CHAPTER

7

The Global Biodiversity of Coral Reefs: A Comparison with Rain Forests

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There has been increasing concern over declining global biodiversity due to overexploitation and habitat destruction by humans, who now consume 20-40% of the global net terrestrial primary productivity (Ehrlich and Ehrlich, 1992; Ehrlich and Wilson, 1991; Wilson, 1992). Tropical communities are particularly important in the global economics of biodiversity, because it is here that human populations are increasing most rapidly, monetary resources will be most strained, and problems of food production, pollution, and environmental change will be most acute during the twenty-first century.

Two of the most diverse natural communities on Earth, coral reefs and rain forests, both occur in the tropics. Coral reefs resemble rain forests in their biologically generated physical complexity, high species diversity, elaborate specializations of component species, and coevolved associations between species. Rain forests and coral reefs usually are considered to represent the two pinnacles of biodiversity on Earth, yet no detailed attempts to quantify the total species diversity on coral reefs have been made. This chapter describes why coral reefs are important for all societies to conserve and manage for the future, addresses the need for training specialists in the systematics of marine organisms (particularly those who would study the rich and poorly known tropical regions), and provides the first quantified estimate of the total biodiversity of global coral reefs as compared to rain forests.

THE VALUE AND CURRENT STATUS OF CORAL REEFS

Although they generally inhabit nutrient-poor waters, coral reefs are one of the most productive ecosystems on Earth (Grigg et al., 1984). Their fishes and

invertebrates traditionally have been and continue to be a critical source of protein for the world's tropical coastal countries. This fact will become increasingly important over the next century and beyond, because it is precisely these countries that are experiencing explosive population growth and some of the most severe coastal degradation. Failure to ameliorate the deterioration of marine waters and to provide management plans for the sustainable use of reef fisheries will remove an essential source of protein for these human populations (Norse, 1993).

In addition, coral reefs form ramparts that enclose lagoons, which are the primary nurseries and feeding grounds for fishes and other organisms. Historically, these protected embayments have facilitated the development of human transportation and commerce systems along tropical coastal areas. Today, they protect human populations from hurricane and wave damage, making coastlines secure for navigation, fishing, and tourism. Bioerosion of the carbonate reef framework and the calcareous shells of reef organisms provide almost all of the sand that comprises most tropical beaches. Tourism on coral reefs is an increasingly important economic resource for developing countries, but such activity must be managed sustainably if tourism is to remain a viable source of income. Geologically, reefs are associated with oil repositories. The diversity on reefs represents a largely unknown and untapped source of genetic material that has potentially great medical, pharmaceutical, and aquacultural use.

However, the coral reefs of the world are endangered by overexploitation, chemical and oil pollution, sedimentation, and eutrophication (resulting from deforestation, construction, and agricultural runoff), as well as large-scale environmental hazards such as increased ultraviolet light exposure and temperature anomalies (Allen, 1992; Hallock et al., 1993; Hughes, 1994; Kuhlmann, 1988; Sebens, 1994). World-wide episodes of coral "bleaching" (loss of symbiotic algae that provide nutrients and increase rates of calcification; Brown and Ogden, 1993; Glynn, 1993; Ogden and Wicklund, 1988; Williams and Bunkley-Williams, 1990), mass mortalities of reef-dwelling organisms (sometimes encompassing entire geographic regions, such as the Caribbean-wide mortality of an ecologically important sea urchin; Hughes et al., 1985; Lessios et al., 1984), and declining abundances of coral and other reef species (Porter and Meier, 1992) have been documented over the last decade.

Some of the above trends have received attention from the media and have been recognized by congressional hearings or other institutional initiatives (e.g., D'Elia et al., 1991). However, the value, risk of loss, and even the amount of biodiversity on coral reefs (and in the marine environment in general) has received relatively little attention by the scientific community, which is based largely in northern temperate zones and is focused primarily on the terrestrial environment (Gaston and May, 1992). Also, although ecotourism and recreation in tropical environments, including coral reefs, has become increasingly popular in recent years, the public generally may be unaware of the urgency and importance of environmental degradation in these tropical marine habitats. In

particular, the public has not been adequately informed of the declining numbers of trained biologists who are capable of estimating the amount of biodiversity on coral reefs, documenting how reef biodiversity is biogeographically distributed, and targeting where the biodiversity on global coral reefs is most at risk.
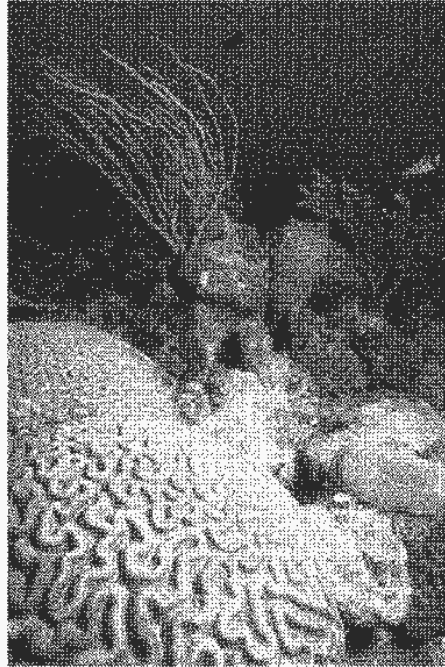
There is a crisis of declining numbers of trained systematists (scientists who analyze the relationships between lineages, the evolutionary trajectories, and the biogeographic distributions of organisms, and signify these patterns in hierarchical taxonomic classifications so that field-caught organisms can be identified and their ecological roles studied). This crisis is especially acute for systematists of marine invertebrates and algae (Feldmann and Manning, 1992; Gaston and May,

Along with rainforests, coral reefs represent the second pinnacle of biodiversity on Earth.

1992; John, 1994). There is an urgent need for major national and international initiatives in the systematics and biodiversity of the global marine biota, particularly of the richest and least known components, the tropical marine biota.

The next section provides an estimate of the global biodiversity of coral reefs and suggests that the lack of prior availability of such information is due to the fact that marine environments in general and tropical marine habitats in particular are understudied and relatively poorly known. This prevents us from assessing which marine habitats of the world are in the most serious jeopardy and, most importantly, prevents us from being able to recognize extinctions if they occur or even from assessing the potential for extinctions. I argue that extinctions in marine macrofauna (particularly on coral reefs) are likely to have been more frequent than we have thought, and that the potential for loss of coral reef species—with all of their inherent genetic and ecological value—over the next 100 years is great.

A QUANTIFIED ESTIMATE OF BIODIVERSITY ON CORAL REEFS

There currently are about 1.8 million described species in all environments on Earth, although various authors have estimated that 5-120 million species

exist and that <10-50% of the Earth's species may be known (Ehrlich and Wilson, 1991; Erwin, 1982, 1988; Gaston, 1991; Grassle and Maciolek, 1992; May, 1988, 1990, 1992; National Science Board Task Force on Biodiversity, 1989; Stork, 1988; Wilson, 1988, 1992). Most international concern over declining biodiversity has been focused on terrestrial environments, particularly the rapidly vanishing rain forests. This concern is justified, given the discoveries over the last decade of how many species are present in these tropical wonderlands, the potential uses of such genetic diversity, the potential effect of burning rain forests on global climate, and the shocking rates—graphically relayed by satellite—at which these habitats are being eclipsed by the activities of humans. Until recently, however, the amount of biodiversity and its possible decline in marine environments has received little attention.

It has been recognized that marine environments have more higher-level taxonomic diversity than terrestrial environments. Among all macroscopic organisms, there are 43 marine phyla and 28 terrestrial phyla (of the 33 animal phyla, 32 live in the sea and only 12 inhabit terrestrial environments), and 90% of all known classes are marine (Angel, 1992; May, 1994; Pearse, 1987; Ray, 1985, 1988, 1991). Many of today's marine animal phyla originated or diversified during the Cambrian evolutionary radiation more than 500 million years ago, whereas plants and then animals invaded land later in the Paleozoic Era (approximately 200-400 million years ago; Signor, 1994). This long separation of evolutionary pathways among marine lineages has resulted in a greater variety of body plans, greater functional and biochemical diversity, and greater "endemism" in major groups of marine compared to terrestrial animals (64% of animal phyla inhabit only the sea, while only 5% of animal phyla live exclusively on land; May, 1994).

In addition to containing great higher-level taxonomic diversity, some marine environments also contain high species diversity. For example, the deep seas are repositories of biodiversity. Based on samples of 1,597 species of marine macrofauna from soft bottoms off the east coast of North America (255 to 3,494 m depths), Grassle and Maciolek (1992) calculated that the global deep sea fauna, because of the huge area it occupies, may include 10 million species (mostly polychaete worms, crustaceans, and molluscs; but see lower estimates in May, 1992, 1994; Poore and Wilson, 1993). Most of these species from the deep sea are rare (90% of the species sampled by Grassle and Maciolek comprised <1% of the individuals, and 28% of the species in the entire fauna were collected only once).

Local marine habitats also contain high numbers of species. Grassle and Maciolek (1992) reported 55-135 species in individual 30 × 30 cm cores of ocean floor sediment at 2,100 m depth. In a shallower soft-sediment environment in south Australia, more than 800 species were found within a 10 m^2 area (Poore and Wilson, 1993). Hughes and Gamble (1977) obtained 350 species from intertidal soft substrates around a reef flat on Aldabra Atoll, and 6 liters of sediment on Oahu yielded 158 species of polychaete worms (Butman and Carlton, 1993).

Coral reef communities also contain high local diversities of species. These communities can be divided into three main components: (1) the suprabenthic fishes; (2) sessile epibenthic organisms that provide the complex structure of the reef (hard and soft corals, sponges, coralline and fleshy algae); and (3) the cryptofauna, which includes organisms that bore into the substrate (primarily sponges, polychaete and sipunculan worms, and bivalves), sessile encrusters living within bioeroded holes and crevices (e.g., bryozoans, sponges, tunicates, polychaete worms), and motile nestlers inhabiting bioeroded holes and crevices (e.g., polychaete and sipunculan worms, echinoderms, molluscs, and especially crustaceans). Although we usually think of coral reefs in terms of the first two components, in fact most of the diversity as well as biomass of coral reef communities is included within the cryptofauna, which is the functional equivalent of insects in the rain forest.

On the Great Barrier Reef of Australia, 350 species of hermatypic (reef-building) corals (33 of them endemic) are recognized, and 242 species are known from one island (Ishigaki) in the Indo-West Pacific (Veron, 1985). Fifteen hundred species of reef fishes have been reported from the Great Barrier Reef (Sale, 1977), 496 species of fishes are known from the Bahamas and adjacent waters (Bohlke and Chapin, 1968), 442 species of fishes have been recorded in the Dry Tortugas (Florida)(Longley and Hildebrand, 1941), and 517 species of fishes occur on Alligator Reef (Florida) alone (Starck, 1968). Using rotenone to sample the fishes on small areas of reef, single collections have yielded 67-200 species in the Bahamas and Palau, respectively (Goldman and Talbot, 1976; Smith, 1978a). Bohnsack (1979) reported 10-23 species of reef fishes living around single coral heads on Big Pine Key, Florida.

The reef-associated cryptofauna also is diverse at several scales. Taylor (1968) found 320 molluscan species in a 31,000 km^2 area of the Seychelles. Peyrot-Clausade (1983) documented 776 species of motile cryptofauna (four phyla) in dead coral from one reef flat in Moorea. One species of coral, *Oculina arbuscula*, in Florida provided habitat for 309 species of organisms larger than 0.2 mm (McClosky, 1970). Fifty-five species of decapod crustaceans have been reported to live in the coral *Pocillopora damicornis* in the Pearl Islands, Panama, and up to 101 species of decapod crustaceans were found in *P. damicornis* in the Indo-West Pacific (Abele, 1976; Abele and Patton, 1976; Austin et al., 1980). Bruce (1976) documented 620 species of shrimps and prawns that are commensal on different species of corals. Jackson (1984) documented 46 species of encrusting cheilostome bryozoans between 0-21 m depth in Jamaica. On a smaller scale, Gibbs (1971) found up to 220 species (8,265 individuals) of boring cryptofauna in single colonies of dead coral, and Grassle (1973) reported 103 species of polychaete worms in one colony of living coral. Thus, although no comprehensive all taxa biodiversity inventories (Yoon, 1993) of coral reef habitats have been made, it seems likely that diversity within as well as between coral reef habitats is extraordinarily high.

The total species diversity on global coral reefs has been difficult to quantify precisely, however. The most current information on the number of species contained within a group of organisms is found in monographic treatments of the systematics and evolutionary biology of individual taxa, but different monographs often target different taxonomic levels (groups of species within a genus, or groups of genera, families, or superfamilies) and usually include species from all of the habitats occupied by the taxon (freshwater, estuarine, terrestrial, marine), making it difficult to tally the numbers of species on global coral reefs among all taxa.

Using the concepts of island biogeography, known and calculated areas of the major marine and terrestrial regions of the globe, and several testable assumptions about the biogeographical distribution and abundance of marine species, one can calculate the described and expected species diversity of coastal marine organisms, tropical coastal marine organisms, and coral reef organisms in comparison to that of rain forests. My laboratory at the University of Maryland is in the process of testing with empirical data the generalities about relationships between species richness in different habitats and biogeographical realms that are present in or inferred from the literature and used in the present calculations. Further additions to the database may alter the numerical results slightly, but are not expected to substantially change the conclusions. Also, the results presented here can be modified and updated easily as more data become available, since the assumptions and mathematical relationships are identified.

Available data and calculations (Table 7-1) reveal that the terrestrial realm includes about 33%, global rain forests 2%, coastal zones 8%, tropical seas 24%, and tropical coastal zones 2% of the global surface area. Global coral reefs

TABLE 7-1   Area Relationships of Coastal Marine Zones and Terrestrial Regions of the Globe (all areas are $n \times 10^6$ km^2)

Zones and Regions	km^2	% of Earth
Global surface area	511	100
Global land area	170.3	33.3
Global rain forests	11.9	2.3
Global oceans	340.1	66.7
Tropical seas	123.0	24.0
Global coastal zones	40.9	8.0
Tropical coastal zones	9.8	1.9
Coral reefs	0.6	0.1

SOURCES: Data were taken or calculated from information provided in Kuhlmann (1988), the Rand McNally Atlas (1980), Ray (1988), Smith (1978b), and Wilson (1988).

comprise about 0.1% of the Earth's surface, 6% of tropical coastal zones, and 5% of the area of global rain forests.

Table 7-2 shows that there are approximately 1,450,000 currently described species of terrestrial organisms (about 78% of the global biota), about 100,000 currently described species of symbiotic organisms (about 5% of the total), and approximately 318,000 described species of aquatic organisms (17% of the global total). Of aquatic organisms, my calculations from data in Pennak (1989) and other sources revealed that about 26,000 species, or about 13% of the species of macroscopic invertebrates overall, inhabit freshwater. Although about 40% of the world's species of fishes occur in freshwater (Ray, 1988), only 5-10% of macroalgal species live in freshwater environments (John, 1994, and personal communication, 1995). The above independently derived figure of about 13% freshwater invertebrates is in good agreement with May's (1994) data (drawn from a tabulation of species in all benthic and pelagic marine and freshwater animal phyla), which show that about 12% of all aquatic species live in freshwater. Consequently, to assess the number of marine species within the relatively little-known microscopic algae, viruses and bacteria, and protistans (all of whose affinities for freshwater or marine habitats might be expected to be closer to that of macroalgae and invertebrates than to fishes), the proportion of marine versus freshwater species was estimated to be about 90% and 10%, respectively.

Thus, of the 318,000 described species of aquatic organisms, a total of about 274,000 species was estimated to be marine (including approximately 180,000 species of macroscopic marine invertebrates; 36,000 species of micro- and macroscopic marine algae; and 58,000 species of other marine groups such as vertebrates, protistans, viruses and bacteria; Table 7-2). Therefore, about 15% of global described species are marine (a figure independently obtained by May, 1994). If only macroscopic marine species are included due to uncertainties in the taxonomy of microorganisms, there would be about 200,000 described species of marine macroalgae, macroinvertebrates, and chordates, or about 11% of the total described global species.

From the total numbers of described species of marine animals and plants (above), one can calculate the number of species in *global coastal zones* by estimating that about 80% of all marine species occur in the coastal zones (National Science Board Task Force on Biodiversity, 1989; Ray, 1988, 1991). This figure probably is conservative. Over 90% of all marine species are benthic (bottom-living) rather than pelagic (May, 1988, 1994). Almost all marine macroalgae live in benthic (John, 1994, and personal communication, 1995) sunlit environments, and oceanic phytoplankton comprise only 9-11% of all algal species (Sournia and Ricard, 1991).

One then can calculate the number of described marine species that should occur in *tropical coastal* and *coral reef* environments based on the global area of these regions and current knowledge of biogeographic patterns. These calculations employ known theoretical and empirical relationships between the rate at

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TABLE 7-2 Species Diversity of Major Groups of Living Organisms

Organisms	Number of Described Species (to nearest 1,000)	% of Total Described Species (@ 1.87 million)
Terrestrial Organisms		
Terrestrial chordates	23,000	1.2
Insects	950,000	50.8
Noninsect and noncrustacean arthropods	80,000	4.3
Other terrestrial invertebrates (molluscs, nematodes, annelids, platyhelminths, etc.)	57,000	3.0
Fungi	70,000	3.7
Terrestrial plants	270,000	14.4
Total Terrestrial Species	1,450,000	77.5
Aquatic Organisms		
Algae	40,000	2.1
All marine algae[a]	36,000	1.9
All freshwater algae[a]	4,000	0.2
Marine macroalgae	4,000-8,000	0.2-0.4
Freshwater macroalgae	450	<0.1
Viruses and procaryotes	10,000	0.5
Marine viruses and procaryotes[a]	9,000	0.5
Freshwater viruses and procaryotes[a]	1,000	<0.1
Protozoa	40,000	2.2
Marine protozoans[a]	36,000	1.9
Freshwater protozoans[a]	4,000	0.2
Macroinvertebrates		
Marine macroinvertebrates	180,000	9.6
Freshwater macroinvertebrates	26,000	1.4
Chordates		
Marine chordates	13,000	0.7
Freshwater chordates	9,000	0.5
Total Marine Species		
All taxa	274,000	14.7
Macrobiota	197,000-201,000	10.5-10.7
Total Freshwater Species		
All taxa	44,000	2.4
Macrobiota	35,000	1.9
Total Aquatic Species	318,000	17.0
Symbiotic Organisms		
Total Symbiotic Species	100,000	5.3
Total Global Described Biodiversity	1,868,000	—

[a]Assumes that the proportions of marine and freshwater species are 90% and 10%, respectively (see text).

SOURCES: Data were taken, calculated, or updated from Barnes (1984), Brusca and Brusca (1990), Ehrlich and Wilson (1991), Hammond (1992), Hawksworth (1991), John (1994, and personal communication, 1995), Margulis and Schwartz (1988), May (1988, 1991, 1992, 1994), Parker (1982), Pearse (1987), Pennak (1989), Raven and Wilson (1992), Ray (1988, 1991), Systematics Agenda 2000 (1994), and Wilson (1988).

which numbers of species change with area ($S=cA^z$, where S is number of species, c is a constant, A is area, and z is a scaling factor that usually falls between 0.2 and 0.3; MacArthur and Wilson, 1967; May, 1975, 1994; Wilson, 1989, 1992). Where $z=0.25$, a reduction of 90% in area coincides with a reduction of about half of the species present, which approximates natural situations for faunas on islands of different sizes or where habitat destruction has reduced the amount of area available to species.

Using the above biogeographical equations and the assumptions that tropical coastal zones are approximately twice as rich in species (or, as modeled here, that z, the exponent in the above equation, is twice as high in tropical as in temperate faunas) and are as well studied as those at higher latitudes, tropical coastal zones should include about 195,000 total described species and 143,000 described species of macrobiota, given their area (Table 7-3). A review of data and inferences in the literature suggests that the assumption of double area-specific diversity in the tropics is realistic but may be conservative. Although data often are not available on an area-specific scale, there are two to at least three times more species in tropical than temperate environments for most (though not all) groups of organisms (Angel, 1992; May, 1986a, 1988; Raven and Wilson, 1992; Rex et al., 1993; Stevens, 1989; Stork, 1988). Also, because of the assumption that the tropical coastal zone is as well studied as the global coastal zone (which likely is not met), the values presented likely underestimate true biodiversity in tropical coastal zones.

Similarly, using the above area relationships and assuming that the complex coral reef substrate contains approximately twice as many species per unit area (or, that z is twice as large) and is as well studied as level-bottom (sand, mud) habitats in the same biogeographical region, there are about 93,000 described species of all coral reef taxa and 68,000 species of described coral reef macrobiota on Earth. Although Abele (1976) reports that 53 species of crustaceans occupy coral habitat (*P. damicornis*) compared to 16 species in sandy beach habitats on the Pacific coast of Panama, biodiversity in coarse- versus level-bottom marine habitats probably needs to be more extensively quantified to document this assumption. Thusly calculated, though, the total described species on coral reefs represents only about 5% of the described global biota.

In contrast, rain forests may account for more than 70% of the described global biota (Table 7-3). If 90% of currently described terrestrial species occurred in rain forests (as do primates; Mittermeier, 1988) and if all groups were as well known as primates, then rain forests would include about 1,305,000 described species. This yields an underestimate of the true number of species in rain forests, however, since about two-thirds of currently described species (mostly insects) are thought to occur in temperate regions (due to more intensive study there), and there probably are two undescribed species of tropical insects for every described species of temperate insect (May, 1986a, 1988). Other estimates, incorporating the high probability that large numbers of undescribed

TABLE 7-3 Calculated and Expected Species Diversity on Global Coral Reefs for all Taxa and Macrobiota

Organisms	Number of Described Species (to nearest 1,000)	% of Total Described Species (@ 1.87 million)
Total Described Marine Species[a]	274,000	14.7
Macroscopic Described Marine Species[a]	200,000	10.7
Animals	193,000	10.3
Algae	4,000-8,000	0.2-0.4
Total Described Coastal Species (if 80% of all marine species are coastal)	219,000	11.7
Macroscopic Described Coastal Species (if 80% of macroscopic marine animals and most marine macroalgae are coastal)	160,000	8.6
Animals	154,000	8.2
Algae	4,000-8,000	0.2-0.4
Total Described Tropical Coastal Species (if communities in the tropical coastal zone are as well studied and twice as diverse as those at higher latitudes; tropical coastal zone=24% of global coastal zone[b])	195,000	10.4
Macroscopic Described Tropical Coastal Species (same assumptions)	143,000	7.6
Animals	138,000	7.4
Algae	3,000-7,000	0.2-0.4
Total Described Coral Reef Species (if reef communities are as well studied and twice as diverse as those on nonreef level bottoms; coral reefs=6% of tropical coastal zone[c])	93,000	5.0
Macroscopic Described Coral Reef Species (same assumptions)	68,000	3.6
Animals	66,000	3.5
Algae	2,000-3,000	0.1-0.2
Global Rain Forest Species (1) if 90% of all currently described terrestrial species[a] live in rain forests	1,305,000	72.5
(2) independent conservative estimate of described and undescribed species in rain forests (see text)	2,000,000	—
(3) potential number of described and undescribed species in rain forests (see text)	20,000,000	—

TABLE 7-3   Continued

Organisms	Number of Described Species (to nearest 1,000)	% of Total Described Species (@ 1.87 million)
Expected Global Coral Reef Species (if coral reefs are as diverse and as well studied as rain forests; global coral reefs=5% of the area of global rain forests[d]):		
From (1) above	618,000	34.3
From (2) above	948,000	----
From (3) above	9,477,000	---

[a]From Table 7-2.

[b]$S=cA^z$; S=number of species obtained empirically from the number of described marine and coastal species above; $z=0.265$ and 0.133 for species in tropical and high latitudes, respectively; A=area known from Table 7-1; and c is provided by solution of the equation.

[c]$S=cA^z$; A is known from Table 7-1; $z=0.265$ and 0.133 for reef and level-bottom tropical coastal habitats, respectively; c is determined above [b], and S is provided by solution of the equation.

[d]$S=cA^z$; A is known from Table 7-1 for rain forests and coral reefs; S is known and c is calculated for rain forests; $z=0.25$ for rain forests and coral reefs; c is the same as for rain forests and S is calculated for coral reefs.

species occur in tropical rain forests, indicate that rain forests likely contain 2 to >20 million species (Ehrlich and Wilson, 1991; Wilson, 1989). Two million species will be used as a conservative estimate of species in rain forests hereafter. Although rain forests cover 20 times more global surface area than coral reefs (Table 7-1), and thus one would expect fewer species on global coral reefs than rain forests, the calculated number of described species on coral reefs (93,000) still is extraordinarily low.

Based on the area of the globe that they occupy compared to that of rain forests, coral reefs should be comprised of about 600,000-950,000 total species (34-53% of currently described global species; Table 7-3), assuming that rain forests have 1-2 million species, that the two environments are equally studied, and that similar ecological and evolutionary processes operate on coral reefs as in rain forests (i.e., coral reefs would have the same biodiversity as rain forests if they occupied equal global area). If rain forests included 10 million species and coral reefs had equivalent area-specific diversity, coral reefs would contain 4,739,000 species; and if 20 million species existed in rain forests, coral reefs would contain more than 9 million species (Table 7-3). The true number of species on global coral reefs probably is at least 950,000, because 2 million species in rain forests is likely to be a conservative figure.

EVALUATION OF THE RESULTS AND THEIR IMPLICATIONS

The difference between the figures for *described* species on global coral reefs (93,000 for all species and 68,000 for macrobiota) versus *expected* total species on global coral reefs (at least 950,000) suggests two hypotheses: (1) only about 10% of all species on reefs have been studied and described, or conversely, that ≥90% of the species on the world's coral reefs remain undiscovered (note that these calculations are based on conservative figures for the number of species in rain forests, so that the expected number of species on coral reefs may be larger and the proportion of described species lower on coral reefs [especially for microorganisms] than is represented here); (2) alternatively, the assumption that similar ecological and evolutionary processes generate and maintain diversity in coral reef and rain forest communities may be incorrect, and coral reefs indeed may have lower area-specific diversity than rain forests due to biological or historical constraints that affect diversification or extinction.

Several lines of evidence suggest that the first rather than the second hypothesis is correct. High numbers of undocumented species are likely in coral reef environments because, being far from the location of most systematists and biologists, tropical environments are less studied than those in temperate latitudes (Diamond, 1989; Erwin, 1988; Gaston and May, 1992; May, 1994; Wilson, 1985, 1988). For example, 80% of ecological researchers and 80% of insect taxonomists are based in North America and Europe, in contrast to 7% in Latin America and tropical Africa, and about 78% of borrowed botanical specimens go to North American and European institutions compared to those in the Neotropics or African tropics (Gaston and May, 1992). Tropical marine environments provide even further barriers to study because they require scuba diving and fairly extensive logistic support for investigation.

In addition, as Gaston and May (1992) have shown, both the number of taxonomists and the level of scientific effort devoted to the systematics of "other" invertebrates (crustaceans, molluscs, echinoderms, cnidarians, sponges, and helminths, most of which are marine) is 2 orders of magnitude less than that devoted to the systematics of tetrapod vertebrates and 1 order of magnitude less than that devoted to plants. These authors also document the aging of the work force (see also Feldmann and Manning, 1992; Manning, 1991). The small numbers within this aging but dedicated and productive cadre of marine systematists are particularly alarming at a time when technological advances and steady progression of knowledge about marine diversity is bearing spectacular fruit.

For example, two new phyla of marine invertebrates, the Loricifera (small worm-like organisms that live between sand grains) and the Vestimentifera (large tube-dwelling worms without a mouth or intestine but a large proboscis-like structure that contains millions of symbiotic bacteria) were described from soft sediments and hydrothermal vents, respectively, as recently as 1983 and 1985 (Grassle, 1986; Raven and Wilson, 1992). Since the communities associated with

hydrothermal vents were first discovered in 1977, more than 20 new families or subfamilies, 50 new genera, and over 100 species have been described (Grassle, 1989). One of the largest species of sharks, the megamouth, was described within a new family as recently as 1976 (Raven and Wilson, 1992).

Recent systematic studies indicate that concealed sibling species (morphologically similar and previously classified within one species) are more common in marine taxa than previously thought. Even in large commercially important decapods, 18 distinct new species were recognized within 2 previous species of deep-dwelling crabs (Feldmann and Manning, 1992). One of the commonest and most important species of reef-building corals in the relatively well-known Caribbean region (*Montastrea annularis*) recently was found to consist of 4 species (Knowlton et al., 1992). Despite only slight morphological differences, non-overlapping biochemical characteristics (coincident with differences in life history) clearly distinguished 6 sibling species in a worm that is a well-known indicator of pollution, *Capitella capitata* (Grassle and Grassle, 1976). Recently established specific differences between the endangered Kemp's ridley sea turtle and the widespread olive ridley (Bowen et al., 1991) demonstrate the lack of systematic effort that has been devoted to marine organisms as well as the importance of systematics in conservation and management issues.

As recently as 1992, researchers discovered in the marine plankton a major new archaebacterial group in which genetic relationships to their nearest rela-

The Smithsonian Tropical Research Institute marine station in the San Blas Islands, Panama.

tives (microorganisms in hot springs) are as distant as those between plants and animals (Fuhrman et al., 1992). Similarly, scientists discovered only in the 1980s that photosynthetic marine picoplankton, too small to have been detected previously, are extremely abundant and account for a significant proportion of global primary productivity. In 1988, Chisholm et al. described a new group of these picoplankton that are free-living relatives of *Prochloron*, the hypothesized ancestor of chloroplasts in higher plants. As recently as 1989, newly discovered marine viruses (bacteriophages) were found to be so abundant that one-third of the marine bacterial population could experience a phage attack each day (Bergh et al., 1989).

Further evidence that large numbers of species on coral reefs remain undiscovered comes from the fact that the percentages of described species (about 10%) generated in the above calculations (Table 7-3) are in the same general range as those found for other relatively little studied or tropical groups in which the number of known versus unknown species were counted or estimated. For example, calculation of the overall proportion of described versus unknown species in the *Systematics Agenda 2000 Technical Report* (1994) shows that only 1-12% are thought to be described (this range represents the percentages obtained when the minimum and maximum estimates of species remaining to be discovered are summed for all groups, divided by the total known plus unknown species, multiplied by 100, and this percentage subtracted from 100%). Tabulation of data for individual groups in the *Systematics Agenda 2000 Techical Report* reveals that only 21% of global crustacean species and 26% of global molluscan species have been described, although these taxa represent some of the best-studied groups of marine invertebrates and are commercially important. In other studies, Grassle and Maciolek (1992) found that 31% of the peracarid crustaceans (mostly isopods and amphipods) had been described in soft sediments from the deep sea off eastern North America. From shallower sediments in southern Australia, however, Poore and Wilson (1993) reported that only 10% of the relatively well-studied isopods were known; they suggest that, due to great regional differences in the extent to which the oceans have been studied, probably only 5% of marine invertebrates are known from the oceans overall. About 36% of the species of polychaete worms and about 63% of the relatively well-known molluscan species in Grassle and Maciolek's (1992) samples from the deep sea off North America had been described. About 17% of the total species of algae have been described (John, 1994; Systematics Agenda 2000, 1994). Only 1%, 1-10%, 4-7%, and 2-3%, respectively, of the estimated total species of the poorly studied viruses, bacteria, fungi, and nematodes are described (Systematics Agenda 2000, 1994).

Among terrestrial organisms, only about 7-9% of the global species of spiders and mites, and only about 9-11% of global species of insects have been described (Systematics Agenda 2000, 1994), despite the fact that entomologists who work on insects and spiders represent about 30% of taxonomists and these

large groups receive considerable taxonomic attention because of their economic importance (Gaston and May, 1992). Estimates within taxa of insects (Gaston, 1991) indicate that 11-33% of beetles are described; only 10-13% of some beetle families (e.g., the speciose staphilinids) have been described, but 25-50% of others (pselaphids, curculionids, carabids, chrysomelids) are known. Up to half of the flies and the large, relatively well-known butterflies and moths probably have been described (but a much lower proportion of the small, more cryptic microlepidopterans are known). Except for the bees (where about half of the species are described), the proportions of described species in the major hymenopteran superfamilies (e.g., ichneumonoid and chalcidoid wasps, ants) are lower, ranging from 17-25%. Similarly, in the hemipteran and some homopteran (cicadellid) bugs, only 20-33% of the total species are described (although about 50% of the economically important coccoid Homoptera are known).

Thus, an estimate of 10% described species on global coral reefs is not unreasonable in terms of what is known of other (especially predominantly tropical) groups. This estimate is further considered realistic because all of the less well-known marine groups are included in this total estimate for coral reefs, the estimate encompasses some very poorly known regions (e.g., areas in the Indo-West Pacific), and marine realms are still relatively little studied.

Additionally, although we tend to think of coral reef communities in terms of their flamboyant fishes, large sessile organisms such as corals, and large colorful benthic invertebrates such as lobsters, most species on coral reefs are small in body size, as shown in Figure 7-1 for reef-dwelling mantis shrimps. Indeed most cryptic species on coral reefs are *constrained* to small body sizes by the sizes of bioeroded holes in the reef, whose refuge they must obtain in order to survive intense fish predation (Moran and Reaka, 1988; Reaka, 1985, 1986, 1987; Reaka-Kudla, 1991; Wolf et al., 1983). Several authors (Hutchinson and MacArthur, 1959; May, 1986b, 1988; Morse et al., 1985) have documented this skewed size distribution, with vastly more small than large species, for almost all groups of animals (but see Fenchel, 1993; May, 1994; and Stork, Chapter 5, this volume; for the microbiota; i.e., those smaller than 1-5 mm).

Small organisms almost always are poorly observed and known (Gaston, 1991; May, 1978; Mayr, 1969) because they often live in cryptic or interstitial environments. This is true in coral reefs as well, where my laboratory has recorded several hundred thousand small macroscopic (>5 mm) motile reef organisms of 12 or more phyla living within holes and crevices in the upper 10 cm of 1 m^2 of reef substrate (Moran and Reaka, 1988; Moran and Reaka-Kudla, 1990; Reaka, 1985, 1987; Reaka-Kudla, 1991; also see other references on cryptofauna given above). In addition to their cryptic habits, these motile organisms often are crepuscular or nocturnal (and thus often are unobserved even by field biologists; Dominguez and Reaka, 1988). Collection of organisms from these three-dimensional calcareous crypts is difficult and labor intensive, leading to their strong underrepresentation in many ecological and systematic studies. Com-
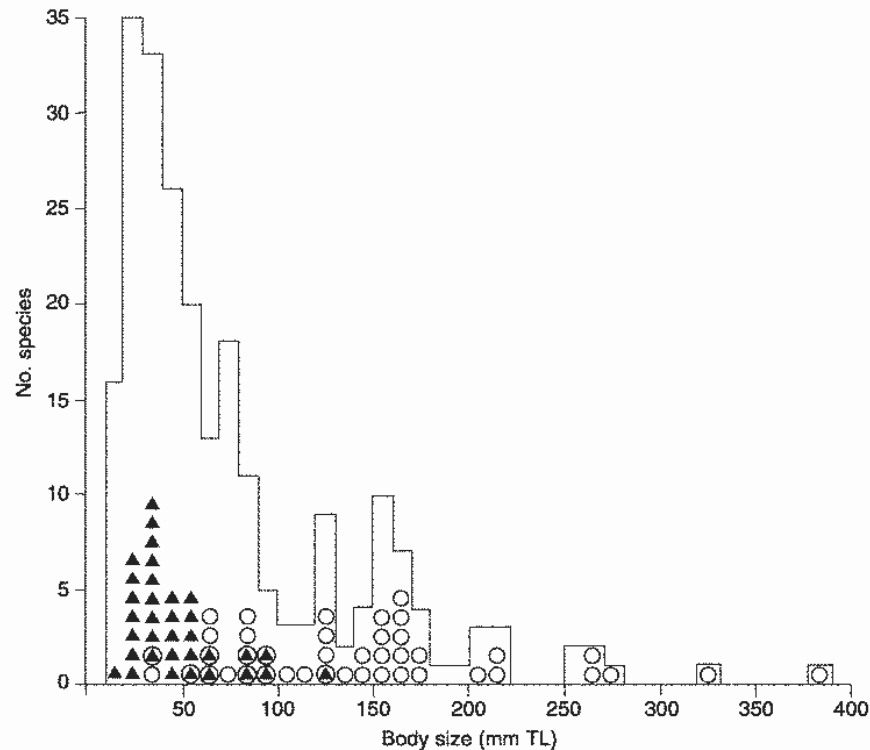
FIGURE 7-1   Size frequency distribution of all species of Atlanto-East Pacific mantis shrimps (Stomatopoda, Crustacea). Closed triangles represent species with known abbreviated larval development, and open circles signify species with known long-distance larval dispersal.

prising the greatest proportion of species on reefs, these cryptic invertebrates are the ecological equivalents of insects in the rain forest, and they usually are overlooked when the diversity of a coral reef is considered.

In addition to inadequate study of these species on local scales, the number of small species is likely to be underestimated on a global scale because of their restricted geographic distributions. One of the strongest correlations in marine biology is the association between small body size of macroscopic marine animals and the production of only a few relatively large larvae that have abbreviated developmental times (where the brooded young either emerge from the parent's protection as relatively large juveniles or the parents produce large larvae with short planktonic stages; both are characterized by short dispersal and restricted geographic distributions; Hansen, 1978; Jablonski, 1986a; Jablonski and Lutz, 1983; Reaka, 1980; Reaka and Manning, 1981, 1987; Strathmann and Strathmann, 1982). In contrast, species that attain large body

sizes within their lineage commonly produce large numbers of small swimming larvae that feed in the plankton for extended periods, resulting in broad geographic distributions.

Figure 7-2 shows that the body sizes of species of reef-dwelling mantis shrimps are significantly correlated with the sizes of their geographic ranges (Reaka, 1980). Fenchel (1993) has suggested that there may be fewer rather than more species at the smallest end of the range of body sizes (1-5 mm), and that these microscopic species have larger geographic ranges, larger population sizes, and may be less vulnerable to extinction than the species just above this size (see also May, 1986b, 1988, 1994; Stork, Chapter 5, this volume). The lack of ecological and detailed systematic knowledge for most of these minute taxa, however, may obscure the number of species and the sizes of the geographic ranges, and this argument does not affect the macrobiota (generally larger than 5-10 mm) discussed in the present study. Therefore, because most macroscopic spe-
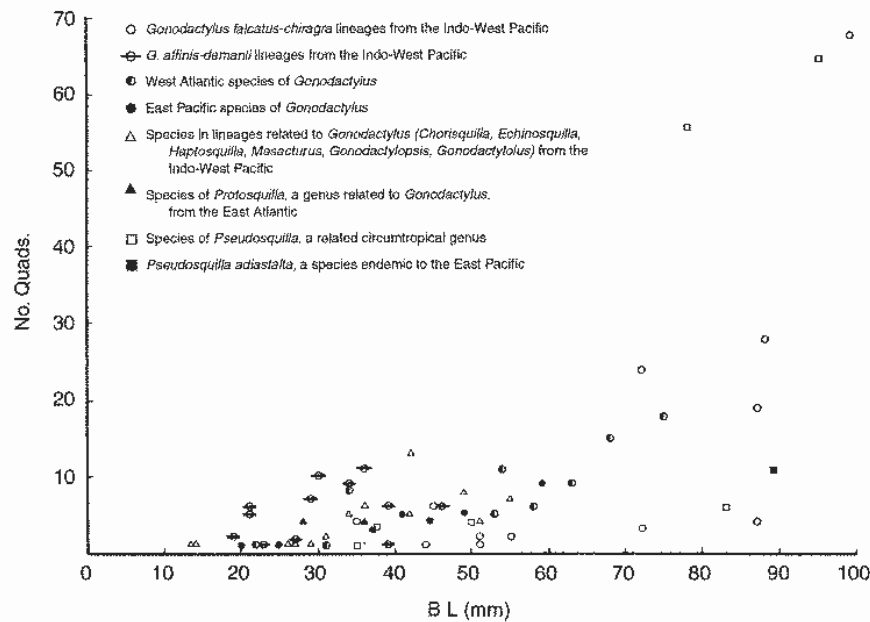

FIGURE 7-2 The relationship between body size (maximum mm total body length) of species and extent of the geographic range (number of $5 \times 5°$ latitudinal $\times$ longitudinal quadrants in which each species has been recorded) in world-wide lineages of coral-dwelling mantis shrimps (Stomatopoda, Crustacea). Each species is signified by one datum, and different symbols represent different taxonomic lineages. See Reaka (1980) for different analyses in which body size of species correlated significantly with other measures of the size of the geographic range for species within and between lineages.

Coral with black band disease.

cies are small (e.g., 10-50 mm) on coral reefs and most small species have relatively small geographic ranges, poorly sampled areas (e.g., some areas of the Indo-West Pacific) are very likely to contain undocumented species with endemic distributions that do not extend into better sampled areas.

It seems highly likely, therefore, that global coral reefs contain a very large number of species that are undescribed. Rapid environmental degradation in coastal environments thus is likely to place at risk great amounts of genetic and species diversity that we have not yet even discovered.

On the other hand, if the ecological and evolutionary processes that govern the diversity of coral reef communities differ from those operating in rain forests, and if coral reefs truly are less diverse per unit area than rain forests (the second hypothesis given in the introduction to this section), the estimate of the number of species expected on global coral reefs (≥950,000), and thus the percentage of unknown species on coral reefs, would be too large.

Although much remains to be learned, considerable evidence suggests, in contrast to the second hypothesis, that many ecological processes governing local diversity in coral reef and rain forest communities are similar (Connell, 1978, 1979; Jackson, 1991; Ray and Grassle, 1991). Both reefs and rain forests are continually exposed to disturbance (including predation), and species diversity is maximized at intermediate intensities of these disruptions (Connell, 1978). On larger scales, similar patterns of recruitment, life history and resource specializations, physical gradients, and other historical factors generate the extraordinary adaptations and species richness seen in both environments (although the specific combinations of these factors affecting diversity of reefs and rain forests at any one time may vary; see Jackson, 1991; May, 1986b, 1988; Ray and Grassle, 1991; Reaka, 1985, 1987; Reaka-Kudla, 1991; and Sebens, 1994, for additional discussions of ecological processes affecting diversity in these environments). Further support for the idea that similar evolutionary processes govern diversity in coral reefs and rain forests is provided by graphs that trace the history of biodiversity in marine invertebrates, vascular plants, vertebrates, and

insects from the Paleozoic Era onward, showing parallel patterns over time (Signor, 1994).

On the other hand, the overwhelming abundance of species of insects (Erwin, 1982, 1988; May, 1978, 1988, 1994; Stork, 1988) and their Paleozoic radiation (apparently even before the rise of the flowering plants)—accompanied by relatively low extinction rates throughout their history and continuing increases in diversification (Labandeira and Sepkoski, 1993)—suggests that something (perhaps related to their small body size and its relationship to their habitat; May, 1978, 1988) fosters exceptionally high diversity in this lineage of terrestrial arthropods. It is probably still too early to know whether or not similar high diversity might be found in comparably sized small marine invertebrates in structurally complex habitats if they were adequately studied.

To accommodate the perceived relatively low diversity of described marine species versus the terrestrial biota, it has been suggested that the geographic ranges of marine organisms are large, extinctions are unlikely, and diversification (at least after the Cambrian radiation of major body plans) is relatively slow because of the presence of a fluid medium. The aqueous medium is considered to buffer local variations and promote long-distance dispersal, which in turn allows recolonization of locally disturbed sites and connects distant populations genetically (see Angel, 1992; Hutchinson, 1959; May, 1994; Norse, 1993; Pielou, 1979). The fact that relatively few marine extinctions have been observed (Carlton et al., 1991) bolsters the opinion that marine organisms are at a relatively low risk of extinction in the modern world compared to terrestrial species. Indeed only 195 molluscs and crustaceans (0.2% of present described species) compared to 229 vertebrates (0.5% of present described species) have been certified as extinct since 1600 (Smith et al., 1993). The latter authors caution, however, that figures of endangered and extinct species strongly reflect the intensity of scientific study devoted to the group and thus should be applied only to well-known groups such as vertebrates and palms.

It is true that dispersing larvae can swamp genetic differences among adjacent populations, retard rates of diversification, and confer resistance to extinction (Hansen, 1978; Jablonski 1986a,b, 1991; Jablonski and Lutz, 1983; Reaka and Manning, 1981, 1987). However, the common inference that most marine species have dispersing larvae and are at low risk of extinction relies on the most conspicuous species in marine environments (e.g., some starfish, crustaceans, molluscs, and fish), which are large in body size and hence produce large numbers of dispersing larvae and have large geographic ranges. This perception ignores the fact that the greatest proportion of species within marine macroscopic lineages are small in body size and thus are likely to have relatively abbreviated larval development and small geographic ranges (Figures 7-1, 7-2). These small, numerous species are relatively vulnerable to extinction.

Paleontological data show that, at normal background levels of extinction, species with restricted geographic ranges are more susceptible to extinction than

those with broader ranges (Hansen, 1978, 1980, 1982; Jablonski, 1980, 1982, 1986a,b, 1991; Scheltema, 1978; Valentine and Jablonski, 1983; Vermeij, 1987; see also Reaka, 1980; Reaka and Manning, 1981, 1987). Vermeij (1993) and Stanley (1986) did not find a correlation between small geographic range and high rates of extinction in certain molluscs, but Stanley points out that species with large geographic ranges can be fragmented by heavy predation into smaller populations which then suffer high extinction, reducing the strength of the correlation in some cases. Also, tropical species are particularly susceptible to extinction, as evidenced by the striking demise of reef communities at each of the major mass extinctions (Jablonski, 1991). The background rates of extinction for marine invertebrates (1-10% of species per million years, Jablonski, 1991) are vastly lower than the extinctions that potentially could result from present-day environmental alterations (Diamond, 1989; Ehrlich and Wilson, 1991; Smith et al., 1993), and the long narrow coastlines of coral reefs are especially vulnerable to habitat degradation and fragmentation.

Therefore, this study proposes that undocumented diversity and—of particular importance at the present time—undocumented contemporary extinctions are likely to be higher than we realize in marine environments because there are many more relatively small, cryptic, and unstudied macroscopic species in coral reef environments than generally recognized. Not only is it likely that undocumented extinctions already have taken place, but the *potential* for future extinction in macroscopic species on coral reefs is higher than generally realized because of the preponderance of diminutive species with small geographic ranges in these environments.

CONCLUSIONS

These analyses suggest that about 93,000 total described species of all taxa occur on coral reefs, which represents about 5% of the described global biota. These numbers are considerably lower than the number of species that are estimated to occur in rain forests. However, coral reefs occupy only 5% of the global area of rain forests. If coral reefs were equivalently studied and contained as much biodiversity as rain forests per km², and if rain forests contained 2 million species, then coral reefs should include approximately 950,000 species. The difference between the numbers of described (93,000) versus expected (950,000) species suggests that coral reefs are repositories of very high undocumented species diversity. Most species on coral reefs are relatively small and cryptic, and difficult to observe and collect. This, in combination with the fact that tropical environments and particularly tropical marine habitats receive less study than those at higher latitudes or terrestrial sites, suggests that many coral reef taxa are indeed very poorly known.

Furthermore, associated with their relatively small size and abbreviated larval dispersal, *most* species on coral reefs are likely to have small geographic

ranges, rendering them vulnerable to extinction. Although coral reef communities do not achieve the phenomenal global diversities found in rain forests because of their smaller area, and although it remains unclear whether or not the cryptic reef biota may rival the extraordinary diversity exhibited by insects per unit area, this study suggests that coral reefs may contain far more species than previously supposed (which is congruent with the elaborate specializations and biological interactions found in reef communities), and that very large amounts of this biodiversity may be lost due to human activities before they are even discovered if appropriate scientific study and conservation measures are not taken.

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