

2. GENERAL BACKGROUND ON CORALS AND CORAL REEFS

2.1 Taxonomy and Distribution

2.1.1 Taxonomy and morphology of scleractinian corals

Stony corals are marine invertebrates in the phylum Cnidaria (Coelenterata) that secrete a calcium carbonate skeleton. Cnidaria is the only phylum that is diploblastic (i.e., two-tissue layers); all higher taxa are triploblastic (three-tissue layers) and thus contain a true mesoderm. The phylum is named Cnidaria because organisms use cnidae (capsules containing nematocysts) for prey capture and self-defense. Organisms in the phylum can be solitary (one polyp) or colonial (many polyps).

Among other groups, the Cnidaria include fire corals (class Hydrozoa, order Milleporina), the blue coral (class Anthozoa, order Helioporacea = Coenothecalia), and true stony corals (class Anthozoa, order Scleractinia). Members of these three orders are represented among the 82 candidate coral species considered in this Status Review Report. The scleractinian corals, along with dinosaurs and mammals, evolved in the middle of the Triassic Era (208–250 million years prior to present [Ma]). The individual building unit in a colony is termed a polyp: a column with mouth and tentacles on the upper side (Fig. 2.1.1), lying above a skeleton of calcium carbonate (usually aragonite but sometimes calcite). Corals in the family Fungiidae exist only as solitary polyps, but the other families exploit the ability to form complex colonies. The rapid calcification rates of these organisms have been linked to the mutualistic association with single-celled dinoflagellate algae, zooxanthellae, found in the gastrodermal cells of coral tissues (Goreau et al., 1979). Scleractinian corals can be hermatypic (significant contributors to the reef-building process) or ahermatypic. The largest colonial members of the Scleractinia help produce the carbonate structures known as coral reefs in shallow tropical and subtropical seas around the world. Massive and branching stony corals are the primary framework builders and a major source of calcium carbonate production of coral reefs. Corals provide substrata for colonization by benthic organisms, construct complex protective habitats for a high diversity of other reef-associated species, including commercially important invertebrates and fishes, and serve as food resources for a variety of animals.

One species under consideration in this petition, the blue coral *Heliopora coerulea*, is of the subclass Octocorallia. Octocorals are generally soft-bodied and distinguished by polyps always having eight tentacles, rather than the multiples of six that characterize stony corals. Blue coral is the only octocoral that forms an aragonite skeleton. *Heliopora coerulea* is the only member of its family and its order known to occur on coral reefs.

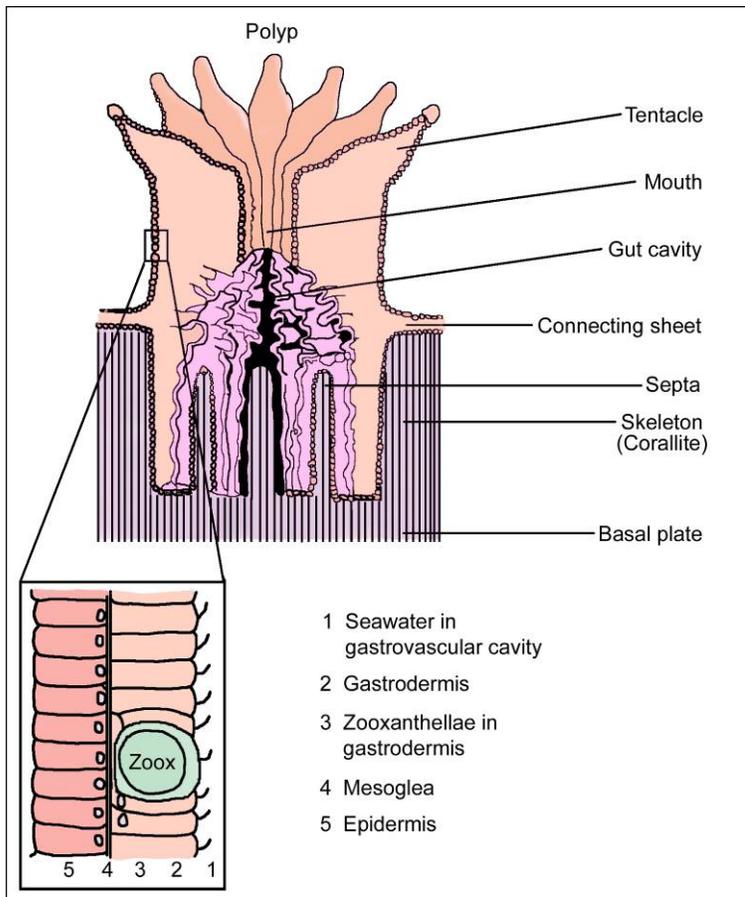


Figure 2.1.1. Schematic view of the anatomy of a coral polyp (corallite) (Sumich, 1996).

2.1.2 Species delineation and uncertainty in corals

The U.S. Endangered Species Act defines a species as a group of organisms that “interbreeds when mature.” The classical biological species concept, in addition to interbreeding (i.e., sharing a common gene pool), requires also that the group be reproductively isolated from other such groups (i.e., their common gene pool is separate and distinct from others). Until the relatively recent development of genetic sequencing techniques, biologists have lacked the capacity to directly quantify reproductive pools or the differentiation of gene pools when identifying and categorizing organisms in the ocean. Rather, classical taxonomy has relied on the similarity and differences in morphological traits (i.e., how does the organism look?) to infer interbreeding and reproductive isolation. Indeed, it is widely known that the sum of an organism’s traits (i.e., phenotype) is determined to a greater or lesser extent by the environment under which it lives, in combination with its genetic composition. Corals are, in fact, especially plastic in their skeletal morphology depending on the environmental conditions under which they live. The degree of environmental vs. genetic determination of morphological characteristics, hence, will determine the degree to which morphologically classified species designations will accurately reflect “true” biological species (i.e., interbreeding and reproductively isolated groups).

The tools of genetic and genomic science have now progressed to the point that they allow direct characterization of connectedness vs. isolation of gene pools. It is not surprising, therefore, that morphological taxonomies have been shown to poorly reflect the genetic species status within many coral genera. Such genetic studies, while advancing rapidly, greatly lag behind what would be required for confident application of the biological species concept to many groups of corals. This presents a challenge in applying the Endangered Species Act. Recent work has begun to elucidate these complex situations in several of the genera addressed in this Status Review Report, specifically *Psammocora* (Benzoni et al., 2010), *Montipora* (Forsman et al., 2010; Van Oppen et al., 2004), *Pocillopora* (Combosch et al., 2008; Pinzón and LaJeunesse, 2011; Souter, 2010), *Seriatopora* (Flot et al., 2008), and *Porites* (Forsman et al., 2009). These studies have yielded contrasting patterns both within and among genera. Some nominal (morphologically defined) species have been congruent with genetically distinct and monophyletic groups [“true” biological species such

as some of the Hawaiian *Montipora* addressed by Forsman et al. (2010)], but such findings appear to be in the minority. Other studies have contained multiple lineages (i.e., previously undescribed species adding to diversity) or found nominal species to be genetically indistinguishable (e.g., within newly described clades within the genera *Montipora*, *Pocillopora*, and *Porites*). In some cases, morphologically defined species have borne no direct mapping on genetic species (Pinzón and LaJeunesse, 2011). Where genetic studies have been available, the BRT has attempted to incorporate them into assessments of extinction risk. In some cases, this has involved subsuming a nominal species (morpho-species) from the petition list into a larger clade when genetic studies have not been able to distinguish among them (e.g., *Montipora dilatata/flabellata/turgescens* and *Porites* Clade 1 forma *pukoensis*). In one case (*Pocillopora elegans*), the BRT has identified likely differentiation within a nominal species, chosen to parse it, and has estimated a Critical Risk Threshold (CRT) for each of these two divisions (eastern Pacific and western/central Pacific which show different reproductive modes, hence likely precluding interbreeding amongst them). In the absence of specific genetic studies, the BRT has treated the remaining nominal species as true species and assessed the likelihood of a species status falling below a Critical Risk Threshold by 2100 according to the information available, recognizing that future genetic studies may render others of these to be inappropriate as biological species.

Another aspect of our general understanding of coral phylogenetics is the concept that the evolutionary history of corals is particularly marked by reticulate processes, meaning that individual lineages show repeated cycles of divergence and convergence via hybridization (Veron, 1995). This potential for hybridization and introgression has been argued to be a characteristic potentially conveying adaptive capacity in some coral species, as an important mechanism of diversification (Vollmer and Palumbi, 2002; Willis et al., 2006) and potential adaptation to changing environments (Richards et al., 2008b)—which could be crucial to species viability in an era of rapidly changing climate and ocean chemistry. It is worth noting that for corals and other taxa with reticulate evolution, the species concept generally applied in the Endangered Species Act is less relevant than for easily distinguished, non-interbreeding vertebrate species. Nonetheless, for the purposes of Endangered Species Act application, the BRT has attempted to distinguish between a “good” species, which has a “hybrid history” (sensu Richards, 2009)—meaning it may display genetic signatures of interbreeding and backcrossing in its evolutionary history (Combosch et al., 2008)—and a “species” that is composed entirely of hybrid individuals. Best information indicates that, while several of the petitioned *Acropora* spp. have “hybrid histories”, there is no evidence to suggest any of them are hybrid species (all individuals of a species being F1 hybrids) as was determined in the previous status review of three petitioned Caribbean *Acropora* spp. In that previous review, *Acropora prolifera* was determined to exist only as hybrid individuals [i.e., all individuals were F1 hybrids (Vollmer and Palumbi, 2002)] and therefore not eligible for listing under the U.S. Endangered Species Act. In contrast, *Acropora cervicornis*, was considered a “good” species though it displays genetic signatures of introgression or backcrossing with *Acropora prolifera* (Vollmer and Palumbi, 2007).

2.1.3 Evolutionary history of corals reefs

While coral reefs have been established for an estimated 240 million years, they have disappeared from the fossil record at least five times. These mass extinction events have resulted primarily from disruptions in the carbon cycle (acidification) on which these calcifying species heavily depend (Veron, 2008). Although many individual coral lineages persisted through these catastrophic events, Earth was rendered relatively “reefless” and it took millions of years for coral reef ecosystems to reestablish themselves following these mass extinction events. This geologic-scale pattern illustrates the potential that coral reef ecosystems may functionally cease to exist without all individual coral species going extinct. This is an important consideration in assessing species’ extinction risk. Current coral reef ecosystems started to develop about 10 million years after the mass extinction at the end of the Cretaceous era (65 Ma), when ~ 33% of all families and ~ 70% of all genera are believed to have gone completely extinct (Veron, 2008). From the little information available, it appears that extensive coral reefs with a low level of diversity (less than 5 scleractinian species; Montaggioni and Braithwaite, 2009) were present as soon as 3–4 million years after the Cretaceous–Tertiary boundary with a substantial increase in diversity from the mid-to-late Eocene. Since the Eocene, coral reefs have developed to the high levels of biological diversity observed in reefs of the modern record. Reefs have often moved through time with changes in sea level. Today’s reef ecosystems are less than 10,000 years old as they are found on shallow seafloors that were dry land during the last glacial period (Siddall et al., 2003).

2.2 Biology

2.2.1 Reproduction and recruitment

The distribution and abundance of scleractinian corals reflect patterns of larval recruitment, asexual reproduction via fragmentation, mortality, and regenerative capabilities (Richmond and Hunter, 1990). Figure 2.2.1 illustrates generalized aspects of coral life histories, their complex stages, and alternative strategies. Interspecific differences in the mechanisms of recruitment, dispersal, and mortality are likely important in determining the species composition of reef corals in different environments; such differences reflect the differential allocation of energy to the basic life history functions of growth (growth rate and rigidity of the skeleton), reproduction (fecundity, mode of larval dispersal, recruitment success), and colony maintenance (intra- and inter-specific interactions, competitive ability, and regeneration) (Bak and Engel, 1979; Connell, 1973; Good et al., 2005; Szmant, 1986).

Although extensive research has been conducted on the diverse reproductive strategies employed by scleractinian corals (Fadlallah, 1983; Richmond and Hunter, 1990; Szmant, 1986), many individual species' reproductive modes remain poorly described. Many stony coral species employ both sexual and asexual propagation. Sexual reproduction in corals occurs through gametogenesis (i.e., development of gametes) within the polyps near the base of the mesenteries. Some coral species have separate sexes (gonochoric), while others are hermaphroditic. Fertilization can occur internally or externally, referred to as “brooding” or “broadcasting/spawning” strategies, respectively (see Fig. 2.2.1). Brooding is a relatively more common strategy in the Atlantic, where nearly 50% of the species are brooders, compared to less than 20% of species in the Indo-Pacific (Baird et al., 2009). Edinger and Risk (1995) speculated that this pattern in the Atlantic was driven by lower rates of extinction of brooders relative to broadcast spawners during the Caribbean Oligocene-Miocene extinction event. In contrast, Glynn and Colley (2008), based on the converse predominance of broadcast spawning species in the eastern Pacific coral fauna, suggest that broadcasters may have greater survivorship in the diverse habitats and extreme fluctuations in environmental conditions characteristic of this region.

Embryonic development culminates with the development of larvae called planulae. For brooding corals, most of the larval development period takes place within the mother colony. With the exception of *Isopora* larvae, brooded larvae contain zooxanthellae and can supplement maternal energy stores (i.e., lipids) with photosynthetic products from these symbionts (i.e., they are “autotrophic”). Generally, brooded larvae are competent to settle shortly after release from the mother colony and may either live for a short time in the plankton (relative to most broadcast larvae) or crawl away from the mother colony. Broadcast spawners, in contrast, undergo fertilization and the entire larval development period (one to several weeks) is outside the parent colonies, much of it with larvae adrift in the ocean. Eggs released by broadcast spawning species from the genera *Anacropora*, *Montipora*, *Porites*, and *Pocillopora* also contain zooxanthellae (and autotrophic capacity), whereas all other spawned larvae (as well as brooded *Isopora* larvae) are “lecithotrophic” and only acquire zooxanthellae after settlement and metamorphosis (Richmond, 1988). There is little evidence to suggest that any coral larvae actually feed (Graham et al., 2008). In either mode of larval development, planula larvae presumably experience considerable mortality (up to 90% or more) from both intrinsic (e.g., developmental abnormalities or energy limitation) and extrinsic (e.g., predation or environmental stress) factors, prior to settlement and metamorphosis (Goreau et al., 1981). In laboratory cultures, Graham et al. (2008) quantified the survival of larvae from five broadcast-spawning coral species and identified three intrinsic survival phases: a bottleneck of high initial rates of mortality, followed by a low, approximately constant rate of mortality, and finally, progressively increasing mortality after approximately 100 days.

High mortality rates early in the larval period decrease the likelihood that larvae transported away from their natal reef will survive to reach nearby reefs, and thus decrease connectivity at regional scales. The importance of connectivity in population persistence is discussed further in Chapter 4, Section 4.6.

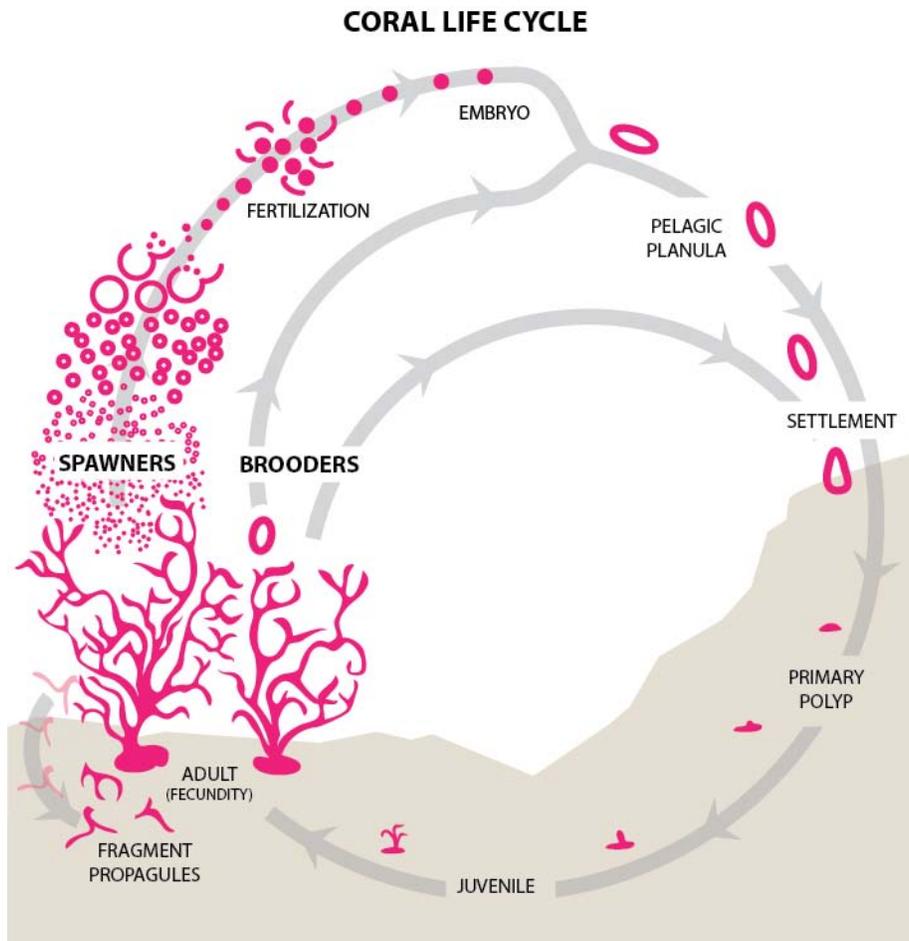


Figure 2.2.1. Diversity of coral life cycle showing different life history stages for broadcast spawners versus brooders, as well as asexual fragmentation. Coral life cycles are replete with vulnerable stages. Spawners have more extensive stages (and bottlenecks) that occur in the water column (fertilization and larval development with at least several days development time to competency). Brooders have internal fertilization (either selfed or with sperm that transits from a nearby colony) and larval development takes place inside the mother colony—hence fewer processes that occur in the water column. Some brooders have “crawl away” larvae that settle in immediate proximity to the parent while others have larvae that can swim for hours to a couple of days. Establishment of fragments from adult colonies is an important asexual mode of reproduction for many coral species. Post-settlement benthic stages are extremely vulnerable and poorly known, given their extremely small size and, in many species, slow growth rates, with the transition from primary polyp to a visible juvenile taking from 3 to 12 months. The transition from visible juvenile to reproductive adult may range from 1 to several (5–10) years. Diagram prepared by Amanda Toperoff, NOAA PIFSC.

Because coral larvae are relatively poor swimmers, their dispersal distances will largely depend on the duration of the pelagic phase and the speed and direction of water currents transporting the larvae (Scheltema, 1986). Brooded planulae can settle shortly (hours) after release (Carlson and Olson, 1993), but can have extended competency periods of 30–100 days (Harrigan, 1972; Richmond, 1987; 1988). Spawned larvae can have much longer competency periods—for example, Graham et al. (2008) documented maximum larval lifespans ranging from 195 days (*Favia pallida*) to 244 days (*Montastraea magnistellata*). The observed extended periods of competency suggest that the potential for long-term dispersal of coral larvae may be substantially greater than previously thought. This may partially explain the large geographic ranges of many species (Hughes et al., 2002), although local retention of larvae is certainly possible (Black et al., 1991; Vollmer and Palumbi, 2007). Detection of increasing mortality rates late in larval life suggests that energy reserves do not reach critically low levels until approximately 100 days after spawning (Graham et al., 2008), although conditions of physiological stress likely increase energy demands of larvae and energy limitation may lead to mortality or poor habitat choice (Vermeij et al., 2006).

In general, on proper stimulation, coral larvae, whether brooded by parental colonies or developed in the water column, settle and metamorphose on appropriate substrates. Some evidence indicate that chemical cues from crustose coralline algae, microbial films, and/or other reef organisms (Gleason et al., 2009; Morse et al., 1996; Morse et al., 1994; Negri et al., 2001) and acoustic cues from reef environments (Vermeij et al., 2010) stimulate settlement behaviors. Initial calcification ensues with the forming of the basal plate. Buds formed on the initial corallite develop into daughter corallites. In some species, it appears that there is virtually no limit to colony size beyond structural integrity of the colony skeleton, as polyps apparently can bud indefinitely. Once larvae are able to settle onto appropriate hard substrata, metabolic energy is diverted to colony growth and maintenance. Because newly settled corals barely protrude above the substratum, juveniles need to reach a certain size to limit damage or mortality from threats such as grazing, sediment burial, and algal overgrowth (Bak and Elgershuizen, 1976; Birkeland, 1977; Sammarco, 1985). Post-settlement mortality can also approach 100% (Harriott, 1985) over the first year for some species and/or habitats. Spatial and temporal patterns of coral recruitment have been intensively studied (Baggett and Bright, 1985; Bak and Engel, 1979; Birkeland, 1977; Chiappone and Sullivan, 1996; Hughes et al., 1999b; Rogers et al., 1984; Sammarco and Andrews, 1989). Biological and physical factors that have been shown to affect spatial and temporal patterns of coral recruitment include substratum availability and community structure (Birkeland, 1977), grazing pressure (Rogers et al., 1984; Sammarco, 1985), fecundity, mode, and timing of reproduction (Harriott, 1985; Richmond and Hunter, 1990), behavior of larvae (Goreau et al., 1981; Lewis, 1974), hurricane disturbance (Hughes and Jackson, 1985), physical oceanography (Baggett and Bright, 1985; Fisk and Harriott, 1990), the structure of established coral assemblages (Harriott, 1985; Lewis, 1974), and chemical cues (Morse et al., 1988). Relatively few studies, however, have examined variation in coral recruitment over larger spatial scales (10–100 km) or among different structural types of reefs (Fisk and Harriott, 1990; Harriott and Fisk, 1987; Hughes et al., 1999b; Hughes and Connell, 1999; Wallace and Bull, 1981). In many studies of western Atlantic reefs, a proxy measure of recruitment success has been the quantification of juvenile coral densities, with juvenile corals defined as newly settled and metamorphosed corals visible underwater to the unaided eye ranging up to 4 cm in maximum diameter (Bak and Engel, 1979). Newly settled corals are visible in the field at approximately 5–10 mm in diameter and, for a range of Caribbean species, colonies approaching 4 cm in diameter are approximately 1–2 years old (Van Moorsel, 1988).

Besides sexual reproduction, many coral species also reproduce asexually. Asexual reproduction most commonly involves fragmentation, where colony pieces or fragments are dislodged from larger colonies to establish new colonies (Highsmith, 1982), although the budding of new polyps within a colony can also be considered asexual reproduction. The successful recruitment of fragments depends greatly on species and habitat conditions, and low survivorship of fragments implies that it is not necessarily an adaptive “strategy” for reproduction (Smith and Hughes, 1999). Fragmentation can occur during storms (Highsmith, 1982; Porter et al., 1981; Tunnicliffe, 1981), with susceptibility to mechanical breakage of colony branches influenced by the boring activities of sponges and lithophagus bivalves. Fragmentation is common and can be the dominant means of propagation in many species of branching corals (Adjeroud and Tsuchiya, 1999; Bak and Crieens, 1982; Davis, 1977; Gilmore and Hall, 1976; Hughes, 1985; Hunter, 1993; Tunnicliffe, 1981). Asexual production of brooded larvae, yielding dispersing planulae that are genetically identical to the parent colony has also been shown for a few scleractinian species (Ayre and Resing, 1986). Accelerating development of genetic tools will likely continue to detect colonies with the same genotype (implying one was produced asexually from the other) within more species.

2.2.2 Nutrition

Reef-building scleractinian corals are active in more than one trophic level simultaneously (mixotrophy) and many act as plants during the day and as animals during the night or some combination of the two at any time. The high gross primary productivity of coral reef ecosystems in oligotrophic environments is maintained by advection processes (i.e., import of nutrients from other habitats; Atkinson, 1992), nutrient recycling (Szmant-Froelich, 1985), and mixotrophy (ability to derive nutritional needs both from photosynthesis of symbionts and from prey) of corals. During the daylight hours, corals can be considered (as holobionts) to function as primary producers. For some species, up to 100% of the daily caloric needs of coral colonies can be provided by photosynthetically fixed carbon translocated from the mutualistic intracellular symbiotic dinoflagellates (Muscatine et al., 1981). However, neither the coral nor the dinoflagellates (zooxanthellae) can actually grow on the energy-rich, nitrogen-poor “junk food” (Falkowski et al., 1984) from photosynthesis that satisfies their caloric needs for maintenance but does not provide needed nutrients. For some corals, advection and uptake of organic sources (dissolved free amino acids) from the water provides 24% and inorganic sources (NH_4^+ and NO_3^-) 74% of the daily nitrogen requirements (Bythell, 1990; Grover et al., 2008). At night, many corals extend their tentacles and feed on zooplankton. These prey provide nitrogen and other nutrients and so predation

on zooplankton can reduce the uptake of free amino acids (Al-Moghrabi et al., 1993) and ammonium (D'Elia and Cook, 1988) by corals.

Excess production of fixed carbon by zooxanthellae can be stored as lipids by some corals, providing as much as 10%–40% of total biomass (Grottoli et al., 2004; Stimson, 1987). This stored supply of lipids can serve as a reserve for some corals during periods of bleaching (Rodrigues et al., 2008) and indeed, lipid stores can provide a better predictor of mortality risk for bleaching corals than chlorophyll-*a* concentrations (Anthony et al., 2007; Grottoli et al., 2004). These energy reserves can be maintained following bleaching when the coral shifts from relying on production of zooxanthellae to predation on zooplankton (Grottoli et al., 2006). It is generally assumed that corals with large polyps tend to be more heterotrophic (feeding on zooplankton) while those with smaller polyps tend to be more autotrophic (the holobiont relying more directly on photosynthesis). Corals with relatively large polyps such as *Montastraea cavernosa* are known to prey upon a diverse assortment of holoplankters and meroplankters (Porter, 1976).

2.2.3 Calcification and reef building

The biodiversity of coral reef ecosystems and high rates of primary production in wide geographic regions with relatively nutrient-poor waters are, to a great extent, the result of the structures built by corals and other calcifying reef organisms (Lewis, 1981). Coral reefs have been defined or characterized in numerous ways on the basis of rigidity, location, framework elements, sediments, and biological diversity. To that end, Fagerstrom (1987) listed several definitive characteristics of coral reefs:

- A rigid framework is present;
- The skeletons of other calcareous microstructures are abundant;
- Structures have positive topographic relief;
- Framework organisms have rapid growth rates; and
- Taxonomic diversity is high, with several ecological functional groups.

Scleractinian corals build reef structures by combining calcium and carbonate ions derived from seawater into aragonite (or calcite) crystals that form their skeletons. Because carbonate (CO_3^{2-}) ions are rare in seawater equilibrium, this process requires metabolic energy (Cohen and Holcomb, 2009). Corals bring bicarbonate (HCO_3^-) from seawater into internal extracellular compartments where the corals physiologically maintain elevated pH that allows the conversion of bicarbonate to carbonate ions for precipitation as calcium carbonate crystals. This effective rapid deposition of calcium carbonate material allows the formation of coral reef skeletons that are often then bound together by cementation (external to the corals) to form coral reefs. The coral skeletons are predominantly composed of aragonite (Stanley, 2006), while reef cements are composed of aragonite and high-magnesium calcite (Rasser and Riegl, 2002). The effectiveness of scleractinian corals at calcifying is directly related to their mutualism with zooxanthellae, either through energetic subsidies from photosynthesis (Pearse and Muscatine, 1971), changes in carbonate equilibrium resulting from photosynthesis (Goreau, 1959), or the removal of phosphate that inhibits calcification (Simkiss, 1964).

It is also important, for the purposes of this Status Review Report, to emphasize that many corals populate nonstructural coral communities (e.g., Riegl, 1999; Semon, 2007), whereby their abundance or growth rates may be too low to accrete reef structure and/or antecedent substrates may be non-carbonate (e.g., volcanic or sandstone).

2.2.4 Clonality and genetics

Most corals are clonal, colonial invertebrates, which distinguishes them from many species that have been considered for listing under the U.S. Endangered Species Act. Colony growth occurs by the addition of new polyps. By the same token, colonies can exhibit partial mortality whereby a subset of the polyps in a colony die, but the colony persists. Colonial species present a special challenge in determining the appropriate unit to evaluate for status (i.e., abundance).

In addition, new coral colonies, particularly in branching species, can be added to a population by fragmentation (breakage from an existing colony of a branch that reattaches to the substrate and grows) as well as by sexual reproduction (see above, and Fig. 2.2.1). Fragmentation results in multiple, genetically identical colonies (ramets) while sexual reproduction results in the creation of new genotypes (or genets). Thus, in corals, the term “individual” can be interpreted as the polyp, the colony, or the genet (Hughes et al., 1992).

In clonal species, there are multiple levels of genetic diversity. Because a coral colony can proliferate by fragmentation, there may be many colonies on a reef, but only one or a few genets; that is, most or all of the colonies may have originated from fragments of a single colony. They share the same genotype, as do identical twins. The first level of analysis of any population genetic study of a highly clonal species would be to determine how many genetically distinct individuals (genets) are represented by the individual colonies found, whether on a given reef or throughout its range. This is termed the “genotypic diversity” and simply indicates the number of genetic individuals. Genotypic diversity is influenced by the relative contribution of sexual vs. asexual reproduction in a population. Because fragmentation (asexual) and sexual reproduction occur simultaneously and to varying degrees in clonal species populations, genotypic diversity can vary widely, even at small spatial scales (Ayre and Hughes, 2000; Baums et al., 2006; Hunter, 1993). Single clones may dominate or exclusively occupy areas of tens to hundreds of square meters. At the other extreme, virtually every colony at this scale might consist of genetically distinct individuals that recruited via sexual reproduction. If there is low genotypic diversity within individual stands and/or across the region, it might suggest that a clonal species’ status is under much greater extinction risk than would be judged from its overall abundance. The importance of genotypic diversity is discussed in Chapter 4, Section 4.4: “Diversity in Corals.”

The next level of analysis concerns the “genetic diversity” at the genet level. The diversity measured at this level is directly comparable to what would be commonly measured in a vertebrate, for example. Genetic diversity describes the number of variants (alleles) of each gene that are present in the population and how these variants are distributed among individuals. Processes such as genetic drift, inbreeding, and selection all influence genetic diversity. Both aspects, genotypic and genetic diversity, are important to consider when assessing extinction risk.

Although scientists are increasingly applying genetic tools to understand the structure of coral populations, this line of research is still in relative infancy. This lack of information, combined with the clonal nature of corals, has profound implications for the consideration of species in an Endangered Species Act petition. For example, a BRT examining the status of killer whales may know all individuals within a population, all of which are genotypically unique, and a salmonid petition may be relatively easily constrained by species boundaries. This is not possible for corals, for which the definitions of a species and a population are to some degree open questions. Therefore, this BRT assessed each candidate coral species based upon the best assessment of range, distribution, abundance, and taxonomy of the species at the time of this Status Review Report (see Section 2.1.2: “Species delineation and uncertainty in corals”).

2.3 Ecology of Coral Reef Ecosystems

2.3.1 Ecosystem roles of coral reefs

A coral reef is a complex three-dimensional structure providing habitat, food, and shelter for numerous marine species and, as such, fostering exceptionally high biodiversity. Scleractinian corals are the primary purveyors of this architectural structure, and thus are foundational species for these generally productive ecosystems. It has been estimated that coral reef ecosystems harbor around one third of all marine species even though they only make up 0.2% in area of the marine environment (Knowlton et al., 2010; Veron et al., 2009). While scleractinian coral species themselves constitute on the order of less than 1000 species worldwide (so far described), existing estimates for reef-associated species range between 1 and 9 million species (Knowlton et al., 2010; Small et al., 1998). It is estimated that between 7.2% and 53.6% of coral reef-associated species have highly restricted ranges (Roberts et al., 2002). Such vulnerable endemics tend to be clustered in geographic centers of endemism, the ten richest of which cover about 16% of the world’s coral reefs but include about half of the restricted-range species (Roberts et al., 2002). Coral reefs are crucial in supporting the high diversity and abundance of these marine organisms and in maintaining a genetic bank for future generations.

Coral reefs serve the following essential functional roles: primary production and recycling of nutrients in relatively oligotrophic seas (Hatcher, 1990), calcium carbonate deposition yielding reef construction, sand production, modification of near-field or local water circulation patterns, and habitat for secondary production, including fisheries (Moberg and Folke, 1999). These functional roles yield important ecosystem services in addition to direct economic benefits to human societies (Moberg and Folke, 1999) such as traditional and cultural uses, food security, tourism, and potential biomedical compounds (Bruckner, 2002). Coral reefs protect shorelines, coastal ecosystems, and coastal inhabitants from high seas, severe storm surge, and tsunamis. Although it is difficult to put monetary values on coral reefs as their intrinsic value is priceless, the goods and services they provide have been estimated at between \$172 billion to \$375 billion (U.S.) per year (Costanza et al., 1997; Martínez et al., 2007). It has been estimated that coral reefs

provide net economic benefits of \$360 million a year in Hawai'i with an overall asset value estimated at nearly \$10 billion (Cesar and Beukering, 2004).

In summary, society relies heavily, both in ecological and economic terms, upon the goods and services provided by coral reef ecosystems. The majority of the ecological functions are dependent on the complex and dynamic interactions between networks of species, such as microbes, plants, herbivores, top predators, and corallivorous predators. However, calcifying coral species are the foundation species in building and maintaining the architectural structures that define coral reef ecosystems.

2.3.2 Habitat requirements of corals and reefs

Coral reefs are formed on solid substrate but only within the narrow range of suitable environmental conditions that allows the deposition rates of corals and other reef calcifiers to exceed the rates of physical, chemical, and biological erosion. Environmental conditions needed to sustain coral reef habitats include relatively narrow ranges of temperature, salinity, turbidity, pH, and light (Kleypas, 1997). At regional and site levels, temperature is a particularly important limiting factor for tropical and subtropical scleractinian corals. Corals occur in a fairly wide temperature range across geographic locations (at least 18°C–32°C), accomplished via either adaptation (genetic changes) or acclimatization (physiological or phenotypic changes). Though there are exceptions, reef corals tend not to thrive in areas with mean temperatures outside a fairly narrow range (typically 25°C–30°C). Short-term exposures (days) to temperature increases of a few degrees (i.e., 3°C–4°C increase above climatological mean maximum summer temperature) or long-term exposures (several weeks) to minor temperature increases (i.e., 1°C–2°C above mean maximum summer temperature) can cause significant thermal stress and mortality to most coral species (Berkelmans and Willis, 1999; Jokiel and Coles, 1990). Such temperature thresholds are variable in both time (e.g., season) and geographic location (i.e., latitude and longitude) and may be nonlinear. For example, in the Arabian Gulf, where corals have adapted to one of the lowest ambient winter temperatures recorded in reef areas, coral mortality occurred when on four consecutive days the water temperature dropped to 11.5°C and stayed at 13°C for 30 days but corals were not damaged at sites where temperature was 12.5°C for 2 days and mean temperatures were 14°C for 5 days (Coles and Fadlallah, 1991). In such locations and other high latitude reefs, such as the Northwestern Hawaiian Islands (Hoeke et al., 2006), corals have adapted to tolerate significant seasonal cycles of temperature of 10°C in magnitude and greater. However, despite adaptation to extremely high summer (and low winter) temperatures, corals in such areas bleach when their normal maximum and minimum temperature tolerances are exceeded. For example, bleaching occurred in the Arabian Gulf in 1996, 1998, and 2002 when temperatures remained warmer than 35°C–36°C for greater than three weeks (Riegl, 2002), and in 2010 corals bleached and died in both the Red Sea and Arabian Gulf (news reports). Over shorter time periods (hours to days), corals have commonly survived water temperatures exceeding the mean maximum temperatures for their area and exposure. For instance, corals in relatively enclosed shallow waters in American Samoa have been shown to survive temperature increases to 35°C, well above the maximum monthly mean (Craig et al., 2001).

Other factors influencing the habitat suitability for corals are light (Yentsch et al., 2002) and water quality (Szmant, 2002), both affected by nutrient enrichment, sedimentation/turbidity, and pollutants. Reef-building corals require light for photosynthetic performance of endosymbionts, though different zooxanthellae strains are specialized to different light regimes. A study on the Great Barrier Reef on the influence of siltation and nutrient enrichment on benthic assemblages revealed that turbid inshore waters can support a high diversity of corals (80% of the hard coral species known to occur in the Great Barrier Reef were recorded) but 50% of the species present at the least nutrient-enriched environment were missing (Fabricius et al., 2005). Within this study, the moderately-resilient, long-lived and relatively bleaching-insensitive families Agariciidae, Mussidae, and Faviidae, and the pioneer family Pocilloporidae were relatively tolerant of poor water quality (Fabricius et al., 2005). Sediments, nutrients and other pollutants can also impair the recruitment of corals (Fabricius, 2005).

Depth distributions of corals are generally limited by light (Graus and Macintyre, 1989; Titlyanov and Latypov, 1991; Yentsch et al., 2002). Each of the 82 candidate coral species are found on shallow tropical and subtropical reefs in depths of less than 30 m (within the upper photic zone), although some may find refugia in deeper or mesophotic reefs. As most research has thus far been conducted in these relatively shallow waters, data on depth distributions for most species are incomplete. Carpenter et al. (2008) reviewed depth distribution data for 845 coral species and listed 49% of those species where depth data were available (681 species) as restricted to shallow water (≤ 20 m) habitats. However, this number is likely an overestimate as mesophotic (depth of 30–150 m) reef research is still in its infancy, and it is possible that many more coral species also occur in these deeper mesophotic habitats. Only recently have scientists begun investigating mesophotic coral ecosystems and gained a greater appreciation for the extent of coral reefs in

mesophotic depths (Kahng et al., 2010; see recent special issue in the journal *Coral Reefs* vol 29, no2; Lesser et al., 2009). This has led to the hypothesis that mesophotic reefs may provide refugia habitat and replenishment potential for presumably more vulnerable shallow reef populations of taxa that can occupy both shallow and mesophotic reef habitats (Bongaerts et al., 2010; Lesser et al., 2009). However, this potential remains mostly hypothetical, and threats and conditions of shallow reef systems are much better characterized. Clearly, at least some of the 82 candidate species occur in mesophotic as well as shallow habitats (Garcia-Sais, 2010; Kuhlmann, 1983), though there is very limited specific knowledge of species abundances or of the extent of their distribution in mesophotic reefs, primarily due to operational challenges and costs associated with working at these depths.

Waves and currents are additional environmental conditions influencing coral habitat and distribution as corals have species-specific tolerances (Dollar, 1982; Geister, 1977a; Graus and Macintyre, 1989). The hydrodynamic conditions that influence coral reefs vary over a broad range of spatial scales from regional (thousands of km) to local (sub-meter), with flows dependent on surface gravity waves (seas and swell), tides, wind, topographic and equatorial upwelling, and large-scale thermohaline circulation. Water motion influences the growth, mortality, and reproductive rate of each species adapted to a specific hydrodynamic zone; for example, in Hawai'i *Pocillopora meandrina* is restricted to high surge or wave energy habitats (Jokiel, 1978). Recent research also suggests that water motion may provide protection to corals by increasing their thermal tolerance to bleaching (Lenihan et al., 2008; Nakamura and Yamasaki, 2005), likely by facilitating diffusion of toxic metabolites and providing increased food supply.

2.3.3 Global habitat condition

There is broad scientific consensus that coral reef ecosystems are being rapidly degraded worldwide (Bellwood et al., 2004; Bruno and Selig, 2007; Wilkinson, 2008). Although scientists debate the relative importance of the many different causes of coral reef degradation (fishing, pollution, disease, climate change), it is clear that in many locations coral cover has decreased dramatically over the past few decades. Coral reefs are at the receiving end of watersheds and are, therefore, subject to multiple threats from both land-conversion in those watersheds and from any coastal development which allows easier land-based access to exploitable marine resources (e.g., Waddell, 2005). Coral reef ecosystems have also deteriorated in response to climate change. Over the last few decades, concerns have primarily focused on increases in water temperature and resulting mass coral bleaching and disease epizootics. More recently, additional attention has been given to the effects of ocean acidification on marine calcifying organisms (Hoegh-Guldberg et al., 2007; Veron, 2008). Current projections about global increases in atmospheric carbon dioxide concentrations and water temperature predict a significant loss of corals and other calcifying marine organisms, resulting in reduced diversity of reef communities and a reduced resilience of corals to local stressors (Hoegh-Guldberg et al., 2007). These threats will be described more fully in the next chapter.

2.3.4 Phase shifts

Coral reefs are described as space-limited systems and, thus, it is thought that competition for space is an important structuring factor. Some types of reef benthic organisms (e.g., macroalgae) have higher growth rates and, hence, potentially greater competitive ability than corals. When disturbances such as disease, predation, or physical damage cause mortality of corals, new habitat (space) becomes available to populations of non-reef-building organisms, such as soft corals, zoanthids or, more often, fast-growing macroalgae (Aronson and Precht, 2006). In extreme cases, "phase shifts" can change the community structure from coral-dominance to macroalgae-dominance (Bellwood et al., 2004; Done, 1992; Hughes, 1994). Such phase shifts may be persistent and difficult to reverse (Mumby et al., 2007b; Sutherland, 1974), as macroalgal occupation of reef space severely impedes recruitment of corals via alleopathy and sediment binding as well as direct occupation of space (Birrell et al., 2008; Kuffner et al., 2006; McCook et al., 2001). Phase shifts may be reversible in theory (Mumby, 2009) and in practice (Ayre and Hughes, 2000; Diaz-Pulido et al., 2009; Hughes et al., 2007; Idjadi et al., 2006), via enhanced grazing, coral growth and/or recruitment. Over the past several decades many reefs, primarily in the Caribbean, have been described as undergoing phase shifts which are attributed to loss of macroalgal control via reduced grazing, to some extent increased nutrient resources for the algae, and/or simply massive increases in available space resources because of widespread coral mortality (Aronson and Precht, 2006; Hughes, 1994; Hughes et al., 2007; Williams et al., 2001). At least at some Jamaica sites, reported phase-shift reversals have been observed as short-lived with a repeated coral cover collapse in association with the 2005 mass coral bleaching event and subsequent predation (Quinn and Kojis, 2008). There is some semantic debate as to what constitutes "macroalgal dominance," whether many reefs are habitat limited, and whether phase shifts are pervasive on global scales (Bruno et al., 2009; Vroom et al., 2006).

In some locations, such as Hawai'i, proliferation of invasive exotic macroalgal species is an added driver of phase shifts (Conklin and Smith, 2005). On some degraded reefs around O'ahu Island, populations of herbivorous fishes have been severely reduced by fishing (Friedlander et al., 2008). The resulting low grazer populations have almost certainly contributed to those reefs' vulnerability to algal blooms (Williams et al., 2007).

Coral reef phase shifts have also been described in which scleractinian corals are replaced by other invertebrates rather than by macroalgae (Aronson et al., 2004; Work et al., 2008) and, at times, have been precipitated by acute anthropogenic disturbances such as shipwrecks (Hatcher, 1984; Work et al., 2008) or by hurricanes (Hughes, 1994; Rogers and Miller, 2006).

2.3.5 Resilience of corals and coral reefs

While the term 'resilience' has appeared in the ecological literature with various shades of meaning (for some review and discussion see Beisner et al., 2003; Moss et al., 2010), the following more or less vernacular definitions will be intended within this Status Review Report. Resilience is the capacity of a reef or population to recover¹ from damage by a major disturbance such as a disease outbreak or tropical storm; in other words, its capacity to "bounce back" from a disturbance rather than assuming an alternate (phase-shifted) state. The term resistance is somewhat different, indicating that the organism or population in question can experience a stressor (e.g., a storm or exposure to a pathogen) without measurable detriment. Resilience is affected by the frequency, intensity, and nature of a disturbance, as well as the life history and status of the organisms involved. Natural communities, including coral reefs, are resilient as there are many descriptions in the literature of rapid natural recovery following disturbances (e.g., storm damage). Based on their high biological diversity, coral reef ecosystems likely have increased functional redundancy, which is expected to provide increased resilience compared with less diverse ecosystems. However, this capacity of organisms and natural systems can be degraded by sequential, chronic, and multiple disturbances, physiological stress, and general environmental deterioration (Nyström et al., 2000). This loss of resilience can also lead to phase shifts. Loss of resilience may take many forms including increased disease susceptibility, impaired reproduction and recruitment, loss of functional diversity/redundancy in communities, and reduced individual growth rates. The complex sexual reproductive cycles of scleractinian corals include many vulnerable stages (Fig. 2.2.1) that environmental stress and disturbance can impair (Ritson-Williams et al., 2009); see discussions on depensation in Sections 4.5 and 4.6.

2.4 Status and Recent Ecological History of Caribbean Reefs

The Caribbean basin is geographically small and partially enclosed, biologically well-connected, and has relatively high human population densities with a long history of disturbances from human activities to coral reef systems across the basin (Mora, 2008; Roberts, 1997). Fishing has affected Caribbean reefs since prior to European contact (Jackson, 1997; Wing and Wing, 2001). A series of basin-scale disturbances, beginning in the early 1980s, has led generally to an altered community state and an apparent loss of resilience in Caribbean reefs. Massive, Caribbean-wide mortality events, apparently from disease conditions, of both the keystone grazing urchin *Diadema antillarum* (Lessios, 1988) and the dominant branching coral species *Acropora palmata* and *Acropora cervicornis* (Aronson and Precht, 2001) spread throughout the Caribbean and precipitated widespread and radical changes in reef community structure (see Section 2.3.4 above on phase shifts). It is likely that the keystone status of *Diadema* (i.e., the overarching importance of *Diadema* grazing on early 1980s Caribbean reefs) was a result of long-term overexploitation of reef fish (Hay, 1984; Knowlton, 1992) and represented an aspect of resilience whereby urchins had functionally substituted for the loss of herbivorous fish. In addition, continuing coral mortality from periodic acute events such as hurricanes, disease outbreaks, and mass bleaching events has added to the depauperate state of Caribbean coral populations (Aronson et al., 2002; Bruckner and Hill, 2009; Miller et al., 2009; Wilkinson and Souter, 2008) and yielded a remnant coral community with increased dominance by weedy brooding species (Aronson et al., 2004; Green et al., 2008).

None of these three important keystone species (*Acropora palmata*, *Acropora cervicornis*, and *Diadema antillarum*) have shown much recovery over decadal time scales. While *Diadema* is now attaining higher densities in some regions of the Caribbean with consequent improvements in reef status (Aronson and Precht, 2000; Carpenter and Edmunds, 2006), its recovery has taken multiple decades and has not yet reached all areas (Chiappone et al., 2002). Nowhere have *Diadema* densities reached levels comparable to pre-dieoff abundances. The two *Acropora* spp. corals have failed to recover at anything like a regional scale, resulting in their Endangered Species Act listing as threatened in 2006. In addition, coral growth rates have been declining over decades. The rate of calcification in *Diploria labyrinthiformis* in

¹ The term 'recover' here is meant in the ecological sense (i.e., an organism, population, or community naturally moving back toward the pre-disturbance state), not in the U.S. Endangered Species Act statutory sense.

Bermuda has decreased by over 25% since 1959 (Cohen et al., 2008), *Acropora palmata* branch extension rates have declined substantially in Curacao (Bak et al., 2009), and juvenile coral growth rates among all species in the U.S. Virgin Islands over the past decade are substantially lower than reported in previous literature (Edmunds, 2007). Caribbean-wide meta-analyses have suggested that the current combination of disturbances, stressful environmental factors, and potentially depensatory states have yielded poor resilience, even to natural disturbances such as hurricanes (Gardner et al., 2005). These wide-scale changes in coral populations and communities have affected habitat complexity (Alvarez-Filip et al., 2009) and may have already begun feeding back in reduced overall reef-fish abundances (Paddock et al., 2009).

In combination, these regional factors were considered by the BRT to contribute to elevated estimates of extinction risk for Caribbean species.

2.5 Contrasts between Caribbean and Indo-Pacific Reefs

The history of diversification and extinction of reef-building corals, starting several million years after the Paleocene-Eocene Thermal Maximum in the early Cenozoic (about 50 Ma), differed greatly among the Indo-Pacific, the eastern Pacific, and the wider Caribbean. In the Indo-Pacific, coral diversity has been substantially increasing since the Eocene (56 to 34 Ma), while the number of hermatypic coral genera has decreased by almost half in the Atlantic, and reefs and hermatypic corals may have periodically been eliminated altogether in the eastern Pacific. Although there were a few endemic genera in the wider Caribbean (e.g., *Mussa*, *Isophyllia*, and *Manicina*, while *Agaricia*, *Mycetophyllia*, *Dendrogyra*, *Diploria*, *Colpophyllia* and others thought of as Caribbean corals were inherited from the ancient Tethys Sea), there has been a general decrease in numbers of genera, especially during two major periods of extinctions. Fukami et al. (2004) have discovered that some of the representatives of different genera in the greater Caribbean are more closely related to each other than they are to their respective congeners in the Pacific, suggesting that some of the genera considered cosmopolitan might be represented by cryptic endemic genera in the Caribbean. Both coral reefs and the number of genera of corals decreased in the late Oligocene, about 24 Ma. The second episode of extinction occurred as carbonate deposition increased and reefs flourished, between 2 and 1 Ma (O'Dea et al., 2007). Of 48 genera of Caribbean hermatypic corals, 23 went extinct in the Cenozoic but are still extant and widespread in the Indo-Pacific (Indian and Pacific Oceans; Paulay, 1997). The eastern Pacific has generally been a region of marginal conditions for coral reefs throughout the Cenozoic. Corals now known only in the Caribbean were found in the eastern Pacific until they all went extinct sometime in the Pliocene (5.4 to 2.4 Ma). Although the provenance of sandy and hard rock habitat fauna in the eastern Pacific is still the western Atlantic (Paulay, 1997), the origin of coral-reef fauna has been the central Pacific since sea level stabilized about 5000 years ago (Dana, 1975; Paulay, 1997).

The Indo-Pacific is enormous and hosts much greater coral diversity than the much smaller Caribbean region (approximately 700 described species compared with 65 described Caribbean species; Table 2.5.1). Size and diversity, as well as some vast expanses of ocean area with only very local, spatially limited, direct human influences, may have provided substantial buffering of Indo-Pacific corals from most of the assaults and declines manifest across the Caribbean. While the reef communities in the wider Caribbean have lost resilience (see Section 2.4), the reefs in the central Pacific, e.g., American Samoa (Birkeland et al., 2008), Moorea (Adjeroud et al., 2009), Fiji (Lovell and Sykes, 2008), Palau (Golbuu et al., 2007), and the Northwestern Hawaiian Islands (Kenyon et al., 2006) appear to remain resilient to date despite major bleaching events, tropical cyclones, and crown-of-thorns seastar (*Acanthaster planci*) predation outbreaks. However, consensus is building that these buffering factors simply have put the Indo-Pacific on a slower journey down a similar road of decline rather than a qualitatively different trajectory (Bruno and Selig, 2007; Done et al., 2008; Galloway et al., 2009; Pandolfi et al., 2003). Indeed, recent meta-analysis of overall coral status throughout the region has indicated that substantial loss of coral cover has already occurred in most subregions of the Indo-Pacific and as of 2002–2003 stand at around 20% live cover (Bruno and Selig, 2007).

Table 2.5.1. Summary of regional coral diversity. Eastern Pacific numbers from Glynn and Ault (2000) but genera and species reduced by 1 each as *Siderastrea glynni* is probably introduced from the Caribbean (Forsman et al., 2005). The other numbers are from Paulay (1997).

Reef-building corals	Indo-Pacific	East Pacific	West Atlantic	East Atlantic
Genera	91	10	25	8
Species	~700	40	65	14

The vast size of the Indo-Pacific region has had at least four additional major effects on the biota. First, while diseases in the wider Caribbean, such as those effecting *Diadema antillarum* (see Section 2.4) and commercial sponges have spread throughout the region within a year, epizootics such as pearl oyster mortality have stayed within Pacific archipelagoes because of the degree of separation of archipelagoes in the basin. Second, the geologic record shows several major bouts of extinction in the western Atlantic during the Cenozoic, but none are known in the Indo-Pacific. At the Oligocene-Miocene boundary (21–27 Ma) and another in the Pliocene-Pleistocene (~ 1.6 Ma), more than 20 genera of corals went extinct in the western Atlantic that are still abundant in the Pacific (relictual endemics, e.g., *Stylocoeniella*, *Pocillopora*, *Stylophora*, *Astreopora*, *Alveopora*, *Goniopora*, *Coscinarea*, *Psammocora*, *Gardineroseris*, *Pavona*, *Galaxea*, *Hydnophora*, *Caulastrea*, *Diploastrea*, *Favites*, *Goniastrea*, *Leptoria*, *Platygyra*, *Trachyphyllia*, *Euphyllia*, *Heteropsamia*, *Turbinaria*) (Edinger and Risk, 1995). It seems the relatively small western Atlantic has always been more vulnerable to mass extinctions than the huge water mass of the west-central Pacific. Third, the distance between archipelagoes facilitates endemism. The greatest numbers of endemic scleractinian species (31) are found in the center of diversity (the Coral Triangle), but the greatest proportions of endemic scleractinians are found in the more remote archipelagoes (20% of Hawaiian scleractinian nominal species are endemic). Fourth, while the wider Caribbean is a relatively homogeneous region, there is a striking gradient in diversity in the Pacific, declining from west to east. For example, the Coral Triangle hosts 581 species, 81 genera, and 16 families of reef-building scleractinians (Veron, 2000), while French Polynesia (Society, Tuamotus, Australs and Gambier Archipelagoes) hosts 163 species, 38 genera and 13 families and the far eastern Pacific (Easter Island, Fanning Island, Galapagos, Malpelo, Clipperton, Cocos, Revillagigedo, and the coast from Mexico to Ecuador) hosts 49 species, 12 genera, and 7 families (Glynn et al., 2007).

2.6 Status and Ecological History of Eastern Pacific Reefs

The eastern Pacific Ocean consists of two primary reef domains: the coastal reefs and nearshore islands, and the offshore islands. These reefs exist from Mexico in the north to Ecuador in the south, and from the coast out to the remote Revillagigedo, Clipperton, Cocos, Malpelo, and Galápagos Islands. All are spatially separated from the reefs of the Indo-West Pacific such that there is little connectivity across the Pacific, isolating the eastern Pacific coral reefs (Glynn, 1982; Glynn and Ault, 2000). Unlike the well-studied Caribbean, much less work has been done on corals and coral reefs of the eastern Pacific and this region was long considered to be lacking of significant coral reef communities, diversity, and structure (Durham, 1966; Stoddart, 1969; Yonge, 1940). More recent work has characterized the corals and coral reefs of the region, describing the significant coral reef resources that exist in the eastern Pacific, while at the same time indicating their high potential for ecosystem transition from one stable state to another and loss of species as discussed below.

In his pioneering work on coral reefs of the eastern Pacific since the 1970s, Glynn and colleagues described the general characteristics of eastern Pacific reefs (Cortes, 1993; Glynn, 1976) and their growth (Glynn and Macintyre, 1977), the first observation of regional-scale mass coral bleaching (in that case related to the 1982/1983 El Niño) (Glynn, 1984), and the first case of a probable extinction of a coral species in recent history (De Weerd and Glynn, 1991). Those studies have revealed an environment that may be one of the least hospitable to reef development and coral biodiversity (Glynn, 1997), even to the point of an almost complete lack of Quaternary fossil reefs (Cortes, 1993). Eastern Pacific reefs and coral populations are hindered from recovery by their extreme spatial separation and distance from source populations of coral diversity (Glynn, 1982; Glynn and Ault, 2000). Durham (1966) even postulated that extinction at the level of genera has been common in the eastern Pacific. Glynn (1997) has documented that since 1980 six of the 40 known reef-building scleractinian and hydrocoral species in the eastern Pacific have possibly become extinct or locally extirpated (Table 2.1 in Glynn, 1997).

After separation from the Caribbean around 3.5 Ma (Cortes, 1993), it is quite likely that earthquakes and fluctuating climate and sea level eliminated extant coral reefs in the eastern tropical Pacific and prevented formation of new ones until the Holocene (Cortes, 1993). Severe climate swings continue to be a hindrance to reef growth today, with major losses of coral cover and even reef loss from Mexico to the Galápagos Islands (Glynn, 1984; 1988a; 1990; 2000; Glynn and Ault, 2000; Glynn et al., 2001; Reyes-Bonilla et al., 2002). Additionally, climatic variability not only has killed corals in recent decades, it has resulted in major loss of reef structure. This has come about through temperature variability (both extreme upwelling and high temperatures during El Niño), storm events, and changes in the abundance, distribution, and behavior of both corallivores and bioeroders (Eakin, 2001; Eakin and Glynn, 1996; Glynn, 1988b; 1990; Reaka-Kudla et al., 1996). After disturbance, eastern Pacific reefs have been among the slowest in the world to recover (Baker et al., 2008; Graham et al., 2011). Additionally, the naturally low calcium carbonate saturation state of eastern Pacific Ocean waters has made these reefs among the most fragile and subject to bioerosion in the world (Manzello, 2010; Manzello et al., 2008). Compared to the Atlantic, the eastern Pacific contains approximately one third as many genera and about half the species (manifestation of vulnerability in this region; Table 2.5.1), less reef area, and a high susceptibility to strong climate variability. For these reasons, the BRT determined corals limited to the eastern Pacific were likely at even higher risk of extinction than those in the Caribbean, based on these regional attributes. Only one candidate coral was limited to the eastern tropical Pacific, that being the broadcast spawning eastern Pacific *Pocillopora elegans*, which the BRT identified as likely a different species from the genetically distinct and brooding central and western Pacific *Pocillopora elegans*. The only other candidate species with a range that extends into the eastern Pacific is *Psammocora stellata*; however, the eastern Pacific is believed to be only a small part of its range.