

6.5 Genus *Montastraea* (Family Faviidae)

Montastraea annularis complex

Taxonomic Issues

The nominal *Montastraea annularis* (Ellis and Solander, 1786) has historically been one of the primary reef framework builders of the western Atlantic and Caribbean. *Montastraea annularis* and its related species seem to have originated prior to the Caribbean coral extinction at the end of late Pliocene to early Pleistocene (~ 2.5 Ma; Budd and Klaus, 2001). Its depth range is from 1 m to over 30 m, and has historically been considered a highly plastic species with multiple growth forms ranging from columnar, to massive, to platy. In the early 1990s, Knowlton, Weil, and colleagues suggested the partitioning of these growth forms into separate species, resurrecting previously described monikers, *Montastraea faveolata* and *Montastraea franksi*. These three sibling species were differentiated on the basis of morphology, depth range, ecology, and behavior (Weil and Knowlton, 1994). Subsequent reproductive and genetic studies have generally supported this partitioning, although with some interesting details. *Montastraea faveolata* is the most genetically distinct, while *Montastraea annularis* and *Montastraea franksi* are less so (Fukami et al., 2004; Lopez et al., 1999). Similarly, hybrid-crossing experiments show the same pattern with *Montastraea annularis* and *Montastraea franksi* showing greater success of hybrid crosses than either with *Montastraea faveolata* (Leviton et al., 2004; Szmant et al., 1997). Isolation between *Montastraea annularis* and *Montastraea franksi* is enhanced by the timing of spawning; *Montastraea franksi* spawns 1–2 hours earlier than the other two. Meanwhile, Fukami et al. (2004) showed some degree of geographic variation in these reproductive and genetic traits with a lesser degree of separation in the Bahamas than in Panama.

While there now is reasonable acceptance that these represent three valid species, long-term monitoring data sets and previous ecological studies did not distinguish among them. Currently, intermediate forms (especially in northern sections of the range) complicate the collection of monitoring data into three species, and so modern monitoring data sets often still group them as “*Montastraea annularis* complex” or “*Montastraea annularis sensu lato*.” The BRT has estimated Critical Risk Thresholds separately for each species, but much of the information available is for the complex as a whole.

Abundance and Trends

The *Montastraea annularis* complex has historically been a dominant species on Caribbean coral reefs, characterizing the so-called “buttress zone” and “annularis zone” in the classical descriptions of Caribbean reefs (Goreau, 1959). Goreau describes *Montastraea annularis* complex as “very abundant” in these zones and constitutes “by far the commonest and often the only fossil framework coral to be found in exposures of the Pliocene Era and more recent coastal reef limestones of northern Jamaica” (Goreau, 1959). There is ample evidence that it has declined dramatically throughout its range, but perhaps at a slower pace than its fast-paced Caribbean colleagues, *Acropora palmata* and *Acropora cervicornis*. While the latter began their rapid declines in the early-to-mid-1980s, declines in *Montastraea annularis* complex have been much more obvious in the 1990s and 2000s, most often associated with combined disease and bleaching events. It should be noted that, given the dramatically low productivity of the *Montastraea annularis* complex (low growth and extremely low recruitment), any substantial declines in adult populations would suggest increased extinction risk since their capacity for population recovery is extremely limited. Figure 6.5 shows only recent trends in aspects of the *Montastraea annularis* complex abundance at select locations, and additional supporting information on longer-term trends is described below. In most cases where examined, additional demographic changes accompany these instances of declining abundance (e.g., size structure of colonies, partial mortality, etc).

In Florida, the percent cover data from four fixed sites have shown the *Montastraea annularis* complex to have declined in absolute cover from 5% to 2% in the Lower Keys between 1998 and 2003 (Fig. 6.5A) and was accompanied by 5–40% colony shrinkage and virtually no recruitment (Smith et al., 2008). Earlier studies from the Florida Keys indicated a 31% decline of *Montastraea annularis* complex absolute cover between 1975 and 1982 (Dustan and Halas, 1987) at Carysfort Reef and > 75% decline (from over 6% cover to less than 1%) across several sites in Biscayne National Park between the late 1970s and 1998–2000 (Dupont et al., 2008). Taken together, these data imply extreme declines in the Florida Keys (80%–95%) between the late 1970s and 2003, and it is clear that further dramatic losses occurred in this region during the cold weather event in January 2010.

Similar declines have also been documented for relatively remote Caribbean reefs. At Navassa Island National Wildlife Refuge, percent cover of *Montastraea annularis* complex on randomly sampled patch reefs declined from 26% in 2002 to 3% in 2009 (Fig. 6.5B), following disease and bleaching events in this uninhabited oceanic island (Miller and Williams, 2007). Additionally, two offshore islands west of Puerto Rico (Mona and Desecheo; Fig. 6.5C) showed reductions in live colony counts of 24% and 32% between 1998/2000 and 2008 (Bruckner and Hill, 2009). At Desecheo, this demographic decline of one-third corresponded to a decline in *Montastraea annularis* complex cover from over 35% to below 5% across 4 sites. Taken together, decadal-scale declines across these remote islands in the central Caribbean constitute over 85% of the populations.

In the U.S. Virgin Islands, recent data from the U.S. National Park Service Inventory and Monitoring Program (Fig. 6.5D) across six sites at fixed stations show a decline of *Montastraea annularis* complex from just over 10% cover in 2003 to just over 3% cover in 2009 following mass bleaching and disease impacts in 2005 (Miller et al., 2009). This degree of recent decline was preceded by a decline from over 30% *Montastraea annularis* complex cover to ~ 10% between 1988 and 2003 as documented by Edmunds and Elahi (2007). Similarly, percent cover of *Montastraea annularis* complex in a marine protected area in Puerto Rico declined from 49% to 8% between 1997 and 2009 (Hernández-Pacheco et al., 2011). Taken together, these data suggest an 80%–90% decline in *Montastraea annularis* complex over the past two decades in the main U.S. Caribbean territories.

While Bak and Luckhurst (1980) indicated stability in *Montastraea annularis* complex cover across depths in Curaçao during a 5-year study in the mid-1970s, this region has also manifested *Montastraea annularis* complex declines in recent years. Bruckner and Bruckner (2006) documented an 85% increase in the partial mortality of *Montastraea annularis* complex colonies across three reefs in western Curaçao between 1998 and 2005 (Fig. 6.5E), approximately twice the level for all other scleractinian species combined. These authors noted that *Montastraea franksi* fared substantially better than the other two complex species in this study. It is likely that *Montastraea annularis* complex populations in Curaçao have fared better than other Caribbean regions but are not immune to losses.

Montastraea annularis complex declines in additional locations can be noted. For example, at Glovers Reef, Belize (McClanahan and Muthiga, 1998) documented a 38%–75% decline in relative cover of *Montastraea annularis* complex across different reef zones between 1975 and 1998, and a further 40% decline in relative cover has occurred since then (Huntington et al., in review). In contrast, *Montastraea annularis* complex populations have shown stable status at sites in Columbia between 1998 and 2003 (Rodriguez-Ramirez et al., 2010), although demographic changes in *Montastraea annularis* complex at both degraded and less-degraded reefs imply some degree of population decline in this region (Alvarado-Chacon and Acosta, 2009).

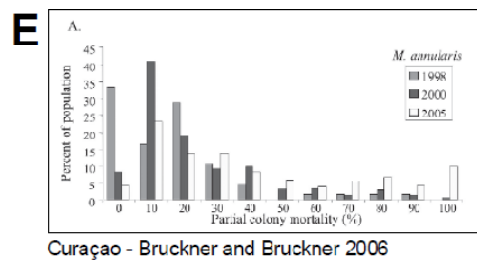
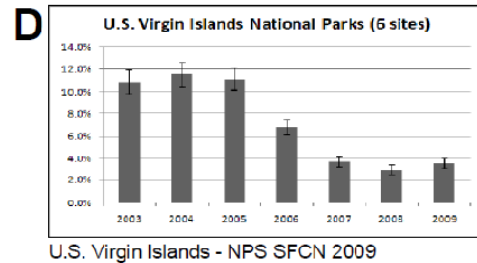
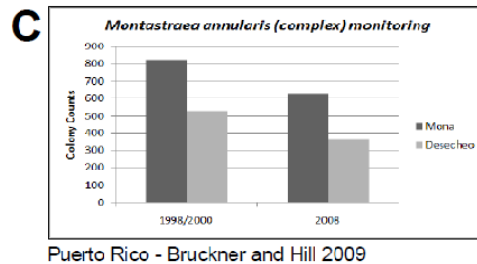
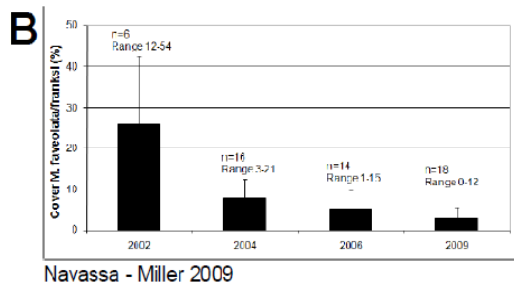
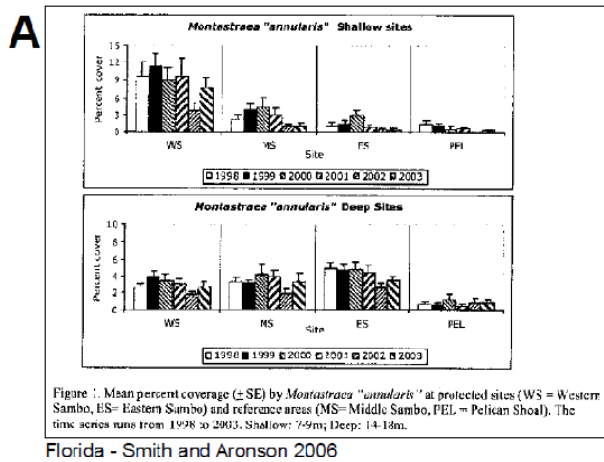
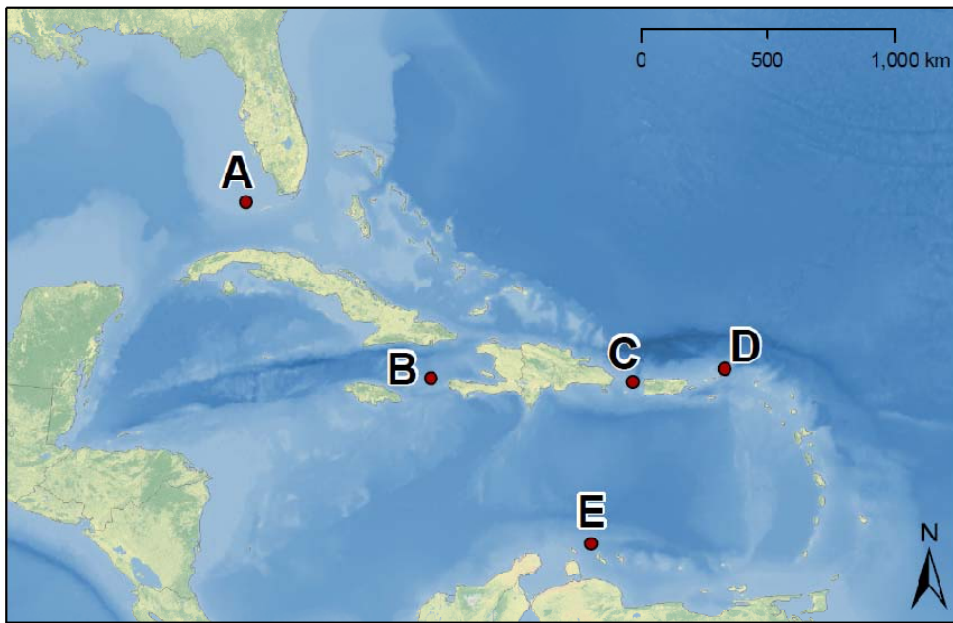


Figure 6.5. Examples of declining abundance of *Montastraea annularis* complex in different regions of the Caribbean in the recent past. A) data from Smith and Aronson (Smith et al., 2006) based on haphazard video transects at two depths at 4 sites in the lower Florida Keys; B) unpublished data from haphazard photo quadrats at randomly selected patch reefs at Navassa Island National Wildlife Refuge (described in (Miller et al., 2005)); C) declines in colony abundance in fixed plots at two offshore islands in Puerto Rico between 1998/2000 and 2008 (Bruckner and Hill, 2009); D) cover data from video transects of six fixed sites in Virgin Islands National Park (unpublished data, National Park Service, South Florida/Caribbean Network); E) increasing proportion of population across three sites in western Curaçao manifesting high levels of partial mortality (Bruckner and Bruckner, 2006) which is accompanied by a lack of recruitment.

Life History

All three of the *Montastraea annularis* complex species are hermaphroditic broadcast spawners, with spawning concentrated on nights 6–8 following the new moon in late summer (Levitan et al., 2004). Fertilization success measured in the field was generally below 15% but was highly linked to the number of colonies observed spawning at the same time (Levitan et al., 2004). Minimum size for reproduction was found to be 83 cm² in Puerto Rico whether as an intact adult or as a remnant fragment of an older colony (Szmant-Froelich, 1985). Szmant-Froelich (1985) estimated this to correspond to 4–5 years of age, and *Montastraea annularis* typically exhibit a linear growth of ~ 1 cm per year (Gladfelter et al., 1978), but increased appreciation for the slow rate of growth of post-settlement stages suggest this age for minimum reproductive size may be an underestimate (M.W. Miller, Southeast Fisheries Science Center, Miami, FL. pers. obs., October 2010). Eggs (~ 310 to 340 µm among the three species; Szmant et al., 1997) and larvae are small and post-settlement growth rates are very slow, both of which may contribute to extremely low post-settlement survivorship, even lower than other Caribbean broadcasters, such as the threatened Caribbean *Acropora palmata* (Szmant and Miller, 2005). There may be a depth-related fecundity cost arising from morphological differences in polyp spacing (Villinski, 2003), suggesting the spatial distribution of colonies may influence population fecundity on a reef.

Successful recruitment by *Montastraea annularis* complex species have seemingly always been rare events. Hughes and Tanner reported the occurrence of only a single recruit for these species over 18 years of intensive observation of 12 m² of reef in Discovery Bay, Jamaica (Hughes and Tanner, 2000) while myriad other recruitment studies from throughout the Caribbean also report them to be negligible to absent (Bak and Engel, 1979; Rogers et al., 1984). Edmunds (2011) asserted that the large, rare, replenishing recruitment hypothesized to operate in these species have never actually been documented on any Caribbean reef since the initiation of quantitative ecological study in the 1960s. Overall recruitment by these species is so low that Edmunds (2011) based an entire publication on the detection of at most nine additional juvenile colonies (constituting a “recruitment pulse”) along the south shore of St. John, USVI in 2008–2009. However, this “recruitment pulse” was limited in spatial extent (Edmunds et al., 2011). *Montastraea* juveniles also have higher mortality rates than larger colonies (Smith et al., 2006). Despite their generally massive form, at least the lobate form (*Montastraea annularis* sensu stricto) is capable of some degree of fragmentation/fission and clonal reproduction. Foster et al. (2007) detected 8% of *Montastraea annularis* genotypes were represented by multiple ramets (up to 14 ramets or separate colonies of the same genotypes) across three sites in Belize.

In St. Croix, growth rates of *Montastraea annularis* were measured along a depth gradient from 3 m to 40 m (Hubbard and Scaturo, 1985). There was a sharp decline in growth rate at a depth of around 15 m with growth rates of 0.7–0.9 cm per year in water depths < 12 m and 0.20 cm per year in depths below 18–20 m. Growth rates, measured as extension rates, in shallow waters (< 15 m) varied between 0.43 and 1.23 cm per year and in deeper waters (> 18 m) between 0.06 and 0.29 cm per year. Also, growth rates were consistently higher in the clear waters of Cane Bay than those at the more turbid and sediment rich waters of Salt River confirming the controlling factors for growth rate of light and sediment load (Hubbard and Scaturo, 1985). Long-term analyses of coral cores have typically shown seasonal variation in growth and a general reduction in *Montastraea* growth rates over the past century, although the reduction may have stabilized over the past few decades (Carricart-Ganivet et al., 2000; Dodge and Lang, 1983; Hudson et al., 1994).

Threats

Because they have traditionally been common and are one of the main reef builders in the Caribbean, *Montastraea annularis* complex species have been the frequent subject of research attention, including responses to and impacts of environmental threats. This body of work is briefly summarized here, but it should be noted that a large body of work exists for these species.

Thermal stress: Published reports of individual bleaching surveys have consistently indicated that *Montastraea annularis* complex is highly-to-moderately susceptible to bleaching (Brandt, 2009; Bruckner and Hill, 2009; Oxenford et al., 2008; Wagner et al., 2010). The species complex is polymorphic with respect to zooxanthellae. Depending on depth and other environmental conditions, colonies can contain clade A, B, C, D, but composition of symbiont assemblages in at least some areas changes in response to bleaching (Rodríguez-Román et al., 2006; Thornhill et al., 2006). Bleaching has been shown to prevent gametogenesis in *Montastraea annularis* complex colonies in the following reproductive season after recovering normal pigmentation (Mendes and Woodley, 2002; Szmant and Gassman, 1990) and leave permanent records in coral growth records (Leder et al., 1991; Mendes and Woodley, 2002). Given the rapidly developing genomic tools for this species complex, cellular and transcriptomic mechanisms for bleaching and thermal stress are being elucidated for this species complex (Desalvo et al., 2008). In addition, certain aspects of geographic and

genetic variability in the molecular responses to thermal stress have been described (Polato et al., 2010), which may enable more accurate predictions of potential evolutionary adaptation to warming. Particularly well-documented mortalities in these species following severe mass-bleaching in 2005 highlight the immense impact that thermal stress events and their aftermath can have on *Montastraea annularis* complex populations (Miller et al., 2009). Using demographic data collected in Puerto Rico over 9 years straddling the 2005 bleaching event (Hernández-Pacheco et al., 2011) showed that demographic transitions (vital rates) for *Montastraea annularis* were substantially altered by the 2005 mass thermal bleaching event. Size-based transition matrix models based on these measured vital rates showed that population growth rates were stable (λ not significantly different from 1) in the pre-bleaching period (2001–2005) but declined to $\lambda = 0.806$ one year after and to 0.747 two years after the bleaching event. Although population growth rate returned to $\lambda = 1$ the following year, simulation modeling of different bleaching probabilities predicted extinction of a population with these dynamics within 100 years at a bleaching probability between 10 and 20%, i.e., once every 5 to 10 years (Hernández-Pacheco et al., 2011). Cervino (2004) also showed that higher temperatures (over experimental treatments from 20°C–31°C) resulted in faster rates of tissue loss and higher mortality in yellow-band affected *Montastraea annularis* complex. Recent work in the Mesoamerican reef system indicated that *Montastraea faveolata* had reduced thermal tolerances in locations and over time (Carilli et al., 2010) with increasing human populations, implying increasing local threats (Carilli et al., 2009a).

Acidification: The only study conducted regarding the impact of acidification on this genus is a field study (Helmle et al., 2011) that did not find any change in *Montastraea faveolata* calcification in field-sampled colonies from the Florida Keys up through 1996. However, most corals studied have shown negative relationships between acidification and growth (Table 3.2.2), and acidification is likely to contribute to reef destruction in the future (Hoegh-Guldberg et al. 2007, Silverman et al. 2009). While ocean acidification has not been demonstrated to have caused appreciable declines in coral populations so far, the BRT considers it to be a significant threat to corals by 2100 (Albright et al., 2010; Hoegh-Guldberg et al., 2007; Langdon and Atkinson, 2005; Manzello, 2010; Silverman et al., 2009). Preliminary experiments testing effects of acidification on fertilization and settlement success of *Montastraea annularis* complex (Albright et al., unpublished data) show results that are consistent with the significant impairments demonstrated for *Acropora palmata* (Albright et al., 2010).

Disease: Both Bruckner and Hill (2009) and Miller et al. (2009) demonstrated profound population declines for *Montastraea annularis* complex from disease impacts, both with and without prior bleaching. Both white-plague and so-called yellow-band diseases can invoke this type of population level decline. Disease outbreaks can persist for years in a population—*Montastraea annularis* colonies suffering from yellow-band in Puerto Rico in 1999 still manifest similar disease signs 4 years later, with a mean tissue loss of 60% (Bruckner and Bruckner, 2006).

Predation: *Montastraea annularis* complex does not suffer from catastrophic outbreaks of predators, such as the effects of *Acanthaster planci* on *Acropora* stands in the Pacific. While *Montastraea annularis* complex can host large populations of corallivorous snails, they rarely display large feeding scars that are apparent on other coral prey, possibly related to differences in tissue characteristics or nutritional value (Baums et al., 2003). However, low-level predation can have interactive effects with other stressors. For example, predation by butterflyfish can serve as a vector to facilitate infection of *Montastraea faveolata* with black-band disease (Aeby and Santavy, 2006). Parrotfishes are also known to preferentially target *Montastraea annularis* complex in so-called “spot-biting” which can leave dramatic signs in some local areas (Bruckner et al., 2000; Rotjan and Lewis, 2006), and chronic parrotfish biting can impede colony recovery from bleaching (Rotjan et al., 2006).

Although it is not predation per se, *Montastraea* colonies have often been infested by other pest organisms. Bioeroding sponges (Ward and Risk, 1977) and territorial damselfishes, *Stegastes planifrons*, can cause tissue loss and skeletal damage. Damselfish infestation of *Montastraea annularis* complex appears to have increased in areas where their preferred, branching coral habitat has declined because of loss of Caribbean *Acropora* spp. (Precht et al., 2010).

Land-based sources of pollution (LBSP): Large, massive, long-lived colonies of *Montastraea annularis* complex lend themselves to retrospective studies of coral growth in different environments so there is a relatively large amount known or inferred regarding relationships of water quality to *Montastraea annularis* complex growth and status. For example, Tomascik (1990) found an increasing average growth (linear extension) rate of *Montastraea annularis* with improving environmental conditions on fringing reefs in Barbados. Tomascik also found a general pattern of decreasing growth rates within the past 30 years at each of the 7 fringing reefs and contributed this decrease to the deterioration of water quality along the west coast of Barbados. Torres and Morelock (2002) noted a similar decline in *Montastraea annularis*

growth at sediment-impacted reefs in Puerto Rico. Density and calcification rate increased from high to low turbidity and sediment load, while extension rate followed an inverse trend (Carricart-Ganivet and Merino, 2001). Eakin et al. (1994) demonstrated declines in *Montastraea annularis* linear extension during periods of construction in Aruba.

Downs et al. (2005) suggested that localized toxicant exposure may account for a localized mortality event of *Montastraea annularis* complex in Biscayne National Park, based on analyses of a suite of cellular biomarkers that yielded signatures of oxidative stress and xenobiotic detoxification response. Meanwhile, *Montastraea annularis* complex was shown to have somewhat lesser sensitivity to copper exposure in laboratory assays than *Acropora cervicornis* and *Pocillopora damicornis* (Bielmyer et al., 2010). *Montastraea faveolata* induces cytochrome p450 and antioxidant enzymes under acute exposure to benzo(a)pyrene (Ramos and Garcia, 2007), but effects of chronic long-term exposure are not known. *Montastraea annularis* skeletons are among those that incorporate toxic heavy metals, making them useful in documenting long-term contamination of reef sites (Medina-Elizalde et al., 2002; Runnalls and Coleman, 2003).

Nutrient-related runoff has also been deleterious to *Montastraea annularis* complex. Elevated nitrogen reduced respiration and calcification in *Montastraea annularis* and stimulated zooxanthellae populations (Marubini and Davies, 1996). Fecal coliform microorganisms were among the bacterial communities associated with *Montastraea* in the Florida Keys (Lipp et al., 2002), suggesting potential sewage impacts to the corals. Elevated nutrients increased the rate of tissue loss in *Montastraea franksi* and *Montastraea faveolata* affected by yellow-band disease (Bruno et al., 2003). Chronic nutrient elevation can produce bleaching and partial mortality in *Montastraea annularis*, whereas anthropogenic dissolved organic carbon kills corals directly (Kuntz et al., 2005).

Overall, LBSP-related stresses (nutrients, sediment, toxins, and salinity) often act in concert rather than individually and are influenced by other biological (e.g., herbivory) and hydrological factors. Collectively, LBSP stresses are unlikely to produce extinction at a global scale; however, they may pose significant threats at local scales and reduce the resilience of corals to bleaching (Carilli et al., 2009a; Wooldridge, 2009b).

Collection/Trade: *Montastraea annularis* complex species have a very low occurrence in the CITES trade databases (CITES, 2010). Hence, collection/trade is not considered to be a significant threat to *Montastraea annularis* complex species.

6.5.3 *Montastraea annularis* Ellis and Solander, 1786

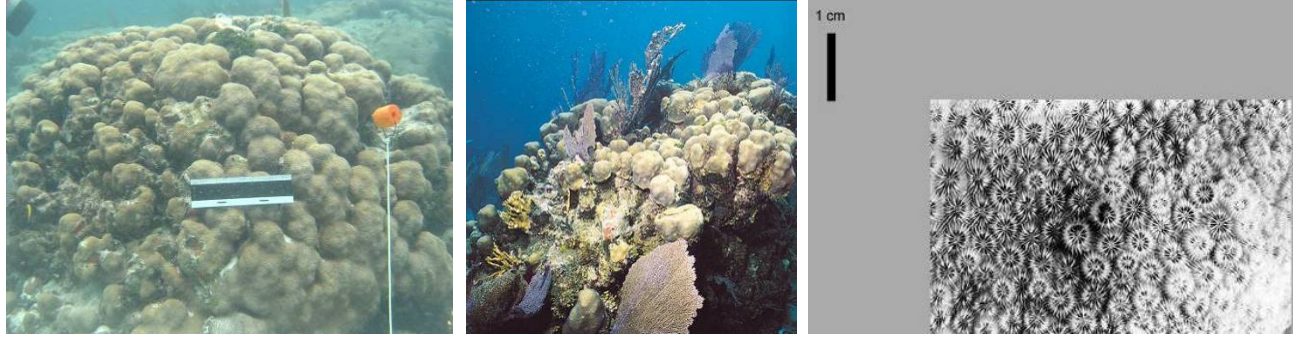


Figure 6.5.7. *Montastraea annularis sensu stricto* photo (middle) and corallite plan from Veron and Stafford-Smith (2002). Large colony photo (left) from NOAA Southeast Fisheries Science Center.

Characteristics

Montastraea annularis colonies grow in columns that exhibit rapid and regular upward growth. In contrast to the other species, margins on the sides of columns are typically senescent (Weil and Knowton, 1994). Live colony surfaces usually lack ridges or bumps. Corallites on tops of columns are closely packed, uniformly distributed, and evenly exsert, with maximum diameters of mature corallites typically 2.1–2.6 mm.

Taxonomy

Taxonomic issues: See Section 6.5: “Genus *Montastraea*.”

Family: Faviidae.

Evolutionary and geologic history: The *Montastraea* genus arose in the Oligocene ~ 30 Ma (Edinger and Risk, 1995).

Global Distribution

Montastraea annularis has a range restricted to the west Atlantic. It can be found throughout the Caribbean, Bahamas, and Flower Garden Banks (Veron, 2000, IUCN), but may be absent from Bermuda (Weil and Knowton, 1994). S. dePutron (Bermuda Institute of Ocean Sciences, St. George’s. pers. comm., May 2010) confirmed the presence of *Montastraea annularis* in Bermuda and categorized its abundance as rare; T. Murdoch (Bermuda Zoological Society, Flatts, pers. comm., May 2010) had not seen this species in Bermuda.

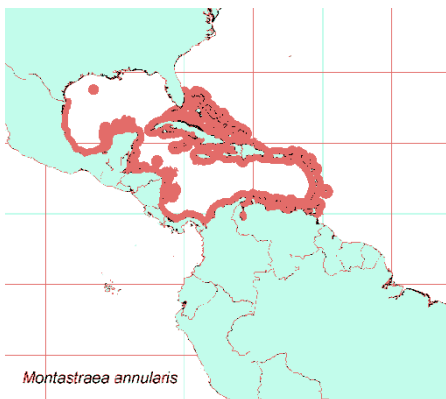


Figure 6.5.8. *Montastraea annularis* distribution from IUCN copied from <http://www.iucnredlist.org>.



Figure 6.5.9. *Montastraea annularis* distribution from Veron and Stafford-Smith (2002).

U.S. Distribution

Montastraea annularis is common throughout U.S. waters of the west Atlantic and greater Caribbean, including Florida and the Gulf of Mexico, within its range including federally protected waters in the following areas:

- Flower Garden Bank Sanctuary
- Dry Tortugas National Park
- Virgin Island National Park/Monument
- Biscayne National Park
- Florida Keys National Marine Sanctuary
- Navassa National Wildlife Refuge
- Buck Island Reef National Monument

Habitat

Habitat: *Montastraea annularis* is reported from most reef environments (Veron, 2000).

Depth range: *Montastraea annularis* has been reported in water depths ranging from 0.5 m to 20 m (Szmant et al., 1997); while *Montastraea* spp. are a common, often dominant component of Caribbean mesophotic reefs (Smith et al., 2010), suggesting the potential for deep refugia. However, *Montastraea annularis* sensu stricto is generally described with a shallower distribution (Szmant et al., 1997).

Abundance

Montastraea annularis has been reported to be common (Veron 2000). See Section 6.5: “Genus *Montastraea*.”

Life History

See Section 6.5: “Genus *Montastraea*.” *Montastraea annularis* is reported to have slightly smaller egg size and potentially smaller size/age at first reproduction than the other two members of the *Montastraea annularis* complex (reviewed in Szmant et al., 1997).

Threats

See Section 6.5: “Genus *Montastraea*.”