, it is appropriate to consider three questions: (1) Is viewing symbiosis in terms of benefits and costs a useful way of assessing the ability of a symbiosis to persist? (2) What are the factors that shift the balance from benefit (+) to cost (−) to the symbiotic association? (3) Are such factors interrelated? Since we are only capable of making crude determinations of relative cost or benefit of a given factor, we cannot realistically provide numbers (limits) for the quantification of benefits and costs. Although this means that the answer to the first question is "no" in most cases, consideration of the relative benefits and costs does facilitate our ability to conceptualize the response of the symbiotic association to changes in any factor.

Exposure to extremes in temperature, oxygen, salinity and nutrient supply are all known to destabilize the symbiosis and result in the loss of zooxanthellae (coral bleaching). Each of these stressors is likely to exact costs of sustaining the zooxanthellae that are too great, so that either the host actively expels them or the zooxanthellae leave on their own accord. The stressor may damage the zooxanthellae, creating a liability for the host if the cells were to remain in their tissues. For example, disruption of photosynthetic membranes by high temperature leads to the uncoupling of photosynthetic energy transduction and the production of damaging reactive oxygen species, killing the zooxanthellae and damaging host cells (Tchernov et al. 2004). As discussed above, nutrients may also result in the active expulsion of zooxanthellae by the host following periods of overgrowth. In this case, symbionts divert carbon from translocate to growth under conditions of nutrient repletion, and algal expulsion serves to keep the host from being overgrown by its less beneficial endosymbionts. A disruption of the balance between the animal host and its zooxanthellae may result in reductions in productivity and coral growth, leading to possible overgrowth by faster-growing organisms, especially seaweeds. Below we discuss some practical examples of how natural and anthropogenic stresses to corals affect the stability of the symbiosis.

The third question was whether factors that affect the net benefit of the symbiosis interrelate with one another. It is possible to define a set of conditions under which a symbiosis will persist, and conversely, under which it will not. Nonetheless, we presently have almost no information regarding synergistic interactions and the effects of multiple stress factors on the net benefits to maintaining the symbiosis.

5.6 Environmental Effects on the Symbiosis

Other chapters in this book review general ecological features relating to corals and coral reefs. Here, we consider the stability of coral/zooxanthellae symbioses with respect to environmental stresses. We approach this topic first from the perspective of local and regional effects, and then from the perspective of global environmental changes and effects through the alteration of the essential factors of sedimentation, light, nutrients, temperature and pH.

5.6.1 Local and Regional Stresses to Symbiotic Corals

In coastal areas, human population densities are increasing at an alarming rate, as people are migrating to within a few hundred kilometers of coasts as was dramatically illustrated by the tsunami tragedy of 2004. This demographic factor is having substantial environmental effects in all coastal areas in temperate and tropical regions, but to date most attention has been paid to temperate areas. That situation is beginning to change (cf Knowlton and Jackson 2008). Numerous meetings of international authorities on coral reefs over the last two decades have concluded that the cumulative effects of local coastal development are presenting more immediate problems than any present global effect such as ozone depletion or enhanced greenhouse effect due to the anthropogenic release of carbon dioxide. This is particularly important because much international policy concern has been focused on controlling greenhouse gases and climate change, while equivalent concern about recognizing on an international level the cumulative threat local stressors has only recently developed (see below).

Human coastal development brings with it increased inputs of nutrients from sewage and runoff. The process of over-enrichment by anthropogenic nutrient inputs ("cultural eutrophication") is widely recognized and is becoming better understood in tropical environments where coral reefs are found. The classic example of this is Kaneohe Bay, Hawaii, where coral reefs suffered greatly from increases in nutrient inputs and sedimentation (Smith 1981). Without recognition or fanfare in the formal scientific literature, remarkable advances in understanding of coral nutrition and maintenance of stable associations has occurred through the work of aquarium hobbyists. Building on the work of scientists seeking to improve public aquarium exhibits, they have revolutionized the ability to maintain and grow corals in their own homes (Borneman 2001). The work of Adey (1983), who recognized the importance of macroalgae in "scrubbing" excess nutrients from aquaria, and Jaubert and Gattuso (1989), who recognized the value of enhancing coupled nitrification and denitrification to maintain a low-N environment, have stimulated the adoption of devices such as the "Jaubert plenum," which is an undergravel biological filter that maintains low N levels in aquaria. The success of this system illustrates the value of controlling serious destabilizing effects of high N levels on zooxanthellate corals. The aquarium hobbyists have also learned how to maintain proper seawater chemistry to maintain and promote the growth (calcification) of corals.

Increased sedimentation and runoff are two of the most pronounced early effects of coastal development, and it has been recognized for some time that global sediment fluxes from land to sea are increasing (Milliman and Meade 1983). In mountainous high precipitation areas especially, clear-cutting of forests and development of agrarian economies result in increased levels of water-borne sediments and nutrients (Sect. 9.2.1), and decreases (or increases in the seasonal variation in) salinity. These activities have been associated with a reduction in coral cover and diversity (Bartley et al. 2014). At the same time, symbiotic corals can provide a useful temporal record of environmental changes within a reef ecosystem because of the dependence of calcification on zooxanthellae; changes in calcification rate due to variation in parameters such as temperature, salinity, turbidity, and pollution are recorded in the density banding patterns of the coral skeletons.

Studies of terrestrial runoff in Kaneohe Bay, Hawaii, and other places suggest that suspended sediment in the water is one of the foremost enemies of reef corals (Chaps. 9 and 11). Although the major effect of sediment on corals is the accumulation of particles on coral surfaces that interferes with feeding, turbidity affects the quantity and quality of light available for photosynthesis, a matter of clear bearing on the persistence of the coral-zooxanthellae symbiosis, and on coral calcification. Alteration of light quality and quantity results both from sediment-related turbidity and indirectly to phytoplankton growth stimulated by increased nutrient loadings (Sect. 9.2) associated with sedimentation and agricultural land practices (increased fertilizer and pesticide application, slash and burn and deep tillage agriculture) (see Sect. 5.2.2 on coral nutrition and calcification).

In addition to the effects on corals, these factors can also affect the trophic structure of the water column overlying reefs. This in turn may affect the nutrition and stability of the symbiosis. The predominant effect of elevated nutrient levels on corals and coral reefs seems to result from altered trophic structure resulting from overgrowth of corals by fleshy seaweeds, high bacterial biomass, increased disease (Chaps. 8, 9, and 11), etc., which are beyond the scope of this chapter.

5.6.2 Global Stresses to Symbiotic Corals

Scientists are increasingly concerned about the effects of global stresses and global change on corals and coral reefs (Hoegh-Guldberg et al. 2007). With respect to the coral-zooxanthellae symbiosis, global stresses of particular relevance include: (1) increased UV irradiation due to a reduction in the ozone layer; (2) temperature increases due to global warming and related changes in oceanic circulation patterns leading to variation in temperature and nutrient inputs; (3) cumulative increases in nutrients and turbidity due to industrial and agricultural development; and (4) reduction in world ocean pH due to CO_2-derived acidification.

The effect of chlorofluorocarbons (CFCs) on the depletion of the ozone layer and the subsequent increase in the flux of ultraviolet (UV) light to the Earth's surface have received substantial attention with respect to coral reefs. Conditions that favor photosynthesis by zooxanthellae expose corals to UV damage. Although corals contain pigments and anti-oxidant defenses that may afford considerable protection from UV, the effective metabolic cost of UV protection for the animal and zooxanthellae with respect to the symbiosis is unknown. If the cost to the symbiosis is greater than the benefit of light-driven photosynthesis, then the symbiosis becomes a liability.

Temperature is a crucial factor affecting the stability of the coral/zooxanthellae symbiosis at the individual level, and certainly, in a larger sense, of coral reefs (Hoegh-Guldberg 1999). Limits of temperature tolerance for corals and well-developed coral reefs are considered to range from a winter minimum of approximately 18 °C to a summer maximum of approximately 30 °C, although to be sure, thriving reefs are found at either extreme that appear to be uniquely adapted to such conditions. Early studies on the effects of temperature stress on photosynthesis and respiration in corals and coral reefs developed from concerns about the thermal effects of power plant effluents on local biota (e.g., Coles and Jokiel 1977). However, over the past 30 years it has become clear that that increases in the frequency of worldwide bleaching events are related to rising global temperatures, due to the enhanced greenhouse effect resulting from anthropogenic emissions of infrared-absorbing greenhouse gases (e.g., Hoegh-Guldberg et al. 2007).

Exposure to temperature extremes may or may not affect the stability of the symbiosis. Both the length of exposure to and the severity of a given temperature stress or anomaly are important factors, as is the particular combination of host and symbiont. As an example, probably the best-known response that indicates a destabilization of the coral/ zooxanthellae symbiosis, "bleaching," depends on all three of these factors (Fitt et al. 2001). Corals bleach, or actively expel their zooxanthellae most typically when temperatures increase sharply for a short period of time (+3-4 °C, several days) or increase moderately for a longer period of time (+0.5-1.5 °C, several weeks) (Glynn and D'Croz 1990; Jokiel and Coles 1990). Since coral calcification, and therefore reef growth, depends on the presence of zooxanthellae, a gradual rise in sea level with global warming might result in the demise of coral reefs at low latitudes and a shift to higher latitudes. The effects of low light and increased nutrient inputs from global changes in atmospheric deposition and oceanic circulation patterns factors are discussed in the previous section.

Whether the global extent of disruption of the coral symbiotic association with zooxanthellae will provide an accurate "barometer" of coral reef degradation due to global climate change remains an issue of debate and uncertainty. Secular increases in ocean temperatures are very likely to increase the number of coral bleaching episodes and the combination of global climate change and local effects is a serious threat to coral reefs (Buddemeier et al. 2004b). Bleaching may simply represent a temporary disruption of the symbiosis that allows each partner to survive the stress on its own. As Baker (2004) states, "…in an era of climate change and global warming, the continued success of [coral reef] ecosystems is dependent on the stable association of these symbionts with the reef-building organisms which depend upon them." The potential for new and more tolerant combinations of partners after bleaching makes this issue more complicated, but does offer some hope that successful combinations may ensue. The recent finding that corals and their zooxanthellae may have greater acclimatory ability than previously thought (Palumbi et al. 2014; see also Chap. 7 by Barshis) adds hope.

A concern now looming on the horizon is the prospect of the "titration" of oceanic pH as a direct effect of anthropogenic CO_2 inputs. Hoegh-Guldberg et al. (2007) used conservative IPCC models to estimate that by the end of this century atmospheric CO_2-driven ocean pH reductions could reach approximately 0.4 units. This change in the ocean's carbonate buffer system could lead to an enhancement of photosynthesis in marine algae by increasing the pCO_2, but it may also decrease carbonate saturation and thereby decrease calcification (Takahashi 2004). The combination of these two effects would have profound effects on the distribution of symbiotic corals by reducing the areal extent of the ocean suitable to sustain coral growth and survival.

5.7 Summary

The symbiotic association with zooxanthellae is clearly beneficial to corals. Increasing evidence has shown that the symbiotic state is accompanied by sensitivity to environmental stress, since a common response to a stress is the disruption of the symbiosis, resulting in coral bleaching. The response is complex, since zooxanthella taxa (or species) and different species or genotypes of coral animals may have different adaptive capabilities and tolerances to environmental extremes, and we are just beginning to understand the role that host-symbiont diversity plays in this process. As the host animal depends on its complement of zooxanthellae for reduced carbon compounds, coral death will ensue if stresses persist for long periods of time or if they are at levels outside of the tolerance range of the coral and of the zooxanthellae. Factors that induce a stress response include: light (quantity and UV), temperature, sewage and run-off inputs (high nutrients, increased turbidity), salinity (freshwater run-off from land due to deforestation and other land-use practices), pH, and physical damage.

Disruption of the symbiotic association, in turn, has potential for use as an indicator of the health of the coral reef ecosystem. Drastic changes in the stability of the symbiosis, as evidenced by changes in the ratio of zooxanthellae to animal biomass in corals, may turn out to be a useful diagnostic indicator of stresses to coral reefs. Present research is leading to improved understanding of how and when this can occur, especially as techniques are being refined to assess relative algal densities non-invasively by in situ fluorescence readings and reef color assessed by satellites.

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Exploring Coral Reefs Using the Tools of Molecular Genetics

6

Nancy Knowlton and Matthieu Leray

Abstract

The tools of molecular genetics have been transformed over the last decades and have in turn transformed our understanding of coral reefs. Initially limited to information on single genes, we are now capable of analyzing entire genomes. These developments make it possible to do many things that were either impossible or extremely difficult before: identify cryptic species, microbes, larvae and gut contents; determine relationships among populations and species; characterize reproductive and dispersal patterns; infer mechanisms of speciation; and soon perhaps embark on genetic engineering. Notably, many aspects of coral reef conservation can and will increasingly benefit from insights derived from the application of molecular genetic tools.

Keywords

Identification • Bioinformatics • Barcoding • Phylogenetics • Speciation

6.1 Introduction

As in other fields of biology, the tools of molecular genetics have transformed our understanding of coral reefs, giving us information that is difficult or impossible to access with the naked eye, or even high-powered microscopes. Though molecular genetics is no substitute for a deep understanding of the natural history of coral reefs, there is also no doubting the transformative advances that these tools have made possible. Indeed, molecular genetic methods have become so commonplace that this chapter can only touch on a few of the many contributions that have been made in this field. Using "DNA" and "coral reef" or "coral reefs" as coupled search terms yields over 600 papers published from 2000 to 2014 on the Web of Science.

Underpinning this progress in understanding have been enormous technical advances, permitting ever more powerful analytic tools to be employed. Those who have witnessed the history over decades of the sequential adoption by coral reef scientists of new genetic tools and approaches (e.g., protein electrophoresis, the polymerase chain reaction, restriction fragment length polymorphism, Sanger sequencing, microsatellites, microarrays, and high-throughput sequencing technologies; see **Glossary**) know that what today seems doable but challenging will be routine in the not-too-distant future. A high-throughput DNA sequencer has even been brought on a ship to analyze samples from some of the most remote reefs of the central Pacific (Lim et al. 2014). In fact, the difficulties and costs associated with collecting molecular data are declining so precipitously that we now face an entirely new challenge, namely how to analyze the massive amounts of data that can be obtained. The biggest obstacles to be overcome are increasingly in the realm of bioinformatics.

With this history of rapid methodological turnover in mind, our chapter will concentrate on important discoveries based on molecular methods, rather than focusing in detail

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on specific techniques. The discoveries to be reviewed fall into seven fields: (1) species identification, (2) ecological relationships, (3) population structure, (4) evolutionary relationships, (5) speciation, (6) sexual systems, and (7) physiology and development. The chapter will conclude with a discussion of how molecular genetics may contribute to the conservation of coral reef organisms in the context of global change.

6.2 Species Identification

Many coral reef species are notoriously difficult to identify because of the problem of cryptic or sibling species, that is species that are difficult to distinguish using conventional morphological traits (Knowlton and Jackson 1994). Factors contributing to this problem include (1) paucity of diagnostic characters, (2) traditional preservation methods that eliminate informative characters such as color pattern, and (3) the fact that in many marine species, mate recognition is mediated by chemical cues rather than traits that are easily recognized by scientists.

The existence of complexes of cryptic species is typically confirmed using molecular genetic approaches (Knowlton 2000), although subtle morphological differences can often be detected in retrospect (e.g., Jackson and Cheetham 1990). Cryptic species complexes discovered using these methods are now so numerous as to defy summary, but they have notably included dominant members of coral reef ecosystems, such as the Caribbean coral *Orbicella* (formerly *Montastraea*) *annularis* (Fukami et al. 2004), the Indo-west Pacific coral *Stylophora pistillata* (Keshavmurthy et al. 2013) (Fig. 6.1), the Indo-Pacific crown-of-thorns seastar *Acanthaster planci* (Vogler et al. 2008), and the snapping shrimp symbiont of corals *Alpheus lottini* (Williams et al. 2003).

In some cases widespread "species" are now recognized as large numbers of geographically circumscribed taxa (e.g., the gastropod *Astralium* in the archipelagoes of the Indo-West Pacific, Meyer et al. 2005); in other cases large numbers of cryptic species are found to be sympatric (e.g., the brown alga *Lobophora* in New Caledonia, Vieira et al. 2014). The criteria for distinguishing cryptic species in sympatry are relatively straightforward. For nuclear genes, fixed differences between groups with no heterozygote individuals is strongly suggestive of the absence of interbreeding. For mitochondrial loci, the strict association of a diagnostic mitochondrial difference with another independent difference (molecular or morphological) is similarly informative. In cases of allopatry, there is more room for argument, as there is no universally accepted genetic definition of a species. However, groups defined by multiple fixed independent differences (e.g., Meyer et al. 2005) or by large genetic differences at a single locus (e.g., Vogler et al. 2008) are often recognized as distinct species.

The facility with which species can be identified by molecular traits has led to the widespread adoption of DNA "barcoding" of standard genetic markers [e.g. for animals, a portion of the mitochondrial cytochrome oxidase I (COI) gene]. The result has been the growth of barcode data in genetic databases [e.g., GenBank, Barcode of Life Data Systems (BOLD)], thereby facilitating the identification of specimens and comparisons across studies. However, the ability of a single mitochondrial gene to reliably define species depends on there being a consistent gap between the amount of variation that typically exists within species versus between species. Studies of cowries, a highly diverse and taxonomically well-known group often associated with coral reefs, suggest that error rates (recognizing taxa that are not distinct species or failing to recognize taxa that are) are not trivial (Meyer and Paulay 2005).

Moreover, some animals, including unfortunately corals, exhibit very little genetic variation in the mitochondrial genome, limiting the utility of COI-based barcoding for these groups (Shearer and Coffroth 2008; Huang et al. 2008). In some cases other genes have been surveyed and show promise [e.g., in octocorals, McFadden et al. (2011)]. Nevertheless, a mixture of genetic and other traits is often needed to distinguish closely related species in these problematic groups, and many unresolved species complexes remain (Prada et al. 2014a). The development of high-throughput sequencing, which allows the routine sequencing of numerous stretches of DNA simultaneously, may make a focus on particular barcoding genes obsolete.

Despite these limitations, DNA barcoding has found a wide variety of applications. For example, even in species that are readily distinguished as adults, barcoding is far more reliable for identifying egg and larval stages (Hubert et al. 2015), although identification efficiency depends on having a good database against which to match sequences, which is lacking for many groups and locations (Puillandre et al. 2009; Leray and Knowlton 2015). DNA barcoding also has the potential to dramatically increase our understanding of coral reef diversity as a whole by expanding analyses beyond the relatively small number of groups that are conspicuous and well known taxonomically [such as those surveyed by Roberts et al. (2002)]. For example, Plaisance et al. (2011) (Fig. 6.2) found 168 barcode-defined species (i.e. Operational Taxonomic Units or OTUs) of brachyuran crabs in just 6.3 m^2 of coral reef samples, a number representing almost 80 % of the diversity of this group for all European seas. These methods are also now being used for coral reef fisheries assessment. In the US, mislabeling of red snapper, a depleted reef fish, was found to be so extensive that 77 % of fish so labeled were likely other species, in some cases from distant locations (Marko et al. 2004).

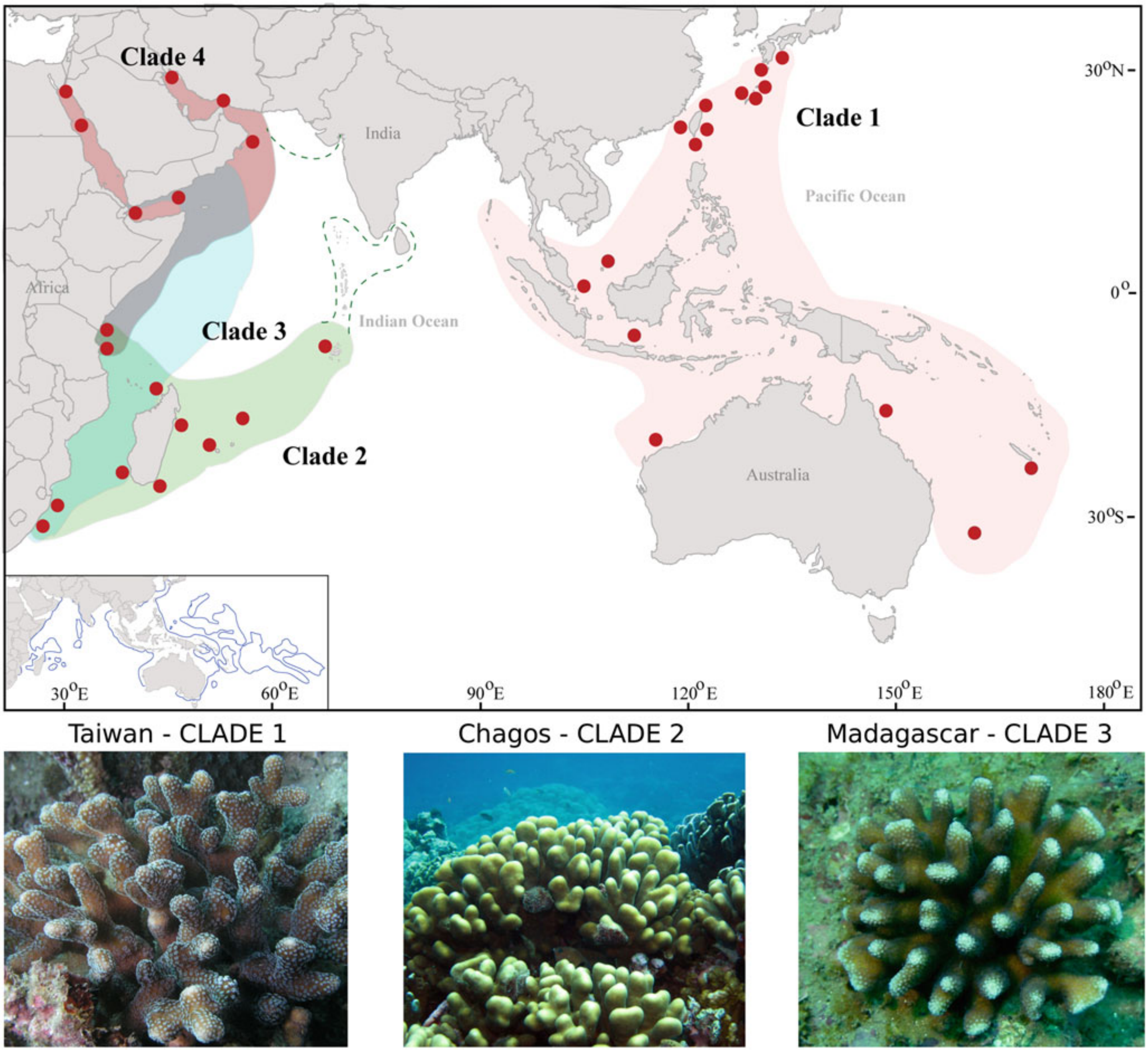


Fig. 6.1 DNA analysis has helped recognize that many species of fish and invertebrates that were once thought to have widespread distributions are in fact made up of multiple distinct genetic lineages. For example, Keshavmurthy et al. (2013, *figure above* modified from Figs. 1 and 2) used DNA barcoding to identify four distinct genetic clades in the widely distributed coral species *Stylophora pistillata*. The degree of differentiation suggests that they diverged from one another 51.5–29.6 million years ago

In Belize, 5–7 % of all fillets tested from markets and restaurants were found to be illegally harvested parrotfish, and 32–51 % of the fillets tested were misidentified (Cox et al. 2013).

Finally, traditional DNA barcoding efforts require identifying organisms one specimen at a time. The relatively recent application of high-throughput sequencing approaches promises to transform this field, because tens of thousands of sequences can be obtained from analyses of a single sample. Censusing diversity by barcoding DNA from samples of the environment containing many organisms is termed metabarcoding. This approach has been widely used to assess microbial diversity based on the 16S rRNA gene (the standard barcode for Bacteria) and has revealed staggering numbers of taxa, including on coral reefs. For example, it was estimated that a single 115 m transect would yield from 135,326 to 468,600 bacterial taxa, with algae harboring an even more diverse community of Bacteria than corals (Barrott et al. 2011). High-throughput sequencing has also been used to detect rare *Symbiodinium* within coral tissues (Quigley et al. 2014). Ironically, metabarcoding of multicellular eukaryotes has been more

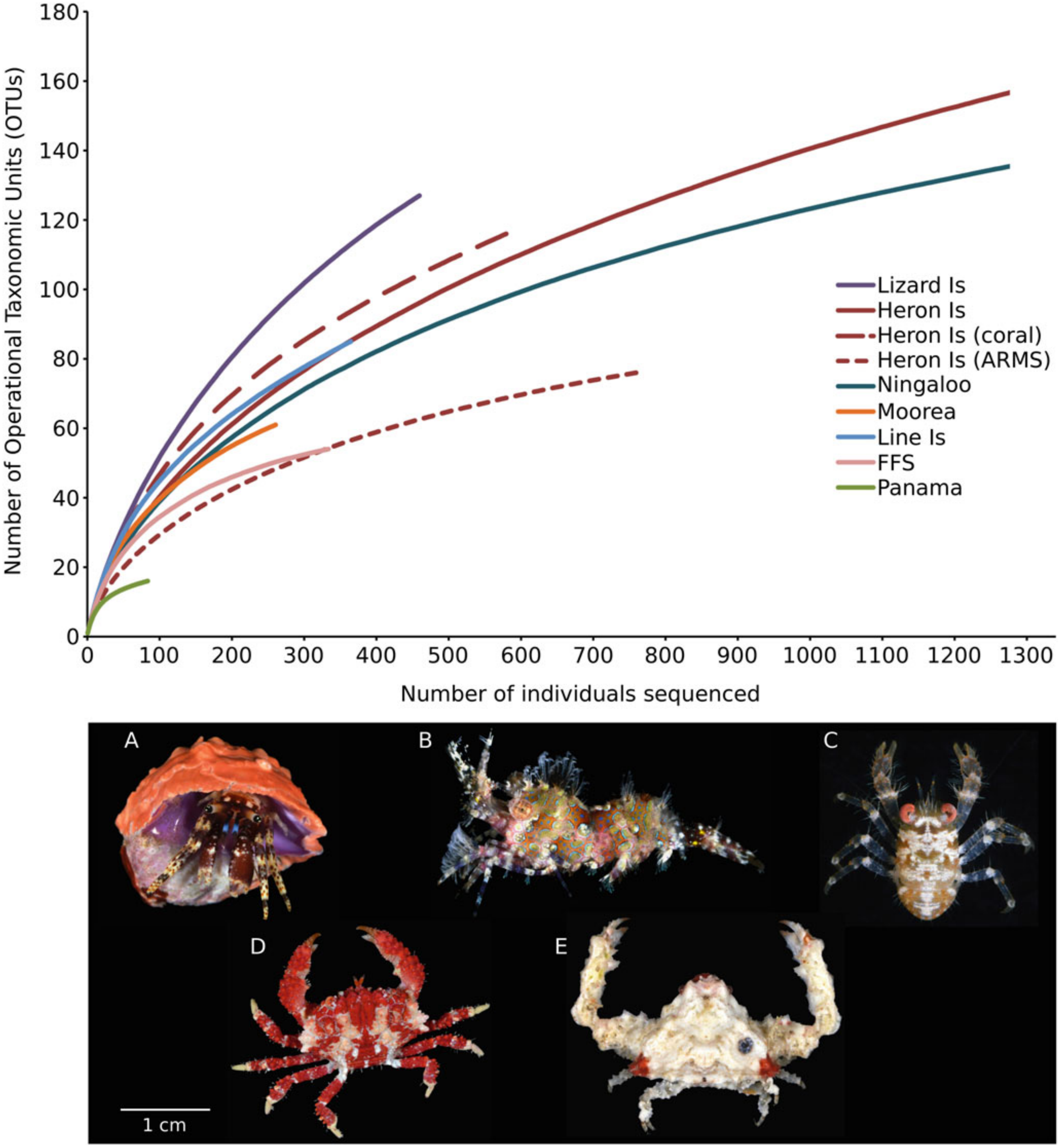


Fig. 6.2 Fish and corals have traditionally been used as surrogates to assess patterns of diversity on coral reefs because they are taxonomically well documented. However, short DNA sequences (*barcodes*) can now supplement traditional morphological approaches when identification can otherwise be time consuming, such as in decapods (*A*: *Calcinus* sp., *B*: *Saron* sp., *C*: *Galathea* cf. *ahyongi*, *D*: *Epiactaea* sp., *E*: *Daldorfia* sp.; all collected in the Red Sea; photo credit: Matthieu Leray). Plaisance et al. (2011, *top panel* modified from Fig. 4) used standardized sampling of dead coral heads and settlement structures (ARMS) with DNA barcoding to describe a gradient of decapod diversity across seven sites; even with large samples diversity had not reached a plateau in most locations

technically challenging, although applications for these organisms are also increasing (Leray et al. 2013; Leray and Knowlton 2015).

6.3 Ecological Relationships

Knowing what species are found where underpins most ecological analyses. For this reason, the identification of species using molecular tools, as described above, has transformed understanding of coral reef ecology in a number of areas where traditional methods for identification are time-consuming or inefficient. Here we review three: microbial symbiotic associations between corals and dinoflagellates, coral disease, and the dietary niches of reef fish.

If one had to choose a single area of coral reef science that has been most transformed by molecular genetics, it would be our understanding of the ecology of the symbiosis of corals and other coral reef organisms with dinoflagellates belonging to the genus *Symbiodinium* (Chap. 5). Indeed, a large proportion of the knowledge reviewed in Chap. 5 is due to the molecular methods that allow one to identify these single celled organisms, many of which cannot be readily discriminated morphologically. It is even possible to extract and sequence *Symbiodinium* DNA from museum specimens of octocorals collected over 150 years ago (Baker et al. 2013).

Previous research spanning decades on host-symbiont associations was upended by the realization that what was once thought to be a single species, *S. microadriaticum*, was in fact many. The initial discoveries were supported by protein electrophoresis and indicated that different hosts harbored genetically distinct symbionts; later work using DNA–based approaches revealed enormous diversity distributed among multiple subgenera of *Symbiodinium* (reviewed by Baker 2003). Multiple surveys have revealed some generalist and many specialist taxa with respect to host, and a wide variety of habitat preferences with respect to light and temperature [e.g. as in a recent survey of the northern Great Barrier Reef, Tonk et al. (2014)]. Discoveries of even more ecological specialization continue as additional cryptic diversity of both hosts and symbionts is uncovered (Prada et al. 2014b). The discovery of novel symbionts in unusually warm waters is of particular interest in the context of global warming [for a recent example see Hume et al. (2015)].

Symbiodinium are, of course, not the only microbial associates of corals and coral reefs. Like dinoflagellates, the Bacteria, Archaea, Fungi and protists found on and in the waters associated with coral reefs can only be easily studied with molecular genetic tools. These organisms have been the subject of especially intensive research of late, in part because of the increasing importance of coral disease on many coral reefs (Chap. 8). Analyses of changes in the microbial communities in corals in response to stress have revealed that manipulations of temperature, pH, nutrients, and dissolved organic carbon each result in distinct changes in the microbial communities (Thurber et al. 2009). Similarly, water samples taken from reefs characterized by different levels of overfishing have distinctive microbial communities, with more potential pathogens in the waters of the most anthropogenically impacted reefs (Dinsdale et al. 2008). DNA-based diagnostic tools for coral diseases have considerable and still largely untapped potential (Pollock et al. 2011).

Turning to the larger organisms on reefs, who eats whom is central to ecological understanding. Because observations of predation events are scarce even for conspicuous species, gut contents have been the traditional source of dietary information for fishes, the only group that has been intensively studied in this regard. However, there have been very few comprehensive analyses due to the diversity of potential prey combined with the difficulty of identifying semi-digested material (Bascompte et al. 2005). Molecular analysis of gut contents eliminates some of these challenges; a barcoding analysis of the gut contents of Mexican lionfish, for example, detected 34 species of prey from 157 individuals (Valdez-Moreno et al. 2012). Metabarcoding approaches (see above) provide even more information because they can characterize DNA from tissue slurries. The power of this approach is exemplified by a recent analysis of 16 reef fish guts (Leray et al. 2013) (Fig. 6.3), which revealed the presence of 334 prey taxa belonging to 14 phyla, 52.5 % of which could be identified to species by matches to genetic databases. Broad-scale application of this approach is likely to reveal diets that are more diverse than has been realized to date.

6.4 Population Structure

Long before molecular genetic data were available, scientists understood that marine species have far greater potential for long-distance dispersal than do terrestrial species. Dispersal typically takes places during the larval stage, but long distances can also be traversed by adults in some species. However, only with molecular genetic data has it been possible to evaluate clearly the extent to which that potential is realized.

Coral reef species vary considerably in this regard. In some cases, genetic data indicate surprisingly little genetic differentiation across large distances, for example across the 5000 km separating the reefs of the central and eastern Pacific (Lessios and Robertson 2006). In other cases, there is far more genetic structure dividing populations separated

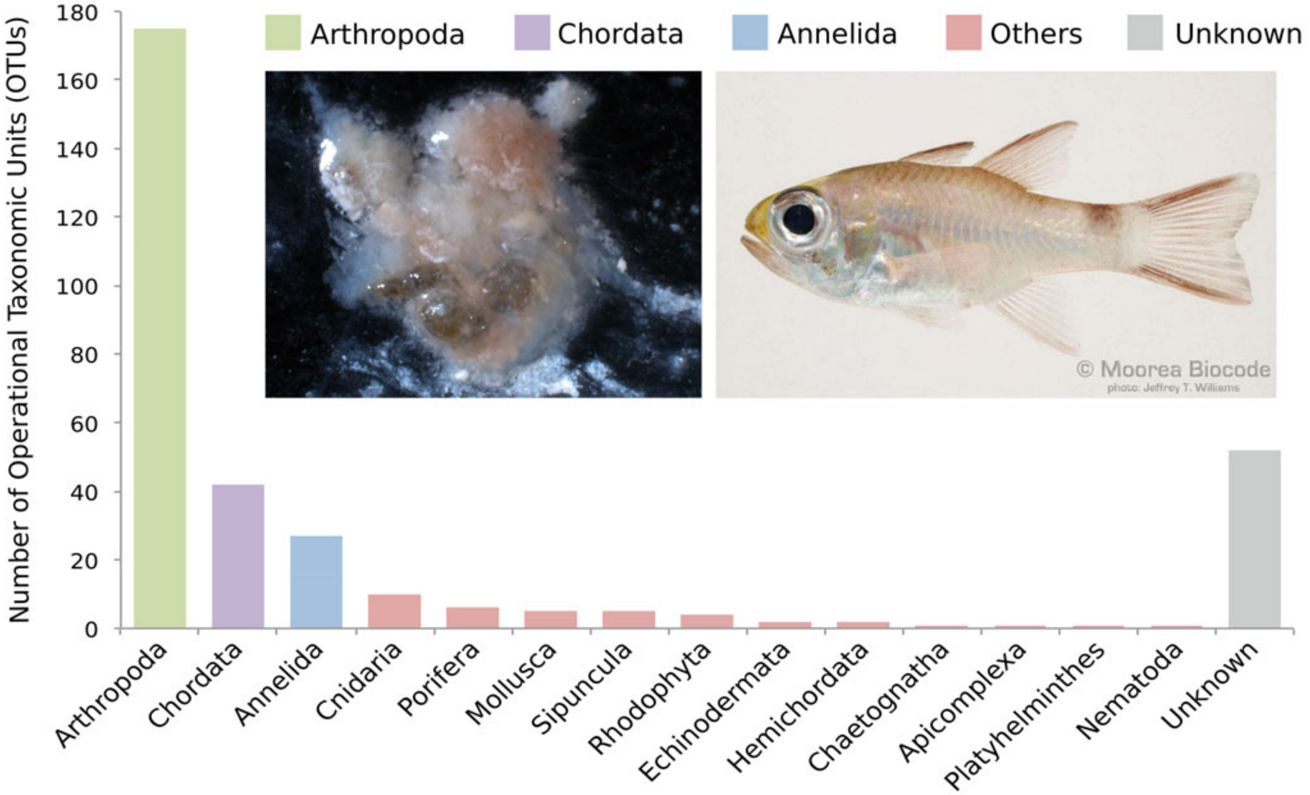


Fig. 6.3 Consumer-resource interactions are difficult to document on coral reefs and have often relied on morphological identification of prey remains in guts. However, genetic analyses have proven very powerful because they allow the detection of prey-specific DNA fragments from unidentifiable prey items (tissue homogenate, *left image*, photo credit: Matthieu Leray) even after several hours of digestion. For example, Leray et al. (2013, *bar graph* modified from Fig. 4a) used high-throughput sequencing to unveil the wide diversity of prey in the gut contents of *Nectamia savayensis* (*right image*, photo credit: Jeffrey T Williams), *Myripristis berndti* and *Sargocentron microstoma*

by short distances than might be expected (Barber et al. 2000; Rocha et al. 2005). Moreover, a recent study showing little difference in genetic diversity between closely related narrowly endemic versus widespread species (Delrieu-Trottin et al. 2014) suggests that genetic connectivity between widely separated populations is less than might be expected based simply on genetic differentiation.

Patterns of genetic connectivity have been of particular interest in the context of knowing the extent to which populations are self-sustaining. Some of the best data come from detailed analyses of anemonefishes, where it is possible to extensively sample adults and juveniles because of the discrete and conspicuous nature of the anemone host habitat. Results based on genetic parentage analysis vary widely depending on the setting, with more isolated sites exhibiting, as expected, more self-recruitment (Saenz-Agudelo et al. 2011). Moreover, even high levels of self-recruitment in contemporary time do not preclude long-distance genetic exchange over evolutionary time. One anemonefish species restricted to three offshore reefs in subtropical Australia had 68–84 % self-recruitment based on microsatellite analyses, whereas past connectivity over evolutionary time explained the shared mitochondrial lineages across locations (van der Meer et al. 2012). In the three-spot dascyllus, not only is some recruitment localized, but a pair of likely full sibs (based on their genetic similarity) were observed to settle together on a single night after spending nearly a month in the plankton (Bernardi et al. 2012).

The extent of routine connectivity between locations has important implications for the design of marine protected areas and other management decisions (Rocha et al. 2007). For example, Almany et al. (2013) (Fig. 6.4) documented that larvae of the squaretail coral grouper, a commercially important fish, often settle within 30 kms of their parents, suggesting that local communities could benefit directly by protecting spawning populations.

Patterns of genetic connectivity are also important for understanding sources of population explosions such as occur in the coral-eating seastar *Acanthaster planci*. One explanation for the temporal patterning of outbreaks is that an initial outbreak would seed secondary outbreaks via larval dispersal. In the central Pacific, unlike the Great Barrier Reef, the genetic distinctiveness of populations from different archipelagoes does not support a seeding hypothesis,

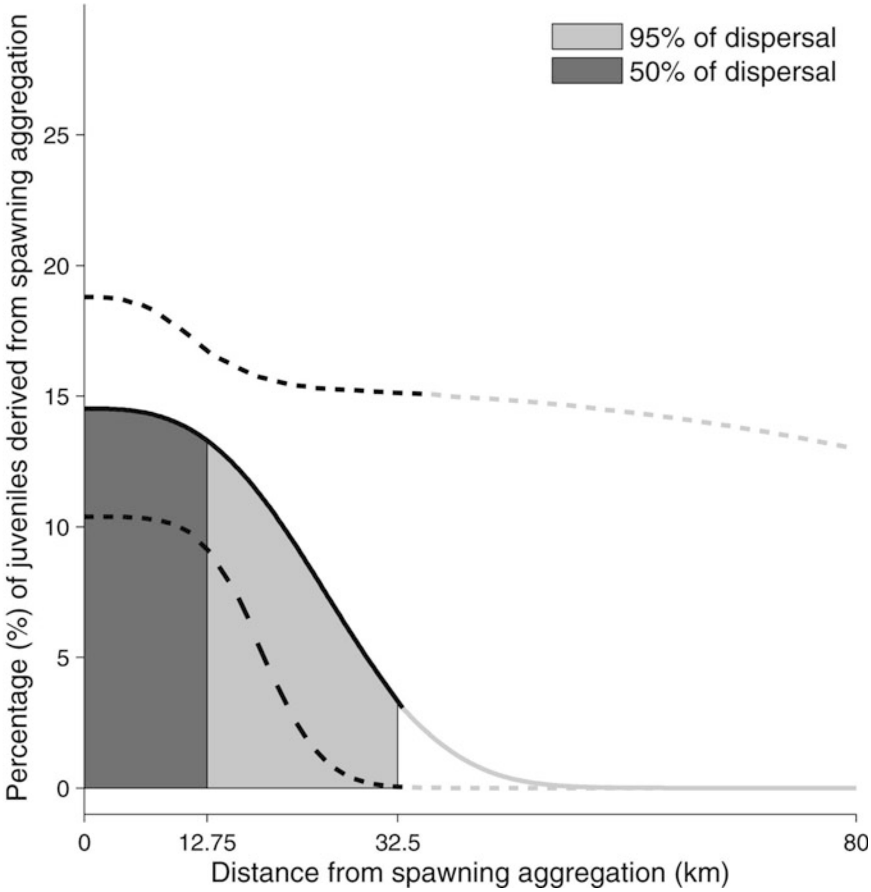


Fig. 6.4 Measuring the benefit of management actions for fisheries requires direct estimates of larval export for the replenishment of adjacent populations. Parentage analysis using microsatellites has been used as a tool to estimate distances of larval dispersal by assigning juveniles to their parents. Using this approach, Almany et al. (2013, panel above from Fig. 2) showed that 50 % of larvae produced by a managed spawning aggregation of squaretail coral grouper (*Plectropomus arelolatus*) settled within 14 kms of the aggregation, suggesting that management can provide fisheries benefits over small spatial scales

suggesting that clustering of outbreaks is instead due to shared environmental conditions (Timmers et al. 2012).

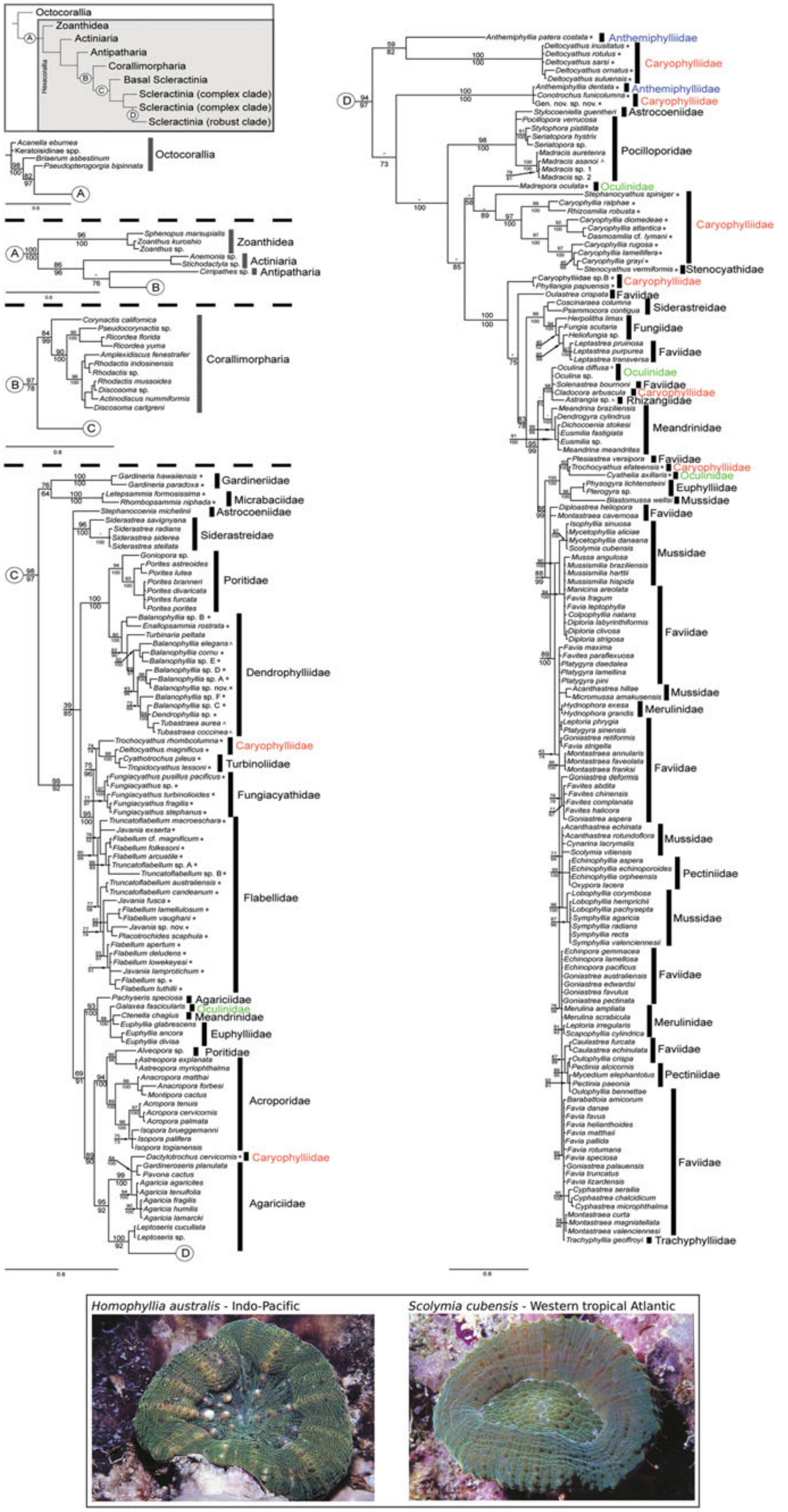
Finally, molecular genetic data allow one to estimate the demographic history of a species based on DNA sequence variation in extant populations. One of the most interesting case studies involves the Caribbean sea urchin *Diadema antillarum*, because of the potential for a genetic bottleneck following the loss of more than 97 % of its numbers due to a disease in the 1980s and because of the possibility that overfishing might have caused it to be more abundant immediately prior to the disease than it was in the more distant past. Surprisingly, genetic analyses supported neither of these scenarios, suggesting that the population of *D. antillarum* expanded more than 100,000 years ago with no loss of genetic variability following the recent population crash (Lessios et al. 2001).

6.5 Evolutionary Relationships

Our understanding of the evolutionary relationships among species has been transformed thanks to the application of molecular genetic methods in many groups, with coral reef organisms being no exception. These studies initially focused on mitochondrial genes, but phylogenetic studies now routinely involve multiple mitochondrial and nuclear genes.

Nowhere has this approach been more revolutionary in its findings than in the corals themselves, and hypotheses about relationships based on traditional morphological characters have been in many cases overturned following the application of molecular methods. One of the first major upheavals came with the establishment that corals could be divided into the so-called robust and complex corals, two highly divergent lineages that represent groupings quite distinctive from traditional arrangements of suborders (Romano and Palumbi 1996). Subsequent molecular analyses confirmed these results and showed that traditional families were also often unsupported (Fukami et al. 2008; Kitahara et al. 2010) (Fig. 6.5). Indeed, molecular genetic analyses have shown that some Atlantic genera conventionally assigned to different families are more closely related to each other than they are to "congeneric" taxa from the Pacific, suggesting a much deeper divide between Atlantic and Pacific reef groups than usually assumed. Considerable work on various sections of the scleractinian tree (e.g. Huang et al. 2014) will be required to sort out the many taxonomic messes that remain at a variety of taxonomic levels.

Fig. 6.5 Molecular analyses have had a profound impact on our understanding of evolutionary relationships of many coral reef organisms, including corals. Kitahara et al. (2010, *tree above* from Fig. 1), in a recent comprehensive phylogenetic analysis of scleractinian corals, showed that deep-sea azooxanthellate species are basal to the group and most recognized shallow-water zooxanthellate families are polyphyletic. In some cases, Atlantic and Pacific species once thought to belong to the same genus, are now placed in different families, such as *Homophyllia* (formerly *Scolymia*) *australis* from the Pacific (Lobophylliidae, *left image*) and *Scolymia cubensis* from the Atlantic (Mussidae, *right image*) (Photos courtesy of JEN Veron)



Taxonomic revisions based on molecular analyses are not limited to corals. Other groups of important coral reef organisms with major reevaluations of relationships based on molecular data include the damselfish (Quenouille et al. 2004), wrasses (Westneat and Alfaro 2005), cowries (Meyer 2003) and cone snails (Puillandre et al. 2014). Where considerable natural history is available to overlay on the phylogeny, it is possible to reconstruct the evolution of other features such as diet. In cone snails, for example, molecular phylogenies reveal that polychaete feeding is the ancestral state, and the ability to feed on mollusks and fishes most likely evolved only once in each case.

These kinds of genetic analyses can also give us insights into the geography of diversification (phylogeography). Coral reefs have played a prominent role in such studies because of their importance in the context of the latitudinal species gradient and attempts to understand why marine diversity is concentrated today in the western tropical Pacific (the so-called Coral Triangle). In evaluating the strengths of competing hypotheses (e.g. the Coral Triangle as a center of origin, center of accumulation, or center of overlap), a recent review (Bowen et al. 2013) concluded that phylogeographic analyses of a wide variety of organisms provide support for all three.

6.6 Speciation

A related controversy concerns the relative importance of allopatric and non-allopatric speciation in the sea (reviewed in Bowen et al. 2013). Impenetrable barriers are uncommon in the ocean, one exception being the Isthmus of Panama, which blocks connections for tropical organisms between the western Atlantic and the eastern Pacific. This situation is a model system for understanding allopatric speciation in the sea (reviewed by Lessios 2008) because closure was relatively recent (~3 million years ago) and because the geology of the area has been extensively studied. Analyses of the extent of molecular divergence between sister taxa on the two sides of the Isthmus showed that the impact of the Isthmus in breaking genetic connections began substantially before final closure, a finding with large implications for the calibration of molecular clocks for various genes and taxa (Knowlton and Weigt 1998).

Increasingly, however, speciation in the absence of complete physical barriers has been documented (Bowen et al. 2013). Cases for coral reef organisms involve speciation across strong ecological gradients (Rocha et al 2005; Duran and Rützler 2006), as a function of host shifts (Duffy 1996; Munday et al. 2004), and as mediated by assortative mating (Puebla et al. 2012) (Fig. 6.6). In each of these cases, genetic analyses have been used to confirm the absence or reduction in gene flow that underpins the speciation event. Speciation in the absence of geographic barriers can happen quite rapidly. For example, two sister species of tropical seastars, one a broadcast spawner and the other a self-fertilizing brooder, are thought to have diverged only 6000 years ago (Puritz et al. 2012).

Molecular methods are also critical to understanding the frequency with which barriers between species break down. Hybridization has been widely assumed in corals and undoubtedly occurs. Indeed, *Acropora prolifera* in the Caribbean is known to be an F1 hybrid of *A. palmata* and *A. cervicornis* (Vollmer and Palumbi 2002), two species that have weak barriers to crossing (Fogarty et al. 2012). In this and other cases, molecular data are crucial for determining the extent to which gene flow occurs across species boundaries and for determining the parentage of larvae resulting from experiments in which eggs are offered a choice between sperm of two species. In several other well studied cases, however, gene flow has turned out to be more restricted than initially assumed, and it is often difficult to distinguish between hybridization and the maintenance of ancestral polymorphisms when individuals carry the genetic signature of two closely related species (Palumbi et al. 2012).

Finally, the mechanistic processes underlying evolutionary diversification can also be analyzed using molecular genetics. For marine organisms, these have been most thoroughly explored to understand gamete recognition in species where fertilization occurs externally (Lessios 2011). Because many marine organisms release eggs and sperm into the water, genes that influence the interactions of sperm and eggs are tightly connected with the process of speciation itself. Sea urchins and abalones have been the best studied, and some of these sea urchins are prominent members of coral reef communities (e.g. *Echinometra*). In sea urchins, gametic compatibility is strongly influenced by the bindin protein and its receptor. The evolution of bindin has been extensively studied, but the receptor is enormous (4595 amino acids) and much less well known. Nevertheless, analyses of bindin and the extremely low incidence of genetically confirmed hybrids in nature suggest that bindin is one of several factors that contribute to interspecific boundaries, and that its evolution may have more to do with intraspecific sexual selection and avoidance of polyspermy (the fertilization of one egg by many sperm) than with prevention of interspecific hybridization (Lessios 2007).

6.7 Sexual Systems

Molecular analyses are also useful for studying mating biology within species, including the identification of partners; indeed when gametes are released into the water column in

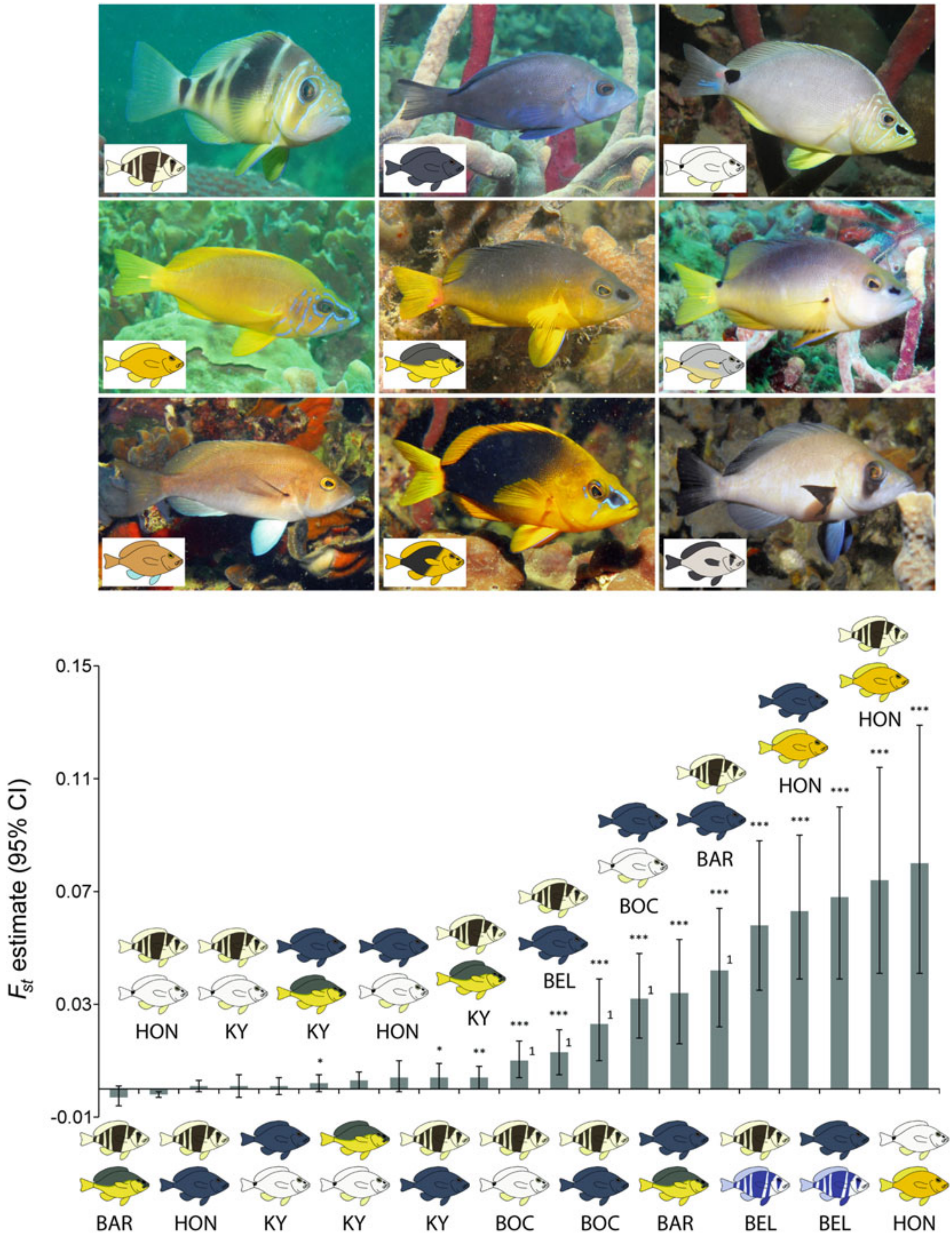


Fig. 6.6 Evolutionary mechanisms underpinning speciation on coral reefs can be readily studied with the tools of molecular genetics. Using behavioral observation, population genetic analysis and individual-based simulation, Puebla et al. (2012, above modified from Figs. 1 and 5) demonstrated the role of sexual selection in driving the evolution of assortative mating in hamlets (*Hypoplectrus* species). Low levels of genetic differentiation (F_{st}) at neutral genetic markers between sympatric color-morphs that occasionally hybridize showed that speciation is occurring in the presence of gene flow

the absence of clear pairing behavior, genetic analyses are the only way to analyze mating success. This approach has been used to determine paternity in spawning fish (Wooninck et al. 2000) as well as in some invertebrates. In one species of stony coral, molecular analyses showed that larvae are often the product of nearby individuals releasing their gametes nearly simultaneously (Levitan et al. 2011). Similarly, in a study of the soft coral *Pseudopterogorgia elisabethae*, most planula larvae appeared to have been sired within the 20 × 20 m of the study area, although closer

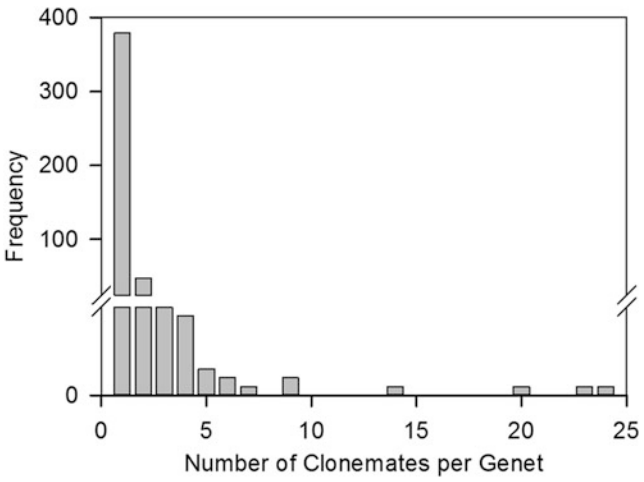


Fig. 6.7 Corals are able to reproduce sexually and asexually but the prevalence of asexual propagation has been difficult to evaluate. Foster et al. (2013, *panel above* from Fig. 2) used microsatellite markers to genotype individual colonies of *Orbicella annularis* and show the contribution of clonal reproduction at various sites across the species' range. They showed that sites varied widely with respect to the number of clonemates per genet (each genet consists of a colony or collection of colonies derived from a single fertilized egg), with asexual reproduction being more common in locations with greater hurricane frequency

or larger males surprisingly did not appear to have an advantage (Lasker et al. 2008). Planula larvae that disperse short distances can lead to aggregations of close relatives, and genetic signatures of inbreeding have been detected in some of these species (Richards and van Oppen 2012; Carlon and Lippé 2011).

Although sexual reproduction is the dominant form of reproduction in corals and many other organisms, asexual reproduction is also sometimes common. Fragmentation produces large numbers of clonemates that can be readily recognized with genetic methods (Foster et al. 2013) (Fig. 6.7). Documenting the geography of clonal reproduction is important because in many mass-spawning corals, self-fertilization is not possible, with implications for reproductive success. A less common form of asexual reproduction is the production of asexual larvae. The best studied case among corals is that of *Pocillopora damicornis*; a recent analysis using microsatellite data suggested that over 90 % of the larvae released were produced parthenogenetically (Combosch and Vollmer 2013).

Of course, asexual reproduction does not prevent the occurrence of mutations. Analogous to the forms of asexual reproduction described above is the clonal reproduction of units within colonies (polyps in corals, zooids in bryozoans, etc.), and growth in general is by its nature a form of asexual reproduction even in non-colonial forms. Recently, interest has increased in determining the prevalence of mutations occurring within individuals due to somatic mutations (mosaicism), a phenomenon that can only be routinely detected with genetic methods. One study using microsatellites found that 10 of 14 colonies of the coral *Acropora hyacinthus* exhibited genetic mosaicism with the potential to transfer this variation to the next generation via eggs (Schweinsberg et al. 2014).

6.8 Physiology and Development

The preceding sections have reviewed the profound contributions of molecular genetics to our understanding of ecology and evolution. At the level of individual organisms, genes control the structure and production of proteins, so it goes without saying that these methods have enormous power to elucidate physiological and developmental processes as well. Until recently, our ability to explore these aspects of coral biology depended on identifying genes known to be associated with certain functions in other metazoans and then using that information to search for related genes in corals. For example, Levy et al. (2007) were able to identify genes related to the ability to sense blue light that could be involved in the synchronization of spawning.

The landscape of what is possible has changed dramatically, however, now that gene expression, transcriptomes (sequences of transcribed genes) and entire genomes can be readily studied in non-model organisms, in particular corals. For example, comparisons of healthy versus diseased *Acropora cervicornis* and *Orbicella faveolata* show distinct patterns of gene expression as a function of coral health (Closek et al. 2014; Libro et al. 2013) (Fig. 6.8). A comparison of gene expression in the bases and branch tips of the closely related *A. cervicornis* and *A. palmata* revealed marked differences in gene expression that may underpin their morphological differences (Hemond et al. 2014). An array of genomic and proteomic data has revealed a suite of 36 proteins likely involved in the formation of coral skeletons (Drake et al. 2013). Gene expression responses associated with algal competition, high temperature, excess nutrients, and ocean acidification are providing a window on the complex physiologic responses of corals to stressors associated with locally driven reef degradation and rising CO_2 emissions (Rosic et al. 2014; Shearer et al. 2014; Moya et al. 2015).

Shinzato et al. (2014) provide a recent snapshot of genomic resources for corals and *Symbiodinium*. For corals, their list contains one published scleractinian genome (*Acropora digitifera*) and ten published scleractinian transcriptomes [four of which were for *Acropora*, two for *Porites*, and one each for *Favia*, *Orbicella* (listed as *Montastraea*), *Stylophora*, and *Pocillopora*]. The *A. digitifera* genome was about 420 Mbp in size and represented over 23,000 coding genes, about 93 % of which could be related to

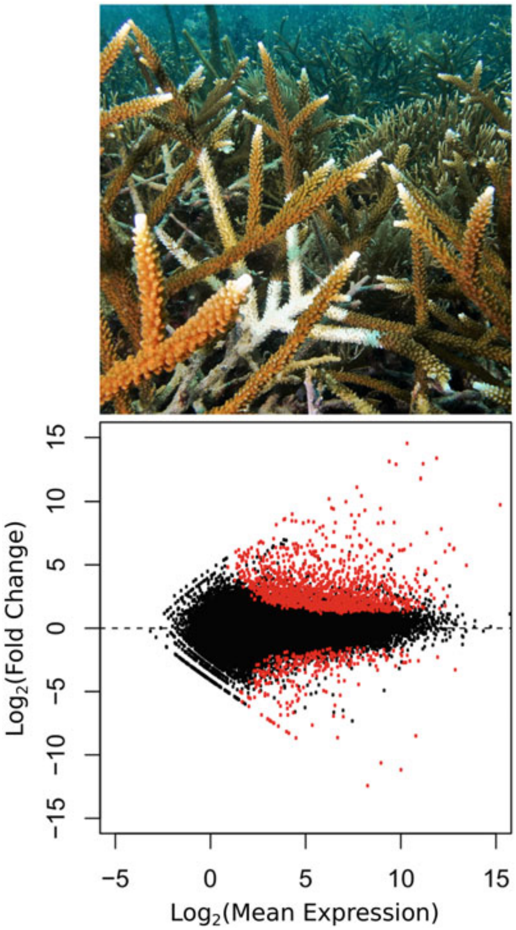


Fig. 6.8 High-throughput RNA sequencing is increasingly used as a tool to understand the physiological response of corals to stressors. Libro et al. (2013, above from Figs. 1 and 2) investigated the immune response of *Acropora cervicornis* to White-Band Disease (*upper photo*) by comparing RNA-seq profiles of healthy and infected tissues. Their approach identified a series up- and down-regulated genes that represent 4 % of the coral transcriptome (plotted in *red* below)

genes in other metazoans. Among these are genes linked to processes associated with calcification, *Hox* developmental genes, genes associated with innate immunity (some of which may be involved in the establishment and maintenance of symbiosis), genes involved in protection against UV damage, fluorescent protein genes, and photoreceptor and circadian clock genes. For *Symbiodinium*, one genome (~1500 Mbp) and 13 transcriptomes were cited in the review (the latter including representatives of the four clades commonly found with scleractinian corals). Our understanding of these data is more limited because of the scarcity of comparative data on dinoflagellate genomes compared to metazoans, as well as the large and peculiar features of the dinoflagellate genome itself. For both corals and *Symbiodinium*, the genomic information landscape is changing so rapidly that any review is almost immediately out of date.

Finally, microbes, being single celled, sit at the intersection of physiology and ecology. Because of their importance in biogeochemical cycling, one way to explore the metabolism of a reef is through analyzing microbial genes. Kelly et al. (2014) using a metagenomic approach found for an array of islands spanning a variety of biological, oceanographic and geographic characteristics, that the type of organisms living on the bottom (especially the amount of living coral) was the best predictor of the taxonomic composition of the microbes, whereas distance from the equator was the strongest predictor of metabolic characteristics of the microbial community.

6.9 Concluding Remarks: Molecular Genetics and the Future of Coral Reefs

Part of what drives science is the desire for technical breakthroughs, and molecular genetics is arguably the scientific field most transformed by such achievements in recent decades. Yet, despite their seductive appeal, it is important to remember that these powerful methods are tools. As with any tool, what really matters are the problems that need solving and the questions that need answering. For this reason, the insights provided by molecular genetics are most compelling when placed in a broader context. In that light, one of the most important frontiers is increasingly the linkage between insights on the functioning of coral reefs provided by molecular genetics and the challenges posed to reefs by the Anthropocene.

Many of the topics reviewed above have clear conservation implications. The dispersal capabilities of fish have important ramifications for the design of marine protected areas (Almany et al. 2013). The identification of stress resistant genotypes could be useful in facilitating adaptation to climate change (Chap. 7, Lundgren et al. 2013; Hume et al. 2015). The characterization of pathogens can form the underpinnings for the management of disease (Pollock et al. 2011). Evolutionary trees can be used to predict the implications of extinctions for the preservation of biodiversity (Huang and Roy 2015). Genetics can play critical roles in the analysis of diet and populations of invasive species (Betancur-R. et al. 2011; Valdez-Moreno et al. 2012) and in tracking the sources of population explosions of native species such as *Acanthaster* (Timmers et al. 2012). Rapid biomonitoring of diversity, including as a response to management, is made possible by metabarcoding (Leray and Knowlton 2015). DNA forensics allows one to assess the extent to which fisheries regulations are being followed (Cox et al. 2013). Indeed, the list is nearly endless.

Could genetic engineering be next? Van Oppen et al. (2015) have considered just that in their thoughtful essay on using assisted evolution to help save coral reefs.

Though they stop well short of the creation of Frankenstein corals, their list of topics to explore includes exposing *Symbiodinium* cultures to mutagens with the goal of producing strains better able to cope with rising temperatures and declining pH.

In sum, the future of molecular genetics in reef studies is bright indeed. One can only hope that these powerful methods will also serve to brighten the future of the reefs themselves.

Glossary[1]

Barcode is a standard short stretch of DNA that is unique to each species and therefore used to delineate species or identify unknown specimens. In animals, the most common barcode is a 658 bp segment of the mitochondrial cytochrome c oxidase subunit I gene.

Barcode of Life Data Systems (BOLD) is an online platform for the storage, analysis and publication of DNA barcode records.

Coalescent theory uses a mathematical model to reconstruct the genealogy of genes back to their common ancestor.

DNA microarray analyses are most commonly used to measure the expression levels of a large number of target genes simultaneously. Microarray chips contain thousands of microscopic spots where specific DNA probes are inserted. The relative abundance of target genes is quantified via fluorescence when target DNA hybridizes to probes.

Environmental DNA is the sum total of DNA in an environmental sample. It comprises not only the DNA from intact organisms in the sample, but also other sources of cellular or extracellular DNA released by an organism into the environment (e.g. in mucus, gametes, feces).

Expressed Sequence Tags (ESTs) are portions of complementary DNA (cDNA) that are constructed from messenger RNA. These fragments of expressed coding genes are used for gene discovery, mapping, gene prediction, gene expression and polymorphism analysis.

GenBank is a publicly available collection of DNA sequences hosted by the National Institute of Health (NIH).

Genome is the entirety of the genetic information contained in an organism.

Genomic library is the collection of DNA fragments representing the genome of an organism stored as short fragments within many individual bacteria or yeast cells. Such collections facilitated early efforts at genome sequencing.

Genomics is the quantitative analysis of the genome.

High-throughput sequencing technologies (i.e. pyrosequencing, semiconductor sequencing) produce millions of sequences concurrently within a few hours. These technologies have drastically lowered the cost of studies that require large amounts of sequence data.

Metabarcoding uses DNA-based species identification and high-throughput sequencing as a cost- and time-effective way to infer the species composition of environmental samples (e.g. plankton, sediments).

Metagenomics is the study of the genetic material collected from the environment. It provides a profile of diversity, including many small organisms that cannot be cultured, and a detailed characterization of the metabolic genes present in an environmental sample.

MicroRNA (miRNA) are short non-coding RNA molecules (approximately 22 nucleotides in length) found in the genomes of plants, animals and some viruses that play a key role in the regulation of gene expression.

Microsatellites are short repeating DNA sequences (two to ten base pairs in length) found across the genome of a species. Because they evolve rapidly, they are especially useful for population studies and individual fingerprinting.

Molecular clock is a mathematical approach that uses the fossil record and rates of DNA sequence evolution to estimate the time since two species or a group of species diverged.

Molecular cloning is a technique that uses a host organism (easy-to-grow bacteria) to replicate a single DNA molecule into multiple identical copies.

Nuclear DNA/organelle DNA/ribosomal DNA are different types of DNA found in the nucleus and organelles (such as the mitochondria, mtDNA) of eukaryotic organisms. Ribosomal DNA (rDNA) refers to the genes that code the RNA that makes up the ribosomes.

Operational Taxonomic Units (OTUs) are low-level taxa often equivalent to species that are defined genetically rather than being identified to species using traditional morphological methods.

Phylogeography is the study of historical processes (i.e. vicariance, population expansion) that explain the present day distribution of populations or species using mitochondrial/nuclear gene genealogies.

Polymerase Chain Reaction (PCR) is used to replicate a single copy of a DNA fragment into millions of copies of the same DNA fragment within a few hours, allowing the DNA to be sequenced.

Primers are strands of nucleic acids used as a starting point for DNA replication during the polymerase chain reaction.

Protein electrophoresis is a laboratory technique used to separate individual proteins from complex mixtures using

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[1] Some terms and concepts useful for understanding molecular genetic studies.

differences in size and electric charge. This was one of the first molecular genetic tools to be used in coral reef studies.

Proteomics is the study of the composition, structure and function of the whole set of proteins produced by the coding genes of an organism.

Restriction-site Associated DNA (or RAD) sequencing is a method used to sample thousands of random parts of the genome of many individuals simultaneously using high-throughput sequencing. Because it analyzes a small fraction of the entire genome, it allows affordable study of many markers across the genome for population genetic studies in non-model species.

Restriction Fragment Length Polymorphism (RFLP) analysis is a DNA profiling technique that uses restriction enzymes to cut stretches of DNA at specific genetic sequences within a gene, followed by analysis of variation in the lengths of the fragments.

Sanger Capillary Sequencing is an automated DNA sequencing technology developed in 1977 by Fred Sanger. It uses a laser to read the position and identity of dye-labeled nucleotides on DNA fragments previously amplified via PCR.

Shotgun Sequencing is a method used to read the sequence of very long stretches of DNA (i.e. genomes). The process involves shearing the long DNA stretch into smaller fragments (<1000 bp) that can be sequenced individually and later reassembled bioinformatically using overlapping regions.

Single Nucleotide Polymorphism (SNP) is a genetic variant at one position in a DNA sequence shared by multiple individuals in a population. The frequency of different SNP alleles can be analyzed with respect to such factors as environment or geographic locale.

Transcriptomics is the study of sets of genes expressed in the genome of a given organism under specific conditions.

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Genomic Potential for Coral Survival of Climate Change

7

Daniel J. Barshis

Abstract

One of the most pressing questions in coral reef biology today is "Will reef-building corals survive climate change?" Critical to this question is the rate at which climate change is progressing and whether that rate will be matched or exceeded by the ability of corals to acclimatize and adapt in their upper stress tolerance limits. The emerging field of genomics (i.e., genome scale genetics) holds great promise for investigation of the raw material needed for coral acclimatization and adaptation to climate change: variation in the gene sequences and activity of the molecular response pathways enabling corals and *Symbiodinium* to maintain key biological functions under environmental stress. A growing number of studies of gene expression signatures and gene frequency distributions are finding a diverse array of potential targets both for acclimatization potential and adaptive natural selection in climate change resistance. Additionally, research is consistently finding greater acclimatization and adaptive potential than previously thought, which when incorporated into models of coral survival in the future significantly improves the short-term outlook for reef persistence. Much remains to be determined about the extent of relevant phenotypic diversity in coral thermal tolerance and resistance to ocean acidification as well as the relative contributions of the coral host, *Symbiodinium*, and associated microbes to increased stress resistance. However, application of these new technologies to the question of coral climate change survival provides new evidence that evolutionary accumulation of adaptive diversity and phenotypic plasticity may give corals increased potential for persistence in the Anthropocene.

Keywords

Adaptation • Acclimatization • Acidification • Climate • Selection

7.1 Introduction

There is no longer a question that climate change is affecting and will continue to affect corals and coral reefs (e.g., Hoegh-Guldberg 1999; Hughes et al. 2003; Carpenter et al. 2008; Doney et al. 2011). The debate now focuses on how extensive these effects will be and whether enough corals possess the ability to withstand these stresses in the coming decades without a precipitous decline in coral abundance and a large-scale loss of reef ecosystems and the services they provide. Central to this debate is the rate at which climate change is progressing and whether the rate of change in the environment will be matched or exceeded by the ability of corals to acclimatize or adapt in their upper tolerance limits.

Hughes et al. (2003) posits a number of scenarios for how corals may respond in the future (Fig. 7.1). The only scenario

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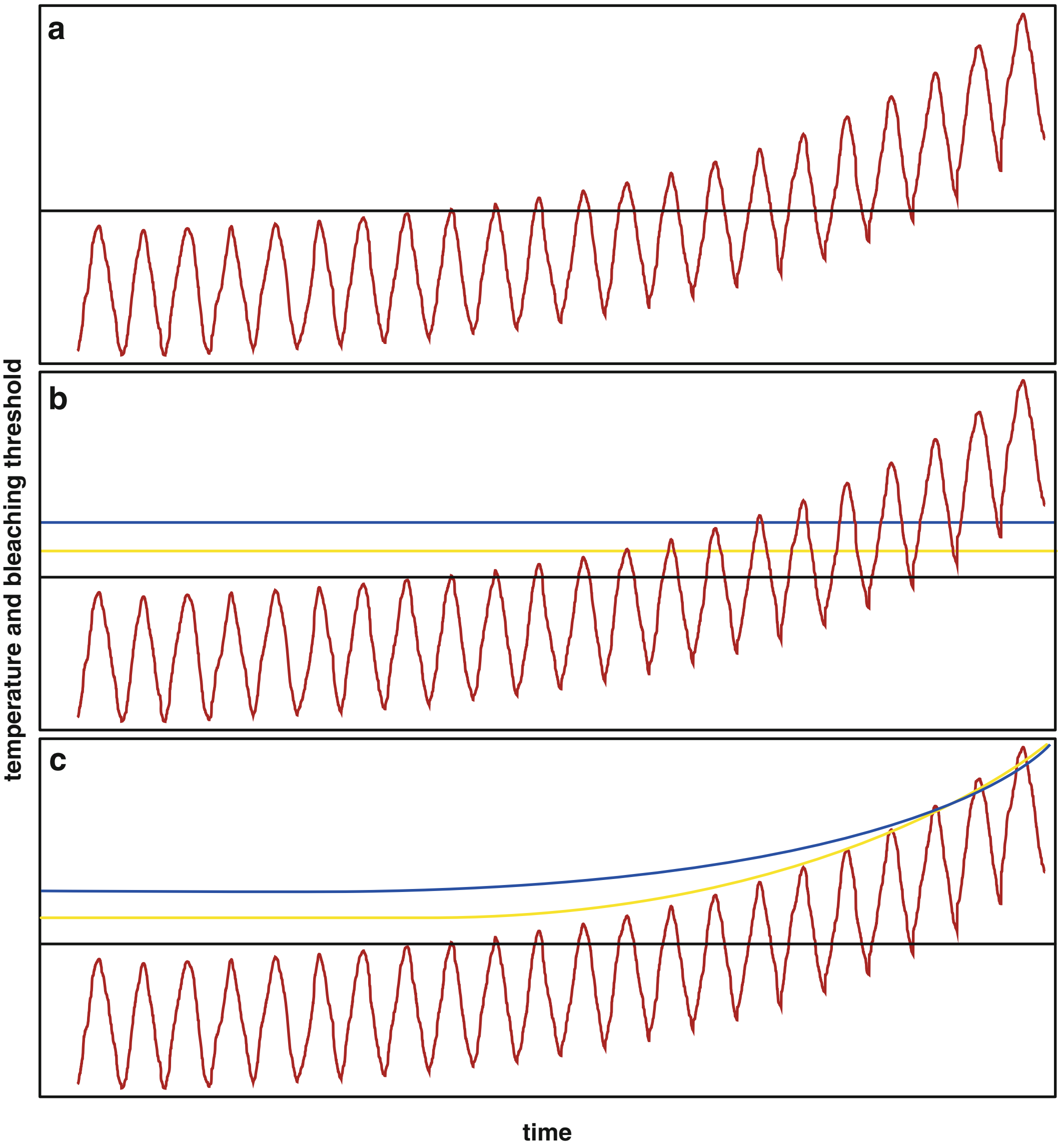

Fig. 7.1 A schematic model representing various scenarios regarding coral bleaching thresholds in relation to future ocean warming. The *red line* represents continued sea surface temperature increase while the *black, yellow, and blue lines* represent theoretical coral thermal thresholds. (**a**) Represents a single thermal threshold for all corals that would be chronically exceeded in the future as sea surface temperatures increase. (**b**) Represents variation among populations and species in the critical thermal threshold. (**c**) Represents the capacity for critical thermal thresholds to change in response to the environment either via acclimatization or adaption to climate change (Figure modeled after Figure 2 in Hughes et al. 2003. Printed with permission from AAAS)

wherein coral bleaching thresholds are able to keep pace with increased ocean temperatures is one that includes the capacity for corals to acclimatize and adapt (Fig. 7.1c). It is generally accepted that climate change will alter ocean temperature and pH such that most corals will experience conditions above their current tolerance limits (Hughes et al. 2003; Hoegh-Guldberg et al. 2007; Pandolfi et al. 2011). What has yet to be determined experimentally and observationally, however, is what capacity corals have to shift those tolerance limits and whether they can be shifted quickly enough and with ample magnitude to keep pace with the changing environment.

Classic ecological and evolutionary theory tells us organisms may respond to environmental change via four main pathways: movement, adaptation, acclimatization, or death/extinction (Holt 1990; Aitken et al. 2008). For the purposes of this chapter we will focus primarily on the As; the ability of corals to adapt or acclimatize to the environmental conditions produced by climate change. Movement relates to larval dispersal and will be touched on briefly near the end of the chapter. Death/Extinction is fairly self-explanatory: conditions may change beyond the tolerance limits and evolutionary capacities of a given organism making survival no longer possible.

For the purposes of this chapter “**adaptation**” refers to evolutionary adaptation, wherein natural selection acts on individuals with heritable genetic mutations that provide increased fitness, the product of which is an increase in survival and reproduction of those advantageous genotypes in the population. “**Acclimatization**” refers to the ability of a single individual to adjust its phenotype during the duration of its lifetime, also referred to as phenotypic plasticity. **Acclimatization** signifies a phenotypic change in response to variation of multiple environmental factors under natural conditions, while **acclimation** refers to a phenotypic shift in response to just a single variable (e.g., temperature only; Prosser 1991). The important distinction between adaptive and acclamatory processes is adaptation acts across multiple generations and is heritable from parent to offspring, while acclimatization acts within a single generation and is generally not heritable from parent to offspring (though see discussion of epigenetics in Brown and Cossins 2011).

7.2 The Role of Genomics in Coral Climate Change Science

Genomics is the emerging field of genome-scale genetics (i.e., examination of a large percentage of the genetic material of an organism rather than a small number of specific gene fragments). Recent advances in sequencing technologies have revolutionized the scale at which hypotheses can be tested and genetics data can be generated. High-throughput (also known at next generation) sequencing technologies are now capable of generating billions of base pairs (single DNA nucleotides) during a sequencing run. This data generation is orders of magnitude greater than previous technologies and allows for the simultaneous investigation of tens of thousands of genes within a single experiment. In terms of corals, these genomic technologies enable examination of the mechanisms behind the adaptation and acclimatization potential of traits that will allow corals to survive climate change: e.g. bleaching resistance, recovery from disturbance, and growth/calcification/reproduction under anomalous conditions (low pH, increased sedimentation, high temperature events). The link between these traits and the environment is the actual material needed for acclimatization and adaptation, i.e., variation in the gene sequences and activity of the molecular response pathways enabling corals and *Symbiodinium* to maintain key biological functions under environmental stress. This chapter provides an updated review of the role of genomics in studies of coral adaptation and acclimatization to climate change. There are a variety of previous, in-depth reviews of these concepts from a broader perspective (e.g. Coles and Brown 2003; Jokiel 2004; Brown and Cossins 2011), hence the purpose here is to provide recent updates to these previous works, as well as a more specific focus on how genomics can lend insight into the raw material responsible for these processes.

7.3 Acclimatization of Corals to Climate Change

The sheer temporal and spatial scales of climate change events make true tests of coral climate change acclimatization difficult, as they would require large-scale manipulations of environmental variables for many years and decades and across hundreds of kilometers of reef. Researchers have thus settled on two main experimental approaches to test coral acclimatization abilities that may be relevant to climate change survival. The first approach focuses on short-term responses by recreating thermal or pH stress events in the lab and assessing changes in response following different acclimatization treatments. This approach enables accurate recreation of the environmental perturbations of various climate change scenarios. However, these experiments are conducted over short time-scales and may not be indicative of the multi-year or decadal scale of actual climate change variation in environmental characteristics. Also, while lab approaches are powerful in their ability to isolate the effect of one or a few variables (e.g. temperature and pH), they generally examine only a subset of the different variables naturally occurring in the environment (e.g. light variability, flow regime, nutrient dynamics, sedimentation, dissolved oxygen, community assemblage interactions) and thus represent an oversimplification of the natural world.

The second approach involves using naturally occurring extreme habitats as a proxy for climate change effects on average environments. This approach is powerful in that corals that have been living in “climate change” like conditions for many generations (i.e., 100s of years) can be compared to neighboring populations from more benign habitats to examine the effects of long-term exposure to environmental stress. These natural, climate change like habitats can take the form of back reef pools regularly reaching high temperatures (Craig et al. 2001), ocean regions like the Persian/Arabian gulf that reach upwards of 36 °C (Coles 1997), or low pH CO_2 seeps (Fabricius et al. 2011), springs (Crook et al. 2013), and reef areas (Shamberger et al. 2014) which approximate future ocean acidification scenarios. The main drawback of these types of experiments is that present day extreme habitats are not exact replicas of future climate change scenarios and thus represent only an approximation of long-term climate change effects. However, the ability to examine the long-term effects of these types of exposures can provide valuable insight into the mechanisms responsible for adaptation and/or acclimatization across the multiple timescales over which they operate.

Brown and Cossins (2011) present a number of key conclusions from both laboratory and field approximation approaches in their review of temperature acclimatization potential in the face of climate change: (a) the ability of corals to acclimatize to changes in climate remains poorly characterized and should not be discounted in future predictions of reef health; (b) a growing number of studies find increases in thermal tolerance following exposure to increased solar radiation and/or sub-lethal elevated temperatures; (c) multiple host and *Symbiodinium*-specific mechanisms exist to facilitate acclimatization; and (d) the role of epigenetics in coral acclimatization is almost entirely unexplored and could represent additional potential for long term acclimatization gains. Since the publication of their comprehensive review, a growing number of studies have found detectable signatures of coral acclimatization, many of which involve increases in bleaching resistance following some type of sub-lethal thermal exposure. Additionally, implementation of genomic tools has opened the door for beginning to understand which genes and physiological processes may be involved in the acclimatization response.

7.3.1 Evidence for and Against Coral Thermal Acclimation

Contrasting ideas regarding acclimatization potential in the face of climate change have been raised over the years in a variety of taxa (including coral). For instance, Stillman (2003) found intertidal porcelain crabs with the highest current tolerance limits actually had the least ability to acclimate to additional heat exposures, suggesting the most thermally tolerant individuals may be the most susceptible to climate change. The opposite was found in a study of European diving beetles, wherein there was a positive relationship between upper thermal tolerance and acclimation ability, with the lowest tolerance populations being the most at risk of future climate change effects (Calosi et al. 2008). In the Mediterranean coral *Oculina patagonica*, Rodolfo-Metalpa et al. (2014) found little to no thermal acclimation ability in populations from four habitats with different thermal regimes, despite 14 weeks of slow exposure to increasing temperature. Additionally, they found little evidence for pre-existing variation in overall thermal tolerance across the various populations, suggesting few adaptive differences across the seascape in this relatively new member of the Mediterranean coral fauna (Rodolfo-Metalpa et al. 2014).

This last finding is in contrast to multiple lines of evidence for thermal adaptation in other Scleractinia (see below Sect. 7.4). In fact, Howells et al. (2013), found historical thermal adaptation in *Acropora millepora* to a warm and cool region of the Great Barrier Reef likely restricted acclimatization capacity following a 14 month transplantation to opposing environmental conditions. Corals from the warmer, northern reef suffered 40 % mortality and grew 74–80 % slower when exposed to cold winter temperatures in the south, while corals from the cooler, southern reef suffered 50 % mortality and grew 52–59 % less in the north than in their native environment. Thus, Howells et al. (2013) postulate long-term adaptation of the coral host and associated *Symbiodinium* to their native environments may limit acclimatization potential in response to novel conditions.

In contrast, a short-term thermal acclimation study by Bellantuono et al. (2012b) showed that a 10-day pre-conditioning exposure of *Acropora millepora* from the Great Barrier Reef to 3 °C below their bleaching threshold (28 °C) resulted in complete bleaching resistance to a subsequent 8-day exposure to 31 °C compared to non-preconditioned corals. This enhanced bleaching resistance was not due to any apparent change in *Symbiodinium* type or microbial associates (Bellantuono et al. 2012b). A follow up study examining the gene expression response following similar preconditioning treatments found only nine differentially expressed genes separated preconditioned and non-preconditioned corals (Bellantuono et al. 2012a). In fact, there was almost complete overlap between the differentially expressed genes in preconditioned and non-preconditioned corals under heat stress. However, out of all of these shared genes, preconditioned corals had lower levels of expression changes compared to non-preconditioned corals, suggesting it is the magnitude of expression change, not the specific genes themselves that may be indicative of acclimation gains in heat resistance (Bellantuono et al. 2012a).

In a field transplant study over multiple years, Palumbi et al. (2014) transplanted colonies of *Acropora hyacinthus* between a highly variable back-reef pool that frequently reaches temperatures 2–3 °C above the local bleaching threshold and a more moderately variable pool with corals known to have lower thermal tolerance levels (Oliver and Palumbi 2011). Following 12–27 months of acclimatization to the different pools, corals that had been transplanted into the highly variable habitat bleached significantly less when exposed to subsequent heat stress, suggesting a strong, positive effect of acclimatization on their heat resistance. However, corals that came from the more moderate area did not display the same levels of heat resistance as corals native to the highly variable habitat despite substantial acclimatization gains in under 2 years, indicating some remaining benefit of long-term acclimatization or potential adaptation of the highly variable natives (Sect. 7.4.2; Palumbi et al. 2014). Investigation of the gene expression differences among corals transplanted to the various environments revealed 74 genes that were different between identical fragments transplanted to the different locations and 72 that were different between the corals native to the two different locations. This is in contrast to the results of

Bellantuono et al. (2012a), where there were no differences in gene expression between the control and preconditioned treatments after 4 and 20 days of exposure. The number of differentially expressed genes due to transplantation observed by Palumbi et al. (2014) may reflect a difference among the acclimatization strategies of the different species (*A. hyacinthus* vs. *A. millepora*), or could be indicative of a fundamental difference in short and long-term acclimatization mechanisms. Regardless of the differences, similar gains in thermal tolerance over short-term, long-term, lab, and field exposures in these *Acropora* spp., combined with the lack of change in associated *Symbiodinium* or microbial communities supports a substantial role for coral host acclimatization gains to contribute to coral survival in the face of climate change.

7.3.2 Unanswered Questions Regarding Coral Acclimatization and Future Directions

It is worth noting that acclimatization potential may come with associated costs. Maintaining the ability for large degrees of phenotypic plasticity is thought to be energetically costly and may affect the ability of a population to evolve optimal phenotypes (DeWitt et al. 1998; Relya 2002). While evidence for costs of acclimatization in corals is scant, Edmunds (2014) found conflicting evidence that thermal acclimation was actually beneficial for massive *Porites* spp. in Moorea, French Polynesia. Instead of evidence supporting the beneficial acclimation hypothesis (Leroi et al. 1994), wherein previous acclimation to a particular environment conveys increased performance during future exposure to the same environment compared to organisms acclimated to any other environmental condition, Edmunds (2014) found only acclimation to increasing temperatures had a positive influence on a corals ability to withstand future thermal stress (similar to many of the examples mentioned above). This was termed the “hotter is better” response, wherein acclimation to increased temperatures has value in responding to a variety of subsequent temperatures (Edmunds 2014). It is worth noting this is one of the first studies to frame investigations of coral thermal acclimation response in terms of the beneficial acclimation hypothesis, and the results of most studies to date of thermal acclimation potential would conform to the hotter is better hypothesis. Additional studies investigating a range of acclimation treatments and subsequent cross-exposures are required before the extent of the hotter is better versus the beneficial acclimation hypothesis can be determined.

7.3.2.1 Little Is Known About Acclimatization to Ocean Acidification

The majority of acclimatization studies have either focused on thermal acclimation potential (discussed above) or photoacclimation potential to different light regimes of coral-associated *Symbiodinium* (discussed below in Sect. 7.3.2.2). While thermal stress is thought to represent the primary coral stressor associated with climate change for corals, decreasing pH associated with ocean acidification represents another important stressor that may influence future coral survival (Chap. 4). A few studies have employed genomic tools to examine coral response to acidification stress and have found substantial overlap in the genes responding to acidification with those responding to temperature stress (e.g., Moya et al. 2012) which suggests acclamatory and adaptive processes for acidification tolerance may operate on similar cellular mechanisms as thermal acclimation. However, Crook et al. (2013) found no evidence for long term acclimatization in calcification of *Porites astreoides* to chronic exposure to low pH submarine springs in Quintana Roo, Mexico, despite these corals spending their entire lifetime in these conditions. This was determined by comparing *P. astreoides* calcification rates to those from neighboring ambient pH areas as well as lowered pH exposures conducted in previous lab studies. They found *P. astreoides* from the submarine springs, which reach lows of pH 7, showed as great a reduction in calcification as the same species from multiple areas across the Caribbean with normal pH conditions when exposed to acidification conditions, suggesting hundreds to thousands of years of natural exposure to reduced pH did not induce an acclimatization response (Crook et al. 2013).

This contrasts with acclimation to low pH observed in the symbiotic anemone *Anemonia viridis*, where *Symbiodinium* gross photosynthesis and chlorophyll increased significantly following exposure to decreased pH (Jarrold et al. 2013). Non-calcifying cnidarians, however, may not be as sensitive to ocean acidification as most Scleractinians, and unifying themes are difficult to draw from these few studies. Future research is greatly needed before we can assess the acclimatization potential of corals to ocean acidification scenarios as well as the molecular machinery behind any potential acclimatization response to reduced pH.

7.3.2.2 Little Is Known About Host vs. *Symbiodinium* vs. Other Microbial Contributions to Acclimatization

There is a wealth of literature concerning the potential for *Symbiodinium* photoacclimation and photoadaptation to changes in light levels and spectral quality (e.g. Dustan 1982; Anthony and Hoegh-Guldberg 2003; Mass et al. 2007), however very little is known about *Symbiodinium* acclimatization potential to changes in temperature and seawater pH. Evidence for both fine-scale and broad-scale differences in *Symbiodinium* thermal adaptation are prevalent in the literature (see Sect. 7.4.2), however direct tests of thermal acclimatization abilities are almost non-existent. The changes in photosynthetic productivity observed in *Symbiodinium* from *Anemonia viridis* in response to acidification as well as the pervasive evidence for various forms of photoacclimation certainly suggest that *Symbiodinium* can acclimate over short time-scales (Jarrold et al. 2013), however whether this applies to short-term acclimation responses to temperature remains to be seen and warrants further investigation. Very little is known as well about true acclimatization responses (i.e., phenotypic shifts within individual genotypes) in other coral microbial associates (e.g., bacteria, fungi, viruses), as most studies have focused on shifts in the microbial community assemblage (i.e., genetic restructuring) rather than phenotypic shifts in a constant assemblage. In fact, we know very little at all about what phenotypes these other associates may express and what functional roles they play in the entire community that comprises a coral (often termed the coral **holobiont**).

7.3.2.3 The Timing and Magnitude of Coral Acclimatization

For acclimatization to effectively aid in coral survival of climate change it must be sufficient in timing and magnitude to alleviate stress caused by subsequent high temperature and low pH exposures. To date, there are multiple lines of evidence supporting both short-term (1–2 week) and long-term (1–2 years) acclimation gains in coral thermal tolerance (e.g. Middlebrook et al. 2008; Bellantuono et al. 2012; Palumbi et al. 2014). Another promising study found that *Pocillopora damicornis* from a highly thermally variable upwelling reef in Taiwan were able to fully acclimate to 9 months of exposure to 30 °C compared to controls at 26.5 °C, suggesting historical, natural exposure to upwelling variability contributed to the acclimation potential to future thermal challenge (Mayfield et al. 2013). However, whether natural sporadic stress events will elicit the same level of acclimatization and whether acclimatization gains will be great enough for coral survival remain to be determined. Also, while Palumbi et al. (2014) found substantial gains in bleaching resistance after 12+ months of exposure to increased variability, they also observed a significant decrease in bleaching resistance when tolerant corals were moved from the highly variable pool to the more moderate location, suggesting acclimation gains may not persist for very long when the driving environmental conditions are removed. Future studies examining a variety of time-scales both in the lab and in the field, as well as comparing gene expression changes in lab-acclimated populations to natural transcriptional profiles of corals during pre-bleaching warming are critically needed before we can accurately predict potential long-term contributions of coral acclimatization to climate change survival.

7.4 Coral Adaptation to Climate Change

If organisms cannot move or acclimatize to climate change, they must adapt to survive (Parmesan 2006), a process sometimes termed "evolutionary rescue" (reviewed in Bell 2013). The concept of evolutionary processes acting as a rescue from population extinction is not new; consider the "rescue" of bacterial populations that evolve genetic resistance to antibiotics. However, scientists historically thought evolution in the environment via natural selection was a slow process, requiring hundreds to thousands of generations to elicit substantial change. Yet a growing number of studies are finding rapid evolutionary changes in nature in response to strong selection pressures over relatively few generations (Carroll et al. 2007). Rapid adaptation is thought to occur via two contrasting mechanisms: (a) rapid generation of novel mutations that confer increased fitness in response to new environmental conditions (termed novel mutation), or (b) rapid increase in the proportion of advantageous genotypes in the population via selection for already existing genetic diversity (termed standing genetic variation; Barrett and Schluter 2008). In the stickleback fish for instance, Barrett et al. (2011) elicited rapid adaptation in cold tolerance in just three generations of strong selection, demonstrating the standing genetic variation accumulated over thousands of years and multiple migrations from fresh to saltwater in these fish was high enough to enable rapid adaptation. For novel mutation, one can consider again the rapid evolution of antibiotic resistance in pathogenic bacterial as an example of how novel mutation (i.e., de novo evolution of a resistant strain) can facilitate rapid adaptation of an entire population when faced with strong selective pressures.

7.4.1 The Contribution of Novel Mutation to Coral Climate Change Adaptation

Generally, it is believed adaptation from novel mutation occurs more slowly than that from standing genetic diversity due to: (a) potential deleterious influence of a particular mutation that has not been present in the environment long enough to be "vetted" under various environmental scenarios, and (b) new mutations likely occur in lower frequency than standing variants and may take longer to become established in a population (Barrett and Schluter 2008). In terms of reef-building corals, their long generation times (years to decades), ability to asexually reproduce, and the persistence of older individuals contributing to the gene pool for hundreds of years all make novel mutation an unlikely contributor to rapid adaptation to climate change. However, the rapid generation time of *Symbiodinium* and massive population sizes across the reef contrast with the coral host, and certainly open the possibility for rapid generation of functional novel mutations. This topic is almost completely unexplored in the literature and thus remains conceptual and speculative at this time, yet the life history characteristics of *Symbiodinium* do not preclude rapid adaptation via novel mutation.

7.4.2 Coral Adaptation from Standing Genetic Variation

For rapid adaptation to occur in a population from pre-existing variation, there has to be sufficient standing genetic diversity in the specific traits needed for survival of a given selection pressure. In the case of corals and climate change this would equate to genetically based differences in thermal tolerance limits and acidification resistance. The strongest, indirect evidence for genetic variation in upper thermal tolerance limits in corals comes from the observation that the bleaching threshold of most coral populations is only 1–2 °C above the mean summer maximum temperature for a given area (Jokiel and Coles 1990; Jokiel 2004). This means the same coral species from different latitudes can have substantially different (>2 °C) bleaching thresholds (Clausen and Roth 1975; Coles et al. 1976; Smith-Keune and van Oppen 2006; Howells et al. 2013). This pattern is repeated across multiple species and multiple locations across the globe, with corals from the warmest reefs on the planet (e.g. the Persian/Arabian Gulf) having the greatest thermal tolerance limits (Riegl et al. 2011, 2012), suggesting substantial standing genetic variation exists in coral bleaching thresholds around the world. Far less evidence, however, has been found concerning potential standing genetic variation in coral tolerance to ocean acidification. Of the three main study areas where coral reefs have been found in naturally acidified seawater, two find demonstrable effects on the structure and function of the coral community, with either a decrease in calcification and increase in bioerosion in the low pH springs of Mexico (Crook et al. 2013), or a reduction in coral diversity in the moderate CO_2 seeps and an absence of reef structure completely in the extreme CO_2 seeps in Papua New Guinea (Fabricius et al. 2011). The third area though, holds promise, where Shamberger et al. (2014) found a diverse coral community and maintenance of calcification in reef communities under chronically low pH (~7.8) in rock island bays in Palau, suggesting these communities have developed mechanisms to maintain calcification and reef building in chronically acidic conditions.

Other studies have found persistent differences in thermal tolerance across much smaller spatial scales than the latitudinal variation discussed above. *Porites astreiodes* in the Florida Keys (Kenkel et al. 2013) and *Porites lobata* and *Acropora hyacinthus* in American Samoa (Oliver and Palumbi 2011; Barshis et al. 2013;Barshis unpublished data) all show greater bleaching resistance in corals from warmer, more thermally variable habitats compared to cooler, more stable areas separated by as little as 500 m–7.5 km. Also, during mass bleaching events there is often survival of scattered colonies, specific communities, or whole reef sections with bleached and unbleached conspecifics found adjacent to one another (Fig. 7.2; Sotka and Thacker 2005). While both small- and large-scale differences in coral bleaching susceptibility indicate the potential for substantial standing genetic diversity in coral thermal tolerance thresholds, most evidence to date is correlative, and comprehensive investigations of the genomic determinants of this phenotypic diversity have only just begun.

7.4.2.1 Is Variation in Coral Thermal Tolerance Genetically Determined and Heritable? The Host Perspective

Unfortunately, linking genotype to complex phenotypes such as bleaching and acidification resistance in coral remains a challenging endeavor. The diversity of genes and molecular processes involved in the coral thermal and acidification stress responses (e.g., Moya et al. 2012; Barshis et al. 2013) indicate hundreds of potential targets that could

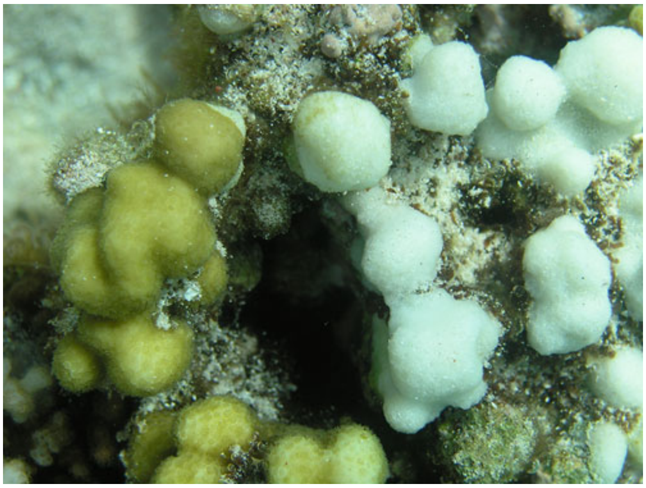

Fig. 7.2 A photo showing differential bleaching susceptibility of adjacent colonies of *Porites randalli* in the Ofu back reef in American Samoa. Bleaching is commonly patchy across a reef and bleached and unbleached colonies are often observed in close proximity. Whether this variability is caused by adaptation or acclimatization of the host or *Symbiodinium* remains to be determined

be causing an adaptive response to stress. In order for selection to result in adaptation, a substantial enough reduction in gene flow between the selected population and unselected neighbors is required, such that selected genotypes are able to increase in the population without continued dilution with less fit genetic variants from neighboring areas. Multiple studies examining neutral markers have found genetic differentiation among coral populations with distinct thermal tolerance limits, which indicates the potential for genetic isolation and accumulation of locally adapted genotypes. For instance, Smith-Keune and van Oppen (2006) found small but significant genetic structuring in nine populations of *Acropora millepora* from distinct thermal ecoregions along the Great Barrier Reef, raising the possibility of enough genetic isolation to accumulate adaptive divergence. These results are only correlative, however, and do not purport to examine genetic differentiation at adaptive markers.

Other studies have found similar genetic differentiation among different thermal habitats, though across much smaller spatial scales. Barshis et al. (2010) found significant genetic structuring in *Porites lobata* that correlated with differences in growth and thermal tolerance between corals native to a more thermally variable back reef vs. a more stable forereef separated by only 5 km in American Samoa (Smith et al. 2007; Barshis unpublished data). Similarly, Kenkel et al. (2013) found thermal tolerance differences and genetic differentiation between *Porites astreoides* from a nearshore reef with warmer conditions and a cooler offshore reef 7.1 km away in the Florida Keys. This genetic differentiation corresponded with constitutive upregulation of metabolic genes in corals from the warmer inshore location during subsequent heat stress, suggesting a potential adaptive role of coral energy management in coral thermal tolerance (Kenkel et al. 2013).

Other studies have taken a more direct approach by either examining genetic differentiation in putatively adaptive gene regions or directly testing differences in stress tolerance among larvae of known genetic composition and parental genotypes. Lundgren et al. (2013) performed a gene mining investigation to find specific candidate genes for adaptive genetic markers in *Pocillopora damicornis* and *Acropora millepora* across the thermal gradient from the northern to the southern Great Barrier Reef. They found significant correlations between allele frequencies (proportion of a particular genotype in the population) and thermal habitat type in up to 55 % of the gene markers examined, representing evidence for one of the first sets of candidate genes for adaptive environmental stress tolerance in corals (Lundgren et al. 2013). A different, transcriptome-wide scan between *Acropora hyacinthus* from a thermally tolerant vs. a more thermally susceptible population in American Samoa (the same populations investigated in Oliver and Palumbi 2011; Barshis et al. 2013; Palumbi et al. 2014), identified 114 highly divergent genetic loci as candidates for environmental selection for heat resistance (Bay and Palumbi 2014). Many of these loci showed significant allele frequency correlations with temperature, in the form of amount of time spent above the local bleaching threshold of 31 °C. Taken together, these investigations are starting to reveal some of the first direct signs of selection in coral genomes that might be responsible for adaptive differences in upper thermal tolerance limits.

An alternative approach to genome scans is direct examination of differences in thermal tolerance among closely related larval crosses to assess the role of genotype in determining thermal tolerance limits. These types of investigations have also found preliminary evidence that variation in thermal tolerance may be genetically-based between closely related families. In larvae from experimental crosses of *Acropora millepora*, two out of six families lost significantly more protein during larval development at increased temperatures, while the other families did not show an effect of temperature (Meyer et al. 2009). In Caribbean *Acropora palmata*, Baums et al. (2013) found significant differences in larval development rate and swimming speed under high temperature among larval families, suggesting genotype may constrain larval performance during thermal exposure. Although neither of these studies directly assessed thermal tolerance differences in the parent colonies, nor the heritability of parental phenotype to the offspring, the finding of significantly different responses to temperature among closely related larval families certainly supports the hypothesis of standing genetic variation in coral temperature sensitivity.

7.4.2.2 Standing Genetic Variation in *Symbiodinium* and the Potential Contribution to Coral Adaptive Tolerance

A comprehensive review of the genetic diversity of *Symbiodinium* and their functional role in coral thermal tolerance is well beyond the scope of this chapter and is well covered elsewhere (e.g., Chap. 5 of this book; Berkelmans and van Oppen 2006; Stat et al. 2006; Stat and Gates 2011). For the purposes of this chapter, a few common themes are relevant to the discussion herein.

First, an extraordinary amount of genetic diversity exists within coral-associated *Symbiodinium* and many physiological differences relevant to climate change stress tolerances have been found among different *Symbiodinium* genotypes. For example, association with some phylotypes of *Symbiodinium* clade D can provide enhanced thermal tolerance to host corals when dominated by these types (reviewed in Stat and Gates 2011). Increased prevalence of certain *Symbiodinium* phylotypes has also been found in habitats characterized by unusually high temperatures and in areas recently influenced by natural bleaching events (Fabricius et al. 2004; Jones et al. 2008; Oliver and Palumbi 2009, 2011). Corals hosting different *Symbiodinium* phylotypes have also been shown to exhibit reduced levels of bleaching and greater maintenance of photosynthetic efficiency during thermal exposure (Berkelmans and van Oppen 2006; Oliver and Palumbi 2011). Although this phenomenon is not universally the same across coral species (Fabricius et al. 2004; Abrego et al. 2008), one potential mechanism for corals to persist in a warming ocean is through association with a more thermally tolerant *Symbiodinium* type (Buddemeier and Fautin 1993; Berkelmans and van Oppen 2006). Additionally, substantial physiological differences exist among specific phylotypes within clades as well as between clades (e.g. Cantin et al. 2009; Howells et al. 2012). Specific strains of a single subtype can show different thermal tolerances and growth rates even in isolated cultures (Howells et al. 2012; Parkinson and Baums 2014), suggesting increased tolerance could be gained via association with a different strain within a subclade type or member of a different clade altogether.

As a whole, there is clearly a substantial amount of genetic variability in coral associated *Symbiodinium*, and we are only just beginning to understand the physiological relevance of the vast majority of this diversity. Genomic investigations have revealed potential candidates for adaptive evolution relevant to temperature tolerance differences among different *Symbiodinium* clades (Bayer et al. 2012; Ladner et al. 2012; Barshis et al. 2014). Highly specific host and *Symbiodinium* combinations exhibit substantial variation in thermal sensitivity (e.g. Abrego et al. 2008; Howells et al. 2012; Parkinson and Baums 2014), which are undoubtedly relevant to coral survival of global warming and ocean acidification. Whether specific host/*Symbiodinium* associations represent true adaptation vs. acclimatization remains debatable and depends on the “heritability” of the intact symbiosis from parent to offspring. Some larvae inherit the full complement of *Symbiodinium* from their parents (“vertical transmission”) while others have to establish the symbiosis de novo from the environment each generation (“horizontal transmission”; Sect. 5.2.3). Thus, the stability of the symbiosis from generation to generation depends on a number of different factors and while certain hosts can show strong fidelity to a particular *Symbiodinium* type, many hosts are more flexible in the associations they maintain, calling into question how persistent more tolerant host-*Symbiodinium* combinations would be in a changing environment (Stat et al. 2008; Putnam et al. 2012).

7.4.3 Coral Climate Change Adaptation in Real Time

Genetic-based changes attributable to recent anthropogenic climate change have been observed in the present-day timing of breeding and migration in animals and flowering in plants, as well as the increased frequency of warm-adapted genotypes in higher-latitude populations (reviewed in Parmesan 2006; Hoffmann and Sgro 2011; Crozier and Hutchings 2014). Evidence of recent adaptation to climate change in corals also exists, though it is correlative in nature. Contrasting bleaching responses of a variety of coral taxa have been observed across years and reefs with recently differing thermal histories. Maynard et al. (2008) found a 30–100 % reduction in bleaching severity across three major coral genera (*Acropora*, *Pocillopora*, and *Porites*) during a severe thermal stress event on the Great Barrier Reef in 2002 when compared to a previous event in 1998. Acroporids and pocilloporids showed the greatest increase in tolerance, despite being more susceptible to thermal stress than *Porites* spp. Similarly, Guest et al. (2012) reported lower bleaching across multiple genera in South East Asian reefs that bleached during 1998 and had greater historical temperature variability and lower rates of warming. Again, *Acropora* and *Pocillopora* were among the most susceptible at the site with highest bleaching (Pulau Weh, Sumatra, Indonesia), yet the least susceptible at an area with a substantial history of thermal stress (Singapore). While both studies are correlative, the authors invoke acclimatization and adaptation in response to recent thermal histories as a likely explanation for the contrasting bleaching responses across sites and years and indicate *Acropora* and *Pocillopora* spp. as likely candidate taxa for rapid acclimatization and adaptation to environmental change.

Natural thermal adaptation to historical temperatures has also been suggested to explain a substantial departure in corals from the Gulf of Aqaba in the Red Sea from the putative “universal” bleaching threshold of 1–2 °C above local mean summer maximum temperatures. Fine et al. (2013) found only mild bleaching (<45 % change in *Symbiodinium* density) after 4 weeks of exposure to 34 °C (7 °C above the summer maxima) and no bleaching after 3 weeks at 31 °C (4 °C above the summer maxima) for five different species (*Stylophora pistillata*, *Pocillopora damicornis*, *Acropora eurystoma*, *Porites* sp. and *Favia favus*). They also developed a stepping stone larval dispersal model and hypothesized coral larvae that reach the northern Red Sea could represent only those that successfully survived passage across the hotter reefs to the south (which can be 5–6 °C warmer than the north). What is particularly fascinating is this mismatch between bleaching threshold and local environmental conditions may have persisted despite thousands of years of exposure to the colder conditions of the Gulf of Aqaba, suggesting either little to no selective cost of maintaining thermal tolerance in cooler conditions or a complete purging of less tolerant genotypes from the population via the heat selective barrier to the south (Fine et al. 2013). The apparent lack of reversion of these thermally tolerant corals in the north could represent a potential climate change refuge, as conditions in the Gulf of Aqaba are not projected to reach the elevated bleaching thresholds of these corals until at least 100 years after their relatives to the south.

Correlative evidence representing possible thermal adaptation such as the above studies has led some to propose more radical manipulative conservation measures based on these results. Multiple authors have suggested that putative thermally adapted genotypes (e.g., those from the Arabian Gulf or Gulf of Aqaba) could be used as source material for restoration of cooler reefs following widespread bleaching and mortality (Coles and Riegl 2013). Termed “assisted migration”, this would involve transplantation of adults and/or larvae to distant areas where native genotypes are not pre-adapted to increased temperatures. Researchers acknowledge that such efforts present several monumental challenges and concerns regarding biodiversity preservation, thus they should only be considered as a last resort when viable alternatives may no longer exist (Hoegh-Guldberg et al. 2008; Coles and Riegl 2013). Alternatives such as selectively cultivating these potential adapted genotypes in coral nurseries (Coles and Riegl 2013), or even cryogenically preserving them for future reanimation (Hagedorn et al. 2012) have also been proposed as possible conservation strategies to combat climate change effects, though these strategies also present substantial logistical and practical challenges.

7.4.4 Unanswered Questions in Coral Climate Change Adaptation

One of the biggest unanswered questions in terms of coral climate change adaptation is what degree of adaptive diversity exists in coral susceptibility to ocean acidification. In a recent review of the potential for adaptation to ocean acidification in all marine organisms, Kelly et al. (2013) suggest that variation in pH across the seascape does not follow as strong and consistent a spatial pattern as variation in temperature, which may not elicit as strong a selective force on intraspecific genetic variation. However, variation among individual genotypes in susceptibility to OA has been observed for some marine species (urchins, bryozoans, oysters, and coccolithophores), and many studies are beginning to find more spatial variability in pH conditions than initially predicted (Kelly et al. 2013). They conclude that our understanding is still limited and additional investigations utilizing genomic approaches and technological advances in pH instrumentation are critically needed before we can begin to ask whether adaptation might rescue vulnerable populations from future acidification effects (Kelly et al. 2013).

For corals, there appears to be significant inter-specific variability in OA sensitivity, with only certain species able to survive in naturally acidified springs and seeps (e.g. Fabricius et al. 2011; Crook et al. 2013), and significant differences among species in susceptibility to lab exposures of low pH (Edmunds et al. 2013). Whether these inter-specific differences reflect similar diversity within species and across populations remains to be determined.

We also have a limited understanding of the spatial scale of relevant diversity in coral thermal tolerance limits. While latitudinal variation in bleaching thresholds indicate the potential for evolutionary rescue of less tolerant populations in cooler regions, there needs to be sufficient dispersal ability between habitats for recolonization to be realistically possible; but not so much dispersal as to dilute the accumulation of relevant adaptive diversity (Garant et al. 2007). The small-scale differences in temperature tolerance observed between inshore and offshore reefs in the Florida Keys (Kenkel et al. 2013) and back reef pools in American Samoa (Oliver and Palumbi 2011) certainly fall within the range of predicted dispersal distances of most corals, but whether ecologically relevant dispersal can realistically occur between thermally adapted populations across latitudinal extremes remains unknown.

Additionally, aside from a few isolated study sites (e.g., Ofu Island in American Samoa, Sugarloaf Key in Florida), very few detailed investigations of small-scale spatial variability in thermal tolerance limits have been conducted and even in these well-studied areas, whether observed differences are truly due to evolutionary adaptation also remains to be determined. Lastly, while a growing number of studies have identified gene expression signatures of acclimatization, only a select few have started to shed light on the genes and molecular processes that may be responsible for adaptive variation in coral thermal tolerance limits. As the evolution of thermal and acidification tolerance in corals is likely determined by a variety of physiological and biochemical processes, substantial additional research is required before we can begin to understand the relationship between current genetic diversity, environmental tolerance limits, and future response of coral populations to climate change influences.

7.5 Summary

Genomics has ushered in a new era of investigation into the molecular mechanisms of coral acclimatization and adaptation potential. Studies of gene expression signatures and gene frequency distributions reveal a complex pattern underlying thermal tolerance differences among corals and mechanisms of acclimatization and adaptation. There is no single gene or gene family implicated in coral temperature tolerance, but variation in both the magnitude and composition of the stress response across a multitude of different physiological and cellular processes. This represents a diverse array of potential targets both for acclimatization potential and adaptive natural selection in climate change resistance.

An increasing number of studies are finding greater acclimatization and adaptive potential than previously thought, which when incorporated into models of coral survival in the future significantly improves the short-term outlook for reef persistence (Donner et al. 2005; Logan et al. 2014). Significant associations between large-scale and small-scale genetic differentiation and temperature tolerance continue to be discovered in corals from different eco-regions and habitats as well as closely related larval families. As a whole, these studies illustrate a substantial amount of diversity in acclimatization ability and adaptive potential in current day coral populations. However, this may only buy reefs a finite amount of time, and without serious conservation actions to mitigate effects of local stressors and reduce global CO_2 emissions, environmental change in the Anthropocene will quickly outpace the ability of corals to acclimatize and adapt.

7.5.1 What Is Ahead?

We are only just beginning to enter the era of coral genomics research. Already, insight from the first generation of studies is dramatically altering previous concepts regarding the extent of acclimatization and adaptation potential in coral survival of climate change. Many important questions still remain to be answered in the coming decades:

- Are genetically based differences in coral thermal tolerance truly heritable from parents to offspring?
- How stable are beneficial host/symbiont associations through time and across generations?
- What is the extent of genetic diversity and acclimatization potential in coral resistance to ocean acidification?
- What are the relevant spatial scales of standing genetic variation in thermal tolerance limits and larval dispersal potential?

Studies to date have focused on relatively few species and genera and predominantly investigated cosmopolitan species of *Acropora* (*A. millepora* and *A. hyacinthus*), *Pocillopora damicornis*, and *Porites* (*P. astreoides* and *P. lobata*). Release of the first coral (*Acropora digitifera*; Shinzato et al. 2011) and *Symbiodinium* (*S. minutum*; Shoguchi et al. 2013) genomes has opened the door for comparative evolutionary studies and investigation of the genotype to phenotype relationship of various corals. With a variety of other draft genomes in progress (*Montastraea cavernosa*, *Acropora millepora*, *Seriatopora hystrix*, *Stylophora pistillata*, *Symbiodinium* clade A-type), our understanding of the genetic determinants of coral physiology and evolution is only just beginning.

7.5.2 A Cautionary Note

Genomics has really changed how we analyze and look at data. We used to visually align genetic sequences and identify mutations by hand. With 100s–1000s of sequences, this was time-consuming but feasible. Now, with datasets routinely consisting of millions to billions of individual sequences, hand curation and analysis is simply impossible. Biologists are increasingly relying on computer programs to interact with and analyze data. We're essentially seeing through the eyes of the computer most of the time, and "seeing" the actual animals of interest and the environment less and less so. A holistic way forward necessitates that we combine approaches and find ways to bridge between specialties and navigate among disciplines (e.g., ecologists, taxonomists, evolutionary biologists, natural historians, and 'omics). Our tools and interpretation are only as good as the sampling and experimental design and knowledge of the animals and system. This is particularly relevant for genomics, given the enormous time and resource investment to obtain, process, and analyze these large datasets.

Similarly, while genomics is revolutionizing the scale at which we can identify the genes and molecular pathways that may be responsible for acclimatization and adaptation to climate change, it can only get us so far. Genome wide scanning and gene expression profiling are powerful tools, but ultimately only describe a correlation between genotypic and phenotypic variability. It is really the fields of quantitative genetics (e.g. controlled crosses, artificially selected family lines) and cell biology (e.g. gene knockdowns, cell cultures, genetic mutants, and genetic modifications) that truly test the effects of genotype on organismal phenotype and ultimately, the contributions of acclimatization and adaptation to coral survival in an uncertain future.

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Diseases of Coral Reef Organisms

8

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Abstract

All coral reef organisms are susceptible to diseases, as are terrestrial organisms, but studying these diseases can be more difficult and much remains to be learned. Although health impairments of corals were first recognized only in the early 1970s, increasing numbers of infectious and non-infectious diseases, causing morbidity and mortality in numerous species of tropical marine organisms, have now been identified in diverse species of algae, plants, invertebrates, and vertebrates. Causes of diseases include biotic, as well as abiotic, factors, but identifying a primary pathogen has been reported in only a few cases, and some of those results have been questioned as additional diagnostic tools have been applied. The multitude of stressors affecting reef organisms, particularly along heavily urbanized coastlines, as well as introductions of species to distant reefs by global transport, are contributing to concerns about extinction risks and loss of biodiversity. This chapter presents an overview of diseases of reef organisms, how diseases have adversely affected coral reefs, and new developments in disease diagnoses. The application of concepts from the field of conservation medicine are aiding our understanding of diseases and their impacts on organisms of these shallow to mesophotic ecosystems.

Keywords

Parasite • Pathogen • Noninfectious • Infectious • Plant • Invertebrate • Vertebrate • Population dynamics

8.1 Introduction

Most people picture reefs, and their associated fauna and flora, as vigorous, flourishing, and healthy, just as we used to see forests, meadows, and even deserts, despite the differences in organisms and physical conditions. Closely tied to this was the realization that increasing human populations were changing these terrestrial ecosystems with agriculture, the growth of big cities bringing people into closer proximities and encroaching on wildlife, fragmentation of habitat into smaller disconnected parcels, and the development of machines to "improve our lives" by industries that have required the extraction of minerals and oil, deforestation, and release of chemicals foreign to the environment (Deem et al. 2001). Many anthropogenic disturbances of terrestrial resources have similarly been recognized in the oceans and produce medium to high impacts on coral reefs (Richmond 1993; Halpern et al. 2008); these will be discussed in Chaps. 9 and 11.

This chapter will discuss the nature of health impairments now recognized to be affecting reef organisms, which often are the direct or indirect result of anthropogenic disturbances and also contribute to disturbances, as well as affect the recovery of coral reef ecosystems. It has only been since 1970 that we have found corals and other reef organisms to

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Box 8.1
"The study of the causes of things must be preceded by the study of things caused."
J. Hughlings Jackson, British neurologist (1835–1911)

be susceptible to diseases caused by pathogens and parasites, as well as to those conditions caused or aggravated by exposures to anthropogenic pollutants and habitat degradation. Perhaps the demise of tropical reefs was delayed only by the more recent colonization of islands and coastlines in the New World and human populations were kept under control by the profusion of their own and zoonotic diseases—e.g., malaria, smallpox, yellow fever, shigellosis, leishmaniasis, schistosomiasis, onchocerciasis, lymphatic filariasis, trypanosomiasis, cholera, dengue fever—mediated by nutritional deficiencies and travel (Armelagos et al. 2005). Examination of peer-reviewed journal articles indicates a recent increase in disease outbreaks in many reef ecosystems and organisms (Harvell et al. 2004; Ward and Lafferty 2004). However, anthropogenic impacts related to overfishing are thought to have begun hundreds of years ago and the reductions in populations of fish and shellfish species may reduce disease transmission in these organisms while increasing the susceptibility of other organisms to diseases (Jackson et al. 2001; Lafferty 2004; Dinsdale and Rohwer 2011).

In these and other studies on diseases of coral reef organisms, multiple physical and chemical stressors are often identified and teasing out their roles in the development of disease with respect to biotic pathogens can be difficult (Ban et al. 2014). Scientists have been busy documenting "things caused" (Box 8.1)—a variety of health impairments in organisms of reef ecosystems—and are now making advances in identifying the "causes of things," the etiologic agents of the diseases, lurking amid the myriad and dynamic natural and anthropogenic stressors present in the reef environment.

8.2 What Is a Disease?

Disease is defined as any impairment (interruption, cessation, proliferation, or other disorder) of vital body functions, systems, or organs. Diseases have at least two of these features: (1) an identifiable group of signs (observed anomalies indicative of disease in a non-human organism) or symptoms (subjective evidence of disease that a human can explain to another human), and/or (2) a recognized etiologic or causal agent, and/or (3) consistent gross or microscopic structural alterations (e.g., developmental disorders, changes in cellular composition or morphology, tumors). The terms "**disease**," and "**syndrome**" (the latter referring to all the signs or symptoms that comprise the disease) are often included in the name of a recognized functional impairment, and it is not necessary to know the causal agent to use either term when identifying a functional impairment of an organism. The term "**health**" is defined as the state of an organism when it functions optimally without evidence of disease or abnormality. Although many refer to "ecosystem [coral reef or other] health," the appropriateness of this is much debated, because ecosystems are dynamic, can exist in multiple stable states, and clear criteria cannot be determined to identify optimal functioning among different ecosystems, which also lack homeostatic mechanisms (Suter 1993; Lancaster 2000; Lackey 2003; Hudson et al. 2006). These are generalized behavioral, physiological, and biochemical responses that may be invoked by an organism over the short or long term, allowing it to adapt to a range of changing conditions while maintaining a preferred state, level (**homeostasis**), or rate of some process (**homeorhesis**) (Stebbing, 1981; McNamara and Buchanan 2005; Sokolova et al. 2012). The counteractive capacity of these adaptive responses will allow an organism to maintain its health while being subjected to changing conditions, leading to resistance to the stressor(s).

Any virus, microorganism, or other substance that causes disease is a pathogen, an etiologic agent. Interactions of a **pathogen** with a **host** (the organism that may develop disease by being affected by an abiotic pathogen or infected by a biotic pathogen) are both always affected by the **environment**. This is the paradigm of **disease** (Work et al. 2008b). Abiotic diseases are those structural and functional body impairments that only result from exposure to abiotic environmental stresses such as changes in physical conditions (salinity, temperature, light intensity or wavelength, sedimentation, oxygen concentrations, currents) or exposures to biotoxins or toxic chemicals (heavy metals, oils, pesticides)—the "other substance" referred to in the above definition of a pathogen (Rougee et al. 2006; Downs et al. 2012). Biotic diseases are those in which the etiologic agent is a living organism such as a microbial, unicellular, or metazoan parasite. If a parasite causes disease and death of the host, then it is known as a pathogen. A variety of organisms normally live in interspecific associations known as symbioses on or within the tissues of other organisms (Amadjian and Paracer 1986). Such associations can range from mutualistic symbioses (beneficial to both organism and host) to parasitic symbioses where the organism derives a nutritional benefit from the host. For example, some symbioses of microorganisms enable their hosts to live in potentially toxic environments or to subsist on nutritionally limited diets. The totality of these associations is now referred to as the **holobiont** (Rohwer et al. 2002). Infectious agents, those that are spread from host to host, include viruses, bacteria, fungi, protozoans (also known as microparasites), and metazoans such as helminths and

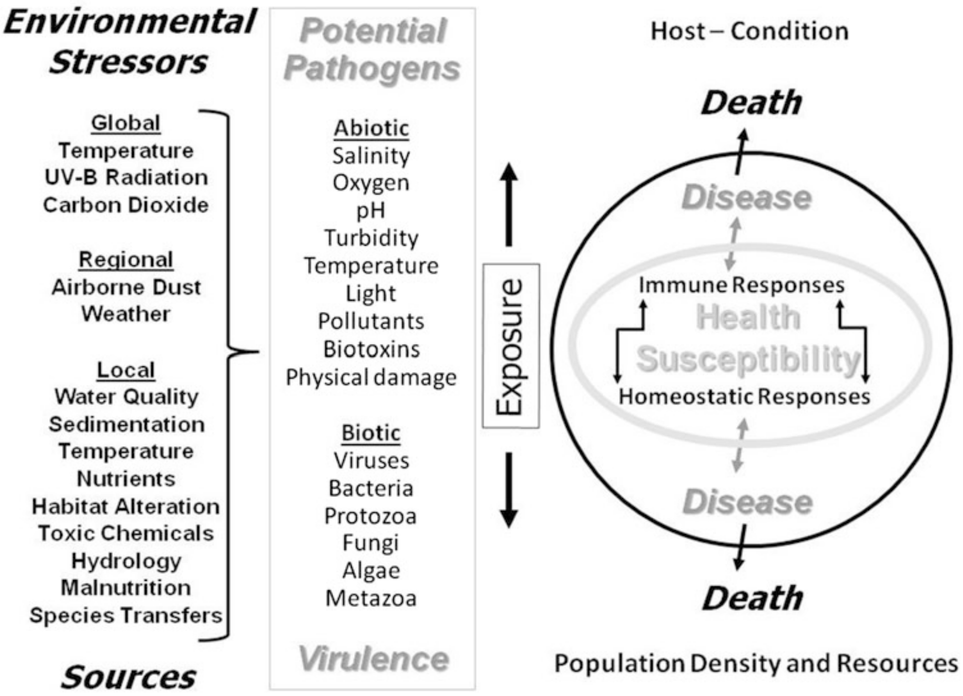

Fig. 8.1 In the "optimum envelope" of health (*center oval*), exposure to stressors is limited to pre-adapted levels in which the organism can retain optimal functioning through its homeostatic mechanisms and immune system; exposure to higher or lower levels of stressors than it is adapted can lead to the development of non-infectious disease or increase its susceptibility to invasion by an infectious agent and subsequent illness; death of cells, tissues, or the diseased host can occur as the result of irreversible damage to its vital functions, organs, or systems caused by the primary pathogen(s) or associated secondary pathogens

arthropods (macroparasites). Zoonotic diseases are those that normally affect animals but can spread to humans. Infectious agents can exist in other organisms (reservoir hosts or vectors) or elsewhere in the environment, to be transmitted to the species they can adversely affect. The interactions of pathogens with hosts within the environments they inhabit and potential outcomes are illustrated in Fig. 8.1.

Exposure to potentially pathogenic levels of abiotic and biotic agents—levels higher or lower than in the range that supports optimal function—may not result in disease. Organisms, including plants, possess a variety of defenses for protection from invasion (non-self recognition) and cellular damage, including innate and (in the case of vertebrates) adaptive, immune systems. These defenses include a surface epithelium of tightly joined cells (e.g., epidermis), the secretion of mucus, ciliary action, production of antibiotic compounds or noxious chemicals that repel or kill parasites, a variety of amoeboid cells that engulf or surround parasites and produce toxicants to destroy them, and in addition to these in vertebrates, the lymphocytes (T, B, and null cells). The degree of vulnerability or susceptibility of an animal to penetration by a pathogen or successful establishment of a parasite resulting in disease may vary between and within species and individuals based on their genetics or may be altered as a result of changes in environmental conditions, nutritional state, developmental stage, and other factors—anything that might impair the optimal functioning of those cells or the products of those cells (Martin et al. 2010). Resistance to infection is characterized by those physiological alterations or responses that occur naturally or develop in the course of invasion by pathogens.

Pathogens cause diseases by acting on the molecules of the organism's cells and tissues, producing microscopic or grossly visible morphological changes (structural) that indicate biochemical changes (functional). Key metabolic processes are attacked, such as aerobic respiration, cell membrane integrity, and the synthesis of proteins, nucleic acids, lipids, and carbohydrates necessary for the organism. A pathologic change in tissue—not normal in structure or function—either external or internal, detected grossly or microscopically, is known as a **lesion**, a sign of disease. The mechanisms by which changing environmental conditions, toxicants, toxins, or microorganisms cause disease are varied (see any general pathology textbook) and will also differ with the species and individual affected. Many interactions between pathogens and their hosts occur without clinical signs of disease, until there is a change in host-parasite ecology (Daszak et al. 2001). Pathogens may cause reversible injuries in organisms, with recovery achieved by metabolic responses limiting damage and restoring normal function (homeostasis). Other associations induce changes in host behavior that may enhance transmission of the parasite. The butterflyfish *Chaetodon multicinctus* preferentially feeds on the "pink pimples" of calcified, pigmented lesions induced in the polyps of *Porites* spp. by the encysted metacercarial stage of the trematode *Podocotyloides stenometra*. The polyps cannot retract into the altered skeleton so the fish consume more coral tissue than when feeding on normal polyps; however, few infections of the juvenile trematodes developed in the fish and measurable effects on host condition and liver energy reserves were not detected, despite the large numbers of metacercarial cysts ingested (Aeby 2002). In other cases they may damage the host's reproductive capabilities (parasitic castration) or seriously affect the functioning of vital organs. Infectious host-specific diseases caused by microbial pathogens may weaken or disable individuals so they are more susceptible to predation or stressful environmental conditions.

However, diseases may also occur as **epizootics** (similar to epidemics in humans), causing disease and mortalities in large numbers of organisms of a single species, due to introducing a new pathogen into a susceptible population, increasing numbers or virulence of pathogenic microorganisms, or lowering the resistance of the host population. Susceptibility and the relative resistance of the host to a biotic pathogen can also change with the size of the population and the genetic constitution of the microorganisms present, but little is known about the regulation of symbiont populations by the host. Furthermore, as parasites and other pathogens influence the abundance of host populations, they exert strong selective pressures on the genetically-based variability of an individual host's resistance or its ability to recover from infection within the population. Thus, the nature of the association may be altered over time (Tompkins et al. 2011). In order to adapt, the host will expend energy for survival, growth, and reproduction. However, as the number of stressors and/or their level of intensity increases, energy expenditures will increase but growth and reproduction will slow or cease. The ability of the organism to deal with stress decreases or disappears as the result of exhaustion of critical biochemical and physiological functions, until finally, disease appears. Death of the organism will result if vital functions are destroyed, i.e., the condition is irreversible.

Although the causal agent of a disease in a tropical marine organism may appear to be either biotic or abiotic, both types of diseases are often closely interrelated. For example, some cases of coral bleaching are caused by certain species of bacteria only when water temperatures are elevated (Kushmaro et al. 2001). Therefore, determining the primary cause of a disease may be difficult. In some cases, a pathogenic microorganism that has infected a host may not harm its host unless the host is stressed by some other biotic or abiotic disease factor (a "stress-provoked latent infection"). Conversely, an abiotic disease can become complicated by secondary infections from normally harmless microorganisms. Lesser et al. (2007) proposed that corals were primarily adversely affected by "opportunistic bacterial infections secondary to exposure to physiological stress that resulted in reduced host resistance and unchecked growth of bacteria normally benign and non-pathogenic." In the tropics, opportunistic pathogens may replicate rapidly and reach the peak of their growth curve in only a few hours. Some studies have identified specific primary pathogens, particularly when biotic diseases develop in specific hosts, such as with viruses. However, the interactions of physiological environmental stressors with host homeostatic mechanisms and immunity complicate the interpretation of causal agents and more data are needed, particularly experiments to demonstrate pathogenesis of agents on hosts, rather than just identifications of associations (Work et al. 2008b). Koch's Postulates or other strength-of-evidence analyses (the application of causal considerations) can be used to help identify the roles of biotic and abiotic stressors in diseases (Susser 1991; USEPA 2000).

Multiple disciplines and tools are needed to identify the pathogen(s) causing a health impairment. Detecting disease in organisms who can't communicate with us requires careful surveillance to evaluate appearance and behavior to understand when they are ADR ("ain't doin' right"), and assess whether changes may be within the normal limits of an organism's life cycle (related to hormonal, seasonal, reproductive, aging, or nutritional factors). Examination of ecological factors is important, what are the abiotic stressors to which the organism(s) has(have) been exposed, key features of the reef where disease is being found, possible microhabitat distinctions, any fluctuations in conditions? Although motile organisms may be able to avoid or limit their contact with pathogens, toxic agents, or adverse physicochemical conditions, sedentary invertebrates generally cannot, but they may produce planktonic larvae to escape. Thus, determining where the organism might have been (e.g., in a crevice, seagrass bed, mangrove forest, marina) is also valuable. After forming a preliminary diagnosis, collection of appropriate samples, both from the affected organism (whole or tissues) and its environment (water, sediment, food, adjacent organisms) and laboratory analyses (behavior, biochemistry, histology, microbiology, immune system responses) are performed to confirm that diagnosis. Timing of sampling to detect the causal agent is critical, because the primary pathogen's presence and effects on the host can be subsequently missed as other bacteria and fungi, for example, multiply and degrade already damaged tissue. After evaluating these results, additional, modified examinations or tests may be necessary, until a final diagnosis can be made (Woebeser 2007). Histology, the study of microscopic anatomical structure from tissue samples using light or electron microscopy, can provide a wealth of information about the functioning of an organism and should be applied in every disease study. Pathological cell and tissue changes have been recognized in several categories (degeneration: necrosis or bleaching; growth: atrophy, hypertrophy, proliferation; inflammation: defense, repair, infectious agents, parasites). But morphologic changes may not completely identify an etiologic agent, requiring the application of methods from microbiology, molecular biology, analytical chemistry, biochemistry, or physiology, to succeed (e.g., Work et al. 2008b; Pollock et al. 2011; Work and Meteyer 2014).

In summary, diseases occur as the result of interactions between a susceptible host, a virulent pathogen, and prevailing environmental conditions. Diseases caused by infectious microorganisms, parasites, and non-infectious (nutritional, environmental, or genetic) disorders have been reported from most phyla of marine plants and animals. However, most of our information on diseases of marine organisms has come from studies of commercially important temperate fish and shellfish species. These studies have received extensive funding and were conducted by multidisciplinary pathobiology teams. For tropical species, many reports in the literature are descriptions of "parasites" where the true nature of the organism's association with the host has not been experimentally determined. There are also a number of reports where the etiologic agent of mass mortalities has not been identified because the disease was not recognized until most of the population was affected and there were few survivors available for study (e.g., the *Diadema antillarum* mass mortalities of 1983).

Among the arguments for using the term "health" in relation to an ecosystem, Rapport et al. (1985) and Rapport (1999) noted that a "healthy ecosystem" would possess the features of relatively rapid recovery when stressed; disturbances or stressors that are present support the maintenance of the ecosystem; maximum biodiversity of native species, productivity, and size of dominant species; sustainable reproduction rates of the native species; minimal pathology among the species; and genetic diversity. Such ecosystems might exist in the time frames of minutes to millennia. What we do know is that ecosystems can change from one type to another and during the period of change we will see alterations in processes and functions at different levels of biological organization as the "optimum envelope" of levels of biotic and abiotic factors shift; diseases may occur. Humans have been responsible for ecosystem degradation that directly and indirectly affects the health of organisms—including humans, particularly with zoonotic diseases. The presence of pathology (diseases) in multiple organisms in an ecosystem indicates it is unstable. What we don't know is the direction of the change, for better or worse.

8.3 Survey of Reef Organism Diseases

This chapter presents some of the most noteworthy diseases of coral-reef organisms that have been studied during the last four decades, but it is not an extensive review, since research, particularly on coral diseases, has increased greatly. As noted in Fig. 8.2, diseases in reef-associated flora and fauna have increased during this time. Anecdotal reports and empirical evidence from long-term surveys on reefs around the world (e.g., Williams and Bunkley-Williams 2000; Santavy et al. 2001; Porter et al. 2002; Lang 2003; Bruno et al. 2007) indicate that this increase is real and that more organisms are being affected by each disease. We remain uncertain, however, about how long some diseases might have been present on reefs but not observed. For example, awareness of sea turtle fibropapillomatosis increased in the mid-1980s as scientists and veterinarians found many affected turtles and began conducting focused studies to determine the prevalence and cause of the disease, especially in the Hawaiian Islands and Caribbean Sea. However, researchers discovered a publication describing this disease in a green turtle in the New York Aquarium as well as three out of 200 green turtles examined at the turtle fishery docks in Key West, Florida, in the late 1930s (Davidson 2001). Another potential factor is the increase in the number of scientists and veterinarians studying these diseases. The reader should consult recent publications and Web sites to further understand the nature and etiology of diseases in tropical marine organisms in the Anthropocene.

8.3.1 Reef Plants

Little is known about biotic and abiotic diseases of marine algae and seagrasses in tropical waters. The turtle grass, *Thalassia testudinum*, in the environmentally stressed Florida Bay, has been affected by a marine slime mold, genus *Labyrinthula* since the 1980s (seagrass wasting disease). This pathogen caused blackened, necrotic lesions on the seagrass blades, reduced the photosynthetic production of oxygen in the plant (Durako and Kuss 1994), and resulted in massive die-offs of this important species (Robblee et al. 1991; Thayer et al. 1994); however, low prevalences of the infections occur and multiple environmental factors, but not predation, may be controlling the disease (Bowles and Bell 2004).

Littler and Littler (1994, 1995) reported the appearance, first in 1992, of coralline lethal orange disease (CLOD), affecting encrusting coralline algae on reefs in the Cook Islands, Fiji, Solomon Islands, and Papua New Guinea. The pathogen was bright orange and spread across the algal surface, leaving behind the bleached carbonate skeletal remains of the coralline algae. When the pathogen reached the margin of the algal thallus, it formed upright filaments and globules, similar to those formed by terrestrial slime molds. Microscopic examination revealed motile gliding rods of a colonial bacterium in a mucilaginous matrix. Experimental studies confirmed that the pathogen globules were highly infectious to a variety of coralline algal species. Littler and Littler (1998) discovered a black fungus covering living thallus tissue of encrusting coralline algae on reefs of

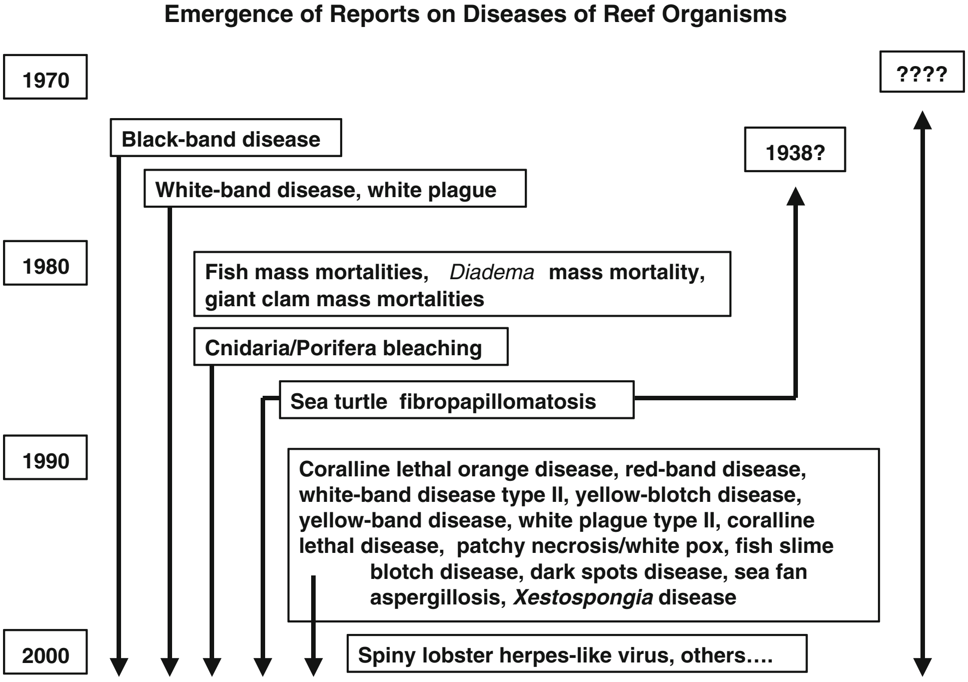

Fig. 8.2 Time-line showing approximate dates of reports of new diseases affecting coral-reef organisms during the past three decades, question marks on right signify uncertainty in how long some of these diseases might have been present, but at such low prevalence that they were not noticed

American Samoa, coralline fungal disease (CFD). In the Caribbean as well as the Indo-Pacific, crustose coralline algae have been observed to lose the pink thallus tissue, with a band of bare carbonate a few millimeters wide remaining next to the thallus; this tissue loss has been named coralline lethal disease, CLD (Goreau et al. 1998). Diaz-Pulido (2000) discovered loss of tissue from three species of the crustose red alga *Peyssonelia* on reefs of the Caribbean and Great Barrier Reef, *Peyssonnelia* yellow-band syndrome (PYBS). A distinct yellow microbial mat composed of gliding filaments of a procaryotic microorganism moved across the surface of the algal thallus, followed by a white mat of the gliding bacterium *Beggiatoa* sp., destroying the tissue. Weil (2004) reported coralline white band syndrome (CWBS=CLD) causing tissue loss in three species of coralline algae in the Caribbean. An investigation of the condition of crustose coralline algae on reefs of U.S.-affiliated Pacific islands by Vargas-Ángel (2010) revealed five categories of grossly visual health impairments in coralline algae: CLOD, CWBS, CFD, coralline target phenomena (CTP), and coralline cyanophyte disease (CCD=PYBS?). Usually found in low prevalences or not detected at most sites, higher prevalences were seen on some reefs with higher human population densities and development. These diseases are also reported from the Caribbean, but little is known about the pathogens that seem to be causing them, although Williams et al. (2014) has identified the CFD etiologic agent as an unculturable fungus in the subphylum *Ustilaginomycetes* (phylum *Basidiomycota*).

These diseases can affect the structure and function of many reef sites, since the dead corallines no longer contribute to productivity and carbonate accretion and cementation processes. More importantly, the coralline algae no longer secrete chemicals that attract coral larvae to settle, and fleshy algae overgrow the dead coralline algae, further inhibiting the settlement and growth of reef-building corals.

8.3.2 Reef Invertebrates

Some of the more prominent members of the coral-reef community and associated tropical marine habitats are the sponges, scleractinian or stony corals, soft corals (alcyonaceans), sea fans and sea whips (gorgonaceans), polychaete worms, a wide variety of bivalve and gastropod molluscs, octopus and squid, spiny lobsters and crabs, sea urchins, sea stars, sea cucumbers, crinoids, and brittlestars. Many species are cryptic, living within spaces of the reef framework, burrowing into the calcium carbonate substrate, or present on or even within other organisms in commensal or mutualistic symbiotic relationships. While we understand much about their ecological roles (see excellent review by Glynn and Enochs 2011), studies of the nature and effects of diseases on these organisms are relatively recent, with reports few or unknown for some phyla (e.g., Annelida), and far from completion.

8.3.2.1 Sponges

While scleractinian corals are usually the most noticeable members of the reef community, at least in size if not numbers, species in the phylum Porifera are numerous and also important mediators of reef productivity (Wulff 2006a). Observations on diseases affecting these organisms had been limited until recently. Primarily the commercial species of the genera *Spongia* and *Hippospongia* were affected by widespread mortalities in the Caribbean in the late 1930s. The timing and distribution of these mortalities followed the major current patterns. Commercial sponge fisheries were effectively eliminated, although some sponges did recover. Affected sponges exhibited "bald patches" followed by "rotting" of tissue beneath the patches, with the entire sponge degenerating within 1 week. The lesions always contained long slender aseptate (without interior walls) filaments that were believed to be a fungus. Studies suggested that bacteria and changes in water temperature might be responsible, but these observations were never confirmed (Peters 1993).

Healthy sponges contain a variety of mutualistic symbiotic bacteria (Webster and Taylor 2012) that may provide nutrition for their sponge hosts or that use metabolic wastes produced by the host. Thus, investigations of the causal agent(s) of diseases in sponges may be complicated by the presence of these microorganisms or by secondary invasions from seawater populations of microorganisms. Sponges possess a variety of cellular defense mechanisms and many sponges can also produce antimicrobial compounds to control pathogenic microorganisms; however, the relationships of sponge-dwelling bacteria and other micro- and macro-organisms with host metabolism and health are poorly understood. Rützler (1988) was the first to report a disease in the mangrove demosponge *Geodia papyracea* from Belize. Apparently, the normal cyanobacterial symbionts of this sponge multiplied out of control, resulting in the destruction of the host sponge tissue. *Aplysina* red band syndrome (ARBS) is another cyanobacterial disease of the Caribbean sponge *A. cauliformis* (Gochfeld et al. 2012), in which a filamentous cyanobacterium (identity still unknown) forms a band around the sponge and spreads along it, killing the live sponge tissue.

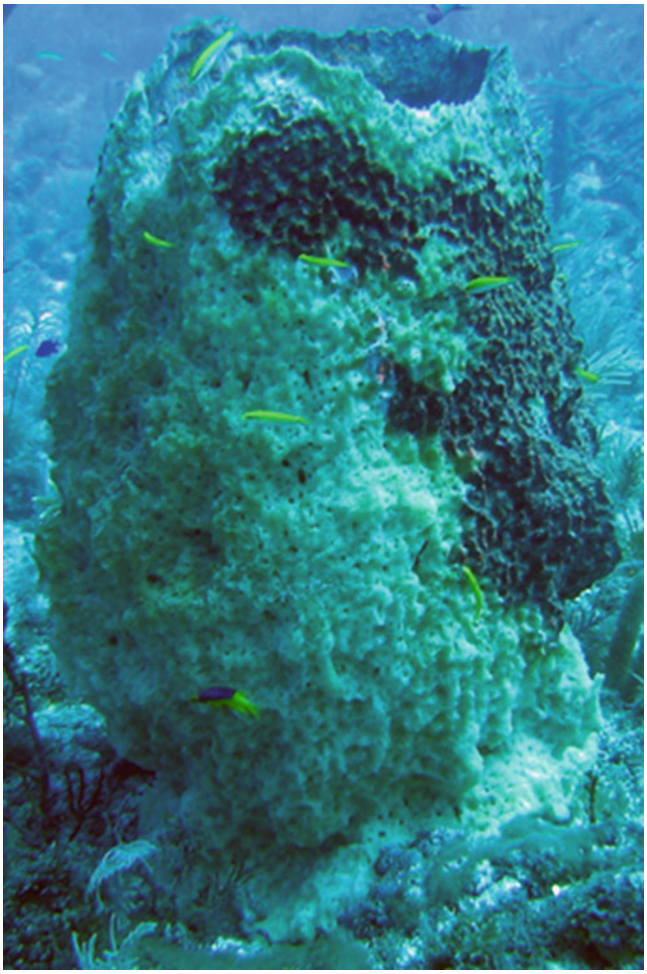

Fig. 8.3 Barrel sponge, *Xestospongia muta*, dying from sponge orange band disease on Aquarius Reef, Florida Keys National Marine Sanctuary, 2011; the cream-colored remnants of spongin fibers are soft and the entire sponge will degrade and disappear

Of more concern has been a sponge disease that has affected many *Xestospongia muta*, the giant Caribbean barrel sponges (Fig. 8.3). Anecdotal reports of paling pigmentation, complete loss of pigmentation and crumbling of the lower portions of these normally rock-hard sponges began to appear on the Coral Health and Monitoring Program Coral-List listserver in the late 1990s. Nagelkerken (2000) described the death of the giant barrel sponge off Curaçao, which had been a tourist attraction for years because its diameter of almost 2.5 m could surround a diver. The same disease signs appeared on this sponge and complete mortality occurred within a few weeks. He noted that the frequent visits and touching by divers might have contributed to spreading a pathogenic microorganism or damaging the sponge and leaving it more susceptible to disease. Paling of the entire sponge and patchy bleaching has also been reported, even when corals were not bleaching. Sampling and microbial community analyses of this sponge orange band (SOB) disease and apparently healthy *X. muta* in the upper Florida Keys and Bahamas by Angermeier et al. (2011) revealed a shift from the stable cyanobacterial consortium to a more heterogeneous mix of cyanobacteria, but experimental infection with diseased sample plugs was unsuccessful. They concluded that a specific pathogen was not responsible for the disease.

Bacterial pathogens (*Pseudomonas* and *Bacillus* spp.) were isolated from *Ianthella basta*, in Kimbe Bay, west New Britain, Papua New Guinea. These sponges were observed dying between 1996 and 2000 at only three sites within 16–20 km of shore and these bacteria were not isolated from healthy sponges, moreover, when inoculated into healthy sponges the same disease signs appeared. Cervino et al. (2006) noted that the closest relatives of these bacteria included terrestrial pathogens used against insects and fungi, and proposed that applications of similar bacteria to agricultural land onshore may have contributed virulence factors to potentially pathogenic marine bacteria strains at these sites near river mouths off palm oil plantations. However, Luter et al. (2010) could not find any shifts in the microbial communities of apparently healthy sponges and diseased *I. basta* collected from sites in the central Torres Strait, but could not completely rule out an infectious agent that might be in low abundance or the high virulence of an existing microbial symbiont.

Bleaching has also occurred in tropical marine sponges that contain photosynthesizing symbionts in their tissues, particularly in the Caribbean during the recent coral bleaching events (Chap. 5). Other sponge diseases have been reported from Indo-Pacific reefs, as well as the Caribbean, with partial or complete loss of pigmentation and tissue breakdown (Harvell et al. 1999; Wulff 2006b; Webster 2007; Angermeier et al. 2011; Webster and Taylor 2012). Study of these lesions is urgently needed to determine what is happening and why.

8.3.2.2 Corals

The tropical zooxanthellate reef-building scleractinian corals not only form the topography of a habitat, but also contribute to its productivity, supporting diverse organisms and protecting land masses as well. Since diseases of corals were first recognized in the 1970s, research has increased greatly as new diseases have been recognized and the number of corals afflicted or killed has also increased. Most of the literature is concerned with scleractinian (hard coral) diseases, but diseases of octocorals (soft or horny corals), particularly the Caribbean sea fan's mass mortalities since the mid-1990s caused by the fungus *Aspergillus sydowii*, have also been studied (e.g., Slattery et al. 2013; Nagelkerken et al. 1997; Kim et al. 2000; Toledo-Hernández et al. 2008). It is now impossible to review all of the developments in this area within the space limitations of this chapter. In addition, new discoveries are being made at a rapid pace. This section will present the current status of a few of these diseases. The reader is directed to books (e.g., Porter 2001; Rosenberg and Loya 2004; Raymundo et al. 2008; Woodley et al. 2015), special issues of journals (e.g., "Diseases of Aquatic Organisms" Volume 69), reviews (e.g., Richardson 1998; Green and Bruckner 2000; Richardson and Aronson 2000; Weil et al. 2000; Williams and Bunkley-Williams 2000; Bruckner 2002; Sutherland et al. 2004; Weil and Rogers 2011), and Web sites, for example, the Global Coral Disease Database (United Nations Environment Program-World Conservation Monitoring Centre: www.coraldisease.org) and the National Oceanic and Atmospheric Administration (NOAA)'s Coral Reef Information System (www.coris.noaa.gov). The literature cited within those sources will also provide a more complete and current understanding of coral diseases.

Contributing to the interest in and research on coral diseases was the organization of the Coral Disease and Health Consortium (CDHC) in 2001, under the direction of Dr. Cheryl Woodley as an activity of the U.S. Coral Reef Task Force, with a workshop held in Charleston, South Carolina, for reef scientists and managers, coral biologists, ecologists, statisticians, toxicologists, biochemists, information technologists, invertebrate pathologists, veterinarians, and medical doctors, to improve the communication and understanding of diseases by interactions among all these disciplines. Committees were formed, plans and procedures were developed (http://www.cdhc.noaa.gov/). *Coral Disease and Health*: *A National Research Plan* (Woodley et al. 2003) is available online (http://cdhc.noaa.gov/_docs/FInal%20CDHC%20plan%2011_07%20correc.pdf) and several more workshops and training sessions have been held to coordinate and inform additional field and laboratory research efforts. The Coral Reef Targeted Research & Capacity Building for Management (CRTR) Program, a partnership between the Global Environmental Facility, the World Bank, and NOAA, organized a Coral Disease Working Group and provided funding to support research by teams of scientists on coral diseases in several localities from 2004 to 2009 (http://www.gefcoral.org/). One of the outcomes of these efforts has been the realization that gross signs of disease in a coral observed in the field fall into one (or more) of these four categories: microbial mat-associated tissue loss, tissue loss, tissue discoloration, or growth anomaly (abnormal skeletal deposition pattern or rate of deposition that may include changes in the number of polyps). Any of these may include abnormal polyp behavior. Tissue loss is not required for a coral to be functionally impaired.

Black-band disease (BBD) was the first microbial mat disease of corals observed on reefs off Belize and Bermuda, but has since been found throughout the Caribbean as well as the Indo-Pacific and Red Sea (Rützler et al. 1983; Antonius 1985; Ravindran et al. 1999; Dinsdale 2000; Barneah et al. 2007). BBD has also been reported on milleporinids (fire corals) and gorgonaceans. Not all coral species appear to be susceptible to this disease. Massive brain corals (*Pseudodiploria* formerly *Diploria*, *Colpophyllia*, *Platygyra*, *Goniastrea*) and star corals (*Orbicella* formerly *Montastraea* spp.) are the most commonly affected members of the families Mussidae and Merulinidae (formerly Faviidae) (Budd et al. 2012), while elkhorn, staghorn, and pillar corals in the Caribbean resist natural infections. Acroporid, poritid, and pocilloporid species are also affected on the Great Barrier Reef (Page and Willis 2006).

Figure 8.4 shows the characteristic appearance of this disease. BBD results from the invasion of coral tissue by a microbial consortium. This consortium is a black mat a few millimeters to centimeters wide, composed of fine cyanobacterial filaments pigmented by phycoerythrin that also contains sulfate-reducing bacteria, sulfide-oxidizing

Fig. 8.4 Black-band disease destroying living coral tissue on a colony of star coral, *Orbicella faveolata*, at Looe Key, Florida Keys National Marine Sanctuary, during the mid-1980s outbreak; the diver on the left is using a suction device to remove the microbial mat from the coral to reduce tissue loss; spreading underwater epoxy along damaged tissue margins and shading affected colonies are more recent treatments (Photo courtesy of H.H. Hudson)

bacteria, other bacteria, and sometimes fungi and protozoans. These microorganisms produce anoxia deep in the band next to the tissue and hydrogen sulfide, as well as microcystins (Richardson et al. 2007; Stanić et al. 2011), which kill the coral tissue and allows the microorganisms to use the organic compounds released by the dying coral cells for their own growth and reproduction (Richardson et al. 1997). The band or mat moves across the surface of the coral at the rate of a few millimeters per day, leaving behind bare coral skeleton that is eventually colonized by filamentous algae. The cyanobacterium was identified as *Phormidium corallyticum*, but recent molecular studies indicate that more than one species of cyanobacterium might be involved among affected colonies within the Caribbean Sea and between the Caribbean and Indo-Pacific Seas (Frias-Lopez et al. 2004) and the Red Sea (Barneah et al. 2007). Different species of cyanobacteria, with greater amounts of red pigmentation, may form the microbial mats in red-band disease of scleractinian corals and sea fans; a yellow-band disease reported from the Arabian Gulf (Korrubel and Riegl 1998) may have been BBD in sulfur-saturated seawater.

Healthy corals can become infected with BBD when in contact with an infected colony, but injured colonies are most susceptible. Aeby and Santavy (2006) found that a coral-feeding butterflyfish could spread the disease during predation or even when the coral was protected from predation in aquarium studies. Most studies have found that less than 2 % of Caribbean and Great Barrier Reef corals are infected with BBD on any given reef area, although there have been outbreaks at several locations, including Looe Key reef in Florida in the mid-1980s, when most corals had lesions and pieces of microbial mats were dispersed through the water. In addition, other stressors, such as nutrients, light levels, higher water temperatures, and bleaching, may increase the susceptibility of corals to infection with the microbial mats (Kuta and Richardson 2002). A BBD epizootic affecting 10 % of *Montipora* spp. colonies with mean percent tissue loss of 40 % at Pelorus Island, Great Barrier Reef, was followed beginning in summer 2006 for 2.7 years. It was linked to seasonal increases in water temperatures and light levels; previous Australian surveys had reported background levels <1 % of susceptible coral populations (Sato et al. 2009).

About the same time that BBD was reported, acroporid (elkhorn and staghorn) corals off St. Croix, U.S. Virgin Islands, exhibited tissue sloughing, which started at the base of the branches and moved toward the branch tip at the rate of a few millimeters per day. In contrast to BBD, however, no consistent assemblage of microorganisms could be found at the junction separating the sloughing brown-

Fig. 8.5 Elkhorn coral, *Acropora palmata*, afflicted with the characteristic basal tissue sloughing of white-band disease at Grecian Rocks, Florida Keys National Marine Sanctuary (Reproduced from Couch and Fournie 1993)

pigmented tissue from bare coral skeleton. This disease was termed white-band disease (WBD), because the sloughing left a broad band of bare skeleton up to several centimeters wide on the colony that was eventually colonized by filamentous algae (Fig. 8.5). These disease signs can be distinguished from predator damage (e.g., fish, gastropod, or worm feeding scars) and have since been observed on acroporid species throughout the Caribbean, the Red Sea, and off the Philippines. Acute tissue loss on many species from the bases or in patches has also been observed on reefs around the world, and variably named WBD or white plague (WP); irregularly shaped patchy tissue loss from elkhorn coral is termed white pox, patchy necrosis, or white patch disease (WPD); acute tissue loss from tabular acroporids in the Indo-Pacific in a wedge-shaped or central pattern is called white syndrome (WS); and other variations in tissue loss based on pattern, species affected, and rate of tissue loss (from 0.5 to 10 cm per day linear), resulting in partial to complete mortality, have been recognized: shut-down reaction, WBD type II, white plague types II and III, rapid tissue loss, stress-related necrosis (Dustan 1977; Patterson et al. 2002; Bythell et al. 2004; Williams and Miller 2005; Ainsworth et al. 2007b). Inconsistent application of the names and descriptive terminology has led to confusion in the literature (Rogers 2010), and research on etiologies has not consistently linked particular signs with pathogens.

Unusual aggregates of Gram-negative rod-shaped bacteria were found scattered in the calicoblastic (skeleton-producing) epidermis that lined the gastrovascular canals of the porous skeleton in WBD-affected acroporids from St. Croix and Bonaire, Netherlands Antilles (Peters et al. 1983). The bacterial aggregates were also found in apparently healthy colonies at St. Croix. Five years later, up to 95 % of the elkhorn corals there had died. The role of this microorganism in the development of disease has not been determined; bacterial cultures or other isolation procedures were not conducted. Bythell et al. (2002) did not find them in their samples, and additional histopathological examinations noted that they occurred in apparently healthy samples and were not always found in diseased samples. Polson (2007) identified Gram-negative *Pseudomonas* spp. bacteria in aggregates from some—but, again, not all—acroporid samples taken during a tissue loss outbreak in the Florida Keys in summer 2003. Ritchie and Smith (1998) discovered *Vibrio carchariae* associated with the bleaching margin found on diseased staghorn coral with WBD type II, which was tested experimentally in the field using cultures of the Gram-negative *V.* (*carchariae*) *harveyi* by Gil-Agudelo et al. (2006), almost all of Koch's postulates were satisfied. Both of these papers also noted that WBD type II could turn into WBD type I and vice versa, lacking the bleaching tissue along the tissue loss margin at times. Another Gram-negative bacterium was identified as the cause of WPD in field experiments by Patterson et al. 2002, *Serratia marscesans*. Extensive work revealed that isolates from infected *Acropora palmata* were identical to a strain found in human wastewater and caused the same tissue loss in laboratory challenge experiments (Sutherland et al. 2011). In WP, a new genus and species of Gram-negative rod-shaped bacterium was identified as the causal agent (Richardson et al. 1998; Denner et al. 2003). Bythell et al. (2002), however, found a coccoid bacterium associated with patchy loss of tissue on *Montastraea* (now *Orbicella*) *annularis*.

Other reports have not found the same microbial communities in WBD- and WPD-affected corals of the same species (Kline and Vollmer 2011; Sweet and Bythell 2012; Lesser and Jarrett 2014), but some comparisons of diseased and apparently healthy colonies of the same species' microbiomes indicate differences that may lead to discovery of the pathogen (Cook et al. 2013; Roder et al. 2013). The causal agent of acroporid white syndrome has been much debated, with some scientists finding tissue loss only due to apoptosis (Ainsworth et al. 2007b) and others identifying vibrio bacteria in the affected corals (Sussman et al. 2008) or ciliates (Work and Aeby 2011; Sweet and Bythell 2012). Cases of acute tissue loss on Red Sea corals that appeared to have the WP disease signs had cyanobacterial mat involvement deep in corallites (Ainsworth et al. 2007a). Work and Aeby (2011) and Work et al. (2012) documented several different types of potential causal agents and host responses to them in *Acropora* and *Montipora* white syndromes using histopathological examinations, including ciliates, helminthes, and fungi, along with fragmentation and necrosis; Ushijima et al. (2012) discovered that *Vibrio owensi* initiated the tissue loss lesions in the latter disease. Casas et al. (2004) sampled apparently healthy and WBD-affected staghorn corals on Panama reefs and identified, using molecular techniques only, a Gram-negative *Rickettsiales*-like bacterium (90 % similarity to uncultured *Rickettsiales* with BLASTN based on cloning and sequencing of bacterial 16S rDNAs). But since it was in all of these samples, as well as in other coral species, they concluded it was not the pathogen of WBD type I. Miller et al. (2014) reported that histopathological examinations revealed the presence of a suspect rickettsia-like microorganism infecting and killing mucocytes of staghorn corals, which might be a chronic primary infection reducing their ability to resist infections by other microorganisms or increasing their susceptibility to other secondary abiotic pathogens that explain the variable patterns and rates of tissue loss. Other scientists have detected virus-like particles in corals affected by tissue loss (e.g., Vega Thurber and Correa 2011; Soffer et al. 2013; Lawrence et al. 2014), but their role in disease is unknown. Much remains to be learned about the nature of tissue sloughing in corals, and how many conditions caused by different pathogens or environmental stresses may actually be represented by the same disease sign of rapid tissue loss.

Tissue discolorations, either a loss of color or a change in color, focally or diffusely throughout a coral colony, indicate that the symbiotic association of the dinoflagellate algae, or zooxanthellae, may be impaired or that other microorganisms may be present (Fig. 8.6). Bleaching, the loss of the algae that normally give the coral tissue a brownish coloration, and/or the loss of their photosynthetic pigments, indicates that this important food resource of the tropical corals has been reduced. Chronic partial or widespread loss of zooxanthellae, for whatever reason, signals a disturbance in the normal metabolism of the coral host and can lead to delayed or reduced reproduction, tissue degeneration, reduced growth, and death of the affected tissue or entire colony (Chaps. 5 and 11; Williams and Bunkley-Williams 2000; Weis 2008; Rogers and Muller 2012). Bleaching of corals, gorgonaceans, alcyonaceans, and anemones has been attributed to exposure to high light levels, increased solar ultraviolet radiation, high turbidity and sedimentation resulting in reduced light levels, temperature and salinity extremes, and other factors. The nature and extent of bleaching vary between individuals and among species at the same location during a bleaching event and have been attributed to different physiological tolerances of the strains (or species, clades) of zooxanthellae and the coral hosts (Rowan et al. 1997; Jones et al. 2008). Discoveries by scientists in Israel include new species of vibrio bacteria that enter coral cells when water temperatures exceed 25 °C and cause lysis of the algae in temperate and tropical corals (Kushmaro et al. 2001; Ben-Haim et al. 2003). A coccidian (Phylum Apicomplexa), a protozoan known to cause disease in other animals, has also been associated with patchy bleaching in corals (Upton and Peters 1986).

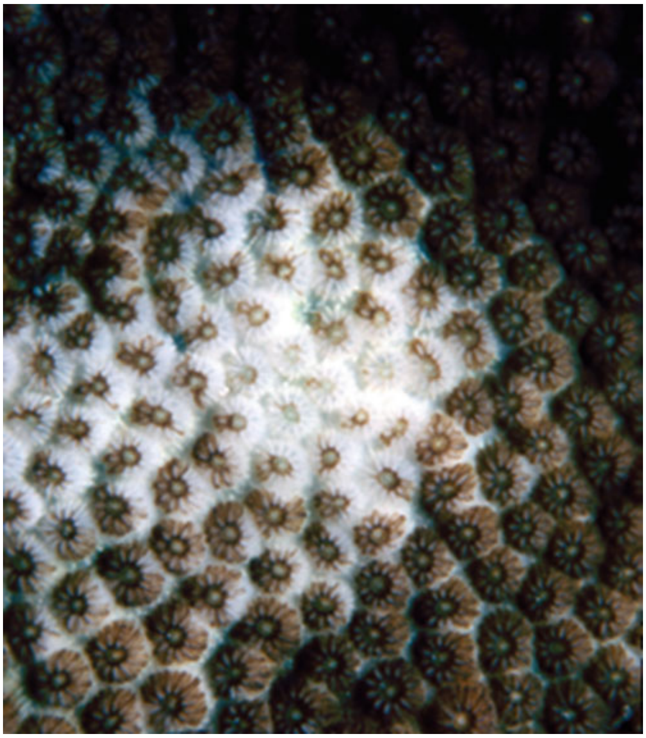

Fig. 8.6 Bleaching of tissue on a colony of *Orbicella faveolata*, Panama, 1996; translucent tissue still covers the skeleton but the zooxanthellae or their pigments are no longer present to color the tissue brown; diverse patterns of bleaching from gradual systemic paling or multifocal acute to chronic discoloration may occur and be accompanied by tissue loss due to many biotic or abiotic factors or combinations of such stressors

Another discoloration condition that is widespread throughout the Caribbean and causing partial mortalities of star corals, *Montastraea* (now *Orbicella*) spp., and other massive framework-building species is known as Caribbean yellow band disease (CYBD), with high prevalences recorded in Panama, Mona Island, the Netherlands Antilles, and the Florida Keys. Signs of this disease are focal to multifocal pale irregularly shaped patches of yellowish lightened tissue or a margin of yellowish lightened tissue a few cm wide adjacent to sediment patches on the colony (Santavy et al. 1999; Weil et al. 2000; Garzón-Ferreira et al. 2001). Similar lesions have been found on several Indo-Pacific coral species, especially *Fungia*. Microscopically, fewer zooxanthellae, with less pigment, reduced mitotic indices, and obvious cellular damage, were present within the lightened tissue compared to normally pigmented areas on the same colony (Cervino et al. 2001); microbiologically, several *Vibrio* spp. have been found in all of these lesions (Cervino et al. 2008).

Instead of showing paling of tissue, several species of corals, particularly the Caribbean *Siderastrea*, *Stephanocoenia*, and *Orbicella* spp., develop darker and often differently colored patches or marginal bands of tissue, which are referred to as dark spots disease or syndrome (DSD or DSS) (Sutherland et al. 2004). Affected areas may stop accreting skeleton with the result that they form depressions on the colony surface, and the dark tissue dies, causing partial mortality in all species. DSS may be a significant source of mortality in some *Orbicella* and *Stephanocoenia* colonies; however, the lesions can disappear in *Siderastrea siderea* colonies over time, suggesting they might be a temporary stress response (see review in Porter et al. 2011). Gross and histopathological observations indicated that in addition to zooxanthellae degeneration, endolithic organisms were present in *S. siderea* skeletons where the darkened tissue lesions occurred (Galloway et al. 2007; Renegar et al. 2008). Microbial communities from apparently healthy colonies and lesions have been examined using cultured and non-cultured (molecular) analyses, with varying results (reviewed in Kellogg et al. 2014). Although vibrios were associated with the lesions, they were also present in healthy tissue; cyanobacteria and an unclassified vibrio were present only in diseased tissue, but they concluded that their data did not show it to be a bacterial disease; they could not identify an isolated suspect fungal sequence. Sweet et al. (2013) had similar results in a study of *Stephanocoenia* DSS, but also identified a fungus similar to a plant pathogen (*Rhytisma acerinum*). Neither of these studies included histopathological examinations. A preliminary look at the histopathology of *Orbicella* DSS, indicates that suspect thraustochytrids on the colony's epidermis (Kramarsky-Winter et al. 2006) are being killed, then the darker tissue of the coral is seen, and the surface body wall atrophies (EC Peters, unpubl observ); but molecular and other analyses still need to be done.

Corals also harbor a variety of protozoan and metazoan microorganisms, some of which may be parasites. One relationship has been examined in Hawaiian corals (*Porites compressa*) containing the metacercarial stage of a digenetic trematode, *Podocotyloides stenometra*. The host for the final stage of this parasite is a coral-feeding butterflyfish, *Chaetodon multicinctus* (Aeby 2002). Parasite-infected coral polyps develop into pink, swollen calcified nodules, reducing the ability of the polyps to retract into their calices. Parasite encystment resulted in reduced growth rates of parasitized corals. Fish fed preferentially on infected polyps, and as a result the altered polyp appearance provided both an enhancement of the parasite's transmission rate and parasite removal from the coral. Healthy polyps then grew back over the feeding scars. Thus, this phenomenon may act as a host strategy of parasite defense.

Anomalous calcification patterns in scleractinian corals may be caused by parasites or commensals. Other examples of enlarged corallites or tumors in the exoskeleton have been attributed to cellular proliferative disorders, including neoplasia (reviewed in Peters et al. 1986). Whitened protuberant calcified tumors have been found on branching acroporid corals in the Caribbean and Indo-Pacific. These skeletal masses have proliferating gastrovascular canals and associated calicodermis (calicoblastic epidermis), the calicoblasts drive the deposition of the aragonite exoskeleton of the coral. As the calicoblastic epithelioma grows, porous skeleton formed by proliferation of gastrovascular canals lined by basal body wall tissue is formed more rapidly than it is in the surrounding tissue, resulting in degeneration of normal polyp structures and loss of zooxanthellae from gastrodermal cells. Mucocytes normally in the epidermis of the coral disappear from the epidermis covering the tumor as the tumor mass grows larger. Having lost the mucous secretory capabilities of the epidermis, the coral is unable to shed sediments and the tissue becomes ulcerated and invaded with filamentous algae. Branches having tumors also exhibit reduced skeletal accretion and growth. Both genetic and environmental factors appear to affect the distribution of tumor-bearing colonies (Peters et al. 1986; Coles and Seapy 1998; Yamashiro et al. 2000).

Additional cases of cellular proliferative disorders generally termed growth anomalies (GAs) have been discovered in coral species worldwide, often with bizarre development of polyps as well as skeletal morphologies (e.g., Gateño et al. 2003; Work et al. 2008a; Burns et al. 2011; Couch et al. 2014). Aeby et al. (2011a) used 937 quantitative coral disease surveys from around the tropical Pacific Ocean and evaluated the prevalence of GAs in relation to several environmental parameters. Strongest correlation of GAs in *Acropora* and *Porites* spp. was with coral colony densities and higher regional human population sizes. Suspected pathogens may include nutrient pollution, fungi (Domart-Coulon et al. 2006), or an infectious agent. Kaczmarsky and Richardson (2007) reported transmission of growth anomaly lesions at the point of contact on two apparently healthy small colonies of *Porites* (*lutea* or *lobata*) studied in aquaria in the Philippines, and one arising without contact that was in an aquarium with an affected coral.

Despite the wealth of data accumulating about all of the coral diseases, it is clear that many questions remain. Multidisciplinary research needs to be conducted on the same samples collected at the same time from the same locations, and this must include epizootiology (epidemiology, distribution and abiotic factors), histopathology (light and electron microscopy), microbiology, molecular biology, biochemistry, and analytical chemistry of environmental and tissue samples. Microbiological or molecular studies of suspected pathogens are not of much value unless histopathological examinations are performed at the same time to provide the necessary "phenotypic anchoring" to describe the condition (= structure) of the host's tissue, detect the presence of microorganisms and microparasites, evaluate how well the host was functioning at the time of sample collection, and aid in understanding pathogenesis and immunity.

8.3.2.3 Molluscs

Diverse species of molluscs live on coral reefs or in adjacent seagrass beds, but few studies have been conducted on these animals, except for the commercially important giant and fluted clams (*Tridacna* spp.), queen conch (*Strombus gigas*), and pearl oysters (*Pinctada* spp.). Diseases of temperate molluscs are caused by viruses, bacteria, fungi, and protozoan and metazoan parasites; nutritional, developmental, and neoplastic disorders are also known. Thus, it is probable that similar diseases are present in tropical molluscs, particularly where reefs are also stressed by abiotic factors.

Giant clams from the Great Barrier Reef were found to contain large numbers of the protozoan *Perkinsus* sp. (Fig. 8.7). It has been suggested that this microorganism, in conjunction with cooler water temperatures, was responsible for observed mortalities affecting up to a third of the giant clams at Lizard Island from 1984 to 1987. However, the protozoan was also found at low levels of infection and not associated with mortalities in other bivalves on the reef (84 species from the families Spondylidae, Arcidae, and Chamidae, as well as the Tridacnidae were examined). These results indicate that there may be species-specific host susceptibilities among the bivalves, several different species of *Perkinsus*, or variations in the prevalence of pathogenic strains of *Perkinsus* (Goggin and Lester 1987). A temperate relative of this protozoan, *Perkinsus marinus*, has been responsible for extensive mortalities of oysters along the east coast of the United States. The relationship of this pathogen to changes in environmental conditions, including salinity and temperature, has been investigated, and careful monitoring and control measures have been undertaken to protect these food resources (Fisher 1988). Further histological studies of the giant clam mortalities off Lizard Island revealed the presence of an unidentified unicellular organism in some of the clams (Alder and Braley 1989), but many questions remain about the nature of this epizootic. *Perkinsus olseni* and an exotic species of *Perkinsus* have been associated with mortalities in ornamental *Tridacna crocea* shipped to the United States for aquaria (Sheppard and Phillips 2008; Sheppard and Dungan 2009). Studies of cultured *T. gigas* revealed that their newly settled veliger larvae are also susceptible to known pathogenic marine bacteria, particularly *Aeromonas*, *Plesiomonas*, *Vibrio*, *Pseudomonas*, *Alteromonas*, and *Alcaligenes* spp., with variability in species/strains for initiating mortality (Sutton and Garrick 1993).

Fig. 8.7 Divers sampling a dying *Tridacna gigas* from North Direction Reef, Great Barrier Reef, Australia during perkinsosis outbreak (Photo courtesy of N. Quinn)

A mass mortality of wild queen conch was reported from the Hol Chan Marine Reserve, Ambergris Cay, Belize, mid-September to mid-November 1991, but the cause was not identified (Williams and Bunkley-Williams 2000). Cárdenas et al. (2005, 2007) discovered an apicomplexan infecting the digestive gland of *S. gigas* at Alacranes Reef, Mexico, and San Andres Island, Colombia, incidentally during a study on their reproduction, collecting 30 specimens monthly for 1 year at each site. Heavy infections were characterized by 75–100 % of digestive tubule cryptic and secretory epithelial cells showing trophozoites, sporocysts, and gamonts containing macrogametes or microgametes and discharged sporocysts present in stomachs. Both populations were affected, the intensity of infections varied from heavy to few infected tubules with the month sampled, but no trend was evident. Although morbidity was not observed, the infections were present in conch throughout the year, and reduced fecundity was associated with the infections.

The commercial market for mother-of-pearl oysters, *Pinctada margaritifera*, in French Polynesia was severely damaged in 1995 by a virus that killed up to a million oysters and culture of *Pinctada* spp. in the Indo-Pacific has been affected by several other diseases associated with viruses, *Perkinsus* sp., or other protistan, bacterial, and metazoan agents (Jones 2007). Larval trematodes of the family Bucephalidae cause parasitic castration or destruction of gonadal tissue in marine bivalves; such infections occur in *Pinctada* spp. and in a burrowing tridacnid clam from the Great Barrier Reef (Shelley et al. 1988). Bott et al. (2005) found digenean trematode parasites from the families Bucephalidae, Gorgoderidae, and Monorchiidae (in low prevalences, overall 2.3 %) in 12 of 47 species of bivalves from Queensland, Australia, waters, including Heron Island and Lizard Island on the Great Barrier Reef some were new host records. Molluscs possess cellular and humoral defense mechanisms that help to control pathogens but investigations of these immune responses have not been performed on their counterparts in subtropical and tropical marine habitats.

8.3.2.4 Crustaceans

Most reef crustaceans are small and inconspicuous or cryptic. Examples include banded coral shrimps (*Stenopus* spp.), cleaner shrimps (*Periclimenes* spp.) associated with anemones, burrowing mantis shrimps (*Gonodactylus* spp., *Callianassa* spp.), snapping shrimps that hide in corals or sponges (*Alpheus* spp.), and a variety of decorator crabs, coral crabs, hermit crabs, and the arrow crab (*Stenorhynchus seticornis*). The spiny lobsters (*Panulirus* spp.) and slipper or Spanish lobsters (*Scyllarides* spp.) are the objects of important subsistence and commercial fisheries in tropical marine waters. However, reports of disease in most of these species are lacking.

Temperate lobsters (*Homarus* spp.), penaeid shrimp, and various edible crabs are known to be susceptible to a variety of pathogens and parasites, as well as abiotic diseases related to poor nutrition and water quality (Sindermann 1990; Stentiford 2011, introduction to special issue on crustacean diseases). Exposure to pollutants and other environmental stressors are known to cause damage to gills (black gill disease) and exoskeletons (shell disease) and reduce the quality of lobster and crab fisheries. Both of these diseases involve ulcerations of tissue with necrosis and bacterial invasion. In shell disease, chitinoclastic microorganisms are responsible for eroding the shell, which may have been damaged by mechanical, chemical, or microbial action, followed by secondary infection of the underlying tissue by facultative pathogens (Shields 2011). Again, most of the research has been performed on commercial species, particularly those held in culture facilities, with a few reports of shell disease, pathogenic microorganisms, and parasites in tropical commercially fished crustaceans.

Crustaceans possess fixed and mobile phagocytic cells in the gills, the pericardial sinus, and at the bases of appendages. They produce bactericidins, agglutinins, and lysins to deal with pathogens and parasites. Bactericidins of the West Indian spiny lobster (*Panulirus argus*) have been examined (see review in Sindermann 1990), and found to be partially nonspecific. Bactericidin activity was enhanced against other Gram-negative bacteria following injections of formalin-killed bacteria. A major concern of the global cultured penaeid shrimp industry has been viruses, particularly white spot syndrome virus (WSSV), and the possibility that some viruses from shrimp pond culture have been released into wild populations through effluent discharges or viruses from wild crustaceans have been introduced into ponds through untreated influent. A survey using sensitive nested PCR screening by Chakraborty et al. (2002) found that multiple species of apparently healthy wild marine shrimps, crabs, and squilla harbored WSSV off the east and west coasts of India, although whether the virus causes mortalities in the wild crustaceans has not been reported.

Shields and Behringer (2004) discovered a viral disease with mean prevalence of 6–17 % of sampled juvenile *P. argus* from sites surveyed in western Florida Bay and along the reef tract in the Florida Keys during different seasons and years (1999–2000). Affected spiny lobsters were lethargic or suffered tremors, could not right themselves, were shunned by other lobsters, and had milky hemolymph that did not clot. Hemocytes (hyalinocytes and semigranulocytes) and connective tissue cells had emarginated condensed chromatin, hypertrophied nuclei, and faint eosinophilic Cowdry-type A inclusions. The inclusions were found to be composed of unenveloped, nonoccluded, herpes-like DNA virus (HLV-PA, PaV1) virions. Injections of raw hemolymph from infected animals into healthy lobsters resulted in morbidity and mortality within 80 days post injection; the virus has now been found in lobsters from the U.S. Virgin Islands, Mexico, and Belize and juveniles are most susceptible (Shields 2011). This disease is of great concern to the commercial fishery for spiny lobster in the Caribbean. Behringer et al. (2012) also discovered that traps baited with sick

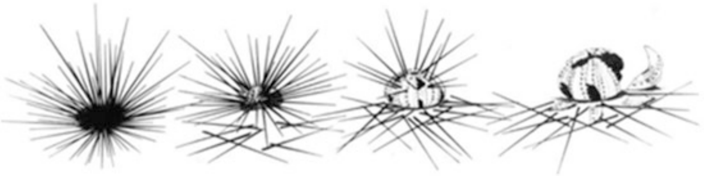

Fig. 8.8 Progressive stages in the death of tropical western Atlantic long-spined sea urchins, *Diadema antillarum*, during the mass mortalities

lobsters attracted fewer lobsters than those baited with apparently healthy lobsters (11 % of the latter tested positive for the virus). Shields (2011) noted that spiny lobsters should be screened for this virus and other infectious agents (bacteria, fungi, protozoans, helminthes, and even other crustaceans) to help prevent their spread as culture of this species increases.

8.3.2.5 Echinoderms

The echinoderms are represented by such diverse animals as crinoids, sea cucumbers, sea stars, sea urchins, and brittle stars, and all are found in tropical marine habitats. Their influence on the structure and function of coral reef ecosystems can be substantial, particularly in food webs and bioerosion (Birkeland 1989). While bacterial and protozoal diseases of temperate sea urchins and sea stars have received much attention from invertebrate pathobiologists, there have been few studies on the etiologies of diseases and mass mortalities in tropical echinoderms, including the most extensive epizootic ever reported for a marine invertebrate.

Two species of echinoids were observed dying in 1981 around Hawaii. *Echinothrix calamaris* displayed drooping spines, loss of spines, and sloughing of the tissue covering the test, beginning on the island of Hawaii, then a few months later at Molokai, Maui, Oahu, and Kauai. Similar signs were observed on *Diadema paucispinum* on Hawaii, but not on other sea urchin species (reviewed in Birkeland 1989). The first mortalities of the long-spined sea urchin *Diadema antillarum* were seen on reefs off the Caribbean coast of Panama in January 1983. Mortalities of only this species subsequently occurred at other sites around the Caribbean and Bermuda for 1 year, in a pattern that followed major water currents from west to east, with a few exceptions (Lessios 1988). Diseased urchins were initially recognized by an accumulation of sediment on their spines and sloughing of the spine epidermis, accompanied by unusual behavior, moving out from their normal hiding places in the reef into the open during daylight, where they were preyed upon by fish. Pigment in the skin covering the spine muscles, peristome, and anal cone then disappeared, and the spines broke off. The tube feet that normally hold the urchin to the sea bed weakened and could not fully retract. Finally, patches of skin and spines sloughed off and the test disintegrated (Fig. 8.8). Diseased urchins died within 4 days to 6 weeks, depending on locality, although some urchins apparently survived the disease and recovered from the broken spines and skin lesions. Overall, adult populations of this urchin were reduced by 85–100 % at sites throughout the tropical western Atlantic Ocean, with juveniles being rarely affected. Localized mortality events were reported affecting the urchins *Astropyga magnifica* and *Eucidaris tribuloides*, in the mid-1980s, in shallow waters of Puerto Rico.

Although numerous studies were conducted on the ecology of the long-spined urchin die-offs in 1983 and on later isolated mortalities of remaining populations of *D. antillarum* off St. Croix, Grand Cayman, and Jamaica, few samples were obtained for histological or microbiological investigations. Gram-positive anaerobic spore-forming rods of the bacterial genus *Clostridium* were isolated from two urchins showing similar signs of the disease that died while in a flow-through seawater aquarium in Miami in 1983. Laboratory experiments with cultures of these bacteria caused death of healthy urchins in 10 h to 6 days, depending on water temperature. Microscopic examination of fixed tissues from apparently healthy and diseased St. Croix urchins collected post-1983 revealed Gram-positive micrococci in mucoid cells of the glandular crypts of the esophagus and in connective tissue and muscle bundles of the peristome, spines, and ampullae. However, bacterial samples were not taken in this study (see Peters 1993 for review). A mass mortality of large *D. antillarum* that occurred in the Florida Keys in April 1991 (Forcucci 1994) provided samples during the event for bacteriological, virological, and histopathological studies, but results proved inconclusive and differed from the earlier observations; the Lower Keys population densities decreased by 88–100 % 6 months later and Middle Keys and Upper Keys reef sites had densities $<0.01/\text{m}^2$ by the summer of 1991, the same as after the 1983 event.

A species-specific waterborne pathogen, perhaps introduced to the Caribbean from the ballast water of ships traversing the Panama Canal and discharged at the Caribbean entrance and at Barbados, was suspected to be the causal agent of the *D. antillarum* epizootic in 1983, since no other species were affected and no adverse changes in environmental conditions were noted at any of the sites (Lessios 1988; Jackson et al. 2014). Perhaps this pathogen is still present and affecting the recovery of the species, although some sites report increasing densities, at others larval recruits disappear and few, scattered adult urchins are found, which probably affects their gamete fertilization success (Edmunds and Carpenter 2001; Miller et al. 2003). Re-occurring outbreaks of disease in other echinoid species have been noted. Echinoderms possess cellular and humoral defense mechanisms in the coelomic fluid and associated tissues that can protect them from invasion by potential pathogens. However, they also usually contain mutualistic bacteria in the gut or other organs. Recent research on immune responses of *D. antillarum*, *Echinometra lucunter*, *E. viridis*, and *T. ventricosus* on reefs of St. Croix, USVI, revealed that long-spined urchins released lower levels of humoral immune molecules when challenged with lipopolysaccharide or several bacteria species compared with the other urchin species (Beck et al. 2009). This suggests that *D. antillarum* may have some molecular, gene-mediated defect in its immunity that contributed to its susceptibility to the suspect waterborne, perhaps bacterial, pathogen; however, more research is needed on its populations throughout the Caribbean to determine the significance of these data.

The coral-eating Indo-Pacific crown-of-thorns seastar *Acanthaster planci* has an unusual bacterium living in its body wall, mucus secretions, and pyloric caecum. When the sea star is held in aquaria, these bacteria become facultative pathogens and leave the animal vulnerable to secondary infections by *Vibrio* spp. and other bacteria. Mass mortalities of juvenile *A. planci* that occurred near Fiji over 3 years were not caused by bacteria, however, but apparently resulted from sporozoan parasites infecting the digestive tract (reviewed in Birkeland and Lucas 1990). Similarly, a wide variety of metazoans have been observed to associate with echinoderms, usually without harming their hosts. In tropical marine species, however, Emson et al. (1985) reported severe damage to brittlestars that were heavily parasitized by copepods. Williams and Wolf-Waters (1990) observed emaciation and lack of gonad development in a Caribbean basketstar in which the stomach was heavily infected by a normally ectoparasitic copepod. Additional investigations of these organisms may reveal new biotic pathogens.

8.3.3 Reef Vertebrates

Although numerous examples of viral and bacterial diseases and epizootics have been reported in temperate marine fishes, particularly commercially gathered species and those species used in aquaculture, few studies have examined their counterparts in tropical species. Besides fishes, sea turtles are globally important tropical marine vertebrates and sea snakes may also be encountered on Indo-Pacific reefs. Some information on the normal physiology, biochemistry, behavior, and diseases has accumulated from research on those tropical marine species popular in aquariums and oceanariums (Stoskopf 1993) and in aquaculture (Glazebrook and Campbell 1990a). Studies on captive fishes and turtles have confirmed their sensitivity to adverse changes in environmental conditions and the importance of appropriate water quality and proper nutrition in maintaining their health (Roberts 1989). Diseases which occur under these artificial conditions tell us little about what occurs on coral reefs and there have been few published field observations.

8.3.3.1 Fishes

Panek (2005) provided a detailed review of the literature for coral reef fish species in the tropical western Atlantic Ocean and Gulf of Mexico, but noted that much remains to be learned about distributions of parasites and pathogens in relation to their hosts, the roles of cleaner fish in limiting parasite harm, mechanisms of pathogen transmission, and environmental issues.

Injured or weakened reef species, such as damselfishes, squirrelfishes, soldierfishes, and angelfishes, may become infected with marine bacteria. Gram-negative *Photobacterium* spp., *Vibrio alginolyticus*, *V. anguillarum*, and Gram-positive *Streptococcus* spp. have been isolated from fishes with skin ulcerations, septicemias, exophthalmias or popeye, and other lesions. Thousands of demersal reef fish washed ashore on beaches of Barbados, Grenada, Saint Vincent, the Grenadines, and Tobago from July to September 1999; the bacterium *Streptococcus iniae* was isolated from a few moribund fish (Ferguson et al. 2000). Keirstead et al. (2013) isolated *S. iniae* from moribund and dead fishes found off St. Kitts and Nevis, West Indies, in January–February 2000. Species affected included snappers (*Lutjanus campechanus*, *Ocyurus chrysurus*), parrotfish (*Sparisoma aurofrenatum*, *Scarus taeniopterus*) and red hind (*Epinephelus guttatus*). Panek (2005) noted that mycobacteriosis of tropical marine fishes has only been reported from the Red Sea, affecting cage-reared and nearby wild rabbitfish (*Siganus rivulatus*). Lymphocystis disease, caused by an iridovirus, is characterized by giant cell “tumors” and has been reported from Australia, Hawaii, the Pacific coast of Panama, Indochina, the South Pacific, and the Caribbean. Other viral diseases, including viral erythrocytic necrosis (VEN) caused by another apparent iridovirus, an infectious pancreatic necrosis-like virus (IPN), and a rhabdovirus infection, have been found in captive tropical marine species such as angelfishes, wrasses, and blennies. However, little work has been done on viruses isolated from these fishes (Stoskopf 1993). Captive tropical marine fishes are also susceptible to fungal infections such as *Ichthyophonus hoferi*.

A wide variety of protozoan and metazoan parasites are known from examination of field-caught and captive tropical marine fishes. They include ectoparasitic flagellates (*Amyloodinium* and *Crepidoodinium* pathogens of gills and skin), trypanosomes, hemoflagellates of the genus

Fig. 8.9 Neurofibromas developing on a bicolor damselfish, *Pomacentrus partitus*, Molasses Reef, Florida; a single, unpigmented, nodular tumor appears on the upper back under the dorsal fin and several small pigmented tumors are apparent near the eyes, on the head

Trypanoplasma, various genera of ciliates, sporozoans (phylum Apicomplexa), microsporidians, myxosporidians (genera *Ceratomyxa*, *Myxidium*, or *Leptotheca* have been found in gallbladders of marine tropical fish), turbellarians, nematodes, digenetic and monogenetic trematodes, aspidogastrids, cestodes, leeches, copepods, and isopods. The trematodes, cestodes, and nematodes require one or more intermediate hosts to complete their life cycle. Many of these parasites do not cause overt disease or mortalities among wild fish (e.g., Bunkley-Williams and Williams 1994; Aeby 2002; Work et al. 2004b) although they may be found in potentially pathogenic numbers during mass mortalities; however, losses of captive fish have been attributed to ectoparasitic infestations, especially "coral fish disease" or "velvet disease" caused by *Amyloodinium* spp. The cleaner fishes and shrimps in tropical marine habitats apparently keep the levels of most pathogens and parasites quite low in wild fish populations, although this has not been demonstrated experimentally.

A few tumors (neoplasms) have been reported in tropical fishes, including hemangiosarcoma, iridophoroma, fibroma, nasal papilloma, reticulum cell sarcoma, and fibropapilloma (Panek 2005). Of particular interest are the neurofibromas, neurofibrosarcomas, and chromatophoromas of the bicolor damselfish, *Pomacentrus partitus* (Schmale 1991; Schmale et al. 2002). Damselfish neurofibromatosis (DNF), which is similar to the disease in humans known as von Recklinghausen neurofibromatosis, is characterized by the appearance of conspicuous hyperpigmented spots on the skin and fins that arise from multicentric peripheral nerve-sheath (Schwann cell) tumors that vary in degree of pigmentation (due to chromatophores, including melanophores). The tumors (Fig. 8.9) were highly malignant, spreading throughout the animal and eventually causing its death as the result of destruction of vital organs or as secondary infections develop. Affected bicolor damselfish have been found only on reefs off South Florida at prevalences of up to 23.8 %. Disease rates remained relatively stable for each reef site examined over a 9-year period. The distribution of tumorous fish and the results of laboratory transmission experiments suggested that an infectious agent, such as a virus, is involved. The virus could be transmitted during the frequent aggressive interactions that occur among neighboring individuals defending their territories. After much work, Schmale et al. (2002) reported identifying an unusual virus characterized by extrachromosomal DNAs (eDNA)—damselfish virus-like agent (DVLA)—from cell lines derived from tumors. Infected cells produced tumors when injected into healthy fish; a similar pattern of eDNA was found in those tumors as well as tumors from spontaneously diseased fish, thus, DVLA is probably the etiologic agent of this disease. Damselfish neurofibromatosis is being developed as an animal model to study neurofibromatosis and possible treatments for humans. Other species of damselfish and other tropical reef species such as snappers in the Florida Keys have also been found to be afflicted with neurofibromas or neurofibrosarcomas (Panek 2005) and chromatophoromas were found in two species of Hawaiian butterflyfish (Okihiro 1988).

The limited observations of disease in fishes in the wild may be the result of predation. Any condition that weakens a fish or changes its normal behavior, or causes its death, would make it susceptible prey. Isolated cases of diseased fish may thus be overlooked. However, there have been mass mortalities of tropical marine fish, with records from the tropical western Atlantic Ocean in 1946; some of these may have been due to exposure to red tide toxins (Landsberg 1995). Mass mortalities of mullet in the mid-1970s near Miami, Florida, were believed to result from infection of their brains with a newly described bacterium that caused twirling and other signs of neurologic disease (Udey et al. 1977). A Caribbean-wide massive fish kill occurred in August and September of 1980, following Hurricane Allen. Tons of dead and dying fishes washed onto beaches. Wild and captive fish exhibited odd behavior suggesting that fishes surviving the mortalities were "sick" for several months. The cause was never identified. Millions of herrings (*Harengula* spp.) died at eight locations around the Caribbean during the 1980s (Williams and Buckley-Williams 1990). These mass mortalities were disjunct over time and geographic location, and examinations of moribund fish did not reveal any bacterial infections or other conditions that might have been responsible. Landsberg (1995) reported results of histopathologic examinations of several affected herbivorous reef angelfish, identifying a ciliate parasite, *Brooklynella hostilis*, as well as bacteria and other microorganisms, as possible etiologic agents of this slime blotch disease first noticed in 1993 along the Florida reef tract. She speculated that biotoxins from dinoflagellates in angelfish food might have contributed to immunosuppression and infections, leading to the mortalities. Williams and Bunkley-Williams (2000) noted that further work linked the ciliate to the disease and it might have caused other moralities of reef fish in the Caribbean.

8.3.3.2 Sea Snakes

Little is known about diseases of the poisonous sea snakes. External parasites include ticks on the skin of laticaudids and a turbellarian on *Pelamis* sp. from the Gulf of Panama. Foraminiferans, hydrozoans, serpulid polychaetes, bivalve molluscs, bryozoans, and barnacles have been recorded as fouling organisms on sea snakes. Most external symbionts are probably dislodged, however, as the result of frequent shedding of the skin and knotting behavior in these organisms (Zann et al. 1975). Endoparasites include chigger mites in the lungs of the semiterrestrial *Laticauda* spp., nematodes, and trematodes (Heatwole 1987; see also Culotta and Pickwell 1993).

8.3.3.3 Sea Turtles

The green (*Chelonia mydas*), loggerhead (*Caretta caretta*), and hawksbill (*Eretmochelys inbricata*) turtles are frequently found on coral reefs and associated habitats, where they feed on seagrasses, macroinvertebrates, and sponges, respectively. Most observations of diseases in sea turtles have also been conducted on oceanarium- and aquaculture-reared animals, with reports consisting primarily of systemic bacterial diseases, metazoan parasites, nutritional disorders, and skin tumors. In one survey of 22 wild turtles obtained from the Torres Strait off Townsville, Queensland, Australia, Glazebrook and Campbell (1990b) found a great number and diversity of parasites. Two species of flukes (Class Digenea: Order Spirorchiidae) were found in the heart and major associated arteries and their eggs were found in other organs and tissues. The presence of the flukes was associated with clinical signs of disease, and muscle wasting, bronchopneumonia, and septicemia-toxemia were present in some of the afflicted turtles. Cardiovascular flukes have also been found in wild turtles in the United States, India, Puerto Rico, and elsewhere in Australia. Seven species of flukes were found in the gastrointestinal tracts of nine wild turtles, but there were no signs of pathological changes. The green sea turtle leech can extensively damage the tissues of its host, but Bunkley-Williams et al. (2008) identified it as infecting a posthatchling juvenile hawksbill sea turtle, and also described sea turtle leech erosion disease caused by superinfection of the loggerhead sea turtle leech in a hawksbill sea turtle.

The most studied disease of sea turtles affects wild green, hawksbill, loggerhead, and the other species of sea turtles from the tropical Atlantic and Pacific Oceans (Balazs and Pooley 1991; Williams et al. 1994). Sea turtle fibropapillomatosis (Fig. 8.10) appears as irregular lobulated tumors (neoplasms), up to 30 cm or more in diameter, on the skin, scales, scutes, eyes, and surrounding tissues, and fibromas also develop internally (Flint et al. 2010). The tumors may interfere with vision, breathing, feeding, and swimming. In the 1980s and 1990s, the condition seemed to be afflicting increasing numbers of turtles and spread geographically. The eggs of parasitic trematode worms occur often, but not always, in dermal capillaries within the tumors. A herpesvirus has been identified in the tumor tissue; however, culture of these virus isolates has not been successful (Lackovich et al. 1999; Lu et al. 2000a). One study was able to cause the tumors by inoculation of cell-free filtrates of tumor homogenates, but their protected status made further experimental evaluation of their etiology difficult. A biotoxin, okadaic acid, produced by dinoflagellates that could be present on turtle grass might also promote the development of these tumors (Landsberg et al. 1999; Davidson 2001). Kang et al. (2008) used in-situ hybridization on tissue sections from fibropapillomas and fibromas of Puerto Rican green turtles to show that the fibropapilloma-associated turtle herpesvirus (FPTHV) was present only in the nuclei of epithelial cells of the tumors, not the underlying dermis fibroblasts. Although the ability of the tumors to cause debilitation in the turtles varies, immunosuppression, with development of systemic bacterial infections consisting primarily of vibrios, probably leads to turtle morbidity and mortality (Work et al. 2004a). The geographic distribution of affected turtles suggests that a combination of abiotic and biotic factors are necessary for the development of this disease.

Other novel viruses have been detected in diseased sea turtles, including herpesviruses (Stacy et al. 2008), papillomaviruses (Manire et al. 2008), and a tornovirus (Ng et al. 2009). The application of new molecular techniques to obtain and sequence DNA or RNA from a variety of

Fig. 8.10 A green sea turtle, *Chelonia mydas*, with large fibropapillomas on its neck and flippers, collected at El Tuque, near Ponce, Puerto Rico (Photo courtesy of L. Bunkley-Williams)

cells may lead to the discovery of other pathogens in the sea turtles.

8.4 Ecological Implications

Early investigations of the structure and function of coral reefs and associated soft-bottom habitats (mangrove and seagrass communities) generally failed to consider the role of pathogens and parasites in population and community development and alterations. Until the 1970s, diseases of tropical marine organisms were virtually unknown. However, whether caused by abiotic stressors or parasites, they are normal in nature. In a review on this topic, Hudson et al. (2006) noted that research has shown parasites and biotic pathogens comprise perhaps half of the biomass of ecosystems, shape community structure and promote ecosystem functioning, and drive biodiversity and productivity. Revisiting the host-pathogen-environment paradigm, we understand that parasites will be affected by anthropogenic changes as well as their hosts, but perhaps in different ways, some surviving better than others, some having the ability to infect new hosts rather than die out, and some better able to change and adapt to new conditions at different stages in their life cycles. We consider them to be problems, and yet host population control is essential so organisms do not exceed the carrying capacity of the ecosystem. The difference is that enzootic (or endemic) levels of disease agents, producing low levels of morbidity or mortality, are not alarming, whereas epizootic (epidemic) levels or outbreaks get our attention. In areas where organisms are adapted to changing conditions, such as temperate zones, the autumnal reduction in light and temperature causes deciduous plants to stop photosynthesis, and their leaves become susceptible to infections with viruses, bacteria, and fungi that will break down the tissue, recycling it into nutrients on the forest floor, while protecting the plant from winter storm (wind and snow) effects. When such infections occur during the spring or summer, damaging the leaves so they cannot support the plant, then the agent is causing disease. Despite our aversion to pathogens, developed from long observations of morbidities and mortalities caused by them and dislike of suffering (our own or others), they are necessary for proper ecosystem functioning (Gómez et al. 2012).

Improvements in recognizing and diagnosing diseases and identifying pathogens have probably contributed to the increase in reports of emerging infectious diseases (EIDs) in terrestrial and aquatic ecosystems (Gire et al. 2012), because disease agents likely have been circulating undetected in ecosystems for years as subclinical infections. With continuing human population growth, urban development, deforestation, point and nonpoint source pollution, and increasing carbon dioxide concentrations in the atmosphere, we have witnessed ecosystem alterations and increasing loss of organisms to abiotic and biotic stressors impairing their health (Vicente 1989; Harvell et al. 1999, 2004, 2007; Selig et al. 2006; Altizer et al. 2013; Ban et al. 2014). Other chapters in this book examine the changes occurring when populations of reef organisms are altered as a result of predation or exposure to adverse environmental conditions. The same principles and effects apply when populations are affected by biotic diseases. This section will review some of the impacts that diseases have on the tropical marine environment, as aptly summarized by the German marine ecologist Otto Kinne in Box 8.2, and additional concerns.

As discussed in other chapters, the demise of even one species of coral-reef organism may have serious repercussions for the structure, composition, processes, and function of a particular community and the reef ecosystem. Diseases of scleractinian corals and coralline algae are perhaps the most important factor in changing the structure and function of coral reef communities because loss of live tissue

Box 8.2
"Diseases affect basic phenomena of life in oceans and coastal waters: for example, life span, life cycle, abundance, distribution, metabolic performance, nutritional requirements, growth, reproduction, competition, evolution, as well as organismic tolerances to natural and man-made environmental stress. In short, diseases are a major denominator of population dynamics." (Kinne 1980, p. 1)

cover not only reduces the number of polyps producing gametes for potential new recruits, but also opens up new hard substratum space for settlement of benthic organisms. However, Kuta and Richardson (1997) found that, in agreement with other studies, BBD caused extensive tissue loss in reef framework coral species, but few benthic fauna colonized the bared skeletal areas in 5 years of observations, and of those, only one was a reef-framework coral species, which could contribute to a shift in community structure over time. Edmunds (2000) followed tagged coral colonies for 11 years on a shallow reef off St. John, U.S. Virgin Islands and reported similar, but very low, rates of recruitment by scleractinians to coral skeletons remaining after being killed by BBD or Hurricane Hugo. This study was undertaken in a bay with a fully protected watershed and relatively pristine reefs, and the only increase in infection rates and loss of tissue occurred during late summer when seawater temperatures were at their peak.

The other coral tissue loss diseases have affected large areas of reef throughout the Caribbean and Florida Keys and now threaten corals in the Red Sea and Indo-Pacific oceans. The population reductions in branching acroporid corals as a result of WBD, with bioerosion of the remaining exoskeletons, changed reef structure (Gladfelter 1982). Aronson and Precht (2001) reported that WBD caused significant mortality of acroporid corals throughout the Caribbean during the past three decades, resulting in changes to the framework of these reefs. The mass mortality of *A. cervicornis* from disease or other causes in the central shelf lagoon of the Belize Barrier Reef during a 10-year period around 1990 was discovered by coring into the substratum. It was the first widespread change in species composition in this region for more than 3,000 years. *Agaricia tenuifolia* replaced the staghorn, but bleached and then was replaced by *Porites porites*. These species do not provide the same high relief habitat and framework as acroporids, and the associated organisms differ as well. In the Florida Keys, changes in corals and other organisms have been documented (Porter et al. 2002; Alevizon and Porter 2014; and others), some associated with disease outbreaks and loss of acroporids, but with high variability among reef sites and uncertainties in understanding the causes (Brandt et al. 2012; Miller et al. 2014). Similar structural modifications are occurring on Indo-Pacific reefs with the loss of the large table acroporids (Hobbs and Frisch 2010) and montiporids (Work et al. 2012) to WS, montiporids to atramentous necrosis (Jones et al. 2004), and many other partial to complete mortalities resulting from diverse diseases in numerous species (see regional reviews by multiple authors in Rosenberg and Loya 2004). Which species are lost before others will affect community structure and function as well (Ostfeld and LoGiudice 2003).

Although community alterations have been observed more often on coral reefs, diseases may also affect a variety of relationships and processes in soft-bottom benthic communities on reefs and in seagrass beds and mangroves. In addition to predation and competition, bioturbation, sedimentation, primary and secondary production, and other phenomena may be changed with the loss of one or more micro- or macro-organisms to biotic or abiotic diseases. During the mass mortality of turtlegrass *Thalassia testudinum* in Florida Bay, more than 23,000 ha were affected, with 4,000 ha of seagrass beds completely lost, especially in protected basins. Many reef organisms are associated with seagrass habitats. They are used by larvae and juveniles as refugia from predators. Soft-bottom invertebrates used as prey may suffer from the loss of the seagrass and they can also be affected by pathogens and parasites, as documented in a review by Sousa (1991). Elevated water temperature, the recent local decline in frequency of hurricanes, elevated salinity, and chronic sediment hypoxia were noted as other factors that may have contributed to the Florida Bay die-off (Roblee et al. 1991), stressors that could also have directly or indirectly affected the other organisms living in this ecosystem.

Parasites and their hosts are embedded in food webs (Hudson et al. 2006). Not only may these organisms affect host responses to environmental stresses, thereby altering population size and geographic distribution, but they can also influence biodiversity and productivity and alter intra- and interspecific interactions of species (Rohde 1993). The dramatic phase shift that occurred following the year-long mass mortality of *Diadema antillarum* adversely affected reefs throughout the tropical western Atlantic, as macroalgae grew with reduced herbivore control, preventing recruitment of corals and other benthic organisms (Lessios et al. 1988). Acroporid corals damaged by Hurricane Allen off Jamaica initially survived as fragments, then apparently succumbed to WBD and macroalgal growth after the *D. antillarum* mass mortality, changing the pattern of predation by coral snails and shifting the roles of other predators there (Knowlton et al. 1990). Marked reductions in multiple species of sponges (51.3 % of species and 42.6 % of total sponge volume), as documented on a shallow reef at Bocas del Toro, Panama, over 14 years and possibly occurring elsewhere in the Caribbean and the Florida Keys, resulted in the loss of several essential ecosystem services, particularly water clarity, nutrient regeneration, and shelter from predators for many species (Wulff 2006b).

Extensive loss of topographic relief has affected fish populations as protective niches and important habitats have been altered. The decline of coral reef fisheries among western Atlantic coral reefs may be related to such structural changes from the loss of acroporids and other coral species, although overfishing has probably contributed to losses of fish species diversity and numbers as well (Rogers 1985; Jackson et al. 2001) argued that human impacts on marine ecosystems, including the phase shifts experienced during the last 20 years on coral reefs in the Caribbean and community changes on other reefs, can be traced back to the continuous fishing activities of humans. Overfishing of large vertebrates and shellfish, to the extent that they are now missing from most coastal ecosystems, resulted from aboriginal, then European, colonization and exploitation, leading to disease in lower trophic levels. Populations of their prey either became so dense that transmission of pathogenic microorganisms was facilitated (e.g., in *Diadema*), or predators of microbes (e.g., suspension feeders) have been removed, facilitating their population explosion now as eutrophication of coastal marine ecosystems increases. Jackson et al. (2014) noted that limiting the blame to climate change as the culprit of disease outbreaks will not lead to appropriate remedies and advocated protection for herbivorous fishes to deal with the macroalgae biomass on many reefs, which has been shown to contribute to coral diseases and reef degradation since the 1980s.

Dinsdale and Rohwer (2011) examined this situation on many degraded coral reefs, where top predators have been "fished down the food chain," and observed that with increased nutrients supporting phytoplankton and macroalgae, the primary productivity that would normally be transferred through herbivores to the predators through the trophic cascade has instead accumulated as particulate and dissolved organic matter, supporting a different, enriched heterotrophic microbial community. Although the top predators' prey are more abundant, the prey's food sources have increased in abundance and cannot be controlled as before. Potentially pathogenic microbes have been identified on algae (Nugues et al. 2004), as well as in the water column, supporting more bioeroders and sponges that may serve as reservoirs of microorganisms implicated in coral diseases (Ein-Gil et al. 2009; Negandhi et al. 2010; reviewed in Webster and Taylor 2012). Bowles and Bell (2004) noted that overfishing of sea turtles was not related to seagrass wasting disease. The numerous other reef organisms that are now being "fished" for food, construction materials, home aquaria, home decorations, and other commercial or socioeconomic reasons are also contributing to the defaunation of coral reef ecosystems, loss of habitat, and disturbances to marine food webs, which will change parasite-host relationships and reduce the ability of organisms to tolerate infections. Another aspect of sorting out the impacts of population reductions on diseases brings us back to the food webs. Diseases can alter the reproductive potential of a population by direct effects on gonad development (e.g., parasitic castration), or indirectly by altering male-to-female ratios and mating or spawning behavior, not to mention reducing population densities and the distribution of individuals that will impair successful reproduction (e.g., Allee effect) (McCallum et al. 2004). What has not been explored are indirect effects on nutrition by reduced intake and absorption of nutrients due to loss of prey or zooxanthellae (contributing nutrients to corals, sponges, anemones) that would also reduce gamete production. And in turn, reducing seasonal releases of gametes and larvae that served as food for other reef organisms. When 90–100 % of *Diadema antillarum* died, how did their loss change food webs that had been dependent on their spawning?

Porter and Tougas (2001, Figure 5 and text) proposed a model of coral disease in which changing environmental conditions are responsible for altering the interactions between hosts and pathogens, as immune systems become compromised because of various stressors. They noted that inclusion of environmental quality was necessary to explain the simultaneous increase in the diseases, species affected, and rates of mortality over large geographic areas, and hypothesized that the incidence of disease would be higher near polluted population centers. This has certainly been shown in widely separated studies on coral diseases, such as in the U.S. Virgin Islands (Kaczmarsky 2005), the Philippines (Kaczmarsky 2006), Abrolhos Bank, Brazil (Francini-Filho et al. 2008), southeast Florida (Dustan et al. 2008), Hawaiian Islands (Aeby et al. 2011a; Couch et al. 2014), and the Great Barrier Reef (Lamb and Willis 2011), as well as coralline algae diseases of Indo-Pacific reefs (Vargas-Angel 2010) at sites where domestic sewage, agricultural, industrial, and stormwater discharges flow onto reefs. In other cases, diseases do not correlate with the level of human influence (Quéré et al. 2014, coralline algae diseases in Curaçao; Gochfeld et al. 2012, *Aplysina* red band syndrome not altered with nutrient enrichment), but these seem to be rare exceptions. Field and laboratory experiments have demonstrated pollution impacts on coral reef organisms. For example, nutrients, organic matter, crude oil, copper sulfate, dextrose, potassium phosphate, and sediment have increased morbidity and mortality in exposed corals, but the addition of antibiotics (in lab experiments) has prevented disease (e.g., Mitchell and Chet 1975; Hodgson 1990; Kuta and Richardson 2002; Bruno et al. 2003; Kline et al. 2006; Voss and Richardson 2006; Brandt et al. 2013), indicating that microbial population control, and its potential for producing anoxia and toxins, is important in addition to the toxicity of the contaminant. In addition, hosts and parasites may have different responses to altered environmental conditions. Increased water temperatures have been found to support growth rates for microbes while damaging plants or animals, with increases in disease outbreaks (e.g., Ben-Haim et al. 2003; Selig et al. 2006; Vargas-Ángel 2010; Muller and van Woesik 2014), but more work is needed on synergistic effects of stressors. For example, Williams et al. (2014) found that the fungal destruction of thallus tissue in CFD was reduced when $p\mathrm{CO}_2$ and water temperature were elevated together, although the coralline algae calcification was reduced by these stressors, adversely affecting resistance to micro-boring organisms.

The first response of many aquatic organisms, particularly corals, when exposed to an irritant is increased production of mucus to form a protective barrier and limit the exposure. The mucus in turn is used by bacteria and other microorganisms for food. The ensuing breakdown of this organic matter can lead to the release of bacterial toxins and anoxia, resulting in disease if the affected organism cannot escape. Different species of corals can produce different kinds and quantities of antimicrobial compounds to control different kinds of surface bacteria (Koh 1997). Sea fans use chemicals to inhibit tissue infection by fungi and cellular defenses to sequester the hyphae (Kim et al. 2000; Petes et al. 2003). Energy for production of mucus or antimicrobial compounds that support a protective microbial community (mechanisms reviewed in Krediet et al. 2014), as well as cellular and humoral immune responses, can be limited in animals when nutritional sources are scarce or metabolic processes are altered by exposure to temperature extremes or pollutants, leaving them susceptible to attack by latent, facultative, or opportunistic pathogens (Hayes and Goreau 1998; Lesser et al. 2007; Mao-Jones et al. 2010). Furthermore, secretion of mucus is suppressed following prolonged exposure to elevated temperatures or pollutants. Metabolism, production of detoxification enzymes, and other physiological and biochemical operations are also altered by exposures to anthropogenic pollutants and changes in water quality (Couch and Fournie 1993), which may also affect prey, resulting in structural and functional changes in tissues leading to morbidity and mortality of resident invertebrate and fish populations.

A study of corals and octocorals from Biscayne National Park, off southeast Florida (USA) in the 1970s revealed high levels of organochlorine pesticides and heavy metals, similar to those levels used in toxicity tests that led to bleaching and mortality of the same reef-building species of corals in the laboratory. One-third of coral colonies sampled from this site exhibited lesions and possibly pathogenic microorganisms were found in their tissues, although the presence of the lesions could not be linked to contaminants in this study (Glynn et al. 1989). Similar studies of corals off Australia (Lewis et al. 2009) and elsewhere have detected uptake of pesticides and heavy metals into tissues; however, the presence of biotic or abiotic diseases in contaminated corals from these sites has not been documented. High tissue burdens of such chemicals resulting from chronic exposures may increase the susceptibility of the organisms to biotic disease agents when additional physical or chemical stresses are encountered. Fish diseases are also increasing in tropical bays and mangrove areas where man-made solid and other wastes are disposed. Observations on commercial fish catches in Biscayne Bay, off Miami, Florida, over 10 years (1970–1982) revealed a variety of surficial lesions and abnormalities, including ulcerations, fin and integumental hemorrhages, fin erosion, eye abnormalities, scoliosis, scale disorientation, parasitoses, emaciation, and tumors, especially in bottom-feeding fishes. Excessive nutrients from sewage; petroleum hydrocarbons from marinas, shipping, port facilities, and industries; and toxic chemicals, pesticides, and polychlorinated biphenyls leaching from landfills, rivers, and canals contributed to the decline in water quality of Biscayne Bay (Skinner and Kandrashoff 1988). Because many young stages of reef fishes use inshore waters that may contain toxic chemicals and high levels of nutrients from sewage disposal and stormwater runoff, as well as heavy sedimentation and turbidity, they may also be susceptible to diseases caused by microbial pathogens and parasites. The role of these diseases in limiting reef fish populations, however, is unknown because appropriate studies have not been conducted. Infectious diseases have decreased in some fish populations as intense fishing has reduced host numbers (Ward and Lafferty 2004), limiting contact and exposure and making disease transmission inefficient. This is the “host-density threshold,” another important aspect of disease ecology.

Fishing top predators can indirectly favor disease transmission in prey populations, however, as prey end up in denser aggregations (Lafferty 2004). In 1982, *D. antillarum* populations were thick on Caribbean reefs, improving the likelihood of infecting another individual. Perhaps their predators were reduced for some reason and perhaps they were starving, which could have further compromised their weak immune systems (McNamara and Buchanan 2005). However, in communities with high biodiversity of potential parasite hosts, a dilution effect has been noted, reducing the risk of vector-borne diseases (Ostfeld and LoGiudice 2003). Loss of biodiversity increases disease transmission by changing the abundance of the host or vector; by changing the behavior of the host, vector, or parasite; or by changing the condition of the host or vector, although more biodiverse communities may contribute novel pathogens (Aeby 2002; Keesing et al. 2010). These concepts have not been explored much in relation to parasites and diseases of coral reef organisms; however, Wood et al. (2014) compared fished and unfished reefs in the Northern Line Islands of the Pacific and found that fishing decreased parasite species, with directly transmitted parasites significantly more affected than those that alternated among hosts, but the effects varied depending on the host species and their sensitivity to fishing impacts. Aeby et al. (2011b) compared *Acropora* WS-affected corals on a reef in the species-poor northwestern Hawaiian Islands with species-rich reefs off American Samoa. They observed high mortality in the monospecific stand of *Acropora* on the Hawaiian reef, whereas the disease could not easily spread among different *Acropora* spp. on the American Samoa reefs, because they differed in their apparent susceptibility to infection and disease severity. Perhaps that was true also of the formerly magnificent monospecific thickets of Caribbean acroporids, facilitating transmission of the agent(s) responsible for WBD, particularly where thickets had been formed by fragmentation of a highly susceptible genotype. Bruno et al. (2007) found that high (>50 %) coral cover on Australian reefs correlated with increased prevalence of WS following exposure to warm temperatures.

Differences in susceptibility to certain diseases as a result of individual or species attributes (genetic or otherwise) are also influential in changing the composition of reef communities (e.g., Koh 1997; Dinsdale 2000; Weil et al. 2000). For example, at some locations, diseased corals show a clumped distribution (Bruckner et al. 1997; Richardson 1998; Sato et al. 2009; Porter et al. 2011), whereas in other areas, diseases have a random distribution (e.g., Edmunds 1991), and exhibit localized adaptation in host infectivity (Grosholz and Ruiz 1997). Muller and Woesik (2012) examined the spatial patterns of yellow-band disease, dark-spot disease, and white-plague disease and suggested that when diseases are not clustered they do not follow a contagious model, rather environmental thresholds are first exceeded that increase corals' susceptibility or the environmental changes create a favorable environment for already present biotic pathogens and increase their virulence (e.g., Remily and Richardson 2006). García et al. (2002) found differences in disease susceptibility not only among coral species in the Parque Nacional Archipiélago de los Roques off Venezuela, but also among different size classes. For example, WP and CYBD was more likely to affect large (older) colonies (0.9–10.8 m^2) and BBD small colonies (0.01–0.09 m^2). Muller and van Woesik (2014) found that white pox was more likely to adversely affect older *A. palmata* colonies after temperature stress. An analysis of constitutive levels of immune-related processes against prevalence and number of diseases affecting different Caribbean coral species revealed that those species studied belonging to older lineages (Siderastreidae, Poritidae, Meandrinidae) tended to resist diseases better than recently divergent lineages (Montastraeidae and Merulinidae, but not Mussidae) (Pinzon et al. 2014), with similar indications in Indo-Pacific species (Palmer et al. 2010). Whether vectors are involved in the spread of pathogenic microorganisms, how they interact with tolerant or susceptible hosts, and whether their own genetics and physiological mechanisms make them susceptible or tolerant to environmental stressors or biotic pathogens, probably also influences the prevalence and intensity of disease outbreaks (Lu et al. 2000b; Panek 2005; Williams and Miller 2005; Aeby and Santavy 2006; Råberg 2014), as well as each organism's holobiont (Mydlarz et al. 2010).

If the complexity of disease ecology within an ocean basin were not enough, another concern is that organisms are being transported out of their home habitat and introduced into similar or new habitats many miles away, often in different regions or even oceans, as the result of global shipping, oceanarium, aquaculture, marine laboratory, and tropical aquarium trade activities. In addition to attaching to the hull of a vessel, larval organisms and potential microbial pathogens can be picked up with ballast water and deposited offshore or in another harbor. Commercial shipments of live organisms contain not only the desired (or target) organisms or their eggs and larvae, but also other organisms that may be parasites or pathogens in the water or seaweed in which they were originally packed and within the target organisms. If placed in flow-through systems, without proper quarantine or treatment of the discharged water, these animals will be released to the sea. Releases of unwanted fish or other animals by tropical aquarists have also led to introductions in foreign lands. If conditions are suitable for survival and reproduction, the species may become established at the new site. Some introduced species have positive effects in their new environment. But the vast majority of documented introductions have adversely affected existing commercial and recreational fisheries as the result of competition, predation, and the introduction of parasites and pathogens (e.g., Carlton and Geller 1993; Chakraborty et al. 2002; Padilla and Williams 2004; Sheppard and Dungan 2009), a phenomenon termed "pathogen pollution." A number of countries developed regulations and procedures to restrict such introductions, including permit and certification requirements; culture using filtered, recirculating sea-water; quarantine procedures; and destruction of diseased stocks (DeVoe 1992), as well as new ballast-water regulations (Gollasch et al. 2007). Controlling individual behavior can be difficult (e.g., the aquarist who dumps unwanted organisms in the ocean; Padilla and Williams 2004). However, Jackson et al. (2014) surmised that the massive losses of Caribbean acroporids and long-spined urchins may have resulted from the "enormous increases in ballast water discharge from bulk carrier shipping since the 1960s" (p. 21) and the fact that millions of years of isolation from the Indo-Pacific may have made them particularly vulnerable to introductions of novel pathogenic microorganisms or ones that had developed increased virulence. For already introduced organisms, such as two species of lionfish (*Pterois*) that are now established (since 1985) and multiplying in the Caribbean Sea and tropical western Atlantic Ocean where they are consuming native fishes (Schofield 2009), perhaps native pathogens and parasites will eventually control them (Albins and Hixon 2013).

Pathogen, nutrient, and toxicant pollution can also be dispersed globally by air. The numerous diseases observed throughout the Caribbean caused scientists at the U.S. Geological Survey to wonder whether disease incidence might be related to dust from the Sahara/Sahel Region of Africa that blows across the Atlantic and is increasing due to drought conditions there. Studies of air samples revealed the presence of viable bacteria and molds apparently shielded from damaging UV radiation by the dust particles. One species of soil fungus found in samples is *Aspergillis sydowii*, identified as the causal agent of the disease aspergillosis in sea fans. Other potentially pathogenic microorganisms have been found in the dust; human cases of respiratory diseases increase on Caribbean islands and elsewhere when dust sweeps into the area (Shinn et al. 2000; Griffin 2007). Furthermore, Hayes et al. (2001) speculated that increased deposition of the iron-rich dust throughout the region since the 1970s, along with local and global climate changes and pollution loading, has probably altered the ability of coastal ecosystems to limit the multiplication of potentially pathogenic microorganisms, resulting in disease outbreaks in marine organisms in these nutrient-enriched areas. Examining multiple environmental and anthropogenic factors on a small scale (e.g., microhabitat) to large scale (e.g., satellite data of sea surface temperatures) will be important in research on diseases of reef organisms (Bruckner 2002).

The complexity of disease, as it is now understood four decades after the first reports of coral diseases, has incorporated a larger role for anthropogenic alterations in the environment, particularly climate change as shallow-water ocean temperatures have warmed and elevated $p\mathrm{CO}_2$ is altering ocean pH. When culture techniques were developed for bacteria, Robert Koch established criteria (Koch's postulates) more than 100 years ago for determining the causal agents of human diseases. Associations of suspected pathogens have been reported in the literature, and some scientists have claimed that they have identified a microorganism or polymicrobial infectious agent by applying Koch's postulates, but experimental tests of Koch's postulates are challenging. Some agents cannot be cultured outside of the host and viruses require special cell lines in which to grow them so they have not been cultured in the laboratory (e.g., herpesvirus of sea turtle fibropapillomatosis, *Rickettsiales*-like organism of staghorn coral). They may also require interactions with other biotic or environmental factors to become virulent (Lackovich et al. 1999; USEPA 2000). Thus, the procedures used to identify pathogenic microorganisms are changing. Molecular tools can now be used to examine DNA sequences and tease out potentially pathogenic microorganisms in comparison to unaffected hosts (e.g., Ritchie et al. 2001; Lesser et al. 2007; Work et al. 2008b; Sutherland et al. 2011; Wilson et al. 2012; Roder et al. 2013; Sweet et al. 2013, 2014; Williams et al. 2014). However, diseases can also result from abiotic, nutritional, or genetic factors. While molecular approaches are providing key insights into the microbiomes of affected species, it is crucial that this research be done in conjunction with histopathological examinations and physiological tests to understand which target cells or organs are being damaged and how pathogenesis occurs. In addition, analytical chemistry is needed to determine whether affected species contain critical body residues of chemical contaminants or biotoxins, which may actually be the pathogen(s) and cause the microbiome to shift to cellular degraders using molecules from the dying cells for their substrates. And, of course, numerous other environmental variables must be considered. The use of tools that integrate stressor exposures and effects, such as biomarkers, may help to identify causal mechanisms for subcellular damage underlying observed effects at the population or community levels (Woodley et al. 2000; Morgan et al. 2001; Richardson et al. 2001); however, the normal ranges for the various parameters must be carefully examined first and laboratory models using cell cultures or whole organisms are needed (Adams 1990; Huggett et al. 1992; Scully et al. 2001). Knowledge of the variability of normal and abnormal structure and function in most tropical marine organisms, both within and between individuals and species, is still lacking. Comparisons that would be useful indicators of environmental stress are few. The study of bleaching in corals and other organisms containing photosynthetic symbionts has increased to the point that algal densities and photosynthetic pigment fluorescence may be useful indicators, as well as molecular biomarkers.

In addition, scientists in tropical marine environments should be aware of the possibility that diseases and mortalities observed locally may actually be major epizootics or mass mortalities that cover large areas of coral reefs or coastal habitats or even regions. D. Faulkner describes a "healthy" patch reef near Eleuthera in the

Bahamas as having numerous *D. antillarum* and other species of urchins, but surprisingly noticed a patch reef not more than 100 m away that appeared "unhealthy" even "bleak," with large dead colonies and algae present, completely lacking urchins. He also could not find *D. antillarum* on Hen and Chickens Reef in the upper Florida Keys reef tract in 1975, and it, too, had dead and dying corals. Although the cause of the reef demise in Florida was suspected to be cold water one winter, he wondered if the lack of urchins had prevented the corals from coming back, as well as whether something had killed the urchins first, resulting in the dying reefs—this was prior to the mass mortality event (Faulkner and Chesher 1979). Could a waterborne pathogen have been present in the Caribbean prior to 1982? What has prevented their return in many areas, particularly the Florida Keys, and where they have returned, are those urchins still susceptible to whatever killed them before (Edmunds and Carpenter 2001; Beck et al. 2009)? Of course, other abiotic and biotic factors may have affected the urchins at these reefs and the sequence of events is unknown. Experience thus far suggests that more extensive networks of scientists need to be developed to track such events and to locate expertise to investigate the role of biotic and abiotic diseases. Both observers in the field and specialists in laboratories are required to respond quickly and gather samples and essential data.

To promote the transdisciplinary and collaborative investigations of the linkages among the health of humans, other animals, and plants (ecosystem health) with environmental changes, the field of conservation medicine developed during the 1990s–2000s (Aguirre et al. 2012). Drawing on data obtained from innovative monitoring strategies, ecological, chemical, physiological, microbiological, histopathological, social science, and other types of research, patterns of shared causes, interrelationships, and the significance of the diseases or mass mortality events can be established to address the conservation of biodiversity. A similar early effort was the Caribbean Aquatic Animal Health Project at the University of Puerto Rico to develop the Marine Ecological Disturbance Information Center (MEDIC) to track reports of major marine ecological disasters (MMEDs) affecting Caribbean aquatic organisms and to alert appropriate experts when field and laboratory studies were required (Williams and Buckley-Williams 1990). Building on this effort, we have seen increased collaborations among experts in different disciplines (CDHC and Targeted Coral Reef Research), more consistency in disease investigations, stakeholder notifications about morbidity and mortality events, incorporation of quarantine or some sort of treatment protocol to prevent spread of disease—particularly from a culture facility to field and vice versa—McCallum et al. 2004), and the realization that human health can be compromised not only by impacts of disease on ecosystem services, but also by direct exposures to zoonotic pathogens. For example, Keirstead et al. (2013) determined antibiotic susceptibility (minimal inhibitory concentrations to various antibiotics) of *S. iniae* to treat fish handlers if they were infected with the bacterium during the 2008 mass mortality of wild reef fish off St. Kitts, Nevis. Other pathogenic microorganisms in tropical marine waters could also infect humans, indicating the need to develop a One Health approach as advocated in conservation medicine. Terrestrial and aquatic ecosystem health linkages must be included (the watersheds, ridges-to-reefs concept).

In summary, investigations of the nature and role of diseases in coral reef organisms have identified diverse agents responsible for morbidities and mortalities. Based on observations of commercially important invertebrates and vertebrates from temperate seas, more diseases and diverse parasites no doubt remain to be discovered, and will also need to be studied. Long-term changes in water quality, such as elevated levels of nutrients, are of particular concern for attached or sedentary invertebrates, since they cannot escape. Loss of important members of a food web will ultimately affect higher predators, as will the loss of those organisms that perform important functions in an ecosystem, such as decomposition, bioturbation, or nutrient recycling, and the loss of organisms that provide protection and specialized habitats. As water conditions and habitats change due to human actions and globalization, with intense mixing and introductions of species to new locations driving exposures and responses to potentially pathogenic agents, multiple factors and scenarios need to be considered. Population losses thought to be tied to overfishing or natural predation may have been the result of disease; diseases may result from population losses that reduce biodiversity and increase malnutrition. Pathogens and parasites exert tremendous pressures on individuals, populations, and communities in their interactions with the host and environmental conditions, and must be taken into consideration in any discussion of the dynamics of coral reefs and associated tropical marine habitats, and in the conservation of reef biodiversity. The contributions of humans to the stressors experienced by reef organisms is unprecedented in this unique period of earth's history, and the Anthropocene is not only changing ecosystems, but how we must think about them.

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Geographic Differences in Ecological Processes on Coral Reefs

9

Charles Birkeland

Abstract

Although basic ecological processes are generally consistent on a local scale, there are geographic differences in geological processes, the physical environment, and dimensions of the areas involved that change the nature of coral-reef systems. The structure of reefs is affected by plate tectonics, e.g., there is a greater prevalence of atolls in the central Pacific and Indian Oceans than in the Atlantic or eastern Pacific. The vast dimensions of the Pacific Ocean produces a sharp gradient of decrease from west to east in species, generic, class, and habitat diversity across the Pacific that is not so pronounced in the smaller western Atlantic and Indian Oceans. Diseases are generally contained within distantly separated archipelagoes in the Pacific but quickly spread across the relatively small and interconnected greater Caribbean. The differences in sediment input into the oceans (2 % west coasts of continents, 82 % east coasts) and the degree to which river output affects biogeographic patterns (eastern vs western coasts of continents), show the overwhelming global influences of trade winds and the Coriolis effect on coral reefs. The relative prevalence of corals and other sessile photosymbiotic invertebrates compared to sessile heterotrophic invertebrates can be affected on a geographic scale as well as locally by the strength and dependability of nutrient input. Adult coral colonies can persevere in areas with substantial nutrient input such as upwelling, but recruitment in these areas is extraordinarily difficult in competition with algae and heterotrophic invertebrates in areas with abundant nutrients. The effects of disturbances and effects of altering the system, for example by reducing the stock of grazers, can be substantially greater in areas of high nutrient input.

Keywords

Trophic • Diversity • Nutrient • Coriolis • Upwelling

9.1 Large-Scale Dynamic Effects of Nutrient Input

Human activities affecting river discharges of nutrients can have international consequences on marine biota. For example, immediately following construction of the Aswan Dam 966 km (over 600 miles) inland from the coast on the Nile, the multinational fisheries catch for the eastern Mediterranean Sea decreased to 3.7 % of its former levels because of the reduction in nutrients flowing into the Mediterranean

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(Aleem 1972). Age-class strength of economically important marine invertebrates and fishes are correlated with river discharge strength (Sutcliffe 1972, 1973; Wolff et al. 1987; Darnaude 2005; Gillson 2011; Dutterer et al. 2012). Terrestrial nutrient inputs have been found to be a cause of outbreaks of *Acanthaster planci* which have had major effects on coral-reef community structure (Brodie et al. 2005; Fabricius et al. 2010).

Striking examples of the magnitude of effects of agricultural nutrients on marine coastal environments are the extensive development of "dead zones" of coastal oceans in recent decades. Fixed nitrogen is essential for making DNA, RNA and proteins and so it is quickly taken up by living organisms and is often in short supply in the natural world. Whereas CO_2 is a low-energy byproduct of processes using energy, and it takes energy such as provided by photosynthesis to remove it from the atmosphere, fixed nitrogen is the end-product of an energetically expensive process and it is quickly taken up when available. Nitrogen is naturally fixed (converted to ammonium) on coral reefs mainly by cyanobacteria using photosynthesis to power the conversion. In the 1950s, the industrial production of fertilizer by use of fossil fuels became a major economic process. The global amount of fixed nitrogen is now twice the natural amount, and this accumulation of molecules high in demand in the biosphere probably does not have precedence in the Phanerozoic record. The excess fertilizer on continents now drains into rivers, which in turn flow to the coastal marine areas. The fixed nitrogen is taken up by phytoplankton, bacteria and other microbes. As the biota grows, the increased biomass respires at night and uses up the available oxygen in the sea. The hypoxic environment causes most of the animals in the area to suffocate, hence the name of the regions "dead zones". The number and area of dead zones doubled every decade since the 1960s, and by 2008 the number of dead zones reached 405, covering a total area of ocean of 245,000 km^2 (Diaz and Rosenberg 2008).

Ryther (1969) estimated that upwelling areas take up only about 0.1 % of the ocean surface, but these small areas provide support for 50 % of the world fishery catch, a 500-fold relative difference in the ratio of average yield per unit area from the world ocean resulting from input of nutrients. Natural abrupt reductions in nutrient concentrations can also have influences on marine biota on an international scale. In 1983, 17 million sea birds of 18 species disappeared from Christmas Island and animals from all trophic levels (zooplankton, squid, planktivorous fishes, marine iguanas, sea birds, fur seals and sea lions) substantially decreased in abundance because of the lower nutrients from the El Niño of 1982 (Glynn 1990). During the 1982–1983 El Niño – Southern Oscillation (ENSO) event, there was a decrease in primary productivity and density of phytoplankton, a temporary closure of the fishing industries, and large-scale mortalities of sea birds (85 % in Peru) and marine mammals (30 % for fur seals in the Galápagos).

9.2 Physical Processes That Bring Geographic Differences to Ecological Processes

9.2.1 Longitudinal Differences

The basic force behind both longitudinal and latitudinal differences in ecological processes on coral reefs is the sunlight falling at a high angle on equatorial regions throughout the year. Since the angle is more direct near the equator, the heat energy is concentrated over a smaller surface area and so the air is warmer on average near the equator (Fig. 9.1a). Although Earth receives an average of

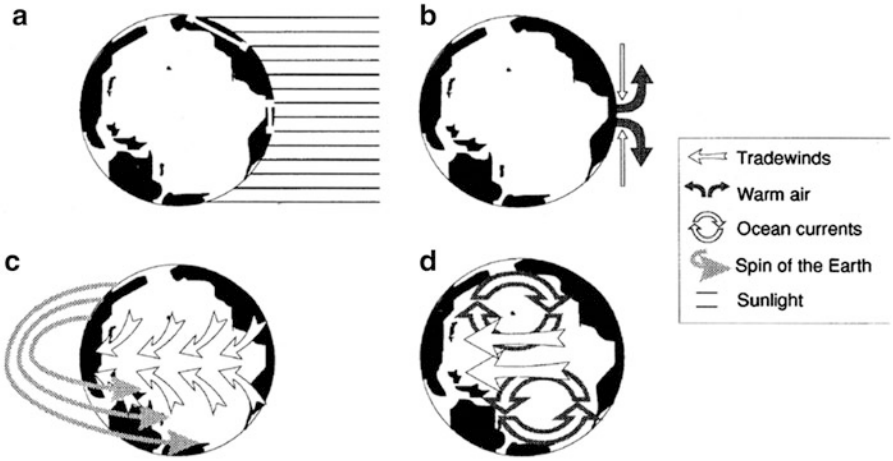

Fig. 9.1 The physical forces that produce the geographic variation in ecological processes of coral reefs. (**a**) Energy from the sun is more concentrated throughout the year in the tropics. (**b**) Excess heat in the tropics produces low pressure, rising air, with replacement air coming from higher latitudes. (**c**) The spin of Earth causes the replacement air to effectively move westward relative to the surface of Earth, creating the trade winds. (**d**) The trade winds and the spin of Earth cause the Coriolis effect, bringing warm seawater and rainfall to the western tropical seas and upwelling of cool nutrient laden water to the eastern tropical seas

12 h per day of sunlight everywhere, the sunlight is distributed more evenly through the seasons in the tropics and so there is no annual cooling.

The climatic and oceanographic patterns of the world are driven by the excess heat in the tropics and the deficit at higher latitudes. As the equatorial air warms, it expands and rises, and is replaced near the surface of Earth by cooler air from the north and south (Fig. 9.1b). Since Earth spins on its axis from west to east, the trade winds (replacement air) effectively (from the perspective of creatures on Earth's surface) move westward rather than directly north or south (Fig. 9.1c). The trade winds blow the main equatorial currents westward. The equatorial currents turn away from the equator in the Atlantic and the Pacific when they are blocked by the continents, moving clockwise in the northern hemisphere and counterclockwise in the southern hemisphere (Fig. 9.1d). This pattern is called the Coriolis effect. This contributes to a striking gradient in diversity of coral-reef organisms across the tropical Pacific from high in the west to less in the east, and it also causes major differences in nutrient input on a geographic scale (Fig. 9.2) which affects the trophic characteristics of the dominant organisms (Fig. 9.3). Heterotrophic sessile animals have an advantage in areas of high nutrient input (upwelling and terrestrial runoff) and animals with photosynthetic symbioses are prevalent in tropical oligotrophic waters (Fig. 9.3).

From the geographic perspective of coral-reef management, the Coriolis effect determines the patterns of nutrient

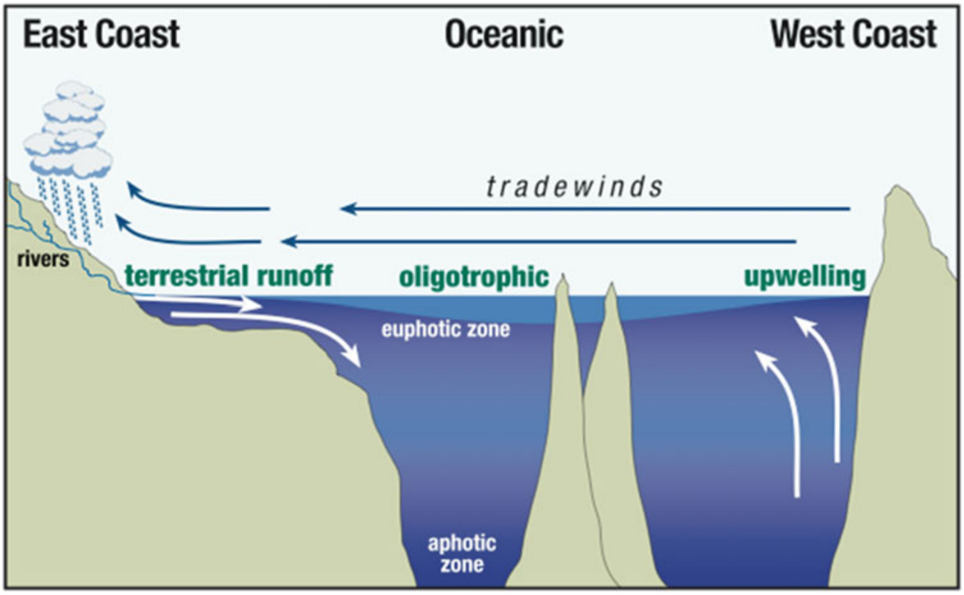

Fig. 9.2 The trade winds bring both upwelling of nutrients to the eastern tropical oceans and rains with terrestrial runoff of nutrients to the western tropical oceans. The oceanic regions tend to have lower concentrations in the surface waters than do continental regions

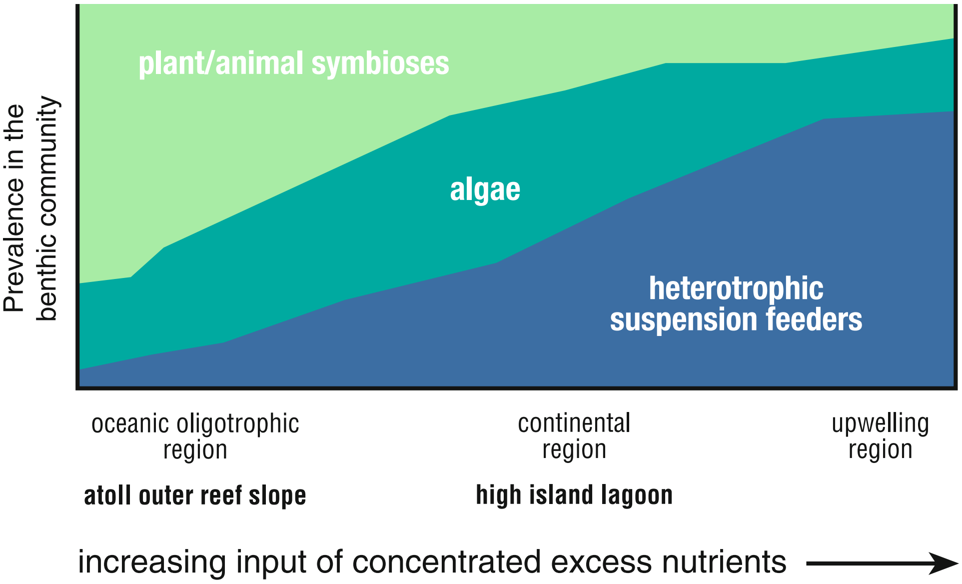

Fig. 9.3 Change in dominant trophic characteristics of coral-reef communities as a function of nutrient input both geographically and locally

input differently in the eastern and western ocean borders (Fig. 9.2). Nutrients generally come up from depths below the photic zone in the eastern borders of oceans (western margins of continents) and come down from land on the western sides of oceans (eastern coasts of continents). On the western coasts of continents, the trade winds push ocean currents away from the coast towards the west. The westward-moving waters are replaced in part by the nutrient-rich upwelling waters from deep below the photic zone. The waters below the photic zone are relatively rich in nutrients because without sunlight, photosynthesis does not happen and so the nutrients are not taken up by phytoplankton. When upwelling brings the water into the photic zone, the rich input of nutrients fertilizes the ocean surface and the primary productivity in shallow water is increased. Sites of upwelling do exist east of continents, for example, on the coasts of Somalia, Yemen, Indonesia, and Venezuela; but major sites of upwelling are prevalent on the western coasts of continents, and this determines major fisheries areas and affects important geographic differences in the nature of coral communities (Fig. 9.3).

A typical influence of nutrients on geographic scale can be witnessed in 1 day by a visitor to Panama. The Pacific and Atlantic coasts are only about 70 km apart at the Isthmus of Panama, yet the Pacific coast supports a large fisheries industry while the Atlantic coast of Panama supports only subsistence fishing and small-scale fishing enterprises. Vast schools of fishes and hundreds of sea birds can be seen on an outing to coral communities in the regions of upwelling along the Pacific coast, while a diverse assemblage of fishes typically in large schools, with each species swimming alone, in pairs, or in small schools, is the usual case on coral reefs in regions with less concentrated nutrient input.

There is also upwelling that occurs along the equator in the center of the oceans. Nutrient-rich waters are pushed by trade winds westward from upwelling areas on the west coasts of continents. As they are carried westward in the Equatorial Current, the Coriolis force moves surface water to the left (southward) in the southern hemisphere and to the right (northward) in the northern hemisphere. As surface waters diverge, they are replaced by cooler, nutrient-rich waters from below. This Equatorial Upwelling produces cooler water with greater rates of primary productivity along the equator in the center of the oceans, but there are few islands or atolls in these regions with upwelling.

By the time the waters in the photic zone reach the oceanic central Pacific, the nutrients have been taken up by phytoplankton and the oceanic waters are generally nutrient poor (Figs. 9.2 and 9.4). In these oligotrophic waters, a relatively high proportion of nutrients is bound to the biomass in the shallow waters that encompass coral-reef communities. On coral reefs of atolls in these central oceanographic regions, there is considerable recycling of nutrients in the coral-reef system and comparatively little input from outside sources (Sect. 1.1).

Trade winds blowing across the tropical ocean waters onto the eastern coasts of continents are laden with moisture (Fig. 9.2). Water has a higher latent heat capacity than does soil, and so the continental land masses heat more rapidly during the summer than do the oceans. The warmer air rises over the continents and the moist air is drawn off the tropical oceans. As these moisture laden monsoonal winds rise over the coastal hills, the moisture precipitates. Therefore, the major rivers that carry sediment into tropical coastal areas are generally on the eastern coasts of continents (Figs. 9.3 and 9.4).

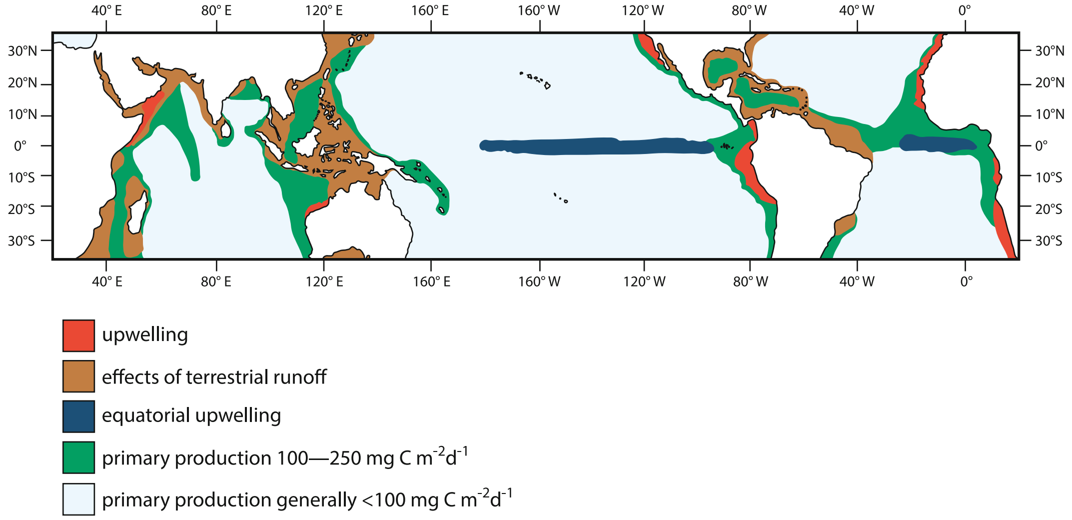

Fig. 9.4 The trade winds bring both upwelling of nutrients to the eastern tropical oceans and rains with terrestrial runoff of nutrients to the western tropical oceans. The oceanic regions tend to have lower concentrations of nutrients in the surface waters than do continental regions

The influence of coastal runoff on coral reefs has been widely studied and clearly have negative effects on reefs (see ISRS 2004; Fabricius 2005). These include documented declines in coral larval settlement and metamorphosis (Hodgson 1990; Babcock and Davies 1991; Gilmour 1999; Birrell et al. 2005; Fabricius et al. 2003; Kuffner et al. 2006).

On the eastern coasts of continents, coral reefs receive sediment and nutrients from higher ground by terrestrial runoff. About 82 % of all the sediment that is carried into the oceans of the world drains off the eastern coasts of landmasses into the western tropical seas (Fig. 9.5); only 2 % drains off the coasts in the eastern tropical seas (Milliman and Meade 1983). Half the sediment being deposited into the oceans of the world is coming off the high islands of the southwestern tropical seas (Milliman 1992), the center of coral-reef diversity. The smaller rivers running off the steeper slopes of the high islands in the southwestern Pacific have greater sediment yields (load per unit drainage basin area) than do larger rivers off the continents because the larger rivers such as the Amazon tend to deposit sediment in their own beds and deltas.

Examples of the abrupt and major effects of rivers on coastal coral reefs are given in Sect. 9.1. Rivers also influence biogeographic patterns. The Amazon River creates a large gap in coral distribution and separates the corals of the western tropical Atlantic into two biogeographic provinces. Likewise, major breaks in the distribution of corals in the Bay of Bengal and Andaman Sea (Indian Ocean) are formed by river outflow.

In contrast, although erosion is a natural process, human activities, especially agriculture and clearing of natural vegetation, has increased the loss of soil into the oceans by more than an order of magnitude. Rates of erosion can increase by as much as 100-fold (Doolette and Magrath 1990). The input of soil from rivers has been over 13.5 billion tons annually (Milliman and Meade 1983). Milliman et al. (1987) calculated that the sediment load of the Yellow River has increased by an order of magnitude because of farming practices in northern China. Approximately four times as much sediment, nitrogen, and phosphorus enter the marine waters off the coast of Queensland than before western agriculture began (Brodie 1995).

Nutrient input has been increasing to an even greater extent than has sedimentation. The rate of input of reactive nitrogen into the open ocean has more than doubled globally, especially in the North Pacific because of the human population growth and rapid industrial development. This doubling of reactive nitrogen is expected to increase primary production and possibly lead to a change in the North Pacific from nitrogen-limited to phosphorus-limited (Kim et al. 2014). Following deforestation in the watershed in the Amazon Basin, the volume of runoff has increased by 30 %, but the concentration of nitrogen doubled and the concentration of phosphate increased nearly eightfold (Hallock et al. 1993). The Mississippi River now carries ten times the concentrations of nitrates and phosphates that it did in the late 1960s (Hallock et al. 1993). The influence of nutrification extends farther downstream than sedimentation. This has been suggested as a primary cause of widespread coral-reef degradation far from concentrations of humans (Hallock et al. 1993).

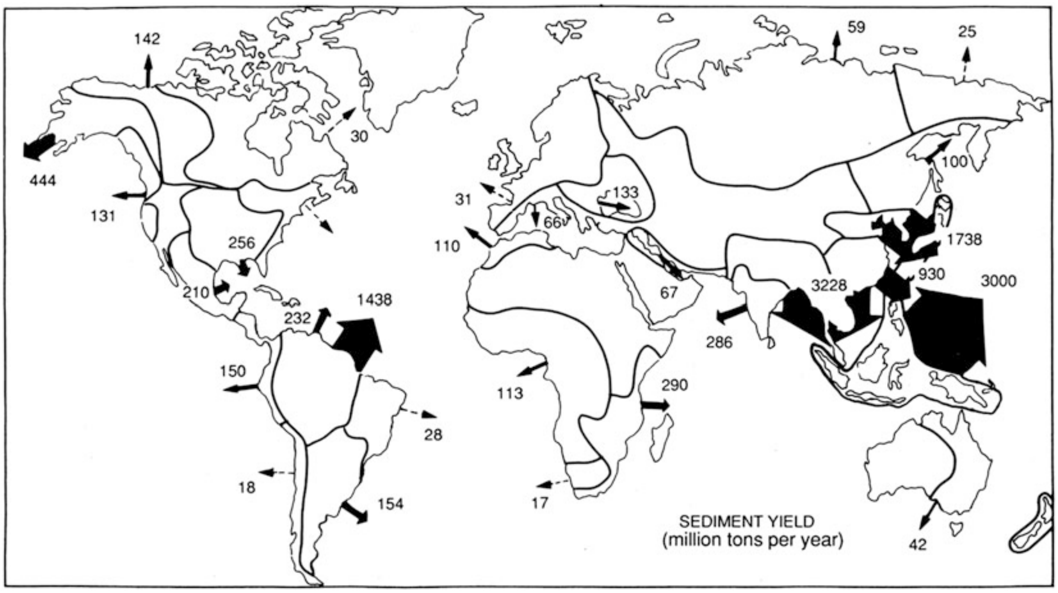

Fig. 9.5 Well over 80 % of the sediment that is deposited into the oceans from the continents is from the eastern rivers in the tropics (From Longhurst and Pauly 1987, modified from Milliman and Meade 1983)

Increased sedimentation and nutrient input into the coastal marine ecosystems may have been causing broad-scale changes in the biotic communities of coastal regions. Paralytic shellfish poisoning resulting from blooms of toxic dinoflagellates was unrecorded in the tropical western Pacific before 1972, but the number of deaths and hospital cases from dinoflagellate toxicity has been increasing rapidly in the continental high islands of the western Pacific and along the coasts of Southeast Asia (Maclean 1984) where so much of the world's sediment input into the world's oceans is occurring.

Geographic and climatic patterns are usually more dependable than are smaller-scale local weather trends, but conversely, when large-scale climatic patterns are disrupted, the effects can be more dramatic. While the Coriolis effect and upwelling in the east are relatively dependable, they can be disrupted by El Niño- Southern Oscillation (ENSO). ENSO can cause major changes in the marine ecosystems, mass mortalities throughout the food web, and long-term deterioration of the coral reefs, especially in the eastern Pacific where the ecosystem normally receives abundant nutrient input (Glynn 1990).

The Coriolis effect also forces typhoons or tropical cyclones to generally move from east to west because Earth spins eastward below the atmosphere in which cyclones are suspended (Fig. 9.1). Typhoons or hurricanes (the names for major cyclones in the Pacific and Atlantic, respectively) are created by rising warm air and rapid replacement by air in "feeder bands" moving in laterally. Since rising warm air creates and provides the energy for cyclones, tropical cyclones will possibly increase in intensity with global warming. Typhoons usually increase in intensity as they move westward. The increases will probably be greater in the western tropical oceans (e.g., Guam) than farther east (e.g., Samoa). This is an example of how warmer seawater might cause differences of some variables along geographic regions might become even greater than they are now.

The Coriolis effect determines the direction of major current patterns away from the equator in the western sides of tropical oceans and toward the equator on the eastern sides (Fig. 9.1d). Thus, coral-reef communities are more easily replenished with recruits from tropical waters after local extinctions in the western tropical oceans, especially at higher latitudes. This is a factor leading to greater species richness in coral-reef communities in the western sides of oceans. Coral-reef communities have a greater latitudinal range in the western sides of oceans because of the northward flow of tropical waters. Aggregations of individuals of species carried by currents to environments with ecological conditions beyond their limits of successful reproduction ("pseudopopulations") are also more frequent at high latitudes in western sides of oceans.

The greater longitudinal extent of the Pacific produces a more observable decrease in species and habitat diversity from west to east across the central Pacific, counter to the main currents. A lesser degree of trophic and population interconnections between coastal habitats in the Pacific than in the greater Caribbean may result partially from less reliable availability of noncoral habitats in Oceania (Birkeland and Amesbury 1988). The occasional ENSO changes direction of prevalent currents and periodically allows for species introductions and replenishment (Richmond 1990).

9.2.2 Latitudinal Differences

Throughout much of their range, coral reefs generally exhibit rates of metabolism and calcification independent of latitude (Smith and Kinsey 1976; Crossland 1988). However, when the latitudinal limits of reef growth are approached, a relatively steep decrease of reef growth with latitude becomes apparent. Gross carbonate production of individual corals and coral-reef accretion by corals decline in a linear fashion as a function of latitude in the Hawaiian Archipelago (Grigg 1982). The point at which the rate of reef accretion becomes less than the rates of reef subsidence and/or erosion, beyond which the reef begins to "drown," is termed the Darwin Point (Fig. 3.7). The Darwin Point is the threshold for oceanic atoll formation, and is potentially at higher latitudes on the western sides of tropical oceans than on the eastern sides.

As a rule of thumb, hermatypic corals are restricted to regions where the average seawater temperatures are 18–30 °C. Because of the Coriolis effect on major current patterns, warm waters and coral reefs extend further from the equator on the western sides of oceans. However, the temperature range tolerated by corals differs among geographic regions, with the lethal limits of particular species being higher where the mean seawater temperature is higher (Jokiel and Coles 1990).

Light penetrates the ocean to greater depths when and where the sun is directly overhead. The proportion of the year in which the Sun is directly overhead decreases with latitude, and the Sun is never directly overhead north of the Tropic of Cancer or south of the Tropic of Capricorn. Therefore, we might have predicted that the maximum depth of reef formation would decrease with latitude. However, this may not be the case (Veron 1995).

9.3 Geographic Differences in Trophic Characteristics of Dominant Species

In regions with rich nutrient input from external sources, small organisms can preempt resources from larger organisms. Whether planktonic or benthic, small plants take nutrients from the water column more rapidly, and grow and reproduce more rapidly, than do larger plants with more complex structural attributes (Odum et al. 1958; Geider et al. 1986). An experimental comparison of two macroalgae of the Ulvophyceae showed that *Ulva curvata* is able to respond to brief inputs of ammonium with more effective uptake and more rapid growth than the more structurally complex *Codium fragile* (Ramus and Venable 1987).

Phytoplankton in the water column can preempt light and reduce the compensation depth of benthic algae under conditions of high nutrient input (Twilley et al. 1985). If the compensation depth of benthic algae were at 100 m in water without phytoplankton, then at a density of only 2 g m^{-3} phytoplankton would raise the compensation depth of the benthic algae to 3.5 m, restricting benthic algae to only the upper 3.5 % of their potential range (Ryther 1963). The single-celled phytoplankters take up nutrients and reproduce rapidly, decreasing both the nutrients and light available to the benthic algae (Geider et al. 1986). In some areas with especially rich nutrient input, phytoplankton virtually exclude the entire benthic algal food web (Kamura and Choonhabandit 1986). Although at least 31 families of coral-reef fishes were present, there were no scarids, acanthurids, siganids or kyphosids (Menasveta et al. 1986). However, herbivorous damselfishes were able to maintain territories in shallow depths (3—4 m), presumably with some filamentous algae.

The same trends can be seen in coral-reef animals. The growth rates of small suspension-feeding animals, such as mussels and barnacles, are strongly associated with the amount of food in the water column (Page and Hubbard 1987). The growth rates of large, colonial, plant-animal symbionts such as hermatypic corals do not respond as rapidly or to as great a degree to concentrated nutrient input (Kinsey and Davies 1979). The growth of small corals has been found to be much slower than previously assumed (Wallace 1985; van Moorsel 1988).

There may be some physiological constraints and rate limits associated with the physiological complexities of plant-animal symbioses (Chap. 5). When primary production of phytoplankton increases, zooplankters can increase rates of consumption and the secondary production of the zooplankton community can increase several-fold (12–16 mg C m^{-2} day^{-1} in tropical oceanic waters to about 75 mg C m^{-2} day^{-1} in upwelling regions (Barnes and Hughes 1988). In contrast, zooxanthellae and corals are in a complex physiological balance (Chap. 5). Increased nutrient input can sometimes cause a rapid increase in zooxanthellae. But this overcrowding can disrupt the physiological conditions of the coral, which may react by expelling the excess zooxanthellae. This constrains a response to nutrient fertilization with more rapid growth.

Community structure on shallow-water tropical hard substrata is determined to a large extent during recruitment. Competition for space among adult colonies is easier to see, but the events during recruitment are of greater effect on the eventual nature of the benthic community. In nutrient-rich upwelling regions in the tropics, the rapid takeover of space and accumulation of biomass by small, fast-growing suspension feeders such as barnacles, bivalves, sponges, ascidians, and bryozoans often preempt space from coral recruits (Birkeland 1977). Although it is not unusual to find adult corals surviving and growing well in regions of upwelling, in nutrient-rich lagoons of high islands, near the mouths of rivers, and near sewer outfalls, these examples are most often individual colonies that had reached a refuge in size. These exceptional cases suggest that the physical environment itself is favorable for growth and survival of corals, but excessive concentrations of nutrients have an indirect effect of differentially favoring the algae and suspension-feeding animals over coral recruits in the competition for space.

Greater rates of nutrient input intensify competition for space by two mechanisms: faster growth of algae and suspension feeders and a greater density of recruitment (Barnes 1956; Sutcliffe 1972, 1973; Birkeland 1977, 1982). In contrast, space is available for a longer period of time in the oligotrophic waters of the western Pacific, and the supply of larvae in the water column, rather than availability of space, is a major determinant of the size of recruitment (Birkeland et al. 1982). Plant- animal symbioses, in contrast, are better adapted to low-nutrient environments (Muscatine and Porter 1977). Coral communities are able to grow to a large size and live for years in clear, nutrient-poor oceanic habitats where active suspension feeders are unable to maintain positive energy budgets (Page and Hubbard 1987). The plant-animal symbioses inherit space in low-nutrient environments by default, not by outcompeting the suspension feeders. Likewise, the benthic algae do not outcompete the phytoplankton, but exist to the extent allowed by the factors that limit phytoplankton standing stock.

Large, massive heterotrophic sponges are typical indicators of “continental” areas such as the greater Caribbean and southeast Asia, including Indonesia, Sulawesi and the Philippines (Figs. 9.4, 9.5, and 9.6). There is no true “oceanic” region in the greater Caribbean because it is tightly enclosed by North and South America. The nutrients from the Amazon and Orinoco affect the Lesser Antilles and occasionally get as far as Mona Channel west of Puerto Rico

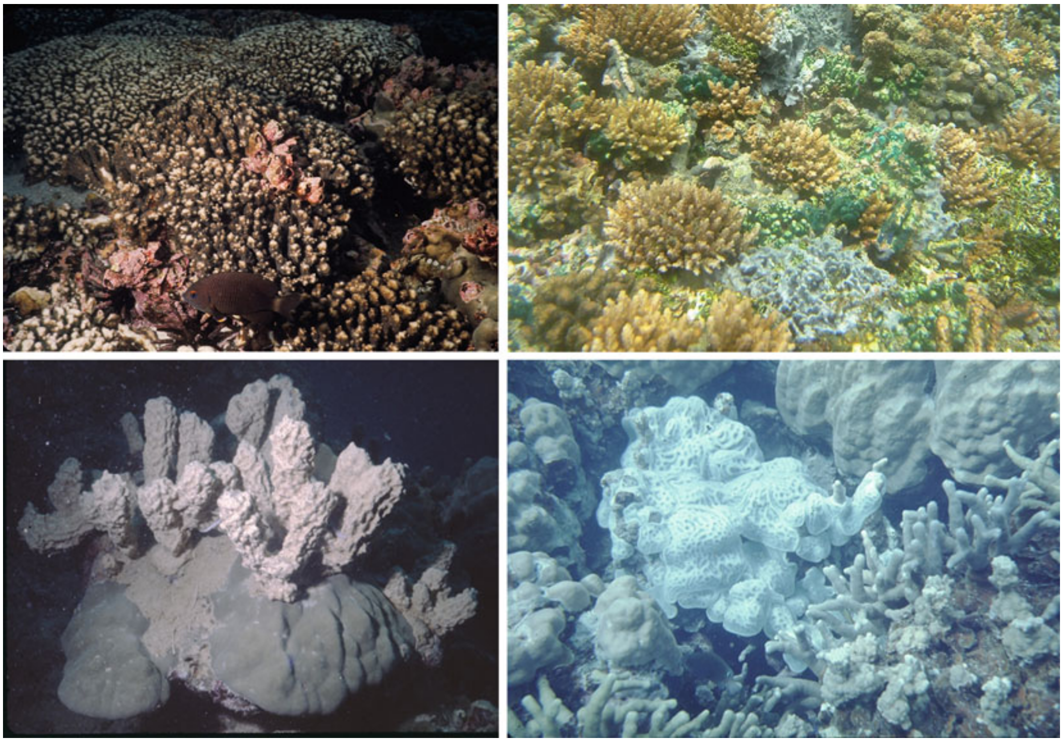

Fig. 9.6 The relative predominance of heterotrophic invertebrates overgrowing scleractinians in nutrient-rich waters (*upper left* – barnacles, Galápagos; *lower left* – heterotrophic sponge, Pohnpei lagoon) and relative predominance of colonial invertebrates with symbiotic photosynthesizers overgrowing scleractinians in oligotrophic waters (*upper right* – the sponges *Lamellodysidea herbacea* and ascidians *Diplosoma similis*, American Samoa; *lower right* – the ascidian *Lissoclinum patella*, Palau)

(Bonilla et al. 1993; Hallock et al. 1993; Chuanmin et al. 2004). The Atchafalaya branch of the Mississippi River affects Flower Garden Bank corals in the northwestern Gulf of Mexico (Dodge and Lang 1983). The Greater Antilles consist of closely-space large ancient islands that fill out the center of the greater Caribbean with "continental" effects, as indicated by the large heterotrophic sponges (Wilkinson 1987; Wilkinson and Cheshire 1990; Wulff 2012) and rapid algal growth (Roff and Mumby 2012). In the southwestern Pacific, large sponges are likely to also be common in the areas around the large continental islands of Indonesia, Sulawesi, and Philippines because of the closely-spaced large ancient islands producing "continental" effects (Figs. 9.4 and 9.5).

Oceanic coral reefs in oligotrophic water are dominated by algal-animal symbionts (Figs. 9.3 and 9.6; Wilkinson 1983). As we move along a gradient of increasing nutrient input, for example, from an atoll to a high island or approaching a sewage outfall, benthic algae and heterotrophs become more prevalent. In regions of even stronger nutrient input, the phytoplankton-based food web dominates and the substratum becomes occupied predominantly by heterotrophic suspension feeders (Smith et al. 1981; Rose and Risk 1985; Kamura and Choonhabandit 1986; Tsuchiya et al. 1986). Even in generally oligotrophic oceanic regions, lagoons can be eutrophic and support large sponges (Fig. 9.6).

The potential biomass of algae on central Pacific coral reefs on islands such as Guam and Maui (Fig. 9.7) is substantial. On Oahu, volunteers have been removing tons of algae from 27 acres of seashore (e.g., 48, 42, 62, 66 tons removed in 2009, 2011–2013, respectively, from Maunalua Bay). Ninety-one tons of algae were also removed from a Marine Life Conservation District shore in the first 3 years of the removal program in Waikiki. In 2005, a large sucker on a barge was developed to remove over a thousand pounds of algae per hour from the reef and has already removed over a million pounds of algae from Kaneohe Bay. Although algal growth rates are generally lower in the Pacific than in the greater Caribbean, and although macroalgal cover can remain relatively low in the Pacific where herbivore biomass has been reduced (Roff and Mumby 2012), the algal biomass can increase by tons per hectare annually on the older massive high islands in the central Pacific and so we should never be complacent.

In striking contrast, when Danielle Jayewardene (2009) set up fish exclusion cages on the leeward coast of Hawaii

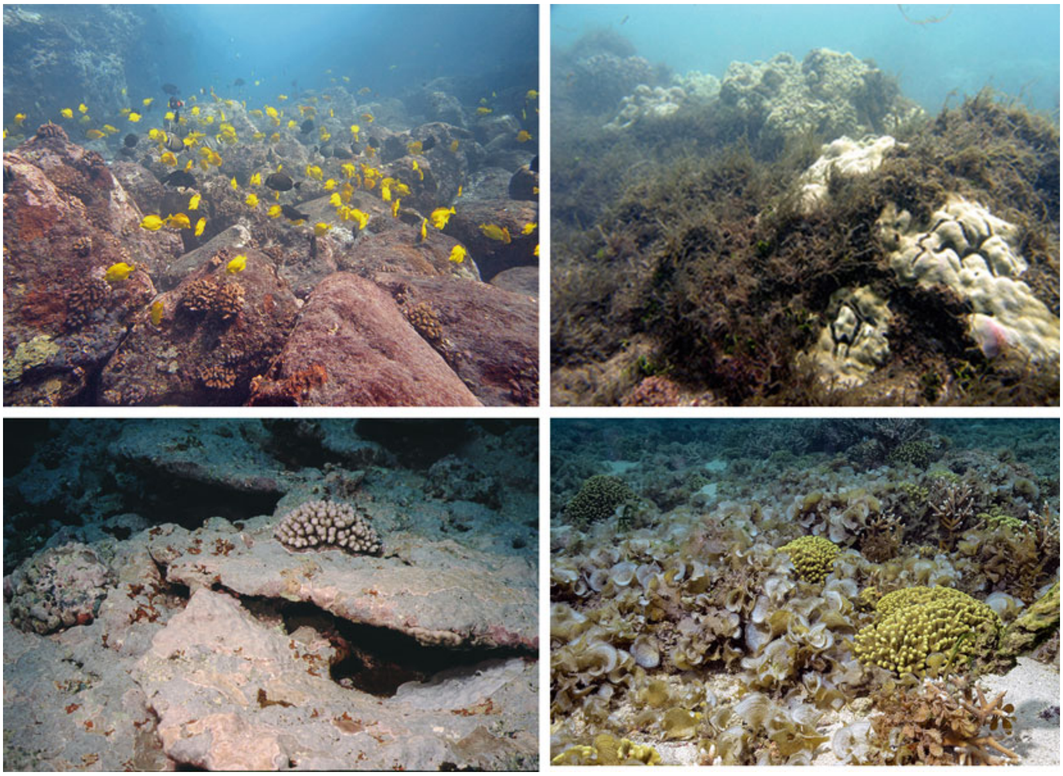

Fig. 9.7 *Upper left* – kona coast of Hawaii Island (Photo courtesy of Bill Walsh). *Upper right* – west coast of Maui Island, about 100 km from Hawaii Island (Photo courtesy of Rssell T. Sparks, DLNR). *Lower left* – American Samoa, 14°S, predominantly crustose coralline algae. *Lower right* – Guam 13.5°N (Photo courtesy of David Burdick)

Island, "Algal biomass within the cages did not increase visibly after the first few months of herbivore exclusion, and fleshy macroalgae were rare." Also along the leeward coast of Hawaii Island, Smith et al. 2001 set up a factorial experiment to examine the relative importance of herbivory and fertilization. The results showed both herbivory and nutrients having significant effects, but even when nutrients were added and herbivory was not allowed, the production did not appear to be on the scale of many tons. The tons of algae on Oahu were introduced species, selected for their capacity for rapid growth, but nevertheless, the nutrients were available on Oahu for repeated rapid and massive algal production. American Samoan reefs are often dominated by crustose coralline algae (Fig. 9.7), although areas of filamentous algae can be maintained within the territories of *Acanthurus lineatus* and *Stegastes* spp. In 1985, the reefs in Fagatele Bay National Marine Sanctuary averaged 57 % cover by crustose coralline algae (Birkeland et al. 1987).

The qualitative nature (life-history characteristics, physiology, morphology) of the dominant biota can influence ecosystem-level processes. The "turn-on/turn-off" point of reefs has been defined as the point at which the dominant processes change from accretion to bioerosion or back (Buddemeier and Hopley 1988). Reefs are generally growing (accretion is dominant) when scleractinian corals and crustose coralline algae are prevalent. Bioerosion becomes more prevalent in areas of high nutrient input (Chap. 4; Highsmith 1980), lower pH (Chap. 4; Wisshak et al. 2012) or up to tenfold greater in areas of both increased nutrients and lower pH (DeCarlo et al. 2015) in which boring bivalves and/or sponges become abundant within the reef framework and sponges and algae become more prevalent than corals on the exposed surfaces.

Hatcher (1997) described how energy and materials from filamentous algae tend to enter the herbivore food web, and energy and materials from more rigidly structured macroalgae tend to enter the detrital food web. Where much of the substrata are covered by living coral and the algae are relatively few, the herbivorous fishes tend to keep algae in the early successional and productive stage in which filamentous algae are most prevalent (Birkeland et al. 1985). After a disturbance when algae take over a greater portion of the substrata and herbivorous fishes a given a choice of algae, their selective feeding tends to advance succession and lead to an increase in less palatable macroalgae. Small plants of relatively simple morphology generally have higher net productivity per unit biomass and a potential for more rapid growth than do larger, more complex algae (Littler and Littler 1980). If smaller organisms of relatively simple morphology have a higher net productivity per unit biomass (Geider et al. 1986), then in view of the prevalence of filamentous algae and small, rapidly growing suspension feeders (mussels, oysters, and barnacles) such as in regions of upwelling, we predict that the net yield from the system may be greater in upwelling regions than in oligotrophic regions where scleractinian corals and crustose coralline algae are relatively prevalent. If the geographic pattern of nutrient input affects the life-history characteristics of the dominant organisms, then these matters should be taken into account when developing resource management program (Chap. 12).

9.4 Regional Differences in Ecological Processes

9.4.1 Grazing and Predation Pressure

Areas with nutrient input from upwelling produce large stocks of fishes (Ryther 1969; Gulland 1976) and the age-class strengths of fishes and invertebrates are often correlated with annual river-discharge strength (Aleem 1972; Sutcliffe 1972, 1973; Wolff et al. 1987), presumably because of increased survival of planktotrophic larvae with a concentrated supply of food. Dense populations of predators and grazers that result from strong recruitment exert intense predation and grazing pressure. The grazing pressure on benthic communities of the Pacific coast of Panama where upwelling occurs is greater than on the Caribbean coast (Glynn 1972; Earle 1972; Vermeij 1978) and this has a major qualitative influence on the structure of the benthic communities and ecosystem processes.

Standardized experimental comparisons of the intensity of grazing on sponges by fishes at three geographically separated locations in both the Caribbean and in the eastern tropical Pacific showed the grazing pressure in the eastern Pacific to average 25 times greater than the grazing pressure in the Caribbean (Birkeland 1987). The eastern Pacific reefs were more densely populated with sponge-grazing angelfishes (*Holacanthus* and *Pomacanthus*) than were Caribbean reefs (Fig. 9.8), and the sponges were smaller and more cryptic in the eastern Pacific even though they grew rapidly when protected from grazing (Birkeland 1987; Fig. 9.9).

Two behavioral changes of predators can occur as population density increases, and these amplify the intensity of grazing and predation pressure. First, the *Holacanthus passer* in the eastern Pacific tend to forage in schools, occasionally as large as four or five dozen, while members of this genus in the Caribbean tend to forage alone or in pairs. This compounds the effects of large populations because each fish

Fig. 9.8 Characteristic views of reef fishes on two sides of the Isthmus of Panamá. On oligotrophic Caribbean reefs, *Holacanthus ciliaris* and many other species are often seen singly or in pairs, whereas on eastern Pacific reefs affected by upwelling of nutrients, *Holacanthus passer* and many other species are often seen in schools of dozens

Fig. 9.9 Intensity of grazing on sponges manually exposed on a reef on Isla Taboguilla, Pacific Panamá, over 3 days. *Upper left* photograph is of a rock which has just been turned over to expose sponges naturally protected from grazing on the underside of the rock. *Upper right* photograph is of the same after 72-h of grazing, mainly by *Pomacanthus zonipectus*. *Lower left* photograph is of a rock which was overgrown on its upper surface by a sponge while in a fish-exclusion cage, from which the rock was just removed. *Lower right* photograph shows the marks of 72-h of grazing at Isla Taboguilla (Note that the sponges on the naturally exposed substrata are very tiny in comparison to sponges inaccessible to fishes on the undersides of rocks or in fish-exclusion cages)

forages more efficiently when it is part of a school than when it is alone (Pitcher et al. 1982; Pitcher and Magurran 1983; Pitcher 1986; Wolf 1987). Concentrated grazing by an aggregation of fishes could also have more intensive effects than the grazing by the same number of individual fishes that are more randomly or evenly distributed.

Second, when population densities of predators and grazers become large and prey become scarce, the consumers must broaden their diet in order to get enough to eat (Ivlev 1961; Werner and Hall 1974). Intense grazing by generalists can set back succession, increasing the proportion of early successional biota with a greater ratio of net to gross productivity (Birkeland et al. 1985). Refuge in patchy distribution and irregular abundance is not as effective for small prey against a variety of common generalist grazers or predators that forage in schools (Pitcher et al. 1982; Wolf 1987), because generalists can forage widely, being maintained on alternative foods between patches of the prey in question. When foraging by generalists is intense, turnover in occupation of substratum increases and many small individuals of a variety of prey species may be grazed indiscriminately.

Chemical and morphological defenses are more characteristic of organisms in nutrient-poor environments (Coley et al. 1985). Morphological and chemical defenses may be ineffective if the prey individual is too small to be recognized by the grazer or predator. If grazing is intense enough, the prey may be bitten off incidentally before they reach a recognizable size. This may apply to coral recruits as well (Sammarco 1980, 1985). Under these circumstances, chemical and morphological defenses may be less effective for survival to reproduction than is rapid growth and early reproduction. As grazing intensity increases along a gradient of increasing concentration of nutrients, the smaller, faster-growing species of benthic organisms are favored both in competition for space and by reproducing before being eaten.

Both the tendency of the predators toward more generalized diets and the responses of the prey toward investing in rapid growth and reproduction rather than defense (Coley et al. 1985)—conditions brought about by concentrated pulses of excess nutrient input—tend to increase net production, increase rates of population turnover, and shorten the food web.

9.4.2 Food Webs

The number of substantial trophic levels in food webs between the primary producers and humans decreases as nutrient input increases (Ryther 1969). Nutrient input tends to shorten food webs by several distinct mechanisms (Hallock 1987). Concentrations of rapidly growing and rapidly reproducing large-celled or chain-forming diatoms are supported in regions with nutrient input from upwelling and terrestrial runoff. These dense concentrations of large-celled phytoplankters support dense concentrations of relatively large herbivores such as anchovy and krill, which are then directly fed upon by tuna, sea birds, and marine mammals. In contrast, in nutrient-poor waters such as the tropical gyres, tiny coccolithophorids and other nanoplankton and picoplankton are the predominant primary producers. The primary consumers of the tiny phytoplankters are usually small, leading to added levels and interconnections in the food web before harvest by the largest animals in the sea.

Although coral reefs exist in tropical regions of upwelling, they are more prevalent in environments with low concentrations of nutrient input. Plant-animal symbioses are favored in competition for space in regions of dilute nutrient input (Muscatine and Porter 1977; Lewin et al. 1983; Wilkinson. 1986; Birkeland 1987). Large colonial animals such as corals add topographic complexity to the habitat. The development of topographically complex biological substrata facilitates the accommodation of more species in the habitat. The diversity of species on coral reefs and the advantages of recycling of nutrients both tend to lead to more complex food webs. On coral reefs, even fish feces have been observed to be fed upon (recycled) by corals and fishes. In fact, Robertson (1982) deduced that some fish fecal material may be recycled through five fishes before it reaches the coral or other benthic substrata.

Hallock (1987) further elaborated on several ways in which a low level of nutrient input leads to habitat diversity and species diversity, and therefore to a more complex food web. Habitat diversity is increased in low-nutrient environments because gradients extend across wider areas and are more stable. Oligotrophic waters are relatively clear and so the gradient in light attenuation is extended over a longer depth gradient. Low-nutrient waters are generally more stable in depth stratification because vertical mixing is characteristic of regions of nutrient input by upwelling and internal waves. A stable pattern of environmental heterogeneity could increase the potential for specialization and species diversity. Regions with strong pulses of nutrient input are less stable, not only because of the fluctuations in magnitude of nutrient input, but because of the physical factors that accompany upwelling (water temperature change) and river discharge (salinity changes, turbidity, and sedimentation).

In regions of short food webs, the ratio of fisheries yield to gross primary production is higher than in complex communities with more trophic levels, such as coral reefs, because energy is lost at each step as matter is passed up the food web. Therefore, in regions of nutrient input such as upwelling areas, the fisheries yield per unit gross productivity would be substantially higher than in oligotrophic areas most favorable to coral reefs (Fig. 1.1). Ryther (1969) assigns one or two steps between phytoplankton and humans in upwelling systems, acknowledging that nutrient-rich areas of the world ocean have the fewest trophic levels in their food webs. Grigg et al. (1984) assigned six trophic levels to coral-reef systems. The implications of these levels for management will be developed (Sects. 1.1 and 12.6.2).

9.4.3 Diversity and Ecosystem Function

The geographic differences among coral reefs that first come to mind concern species richness. The diversity of species, genera, and families of corals, fishes, and most other taxonomic groups of coral-reef animals are very much greater in the western Pacific compared to the Atlantic or eastern tropical Pacific (Paulay 1997), and most of the causal explanations for these differences involve multiple factors of geographic patterns and processes such as isolation and current direction (Bowen et al. 2013). But does the diversity of corals affect the growth of the reef? It is certainly important that species are present to handle the complete array of essential roles, such as herbivory and provision of topographic complexity of reef structure; otherwise coral-reef communities are not resilient to disturbance (Bellwood et al. 2004; Roff and Mumby 2012). But do reefs in Japan grow substantially faster than those in French Polynesia? About 400 species of hermatypic corals occur in Japanese waters (Veron 1993), while a total of only about 155 species occur in French Polynesia (Society Islands, Tuamotus, Gamblers, Australs, Marquesas; see Chevalier 1982).

Notwithstanding the spectacular differences among geographic regions in size, age, and species richness (Paulay 1997), these characteristics do not appear to affect the overall growth or physiology of coral reefs (Kinsey 1983; Crossland 1988). The reefs and atolls of French Polynesia often appear to be accreting or growing at the same rate or better than those in Japanese waters. Likewise, Caribbean and other western Atlantic reefs have only about 65 species of hermatypic corals, about one-sixth the species richness of

Japanese waters, yet the reefs in the Atlantic seem to be accreting at rates comparable to those in the Pacific (Kinsey 1983), at least prior to the stress of global changes in the more recent three decades. The characteristics of the physical environment overshadow the influence of differences in biodiversity on the functioning of coral reefs, as long as representatives of each of the performers of key ecological roles are present. Primary productivity and fisheries yield are most strongly influenced by local physical environmental factors and human activities, not obviously greater or lesser on Atlantic reefs than on more diverse reefs in the western Pacific.

Despite the concept of convergent evolution, the richer species pool in the western Pacific provides kinds of predators with no counterparts in the western Atlantic; the crown-of-thorns seastar, *Hymenocera* (shrimp that prey on large seastars), giant clams, anemone fishes, schooling catfishes, and sea snakes are examples. Some of the individual species such as the crown-of-thorns starfish *Acanthaster planci* (Indo-West Pacific), *Diadema antillarum* (western Atlantic), and *Eucidaris thouarsii* (Galapagos Islands) cause large-scale phenomena that are unique to the particular geographic region (Carpenter 1997). Mutualistic associations are also more diverse in the western Pacific, with some groups of associations, such as giant clam-zooxanthellae and anemone-anemonefishes, being characteristic of the Indo-West Pacific (Vermeij 1978), but not the Atlantic or eastern tropical Pacific.

Some entire classes, orders, and families of organisms are absent from coral reefs in the central Pacific, but present in the western Pacific. There are at least 91 species of crinoids in the shallow waters of Indonesia, at least 55 in the Philippines, 21 in Palau, 6 in Guam and the Marshall Islands, and none at all on coral reefs in Hawaii, French Polynesia, the Line Islands, or the eastern tropical Pacific (Birkeland 1989). Although individual species of echinoderms have overwhelming influences on the functioning of the coral-reef ecosystems in their respective regions, some other species in their classes do not, and the overall species diversity of their classes does not seem to have any ecological effects (Birkeland 1989).

Nevertheless, coral-reef communities appear susceptible to diseases when large monocultures exist. Diseases of commercial sponges have spread widely in the tropical western Atlantic about six times since the mid-nineteenth century. A disease killed about a million mother-of-pearl-producing oysters in the Gambier and Tuamotu archipelagoes in the late 1980s (Sect. 1.3). A massive mortality *of Diadema antillarum* occurred in the tropical western Atlantic in the early 1980s. The density of *D. antillarum* prior to the mortality may have been unnaturally high as a result of fishing pressure on predators of urchins (Hay 1984; Hughes 1994). Evenness in species abundance is an aspect of diversity. Regardless of species richness, the thin dispersal of species may facilitate stability of the system by reducing the spread of communicable disease and making the overexploitation of certain species uneconomical.

9.5 Management Considerations

The tropical western Atlantic is only about a tenth the area of the tropical western Pacific. The interconnectedness of the entire tropical western Atlantic, as evidenced by the spread of diseases of urchins and sponges throughout the region within a year on each occasion, and by the relatively uniform faunal distribution compared to the tropical Pacific, indicates that management of coral-reef resources requires international cooperation. Sea turtles from nests in one country may never return because they have been harvested by hunters in other countries. As exemplified by the effects of the Aswan Dam on the fisheries of the eastern Mediterranean, a project undertaken hundreds of kilometers inland in one country can have major effects on the marine fishery resources of several other countries (Aleem 1972). Unfortunately, there are presently no international legal mechanisms analogous to domestic court cases that can be applied to prevent international downstream damages. Each nation is an independent legal unit in an ecological continuum.

The coral reefs of the world cover about one-sixth of the world's coastlines, have greater gross productivity, and have a far greater standing stock of fishes than the combined stock of all the regions of upwelling. Yet upwelling favors abundant recruitment that potentially supports sustainable industrial fisheries, while most commercial export fisheries on coral reefs have been comparatively vulnerable to overexploitation. Because of the spectacular standing stock of coral-reef fish biomass, government agencies often consider it their mandate to develop export fishing industries to help improve the economies and standards of living of the indigenous people. Although well intentioned, these government agencies most often bring principles of fisheries science from temperate regions to coral reefs, and this often undermines more effective and appropriate management systems already in existence, having been developed over centuries by the indigenous people (Sect. 12.6.3).

Why are principles of fisheries science from the temperate regions often inappropriate for coral-reef fisheries? The large numbers of species and topographic complexity of coral reefs make wholesale harvest and processing relatively uneconomical. Although the biodiversity, the large number of steps in the food web, and the life-history characteristics of species adapted to low-nutrient environments all contribute to the maintenance of high-standing stocks of many species per unit of gross production, a relatively small portion of this gross production is transformed into secondary production that is meaningful for human consumption (Sects. 1.1 and 12.6.2). Furthermore, the life-history traits of target species of coral reefs (residential postlarval stages, slow growth, long life, dependence on multiple reproduction) make coral-reef animals particularly vulnerable to overexploitation (Sect. 12.5). In Chap. 12, a paradigm for resource management is presented for coral reefs that takes into account the *unique* aspects of coral-reef ecosystems.

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Reef Fishes, Seaweeds, and Corals

10

A Complex Triangle

Mark A. Hixon

Abstract

The coral-seaweed-herbivore triangle is an accepted generalization embedded within a highly complex web of biotic interactions and abiotic conditions that bring exceptions. The pattern is confirmed by observations that herbivorous fishes and urchins can have very strong effects on the standing crop of reef macroalgae, thereby opening space for corals to thrive. However, other factors, such as the abundance and distribution of territorial damselfishes, shelter for schooling herbivores, water motion, and nutrient flux, as well as multiple stressors on corals, can modify this basic pattern, sometimes strongly. High levels of herbivory lead to dominance by low-lying algae, including crustose corallines that may foster coral settlement. The intensity of herbivory by schooling fishes often varies unimodally with depth: low in very shallow water due to wave stress and other factors limiting accessibility by fishes, high at moderate depths, and low in deeper water where coral growth that provides shelter for fishes declines. Dense stands of macroalgae tend to thrive where herbivores are rare due to lack of habitat complexity that provides refuges from predation. Herbivorous damselfishes can act as natural cages by inhibiting schooling grazers and maintaining a high diversity of mid-successional algae within their territories via moderate grazing (intermediate-predation effect). These algal mats not only inhibit coral growth, but also serve as localized refugia for small invertebrates and newly settled fishes. Nutrients also play a pivotal role in structuring benthic algal productivity, standing crops, and species assemblages. Besides directly consuming corals or algae, reef fishes can also affect invertebrate corallivores and herbivores, causing subsequent indirect effects on reef benthos. Examples include predation on the corallivorous crown-of-thorns seastar and herbivorous sea urchins, the latter causing halos around patch reefs where urchins remain near cover. From a management perspective, conserving herbivores is clearly important for keeping reef algae in check. Maintaining both the abundance and species diversity of herbivores of a variety of sizes, especially via marine reserves, is likely the best means of ensuring that macroalgae do not displace corals. Such rules of thumb are likely essential for fostering the ecological resilience of coral reefs, especially in the context of a warming and acidifying ocean.

Keywords

Herbivore • Corallivore • Territorial damselfish • Phase shift • Trophic cascade

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10.1 Introduction

10.1.1 Fishes and Coral Reefs

Besides the corals themselves, fishes are perhaps the most conspicuous and beautiful inhabitants of coral reefs. Their diversity is amazing. It has been estimated that over 5,000 species of fish inhabit coral reefs worldwide (Cowman and Bellwood 2013), and locally, hundreds of species can coexist on the same reef. For example, Smith and Tyler (1972) found 75 species occupying a 3-m diameter patch reef in the Caribbean, which is not a particularly speciose region compared to the Indo-Pacific (Paulay 1997).

The variety of sizes and shapes of reef fishes is as remarkable as their species diversity. The smallest vertebrate is a goby less than 10 mm long that inhabits Indian Ocean reefs (Winterbottom and Emery 1981), whereas at the other extreme, reef sharks, groupers, barracudas, and even wrasses and parrotfishes can reach startling sizes measured in meters. Fishes exploit virtually every conceivable microhabitat and food source on reefs, from incoming oceanic plankton, to a wide variety of benthic organisms, to other fishes (see reviews in Sale 1991, 2002). Moreover, reef fishes often occur in high standing stocks, with 8 mT/ha being near the likely present maximum, observed on uninhabited Jarvis Atoll in the Pacific (Sandin et al. 2008). Not surprisingly, reef fishes are an important food source for many tropical nations (reviews by Russ 1991; Polunin and Roberts 1996).

It seems almost a foregone conclusion, then, to assert that fishes have strong effects on the dominant benthos of reefs: corals and macroalgae. As reviewed below, herbivorous fishes normally do substantially affect the distribution and abundance of algae on reefs that are not overfished. Although relatively few major direct effects of corallivorous fishes on corals have been found, newly reported cases of corallivory are increasing, and the indirect effects of herbivorous fishes on corals can be substantial and perhaps essential for the ecological resilience of reefs. Additionally, there is evidence that various fishes affect the distribution and abundance of invertebrate herbivores and corallivores, further affecting reef algae and corals indirectly.

10.1.2 Coral-Seaweed-Herbivore Triangle

A popular yet somewhat controversial hypothesis is that herbivorous fishes (and some macroinvertebrates, especially sea urchins) facilitate dominance by corals on reefs by preventing macroalgae (or equivalently, “seaweeds”, with apologies to phycologists) from outcompeting or otherwise hindering corals (e.g., Hughes 1989, 1994; Carpenter 1990; Done 1992; Knowlton 1992; Tanner 1995; McClanahan et al. 1996; Lirman 2001; Burkepile and Hay 2008, 2010; Barott et al. 2012). Indeed, there is some evidence that the evolution of modern herbivorous reef fishes may have been a prerequisite for dominance by reef-building corals. Bellwood and Wainwright (2002: 30) conclude from the fossil record that “the inferred scenario is one of increased herbivory, both in intensity and excavation depth, with a concomitant decrease in the abundance of macrophytes. This results in a system dominated by close-cropped turfs, where decreased competition between algae and corals permits coralline algae and corals to proliferate.” Thus, herbivores, seaweeds, and corals can be viewed as an important interaction web on healthy reefs, whereby predators (herbivores) control the dominant competitors for space (macroalgae), allowing subordinate competitors (reef-building corals) to thrive (Fig. 10.1a).

At the risk of proliferating ecological jargon, let us call this concept the **coral-seaweed-herbivore triangle**. Overfishing of herbivorous fishes combined with the loss of herbivorous macroinvertebrates can degrade this triangle, facilitating the replacement of corals by macroalgae as the dominant benthos (Fig. 10.1b). This change is often characterized as a “**phase shift**” that contributes to the demise of coral reefs (reviews by McCook 1999; McManus

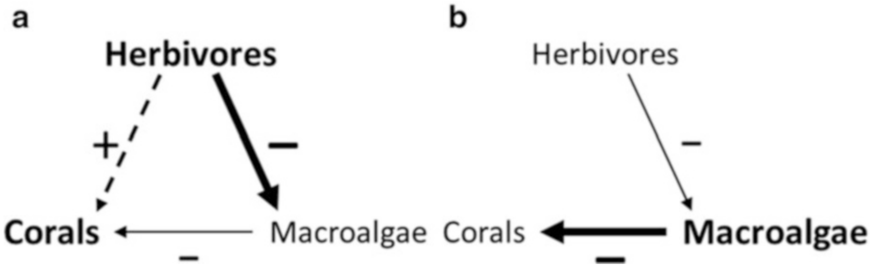

Fig. 10.1 The coral-seaweed-herbivore triangle as a simple interaction web, showing positive (+) and negative (−) direct effects (*solid arrows*) and indirect effects (*dashed arrows*). *Arrow thickness* depicts the relative strength of interactions, and font size represents relative biomass between scenarios. (**a**) The triangle on a reef that is relatively healthy from a human perspective: many herbivores indirectly cause high live coral cover. (**b**) The triangle on a reef that is relatively degraded from a human perspective: macroalgae overgrow corals in the absence of substantial herbivory

et al. 2000; Nyström et al. 2000, 2008, 2012; McManus and Polsenberg 2004; Pandolfi et al. 2005; Ledlie et al. 2007; Mumby et al. 2007b, 2013; Mumby and Steneck 2008; Bruno et al. 2009; Cheal et al. 2010; Hughes et al. 2010; Roff and Mumby 2012; Graham et al. 2013). Such phase shifts may represent "alternative stable states" in that a positive feedback loop can develop following the loss of herbivores in which more algae and less coral means less shelter for fishes and macroinvertebrates, which inhibits further recruitment of herbivores, which means continuing low herbivory, high algal growth, and less coral (review by Petraitis 2013). Of course, degradation of the triangle is only one of a multitude of threats to coral reefs, as detailed elsewhere in this volume.

There is some controversy regarding the generality of the coral-seaweed-herbivore triangle. First, it has been debated whether macroalgal standing crops on reefs are controlled more from the top-down by herbivory or more from the bottom-up by nutrient flux (Lapointe 1997, 1999; Hughes et al. 1999; McCook 1999; Miller et al. 1999; Aronson and Precht 2000; Belliveau and Paul 2002; Jompa and McCook 2002; McClanahan et al. 2002; Diaz-Pulido and McCook 2003; Lapointe et al. 2004; Sotka and Hay 2009), although meta-analyses have indicated that herbivores are typically more important than nutrients (Burkepile and Hay 2006). Nonetheless, there are reef systems where both top-down and bottom-up factors are simultaneously important (e.g., Smith et al. 2001, 2010; Stimson et al. 2001; Thacker et al. 2001), a pattern that is also evident in meta-analyses (Gruner et al. 2008).

Second, the extent to which macroalgae outcompete or otherwise inhibit corals is also somewhat controversial (Miller 1998; McCook 1999; McCook et al. 2001; Williams et al. 2001; Birrell et al. 2008), with lab and field experiments both demonstrating such effects (Hughes 1989; Tanner 1995; Lirman 2001; Birrell et al. 2005, 2008; Kuffner et al. 2006; Box and Mumby 2007; Arnold et al. 2010) and failing to do so (Jompa and McCook 1998; McCook 2001). Dominance in competitive interactions between turf algae and corals varies with human presence, likely due to effects of fishing on herbivores (Barott et al. 2012). The effects of parrotfish consuming both seaweeds and corals can make it difficult to detect seaweed-coral competition (Miller and Hay 1998), and competition between sea urchins and herbivorous fishes further complicates these interactions (McClanahan 1992; McClanahan et al. 1996). Rather than extending such debates, my intent is to examine the complex role of reef fishes in structuring coral-reef benthos.

It is important at the outset to stress that the coral-seaweed-herbivore triangle may often not be as simple as depicted in Fig. 10.1 because this triad does not occur in isolation from the remainder of the reef ecosystem. All three groups of organisms are affected by a variety of other organisms and abiotic factors that act in concert with interactions inside the triangle. Indeed, the coral-seaweed-herbivore triangle is part of the vastly complex interaction web that we call a coral reef ecosystem, involving a variety of direct and indirect effects among herbivores, seaweeds, corals, and their biotic and abiotic environment is ways that defy simplistic explanations (as detailed below). For example, herbivorous fishes can actually aid the dispersal of macroalgae, fragments of which may survive gut passage and reattach to the reef (Vermeij et al. 2013). Unfortunately for present-day scientists, much of what we know of reef ecosystems is a recent remnant of far richer systems that included numerous mega herbivores, including sea turtles, manatees, etc. (Jackson 1997).

Given this context, this chapter focuses on the myriad effects of (1) herbivorous fishes on the distribution and abundance of reef algae, and indirectly, corals, (2) corallivorous fishes that directly consume reef-building corals, and (3) fishes that consume and compete with invertebrate herbivores and corallivores, thereby indirectly affecting macroalgae and corals. The overall conclusion is that, beyond useful yet not quite universal concepts like the coral-seaweed-herbivore triangle, the immense complexity of coral reefs – combined with numerous synergistic threats to these ecosystems – makes explicitly detailed guidelines for conservation and management difficult. Nonetheless, there is sufficient generality that rules of thumb – such as maintaining high diversity and large populations of herbivores of a variety of body sizes – should be widely implemented to bolster the ecological resilience of coral reefs.

10.1.3 Scope of Review

This chapter focuses on the one-way effects of fishes upon reefs, emphasizing the mechanisms and constraints under which fishes cause shifts in the relative dominance of benthic organisms. However, it is important to realize that this limited perspective ignores most of the complex interactions between fishes and the reefs they inhabit. Indeed, the reciprocal effects of reefs upon fishes (e.g., interaction arrows that would flow in the opposite directions as those in Fig. 10.1) are a matter of life and death for many species; many fishes are obligatory denizens of coral reefs and derive all their food and shelter from this habitat. The demise of a reef certainly has repercussions for reef fishes (review by Sale and Hixon 2014). For example, macroalgal overgrowth of reefs may reduce the density of both herbivorous and carnivorous fishes in Kenya (McClanahan et al. 1999). Indeed, Reese (1981) proposed that the density of obligate coral-feeding fishes can be used as a bioindicator of the general health of a reef, yet this idea stirred considerable controversy (Bell et al. 1985; Bouchon-Navarro et al. 1985; Williams 1986; Roberts et al. 1988; Sano et al. 1987; White 1988; Bouchon-Navarro and Bouchon 1989; Clarke 1996; Kokita and Nakazono 2001). The close association of fishes and corals was documented by Harmelin-Vivien (1989), who noted a significant linear relationship between the number of fish species and the number of coral species among reefs across the Indo-Pacific region, but no such relationship with the number of algal species. In any case, the death and collapse of a coral reef reduces living space for fishes, which in turn may reduce local populations of herbivores, thereby inhibiting reef recovery (Mumby and Steneck 2008; Nyström et al. 2012; Sale and Hixon 2014).

Other potentially important interactions between fishes and reefs that will not be covered here are, first, assessment of the relative effects of fishes vs invertebrate herbivores (Hay 1984; Carpenter 1986; Foster 1987; Morrison 1988; Klumpp and Pulfrich 1989), and second, the role of fish defecation and excretion fertilizing reef benthos (Meyer et al. 1983; Meyer and Schultz 1985a, b; Polunin and Koike 1987; Polunin 1988; Harmelin-Vivien et al. 1992; Burkepile et al. 2013). Finally, space limitations preclude exploration of the many fascinating and ecologically important interactions among fishes and the community structure of reef fishes per se. For example, changes in the abundance of predatory fishes could result in reciprocal shifts in the density of herbivorous fishes, with ramifications for the benthos (Graham et al. 2003; Mumby et al. 2006, 2012). Fortunately, volumes on these topics edited by Sale (1991, 2002) and Mora (2014) are unparalleled and recommended for those desiring a detailed introduction to reef-fish ecology, just as Polunin and Robert's (1996) edited volume covers reef fisheries.

This review, then, is by no means exhaustive. Previous reviews detailing interactions among reef fishes, seaweeds, and corals include Hixon (1986), Hutchings (1986), Glynn (1988, 1990), Steneck (1988), Horn (1989), Hay (1991, 1997), Jones et al. (1991), and McCook (1999). This review summarizes relevant literature published through 2013, emphasizing earlier foundational studies that are not always readily available on-line.

10.2 The Players: Corallivorous and Herbivorous Reef Fishes

Only a handful of families of fishes have been documented to have obvious direct effects on reef corals (Fig. 10.2). Although about 10 families and over 100 species of fish are known to eat coral polyps, there are relatively few groups that feed strictly on corals (reviews by Robertson 1970; Randall 1974; Cole et al. 2008; Rotjan and Lewis 2008). This pattern may be due to coral polyps being relatively unpalatable compared to other prey in terms of their chemical composition, their protective nematocysts, and their calcium-carbonate skeletons. The predominant **corallivores** are butterflyfishes (Family Chaetodontidae, Cole et al. 2011); about half of the over 100 species eat corals (Allen 1981; Cole et al. 2008; Rotjan and Lewis 2008). Other relatively large fishes that regularly consume corals are triggerfishes (Balistidae), filefishes (Monacanthidae), and puffers (Tetraodontidae) (e.g., Jayewardene et al. 2009). Whereas the butterflyfishes delicately extract individual polyps from the coral skeleton, triggerfishes and puffers tend to scrape or excavate pieces of the coral colony with their beak-like mouths. Smaller corallivores include at least one goby (Gobiidae; Patton 1974).

Among the corallivores, the social systems of the butterflyfishes are best documented, often comprising territories defended by male-female pairs (Reese 1975; Hourigan 1989; Roberts and Ormond 1992). About 8 species of wrasse and about 20 species of parrotfish (both Labridae) also consume living coral tissue (Bruckner et al. 2000; Rotjan and Lewis 2006, 2008; Cole et al. 2008, 2010; Mumby 2009; Rotjan and Dimond 2010; Bonaldo and Bellwood 2011; Cole and Pratchett 2011a; Burkepile 2012), especially the largest species, the endangered bumphead parrotfish *Bolbometopon muricatum* (Randall 1974; Choat 1991; Bellwood et al. 2003). About a third of the species of corallivorous reef fish feed almost exclusively on corals (Cole et al. 2008).

In contrast to the corallivores, **herbivores** are relatively speciose (Fig. 10.2). As collated by Allen (1991) and Choat (1991), the predominant consumers of benthic algae are most of the approximately 75 species of surgeonfishes (Acanthuridae), all 27 species of rabbitfishes (Siganidae), all 79 species of parrotfishes (formerly Scaridae, now the Subfamily Scarinae of the Family Labridae), and over half of the approximately 320 species of damselfishes (Pomacentridae). Other herbivorous families include smaller fishes, such as combtooth blennies (Blenniidae), and even batfish (*Platax pinnatus*, Bellwood et al. 2006). The geographic distribution of herbivorous reef fishes is likely limited by temperature-related feeding and digestive processes (Floeter et al. 2005).

The feeding modes of herbivorous reef fishes are highly variable (reviews by Ogden and Lobel 1978; Horn 1989; Glynn 1990; Choat 1991; Wainwright and Bellwood 2002; Choat et al. 2002, 2004). Surgeonfishes and rabbitfishes tend to crop seaweeds in a browsing mode that leaves algal holdfasts intact. Parrotfishes, on the other hand, have highly modified jaws and fused teeth. With these beaks (which inspired their name) and depending upon the species, parrotfishes superficially scrape or deeply excavate the substratum and remove algal holdfasts along with the dead coral to which the algae attach, and occasionally, live coral

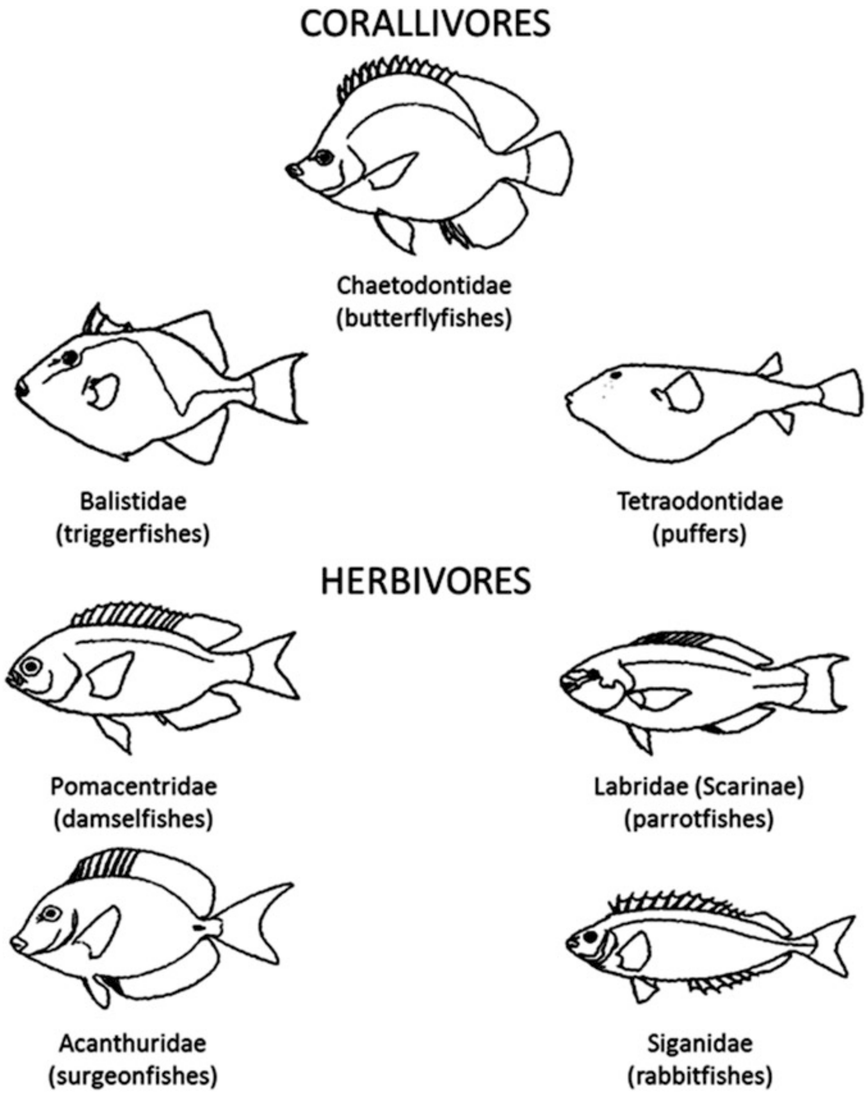

Fig. 10.2 Families of larger-bodied reef fishes that include the most corallivorous and herbivorous species. Note that members of all the listed corallivore families include species that do not consume corals, and about half the species of damselfish are not herbivorous. Certain species in numerous other families also consume corals and/or algae. Note that parrotfishes are increasingly documented to consume live coral as well as algae (Modified from Hixon 1997)

(Bellwood and Choat 1990; Bruckner et al. 2000; Rotjan and Lewis 2006; Bonaldo and Bellwood 2009; Mumby 2009; Rotjan and Dimond 2010; Burkepile 2012). This activity makes parrotfishes the major source of bioerosion (and producer of coral sand) among reef fishes (reviews by Hutchings 1986; Choat 1991, Chapter 4). Different species of algae are differentially consumed by different species of herbivore, indicating that herbivore diversity is important in controlling the overall standing crop of seaweeds (Mantyka and Bellwood 2007a, b; Burkepile and Hay 2008). Surgeonfishes, rabbitfishes, and parrotfishes exhibit variable social systems, from individual territories to transient foraging aggregations (e.g., Ogden and Buckman 1973; Robertson et al. 1979; Robertson and Gaines 1986).

Most herbivorous (actually, omnivorous) damselfishes maintain permanent individual territories, measuring about a square meter in area, which they defend vigorously against other herbivores (e.g., Low 1971). This defense, combined with moderate browsing and even "weeding" behavior (sensu Lassuy 1980), often maintains a distinctive mat of erect algae within the territory. By forming large schools, parrotfishes and surgeonfishes can sometimes overwhelm and denude damselfish territories (Jones 1968; Barlow 1974; Vine 1974; Robertson et al. 1976; Foster 1985; Reinthal and Lewis 1986).

Overall, both corallivorous and herbivorous fishes display a wide variety of feeding modes and behaviors, suggesting that the ecological effects of these consumers are bound to vary widely from species to species and from reef to reef. This immense functional diversity indicates likely complementary, synergistic, and redundant roles of multiple species in maintaining the resilience of what humans consider to be healthy coral reefs. What follows, then, are summaries of specific studies that can be generalized only with caution.

10.3 Effects of Fishes on Seaweeds

10.3.1 Schooling Herbivores

Parrotfishes, surgeonfishes, and rabbitfishes often occur in dense aggregations that have obvious effects on reef macroalgae. Densities can average well over 10,000 herbivorous fish per hectare (review by Horn 1989), standing stocks on unfished reefs in the Great Barrier Reef can reach 45 metric tons per km^2 (Williams and Hatcher 1983), and secondary productivity can approach 3 metric tons per km^2 per year (review by Russ and St. John 1988). At Orpheus Island on the Great Barrier Reef, the entire area of the reef crest can be grazed by the parrotfish *Scarus rivulatus* monthly (Fox and Bellwood 2007, 2008). In the Caribbean, parrotfishes can graze at rates of over 150,000 bites per m^2 per day (Carpenter 1986), although it has been estimated that these fish can maintain only 10–30 % of a structurally complex fore-reef in a grazed state (Mumby 2006). At lower algal productivities on reefs in the Florida Keys, herbivorous fishes may consume up to 100 % of the entire daily production, ranging as low as about 30 % in some microhabitats (Paddack et al. 2006). Hatcher (1981) estimated that about half the net algal production on One Tree Reef, Australia, was consumed by fishes. At the same site, Hatcher and Larkum (1983) demonstrated that algal standing crop was controlled by grazing fishes during both autumn and spring on the reef slope (10 m depth), but only during spring in the lagoon (2 m depth). In autumn, inorganic nitrogen limited the standing crop of lagoon algae despite the continued presence of fishes (Hatcher 1997). In some systems, such intense herbivory enhances local primary productivity by maintaining algae at an early-successional stage (Montgomery 1980; Birkeland et al. 1985; Carpenter 1986).

In addition to seasonal variation, an apparently general trend is that the spatial distribution of herbivory by fishes varies inversely with tidal exposure and/or wave action (Van den Hoek et al. 1975, 1978) and directly with the availability of shelter for the herbivores from predatory fishes (Hay 1981a; Lewis 1986), with both turbulence and shelter often decreasing with depth. Thus, as documented in Guam (Nelson and Tsutsui 1981), the Caribbean (Hay et al. 1983; Lewis and Wainwright 1985), the Great Barrier Reef (Russ 1984a, b), and the Indian Ocean (Sluka and Miller 2001), the depth distribution of herbivores and grazing intensity may often be unimodal: low in very shallow water due to limited accessibility by fishes, high at intermediate depths due to high accessibility and shelter, and low in deep reef areas (greater than about 10 m), where the abundance of coral shelter for fishes typically decreases. However, in areas where intense fishing has greatly reduced the abundance of piscivores, herbivorous fishes may be active at greater depths, with algal standing stocks consequently being lower than usual at those depths (Hay 1984). The unimodal depth distribution of herbivorous fishes may explain the bimodal zonation of erect algal cover found on reefs such as those in Curacao (Van den Hoek et al. 1978): high cover in the eulittoral zone (0–1 m depth), low on the upper reef slope (1–30 m), and high again on the lower slope (30–50 m).

Lack of shelter for grazing fishes probably also explains the existence of extensive algal plains occurring on sand bottoms below and between reefs, as well as high algal densities on very shallow reef flats lacking adequate shelter for fishes (Van den Hoek et al. 1978; Hay 1981b; McCook 1997). Overall, it appears that the risk of predation limits the grazing activities of smaller reef fishes to areas providing structural refuges (reviews by Hixon 1991, 2015).

At the microhabitat scale, schooling herbivores may invade territories of damselfish, which harbor higher standing crops of seaweeds than the surrounding seascape (Jones 1968; Barlow 1974; Vine 1974; Robertson et al. 1976; Foster 1985; Reinthal and Lewis 1986). However, herbivores may spend less time foraging where macroalgal stands are particularly dense (Hoey and Bellwood 2011). At broader regional scales, on the Great Barrier Reef, inner-shelf reefs support both high macroalgal cover and high densities yet low biomass of parrotfishes, whereas outer-shelf reefs support the opposite patterns (Hoey and Bellwood 2008; Wismer et al. 2009), although other schooling herbivores are more abundant on the outer reef than inshore (Williams and Hatcher 1983; Russ 1984a, b). The mechanisms underlying these patterns appear to be related to between-region differences in the palatability and productivity of reef algae (Roff and Mumby 2012). (Chap. 9 provides a general review of regional variation in coral-reef processes.)

Regionally, comparisons among reefs have shown clear inverse correlations between the biomass of herbivorous fishes and the percent cover of macroalgae in the Caribbean (Williams and Polunin 2001) and the Great Barrier Reef (Wismer et al. 2009). Locally, herbivores can be more abundant inside marine reserves, with consequent declines in macroalgal abundance relative to fished areas, as documented in the Bahamas (Mumby et al. 2006), but not in Belize (McClanahan et al. 2011b). In the Bahamas, this pattern can lead to a trophic cascade that benefits corals (Mumby et al. 2007a). Field experiments pioneered by Stephenson and Searles (1960) and Randall (1961), in which herbivorous fishes are excluded from reef plots by cages, have shown that such correlations are a case of cause and effect. Typically, heavily grazed dead coral surfaces become dominated by grazer-resistant algal crusts or turfs, whereas caged but otherwise identical surfaces become covered by high standing crops of erect algae (Vine 1974;

Wanders 1977; Lassuy 1980; Sammarco 1983; Hixon and Brostoff 1985; Carpenter 1986; Lewis 1986; Morrison 1988; Scott and Russ 1987; McCauley et al. 2010). Essentially, erect algae competitively exclude crusts in the absence of grazing, but crusts are more resistant to grazing (Littler et al. 1983; Steneck 1983). Overall, the local species diversity of algae on exposed flat surfaces declines with increasing density of schooling herbivores (Day 1977; Brock 1979), an effect that is ameliorated on surfaces where algae can grow in crevices (Brock 1979; Hixon and Brostoff 1985; Hixon and Menge 1991).

A yearlong experiment off Hawai'i examined the benthic successional sequences and mechanisms that cause these general patterns (Hixon and Brostoff 1996). Succession was followed on dead coral surfaces subjected to each of three grazing treatments: protected within grazer-exclusion cages, exposed to moderate grazing inside damselfish territories, and exposed to intense parrotfish and surgeonfish grazing outside territories. The ungrazed successional sequence inside cages was an early assemblage of filamentous green and brown algae (including *Entermorpha* and *Ectocarpus*) replaced by a high-diversity assemblage of mostly red filaments (including *Centroceras* and *Ceramium*), which in turn was replaced by a low-diversity assemblage of mostly coarsely-branched species (including *Hypnea* and *Tolypiocladia*). Plotted in a multispecies ordination (detrended correspondence analysis), ungrazed succession followed a distinct trajectory over the year (Fig. 10.3a). Intense herbivory by parrotfishes and surgeonfishes outside damselfish territories caused succession to follow a very different path, where the early filaments were replaced immediately by grazer-resistant crustose species, including the red coralline *Hydrolithon* (Fig. 10.3a). This result suggests that heavy grazing deflected the normal trajectory of succession toward herbivore-resistant algae (Hixon and Brostoff 1996). Other experiments showing the important role of herbivores in benthic algal succession include McClanahan (1997) in Kenya, Ceccarelli et al. (2005) in Papua New Guinea, and Burkepile and Hay (2010) in Florida.

In summary, intense herbivory, especially where an abundance and variety of herbivore species are present, strongly influences the standing crop, productivity, and community structure of reef algae. It also appears that selection for resistance to such herbivory may compromise competitive ability among algal species (Littler and Littler 1980; Hay 1981b; Lewis 1986; Morrison 1988). Off the Caribbean coast of Panamá, fishes may prevent competitively dominant (but highly palatable) sand-plain species from displacing competitively subordinate (but grazer-resistant) reef algae (Hay 1981b; Hay et al. 1983). This dichotomy may act to maintain between-habitat diversity in algae (Hay 1981b, see also Lewis 1986).

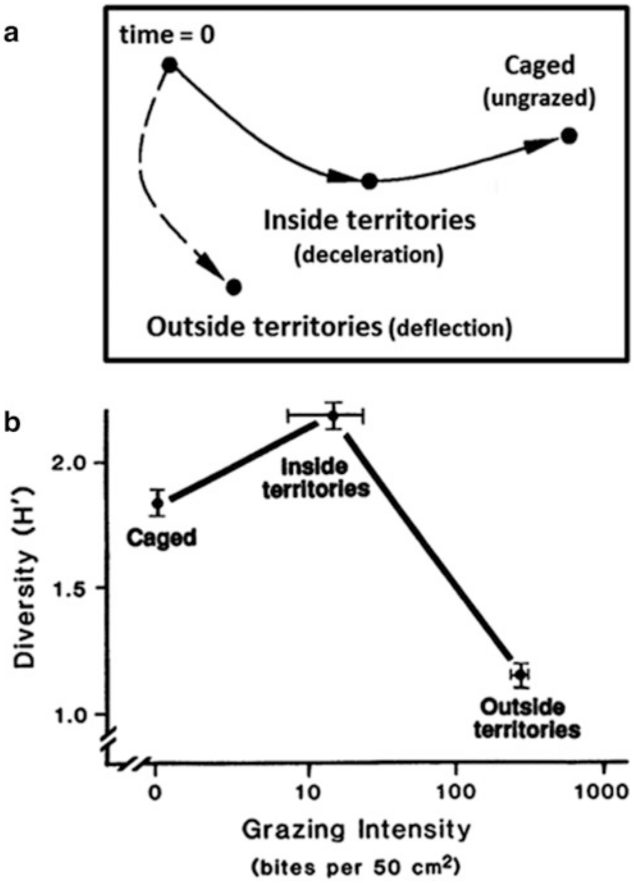

Fig. 10.3 Patterns of macroalgal succession and local species diversity on a Hawaiian coral reef under three levels of grazing by macroherbivores: caged (none), inside damselfish territories (moderate), and outside territories (intense). (**a**) Succession as a stylized ordination of macroalgal communities through time in species space (i.e., each curve shows community change in species composition and relative abundance through time). The pattern of ungrazed succession (caged) is decelerated within damselfish territories, whereas succession is deflected onto a new trajectory toward crustose algae outside territories. (**b**) Macroalgal species diversity after 1 year, indicating an intermediate-predation effect within damselfish territories, such that the damselfish is locally a keystone species (Modified from Hixon and Brostoff 1983, 1996)

10.3.2 Territorial Damselfishes

By defending small patches of dead coral, and grazing or "weeding" the algae in these patches in a particular way, territorial damselfishes often establish and maintain visually distinct mats of macroalgae on reefs (Vine 1974; Brawley and Adey 1977; Lassuy 1980; Montgomery 1980; Hixon and Brostoff 1996; Hata and Kato 2003). In general, these mats are sites of greater primary productivity than comparable areas outside territories (Montgomery 1980; Russ 1987; Klumpp et al. 1987). This production is an important food source for not only the resident damselfish, but also small invertebrate herbivores inhabiting the mat and larger intruding herbivores (Russ 1987; Klumpp and Polunin 1989).

Given that territory mats can cover well over 50 % of shallow reef tracts on some reefs (Sammarco and Williams 1982; Klumpp et al. 1987), the local effects of damselfishes on the benthic community can be substantial. In particular, the defense, grazing, and weeding activities of damselfish (possibly combined with localized fecal fertilization) strongly affect the local species diversity of reef algae. This general effect has been demonstrated by three similar experiments in Guam (Lassuy 1980), Hawai‘i (Hixon and Brostoff 1983), and the Great Barrier Reef (Sammarco 1983). Each experiment compared algal diversity on dead coral surfaces exposed to each of three different treatments: accessible to mostly damselfish grazing inside territories, accessible to intense grazing by other herbivores outside territories, and protected within fish-exclusion cages outside territories.

Although strict comparisons are precluded by differences in experimental design and laboratory analyses, some general patterns do emerge. For both damselfish species he studied (*Stegastes lividus* and *Hemiglyphidodon plagiometopon*), Lassuy (1980) found that caged surfaces exhibited the greatest algal diversity after 2 months. Both Hixon and Brostoff (1983) and Sammarco (1983) obtained the same result from samples taken after 2–6 months and 3 months, respectively. However, after a year both the latter studies found that algal diversity was greatest inside damselfish territories. These data, combined with the fact that Sammarco studied one of the same species as Lassuy (*H. plagiometopon*), suggest that Lassuy's (1980) samples may have represented relatively early successional stages.

In the Hawai‘i study, Hixon and Brostoff (1996) showed that moderate grazing by the damselfish *Stegastes fasciolatus* (now *S. marginatus*) slowed and appeared to stop succession at a high-diversity middle stage dominated by red filaments (Fig. 10.3a). Thus, rather than deflecting the successional trajectory like more intensive grazers (see above), damselfish appeared to simply decelerate algal succession. Territorial fish may maintain the mid-successional algal community because these species provide a superior food source for the damselfish (Montgomery and Gerking 1980) and/or a source of invertebrate prey and palatable epiphytes (Lobel 1980).

Hixon and Brostoff (1983, 1996) further showed that grazing by damselfish inside their territories was of intermediate intensity relative to that within cages and outside territories. Correspondingly, the standing crop of algae was also at intermediate levels inside territories, whereas local species diversity was at its maximum. These results thus corroborated the **intermediate-predation hypothesis** (review by Hixon 1986). At low levels of grazing within cages, a few dominant competitors (coarsely branching species such as *Hypnea* and *Tolypiocladia*) were capable of locally excluding most other species. At high levels outside territories, only a few crustose species persisted. Inside damselfish territories, the coexistence of many algal species was maintained because their densities were apparently kept below levels where resources (presumably mediated by living space) became severely limiting (Fig. 10.3b).

Given that territorial damselfish can locally enhance species diversity, they can be considered "**keystone species**" (sensu Paine 1966, see also Williams 1980). However, unlike the normal kind of keystone species, which enhance diversity by increasing predation intensity on a prey assemblage, the territorial behavior of damselfish enhances diversity by decreasing predation overall (Fig. 10.3b). That is, in the absence of a normal keystone species, predation is low and diversity is low because a few prey species competitively exclude most others from the local system (e.g., Paine 1966). However, in the absence of damselfish ("keystone species in reverse"), predation is high (due to schooling herbivores) and diversity is low because few prey are able to survive intense herbivory.

There is evidence that this pattern documented in Hawai‘i is common. Assuming that grazing intensity was intermediate inside damselfish territories in Sammarco's (1983) study, *Hemiglyphidodon plagiometopon* is a keystone species where it is abundant at the Great Barrier Reef, and possibly Guam (Lassuy 1980). It has also been found that species diversity of macroalgae in territories of other damselfish, including *Stegastes planifrons* off Puerto Rico (Hinds and Ballantine 1987) and *Stegastes fuscus* off Brazil (Ferreira et al. 1998), decline in when caged, also suggesting a keystone-species effect. Note, however, that not all damselfishes enhance local algal diversity; some species maintain near monocultures within their territories by intense nonselective grazing (Montgomery 1980) and/or weeding (Hata and Kato 2002; Hata et al. 2002). Although *Stegastes nigricans* maintains strong dominance by *Womersleyella setacea* in its territories in Okinawa, the abundance and species diversity of benthic foraminifera is greater inside territories than outside (Hata and Nishihira 2002).

Regardless of whether damselfishes enhance local algal diversity, the greatly increased standing crop of erect algae inside their territories (compared to more heavily grazed surfaces outside) has important secondary effects on reef benthos. The algal mat serves as a refuge for invertebrate microfauna and/or various epiphytes (Lobel 1980; Hixon and Brostoff 1985; Zeller 1988), as well as newly settled fishes (Green 1992, 1998). Also, because accretion by crustose coralline algae adds to the reef framework and such algae are overgrown by the algal mat, damselfish territories may be sites of weakened reef structure (Vine 1974; Lobel 1980). Crustose corallines also provide settlement substratum for some reef-building corals (Morse et al. 1988; Heyward and Negri 1999), so damselfish territories may additionally inhibit coral settlement.

Damselfish territories may also indirectly affect nitrogen fixation on reefs, although available data are somewhat contradictory. During the same study as Sammarco (1983) described above, Wilkinson and Sammarco (1983) found that nitrogen fixation by blue-green algae (cyanobacteria) was positively correlated with grazing intensity on the Great Barrier Reef, being lowest within cages, intermediate inside damselfish territories, and greatest outside territories. However, both Lobel (1980) and Hixon and Brostoff (unpublished) found considerably more blue-green algae inside than outside territories in Hawaiʻi. Finally, Ruyter Van Steveninck (1984) found no differences in the abundance of filamentous blue-green algae inside and outside damselfish territories in the Florida Keys. These discrepancies suggest possible regional differences in local distribution and abundance of blue-green algae.

10.3.3 Conclusions Regarding Effects of Fishes on Seaweeds

Herbivorous fishes can strongly affect the distribution and abundance of reef macroalgae. Where there is ample shelter from predation and protection from strong turbulence, schooling herbivores can consume reef algae to very low standing crops, leaving mostly grazer-resistant forms such as crusts, compact turfs, or chemically-defended species. Such intense herbivory may be essential for reef-building corals to flourish. Describing the coral-seaweed-herbivore triangle, Glynn (1990: 391) concluded that the "maintenance of modern coral reefs may be due largely to the activities of fish and invertebrate herbivores that prevent competitively superior algal populations from dominating open, sunlit substrates." Nonetheless, it is important to realize that a myriad of factors are involved in these and other switches in dominance among algal growth forms and between algae and corals. For example, Littler and Littler (1984) saw nutrient levels as pivotal in determining whether and how herbivory will determine the dominant benthos on reefs, and subsequent experimental work showed that nutrient levels may or may not affect these interactions (Smith et al. 2001; Stimson et al. 2001; Thacker et al. 2001). Thus, a synergistic combination of "top-down" factors (herbivory) and "bottom-up" factors (nutrients) likely determine whether corals or seaweeds dominate reef benthos (Hatcher 1990; Szmant 2001; McClanahan et al. 2002). Additionally, by providing spatial refuges from predation for both corals and seaweeds, the physical structure of the habitat (holes and crevices) affects local grazing rates, with further ramifications for benthic community structure (Littler et al. 1989; Hixon and Menge 1991).

Besides schooling herbivores, territorial damselfishes have particularly strong local effects on shallow reef algae, effects which can cascade through the entire benthic community. The defensive and grazing activities of damselfishes and the resulting dense algal mats they defend can substantially affect reef accretion, nitrogen fixation, epiphytes and small invertebrates that inhabit the algae, and, as will be seen in the next section, corallivores (Fig. 10.4). Clearly, herbivorous fishes are major players determining the character of shallow coral-reef communities, and territorial damselfishes in particular can act as keystone species.

10.4 Effects of Fishes on Corals

10.4.1 Direct Consumption

The genera of corals most commonly grazed by reef fishes are *Acropora*, *Pocillopora*, *Montipora*, and *Porites* (reviews by Cole et al. 2008; Rotjan and Lewis 2008). Compared to the effects of herbivores on algae, surprisingly few studies have demonstrated that corallivorous fishes influence the distribution and abundance of reef-building corals. For example, although butterflyfishes are among the most obligatory of corallivores (Reese 1977), these fishes originally appeared to have a negligible effect on coral standing crops (Harmelin-Vivien and Bouchon-Navarro 1981, 1983). At Aqaba in the Red Sea and Moorea in the South Pacific, butterflyfishes occurred at average densities of 69 and 51 fish per 1,000 m^2, yet consumed an average of only about 10 and 28 g of coral polyps per 1,000 m^2 per day, respectively. It appears that corals often retract all their polyps in response to predation by butterflyfish, making polyps locally unavailable to predators for considerable periods. Such factors may preclude high densities of large-bodied obligate corallivores, perhaps necessitating the large feeding territories defended by butterflyfishes (see Tricas 1989; Roberts and Ormond 1992). More recently, however, it has been documented that butterflyfishes on the Great Barrier Reef can consume up to 79 % of the annual productivity of tabular acroporid corals (Cole et al. 2012).

The local distributions of several coral genera are strongly affected by coral-feeding fishes. Neudecker (1979) provided one of the first experimental demonstrations that fishes can potentially affect the depth zonation of corals. Off Guam, he transplanted small colonies of *Pocillopora damicornis* from a relatively fish-free lagoon (1–2 m depth) to reef slopes (15–30 m depth) where this coral was naturally absent and corallivorous fishes were common. Coral transplants survived well when caged, but exposed colonies were partially consumed by butterflyfishes and triggerfishes within 1 week (see also Hixon and Brostoff 1996). Additionally, butterflyfishes may negatively affect corals indirectly by being vectors for diseases (Raymundo et al. 2009).

Locally high densities of corallivorous fishes can clearly stress their particular host corals (Cole and Pratchett 2011b), and these predators may selectively target colonies with high

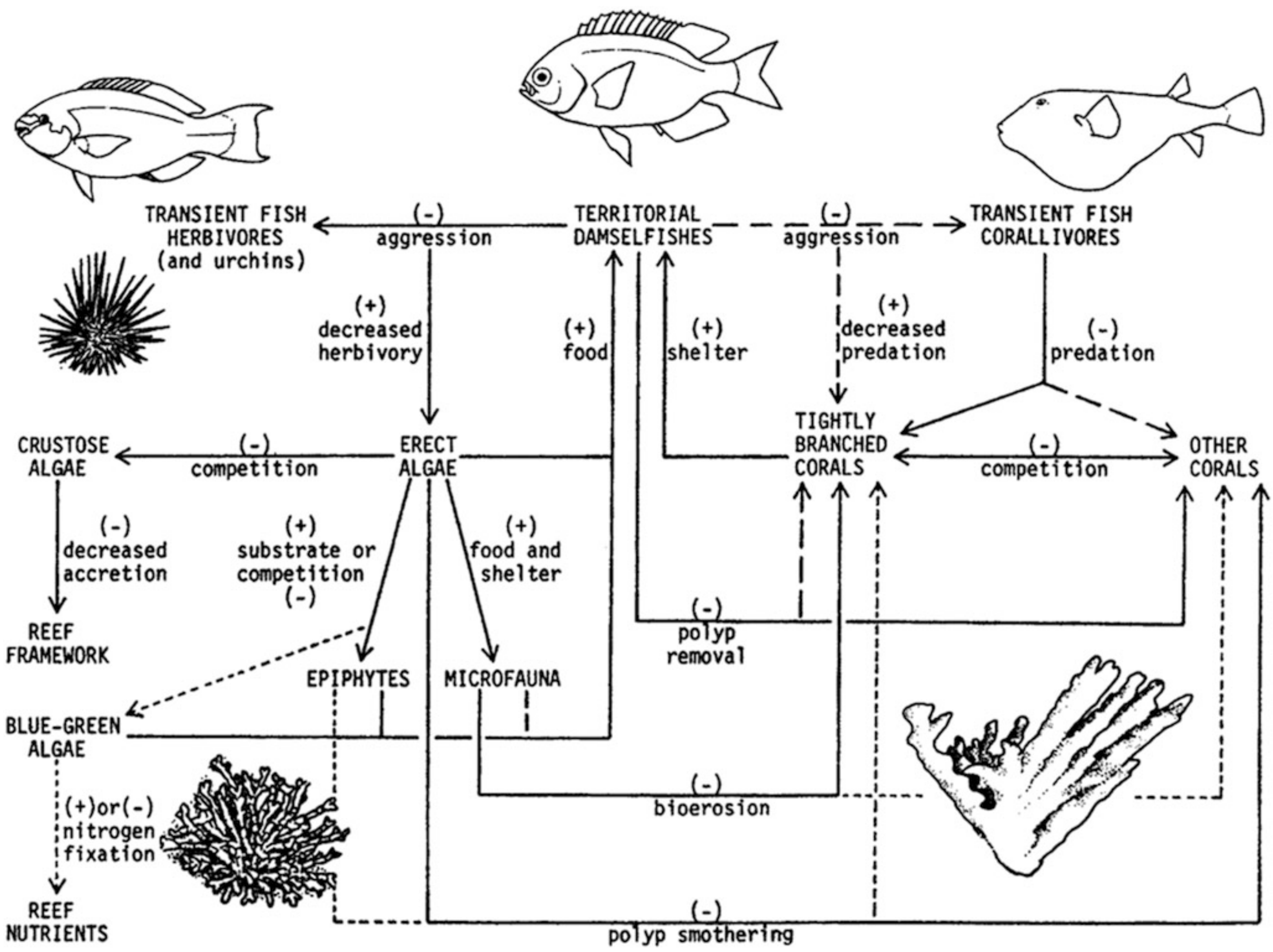

Fig. 10.4 Flowchart synthesizing the interactions between fishes and benthos on a shallow coral reef where territorial damselfishes are abundant. *Arrows* indicate positive (+) and negative (−) effects. *Dashed lines* indicate relatively weak effects, and *dotted lines* indicate effects that are poorly documented and/or controversial. Where territorial damselfishes are rare, some of these effects reverse. In particular, erect algae and their associates are often replaced by grazer-resistant crustose algae (which may serve as settlement habitat for corals) due to intense grazing by transient herbivores (Modified from Hixon 1983)

densities of macroboring organisms (Rotjan and Lewis 2005). Such differential effects can have ramifications for interactions among corals. For example, off Hawai‘i, Cox (1986) showed that the feeding preference of the butterflyfish *Chaetodon unimaculatus* for the coral *Montipora verrucosa* can reverse the competitive dominance of this coral over another coral, *Porites compressa*. Inside fish-exclusion cages, *Montipora* overgrew *Porites*, yet outside cages, this dominance sometimes reversed due to differential grazing of *Montipora* by the butterflyfish.

Besides the strict corallivores, herbivorous fishes may also directly affect corals by occasionally consuming or otherwise killing them. Territorial damselfishes are known to remove polyps, thereby killing patches of coral on which the damselfish establish their algal mats. In the Caribbean, the damselfish *Stegastes planiforns* was observed killing *Orbicella* (formerly *Montastraea*) *annularis* and *Acropora cervicornis* (Kaufman 1977). Knowlton et al. (1990) suggested that such predation dramatically slowed the recovery of *A. cervicornis* off Jamaica following Hurricane Allen, inhibiting the usual dominance of this species. Similarly, off the Pacific coast of Panamá, *Stegastes acapulcoensis* killed patches of *Pavona gigantea* (Wellington 1982). Wellington’s study demonstrated how this direct effect, combined with various indirect effects, strongly affected coral zonation (see below).

Outside damselfish territories, there can be direct consumptive effects of herbivorous fishes on corals. Field observations have noted grazing fishes damaging juvenile corals (Randall 1974; Bak and Engel 1979), although Birkeland (1977) documented herbivores avoiding coral recruits. Littler et al. (1989) suggested that parrotfishes (*Scarus* spp. and *Sparisoma* spp.) substantially influence the local distribution of *Porites porites* off Belize by eliminating this delicately branching species from areas where these fish are abundant. They proposed that a combination of differential consumption of *P. porites* by parrotfishes and the relative availability of refuge holes for grazing fishes of different sizes among different microhabitats determined whether back-reef bottoms were dominated by macroalgae, *P. porites*, or the relatively mound-shaped and grazer-resistant *P. astreoides*. Similarly, recently recruited coral colonies survived intense parrotfish grazing in laboratory mesocosms in Hawai‘i only when structural refuges from grazing were provided (Brock 1979). Indeed, although it was long believed that only the largest species of parrotfish, the Indo-Pacific *Bolbometopon muricatum*, consumes substantial amounts of live coral (Randall 1974; Choat 1991), individually consuming about 2.5 metric tons of living coral per year (Belwood et al. 2003), there is increasing evidence that smaller parrotfishes may also negatively affect corals (Bruckner and Bruckner 1998; Bonaldo and Bellwood 2011; Burkepile 2012, but see Mumby 2009).

A poorly documented yet possibly substantial source of coral mortality is consumption of coral spawn by planktivorous reef fishes, especially on the Great Barrier Reef (Westneat and Resing 1988; Pratchett et al. 2001). Less directly, parrotfish of the genus *Sparisoma* may differentially target gravid polyps of *Orbicella* in the Caribbean, thereby lowering the fitness of grazed coral colonies prior to spawning (Rotjan and Lewis 2009). Also poorly documented yet potentially important are the combined negative effects of corallivory and bleaching on the condition and recovery of corals. Fish may (or may not) target bleached corals (Cole et al. 2009), and bleached corals that have been previously grazed by parrotfish may show a persistent reduction in the density of endosymbiotic zooxanthellae compared to bleached colonies that have not been grazed (Rotjan et al. 2006).

10.4.2 Indirect Effects

Available experimental evidence suggests that indirect effects of herbivorous fishes influence the local distribution and abundance of corals more extensively than direct consumption by corallivores. As reviewed in the introduction to this chapter, schooling herbivores can benefit corals indirectly by reducing the standing crops of seaweeds that compete with corals via the coral-seaweed-herbivore triangle (Fig. 10.1a). For example, Lewis (1986) noted that macroalgae overgrew corals of the genus *Porites* when herbivorous fishes were excluded by fencing from a shallow reef off Belize for 10 weeks. Lirman (2001) documented that more than 50 % of the basal perimeter of *Siderastrea siderea*, *Porites astreoides*, and *Orbicella faveolata* in the Florida Keys was in contact with macroalgae. Excluding herbivores by caging these perimeters resulted in increased algal biomass, accompanied by decreased growth rates of *Porites* and increased mortality of *Orbicella*. However, *Siderastrea* was unaffected by seaweeds. Following a coral bleaching event on the Great Barrier Reef, algal cover increased and live coral cover decreased in plots caged to exclude herbivorous fishes, indicating the important role of herbivores in fostering ecological resilience (Hughes et al. 2007). Inside a marine reserve in the Bahamas, herbivory was greater, macroalgal abundance was less, and coral recruitment was greater than in adjacent fished areas, yet overall coral community structure was no different (Mumby et al. 2006, 2007a). Following the massive coral bleaching event in 1998, which shifted benthic dominance from corals to seaweeds on many reefs, a marine reserve harboring herbivorous fishes recovered at a rate no greater than fishes reefs (McClanahan 2008).

By defending and maintaining their algal mats, territorial damselfish produce patches in which juvenile corals are often smothered (Vine 1974; Potts 1977). Additionally, the algal mat provides microhabitats facilitating various boring organisms, which intensifies bioerosion of the coral framework (review by Hutchings 1986, Chapter 4). However, some coral species seem to recruit more successfully to damselfish territories than to adjacent undefended areas, suggesting that the territories may provide at least a temporary refuge from corallivores (Sammarco and Carleton 1981; Sammarco and Williams 1982; Wellington 1982; Suefuji and van Woesik 2001). If for any reason coral colonies manage to reach a certain size, they may become invulnerable to algal overgrowth (Birkeland 1977).

Given that damselfishes may have both positive and negative effects on corals, complex interactions can result. An example is provided by a study of coral zonation on the Pacific coast of Panamá by Wellington (1982). In this system, branching *Pocillopora* corals dominated shallow areas (0–6 m depth), while the massive *Pavona gigantea* dominated deeper areas (6–10 m depth). Combining field observations and experiments, Wellington discovered an interactive feedback loop whereby the damselfish *Stegastes acapulcoensis* may directly and indirectly cause this zonation (Fig. 10.5). When establishing territories in the shallow zone, damselfish differentially kill *Pavona* by polyp removal and maintain their algal mats on the exposed substrata. However, *Pocillopora* is apparently protected by its tightly branched morphology and rapid polyp regeneration. Additionally, *Pocillopora* colonies within the periphery of territories are protected from corallivores by the defensive behavior of the damselfish. These factors enhance the ability of *Pocillopora* to competitively dominate *Pavona* in shallow areas. The *Pocillopora* framework, in turn, provides the damselfish with shelter, a necessary requisite for a territory. In the deep zone, shelter sites and thus damselfish densities

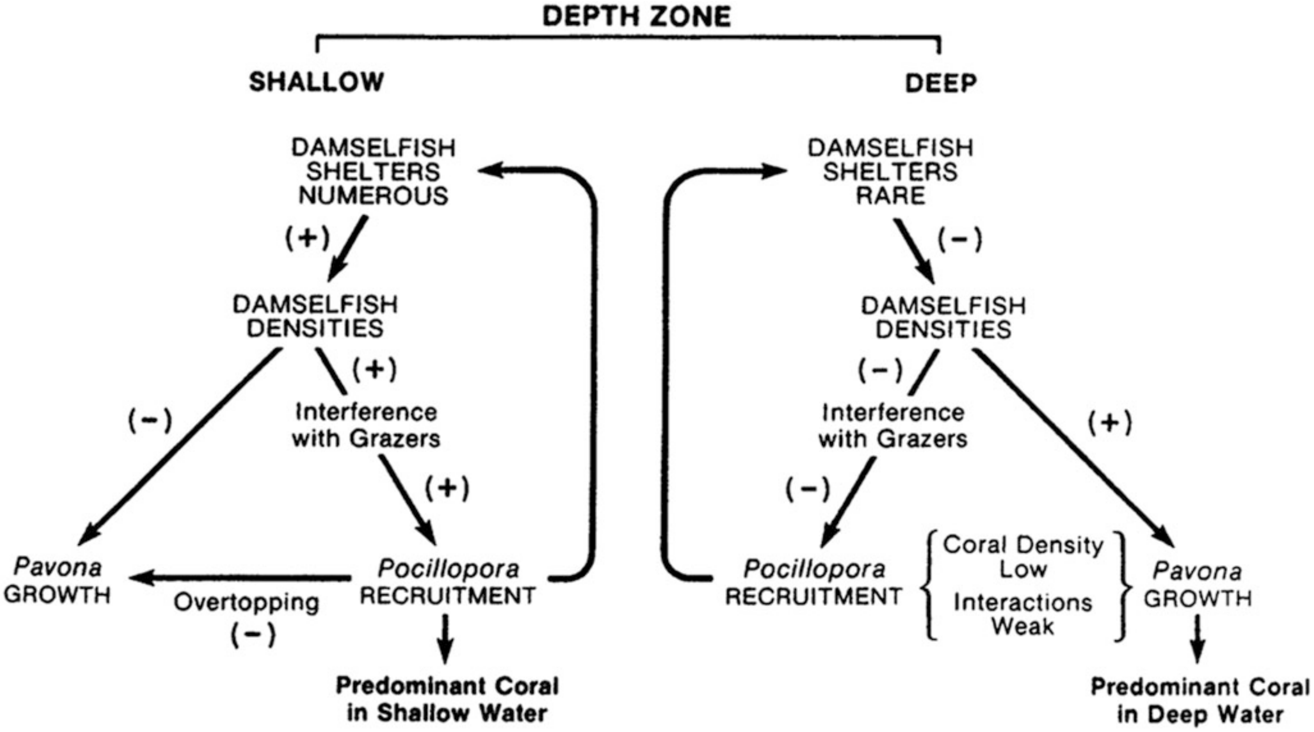

Fig. 10.5 Interactive feedback loops influencing the depth zonation of *Pocillopora* and *Pavona* corals off the Pacific coast of Panamá. *Arrows* indicate positive (+) and negative (−) effects. The direct negative effect of territorial damselfish on *Pavona* in shallow water is due to polyp removal, whereas the "direct" positive effect in deep water is actually an indirect effect mediated by the scarcity of damselfish shelters (From Wellington 1982)

are low because overall coral cover (and thus between-coral competition) is low, apparently due to physical factors (attenuated light, reduced water motion, etc.). Here, transient fish corallivores (mostly puffers) differentially eat *Pocillopora*, whose branches they can ingest and masticate, leaving *Pavona* as the dominant coral.

Finally, a variety of reef fishes have been observed feeding on diseased *Acropora* coral tissue affected by black-band and brown-band disease, which could potentially spread these diseases from head to head and/or foster recovery of infected heads (Chong-Seng et al. 2011).

10.4.3 Conclusions Regarding Effects of Fishes on Corals

Truly corallivorous fishes have been shown to affect the local distribution and abundance of some corals directly via consumption. However, the indirect effects of the coral-seaweed-herbivore triangle and the territorial activities of herbivorous damselfishes appear to have more substantial effects on corals in shallow water. In any case, direct interactions between fishes and corals seem to be largely indeterminate. It appears that, on exposed reef surfaces, coral recruits may initially experience enhanced survival where they are protected from intensive fish grazing, such as within damselfish territories, but will often be eventually overgrown by algae in the absence of substantial herbivory. Those coral larvae settling on surfaces exposed to grazing by herbivorous fishes outside territories may or may not initially suffer high mortality, depending on whether they are consumed along with targeted prey, but some colonies normally reach an invulnerable size where they are both immune to incidental predation and freed from competition with algae. Rotjan and Lewis (2008) suggest that, as reefs continue to be degraded by various human activities, corallivory will become increasingly important as an agent of reef decline.

10.5 Effects of Fishes on Invertebrate Corallivores and Herbivores

Besides directly consuming corals or algae, reef fishes can also affect invertebrate corallivores and herbivores, causing subsequent indirect effects on the dominant reef benthos. Most obviously, some fishes directly consume these organisms, including the major invertebrate corallivore – the crown-of-thorns seastar (*Acanthaster planci*) – and the major invertebrate herbivores: sea urchins (reviews by Jackson 1994; Roberts 1995). At the Great Barrier Reef, Pearson and Endean (1969) noted planktivorous damselfish consuming early developmental stages of *Acanthaster*. In the Red Sea, Ormond et al. (1973) documented that triggerfishes and puffers killed 1,000–4,000 *Acanthaster* per hectare each year, a rate that accounted for an observed decline in the *Acanthaster* population. However, experiments on the Great Barrier Reef detected no effects of fish predation on juvenile *Acanthaster* (Sweatman 1995).

Triggerfishes and puffers also consume sea urchins, as do large wrasses and porcupinefishes (Diodontidae, Randall 1967). Field experiments have demonstrated that such predation can be intense (Glynn et al. 1979) and force urchins to remain near shelter (Carpenter 1984). Thus, the risk of predation by fishes limits the area over which urchins can overgraze algae and seagrass, resulting in discrete barren zones or "**halos**" around Caribbean reefs (Ogden et al. 1973). Hay (1984) suggested that overfishing of large wrasses and triggerfishes caused the unusually high urchin densities in populated regions of the Caribbean before the mass mortality of *Diadema antillarum* in 1983 (Lessios 1988). Mumby (2006) calculated that, following the ecological extinction of *Diadema*, parrotfish grazing alone was insufficient to prevent macroalgae from displacing corals.

Besides the mechanism of direct consumption, fishes may negatively affect invertebrate corallivores and herbivores by competitive interactions. In defending their territories, several damselfish species in the South Pacific exclude *Acanthaster* (Weber and Woodhead 1970). This exclusion apparently results in the preferred prey of the seastar (mostly acroporid corals) being more abundant and more diverse inside territories than outside (Glynn and Colgan 1988). In contrast, the species diversity of new coral recruits on the Great Barrier Reef was smaller inside territories of the damselfish *Hemiglyphidodon plagiometopon*, although the density of coral recruits (mostly acroporids) was greater there (Sammarco and Carleton 1981).

In the Caribbean, the damselfish *Stegastes planiforns* can exclude *Diadema* urchins from their territories (Williams 1980, 1981), which may also serve as refuges for certain corals (Sammarco and Williams 1982). Corals such as *Favia fragum* can apparently withstand competition with the macroalgae that dominate inside territories. Given that, first, damselfish can prevent urchins from overgrazing their territories, and second, that the algae growing within the territories provide food for the damselfish, Eakin (1987) concluded that the relationship between damselfish and their algal mats is a case of mutualism.

Parrotfishes and surgeonfishes also compete with *Diadema* on Caribbean reefs, although the urchin appears to be the dominant competitor in this case (Carpenter 1986). In particular, increases in the local abundances of these fishes have been documented following experimental removals of or natural declines in populations of the urchin (Hay and Taylor 1985; Carpenter 1990; Robertson 1991; Hixon and Beets, unpublished).

Finally, complex interactions between invertebrates and fishes can occur. Outbreaks of *Acanthaster* can kill large tracts of coral, presumably increasing the availability of substrata for macroalgal growth, which in turn may increase the local densities of herbivorous fishes and decrease densities of corallivorous fishes. This sequence was documented for some fishes both at the Great Barrier Reef (Williams 1986) and off Japan (Sano et al. 1987), although the response of herbivorous fishes was negligible. Clearly, there are many possible ecological linkages among algae, corals, invertebrate herbivores and corallivores, and reef fishes.

10.6 Implications for Reef Management and Conservation: A Complex Triangle

As a generality subject to exceptions, the coral-seaweed-herbivore triangle on healthy reefs (Fig. 10.1a) is confirmed by observations that herbivorous fishes and urchins can have very strong effects on the standing crop of reef macroalgae, thereby opening space for corals to thrive. However, other factors, such as the abundance and distribution of territorial damselfishes, shelter for schooling herbivores, water motion, and nutrient flux, as well as multiple stressors on corals, can modify this basic pattern, sometimes strongly (Szmant 2001; Cheal et al. 2010; McClanahan et al. 2011a). The degradation of the coral-seaweed-herbivore triangle (Fig. 10.1b) is also reasonable generality, in that overfishing of herbivores (or loss by other factors) can facilitate the overgrowth of corals by macroalgae. Again, however, there are exceptions and conflicting results. For example, although a negative correlation was documented between the density of herbivorous fishes and the cover of seaweeds on Caribbean reefs, the abundance of seaweeds was high even on lightly fished reefs (Williams and Polunin 2001; see also Cheal et al. 2010).

In New Caledonia and elsewhere, there may be little correlation among reef protection status (especially in lightly fished regions), coral recovery, and relative macroalgal development following severe storms and bleaching events (Carassou et al. 2013). Also problematic is determining whether seaweeds truly outcompete corals, or merely colonize dead coral surfaces after a polyp colony is killed by other factors (McCook 1999; McCook et al. 2001), including algae fostering coral disease (Smith et al. 2006). Additionally, there are sufficient differences between Caribbean and Indo-Pacific reef ecosystems and their respective stressors that extrapolating findings between ocean basins may be unwarranted (Roff and Mumby 2012).

Given the variety of factors that may modify the simple coral-seaweed-herbivore triangle (Fig. 10.1a), it may be more prudent to include the many biotic and abiotic environmental factors that can affect the outcome of the basic interaction web. Figure 10.6 is offered as an image of the

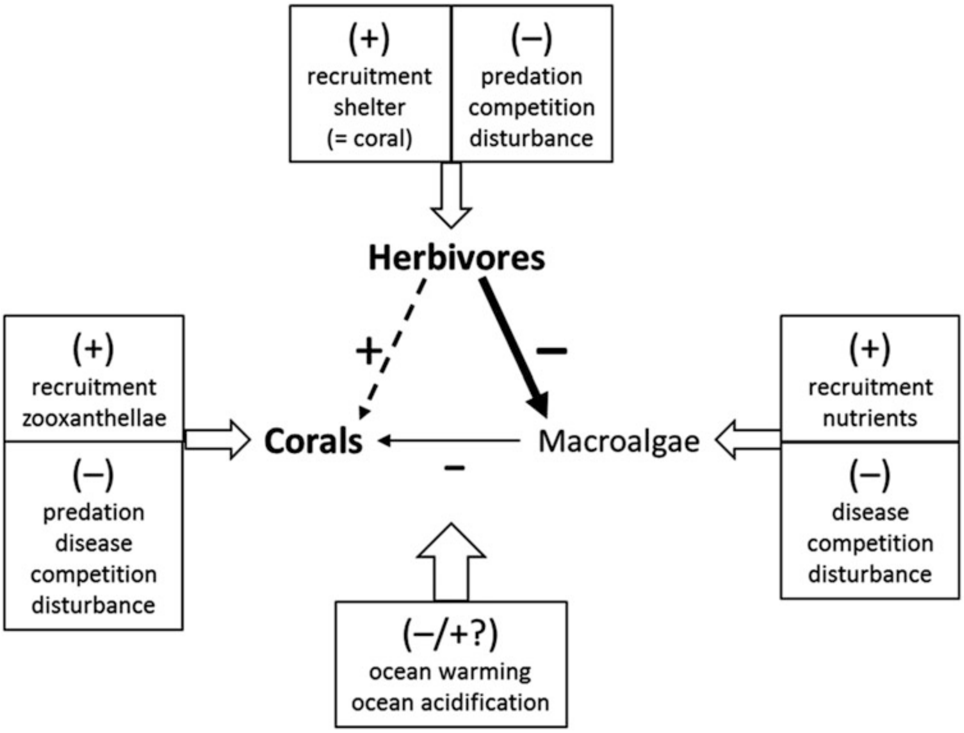

Fig. 10.6 The coral-seaweed-herbivore triangle including some of the major complicating factors that affect each member of the triad. Note that "predation" can include disease, parasitism, carnivory, and fishing mortality, and "disturbance" can include wave surge, sand scour, sedimentation, and pollution. Ocean warming and acidification will affect all members of the triad in ways that are likely to be negative for corals (and perhaps fishes) and may be positive for macroalgae. The relative strengths of all direct and indirect interactions among all these factors (among others) will ultimately determine whether or not the triangle is dominated by interactions illustrated among herbivores, macroalgae, and corals. Given the number of factors involved and high variation in their intensities, the simple coral-seaweed-herbivore triangle is unlikely to operate in every system, despite its broad relevance

more realistic triangle, including some of the more important complicating factors (see related figures by Mumby and Steneck 2008; Nyström et al. 2012; Burkepile et al. 2013). Recent models have attempted to address some of this complexity (Mumby 2006; Mumby et al. 2007; Ruiz Sebastián and McClanahan 2013).

From a management perspective, conserving herbivores is clearly important for keeping reef seaweeds in check (Mumby et al. 2007a, b; McClanahan et al. 2012). Given that seaweeds have evolved a variety of structural and chemical defenses that inhibit particular herbivores (reviews by Hay and Fenical 1988; Steneck 1988; Duffy and Hay 1990; Hay 1991, 1997), maintaining both the abundance and species diversity of herbivores of a variety of sizes is likely the best means of ensuring that seaweeds do not displace corals, as demonstrated experimentally by Burkepile and Hay (2008, 2010) and suggested by the modeling studies of Mumby (2006) and the correlative field studies of Cheal et al. (2010). Parrotfishes, especially larger individuals, are often seen as a particular conservation target for enhancing the ecological resilience of coral reefs (Bellwood et al. 2004, 2012; Mumby 2006, 2009; Mumby et al. 2006, 2007a, b). Larger parrotfish are particularly important in controlling macroalgal biomass (Jayewardene 2009).

Beyond the general rule of thumb of "conserve and foster herbivores," the complexity of interactions among fishes, seaweeds, corals, and their reef environment makes it difficult to provide explicitly detailed predictions relevant to the management and conservation of coral reefs. For example, before predicting how fishing will secondarily affect the benthic community on a reef explicitly, one must know how different fish populations will respond to exploitation, and as a prerequisite, what determines the local population sizes of fishes in the absence of fishing. Understanding of the mechanisms driving and regulating the population dynamics of coral-reef fishes is an onerous undertaking (e.g., Hixon et al. 2012). Nonetheless, it is clear that both corallivores and herbivores are often subjected to intensive overfishing (review by Russ 1991; Roberts 1995; Polunin and Roberts 1996; Bellwood et al. 2012), so rules of thumb are essential for fostering the reef resilience.

The immense complexity of coral-reef ecosystems means that the demise or outbreak of a single species or functional group of species due to human activities may have unanticipated and possibly severe consequences for the remainder of the system (Chap. 11). Reef fishes, in particular, manifest a very complex variety of direct and indirect effects on the benthos of coral reefs (e.g., Figs. 10.4 and 10.5) – far more complicated than the simple triangle illustrated in Fig. 10.1, or even the complex triangle illustrated in Fig. 10.6. The numerous indirect interactions between fishes and the reefs they inhabit may simultaneously be both positive and negative from a human perspective. For example, damselfish territories may be sites of high productivity and species diversity of seaweeds and associated fauna, including new recruits of reef fishes, but may also be sites of reduced coral growth and weakened reef framework. The multitude and complexity of these effects severely limits our ability to predict the precise outcome of active management of any particular species, let alone multiple species.

Although reef systems may be too complicated to allow us to predict explicit outcomes of human activities beyond basic concepts like the coral-seaweed-herbivore triangle, the patterns summarized in this and other chapters of this volume do provide an important lesson: managers should cast a skeptical and cautious eye on proposals to strongly reduce the abundance of any native coral-reef inhabitant. The secondary results of such alterations may be both unexpected and undesirable. Perhaps more than any other natural system, coral reefs verify John Muir's (1911) axiom: "When we try to pick out anything by itself, we find it hitched to everything else in the universe." Given the widespread degradation of coral reefs occurring worldwide, perhaps the most effective approach to the conservation and management of these amazing and valuable ecosystems is to ensure that some reefs – especially those buffered from or adapted to ocean warming and acidification – are fully protected from regional human impacts (both extractive and nonextractive) in large marine reserves, thereby ensuring substantial local populations of herbivorous fishes and other resilience mechanisms (Pandolfi et al. 2005; Hughes et al. 2006; Mumby and Steneck 2008; Steneck et al. 2009; Edwards et al. 2010; Selig and Bruno 2010).

Marine reserves may harbor more coral-reef piscivores that may inhibit increases in herbivore populations (Graham et al. 2003), but there is ample evidence that piscivores also play an important role regulating and thus stabilizing the population dynamics of their prey (Hixon and Jones 2005). Of course, marine reserves are necessary but not sufficient for saving reefs; multiple sources of protection and active management are essential (Pandolfi et al. 2005; Nyström et al. 2012; Carassou et al. 2013). In any case, despite broad protections in substantial regions such as the Great Barrier Reef Marine Park in Australia and the Papahānaumokuākea Marine National Monument in Hawai‘i, humankind has by-and-large been woefully slow in fostering the resilience of our remaining coral reefs (Mora et al. 2006; Hughes et al. 2010). Time is short to reverse this dangerous trend.

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Coral Disturbance and Recovery in a Changing World

11

Margaret W. Miller

Abstract
Much of the historical development of ecological thought has revolved around disturbance and the responses of organisms, species and assemblages. Coral reefs have figured prominently in this intellectual development. Historically, observed coral populations and communities have been understood as displaying the net balance (though rarely reaching an equilibrium) between disruptive forces and those leading to recovery of coral abundance and composition. The fact of drastic coral decline over the past few decades implies a shift in this balance toward greater influence of disturbance and/or lesser effectiveness of recovery. This chapter examines the likelihood that both expanding disturbances (in identity, scale, intensity, and/or frequency) and impaired recovery processes (resulting at least partially from expanding chronic disturbances) are likely contributors to this shift. The contemplation of progressively more radical management interventions to combat expanding disturbance and faltering recovery invokes a need for targeted research to clarify and minimize risks while maximizing benefits of such intervention strategies.

Keywords
Resilience • Chronic • Bleaching • Disease • Storms

11.1 Introduction

The concepts and theory of disturbance and recovery are seminal in the field of community ecology and much of this theory is based on coral reefs as a model system. These concepts came to the forefront in the effort to explain the origin and maintenance of species diversity in communities. That is, how do so many species, especially species that appear to make their living in a similar manner (i.e., have similar niches) persist in equilibrium? Several pivotal works in the 1970s revealed that periodic repeated disturbances at different scales generally preclude equilibrium, climax conditions in marine benthic communities (including coral reefs) where space and light are the primary limiting resources (Dayton 1971; Sutherland and Karlson 1977; Connell 1978). By preventing an equilibrium climax community, disturbance is understood to allow the maintenance of high species diversity by precluding competitive exclusion (Connell 1978).

Disturbance, by definition (Box 11.1), is bad for the status quo but not uniformly bad. The effects of a given disturbance event will depend not only on the nature of the disturbance but also on the previous experience of the present assemblage (Hughes and Connell 1999; Mumby et al. 2011). In addition, the variable nature of biotic populations and species implies that the experience and therefore the effects of disturbance will vary between species and among individuals within a species according to their tolerances. These tolerances clearly change over time as genetic or physiological adaptation may adjust the tolerance of individuals within a species and changing species

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Box 11.1

For the purposes of this review, **disturbance** will be referenced as "*killing, displacement, or damaging of one or more individuals (or colonies) that directly or indirectly creates an opportunity for new individuals (or colonies) to become established.*" (Sousa 1984, p. 356).

Box 11.2: Typologies of Disturbance

Natural vs. Anthropogenic: As denoted by the concept of an 'Anthropocene' age, nothing is truly free of anthropogenic influence. We have increasing understanding that 'natural' processes determining carbonate chemistry, storms, disease, etc. are all affected by the rapidly changing atmospheric/CO2/ climate system. Most everything is BOTH

Biotic vs. Abiotic: Similarly, changes in fundamental ocean chemistry and climate interact with the biology of organisms in ways that substantially blur this distinction. For example, increased river runoff from extreme rainfall events has been convincingly linked with destructive outbreaks of corallivores (Fabricius et al. 2010).

Global vs. Local: Climate and chemistry-based disturbances are clearly global in origin, but the experience of them is also local. This distinction may be important from a patch dynamics or metapopulation perspective, but several important threats (especially disease and often bleaching) appear to operate at multiple scales

Chronic vs. Acute: This is a highly relevant dichotomy as these likely have distinct consequences for recovery and evolutionary outcomes. Both types are probably increasing (e.g., extreme thermal bleaching events AND nutrient loading are likely increasing in many reefs). However, as the frequency of acute disturbances increases, as expected for thermal bleaching over the next two decades, it also blurs to a chronic disturbance.

composition may adjust the tolerance of the extant community. Such shifts in species and community tolerance can happen rapidly, especially within the context of rapid environmental changes, and are crucial interactors with disturbance and recovery (discussed more completely in Chap. 7).

The consequence, however, of disturbance being bad for the status quo is that it creates opportunities for newcomers, both species and individuals. The effective utilization of such opportunities requires successful recruitment and growth of the newcomers. For corals, successful recruitment is determined by a complex interplay of fecundity, fertilization, connectivity, settlement and post-settlement survival (Ritson-Williams et al. 2009). Clearly, the community observed at a given point of space and time represents the balance of loss to recent disturbances and the relative progress of newcomers in recruitment and growth, which will be referred to as recovery. In the classical conception of a coral reef as a stable system with high coral cover and high community diversity, a favorable balance of disturbance and recovery gave the 'illusion' of equilibrium.

In the past two to three decades, as coral reef ecosystems and corals in particular have begun and proceeded quite far down a course of decline, this balance of disturbance and recovery processes appears to be shifting toward dominance by the former. The progression of ecological theory during this period has been dominated by the growing recognition and discussion of tipping points, alternate stable states, and resilience. Recovery processes may fail to return the community to a pre-disturbance state (i.e. failure of resilience) either because recruitment and growth of newcomers are failing or because the disturbances are too frequent, intense, and/or diverse for recovery to run its course. The result may be an alternate stable state if punctuated acute disturbances are most important, or a slow, steady decline if chronic disturbances dominate (Hughes et al. 2012). The trajectory of reefs at Discovery Bay, Jamaica (Fig. 11.1) provide the archetypal example of lost resilience in the face of both acute (hurricane) and chronic (impaired grazing due to overfishing and collapse of grazing urchin populations) disturbances (Hughes 1994).

This chapter will evaluate trends in both disturbance and recovery processes in the radically changing coral reef environments of the 'Anthropocene'.

11.2 Disturbances: Types and Impacts

Many different typologies of coral reef disturbance have been discussed in previous works. Several of these differentiations are losing meaning in an era wherein human influence on otherwise 'natural' or 'abiotic' systems (e.g., climate or ocean carbonate equilibrium) is becoming predominant (Box 11.2). The dichotomy of acute vs. chronic disturbance will be maintained in the current discussion as it retains strong influence on both the recovery processes and on the potential evolutionary responses that result. It should be noted that various disturbance types may occur as both chronic and as acute events, and hence interact and compound each other in complex ways.

Various modeling studies have projected effects of various disturbance types or frequencies on coral assemblages. For example the model of Wakeford et al. (2008), based on observed coral mortality, recruitment, growth, and competitive outcomes in a reef patch at Lizard Island between 1981

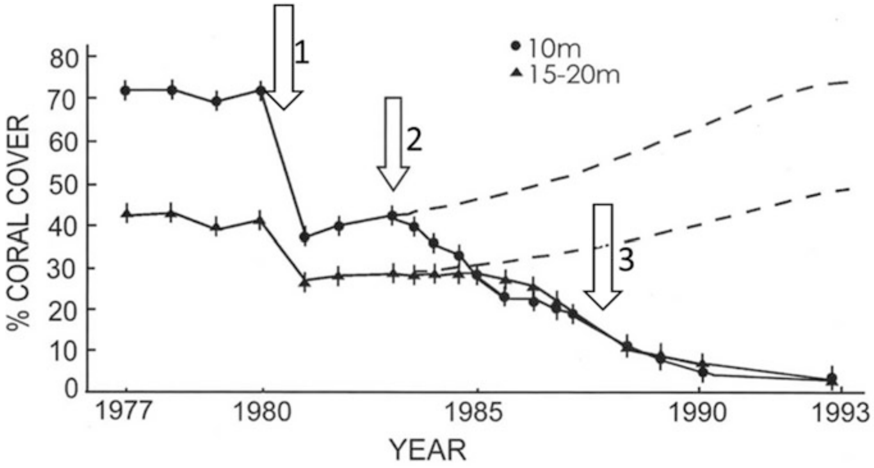

Fig. 11.1 Coral cover response to sequential disturbances in the archetypal example of Discovery Bay, Jamaica. The severe acute disturbance of Hurricane Allen (*1*) precipitated significant coral mortality, after which some recovery was evident, and at a pace that could have returned coral cover (not necessarily community or population structures) to the pre-Allen baseline in less than 15 years (*dotted lines*). However, the acute mass mortality of *Diadema antillarum* (*2*) resulted in massive macroalgal proliferation (a chronic disturbance) which curtailed coral recovery. A following hurricane, Gilbert (*3*) continued coral mortality. Subsequent recovery of *D. antillarum* (at least in small patchy sites) has been reported to have decreased macroalgal cover and greatly increased coral juvenile density in this region (Edmunds and Carpenter 2001) (Redrawn from Hughes 1994)

and 2003, indicates that the actual assemblage was maintained when mortality was concentrated in acute disturbance events (cyclones and/or predation outbreaks) up until 1997. After this date, the observed coral assemblage was only emulated in the model by incorporating additional chronic mortality factors into the model. These authors suggest a fundamental shift in the disturbance regime and/or resilience capacity of this reef during the 1990s decade.

11.2.1 Acute Physical Disturbance

Tropical storms and cyclones are the quintessential physical disturbance, though various degrees of water motion (from swell to tsunamis) and/or substrate disturbance (e.g., earthquakes or ship groundings) may have similar disturbance effects (i.e. killing coral and/or smashing substrate). Their effects can be dramatic but patchy, with the more severe events also causing additional physiographic or geological changes (Stoddart 1963; Connell et al. 1997). Events causing damage to underlying substrate or flow regimes further challenge the recovery potential and time frame. However, over historical times, recovery from storm damage to coral communities was presumed, and many aspects of coral life history, dynamics and genetic structure were attributed to the influence of storm events and their variable effects in time and space (e.g., Hunter 1993; Hughes and Connell 1999; Highsmith et al. 1980; Foster et al. 2013). Tabular or branching coral species show greater susceptibility to storm damage than encrusting or mounding corals. Depth and other habitat characteristics as well as recent history strongly influence the amount of coral damage. For example, Hughes and Connell (1999) delineate the sequence of storm events and their relative impacts in different habitat types in two long term data sets. The effects of repeated storm impacts in both Heron Island, Australia, and the north coast of Jamaica, varied strongly according to the habitat type, the relative dominance of vulnerable (branching or tabular) coral species, and, relatedly, the duration and nature of recovery from the previous disturbance. In both study regions, vast changes in coral composition as well as reduced abundance resulted from storm disturbance when tabular (generally *Acropora* spp.) corals dominated and little change in composition (and much less change in abundance) was wrought by storms when massive corals comprised the bulk of the community (Hughes and Connell 1999).

Gardner et al. (2005) conducted a large meta-analysis of hurricane effects on Caribbean coral reefs from 1980 to 2001. They estimated that Caribbean reefs affected by a hurricane during this period lost an average of 6 % coral cover per annum in comparison to 2 % per annum for sites not affected by storm damage, a significant difference largely attributable to an average 17 % loss in coral cover in the year following a hurricane impact. Variation in these rates of loss showed positive correlation to storm strength and duration since the previous storm impact. Gardner et al. (2005) also noted a greater difference between the fate of hurricane impacted vs. not-impacted sites in the 1980s decade in comparison to the 1990s, when all sites showed similar rates of decline suggesting non-hurricane factors came to dominate coral trends. On Australia's Great Barrier Reef, comprehensive monitoring of 214 sites between 1985 and 2012 yielded estimates of average mortality of 1.63 % coral cover per year to cyclones, which was marginally higher than the mortality estimates for predation (1.42 % per year) and substantially higher than that for bleaching (0.34 % per year) (De'ath et al. 2012).

In more recent times, storm-induced coral disturbance has often resulted in follow-on mortality rather than rapid recovery. Evidence is mounting of the linkage of physical disturbance with subsequent coral mortality from disease and/or predation, at least in the Caribbean (Brandt et al. 2013; Knowlton et al. 1981; Bruckner and Bruckner 1997) though the mechanisms behind this interaction, particularly for disease, are not well documented. It is clear, however, that continuing coral mortality following a storm, including mortality of potential fragment propagules, greatly hinders recovery (Williams et al. 2008a). Additional ensuing threats impairing post-storm recovery include the dispersal and propagation of the excavating sponge, *Cliona tennis* (Lopez-Victoria and Zea 2004) and increased impact from generalist coral predators that may concentrate on reduced or injured populations of preferred prey (Knowlton et al. 1990; Bright 2009)

While the effects of storm disturbances may be increasing over time, there is also the question of whether these disturbance events, themselves, are increasing in frequency or intensity. Additional heat in the ocean/atmosphere system may be expected to drive more tropical cyclones and, indeed, Grinsted et al. (2012) report a significant correlation of large Atlantic cyclone occurrence with warm years and a significant increasing frequency of such events since 1923. A significant increase in the number and proportion of strong tropical cyclones, but not frequency of all cyclones, was detected across all ocean basins over a 35 year period of warming seas (Webster et al. 2005; Emanuel 2005). Meanwhile, Mumby et al. (2011) conducted a spatio-temporal analysis of hurricane occurrence in the Caribbean and showed that Atlantic storms from 1901 to 2010 have been temporally clustered in certain areas, yielding lesser overall reef damage/decline than if storms were randomly distributed. However, the specter of more damaging storms in the future, combined with apparently growing interactions of physical disturbance with other sources of mortality suggests worsening ultimate effects.

11.2.2 Acute Thermal Stress and Mass Bleaching Events

Thermally induced mass bleaching events have become the hallmark of global warming effects on coral reefs, but regional-scale bleaching/mortality events can also result from other environmental stressors such as cold temperatures (Lirman et al. 2011) or low salinity runoff events (Haapkylä et al. 2013). Coral bleaching, the breakdown of symbiosis between the coral host and its zooxanthellae endosymbionts resulting in lost energetic subsidy to the host, can occur following a range of physiological stresses. Comprehensive reviews of bleaching causes and consequences have been provided by Brown (1997) and Baker et al. (2008). Mass bleaching events can be predicted on the basis of cumulative thermal stress measured as Degree Heating Weeks (DHW) over the long term monthly maximum. Generally, coral bleaching risk is considered to be elevated at doses above 4 DHW, i.e. 1 °C for 4 weeks or 4 °C for 1 week (Liu et al. 2006). Recent trends in thermal stress dosage have been increasing at large regional scales with considerable variation at individual sites. Figure 11.2 shows annual maximum DHW averaged over the Caribbean region with larger peaks evident over time corresponding to severe mass bleaching events (Eakin et al. 2010). Similar increasing regional trends in mean temperature or thermal stress dosage have been documented in the Coral Triangle (Penaflor et al. 2009), the Arabian Gulf (Riegl et al. 2011), and globally (Lough 2000). Increasing temperature trends are expected to continue with the frequency of mass bleaching disturbances predicted to increase over the coming decades, possibly to annual or nearly so (e.g., Donner et al. 2005) with dire consequences for coral populations and coral reefs (McClanahan et al. 2007; Hoegh-Guldberg 1999).

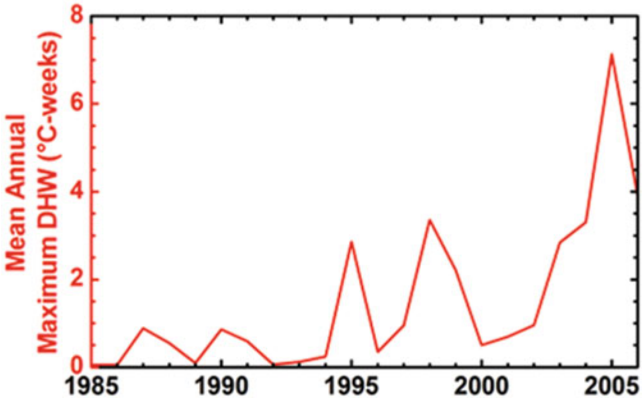

Fig. 11.2 Cumulative warm thermal stress in Degree Heating Weeks (DHW) over two decades averaged over the Caribbean basin (0.5° map pixels containing coral reefs, bounded by 35°N, 55°W, and the coast of the Americas). Severe regional mass bleaching events occurred in 1995, 1998, and 2005 (Source: Eakin et al. 2010)

The first recognized global-scale mass bleaching events were associated with El Niño warming events in 1982–1983 and 1997–1998. Additional basin-scale events were documented in 2005 in the Atlantic/Caribbean (Eakin et al. 2010) and 2010 throughout Southeast Asia and Arabian Gulf regions (Riegl et al. 2011; Guest et al. 2012). Cumulative thermal stress events as well as corresponding bleaching events in the Caribbean region appear to be intensifying over time (Fig. 11.2; McWilliams et al. 2005).

Differential thermal bleaching susceptibilities among taxa (Marshall and Baird 2000; McClanahan et al. 2007; McField 1999) and among members within a species either based on factors such as symbiont type, latitude or habitat (Ulstrup et al. 2006), and prior thermal history (Guest et al. 2012; Middlebrook et al. 2008; Thompson and Van Woesik 2009) clearly influence the patterns of bleaching and resultant mortality. Generally, colonies or taxa previously exposed to moderately fluctuating or moderately extreme temperatures appear to show greater thermal thresholds and lesser severity of bleaching.

The direct mortality caused by bleaching is generally poorly quantified, but represents the most severe aspect of this disturbance. Meanwhile, bleaching itself represents disturbance as ‘damage’ (Box 11.1) which can manifest as increased disease susceptibility (discussed below) or impaired reproduction. Thermal stress and bleaching of parent colonies have been shown to limit subsequent reproductive success, primarily via reduced fecundity (Szmant and Gassman 1990; Baird and Marshall 2002) and possibly reduced fertilization (Omori et al. 2001). Baird and Marshall (2002) is one of the few studies to quantify both mortality and reproductive impacts by following the fate of bleached colonies of four species after the 1998 bleaching event. Two *Acropora* species (*hyacinthus* and *millepora*) showed greater whole colony mortality than *Porites lobata* and *Platygyra daedalea*. These two *Acropora* spp. also varied in their subsequent reproductive impairment with only 45 % of bleached *A. hyacinthus* colonies gravid the following year, compared with 88 % for *A. millepora*. Hence, bleaching susceptibility, associated mortality, and subsequent reproductive impairment are all known to vary greatly among species.

Like physical disturbance, thermal stress and bleaching are often associated with follow-on mortality from coral disease. For example, bleached corals in the US Virgin Islands suffered over 60 % mortality several months after the 2005 bleaching event (Miller et al. 2009). Individual bleached colonies also show greater likelihood of manifesting disease mortality (Brandt and McManus 2009; Muller et al. 2008). Ritchie (2006) describes a possible mechanism for increased disease susceptibility of bleached corals in that the usual antibiotic activity of mucus-associated microbes was found to be absent in mucus from bleached colonies.

11.2.3 Acute Disease Outbreaks

The profound effect of acute diseases (those causing rapid tissue mortality) on coral assemblages and coral reef communities, especially in the Caribbean basin, in the past three decades is difficult to overstate, yielding massive changes in the overall makeup of coral communities. Beginning in the early-mid 1980s and with progressive extent and effect through the next two decades (Sutherland et al. 2004) disease has ravaged coral populations including the major reef-builders, *Acropora* spp (Aronson and Precht 2001; Gardner et al. 2003) and later *Montastraea* (now *Orbicella*) spp. (Miller et al. 2009; Bruckner 2012). Impacts of disease outbreaks in the Indo-Pacific region have been less severe, but added scrutiny of coral disease phenomena throughout the Indo-Pacific basin in recent years has revealed that coral disease affects most regions at increasing prevalence and in greater varieties with time (Raymundo et al. 2008). Coral disease impacts have been reported even in the most remote Pacific reefs (Williams et al. 2008b; Aeby 2005). Outbreaks occur both in concert with other acute (discussed above) and chronic disturbances such as nutrient or sewage pollution (Kaczmarsky and Richardson 2011), but can also occur in apparent isolation (Richardson et al. 1998; Nugues 2002; Roff et al. 2011; Miller and Williams 2006; Williams et al. 2008b).

The apparent disease-induced range-wide mass mortality of grazing urchins, *Diadema antillarum*, also in the early 1980s, is the other disease event of profound importance in the recent history of Caribbean reefs. The loss of grazing capacity on most reefs was a major contributor to described lack of recovery on these reefs (Fig. 11.1; Lessios 1988).

11.2.4 Acute Predator Outbreaks

The most influential predator on Indo-Pacific corals, the crown-of-thorns seastar (COTS; *Acanthaster planci*) undergoes dramatic population outbreaks which kill large amounts of coral. COTS display strong and consistent preferences among different coral prey, yielding highly selective mortality of Acroporids and other tabular growth forms in affected reefs with potentially strong effects on coral community structure. COTS outbreaks are common, regional scale acute disturbances across the Indo Pacific region (Birkeland and Lucas 1990; De’ath and Moran 1998), though their relative influence may be underappreciated in regions with less rigorous monitoring (Baird et al. 2013). Across Australia’s entire Great Barrier Reef, it is estimated that COTS are responsible for an annual decline of 1.43 % of total coral cover, second only to cyclone mortality and over four times higher than mortality attributed to bleaching (De’ath et al. 2012). Recent studies provide strong evidence for the early hypothesis (Birkeland 1982) that local environmental factors, specifically nutrient loads driving planktonic productivity fostering high larval recruitment, are most responsible for outbreaks (Fabricius et al. 2010; Brodie et al. 2005), as opposed to autogenous genetic factors in 'rogue' populations which might lead them to outbreak (Timmers et al. 2012). There is also some evidence that tropic cascades related to fishing may also enhance COTS outbreaks (Sweatman 2008). These factors point out the strong anthropogenic influence even in this 'natural, biotic' mechanism of acute disturbance.

While corallivores can be influential in some Caribbean reefs, they do not seem to undergo the outbreak dynamics associated with COTS or, to a lesser extent, Pacific corallivorous gastropods, *Drupella* spp. (Turner 1994). Outbreaks of *Drupella* snails have been reported to impose up to 75 % coral mortality but such reports are rare relative to COTS. Largely ecologically analogous corallivorous snails in the Caribbean, *Coralliophila abbreviata*, can impose substantial coral mortality, but acute predation seems to be more related to coral population declines (Knowlton et al. 1990), rather than corallivore population increases. Fish can certainly also disturb corals, either by predation or territorial activities (Chap. 10) but these are generally of a chronic nature causing relatively small amounts of mortality but potentially enhancing other disturbances and causing some reproductive impairment (e.g., Rotjan et al. 2006; Rotjan and Lewis 2009)

11.2.5 Chronic Disturbances

While certain sorts of chronic stressors may cause direct mortality (e.g., severe sedimentation), most often, their disturbance effects are manifest as sub-lethal damage. From our definition of disturbance (Box 11.1), this means that the opportunity provided for other organisms may be indirect (e.g., via lower production of offspring) or slower to manifest via delayed mortality. Such indirect effects of chronic disturbance, particularly on reproduction and recruitment, greatly influence the recovery side of our balance as discussed in the next section.

It is also axiomatic that any acute disturbance can also be experienced in background levels as a chronic effect. Wave damage, predation, disease, and to some extent, bleaching can all cause small scale disturbance/mortality which, due to its ubiquitous patchiness over time and space, should recover seamlessly. On the other hand, increasing frequencies of acute disturbances, such as predicted annual occurrence for thermal mass bleaching, may yield a dire situation of 'constant acute' disturbance, which perhaps should still be distinguished in effect from chronic disturbance.

11.2.5.1 Water Quality Decline

Anthropogenic, land-based inputs to the coastal ocean broadly include sewage and runoff as the major routes of introduction, but introduce a host of constituent stressors including sediment, nutrients, pharmaceuticals, pesticides and other toxicants, microbes, etc. Direct causal evidence of coral mortality or damage is difficult to determine in open ocean environments, but it is clear that this range of factors, especially in combination, have a negative effect on corals (Fabricius 2005). Evidence for combined interaction of poor water quality (or a surrogate of nearby human population density) with coral impairment and disease is increasing (Haapkylä et al. 2011; Kline et al. 2006; Downs et al. 2005; Aeby et al. 2011).

As Fabricius (2005) states 'In most cases where terrestrial runoff causes reef degradation, disturbances other than eutrophication were the proximate causes of coral mortality, and runoff effects only became obvious when hard corals failed to reestablish after such disturbances' (p. 134). Reproductive impairment, both via direct stress on the parent colonies and on larvae themselves, may be the most influential effects of poor water quality (Richmond 1997). Increased intensity of land use and coastal development in many regions has clearly resulted in decreasing water quality over time (McKergow et al. 2005), including the introduction of completely novel substances such as pharmaceuticals (Richardson et al. 2005). Most sources of water quality decline such as sewage, agriculture, and other land-use changes are directly related to human population densities, especially in coastal areas, but also inland. As such, these chronic disturbances are expected to increase over time with human population abundance and consumption levels. However, land-based pollution is also a factor that can be managed effectively and so has the potential to decline in well-managed localities.

11.2.5.2 Fishing and Trophic Disruption

A nigh-ubiquitous disturbance that affects coral reef ecosystems is the trophic disruption that results from artificial removal of biomass by fishing. While corals are directly removed in some locations, local protection and management are most often able to curb this direct disturbance and so the effects of fishing on corals are largely indirect, and hence, more difficult to quantify. For example areas where grazers are intensively removed are more prone to 'phase shifts' to persistent seaweed dominated reefs when acute disturbances cause coral mortality (Jackson et al. 2001; Hughes et al. 2007; Hughes 1994). Conversely, various modeling studies have described how maintaining high levels of grazing can mitigate other disturbances' (e.g., hurricanes or bleaching mortality) effects on coral decline (Edwards et al. 2010; Mumby et al. 2007). Similarly, some evidence suggests that more diverse fish trophic webs in no-take reserves can reduce the spread of coral diseases, likely via reduced transmission by coral-feeding butterflyfishes (Raymundo et al. 2009). The intensive, long

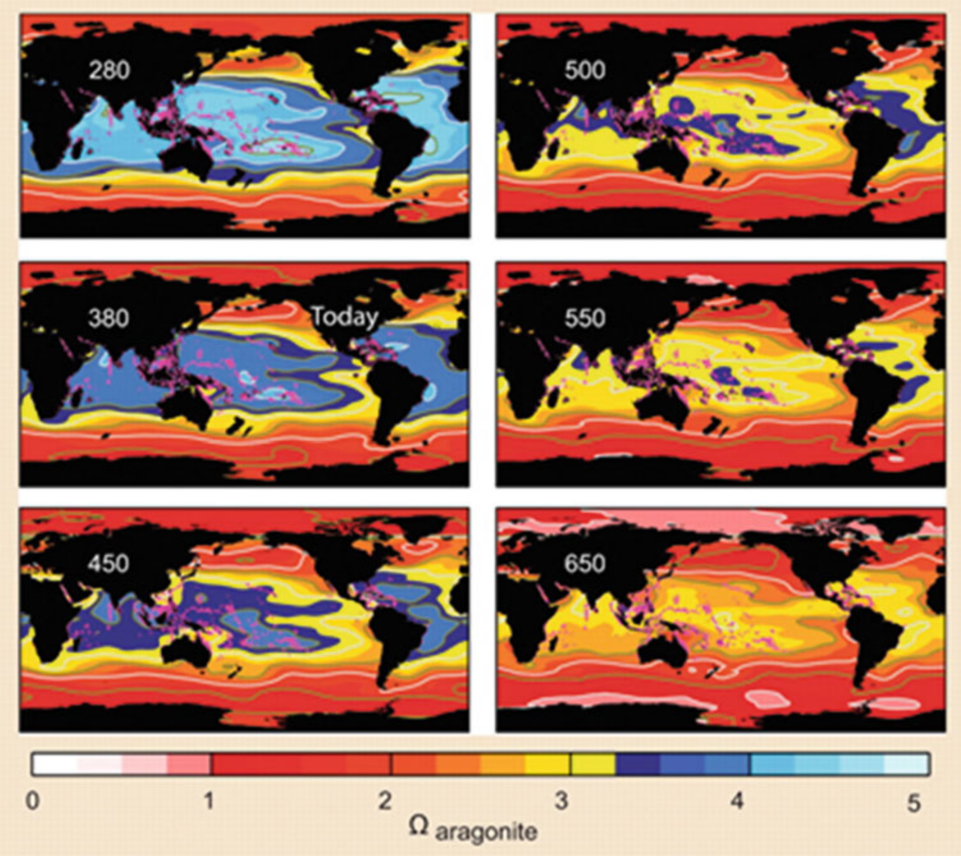

Fig. 11.3 Projected global patterns of aragonite saturation state (Ω) showing expected progressive expansion and intensity of chronic ocean acidification disturbance throughout tropical seas. Simplistically, calcification requires greater energetic investment by corals under lower levels of Ω (From Hoegh-Guldberg et al. (2007). Reprinted with permission from AAAS)

standing, and ubiquitous changes in coral reef food webs from overfishing have been posited to have wrought such profound alterations of trophic structure that microbial and organic carbon dynamics have been disrupted (Jackson et al. 2001) which can also induce coral mortality and disease (Smith et al. 2006; Kline et al. 2006). Although manageable, fishing pressure is also likely to increase with human population and is thus likely to grow in the foreseeable future.

11.2.5.3 Carbonate Chemistry Changes

Ocean acidification is the term used to describe the process of absorption of excess CO_2 from the atmosphere into the ocean yielding alterations in the carbonate chemistry equilibrium of ocean waters. The resulting reduced pH and saturation levels of aragonite (the carbonate mineral form of which scleractinians build their skeletons) are expected to impair coral calcification (Cohen and Holcomb 2009), possibly their resistance to physical disturbance (Chap. 4), and their reproduction (though likely via indirect mechanisms such as increased fertilization limitation (Albright et al. 2010), altered settlement cues (Doropoulos et al. 2012), and slowed post-settlement growth rates (De Putron et al. 2010; Suwa et al. 2010; Nakamura et al. 2011). Modelling projections (illustrated in Fig. 11.3) clearly show the anticipated increase in severity and geographic extent of this stressor over the remainder of the twenty-first century.

11.2.6 Ecosystem Effects of Disturbance

The dramatic disturbance-induced coral declines of recent decades beg the question of how coral reef ecosystems are affected. Certain obligate corallivores or coral-dwellers (Stella et al. 2011) clearly suffer when coral is disturbed. Live coral cover, itself, does significantly enhance reef fish communities (Coker et al. 2012), though the loss of physical structure probably has more profound effects and the maintenance of the skeletal structures of even dead coral contribute greatly to habitat value and ecosystem function of reef habitats (Graham et al. 2006; Wilson et al. 2006). Indeed, the more novel sources of disturbance mortality (bleaching and disease) largely leave skeletal structures in place. However, without living coral to maintain/replace this structure, erosive forces will inevitably whittle it away (Chap. 4). Graham et al. (2008) in a meta-analysis of reef change across nine regions of the Indian Ocean showed a strong correlation of coral cover loss (the primary driver being the 1998 mass bleaching) and loss of structural complexity within 7 years of the acute disturbance. Large scale meta-analyses for Caribbean reefs indicate a long term decline in the architectural complexity of Caribbean reefs (Alvarez-Filip et al. 2009) and simultaneous declines in fish communities that appear to be better explained by habitat degradation than direct fishing pressure per se (Paddack et al. 2009). Combined with poorer cementation/accretion and reduced coral growth rates under declining carbonate saturation environments and potentially increased dissolution and bioerosion rates due to acidification (Andersson and Gledhill 2013), the structural degradation of coral reefs and hence degradation of carrying capacity for associated species is likely to accelerate under increasing CO_2 futures.

11.3 Recovery Processes

Recovery of reef ecosystems in the modern ecological literature has substantial overlap with the term 'reef resilience', the speed or effectiveness with which a given reef returns to a pre-disturbance state. There is broad consensus that fundamental ecological processes such as grazing, or other complex interactions affecting coral recruitment and growth are the primary determinants of reef resilience. In the past few decades, the literature is replete with examples of lack of recovery, particularly on Caribbean but also Indo-Pacific reefs. As early as 1997, a synthesis of reef recovery studies indicated a more or less complete lack of recovery on disturbed West Atlantic reefs (Connell 1997). In addition to the intensifying cycles of disturbance described above, the proliferation of macroalgae and lack of coral recruitment, particularly for reef-building species, are associated with poor recovery. The fact of coral reef degradation throughout most all regions of the world implies that the processes of coral recovery lag the combined effects of disturbances. The previous section described many types of disturbance effects, many of which are understood to be increasing individually, and are most certainly increasing in combination. Whereas acute disturbances often occur very rapidly (e.g., days to weeks), are obvious, and relatively easy to quantify, the processes whereby corals recover are slow (e.g., decades) and important stages (e.g., coral larvae and post-settlers) are difficult or impossible to observe directly. This means that our general understanding of recovery processes and potential trends are much more poorly understood.

Graham et al. (2011) review ecological studies of reef recovery from the 1960s to 2009, analyzing five categories of predictors for reef recovery (in this case, measured as coral cover); disturbance characteristics, reef characteristics, reef connectivity, ecological characteristics and anthropogenic influences. Interestingly, they document an exponential increase in the number of published recovery studies in the latest decade as well as in the diversity of instigating acute disturbance types. Their analyses of reef studies with positive recovery trajectories indicate that geographic region (lowest in the Eastern Pacific, followed by the Caribbean), management status of the reef (lowest in fully protected MPAs, possibly an artifact of prior reef condition rather than an effect of management itself), and the post-disturbance coral cover (faster recovery from 6 % to 10 % cover than <5 % or >10 %) were the important factors in influencing rate of coral recovery, which had an overall mean of 3.56 % per year (95 % CI = 2.89–4.43). The type of disturbance and the physiographic reef type or zone had limited influence on recovery rate, as did the adjacent human population density. These characteristics are derived from a subset of resilient reefs, however, and it would likely be instructive to perform a similar analysis comparing similar characteristics with instances where reefs failed to recover over similar time scales. Indeed, Ateweberhan et al. (2013) contrast recovery of coral cover after the 1998 bleaching event between the remote, nearly pristine Chagos archipelago (less than a decade) and the Seychelles with higher human disturbance (minimal recovery observed over ~15 years) despite similar latitude, pre-disturbance coral cover, and disturbance related declines.

The importance of biogeographic variation in reef recovery processes is highlighted by Roff and Mumby (2012) who discuss evidence and a range of explanatory hypotheses for the apparent lesser recovery potential of Caribbean versus Indo-Pacific reefs. The semi-enclosed Caribbean basin has experienced more intensive human occupation and influence, including intensive fisheries extraction disrupting trophic structure over centuries (Wing and Wing 2001; Jackson 1997). However, the lower Caribbean species diversity in guilds of both fast growing corals and reef herbivores yields a lower functional redundancy. Hence, the sequence of acute disturbances in the Caribbean which have rendered both fast-growing acroporid corals and the important grazing urchins functionally extinct in this region, has yielded a basic loss in the recovery capacity of these reefs. Roff and Mumby (2012) also compile evidence from a range of studies showing a dramatically higher rate of seaweed recruitment and productivity under experimental conditions of reduced grazing in the Caribbean versus Indo-Pacific. Despite this inherent robustness of Indo-Pacific reef resilience, the repeated patterns of coral decline across subregions (Bruno and Selig 2007; De'ath et al. 2012; Riegl et al. 2012) point to at least a similar trend of increasing imbalance with the pace of recovery lagging the pace of cumulative disturbance.

Of course conclusions about the progress or trends in coral recovery will depend also on the currency one uses. While the most data are available on percent cover, recovering population structure of long-lived organisms will necessarily take a very long time (see Fig. 11.1). More importantly, there are numerous examples that occasions of apparent rapid recovery of coral cover to a pre-disturbance level may mask fundamental changes in species composition, with sensitive species (often *Acropora* spp.) being largely replaced by more tolerant ones (Berumen and Pratchett 2006; Burt et al. 2008; Hughes and Connell 1999).

11.4 Coral Replenishment

The most basic processes of coral recovery involve the recruitment of new propagules and the re-growth of remnant tissue left from partial mortality on colonies. If the pattern and scale of disturbance allows for this latter mechanism to be effective, recovery can indeed be very rapid (one to a few years) (Diaz-Pulido et al. 2009) or greatly accelerated (Gilmour et al. 2013). The intensity and scale of many reef disturbances dictates that recovery will depend on the influx of new population members, likely larval recruits, highlighting the importance and influence of larval supply from upstream populations. Many, if not most, disturbances also have direct effects on coral reproduction and recruitment success, further impairing coral recovery and widening the potential imbalance in disturbance and recovery processes in coral reef systems. Climate change-related disturbances likely affect coral replenishment by impairing coral larval production (fecundity and fertilization), dispersal, settlement success and juvenile growth (summarized in Birkeland et al. 2013). Early life phases of corals commonly show direct susceptibility to warm temperature stress including reduced fertilization for some species, developmental abnormalities and reduced larval survivorship, and reduced settlement success (Randall and Szmant 2009; Polato et al. 2010; Negri and Hoogenboom 2011; Negri et al. 2007). Trophic disturbance of reef systems (via fish extraction or mass mortality events) generally impedes coral replenishment by degradation of settlement habitat, especially via proliferation of benthic macroalgae (Kuffner et al. 2006; Birrell et al. 2008). Disturbance from water quality degradation and sedimentation can impede coral replenishment both via larval supply (fecundity, larval survivorship), and via degradation of settlement habitat (Fabricius 2005; Birrell et al. 2005).

At some scales, both chronic and acute disturbances inherently impair coral replenishment by reducing the production of propagules via both mortality and physiological stress (described in the disturbance sections above and illustrated in Fig. 11.4). Evidence for stock-recruitment relationships in coral populations is often obscured by multiple stressors and the potentially wide scale of dispersal. However, a positive stock-recruitment relationship of acroporid corals driven largely by fecundity, rather than abundance, was shown across broad scales of the Great Barrier Reef in the late 1990s (Hughes et al. 2000). Because corals are sessile, mass mortalities from acute disturbances likely increase fertilization limitation by decreasing adult colony density (Birkeland et al. 2013). Chronic disturbances such as trophic disruption, declining water quality, ocean acidification, and rising mean temperatures also exert physiological stress and impair reproductive success across a range of early life stages. Such feedbacks are influential in instances of lack of coral recovery and suggest a reinforcing downward spiral in coral status (Fig. 11.4).

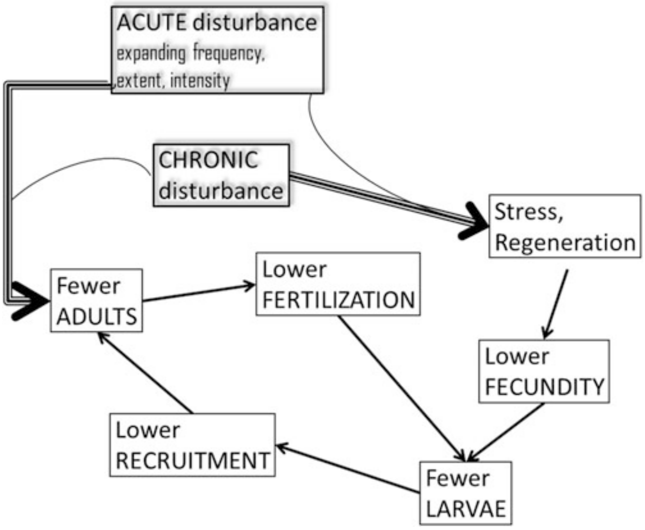

Fig. 11.4 Hypothesized feedback of disturbance cycles leading to coral decline. Acute disturbance primarily kills living coral with lesser impacts by reducing coral replenishment whereas chronic disturbances' primary influence is by reducing coral recovery

There is ample empirical evidence of reduced coral recruitment or juvenile success in chronically disturbed sites (e.g., Salinas-de-León et al. 2013; Wittenberg and Hunte 1992). There is also evidence of a temporal trend (generally decadal) of recruitment failure and/or declining success of juvenile corals (Guzner et al. 2012; Edmunds 2007; Vermeij et al. 2011; Hughes and Tanner 2000). While the cause of such declines is no doubt multifaceted, it bodes poorly for coral recovery in a regime of increasing disturbances. However, there are also many cases, including some exceptional cases in the Caribbean region, where effective coral recovery from disturbance has been documented (Manfrino et al. 2013; Graham et al. 2011). Low levels of local human influence are often cited to account for recent examples of rapid coral recovery (Manfrino et al. 2013; Ateweberhan et al. 2013; Gilmour et al. 2013).

11.5 Implications

From the realization that coral disturbance regimes are worsening while recovery capacities are waning, it follows that management strategies might beneficially focus on both of

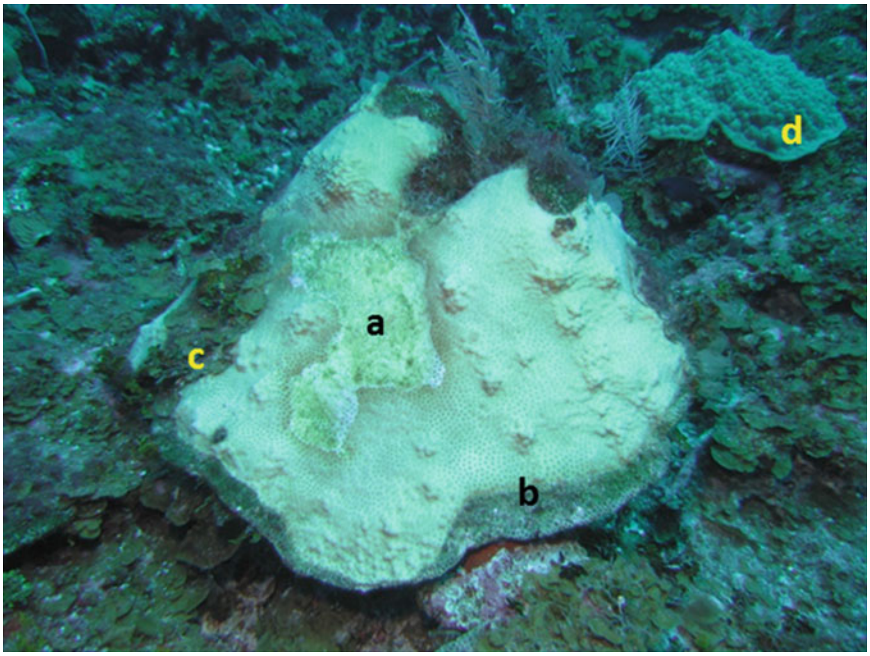

Fig. 11.5 Example of multiple acute and chronic disturbances at the colony scale. This bleached colony of *Orbicella faveolata* also displays (**a**) recent partial mortality from active disease, (**b**) old, unrecovered partial mortality from a prior unknown source, and (**c**) active macroalgal encroachment along colony margin. A normally pigmented coral of a hardier species, *Porites astreoides* (**d**) is visible in the background for reference (Photo by M. Miller)

these processes. The management strategy coined 'reef resilience' stresses this point. The recognition of complex interactions of disturbances and other factors that impair recovery invokes a need for management focus on both reducing local disturbances and managing for conditions that may enhance recruitment and recovery of corals. For example, land use and watershed management to reduce nutrient and/or toxicant loading can bolster organismal tolerance and increase thermal thresholds which apply to both bleaching disturbances (Wooldridge and Done 2009; Carilli et al. 2010) and coral larval success (Negri and Hoogenboom 2011). Other examples of management strategies to enhance replenishment most commonly include management actions to maintain herbivory as a necessary factor for coral recruitment as well as designing reserve networks to enhance connectivity and larval supply (Hughes et al. 2005; Nystrom et al. 2008; Mumby et al. 2012; McClanahan et al. 2012). However, these 'managing-for-resilience' strategies are still based on the premise that if local, anthropogenic disturbance regimes (but see Box 11.2) are appropriately managed, the recovery processes of coral communities are still capable of maintaining coral reefs within a range of states that sustain ecosystem services (i.e. corals are still resilient).

There is also a growing suspicion that resilience of coral species and assemblages is truly being lost in the onslaught of co-occurring disturbances of increasing frequency and intensity (Figs. 11.4 and 11.5). Loss of resilience suggests a need for more proactive measures to regain balance of disturbance and recovery and maintain biodiversity and ecosystem services provided by coral reefs. Parallel with the resilience strategies, proactive strategies can also be categorized as those mitigating disturbance impacts and those manipulating recovery. For example, interventions to increase the tolerance of organisms via selection for genes involved in increased environmental tolerance (Lundgren et al. 2013) or active manipulation of microbial (Teplitski and Ritchie 2009; Atad et al. 2012) or dinoflagellate symbionts (but see Coffroth et al. 2010) could enhance resistance to disturbances such as warm temperatures, pathogens, or toxicant exposure. Meanwhile most other proactive strategies relate to more fundamental manipulations of recovery and recruitment processes, including culture/restocking and 'gardening' for depleted populations of both corals and key grazers such as *Diadema antillarum* (Rinkevich 2008; Office of National Marine Sanctuaries 2011), or 'assisted migration' interventions to aid corals in the colonization of new habitats such as thermal refugia at higher latitudes (Riegl et al. 2011; Hoegh-Guldberg et al. 2008). While such strategies may seem far-fetched or radical at the current time, the rate of environmental change dictates a prompt research agenda to validate strategies that might be successful and ensure they can be implemented in ways that minimize risk of unintended consequences when and if coral reef status reaches a point that they seem prudent or necessary, if no less radical.

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Biology Trumps Management: Feedbacks and Constraints of Life-History Traits

12

Charles Birkeland

Abstract

The geologic record suggests a diverse array of reef-building corals will survive increasing CO_2, but the relative prevalence of different types will shift and the reefs will become degraded and eroded. Although many corals may not go extinct, if pH decreases effectively, reef ecosystem services will deteriorate because bioerosion will accelerate and, for some coral species, net skeletal construction will require more energy when the aragonite saturation state decreases. A similar pattern of many genera of reef-building scleractinian corals surviving, but with relatively little reef accretion, was seen through the roughly 140 million years from the Late Jurassic to the late Paleogene when the calcite seas (Mg/Ca mole ratio <2) and pH <7.8 were unfavorable for aragonitic reef accretion. The geologic record suggests that the corals most vulnerable to extinction were the fast-growing branching species because the traits that provide fast growth have tradeoffs with traits that provide tolerance of stressful environments. Iteroparous animals such as corals are adapted for survival under stressful conditions at the expense of fecundity. Surveys have recorded widespread decreases in living coral cover, but the less visible decrease in fecundity from stress may be more insidious to population recovery. Reduced fecundity and less dense population distribution can act synergistically to produce Allee effects in sessile animals such as corals. Natural coral-reef ecosystems give the appearance of inverted trophic pyramids, but when fished down by about 80 %, recovery has usually not happened, possibly because the larger individuals in the populations were a major source of fecundity. Although biomass of eukaryotes appear to be in inverted trophic pyramids, the turnover and energy is in the form of standard pyramids and although large individuals in the upper trophic levels are especially sensitive to exploitation, subsistence economies can be maintained by harvesting the medium-sized individuals. Large individuals matter more than population biomass because of the distinct roles of large individuals in ecological processes maintaining coral-reef ecosystems and the relatively large reproductive potential of big fishes. The functional traits of both the coral-reef ecosystem and its component animals provide a greater potential for exploitation by globalization in a service-based economy than with an extractive economy, as exemplified by Palau.

Keywords

Fecundity • Extinction • Tradeoffs • Slot limits • Big fish

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12.1 Fecundity and the Loss of Community Resilience

In 1928, a relatively dense population of pearl oysters *Pinctada margaritifera* was found on Pearl and Hermes Reef in the Northwest Hawaiian Islands. About 150,000 oysters were taken during the next 2 years. A survey was done the following year, 1930, and again in 1994, 2000, and 2003. Although pearl oysters were still present and reproducing, the overall population density was still similar in 2003 to that right after the harvest in 1930 (Keenan et al. 2006). For species in which the adults are sessile, fertilization success decreases when the population density falls below a threshold (Fig. 11.4; Sect. 11.4; Birkeland et al. 2013). Although fecundity may be at normal levels in individuals in the population, the reproductive potential of the population as a whole may become too low to provide enough successful recruitment beyond the cost of mortality of larval and juvenile stages to allow the population to expand and recover to its previous size. Many marine species are "boom and bust" (Uthicke et al. 2009) and episodic abundant recruitment of normally rare species can occasionally allow benthic coral-reef invertebrates such as sponges, corallimorpharians, didemnid tunicates, and *Acanthaster planci* to swamp the usual rates of larval and juvenile mortality and allow the species to recover to the higher level. Hughes et al. (2000) found that the amount of recruitment to coral populations on the Great Barrier Reef was not associated with the number of adult colonies (living coral cover) but with fecundity of the existing colonies. In corals, fecundity decreases as the colony is stressed (Sect. 12.2.2) and the potential of coral communities to provide increased recruitment that exceeds the normal rates of larval and juvenile mortality and thereby recover from disturbance may decrease with stresses and with added energy demands of climate change, lower ocean pH, and effects of human activities.

Although fishes are motile and therefore not as vulnerable to decreased fertilization when their populations decline, once below a threshold population size, fish are also usually unable to meet the normal rates of larval and juvenile mortality and many populations show no sign of recovery even decades after the fishing pressure was removed (Sect. 12.5; Hutchings and Reynolds 2004). The lower reproductive and recovery potential of motile fish populations may result from the selected harvest of the larger individuals. Fecundity increases exponentially with body size in fish. The fish associations of coral reefs are characterized in their natural state as inverted trophic pyramids with the top trophic level, piscivores, making up four fifth of the biomass (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008; Fenner 2014). Fishing effort focuses primarily on the larger individuals which are especially vulnerable to modern fishing technology (Fenner 2014). Once the larger individuals are gone, the fecundity is greatly reduced. There are "no quick fixes" (Craig 2005) and the inverted trophic pyramids have generally not reappeared (Sect. 12.5). Many coral reefs lost these natural characteristics of coral-reef systems hundreds of years ago (Jackson 1997; Wing and Wing 2001). In the last half century, most populations of large fish have not recovered even after the fishing pressure was removed (Sect. 12.5). Hutchings and Reynolds (2004) analyzed more than 230 populations of fishes with a median decrease in population size of 83 % and found that most exhibit little or no change for at least 15 years after the collapse.

12.2 Natural Selection Favors Survival over Reproduction in Corals

12.2.1 Unreliable Recruitment Leads to Multiple Reproductive Attempts

Lamont C. Cole (1954) explained how age at which reproduction begins is one of the most important characteristics determining the potential of a species to increase rapidly in abundance. Starting reproduction soon, e.g., within a year, gives a species a potential for exponentially greater number of offspring after several years than species that take two or more years to mature. If the offspring of the species are also reproducing when the parents would potentially reproduce a second time, then the selective importance of the parents would be relatively low after the first reproduction because it would be just one of a number of progenitors. For example, a Chinook salmon can produce 15,000 eggs. If it were probable that one percent of its first batch of offspring survived to reproduce, the importance of the parent's contribution to future generations from a second year's reproduction would be only 1/150 of the importance of its first reproduction. If the offspring carried genes that do not favor future reproduction and fitness of the elderly, the 150 could have passed on these genes without selection against them. For a second example, if human parents often successfully started families by early to mid-20s, and their offspring were also generally successful in starting families by their early to mid-20s, then the selective pressure to maintain fecundity after their mid-40s or early 50s (i.e., postponing menopause), or avoiding Parkinson's or Alzheimer's disease would not be strong. Natural selection for rapid population growth strongly favors reproducing successfully as soon as possible, with little selective pressure towards reproducing after the next generation is reliably established. In contrast to species adapted to rapidly expand populations, most of the

Fig. 12.1 A *Porites* (cf. *lutea*) colony in American Samoa. It must be quite old because *Porites* mounds grow an order of magnitude slower than some branching corals and this colony began life at about 14 m (46 ft) depth with less light than the shallower habitats would allow (Photo courtesy of Larry Basch)

dominant animals on coral reefs take longer than a year to mature and then live to reproduce multiple times.

An analysis of data from 251 species of fishes (Longhurst 2002) showed that as recruitment success becomes less reliable, the traits of late maturity, increased longevity, and iteroparity substantially increases (Murphy 1967; Schaffer 1974; Jennings et al. 2001). The number of years of reproductive activity typical of a species might indicate the usual degree of risk of failure to produce successful recruitment and the length of life and number of reproductive attempts to accommodate the risk. In complex coral-reef communities with large standing stocks and relatively low concentrations of nutrient input, intense and ubiquitous predation and competition make recruitment hazardous and unreliable for many species. Since many reef-building corals can live for decades (Fig. 12.1), it seems reasonable that when stressful or disruptive environmental conditions prevail, committing resources towards survival until a time in which conditions for recruitment are more likely to be successful should be favored by natural selection. Coral-reef fishes are also exceptionally long-lived, in contrast to larger, faster-growing, pelagic fishes (Sect. 12.5.3) and the traits of offspring (egg size, egg quality, larval size, larval quality, length of time before dying of starvation) of many species of coral-reef fishes actually increase with the mother's age (Hixon et al. 2013). Perhaps early reproductive success is not likely, so it is worth "bet-hedging".

If settling planulae and juvenile corals are just as vulnerable to stressful conditions as adults, then natural selection might favor adult corals that survive until favorable conditions occur and then reproduce many times. The planulae or juveniles of 1 year may not survive if conditions are stressful. Immature immune systems (Frank et al. 1997) and lack of an adequately developed protective microbial association (Apprill et al. 2009; Sharp et al. 2010) make juvenile corals especially susceptible to harmful microbes (Vermeij et al. 2009; Marhaver et al. 2013). Newly settled coral recruits are especially vulnerable to lower seawater pH (Webster et al. 2013), lower availability of carbonate ions (Kleypas et al. 1999a, b; Albright et al. 2008), reduction of aragonite supersaturation (Cohen and Holcomb 2009), and greater difficulty for the precipitation of calcium carbonate skeletons associated with increased CO_2 (Albright et al. 2010). Low pH of seawater can especially affect coral recruits during their first $CaCO_3$ deposition. For certain coral species, crustose coralline algae attract recruits (Morse et al. 1988), but increased CO_2 also adversely affects crustose coralline algae (Kuffner et al. 2008), thereby adversely affecting coral recruitment (Doropoulos et al. 2012; Webster et al. 2013).

In fact, planulae settling near adult colonies of their own broadcast-spawning species have lower survival because of harmful microbes that are associated with the adults (Marhaver et al. 2013). Although elegant experiments in both field and laboratory have shown that broadcast-spawning species are vulnerable to microbes associated with adult colonies of their own species (Marhaver et al. 2013), brooding corals may have an advantage of inoculation. The planulae of *Heliopora coerulea* are brooded on the surface of the adult colony for 6–14 days (Babcock 1990). During these days, the large (3.7 mm long) bright white planulae attract several species of butterflyfishes that prey upon them for extensive periods of time (at least 30 min, Villanueva and Edwards 2010). In the converse of the Janzen-Connell model in which species diversity is favored by seeds and seedlings being less favored to survive near adults of their species because of species-specific predators and pathogens attracted to adults (Marhaver et al. 2013), it is the larval *Heliopora* that attract predators. The larvae of brooding *Pocillopora damicornis* have been seen to successfully settle and live next to adult colonies of *P. damicornis* transplanted on a terra cotta brick into heavily sedimented Ylig Bay, Guam, where the species was not otherwise found (pers. obs.). Likewise, over three hundred spat were observed to have settled on a plastic tray to which a single adult *P. damicornis* was attached in a water table at the University of Guam Marine Laboratory. The advantages in inoculation of brooding larvae over the vulnerabilities of broadcast-spawning might be analogous to breast-feeding in humans over feeding infants on formulae in bottles.

12.2.2 Tradeoff Between Survival and Fecundity

An often accepted definition of coral-reef "resilience" is "…the ability of reefs to **absorb** recurrent disturbances. . .**and** **rebuild** coral-dominated systems" (Hughes et al. 2007). This definition combines two processes, "absorb" (tolerance, acclimatization, adaptation) and "rebuild" (reproduce, successfully recruit, repair, heal) that often trade off against each other. For example, the decrease of available energy because of turbidity and/or the increased energy expenditure for shedding sedimentation results in a reduction in gametogenesis (Kojis and Quinn 1984). The expenditure for repair of tissue damage can take enough energetic resources to prevent gametogenesis for several years (Lirman 2000). When conditions become stressful and the adult coral requires additional energy to survive, gametogenesis is often reduced to provide the extra energy needed for adult survival (Kojis and Quinn 1985; Van Veghel and Bak 1994). When corals recover from stress that caused bleaching, it can be 4 years before they spawn again (Levitan et al. 2014). The metabolic energy expenditure for recovery of the adult colony from bleaching in response to warm seawater is also paid for by reduction in fecundity (Michalek-Wagner and Willis 2001; Ward et al. 2002), gamete quality (Omori et al. 2001), or gametogenesis the following year (Szmant and Gassman 1990). Likewise, energy spent for survival of the colony in physiological response to elevated levels of nutrients (Ward and Harrison 1997, 2000) results in fewer larvae or eggs per colony. Increased ammonium stopped planulation in the brooding coral *Pocillopora damicornis*. Planulation resumed 3 months after the ammonium input was halted. Increased ammonium caused a significant reduction in the size of eggs spawned by the coral *Montipora capitata* (Cox and Ward 2002). There is a general reduction in gametogenesis and larval development along a gradient of increased eutrophication (Tomascik and Sander 1987; Tomascik 1991; Hunte and Wittenberg 1992; Wittenberg and Hunte 1992). Kojis and Quinn (1984) suggested variation in coral fecundity can be used to monitor environmental stress on corals.

Chronic disturbances brought about by increased CO_2, such as ocean warming, ocean acidification, and lowering of the aragonite saturation state, have been projected to move continuously outside the historical bounds at any given site on Earth by 2069 (±18 years s.d., Mora et al. 2013). This trend will probably not be reversed for about 1,000 years after the anthropogenic emissions stop (Archer and Brovkin 2008; Solomon et al. 2009). Ultimately, it is a proper combination of survival and gametogenesis that will be favored in surviving corals. But selection for survival responds to current environmental factors that are changing rapidly and may select against the proper combination of characteristics needed in the future. The tradeoff of increased survival at a cost of reduction in fecundity that is frequently observed these days does not appear to accommodate the general increase in the chronic nature of disturbances (Chap. 11). With long term chronic change, survival of adult colonies or clones by acclimatization (physiological adjustment of the colony), does not necessarily enhance adaptation (population genetic adjustment).

12.2.3 Chronic Stress Potentially Leads by Positive Feedback Processes to Decline in Recruitment and Connectivity

If stressful conditions are chronic, a positive feedback system can develop that drives the system into a continuous decrease in corals (Fig. 11.4, Sect. 11.4). Continuous energy loss with physiological stress or repair lowers fecundity which in turn leads to fewer larvae and fewer successful recruits and thereby fewer adult colonies. Fewer adult colonies then leads to a self-reinforcing (positive feedback) sequence because fewer sessile adults diminishes both population fecundity and success in fertilization. The decrease in fertilization success results from fewer adults because a lower number of adult colonies most often lowers population density of adult colonies which, because coral colonies are sessile, leads to a greater average distance between colonies. Field observations of a broadcast-spawning species indicated that if the effective distance between colonies falls below one spawning colony of a species within 100 m^2, the probability for fertilization would be nearly zero (Levitan et al. 2004). If only 20–30 % of the corals of a species spawn on a particular night (Levitan et al. 2004), the lowest absolute population density for successful fertilization would be more like 3 or 4 colonies per 100 m^2.

Lower fecundity also leads to less connectivity among populations (Fig. 12.2). Although many, perhaps the majority, of coral species have potential larval pelagic duration periods of weeks (Harrigan 1972), some over 200 days (Harrigan 1972; Graham et al. 2008), most of these same species show maximum settlement within the first 3 days (Harrigan 1972). For example, the planulae of *Pocillopora damicornis* can survive for at least 212 days, but an average of 24 % settle within the first 4–8 h and the majority (70 %) settle within first 24 h (Harrigan 1972). In the near future, the warming of seawater may further shorten substantially the pelagic larval duration of coral planulae. Harrigan (1972) noted the average free-swimming period for *P. damicornis* planulae in Palau (26–30 °C) is half of that in Hawaii (24–27 °C) and Harrigan's laboratory records provided evidence for shortened pelagic duration in warmer water.

Although coral reefs are not completely self-recruiting, genetic studies have indicated that a substantial portion of larvae often recruit back to their population of origin (Sammarco and Andrews 1989; Swearer et al. 1999, 2002; Jones et al. 1999, 2005, 2009; Warner and Cowen 2002; Poulin et al. 2002; Cowen et al. 2000, 2006; Almany et al. 2007; Gerlach et al. 2007; Planes et al. 2009;

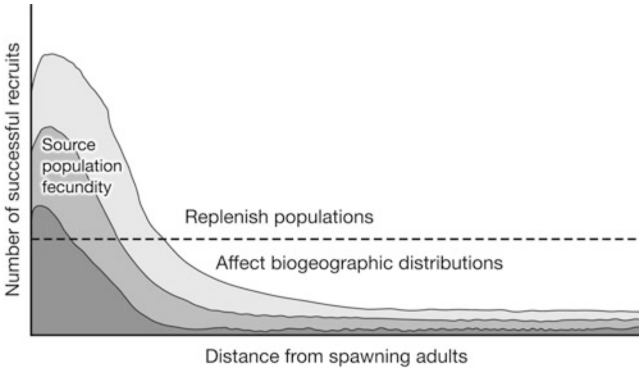

Fig. 12.2 A large proportion of planulae recruit near their population of origin. As the fecundity of the population is substantially reduced by stress or mortality, the absolute number of larvae that are transported great distances decreases and so stress or mortality also decreases connectivity (Figure is modified from Steneck 2006). The horizontal dotted line represents the number or recruits necessary to meet local mortality, so the source population fecundity must be protected to sustain local populations. Natural selection favors fidelity to the parental population, but incidental "leakage" to distant sites, though selected against, is probably sufficient to spread risks from local disasters among descendants (Strathmann et al. 2002)

Underwood et al. 2009; Shanks and Shearman 2009; Harrison et al. 2012; Golbuu et al. 2012; López-Duarte et al. 2012). In addition to the tendency of planulae to settle near home, the rates of mortality of coral larvae are especially high early in life, and so the connectivity at regional scales is less than assumed (Graham et al. 2008). Furthermore, at least in some cases, the probability of successful dispersal declines substantially after 1 km (Buston et al. 2011). The distance of population connectivity is not as reliably predicted by pelagic larval duration as is usually assumed (Weersing and Toonen 2009). Even for species with larvae that have long-pelagic duration, successful long-distance dispersion is a byproduct of large parental populations (Fig. 12.2; Strathmann et al. 2002).

Even when planulae succeed in reaching a disturbed area, survival of coral recruits is severely reduced by unwelcoming conditions such as sedimentation and prevalence of algae (Fabricius 2005). Rates of successful settlement and metamorphosis of corals are nearly zero in areas with sediment. Macroalgae and filamentous turfs preempt available space, trap sediment, intercept light, physically abrade the small coral recruit, transmit coral diseases and allelopathic chemicals, increase the growth of microbes on the surface mucus of corals and potentially affect the small recruits in additional ways (Littler and Littler 1997; Szmant 2002; Nugues et al. 2004; Kuffner and Paul 2004; Fabricius 2005; Smith et al. 2006; Birrell et al. 2008; Kline et al. 2006; Ritson-Williams et al. 2009). But negative settlement clues that trump positive settlement cues may be an adaptation to preempt mortality of coral recruits from sedimentation, algal dominance, or other fatal factors.

Coral communities develop quickly and well on flat basalt with no topographic complexity (Fig. 12.3), a substratum that obviously attracts coral recruits. Roughened plexiglass sometimes attracts more successful coral recruits than does the surrounding $CaCO_3$ reef surface (pers. obs. with Birkeland 1977; Birkeland et al. 1981). *Pocillopora damicornis* often grows on rope, pilings, cement and other artificial structures in harbors (pers. obs.) and Jokiel (1990) found corals attached to pumice and other floating objects. It may be that planulae are not actually attracted to anthropogenic artificial materials or to basalt or pumice. Rather, these materials lacked negative warning cues associated with factors on disturbed reefs. In experiments with biofilms associated with materials from the Great Barrier Reef (GBR), Prescott et al. (2014) found that *Acropora millepora* and *Pocillopora damicornis* settled significantly more on untreated laboratory biofilms than on biofilms that had developed in the presence of particulate organic matter or sediment on the GBR. Her DNA analysis of the microbial communities on the surfaces on which the planulae favored for settlement and those on which they apparently avoided for settlement and metamorphosis indicated that the patterns of association were mostly negative, i.e., the negative associations were strong and determinant while positive association were weak and apparently trumped by the negative associations. Signals of dangers might have more immediate and strong selective value than signals of potentially favorable sites. Passing a potentially favorable site to search for another might often be favored over death. Corals are probably not selectively settling on plexiglass, basalt, rope and pumice, but may be settling because the biofilms are not of the types associated with negative factors on disturbed reefs.

The effects of coastal runoff on coral reefs have been widely studied and clearly have negative impacts on reefs (see Fabricius 2005; Fabricius et al. 2013 for reviews). These include documented declines in coral larval settlement and metamorphosis (Hodgson 1990; Babcock and Davies 1991; Gilmour 1999; Birrell et al. 2005; Fabricius et al. 2003; Kuffner et al. 2006). The mechanisms that allow avoidance of coral larval settlement under poor water quality conditions are just starting to be investigated. The findings of Prescott et al. (2014) indicate that the spatial distribution of *A. millepora* and *P. damicornis* larval settlement and metamorphosis are guided by negative cues rather than positive settlement cues.

In an array of controlled field and laboratory experiments, Dixson et al. (2014) determined that coral larvae from three species of *Acropora* and larvae from six families of reef fishes all showed significant recruitment preferences for water samples from a marine protected area with abundant coral over water samples from an unprotected area dominated by macroalgae. The larvae of fishes from all six

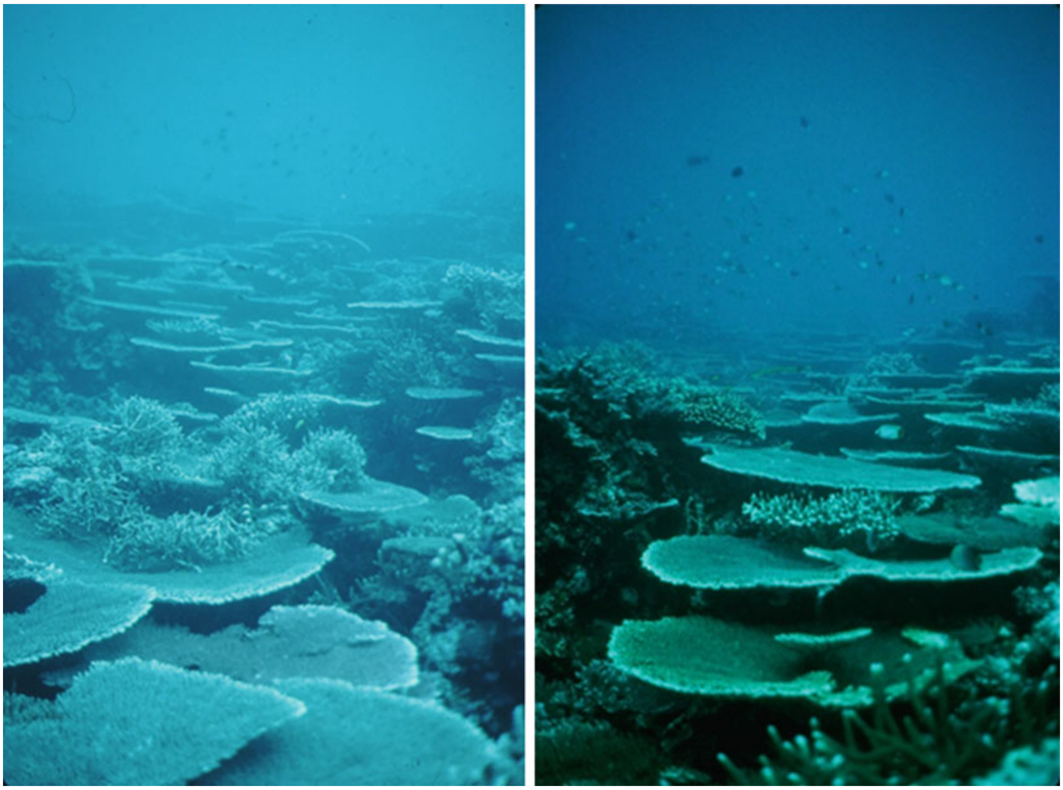

Fig. 12.3 A coral community, mainly composed of *Acropora* spp., rapidly colonized and became established on a 70,000 m^2 lava flow. A volcano covered the site with lava on 9 May 1988. These photographs were taken in November 1994. Tomascik et al. (1996) calculate the tabulate *Acropora* colonies must have grown by 30 cm y^{-1} (a radial extension of 15 cm^{-1}). *Acropora* spp. have no defense to lava, but they can recolonize and grow rapidly, becoming the dominant genus of coral

families showed very similar strong preferences for association with *Acropora* over *Porites* and over *Pocillopora*. Whereas *Acropora* is sensitive to stresses (Sect. 12.3), *Porites* is renowned for its relative tolerance of conditions of stress, and *Pocillopora*, although also stress-sensitive, tended to be a rapid colonizer and therefore potentially indicative of recent disturbance. Dixson et al. (2014) interpreted larval behavior as selecting *Acropora* as an indicator of a healthy undisturbed reef community. The fishes from all six families were also strongly selective for association with some genera of benthic algae over others.

12.2.4 Environmental Stress May Facilitate Reticulate Evolution

The numbers of larvae that potentially self-recruit or recruit to sites farther away are proportional; the absolute numbers are based on proportion times the fecundity of the reproductive source population (Fig. 12.2). The numbers of larvae are also affected by pelagic larval duration and survival. As water temperatures increase, the larvae may develop faster and/or abnormally. During times of environmental stress to corals, the fecundity of corals tends to decrease (Sect. 12.2.2) and the fewer larvae tend to replenish only populations nearer the reproductive source and seed populations at lesser distances from the source. Along with climate change, pollution, sedimentation, and other aspects of environmental stress that reduce fecundity on individual coral colonies, increased patchiness and distance between habitats suitable for successful recruitment brought about by coastal construction and overfishing of herbivores augment the effect of lower fecundity in decreasing connectivity among populations of corals (Steneck 2006).

Veron (1995) proposed that this periodic decrease in connectivity might explain the geographic variations observed in dominant and widespread species of corals that form “species complexes” (Fig. 12.4), such as *Orbicella* spp. and *Acropora* spp. Since adult corals are sessile, like plants, the genetic connectivity depends on dispersion of gametes and larvae rather than behavioral coming together of adults. Veron championed the concept of “reticulate evolution” for “species complexes”. When the environment is favorable to corals and fecundity is high in areas of strong water currents, closely related species tend to disperse more widely (Fig. 12.2) and interbreed, bringing about more uniform, genetically integrated species. Alternatively, when conditions are stressful and fecundity is low, populations

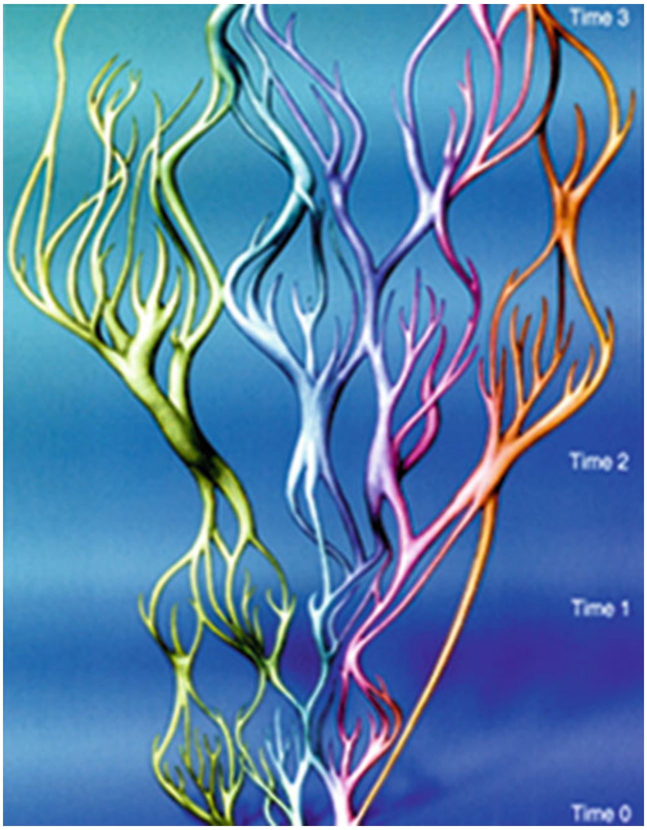

Fig. 12.4 Veron's (1995) diagram of the blending together through hybridization and separation by isolation, then further separation by genetic drift or local selective forces, of closely related coral species (in a "species complex") through time in reticulate ("netlike") evolution. The blending together might be facilitated by faster large-scale water currents and/or by more benign conditions favoring high fecundity or, separation might be facilitated by warmer waters causing more rapid larval development and thereby less time in the water column, by stressful conditions reducing fecundity (Fig. 12.2) or more stagnant water conditions (© Australian Institute of Marine Science and CRR Pty Ltd [2000]. The Australian Institute of Marine Science does not necessarily endorse any modification to that material)

may tend to become isolated and genetically diverge by genetic drift or by local selective forces. Isolation can be further enhanced by habitat deterioration causing patchiness and reduced pelagic larval development time reducing connectivity.

Molecular genetic evidence and patterns of natural hybridization are consistent with the concept of reticulate evolution (Kenyon 1997; Hatta et al. 1999; Diekmann et al. 2001; van Oppen et al. 2001; Frank and Makody 2002). However, these studies were on *Acropora* or *Madracis* which were already known to be "species complexes" so it is not yet known whether metapopulations of broadcast- spawners become more genetically distinct or "structured" under stressful conditions when fecundity is low, appropriate habitat is more patchily separated and scarce, and planulae spend less time in the water column as temperatures rise.

12.2.5 Constraints of Biology on Management

Fundamental forces acting against coral reef ecosystems today, e.g., growth in human populations multiplied by the per capita burden of increased growth in economic demands and needs for natural resources, and the resulting global environmental effects of seawater warming, lowering of seawater pH, and climate changes seem to be considered too daunting to address directly. Coral-reef managers almost always focus actual efforts towards manageable local processes, attempting to control overfishing, sedimentation, and pollution, etc., in hopes that these procedures will increase the local resilience of corals to global changes. Particular areas are selected for protection with the thought that fecundity will be substantial in protected areas and so these populations can replenish downstream disturbed areas.

We cannot rely entirely on improving local situations and setting aside protected areas, depending on sufficiently developed resilience to stress and replenishment of populations by larvae from upstream sources. There are two basic aspects of coral biology that are not supportive of large-scale downstream connectivity. First, although planulae of many coral species can potentially survive for over 200 days and potentially drift thousands of kilometers, it is a characteristic of coral biology that a major portion of the actual surviving larvae replenish local or nearby populations (Sect. 12.2.3). Second, the areas outside the protected areas that are disturbed and have undergone phase shifts can be unfavorable for successful larval recruitment (Sect. 12.2.3; Dixson et al. 2014; Prescott et al. 2014). We must begin to search for effective ways to directly address the deteriorating global conditions. As Ove Hoegh-Guldberg has said, "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".

12.3 Selection Favors Rapid Growth over Survival in Acroporids

12.3.1 Fast Growth Favored by Less Complexity

This section starts by documenting the observation that corals of the genus *Acropora* have jettisoned their ancestors' usual mechanisms of defense and tolerance that would have favored survival, possibly in exchange for rapid growth. This seems to have also happened at other times in the Mesozoic, in other scleractinian families (Sect. 12.3.2). Ancestors of *Acropora* probably included stress-tolerant encrusting acroporid corals such as *Astreopora* that were capable of surviving the Cretaceous/Paleogene (K-Pg)

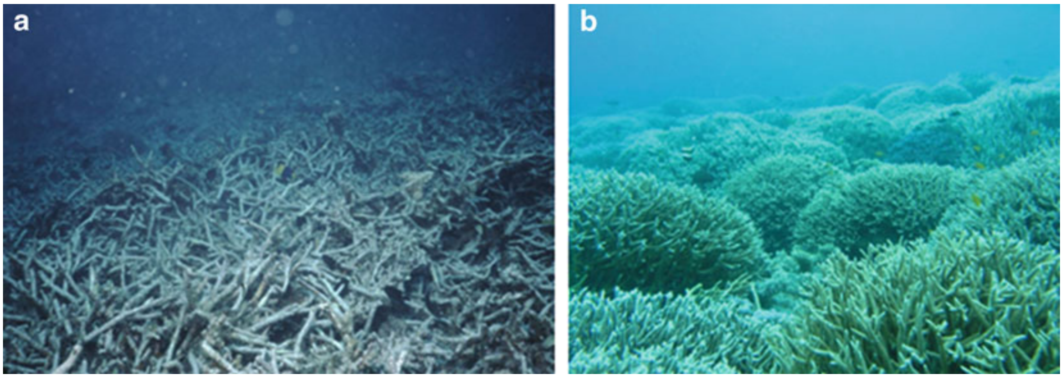

Fig. 12.5 A community of *Acropora* spp. on Ngederrak Reef in Palau. (**a**) In 1999, the coral community had been devastated by predation by *Acanthaster planci* in 1979. (**b**) By 2005, the *Acropora* spp. (mostly *Acropora muricata*) took over by rapid growth

mass extinction (formerly called the Cretaceous/Tertiary [K-T] mass extinction), but when environmental conditions again favored reef production, *Acropora* may have evolved by losing the defenses or tolerances typical of most scleractinians in exchange for rapid growth (Fig. 12.3).

A striking example of the lack of investment in defense by *Acropora* spp. is their vulnerability to predation. Despite the diversity of corallivores (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)), only 28 of the genera of reef-building Scleractinia have been recorded as prey, leaving 83 genera that appear to be entirely avoided as prey (Stella et al. 2011). Defense against predation appears to be the norm for corals. Yet nearly all phyla of corallivores easily prey on *Acropora* spp., and among the important groups of corallivores, *Acropora* is actually preferred. *Acropora* species are the preferred prey of the seastar *Acanthaster planci*, decapod crustaceans, gastropods such as *Drupella* spp. and *Coralliophila* spp., the polychaete *Hermodice carunculata*, the polyclad flatworn *Amakusaplana acroporae* (Rawlinson and Stella 2012), and fishes such as blennies *Exallias brevis*, damselfish *Stegastes planifrons*, and 69 species of butterflyfishes *Chaetodon*. Considering the magnitude of the effects of predation on *Acropora* (Fig. 12.5a) it is surprising that natural selection has not favored resistance to predators; but *Acropora* can grow back rapidly (Fig. 12.5b).

Acropora spp. are also especially susceptible to diseases such as the white-band disease which, since the early 1980s, has substantially reduced the abundance of *Acropora palmata* and *Acropora cervicornis* throughout the greater Caribbean. Other reef-building scleractinians are affected by disease, but *Acropora* spp. are among the most seriously affected (Aronson and Precht 2001). It is possible that being favored prey for several phyla of corallivores facilitates infection by disease and recruitment of bioeroders by increasing the frequency of tissue penetration and the baring of skeleton, respectively.

Nearly all genera of corals are susceptible to bleaching when exposed to extraordinarily warm temperatures, but *Acropora* is ranked among the most susceptible (Marshall and Baird 2000; McClanahan et al. 2007). The hydrocoral genus *Millepora* is sometimes the only reef-building genus that is more susceptible than the scleractinian *Acropora* (Marshall and Baird 2000). *Acropora* was a dominant genus throughout the Indian Ocean until it suffered major losses in the 1997/1998 bleaching event (McClanahan et al. 2007).

The elevated morphology of branching and tabular *Acropora* species and their porous skeletons make them particularly susceptible to the strong waves of hurricanes or typhoons (Hughes and Connell 1999; Fig. 12.6a), but they grow back rapidly (Fig. 12.6b). Fast-growing corals were shown by Comeau et al. (2014) to be more sensitive to ocean acidification than were slow-calcifiers.

Even the larval stage of *Acropora* species appears to be less adapted for survival than the larvae of other coral genera. Graham et al. (2008) quantified the survival of larvae from five genera of broadcast- spawning scleractinians. Although larvae of the representative acroporid *Acropora latistella* lived as long as 209 days, the median survival was 4 days. The larvae of the other genera also lived a maximum of about 200 days, but their median survivals were substantially longer. For example, the larvae of *Goniastrea aspera* lived a maximum of 215 days, but the median survival was 138 days.

Denis et al. (2013) found that fast growth was prioritized in *Acropora* in a tradeoff against regeneration of tissue. The energy and biochemical materials saved by not developing as many effective survival mechanisms against predation, disease, extraordinarily warm seawater, or hurricanes as do most scleractinian corals, perhaps allowed *Acropora* spp. to allocate more metabolic energy for rapid growth. The tissues of branching corals such as *Acropora* and pocilloporids average less than a third the thickness of the tissue of massive corals (Loya et al. 2001) and the biomass as

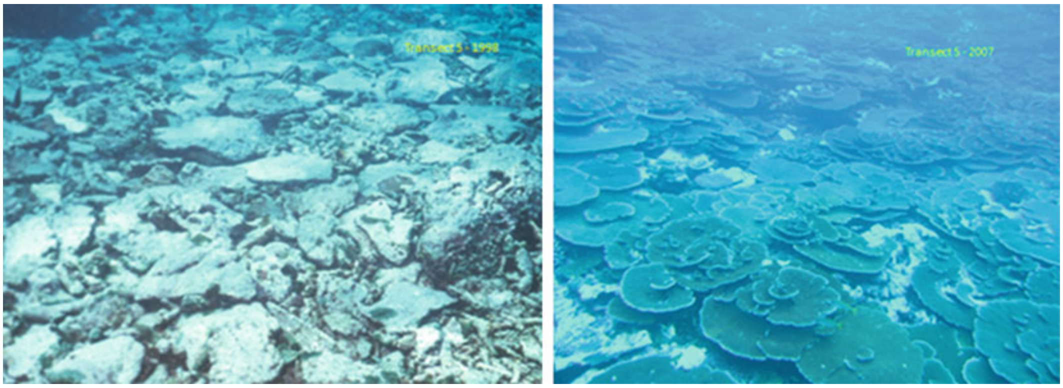

Fig. 12.6 A community of mostly *Acropora hyacinthus* with a few *A. cytherea* and other *Acropora* spp. on Transect 5 in Fagatele Bay, American Samoa. Although *Acropora* colonies are susceptible to hurricanes, rapid growth enables them to quickly become dominant following disturbance

measured by ash-free dry weight of *Acropora* spp. was lower than the biomasses of other genera of corals tested (Thornhill et al. 2011). The Caribbean *Acropora* spp. show lower metabolic rates, lower rates of protein turnover, and less capacity to acclimatize than some mound corals, but are able to grow substantially more rapidly (Gates and Edmunds 1999). The skeleton of *Acropora* spp. is extraordinarily porous (Gladfelter 1982) and grows an order of magnitude faster than other genera measured (Gladfelter et al. 1978). Initially, it would be reasonable to surmise that less investment in tissue biomass and repair may facilitate faster growth by allocation of more metabolic energy or nutrients to growth.

Pocillopora spp., to a lesser extent than *Acropora* spp., are also fast-growing, branching corals with thin tissue (Loya et al. 2001) and substantially lower organic content of tissue than the other coral general tested (Glynn and Krupp 1986). Yet *Pocillopora* spp. are still preferred prey. How could *Acropora* and *Pocillopora* be preferred prey when their tissues are relatively thin and possibly less nutritious? Glynn and Krupp (1986) found that although *Pocillopora* tissue had low organic content, it provided the highest energetic return to the predator. The tissues of *Acropora* and *Pocillopora* are superficially located on the skeleton and therefore may be more accessible, and fewer complex secondary metabolites for defense in the tissue may cause them to be less metabolically resistant.

But what is the resource involved in the tradeoff between survival and fast growth? Light and nutrients are critical resources required by the zooxanthellae that fuel coral growth and calcification. Nevertheless, there is typically a superabundant supply of light in shallow water over coral reefs where *Acropora* spp. are dominant. Moreover, corals do not respond to changes in nutrients as immediately and strongly as do more simple organisms, i.e., organisms that are less complex physiologically and more distinctly autotrophic or heterotrophic. The growth rates of purely heterotrophic animals, such as mussels, barnacles, bryozoans, and many sponges, and purely autotrophic algae, are strongly associated with the amount of food or nutrients in the water column (Widdows et al. 1979; Ceccherelli and Rossi 1984; Rose and Risk 1985; Page and Hubbard 1987). The growth rates of corals do not respond so quickly and substantially to nutrient input (Kinsey and Davies 1979; Koop et al. 2001). Although adult coral colonies can live well in areas of nutrient input such as upwelling, the recruitment of corals is very difficult in these areas because the recruits of simple heterotrophic animals and algae respond more immediately and substantially to nutrient pulses, grow at substantially greater rates, and can plow away or overgrow recruits of corals which do not respond as quickly and substantially (Birkeland 1977).

Simplicity may be an important a factor in competition for space because it facilitates speed of response to either nutrients or calories from photosynthesis. The symbiotic system of a holobiont (the combination of coral animal, dinoflagellates, and prokaryotes) is too complex to respond as quickly to a pulse of nutrients as do benthic autotrophic algae and sessile heterotrophic animals. Single-celled algae in the phytoplankton can rapidly increase with input of nitrogen and phosphorus, but the density of single-celled algae in the cells of corals is relatively constant within any set of environmental conditions associated with depth. Enhancing the growth rate of zooxanthellae can upset the complex physiological balance in the symbiosis and the corals might dampen the response of the system by expelling the excess zooxanthellae (Muller-Parker and D'Elia 1997).

Simplicity has two aspects. First, complexity requires that metabolic processes have more regulations and time-consuming steps. Second, complexity in terms of additional secondary metabolites requires a greater expense of production. Organisms that are less complex morphologically and/or invest fewer resources into secondary metabolites for defense are generally able to respond more quickly to pulses in resource availability and grow faster than phylogenetically related species that are more complex. The structurally simple green alga *Ulva curvata* responded to inputs of ammonium with more effective uptake and more rapid growth than did the more structurally complex green alga *Codium fragile* (Ramus and Venable 1987). Algae with relatively simple morphology generally have higher net productivity per unit biomass and a potential for more rapid response and growth than do algae with more complex structure (Littler and Littler 1980). Diatoms tend to be favored as food for many animals and can grow up to three times as fast as dinoflagellates of the same size under similar conditions (Banse 1982). Although diatoms can produce toxins and are motile with microfibrils, dinoflagellates tend to be more complex, producing secondary compounds that result in toxic red tides and ciguatera, and likely expend more energy on motility driven by two large flagellae. Many dinoflagellates are also more complex because they are mixotrophic (capable of both autotrophy and heterotrophy in the same organism). Mixotrophy requires extra energy to maintain both trophic processes in the same system (Stoeker 1999; Dolan and Pérez 2000). Mixotrophy is advantageous in nutrient-poor environments where solar energy is unlimited (such as shallow-water coral reefs), but organic carbon and dissolved inorganic carbon are limiting (Hallock 1981, 2001). An increase in dissolved inorganic nitrogen not only shifts the advantage to more rapidly growing simple autotrophs and heterotrophs, but it throws the more complex mixotrophic system out of balance and can stimulate bleaching in corals (Wooldridge 2009).

Simple systems are normally advantageous in nutrient-rich environments. In environments with low resource availability or stressful conditions, plants that are favored have slow growth rates and major investments in antiherbivore defenses because they must defend what they already built at such great cost (Coley et al. 1985). In contrast, when resources are abundant or environmental conditions are benevolent, organisms often tend to invest in rapid growth and increased fecundity at the expense of defense. For corals, rapid increase in colony surface area and number of polyps can potentially produce a rapid increase in fecundity and the increased number of early potential progeny might be favored. So while most corals are adapted to survive during periods of stress, corals in the genus *Acropora* are especially vulnerable to predation, disease, unusually warm seawater, and hurricanes. Yet they have often been the dominant corals because of their rapid growth and elevated morphology (Fig. 12.3). While most corals invest in survival (tolerance) at the expense of reproduction (recovery), corals of the genus *Acropora* invests in rapid growth (recovery) at the expense of survival (tolerance). This is consistent throughout the history of scleractinians since the Triassic.

12.3.2 Fast Growth Favored over Survival in Productive Times

There have been three periods especially favorable for scleractinian reef-building: the Late Triassic, the Middle Jurassic, and the Neogene (Kiessling 2009). These periods of prevalent reef-building are associated with “aragonite seas” (Sect. 2.7, 2.9.3, 2.9.4, and 2.9.5; Stanley and Hardie 1998) and with the prevalence of relatively rapidly growing corals. During mass extinctions, rapidly growing corals did not survive. Survivors were generally massive or mound-shaped corals. Conversely, about 15 million years after the Triassic mass extinction and 30 million years after the Cretaceous-Paleogene mass extinction in aragonite seas, a large number of new scleractinian genera originated and reef-building accelerated while the survivors of the mass extinctions showed substantial rates of elimination. The conditions favoring increased rates of reef-building were beneficial for newly evolved fast-growing corals, while these conditions were detrimental for stress-tolerant, slower-growing survivors of mass extinctions.

On Late Triassic (Norian and Rhaetian) reefs, *Retiophyllia* spp. may have been somewhat ecologically analogous to *Acropora* spp. on modern reefs in that it was a “very speciose branching (phaceloid, see Box 12.1 and Fig. 12.7) genus” (Caruthers and Stanley 2008) that was one of the dominant, reef framework-building scleractinians. In the Late Triassic, “Some branching [phaceloid] corals probably grew rapidly, and reached over 10 m high, but bore thin branches only 5–10 mm in diameter” (Wood 1999, p. 104). *Retiophyllia* spp. were widespread, found in Japan, central and northeast Asia, Indonesia, Russia, the Caucasus, the Alps, Europe, and western North and South America from Alaska, Yukon, Vancouver Island, Oregon, Idaho, Nevada,,

Box 12.1: Branching Corals

Although erect corals in the Triassic and Jurassic were mostly “phaceloid” (each branch produced by a single polyp), or sometimes “dendroid” (single-polyp branches coming off a common stem), they are sometimes referred to as “branching” or “ramose” corals. “Branching” corals are presently considered more precisely as corals with each branch being continuously covered by a sheet of polyps, i.e., “multiserial erect”. Branching corals become more prevalent abruptly in the late Cretaceous (Turonian Age), but *Oculina* was the only branching coral that survived the Cretaceous/Paleogene mass extinction. *Acropora*, *Pocillopora*, and other extant genera of branching corals originated in the late Paleocene, early Eocene, or more recently.

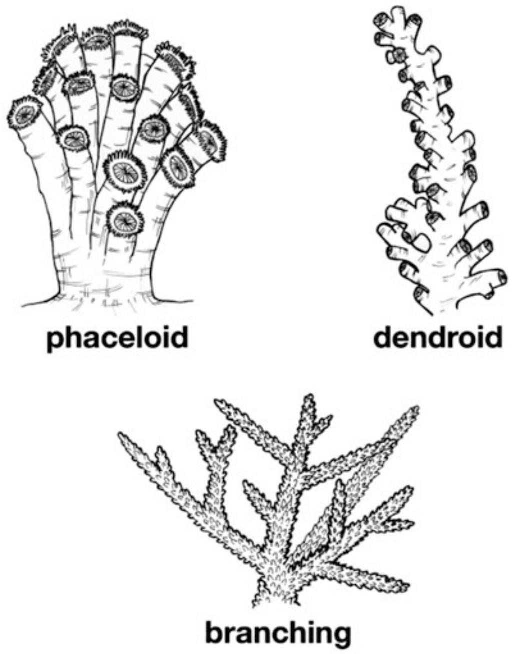

Fig. 12.7 The morphology of the predominant erect corals through the geologic record (Box 12.1)

northern Chile, and Peru (Caruthers and Stanley 2008). These fast-growing dominant corals fell victim to the mass extinction at the end of the Triassic.

The corals that survived the Triassic/Jurassic mass extinction were solitary or massive or smaller phaceloid types and did not appear to be fast-growing or dominant. Of the 20 genera that passed from the Triassic to the Jurassic, one (*Alakiria*) went extinct in the first age that followed (Hettangian). It may have been what Jablonski (2002) called a "dead clade walking". Another genus, *Dimorphastraea*, persisted into the Late Cretaceous. The remaining 18 scleractinian genera lived about 15 million years, and each went extinct when conditions became favorable for reef-building corals (Lathuilière and Marchal 2009), beginning in the late Early Jurassic when the Jurassic scleractinians were becoming diverse, with at least 100 new coral genera having originated by the Middle Jurassic (Heckel 1974). The time of greatest rate of origination of scleractinian genera (Kiessling and Barin-Szabo 2004) and greatest rate of reef-building (Kiessling 2009) in the Mesozoic era was in the latter half of the Jurassic period. Corals with the physiological capabilities to survive the Triassic mass extinction were unable to survive in conditions exceptionally favorable to newly evolved scleractinians. One possible explanation is that the usually solitary, massive or encrusting survivors were crowded out by the relatively fast-growing Jurassic corals (Fig. 12.8). However, although competition for space between corals can affect their distributions and community structure (Cox 1986; Pandolfi et al. 2002), I have never documentation of corals driven to extinction by competition.

Although reef-building corals in the Jurassic grew substantially slower than modern corals, averaging about a third the growth rate (Leinfelder 2001), the dominant phaceloid corals were still relatively fast-growing in their time. A main reef-builder throughout the Tethys region in the Middle Jurassic was *Thamnastria dendroidea* which often formed dense monospecific thickets. "The growth of branches was directed upwards, but also frequently sideward, forming an overtopping morphology.... *Thamnasteria dendroidea* is therefore interpreted as an "aggressive coral"... Compared with other Mesozoic (Late Jurassic) corals . . . its growth rate is very high" (Helm and Schŭlke 2000). Leinfelder et al. (2012) found extensive meadows of erect *Calamophylliopsis* spp. or thickets of *Actinastrea crassoramosa* in Late Jurassic coral communities. When reef construction is active, "aggressive" erect corals seem to be prevalent.

Near the end of the Jurassic, the increase in volcanism with more rapid seafloor spreading caused high rates of CO_2 emissions while magnesium was taken up in the hot basalt, lowering the Mg/Ca ratio in the seawater and shifting the seawater from aragonitic to calcitic (Sect. 2.5, 2.7, Fig. 2.1; Stanley and Hardie 1998). With the shift to calcite seas, there was a substantial drop in production of coral reefs for about 140 million years from the later Jurassic throughout the Cretaceous and through to the early Paleogene.

However, as explained by Kleypas et al. (2001), a diverse coral community may be performing well ecologically even while performing poorly geologically (Fig. 12.3). While the scleractinian fauna in the Cretaceous produced unimpressive reefs compared to those in aragonitic seas, the rudist bivalves produced volumes of massive calcium carbonate relatively rapidly. These three-dimensional hard substrata above the sediment allowed scleractinian corals to increase in diversity and maintain widespread distribution throughout (Götz 2003). The corals, in turn, helped stabilize the rudists by binding them together (Götz 2003). In modern times, crustose coralline algae (CCA) form algal ridges in areas of consistent wave action and are an agent of binding of coral skeletons while in the Cretaceous, scleractinian corals were more prevalent in areas of consistent wave action and were an agent of binding and stabilization of rudist shells (Götz 2003).

When volcanism decreased and the seafloor spreading slowed, the Mg built up to $Mg/Ca > 2$ and the oceans became aragonitic during the Oligocene, about 30 million years ago, and reefs began to develop more vigorously. Although *Acropora* originated in the Later Paleocene – Early Eocene, it did not begin dominating reef frameworks until the Oligocene (Wallace and Rosen 2006) when atmospheric pCO_2 dropped below 500 ppm and seawater pH rose

Fig. 12.8 In conditions favorable to growth of coral reefs, the faster growing branching corals sometimes overwhelm the more slowly growing massive corals. This process affects community structure and local distribution of species, but it is not known whether it ever leads to extinction

to over 8.0 (Pearson and Palmer 200) and reef production became vigorous.

As with 18 of the 20 scleractinian genera that survived the Triassic/Jurassic mass extinction but went extinct in the Middle Jurassic when the scleractinians were greatly increasing in diversity and major reef construction was occurring, the family Actinacididae survived the K-Pg mass extinction and continued for 30–40 million years until the Oligocene when conditions for vigorous reef growth and domination by branching species began to occur, at which time this scleractinian families went extinct. At least 11 scleractinian genera from several families also went extinct in the Oligocene and at least 10 genera went extinct in the Miocene when reef production was increasing and at least 40 new scleractinian genera were originating (Fig. 12.9; Wells 1956).

Edinger and Risk (1995) attribute extinctions in the Oligocene and Miocene in the greater Caribbean to be caused by a major increase in upwelling, and this is may be true, but some of these genera also went extinct in other oceans at about the same time. For example, *Antiguastrea* that originated in the Jurassic also went extinct in the Miocene in Australasia, southern Europe and northern Africa (data in corallosphere.com at the British Museum of Natural History). *Trochoseris* that originated in the Cretaceous also went extinct in the eastern tropical Pacific (López-Pérez 2005). *Lamellastraea* went extinct in east Asia (corallosphere.com) and *Leptomussa* in Italy (Wells 1956). *Actinacis*, *Siderofungia*, *Stylangia*, *Cyathoseris*, and *Rhizangia* all originated in the Cretaceous and went extinct in Europe or Asia when reef-building was accelerating and new genera were originating (Wells 1956). Budd (2000) listed 21 new genera of scleractinians that appeared in the Caribbean in the Oligocene to the middle Miocene, while 15 genera went extinct. Another six genera originated in the late Miocene.

Scleractinians seem to be improving over time in their abilities to survive mass extinctions in comparison to other marine invertebrates. In contrast to the poor showing in the Triassic/Jurassic mass mortality of scleractinian coral genera (27 % survival, i.e., 20 survived out of 73, Lathuilière and Marchal 2009), 70 ± 4 % of scleractinian genera and over half the species survived the K-Pg mass extinction (Kiessling and Baron-Szabo 2004). The general extinction of marine genera was about 47 % for both the Triassic/Jurassic and K-Pg extinctions (Bambach et al. 2004), so the scleractinians shifted from one of the most vulnerable groups to among the more resilient. Not only did some of the massive and encrusting corals that developed in the Cretaceous survive the K-Pg mass extinction, but also the Paleocene-Eocene Thermal Maximum, the Pliocene-Pleistocene accelerated turnover and extinction in the greater Caribbean (Budd et al. 1996), and they are still prevalent on contemporary coral reefs (Fig. 12.9). Nine of the scleractinian genera of corals that prevailed from the Cretaceous to the present were previously grouped together in the

Fig. 12.9 Geologic history shows that mound or encrusting corals are more frequently seen to be the survivors of mass mortality events, and the dominant, fast-growing, branching species more often go extinct with events of mass extinction, then new genera of branching corals originate in the geologic period following the mass extinction. The data are mainly from Wells 1956. The genera in parentheses are from Ma 1959. Additional genera mentioned by Veron (1995) and Paulay (1997) with question marks are included with question marks and no parentheses. At least a dozen extant survivors from the Cretaceous are not listed because they are deepwater or solitary

	Survived Mesozoic LAZARUS CORALS	Originated Cenozoic FAUSTIAN CORALS	
Massive or encrusting	*Stephanocoenia*		
	Madracis		
	Astreopora		
	Siderastrea		
	Dichocoenia		
	(*Dendrogyra*)		
	Cycloseris ?		
	Astrangia		
	Hydnophora		
	Favia		
	Diploria		
	Montastraea		
	Diploastrea		
	(*Favites*)		
	(*Goniastrea*?)		
	Leptoria		
	(*Leptastrea*)		
	(*Oulastrea*)		
	(*Plesiastrea*)		
	Goniopora		
	(*Alveopora*)		
	Porites ?		
	Heteropsammia ?		
	Heliopora		
Phaceloid	*Cladocora*		
Branching	*Oculina*	*Stylophora*	(Paleocene)
		Pocillopora	(Eocene)
		Acropora	(Eocene)
		Seriatopora	(Miocene)
		Anacropora	(recent)
		Palauastrea	(recent)
		Paraclavarina	(recent)

family Faviidae (Wells 1956; Veron 2000), but these nine genera have now been distributed among four families by genetic analyses (Budd et al. 2012). Jackson and McKinney (1991) documented that corals have become more "integrated" in colony morphology with time, but the potential relationship of survival with integrated colonial morphology still needs to be determined. New genera of solitary (*Scolymia*, *Homophyllia*, *Heterocyathus*, some fungiids) and phaceloid (*Caulastrea*, some *Galaxea*, some *Lobophyllia*) corals have originated in the Cenozoic so the less "integrated" corals keep returning anew.

The 54 scleractinian genera from the Cretaceous that are briefly described in Wells (1956) are typically solitary, massive, encrusting, or phaceloid. However, Jackson and McKinney (1991) reported a sudden increase in branching corals in the final 10–15 million years of the Cretaceous; a sudden increase of branching corals to percentages of the coral community without precedent. Nevertheless, the corals surviving the K-Pg mass extinction were generally solitary, massive or encrusting (Fig. 12.9). *Oculina* might be considered branching or dendroid and *Cladocora* might be considered phaceloid, but neither counts as a good representative of "aggressive" branching reef-builders and are often without zooxanthellae (Bernecker and Weidlich 2005).

Some massive or encrusting scleractinians that survived the Cretaceous-Paleogene mass extinction (Fig. 12.9) are called "Lazarus taxa" by Wood (1999) and Rosen (2000). The fast-growing, branching corals that have attributes that allow them to dominate the scene today, originated after the mass extinction. They were given the traits that allow them to dominate and live gloriously, but they are the first to die, reminding us of the story of Faust. Van Woesik et al. (2012) noted that dominant and widespread branching corals in the Caribbean in the Pliocene, *Stylophora* and *Pocillopora*, became extinct in the Pleistocene, indicating that being abundant and widespread does not protect species from extinction. Likewise, Pandolfi et al. (2001) reported on the extinction of two widespread and dominant corals and the survival of some of the rare species within the recent 82,000 years.

Ultimately, the best "strategy" for selection would be the best combination of survival and reproduction. But natural selection does not act as a "strategy" for the future, but rather works at the individual colony level, favoring traits that provide more successful recruitment in the present. Natural selection on dominant corals during benevolent times seems to favor the increase in rate of growth at the expense of defense and/or tolerance because the more rapid increase in surface area can increase the number of polyps, and thereby increase fecundity. Tabletop morphology of some *Acropora* allows for increase in diameter of up to 30 cm per year through radial expansion (Tomascik et al. 1996) and the cylindrical branches of arborescent *Acropora* allow polyps over the entire surface in contrast to encrusting or mound corals can have polyps on only the unattached surface. We are used to considering competition for space to be a major selective force in the evolution of corals, but in the case of *Acropora*, competitive superiority might be a spinoff of rapid growth and elevated morphology selected for increased fecundity, i.e., the rapid production of greater numbers of potential offspring.

While proximal selection was indirectly successful in making the *Acropora* species dominant, the ultimate effect of reducing investment in defense and tolerance may result in the dominant species being more susceptible to extinction with change in climate (Birkeland et al. 2013) as it seems to have done with erect, dominant corals, in the Mesozoic. On the other hand, the slower-growing, more tolerant corals that survived the mass extinctions seem to have sometimes continued to live for millions of years only to go extinct when the environment becomes especially favorable for reef-growth and new genera of scleractinians arise. Investments in tolerance may have cost them rapid growth and thereby made them susceptible to being crowded out by new families of more rapid-growing dominants in times of major reef growth. The fast-growing dominant corals go extinct when times are bad (e.g., mass extinctions), while some of the especially tolerant corals go extinct when times get especially good for reef production.

Favoring rapid growth at the expense of survival in *Acropora*, just as favoring survival at the expense of fecundity in other corals, may have allowed sessile species like corals to survive when disturbances or stressful conditions were acute, but brief. But when stressful conditions become chronic (Chap. 11), as with the influence of overfishing and coastal construction, sedimentation, pollution and increased CO_2, resulting from the growth of human populations, the periods of time between successful reproduction and recruitment may become too long for these corals to persist.

12.4 We May Keep the Corals but Lose the Reefs

12.4.1 Many Coral Species May Not Go Extinct

> What doesn't kill you makes you stronger. (Friedrich Nietzsche)

Although coral reefs are likely to continue to deteriorate and become less topographically complex for the foreseeable future (Kleypas et al. 1999a, b; Alvarez-Filip et al. 2009; Fabricius et al. 2011; Kennedy et al. 2013), no longer providing environmental services such as optimal habitat for fish and providing protection against wave action as sea level rises, we need not assume most corals will go extinct. Many studies document the increased tolerance of corals to stressful conditions by acclimatization (physiological or behavioral adjustments of individual colonies) or adaptation (genetic adjustment of populations). In a series of major bleaching events in the eastern tropical Pacific (Glynn et al. 2001; Podestá and Glynn 2001; Jimenez et al. 2001; Cortes and Jimenez 2003; Zapata and Vargas-Ángel 2003), French Polynesia (Adjeroud et al. 2009), Great Barrier Reef (Maynard et al. 2008), and Phuket, Thailand (Dunne and Brown 2001), corals appeared to become more tolerant of warm temperatures with experience (Brown 1997a, b; Coles and Brown 2003; Brown and Cossins 2011; Palumbi et al. 2014; Barshis Chap. 7). Indeed, corals closer to the equator have higher thermal limits than do populations of the same species in subtropical parts of their range (Coles and Jokiel 1978; Oliver and Palumbi 2009, 2011). Berkelmans (2002) determined stress-response thresholds for bleaching from 13 sites on the Great Barrier Reefs across 22° of latitude over 10–12 years and concluded that thermal adaptation had taken place over both small (10s of km) and large (100s–1,000s of km) scales of distance.

The ability of diverse assemblages of corals to survive frequent exposures to high water temperatures is common (Brown 1997a; Berkelmans and Willis 1999). In shallow pools on the small island of Ofu in American Samoa, the water temperature can fluctuate by 6.3 °C daily, reaching 34.5 °C (Craig et al. 2001). Although *Millepora* spp., *Acropora* spp., and some corals of other genera occasionally bleach at Ofu, 85 species of coral seem to generally thrive in these pools of fluctuating temperatures. The 85-species assemblage in these pools is comparable to the diversity on the reef front. Coles (1997) observed that a robust assemblage of 24 species of corals occupying 50–75 % of the substrata seemed to survive daily fluctuations of 8.2 °C with no signs of stress. Riegl et al. (2011) documented that in the central region of the Arabian/Persian Gulf, corals did not bleach until exposed to temperatures above 34 °C for 8 weeks, with three of the weeks above 35 °C.

Some of the presently predominant genera of reef-building corals that lived in the Cretaceous (Sect. 12.3.2; Fig. 12.9) probably lived at seawater temperatures 32–36 °C (Poulsen et al. 1999, 2001; Wilson et al. 2002; Schouten et al. 2003; Littler et al. 2011; DeCarlo et al. 2015) or possibly as high as 42 °C (Bice et al. 2006) and also at lower pH, often 7.4–7.6 (Pearson and Palmer 2000; Zeebe 2001; Hönisch et al. 2012) in calcite seas (Mg/Ca mole ratio <2). The source of massive CO_2 input was the extensive and chronic volcanism that was producing new seafloor and pushing apart the Americas from Europe and Africa. This was compounded by the volcanism that was producing the Deccan Traps at the end of the Cretaceous and the bolide that hit the Yucatan Peninsula during this time.

Likewise, during the Paleocene and early Eocene, atmospheric $p\mathrm{CO}_2$ was 2,000–3,500 ppm and sea surface pH was between 7.4 and 7.6 (Pearson and Palmer 2000) as it was in the Mesozoic (Hönisch et al. 2012). This time, the input of CO_2 by volcanism was augmented by the rapid input of about 2×10^{12} metric tons of C into the atmosphere as methane which assisted the rapid lowering of pH and massive dissolution of sea-floor carbonate (Zachos et al. 2005). Seawater temperatures increased 5 °C in the tropics and but reached 24–26 °C near the North Pole (Moran et al. 2006). The increase in seawater temperature was several times greater in polar latitudes than in the tropics and this brought about a lesser latitudinal gradient in seawater temperatures. This suggests that there may be some kind of "ocean thermostat" that puts limits on tropical seawater temperature rise, at least in some areas (Kleypas et al. 2008). If seawater in much of the tropics in the Cretaceous was 32–36 °C, then the future limits to tropical seawater temperatures in large basins (i.e., oceanic atolls and islands) lie within the range to which modern corals can adapt (Riegl et al. 2011) .

The two dozen or so genera of reef-building scleractinians represent about 17 families that have survived the harsh conditions of the Cretaceous, the Cretaceous-Paleogene mass extinction, the Paleocene-Eocene Thermal Maximum and are still predominant on modern reefs. It seems reasonable to have hope that some descendants will adapt to the "norm" (diverse scleractinians without reefs) and not go extinct. This does not apply to fast-growing species that originate after mass extinctions. They are more prone to extinction (Sect. 12.3.2).

Montastraea is first found in the Upper Jurassic (~150 mya), *Diploastrea* in the Early Cretaceous (Aptian Age, ~115 mya) (Wells 1956), and *Heliopora* in the Cenomanian Cretaceous (~95 mya) (Eguchi 1948). Skeletal morphology is not a reliable way to categorize coral genera (Budd et al. 2012), yet they are most likely ancestors to the genera with their names. For example, although *Heliopora* in the Lower Cretaceous is not morphological distinguishable from *Heliopora coerulea* in the present (Eguchi 1948; Colgan 1984), it is almost certain that the species has evolved to the extent that if biochemical data were available for comparison, they would be considered different species. Nevertheless, the continuous fossil record indicates that representatives of a number of genera of reef-building scleractinians survived a long history of extensive stressful times and mass extinctions (Wells 1956) and so it seems reasonable to hope that some will survive the present trajectory because their genome may contain substantial relics from their ancestors. This would not necessarily apply to those genera that shed defenses and tolerances when they originated in favorable times (Sect. 12.3.2).

Since corals previously experiencing stress often acclimatize or adapt to become more tolerant (Palumbi et al. 2014), Steve Palumbi and his lab are planning to transplant selected coral colonies that have adjusted to higher temperatures or other stresses to set up "designer reefs", groups of experienced colonies that are likely to survive where the ordinary corals might not (Mascarelli 2014; van Oppen et al. 2015). Likewise, Hernández-Delgado and Suleimán-Ramos (2014) have also been maintaining a community-based program of coral farming and outplanting for reef rehabilitation in Puerto Rico. Transplanting colonies bypasses the problems of connectivity, i.e., reduced fecundity, reduced fertilization of gametes from sessile adults as disturbance thins their population densities, shortening of development time in warmer water, early and local settlement behavior of many larvae despite potential for long pelagic duration, and reduced acceptability of disturbed habitats for successful recruitment (Sect. 12.2.3). However, paleontology indicates that although corals can adapt physiologically to the effects of CO_2 (such as temperature) and survive, they have not been able to adapt the relative rates of bioerosion and calcification to the effects of low pH and Mg/Ca mole ratio <2 so it seems likely that many genera of corals will survive, but reefs will deteriorate.

12.4.2 Reef Structure Will Deteriorate, as in the Cretaceous and Paleogene

> Like obesity, a massive reef accumulation may be the result of remaining stationary for too long under good conditions. (RW Buddemeier and RA Kinzie III (in Kleypas et al. 2001))

If the temperatures of tropical seas become warmer and the pH of shallow seawater becomes lower, most corals may not go extinct in the near future (Sect. 12.4.1), but bioerosion will certainly increase (Chap. 4), accretion by some corals may decrease, and the topographic complexity will decline (Alvarez-Filip et al. 2009; Fabricius et al. 2011), causing many reef ecosystem services to deteriorate. Glynn and Manzello (Chap. 4) explain that coral reefs are in a dynamic and delicate balance between $CaCO_3$ deposition and bioerosion and dissolution. With increased atmospheric pCO_2, the uptake of CO_2 by the ocean lowers the pH of seawater and accelerates bioerosion while sometimes also reducing the rate of calcification. With decreased pH, rates of bioerosion do increase in low-nutrient waters (Wisshak et al. 2012), but in high-nutrient waters (>1 μM nitrate), bioerosion increases tenfold (DeCarlo et al. 2015). Lower pH decreases the saturation state of aragonite, i.e., decreases the ease by which corals secrete calcium carbonate. Models predict that calcification rates of corals will decrease by 30±18 % in 30–50 years (Kleypas et al. 1999a, b). No matter how successful we will be in abruptly halting local problems such as overfishing, sedimentation, pollution, etc., the increased rates of bioerosion with possibly reduced rates of calcification will lead to severely reduced structural habitat complexity, and ecosystem services of coral reefs. Adapting to ocean acidification by itself is facing an indifferent non-responsive physical factor, but adapting to bioeroders is coevolving in an arms race. There has already been a Caribbean region-wide substantial loss of topographic complexity in the past four decades (Alvarez-Filip et al. 2009), and so although no corals have gone extinct in the Caribbean, the reefs are becoming substantially degraded and less functional ecologically.

Are coral reefs now returning to a "normal" situation in which reef-building is negligible (Kleypas et al. 2001)? The past interglacial period was extraordinarily favorable for scleractinian reefs, and not typical of the 224 million years of scleractinian existence (Hay et al. 1997; Buddemeier and Kinzie 1998; Pearson and Palmer 2000; Berner and Kothavala 2001; Kleypas et al. 2001). The late Jurassic through the late Paleogene was roughly 140 million years in which the Mg/Ca mole ratio of seawater was below 2 (Stanley and Hardie 1998), and so bioerosion increased tremendously (Vermeij 1987) and accretion of coral (aragonite) reefs became reduced (Stanley and Hardie 1998; Kiessling 2009). Although the diversity of reef-building genera of scleractinians increased (Sepkoski 2002; Kiessling and Szabo 2004), atmospheric concentrations of CO_2 were higher than today (may have ranged between 600 and 2,400 ppm), seawater temperatures may have ranged between 32 and 36 °C and seawater pH was usually between 7.4 and 7.6 (Pearson and Palmer 2000), so conditions were not favorable for substantial reef accretion. In the present, as the pH in warm surface ocean waters is likely to drop, bioerosion will certainly increase while accretion of reefs by corals may become more costly energetically.

Kleypas et al. (2001) emphasize that there is not a correlation between how well a coral community is performing biologically and how well it is performing geologically (building reefs). In the calcite seas of the Cretaceous, other creatures such as rudist bivalves provided three-dimensional substrata that corals could use (Götz 2003). Sepkoski (2002) and Kiessling and Baron-Szabo (2004) found scleractinian diversity to be high in the Cretaceous, and even if there were sources of error in Sepkoski's compilations, the general pattern of diverse scleractinians with eroded minor reefs was the situation during most of the existence of scleractinians. Now as the atmosphere, and then the oceans, take up more CO_2, corals may return to the "norm" of diverse assemblages of scleractinian corals on eroded reefs with minor rates of accretion. The basic message is that we have just been through about 10,000 years of abnormally prolific reef-building, but scleractinians may now return to the pattern in the later Mesozoic. Although a drop in Mg/Ca mole ratio to less than 2 and a drop in pH are very different chemical processes, they may have the same effects of accelerating bioerosion while reducing scleractinian reef accretion.

Corals do quite well without reefs (Fig. 12.3). Corals recruiting to basalt, plexiglass, pumice and many other substrata do as well, and sometimes better, than recruits to coral reefs (Sect. 12.2.3). The past few thousand years have been extraordinarily favorable for reef accretion and preservation (Kleypas et al. 2001) and this favorable period is representative of only 10 % of the past few million years (Hay et al. 1997). Since the origin of scleractinian corals about 224 million years ago, there have been only three periods of major reef construction (Kiessling 2009). However, the greatest diversity of scleractinian corals developed during a time in the later Cretaceous when most of the calcium carbonate structures were being formed by bivalve molluscs (rudists). Reefs are not an extended phenotype of corals like nests are of birds or dams are of beavers (Dawkins 1982), but are a byproduct of long period of good conditions (Buddemeier and Kinzie 1998).

12.5 Importance and Vulnerability of Big Fishes on Coral Reefs

12.5.1 Previous Stocks and Their Failure to Recover

Undisturbed coral reefs can appear to be characterized by inverted trophic biomass pyramids with up to 80 % (DeMartini et al. 2008) or 85 % (Sandin et al. 2008) of the fish biomass in the top level of piscivores and with fishes in all lower trophic levels pooled together constituting only 15–20 %. Although there is controversy as to whether inverted trophic biomass pyramids actually exist (Sect. 1.1), the disparate array of methods for surveying fishes all converge (Rizzari et al. 2014) on the same conclusions that population densities of large fishes are inversely related to the population densities of humans (Friedlander and

DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008; Nadon et al. 2012; Fenner 2014). The apex predators are the initial focus of the fishing activities and the larger fishes are especially vulnerable to modern fishing technology (reviewed in Fenner 2012, 2014). A few fishermen are able to change the trophic structure of a coral-reef ecosystem in very little time with modest effort (Fenner 2014), but the return of large fishes and the recovery of the inverted trophic pyramid usually takes decades if it happens at all (Hutchings and Reynolds 2004; Abesamis et al. 2014). Even subsistence fishing significantly reduced the upper trophic levels and total vertebrate biomass on coral reefs in the Caribbean at least 1,300 years ago (Wing and Wing 2001). By the 1800s, there had been a major decrease in large coral reef and seagrass-associated vertebrates and by the 1950s, the predatory and herbivorous coral-reef fishes of the greater Caribbean were mostly of small size (Jackson 1997).

The Nassau grouper *Epinephelus striatus* was historically one of the most important food fishes in the western tropical Atlantic. It served as a main source of food and income for shore communities throughout the greater Caribbean (Sadovy 1993). Spawning aggregations consisted of as many as 100,000 individuals (Smith 1972). Now, in the greater Caribbean, some spawning aggregations have disappeared. In Bermuda, the catch of Nassau grouper declined by 93 % in 14 years (Sadovy 1993). Nassau groupers used to reach a weight of 22.7 kg (50 lbs) or more, but now most are taken as juveniles. The World Conservation Union (IUCN) considers the Nassau grouper endangered.

Despite the loss of larger individuals in Caribbean coral-reef fish stocks, as recently as the early 1980s the biomasses of populations of coral-reef fishes were still estimated to be as high as 160–200 metric tons km^{-2} in the Atlantic (Randall 1963; Munro 1983) and as high as 93–237 metric tons km^{-2} in the Pacific (Goldman and Talbot 1976; Williams and Hatcher 1983). The mean harvests on reefs of a couple of small islands in the central Philippines over a 5-year period were found to be 11.4 and 16.5 metric tons km^{-2} year^{-1} (Alcala and Luchavez 1982). The shoreline fishery of American Samoa has yielded up to 26.6 metric tons km^{-2} year^{-1} (Wass 1982). Despite the reduction in stocks of larger fishes on coral reefs, the standing stocks of coral-reef fishes are still about 30–40 times greater than standing stocks on demersal fishing grounds in Southeast Asia, the Mediterranean, or other temperate regions (Russ 1984).

Although the biomasses of fish populations on coral-reefs three or four decades ago remained high in many places, coral-reef fish stocks in many locations dropped by 70–80 % and have remained low since the 1980s. The development of fishing technology made catching fishes easier, so the catch-per-unit-effort (CPUE) often underestimates the actual decrease of reef fish populations in the past three decades. The CPUE of the shoreline fishery of American Samoa dropped 70 % between 1979 and 1994 while the number of common fishes decreased by 75 % and the relative abundances among fishes changed drastically, with a decrease in commercially preferred fishes (Craig et al. 1995). Likewise, in fisheries monitored over a 4-year period in the Philippines, the numbers of adult fishes dropped 80 % and the number of species known to reach adulthood dropped 33 % (McManus et al. 1992). The CPUE on a bank south of Jamaica also declined by 82 % over a 15-year period (Koslow et al. 1988). The Guam nearshore fisheries CPUE decreased 78 % between 1985 and 1997 (Birkeland 1997). Data in Sandin et al. (2008) show that the biomass of reef fishes at Tabuaeran dropped by 68 % and at Kiritimati dropped 75 % in the past two decades. The stocks of coral-reef fishes in the main Hawaiian Islands are at most 20–25 % of what they were a century ago (Shomura 1987; Harman and Katekaru 1988; Smith 1993).

Once the drop in the range of about 80 % in standing stocks of reef fishes occur, the recovery may take decades if at all (Abesamis et al. 2014). The *Bolbometopon muricatus* were spectacular on Guam in the mid-1970s, but were essentially eliminated by overfishing in the late 1970s and still almost none are found 34 years later. The scenario is similar in American Samoa. Craig (2005) noted that corals recover from hurricanes, *Acanthaster*, and bleaching, but the fish populations are not recovering. A visiting marine ecologist commented that American Samoan reefs were like a lovely mansion of corals, but the mansion was empty. Where are the fishes? Like many coral reefs around the world, there are actually still many colorful small fishes; it is the big fishes that are gone. Craig (2005) noted there is “no quick fix” and that what we see today is “a shadow of former population abundances”. This pattern is not unique to coral reefs. Hutchings and Reynolds (2004) analyzed data from more than 230 fish populations that had a median breeding population reduction of 83 % from known historical levels and found little or no change in abundance for at least 15 years.

The diverse stocks of fishes on coral reefs are impressive, especially the stocks in relatively untouched areas that appear to have an inverted trophic biomass structure. This unfortunately encourages the investment into fishery-based economies. A journal The Economist stated that commercial trade in large coral-reef fish is a “gold rush”, a boom and bust, “. . .an extractive industry that eventually exhausts the resource it exploits” (Anonymous 2000).

12.5.2 Influence of Large Fishes on Community Structure

Coral reefs operate differently than do large-scale pelagic current systems in which concentrated pulses of nutrient input from upwelling act as physical oceanographic drivers of the foodweb. If the pelagic fishes are overharvested, it does not necessarily cause long-term fundamental changes in the system and the populations can replenish themselves with the next upwelling. The relatively low diversity system (two trophic levels between primary production and humans Sect. 1.1) of pelagic fisheries in eastern oceans is relatively simply based on nutrient input from upwelling and are relatively unstable because of the dependency on nutrient input. When there is a major El Niño Southern Oscillation (ENSO) which dampens upwelling, there is a failure of the anchoveta and tuna fisheries, hundreds of thousands of seabirds and at least hundreds of sea lions and seals die, but the system is resilient and recovers with the return of nutrient input from upwelling. Although the pelagic system is unstable because of its dependence on nutrient input, it is resilient because it does not depend on species interactions to prevent shifting to alternative states.

In the more complex and diverse coral-reef ecosystems, internal biological interactions such as grazing, predation, and competition have dominant roles in community structure. This may provide the communities of coral reefs with general stability because herbivores can potentially control the algae and predators can potentially control outbreaks of herbivores or corallivores. But diverse systems are less resilient because they can fall into alternative stable states. If herbivores are overfished, algae can take over and dominate when a disturbance decreases the cover of living coral and the algal dominance can persist by the effects of algae on coral recruitment (Sect. 12.2.3). There is no alternative steady state in most simple systems. Since coral-reef systems are complex, with species interactions that can maintain the stability of the system, they are less resilient to overfishing or severe disturbances because it is these species interactions that prevent the system from shifting to alternative states.

Long-term studies by McClanahan (2014) on the coast of Kenya found that the piscivores regained their biomass after about 20 years of protection, but the biomass of herbivorous fishes was slow to recover and the functional groups in the coral-reef system had still not fully recovered after 35 years of protection. Even if the biomass of herbivores is recovered, the “functional groups” may not recover unless the large individuals are present. Even at lower trophic levels, the size of the individual fish is of key importance. Parrotfishes below 15–20 cm in length nibble at algae to feed themselves, but those above 15–20 cm in length scape or excavate the substratum, removing algae and creating bare substrata appropriate for successful coral larval recruitment (Bruggemann et al. 1996; Bonaldo and Bellwood 2008; Lokrantz et al. 2008; Ong and Holland 2010).

Hunting the largest individuals not only affects the coral-reef ecosystem, but also has direct and indirect effects on the other fishes associated with targeted fish. Reducing the size and abundance of the predatory fishes led to the fishes at lower trophic levels to increase in average size and longevity (Ruttenberg et al. 2011), and to be in generally better condition. Sex change for protogynous species occurred at a larger body size when there were fewer apex predators (DeMartini et al. 2005). For a given body length, fishes at lower trophic levels had greater body mass, greater liver mass, and more energy reserves on reefs in which the predators at upper trophic levels were less common (Walsh et al. 2012).

The reason for the lower energy reserves and lower body and liver mass per unit length in coral-reef fishes on reefs where the top predators are in their natural abundances is likely to be the high risk of predation restricting the time and distance the potential prey species forages for food away from refuges from predation. Thus the removal of top predators potentially affects the benthic community by allowing the herbivores to forage greater distances from shelter and thereby increasing the distances that barren grounds or haloes separate reefs from seagrass (Randall 1965). Although herbivorous fishes become more predominant where the higher trophic levels have been fished down, this does not mean that the herbivores have higher biomass. The herbivores might also be fished down, but not to the extent of the top predators (Friedlander and DeMartini 2002).

Natural, undisturbed coral reefs are typically characterized by what appears to be an inverted trophic biomass pyramid, where upper trophic levels consist of large predators with relatively slow turnover, and the populations of fishes at lower trophic levels of herbivorous and planktivorous fishes consist of fewer and smaller fishes (DeMartini et al. 2008). The inverse pyramid is sustained because top predators have relatively slow turnover and the lower trophic levels (prey) have relatively rapid turnover. But this makes the system especially vulnerable to overharvesting of the slow-growing species in the upper trophic levels. It is the diversity of consumers and the large number of trophic levels that provide the mechanisms behind the unique structure of coral reefs of large gross primary production and mediocre net production or fisheries yield (Fig. 1.1; Sect. 1.1).

12.5.3 Importance of Large Fishes to Population Sustainability

The number of years of reproductive activity typical of a species indicates the usual degree of risk of failure to produce successful recruitment (Sect. 12.2.1). Analyses of data from 251 species of fishes showed that as recruitment success became more variable, the traits of late maturity, increased longevity, and iteroparity substantially increased (Longhurst 2002). Recruitment to complex coral reefs is hazardous for larval or juvenile fishes. Planktivorous fishes form a "wall of mouths" during the day (Hamner et al. 1988) and scleractinian corals, zoanthids, and anemones form a "wall of mouths" at night (Fabricius and Metzner 2004). There have been many studies of the effects of predation by resident fishes on the survival of newly arrived juveniles (Hixon 1991; Hixon and Beets 1993; Hixon and Carr 1997; Holbrook and Schmitt 2002; Hoey and McCormick 2004; Dixson 2011) and on the effects of competition among the recruits (Holt 1984, 1987; Jones 1997; Hixon 1991; Holbrook and Schmitt 2002). The proportion of successfully settled *Haemulon favolineatum* surviving through the first year was determined to be 0.008 (Ogden 1997). The survival of successfully settled *Acanthurus lineatus* through their first year has been found to be 0.007 (Craig 1995), but once established as an adult, it can live 42 years (Choat and Robertson 2002).

The hazardous and unreliable successful recruitment on coral reefs is probably the reason that coral-reef fishes are adapted to live long enough to attempt reproduction many times (Sect. 12.2.1). Acanthurids often live to 30 or 40 years (Choat and Robertson 2002) as do some lutjanids (Newman et al. 1996). Individuals of the genera of groupers (Serranidae) such as *Epinephalus*, *Mycteroperca* and *Cephalopholis* live 30–50 years, 33 years and 26 years, respectively. The relatively short-lived *Plectropomus* spp. still live over a decade (Ferreira and Russ 1994). The holocentrid *Myripristis amaena* becomes mature after 6 years and lives at least 14 years (Dee and Parrish 1994). Even damselfishes and parrotfishes have lifespans generally between 5 and 20 years, with *Stegastes acapulcoensis* having a maximum age of 32 years (Meekan et al. 2001). *Bolbometopon muricatum* takes about 7–8 years to reach sexual maturity at about 60 cm length, with a lifespan of about 40 years (Hamilton et al. 2008; Hamilton and Choat 2012).

The larger individuals among coral-reef fishes are particularly important, not only for maintaining ecosystem structure, but for sustaining their own populations. The fecundity of fishes increases exponentially with body size (Fig. 12.10); and so in natural populations where recruitment is sparse and uncertain and small fishes are at risk of being consumed by predators, the selective pressure strongly favors large body size, long life, and multiple reproductions. When the species that formerly had a refuge in size is now the prey of humans, however, the probability of living long enough to reproduce

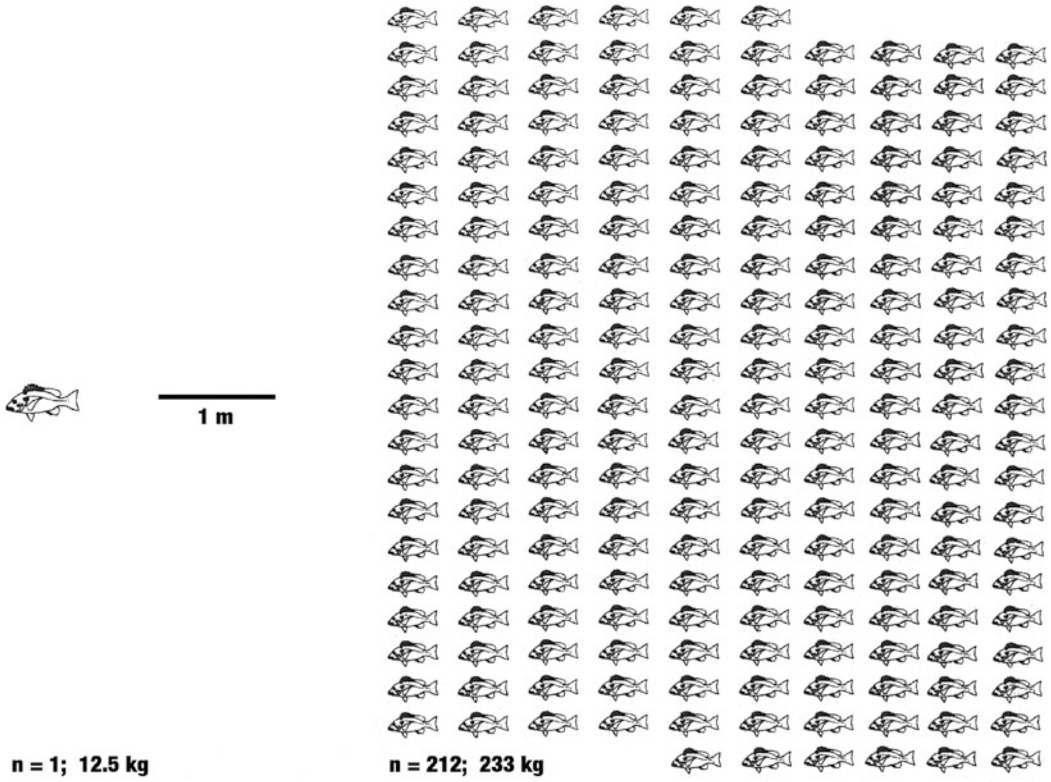

Fig. 12.10 Fecundity increases exponentially with body length in fish. One 61-cm female red snapper (lutjanid) produces the same number of eggs as 212 females at 42 cm each, or 12.5 kg of large snapper produces the equivalent number of eggs as 233 kg of medium-sized snappers. Each smaller snapper is 69 % the length of the larger one (Bohnsack 1998). The reproductive potential of a population is disproportionately affected when fishermen target large individuals. This is especially true for protandrous species

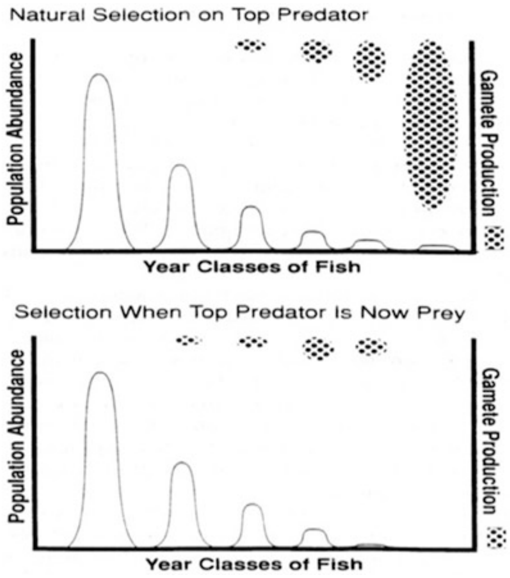

Fig. 12.11 There is a strong selective advantage for a top predator to grow large because fecundity increases exponentially with body size. When the top predator becomes prey to humans, selection turns to favoring early reproduction. Effective reserves protect the intraspecific genetic diversity of populations (Bohnsack 1998)

at a large size becomes small (Fig. 12.11); and selective pressure can shift to favoring rapid growth, early reproduction, and smaller size.

In contrast, recruitment to fisheries in pelagic systems is relatively reliable with the exception of periods of ENSO every few years and so lifespans of less than a decade should allow the adult fish populations to reproduce relatively reliably in abundance during non-ENSO years. Pelagic fishes such as mahimahi (*Coryphaena hippuros*) often live 2 years and grow to 14 kg (31 lb) on the In contrast, recruitment to fisheries in pelagic systems is relatively reliable with the exception of periods of ENSO every few years and so lifespans of less than a decade should allow the adult fish populations to reproduce relatively reliably in abundance during non-ENSO years. Pelagic fishes such as mahimahi (*Coryphaena hippuros*) often live 2 years and grow to 14 kg (31 lb) on the average, and can live a maximum of 4 or 5 years and grow to a maximum of 39.5 kg (87 lb). The pelagic *Thunnus albacares* (yellowfin tuna) has a lifespan of up to 6.5 years (Lehodey and Leroy 1999) and can grow to over 181 kg (almost 400 lb).

Pelagic fishes possibly grow faster in part because they continually search for dense concentrations of food and sometimes have the opportunity to consume food much more intensely than do coral-reef predatory fishes. When tuna find a mass of fish, they devour their prey intensely, consuming as much as 25 % of their body weight in one day, which partially explains their rapid growth. Coral-reef fishes cannot find prey in such concentrations because the topographic complexity provides refugia for their prey and so they feed on an occasional individual prey that wanders too far from their shelter. The introduced predatory reef fish *Cephalopholis argus* on the island of Hawaii, where it grows faster than in its native range, is found to consume on the average 0.8 % of its body weight per day (Dierking 2007). Groupers generally grow slowly, rarely over 0.5 kg per year. Yellowfin tuna can average 28 kg per year or 56 times faster growth than coral-reef groupers. When we compare the rate of growth and found to consume on the average 0.8 % of its body weight per day (Dierking 2007). Groupers generally grow slowly, rarely over 0.5 kg per year. Yellowfin tuna can average 28 kg per year or 56 times faster growth than coral-reef groupers. When we compare the rate of growth and potential longevity of coral-reef fishes such as *Acanthurus lineatus* that can live 42 years (Choat and Robertson 2002) to grow to a maximum size of 2.7 lb (1.24 kg), we can perceive how the ratio of fisheries yield per unit gross primary productivity for the Peruvian upwelling can be about 20–60 times greater than is this ratio for coral reefs (Fig. 1.1; Nixon 1982). There are some exceptions. The larger marlin and bluefin tuna can live 25 and 40 years, respectively. Bluefin tuna take several years to reach maturity and, like large coral-reef fishes, are more vulnerable to overfishing and most populations have decreased over 90 %.

Even the larger individuals of smaller species on coral reefs are important for fecundity. For example, the yellowstripe goatfish *Mulloides flavolineatus* is a schooling predator of small, soft-bodied invertebrates in the sand. It reaches sexual maturity within 1 year after hatching and has a long period of repeated spawnings each year. The local fishermen on Guam probably do not realize that fishing pressure has been drastically reducing the reproductive potential of the goatfish each year. By 1991, the reproductive potential of *M. flavolineatus* was only 5 % of its unfished potential (Davis 1992). By harvesting the larger individuals of even the smaller, more rapidly maturing fishes, a greater portion of the breeding stock is taken than is perceived by fishermen.

Although the importance of larger individuals may have been taken into account by Pacific islanders who knew the natural history of their fishes centuries ago, in modern times this is a particular problem because state fishing regulations are often not based on the natural histories of the fishes concerned and therefore allow the taking of important species such as parrotfishes before they have a chance to reproduce for the first time (Howard 2008). Important additional components of this loss of sustainability are the development of technologies such as refrigeration that allowed the switch from local subsistence to a global market economy. New

Fig. 12.12 One night's catch of *Bolbometopon muricatum* at Tetapare Island in the Solomon Islands (Photo courtesy of Richard J. Hamilton)

technologies such as scuba and underwater lights provided the means to overharvest large species such as *Bolbometopon muricatum* while they sleep, eliminating previous natural refuges for breeding stock (Fig. 12.12; Hamilton and Choat 2012).

Westerners' tendencies to focus harvesting on the largest individuals is as deleterious as the elimination of natural refuges and the switch to a global market. This can reduce the potential for population replenishment by drastically lowering fecundity, shortening the reproductive season, thus preventing the "bet-hedging" that allow some of the larvae to encounter favorable conditions, and in some cases reducing the average growth rate and endurance strength of larvae (Berkeley et al. 2004a, b; Bobko and Berkely 2004; Hixon et al. 2013). Overharvesting of larger individuals can also lead to the loss of genetic heterogeneity, potentially leading to reduced adaptability (Hauser et al. 2002). In recent decades, selective fishing pressure on the larger (older) individuals has caused a rapid evolution of smaller body size and lower fecundity in some harvested populations (Handford et al. 1977; Ricker 1981; Olsen et al. 2004).

12.5.4 What Does This Mean for Management Practices?

Isolated peoples can be in situations in which they must exploit coral reefs for subsistence. How should fish be taken while still maintaining the integrity of coral reef systems? Fish should be exploited with two forms of moderation: the use of slot limits on sizes taken and shift the focus from harvesting the capital to harvesting the interest or yield (Fig. 12.13). Slot limits guide the taking of intermediate size classes of a species, but leaving the largest individuals as highly fecund brood stock and leaving the juveniles to manifest their potential for rapid growth.

The yellow tang *Zebrasoma flavescens* is the economically most important aquarium fish in Hawaii and it is compelling to surmise that its spectacular success may be facilitated by effective slot limits. Well over 200,000 yellow tang are taken from the Kona Coast of Hawaii each year by the aquarium trade (280,125 in 2013 [William Walsh unpubl. data]). About 89,000 are taken as prey by roi (Dierking 2007), the introduced predatory grouper, *Cephalopholis argus*. This is an approximate total of 370,000 taken in 2013. Of course, this is an approximation and it must vary from year to year, but it does indicate that the population of yellow tang has been sustaining itself well. On a 217-km continuous reef, the take would be over 1,700 yellow tang per km of coastline per year.

This sustainability has certainly been aided by the establishment of zones in which some of the brood stock of aquarium fishes cannot be taken and there also must be habitat and oceanographic conditions favorable for recruitment. But the yellow tang still stands out as more productive than the other species in these environmental conditions taken for the aquarium trade and taken by predatory fishes. Part of the reason for the sustainability and extremely productive success of this system might be because both roi, the introduced predator, and the aquarium industry favor medium-sized individuals over the larger and the smaller individuals. Meyer and Dierking (2011) documented that *Cephalopholis argus* on the Kona Coast fed mainly on prey between 3 and 15 cm length ($n = 135$), while yellow

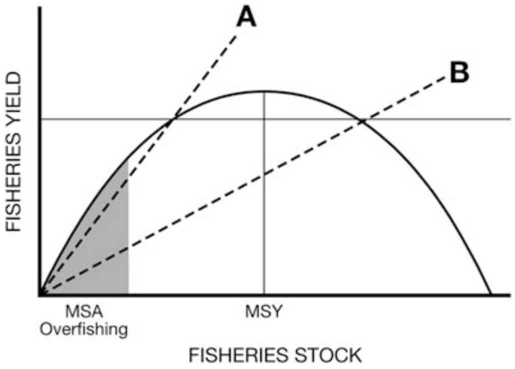

Fig. 12.13 Traditionally, the optimal harvest was considered to be to the left of the maximum sustainable yield (MSY). Overfishing has sometimes been defined by fishery councils under the MSA as spawning biomass reduced to 20 % of its unfished level. The fishery would be more stable if the same yield is taken from the right of the maximum sustainable yield (Courtesy of Joan Roughgarden. Modified and redrawn from Roughgarden and Smith 1996 with permission Copyright (1996) National Academy of Sciences, USA)

tang grow to 20 cm (Randall 2007). The aquarium trade also finds medium-sized yellow tang (8–15 cm) more marketable for household aquariums than older larger individuals (15–20 cm). By leaving the larger individuals which have the exponentially greater fecundity, and also leaving the smaller individuals which have the greatest proportional growth rates, harvesting the intermediate size classes is the most sustainable (Fig. 12.10).

Of 117 definitions of "overfishing" reviewed by an international panel of experts for the National Marine Fisheries Service, essentially all of them allowed fishing to reduce the stock well below the point of maximum sustainable yield (Darcy and Matlock 1999). For fishery councils operating under the Magnusen-Stevens Act (MSA), it is not uncommon for overfishing to be considered to begin when the spawning biomass is reduced to 20 % of its unfished level. This might not be appropriate for coral-reef fisheries because, as indicated by the longevity and multiple years of spawning typical of reef fishes (Sect. 12.2.1), successful replenishment of the fisheries catch may not be as reliable for coral-reef fisheries as for the target stocks on which theory is based. Roughgarden and Smith (1996) pointed out that when the limits to fishing down the population to the left of MSY (maximum sustainable yield), there is lower reproductive stock and theory indicates that this leads to a very unstable ecological equilibrium, "as difficult to maintain as balancing a marble on top of a dome". A coral-reef fisheries should be managed to promote stability because of the unreliability of successful recruitment. If the take is limited to the right of MSY, where the reproduction is affected by crowding, the fishery is "as easy to maintain as keeping a marble near the base of a bowl". Figure 12.13 illustrates how the fisheries yield is potentially the same on either side of MSY, but if we harvest the capital (line A) as in most commercial fisheries, the system is very unstable and difficult to manage. If we harvest the interest (line B) as in many indigenous subsistence fishers, the system is stable with "natural insurance" (Roughgarden and Smith 1996). A caveat for any fisheries theory that refers to MSY is that it is a moving target that is difficult to observe. A quantitative estimate of MSY requires a lot of data repeatedly because it changes frequently. Indigenous subsistence fishers did not need a quantitative estimate of MSY. They could observe if the larger individuals were still present.

Bob Johannes (1998) once pointed out that data-less resource management was the most effective approach to the complex and unpredictable interactions of resource management. For example, to adequately survey Indonesia for fish abundance or biomass would require over 400 man-years and the system being surveyed would change before the survey was complete. Are the quantitative values of abundance or biomass relevant? A hundred kilograms of small goatfish may have an order of magnitude lower fecundity than the same biomass of fewer larger goatfish. A hundred kilograms of parrotfishes <20 cm in length would have relatively little effect on the benthos while the same biomass of fewer larger parrotfishes would be removing algae and clearing substrata for coral recruitment. The information that is necessary to evaluate potential replenishment of marine resources should rely not on statistical analyses of surveys of biomass or population densities of stock or assessments of CPUE, but rather on the straightforward observation of whether the big ones are still there.

12.5.5 Coral Reef Ecosystems Are Not for Export, but Rather for a Service Economy

Although coral reefs have the greatest gross productivity of any ecosystem in the tropical seas, the sustainable fisheries yield and net system productivity are relatively low (Fig. 1.1). Far less than 1 % of the gross primary productivity of a natural coral reef is converted to production that is meaningful for human consumption (Hatcher 1997). The ratio of fisheries yield per unit gross primary productivity for the Peruvian upwelling is about 20–60 times greater than is this ratio for coral reefs (Fig. 1.1; Nixon 1982). The average ratio of gross productivity (P) to respiration (R) is close to 1 (P/R = 1) and the positive excess production, or potential yield from the system, is very close to zero (Sect. 1.1).

The number of trophic levels in food-webs decreases as nutrient input increases. Hallock (1987) explains mechanisms by which chronically low-levels of nutrient input leads to habitat and species diversity. Ryther (1969) assigned one or two steps between phytoplankton and man to upwelling systems and acknowledged that the upwelling regions of the world have the shortest food-webs. Grigg et al. (1984) assigned six trophic levels to coral reefs, probably the most complex of marine systems. Much of the assimilated energy is lost in respiration at each step in the food-web so that it is understandable that there would be less excess production in a system with six trophic levels than in a system with two.

There was a widespread concern in Bermuda that the coral reefs were deteriorating because of commercial fishing, even though the fisheries economy and number of people employed in extractive fisheries was small compared with tourism. Tourism and recreation related in Bermuda grossed more than $9 million in 1988. The hotel owners, charter-boat fishermen, dive and tour-boat operators and other businesses felt the incomes of many were threatened by the activities of a few fishermen. In 1990, considering evidence that the catches were declining substantially and the reef communities were deteriorating, the Government of Bermuda offered payment of up to $75,000 per fishermen, in addition to compensating them for hardware such as pots and winches, in order to close the coral reefs of Bermuda to pot fishing (Butler et al. 1993). This was not popular with commercial fishermen and was considered by some to be draconian. But with the establishment of a number of offshore fish-aggregation devices, some fishermen found alternative livelihoods with recreational charter fishing, offshore longlining for pelagic fishes, and deep-water trapping for crabs and prawns. Unlike fishing on coral reefs which is naturally subsidized by alternative species when the preferred species become scarce, the alternative fisheries each targeted certain types of fish and therefore was relatively self-limiting, requiring healthy stocks in order to have a viable fishery.

The money exchanged in world tourism in 1992 was 1.9 trillion, over 27 times the 70 billion of the world marine fisheries revenue (Weber 1993). In 2012, international tourism alone grossed 1.3 trillion, about 16 times the world marine fisheries which grossed 80 billion. To participate in the world economy, the islands of Oceania can be highly competitive for the high spenders in tourism, while geography (transportation costs for export fishery products), ecology (low sustainable yield and effects of overfishing on ecosystem processes), and biology (life-history characteristics of the species) work against commercial export fisheries from coral reefs. The infrastructure for commercial fisheries (processing, refrigeration, transportation) is more expensive and risky than the commitment to ecotourism. The cost of airfares are paid by the tourists themselves and create local employment, in contrast to the subtraction of air transport costs from the profit on exported fish sales. Analogous to the great diversity and biomass of species supported by reefs in regions of low rates of nutrient input, a greater number of people and jobs can be supported sustainably by coral reefs if economies are based on the natural attributes of the species and ecosystem.

I have been told by fisheries scientists that once a fish is dead, it does not matter whether it is used for subsistence or commercial export. But it takes at least an order of magnitude more fish to support a few commercial fishermen than it does to support a population by subsistence because most of the proceeds from the sale of fishes goes to supporting the marketing and transportation infrastructure. Coral-reef resources can sustain a much greater number of people or careers in the world economy if used in nonexportive enterprises. The nonexportive, service-oriented approaches of Bermuda and Palau (Sect. 12.6.3) are compatible with the attributes of coral-reef ecosystems and species, and with the demands of the growing human populations, growing economies, and urbanization.

Much of the great increases in marine fisheries of the world in the 1950s and 1960s came from the shift in emphasis in fisheries from the predatory fishes to the more plentiful fishes lower in the food-web. The catch of anchoveta (*Engraulis ringens*) in the Peru upwelling increased from about 200,000 metric tons in 1955 to 12 million tons in 1970, a 60-fold increase (Larkin 1978). In view of these successes, Grigg et al. (1984) suggested a series of important principles of resource management of coral reefs, in which the first was "To maximize efficiency, harvest at levels of sustained yield as low on the food chain as possible. Cropping predators would increase potential yield." Likewise, at a UNESCO meeting in Sri Lanka, I heard that local fishermen would prefer not having coral reefs because the slower growth of the resident fishes provided less turnover and therefore less sustainable yield, the higher diversity made harvesting and processing less efficient, the residency made replenishment less reliable, and the reefs themselves were a hazard to navigation. If our objective is to feed the growing human population, coral-reef fisheries are too easily overharvested, are too diverse for economically efficient processing, and unlike the pelagic fisheries, overfishing can affect the ecosystem. Although the Palauans and Bermudans agree that coral reefs are susceptible to overfishing and do not provide for a sustainable export economy, they had a rational view that coral reefs actually provide a solid economic basis for globalization with a service-based economy.

12.5.6 Palau, an Exemplary Case of Coral-Reef Management

> I believe the evolution of a social system that was built around knowledge has been the true treasure of Palauans. This, in my opinion, is also why Palau has had such great leaders and will continue to benefit for many years to come. (Gerald W. Davis)

Palauans display a more successful insight than any other people of which I am aware into adapting their solid understanding of the natural history of their resources to the changing conditions imposed by globalization of economics. Their policies of resource use appear to be developed by a society with knowledge of how ecosystem processes of coral reefs (Sect. 1.1) and life-history characteristics of animals in coral-reef communities (Sect. 12.5.3) are more sustainable and profitable with a subsistence and service –based economy (tourism) than with an export-based economy. On only a few hundred meters of reef at Blue Corner and nearby Ngemelis Dropoff, Palau earned about $7,000 per day on the average and up to $14,000 per day in peak season from diving tours back in 1992 (C. Cook, The Nature Conservancy – Palau Office, pers. comm.). A major contribution towards these earnings was a large humphead wrasse that allowed tourist photographers to approach closely. The Palauans were aware that this fish was much more profitable economically as a continuous tourist draw at thousands of dollars per day than it would be as a one-time fisheries yield, and so shooting this individual wrasse for sale in the fish market would have been socially unacceptable. Even dog-tooth tuna and grey reef sharks came close to photographers at Blue Corner. Diving activities by tourists brought in over $12 million to Palau in 1992 (not counting additional expenditures such as hotels, meals, and transportation). In 2010, scuba tourism brought $85 million to Palau (Vianna et al. 2010), and at least 50 % of tourists are scuba divers and close to 90 % go snorkeling or swimming (N. Singeo – Palau Visitors Authority, pers. comm.) (Figs. 12.14 and 12.15).

With its Shark Haven Act of 2009, Palau had the remarkable insight to set up the first major sanctuary for sharks, banning all fishing for sharks throughout its 600,000 km^2 exclusive economic zone (EEZ). A study by the Australian Institute of Marine Biology found that 39 % of Palau's gross domestic product ($218 million) was from scuba-tourism ($85 million) and 21 % ($17.9 million) of diving tourists said their primary purpose for choosing Palau was specifically to see sharks. Vianna et al. (2010) estimated that the main tourist dive sites hosted approximately 100 sharks. Therefore, they concluded an individual live shark brings in about $179,000 in revenue per year in the tourist industry, or a lifetime value of about $1.9 million, compared to $108 as a fisheries catch. The tax revenues to Palau from scuba-diving activity during which the observation of sharks was the major objective was 24 times higher than the total revenues from the fishing industry (Vianna et al. 2010).

Because of their economic and biological insight in developing a service-based economy rather than an extraction-based economy for coral reefs, Palau was given the prestigious Future Policy Award of 2012 for the best ocean policy of all nations. Palau's intelligent practice of bringing in substantially more revenue with relatively little capital investment, as well as the understanding that the life-history of sharks makes them especially vulnerable to harvest, encouraged similar actions by other nations. In 2010, the year following Palau's Shark Haven Act, the Maldives established their 90,000 km^2 EEZ as a shark sanctuary and Hawaii became the first state in the US to prohibit the sale of shark fins. In 2011, the rest of Micronesia (the Marshalls, Kosrae, Pohnpei, Chuuk, Yap, the Commonwealth of the Northern Marianas, and Guam), Tokelau, Honduras, and the Bahamas established shark sanctuaries throughout their EEZs. French Polynesia (4.7 million km^2) and the Cook islands (1.9 million km^2) followed suit in 2012 and the British Virgin Islands in 2014. The Bahamas now advertises itself to tourists as the shark-diving capital of the world.

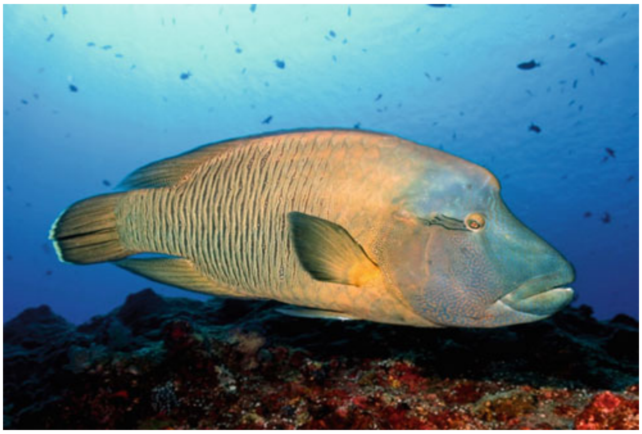

Fig. 12.14 "Tame" *Cheilinus undulatus* humphead wrasse that allows tourists to photograph it at Blue Corner, Palau (Photo courtesy of David Burdick)

Scuba-diving and snorkeling on coral reefs form a major base of the economies of a several countries. Over 31,000 tourists observe the reefs of Bonaire with scuba annually and the revenue from scuba-related tourism brings in about $23 million each year, about half their gross domestic product. The annual expenditure in reef protection by Bonaire is $0.67 million per year (NOAA Coral Reef Valuation Database), so the return on investment is substantially better than it would be for extractive fisheries. Service-based economies are not only substantially more profitable both in total income and in the ratio of profit to investment, but they are more sustainable for coral reefs because of the life-history characteristics of coral-reef species (Sect. 12.5.3).

Charter-boat sport-fishing of offshore pelagic fishes brings in considerably more money per fish than direct sales of fish. I knew a person who moved to Guam from Florida in hopes of making a living as a commercial fisherman. The expense of ice, diesel fuel, marketing, upkeep of the boat, docking fees, and the cost of living on Guam made it too difficult to compete with fishers in the Philippines who

Fig. 12.15 *Carcharinus amblyrhynchos* (*grey* reef sharks) and *Caranx sexfasciatus* (bigeye trevally) at a popular tourist dive site Siaes Corner, Palau (Photos courtesy of David Burdick)

could live and operate on substantially less. Philippine fishers could undersell fishers on Guam despite the added daily cost of air-freighting their fish to the market. Therefore, the person I knew supported his goal of occasionally being a commercial fisherman by actually making his income by chartering his boat for offshore sport-fishing.

In 1980, Japan AID contributed 11 diesel fishing boats and other fishing gear to Palau to promote export of reef fishes. After a year, thousands of dollars were being exchanged in the marketing of reef fishes, but after expenses in operating the boats, marketing and processing the fish, the fishermen were netting only US$ 0.20 per fish. In the export business, fishermen would have to sell about 5 kg of reef fish to purchase 0.2 kg of canned tuna at the supermarket. It was clear that exporting fishes was far less profitable, and well as being in competition with subsistence fishing, recreational fishing, tourism, and selling fishes to local restaurants and hotels.

In view of the more sustainable economic use of resources in subsistence and tourism than in export of biomass, the Government of Palau has passed legislation called the "Marine Protection Act of 1994" to gradually phase out the export of coral-reef fishes. "The purpose of this Act is to promote sustainability and develop marine resources of the Republic while also preserving the livelihood of the commercial fishermen of the Republic." At this time, commercial export of reef-fishes from Palau is illegal during the months of March through July which are the spawning seasons for important reef-fish species. The local fishermen are encouraged to switch completely to other forms of endeavor, e.g., chartering for sport fishing or selling fish locally to hotels and restaurants. The money stays in Palau when the fish are sold locally, the fisherman can make a lot more money per fish by cutting the costs of shipping and middlemen, and the quality of fish in the local hotels and restaurants is greater when they do not have to compete with the export market.

Palau has a strong tradition of a marine tenure system. Resource management regulations may still be put in place by traditional chiefs in each state. A traditional closure is called a "bul". In support of this tradition, the constitution of the Government of Palau recognizes that each state has the responsibility to manage all activities within their lagoons, inshore areas, and reefs extending 12 nautical miles seaward of the shore. The national government holds an advisory role to the state on all matters of resource management. Access to fish within a state is granted by the traditional leader's authority.

When a local community establishes restrictions, this helps the Government understand what policies are needed by the local communities. In 1988, before the banning of exports of coral-reef invertebrates (other than those produced by aquaculture) and reef-fishes during their breeding seasons, a "bul" on the export of sea cucumbers was promoted by groups of women who collected them for subsistence (Gerald Davis, pers. comm.). Sea cucumbers are a very popular and commercially valuable food in Asian countries. An Asian entrepreneur came to Palau and began exporting the more valuable species. This quickly depleted the stocks. Women who glean the reefs for subsistence realized how these commercial exports were substantially reducing their abilities to take food home. Their lobbying for a "bul" on the exportation of sea cucumbers made the Government of Palau aware of the need for regulations in cooperation with the local communities (Gerald Davis, pers. comm.). The Marine Protection Act of 1994 was thereby developed from a responsible tradition of cultural regulation of local resources.

Communication between villages and the Government of Palau has been remarkably two-way. Just as the Government pays attention to a local "bul", the people pay attention to their leaders. The seawater warming of 1997–1998 caused substantial coral mortality. The coral was replaced by algae which inhibited coral recruitment. Tommy Remengesau, Jr., then Vice President of Palau, published advice in the local newspaper to avoid taking herbivorous fishes for food, but rather take predators or omnivores, because the herbivores can control algae and this should facilitate coral recruitment. He also asked people not to step on living corals because in doing so they would damage the brood stock needed for recovery of coral populations. The reefs recovered substantially, so perhaps his advice was heeded. He also initiated the Micronesia Challenge in which Palau and the other nations of Micronesia all pledge to conserve effectively at least 30 % of their nearshore marine resources and 20 % of their terrestrial resources by 2020. In 2014, the President of Palau announced his intention to establish the first nation-wide marine sanctuary that fully protects more than 80 % of its EEZ. Remengesau, now President of Palau, was winner of the Champions of the Earth award by the United Nations for the policies of Palau that promise to sustain economic resilience while maintaining natural resources.

There has also been a two-way communication between Palauan cultural knowledge of the natural history of the coral-reef resources and western science. Bob Johannes (1981) championed the knowledge of Micronesian fishermen and quoted other scientists as well who noted that local fishermen know more about the natural history of their resources than is known in science. The Palauans have special talents to combine traditional culture and economics with science and natural history to get the best results. They accept technical support with an open mind. For example, Noah Idechong received an education in economics, but he grew up knowing Palauan fisheries and was awarded a Pew Fellowship in 1997 to work on marine conservation. National Marine Fisheries Service awarded him a grant to develop a sustainable sport fishery that provided the best use of the inshore fishery resources of Palau.

Noah led the founding of the Palau Conservation Society (PCS), a nongovernmental organization with the goal of solidifying the local communities' capacities for stewarding their natural resources. PCS takes the comprehensive (marine and terrestrial) ecosystem approach and helped to develop the Protected Areas Network (PAN) in cooperation with the local communities and the national government of Palau. PAN sites are the Palauan commitment towards the Micronesia Challenge. The Palauan Government established a Green Fee, a fee that is paid by anyone leaving Palau. Diving tourists are nearly always happy to pay a coral-reef resource management tax as long as it is directly used for the stated purpose rather than to general government account. The Green Fees of Palau are restricted to a PAN Fund. States, communities or private protected areas may apply for support to develop and manage a PAN site. PCS worked with the government, states and the NOAA Pacific Islands Fisheries Science Center to develop criteria for management plans and monitoring protocols.

The other peoples of the Caroline Islands (Yap, Chuuk, Pohnpei, Kosrae and their numerous associated atolls) also have solid knowledge of their resources. In Yap, they directly manage their terrestrial resources by planting vegetation or raising livestock or poultry to replace what is harvested, but they manage their harvesting of marine resources indirectly by managing their fishing practices because they know they must depend on the whims of natural processes to replace what they harvest. Traditional social organizations of marine tenure, rights of harvest, control of fishing methods vary among the many islands and atolls. However, Palau stands out as leading in adapting management of resources to the changing global economy.

The most important value of coral reefs in the lives of local people is usually not recognized by outsiders. This is the stabilizing effects 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 has been said that reefs may be more important in providing the opportunity for fishing activities than in providing the catch. Fishing and reef-gleaning are 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 food 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 these costs of the deterioration of coral reefs are ultimately paid by all of us.

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