



Bonaire and Curaçao

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Abstract

Bonaire and Curaçao are oceanic islands surrounded by coral reefs on their leeward sides extending steeply down to mesophotic depths (30–150 m). Easy access from shore, as well as the geopolitical context of the two islands, has made the mesophotic coral ecosystems (MCEs) of Bonaire and Curaçao among the most well studied in the world. MCE research has been conducted in the region since the 1970s, and ongoing research employs state-of-the-art exploration technologies such as manned submersibles, autonomous underwater vehicles, and mixed-gas, rebreather technology. Mesophotic coral communities in Bonaire and Curaçao are typically dominated by agariciids, with *Agaricia lamarcki* and *A. grahamae* covering a substantial proportion of the substrate at upper mesophotic depths (30–60 m), while the lower meso-

photic (>60 m) consists predominantly of *A. grahamae* and *A. undata*. Although much of the habitat is dominated by sediment with only patchy coral growth, in some locations coral assemblages can cover up to 100% of the sea-floor down to depths of 70–85 m. Recent biodiversity studies, mostly focusing on fishes, sponges, and corals, documented only limited overlap between shallow and mesophotic reef communities, and that MCE biodiversity is strongly structured by depth. Since MCEs in Bonaire and Curaçao harbor highly specialized communities facing specific threats deriving from their proximity to urbanized land, these ecosystems warrant new management policies and conservation measures. These measures should protect the whole extent of these reefs, which rank among the healthiest in the Caribbean region.

Keywords

Mesophotic coral ecosystems · Dutch Caribbean · Caribbean Netherlands · Submersible · Pristine reefs

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9.1 Introduction

Bonaire and Curaçao are two neighboring oceanic islands in the southern Caribbean, located approximately 60 km north of Venezuela and 12° north of the equator (Fig. 9.1). After the dissolution of the Netherlands Antilles in 2010, Bonaire became a special municipality of the Netherlands, whereas Curaçao became a constituent country of the Kingdom of the Netherlands. Both islands are surrounded by narrow fringing reefs extending up to 300 m offshore. Mesophotic coral ecosystems (MCEs) on Bonaire and Curaçao can therefore be easily accessed directly from shore. This accessibility has contributed to some of the islands' MCEs being relatively well charted and studied; to date, more than 50 peer-reviewed publications have resulted from MCE research focused on Bonaire and Curaçao. This chapter provides a summary of what is known about the ecology, biodiversity, threats, and conservation of the MCEs fringing these islands.

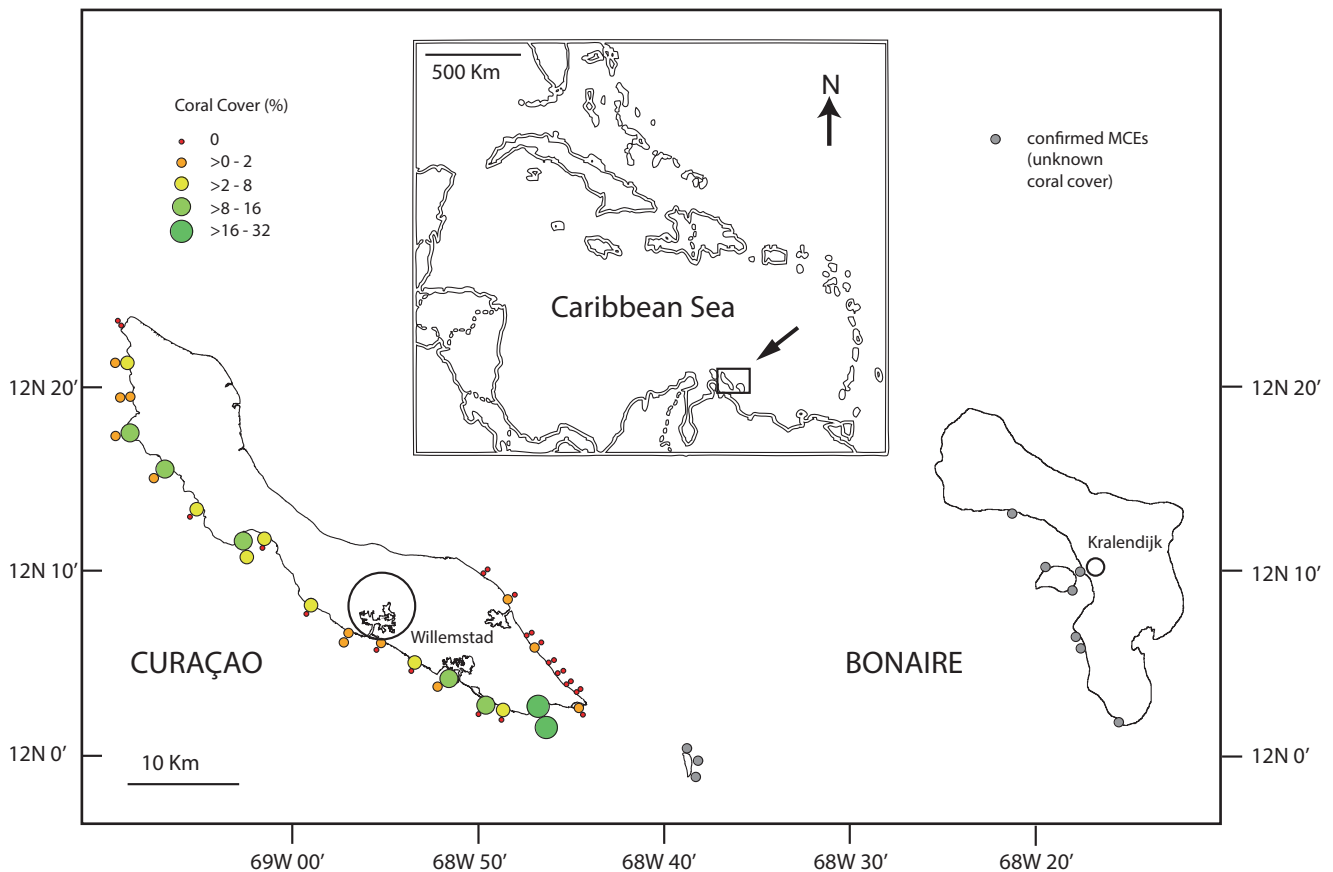


Fig. 9.1 Map of Bonaire and Curaçao (see inset for position within the Caribbean Sea) showing locations of confirmed MCEs. Colored circles represent the percentage coral cover for upper (30–60 m depth) and lower (>60 m depth) MCEs around Curaçao. Coral cover estimates were made from footage taken by a camera dropped down along a rope at 26 locations around Curaçao, with depth being determined by sonar (Waitt Institute and University of the Virgin Islands unpubl. data). The deepest observation was made at 111 m. For each location the closest circle to the shore represents upper MCEs, and the furthest represents lower MCEs ($n = 2-6$ per circle, except for a few locations along the north coast of the island, where $n = 1$). Gray circles represent confirmed occurrence of MCEs made by the authors. Around Bonaire, habitat available for potential MCE occurrence includes most of the leeward coast and parts of the southeast coast of the island

9.1.1 Research History

Research on Bonairean and Curaçaoan MCEs has contributed greatly to knowledge of Caribbean MCEs. Both islands as part of the Netherlands Antilles territory were visited by Europeans pioneering SCUBA diving, including deep diving, as early as the first half of the twentieth century. The history of underwater exploration in Curaçao and Bonaire therefore overlaps to a large degree with the history of diving and underwater photography itself. By the 1920s, a researcher from the University of Amsterdam (The Netherlands), van der Horst, had studied the shallow-water corals of Curaçao wearing only a diver's helmet (Roos 1964). Hans Hass, one of the earliest SCUBA diving pioneers, visited the islands in the late 1930s, where he took the first underwater photographs of sharks in the wild (Hass 1941).

The Caribbean Marine Biological Institute (CARMABI), later renamed to Caribbean Research and Management of Biodiversity, was founded on Curaçao in 1955. CARMABI

provided a base for natural science research in the Netherlands Antilles, especially on Curaçao, and is still active today. With the establishment of STINAPA (Netherlands Antilles National Park Foundation) in 1962, parks on all islands of the Netherlands Antilles could be managed. With the creation of the Bonaire National Marine Park (BNMP) in 1979, shallow and upper mesophotic reefs on Bonaire (down to 60 m depth) became effectively protected. The BNMP was one of the first marine protected areas worldwide to specifically incorporate MCEs, and this long-term protection is widely regarded as a primary reason for the high abundance of coral reef fishes on Bonaire (Jackson et al. 2014; Steneck et al. 2015).

The ecology of coral reefs was still rarely considered during scientific research on Curaçao and Bonaire until the 1970s and was restricted to the shallowest 20 m of the reef (Scheer 1960; Roos 1964, 1971). In 1970, the creation of a new science program focused on coral reef studies, led by Rolf Bak at the CARMABI Foundation in Curaçao and

sponsored by Dutch Academia, resulted in a large increase in reef research and the first studies of the Netherlands Antilles MCEs (Bak 1975, 1977; Bak and Luckhurst 1980). This early work focused on the growth and morphological variation of mesophotic corals, changes in community composition across large depth gradients, and the regeneration capacity of corals. Through this scientific program, CARMABI hosted a growing number of international researchers, such as Thomas Goreau's group in 1969 (Rolf Bak, pers. obs.). This initial interest in the ecology and biodiversity of MCEs quickly attracted other scientists working on organismal groups other than corals, such as algae (van den Hoek et al. 1978). From the 1980s onwards, graduate students from universities in The Netherlands and elsewhere have further contributed to MCE research, especially upper MCEs (30–60 m). This research often included comparisons of community structure across depths for various taxonomic groups including algae (Nugues and Bak 2008), corals (van Duyl 1985; Diekmann et al. 2002; Vermeij and Bak 2002), sponges (van Soest 1978; Kobluk and van Soest 1989; Meesters et al. 1991), mollusks (Potkamp et al. 2017), crustaceans (Snijders and Fransen 2010; van Tienderen and van der Meij 2016), fireworms (Wolf et al. 2014), and fish assemblages (Dorenbosch et al. 2004; Bohm and Hoeksema 2017). Recent research encompassing MCEs on Curaçao has focused on numerous topics including the evolutionary ecology of coral species complexes (Vermeij and Bak 2003), the functional diversity of coral symbionts (Frade et al. 2008a), and nutrient cycling (van Duyl and Gast 2001), and also the biodiversity, taxonomy, and ecology of reef fish assemblages (Pinheiro et al. 2016; Tornabene and Baldwin 2017). Rolf Bak's ongoing work (early 1970s to the present) on monitoring community changes through time, including upper MCEs (30–40 m) on Bonaire and Curaçao, has resulted in the longest coral reef time-series dataset in the world (Bak and Luckhurst 1980; Bak and Nieuwland 1995; Bak et al. 2005; de Bakker et al. 2016).

State-of-the-art deep-reef exploration technologies are revealing the secrets of MCEs in Bonaire and Curaçao. At the end of the 2000s, Bonaire's MCEs were surveyed by a pioneering US National Oceanic and Atmospheric Administration (NOAA)-sponsored expedition using multiple autonomous underwater vehicles (AUVs) that aimed to understand the reasons for the presence of the "most pristine coral reefs in the Caribbean" around the island (NOAA 2008). Research using AUVs is ongoing on the MCEs of Bonaire, focusing on geoacoustic data as proxy to estimate habitat features such as hard coral cover (Trembanis et al. 2017). These data are providing a useful new tool to quantify the extent of MCEs and to monitor future changes to these systems at large spatial scales (Fig. 9.2). In addition, the recent establishment of a manned submersible station at the Curaçao Sea Aquarium, Substation Curaçao, in 2010 has

brought new possibilities for the investigation of MCEs (Bongaerts et al. 2015b). Operated independently or in conjunction with its mother ship, the RV *Chapman*, the *Curasub* submersible (Fig. 9.3) provides a unique platform to access reefs down to 300 m depth anywhere in the Caribbean (Becking and Meesters 2014). As the *Curasub* is equipped with a large viewport for conducting visual censuses and hydraulic arms that enable the capture of specimens, this has allowed for the collection of thousands of specimens and species/depth data records for mesophotic and deeper reefs. Working from the *Curasub*, researchers, especially from the Smithsonian Institution, have recently discovered numerous new species of fishes, crustaceans, mollusks, and sponges between depths of 70 and 300 m (Hoeksema et al. 2017b). Since 2012, Smithsonian scientists have been deploying and annually retrieving moored temperature loggers off Substation Curaçao (11 depths between 50 and 250 m), which is resulting in a unique dataset of temperature changes on a shallow-to-deep reef slope. Furthermore, they have expanded the global use of autonomous reef monitoring structures (ARMS, e.g., Knowlton et al. 2010) into the mesophotic zone at Curaçao using the *Curasub*.

9.2 Environmental Setting

Located within the Southern Caribbean Dry Zone, the islands of Bonaire (294 km²) and Curaçao (444 km²) experience a semiarid climate, with an average annual precipitation of less than 500 mm (Meteorological Department Curaçao 2017). The islands have distinguishable dry and rainy seasons (February–June and September–January, respectively), with sustained moderate to fresh easterly trade winds. Consequently, the eastern and northeastern coastlines are consistently exposed to wave heights of 2–3.5 m above sea level (van Duyl 1985), whereas the south, southwest, and west coasts are sheltered (waves <1 m). Surface seawater temperature around the islands averages ~27 °C, with an average of 25.9 °C in the coldest months (February–March) and 28.2 °C in the warmest months (September–October). The peripheral location of the islands within the Caribbean hurricane belt means the islands rarely experience severe storms (Meteorological Department Curaçao 2017).

Both Bonaire and Curaçao are surrounded by coral reefs on their leeward sides (Fig. 9.1). Reefs along the islands' windward shores are generally less developed (van Duyl 1985). According to a recent compilation of scientific literature on the state of Caribbean reefs, the islands' coral reefs rank among the best remaining in the region (Jackson et al. 2014). In particular, reefs along the non-inhabited sections of the islands remain in surprisingly good condition. Estimated coral cover for Curaçao's leeward coast averages ~16% according to a survey performed at a depth of about 10 m in

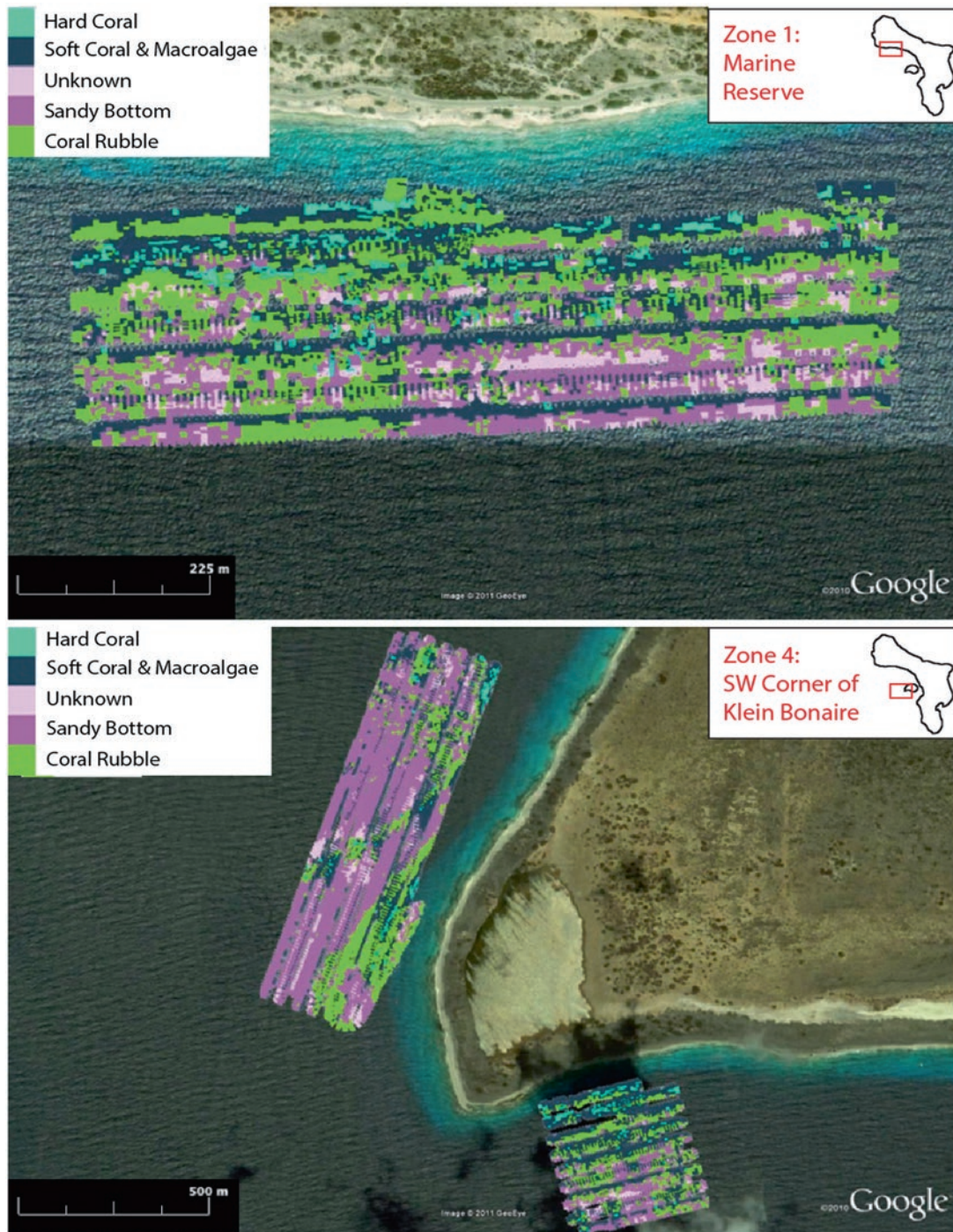


Fig. 9.2 Example of acoustic class maps highlighting patchiness of hard coral cover (turquoise color) on MCEs for two locations off Bonaire: the marine reserve and the southwest corner of Klein Bonaire. MCE substrates were geoaoustically inferred from data on depth, acoustic backscatter intensity, seafloor slope, and rugosity collected by an AUV. For further methodological description, see Trembanis et al. (2017). Stations in the marine reserve and the southwest corner of Klein Bonaire are part of zones 1 and 4, respectively, in the study of Trembanis et al. (2017). The primary zone of MCE occurrence is between 25 and 150 m depth

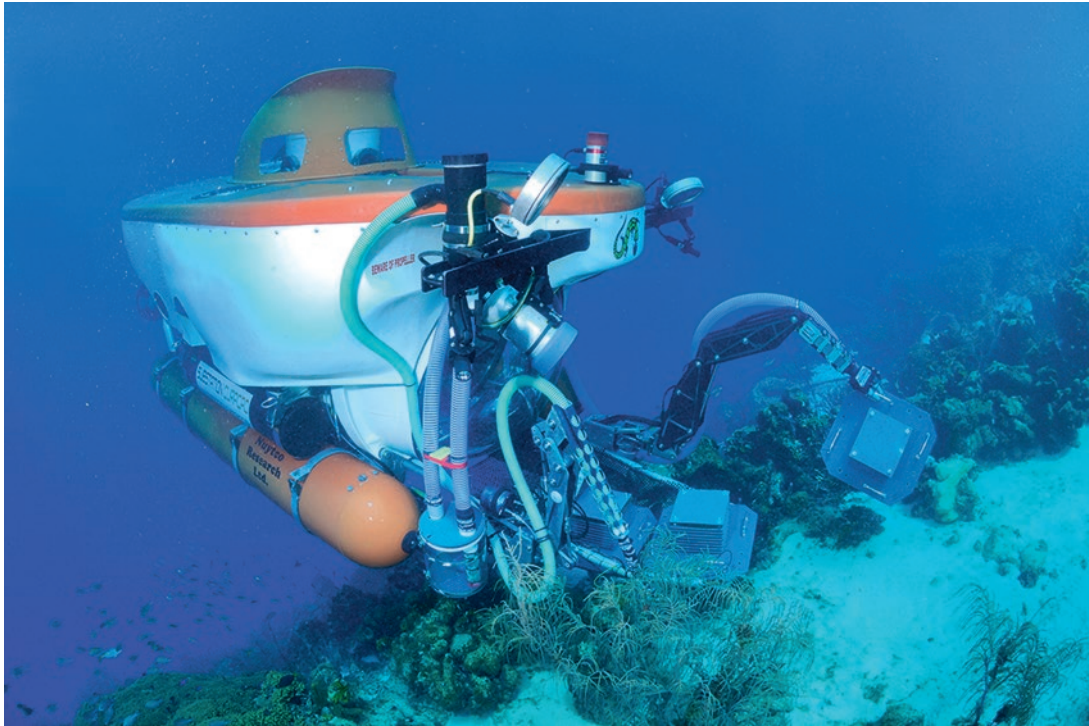


Fig. 9.3 The *Curasub* submersible uses its hydraulic arm to handle ARMS (autonomous reef monitoring structures) that will be deployed at several depths down the MCEs of Curaçao. Note presence of more ARMS on the *Curasub* front basket. ARMS are part of the Deep Reef Observation Project of the Smithsonian Institution. (Photo credit: ©Barry B. Brown, can be reused under the CC BY license)

2015 (Waitt Institute 2017). While this is substantially lower than the ~34% cover reported in the early 1980s (van Duyl 1985), some large stretches of coast reach an average coral cover of 20–30%, with a few individual sites standing above 40% (Waitt Institute 2017). For Bonaire, overall coral cover was recently reported to be 38%, the highest in the Caribbean (Steneck et al. 2015). However, more representative surveys undertaken in 2014 and spanning a broader extent of the leeward coast of Bonaire found only 19% average coral cover at about 10 m depth (Zanke and de Froe 2015).

A deep-water trench reaching depths of 4000–5000 m separates the islands from the South American mainland and from each other, and therefore the islands are strongly influenced by deep oceanic water. Both islands are affected by upwelling occurring along the coast of Venezuela, primarily between December and April due to the strengthening of the trade winds, as well as a mid-year upwelling during June–August (Rueda-Roa 2012). This upwelling causes the pulsed delivery of oceanic sub-thermocline water (Bak et al. 2005), as well as prolonged nutrient supply affecting the MCEs of Bonaire and Curaçao from December to August, with a peak in phytoplankton and bacterioplankton coastal biomass in spring (Gast et al. 1999; Lapointe and Mallin 2011).

9.3 Habitat Description

The leeward reefs around Bonaire and Curaçao have similar geomorphological features. The shore mostly consists of steep cliffs and rubble beaches resulting from long-term erosion on terraces formed during the Pleistocene due to substantial changes in sea level (de Buissonje 1974). From the shore, a 50–200 m wide, shallow reef flat with only scattered patchy coral communities gradually slopes to a drop-off starting at 7–15 m depth (Bak 1975). From here, the fore reef slopes steeply downward mostly at 30–40° but occasionally steeper (van Duyl 1985). In most locations, the first drop-off turns into a sandy terrace around 50–60 m that gently slopes to deeper water until a second drop-off at around 80–90 m. In other places, this terrace may be absent, and the seafloor consists of a single steep slope down to the second drop-off (Bongaerts et al. 2015b). Observations taken for the MCEs off Bonaire have revealed that leeward reef slopes sometimes have a minor secondary break at 50 m (Trembanis et al. 2017).

The windward eastern and northern shores usually exhibit gentle slopes, which adjoin a sandy terrace at 40 m depth (Bak 1977). Reefs here are generally poorly developed but may exhibit locally well-developed coral communities interspersed with dominant organisms such as crustose coralline algae,

Sargassum, and gorgonians (van Duyl 1985; Sommer et al. 2011; Waitt Institute 2017). Otherwise, *Sargassum* dominates most of the windward shore communities. The southeast of Bonaire is an exception and presents well-developed coral reefs similar to those of the leeward coast along about one-third of the island's latitudinal range. The central east and north coasts of Bonaire are thought to have supported well-developed reefs that were impacted by severe strong wave events up to 4200 years ago, culminating in substantial onshore deposits of coral reef fragments (Scheffers et al. 2006).

On both islands, the leeward shore was formerly characterized by dense shallow coral communities dominated by *Acropora palmata*, *A. cervicornis*, and gorgonians, in addition to the typical *Orbicella annularis* (Hass 1941; Bak 1975, 1977). However, the *Acropora* communities were severely affected by white band disease from the late 1970s to the mid-1980s (Aronson and Precht 2001), and at Bonaire hurricanes, Lenny (in 1999) and Omar (in 2008) caused near complete obliteration of coral in some restricted areas (IUCN 2011). In general, coral cover and diversity along the leeward coasts increases from the high-water mark toward the first drop-off, where the habitat changes from a sandy bottom to a consolidated reef of Pleistocene limestone rock covered by sand, coral rubble, turf algae, gorgonians, and living stony corals. This shallow-water coral community is currently dominated by *Madracis mirabilis*, *Orbicella faveolata*, *O. annularis*, and *Agaricia agaricites* (Bak 1975; Waitt Institute

2017). Coral cover and diversity remain relatively high after crossing the drop-off down to mesophotic depths (below 30 m), after which both decrease to around 80 m where coral cover becomes sparse. Recent surveys showed coral cover ranging between 9% and 13% on the shallow reef down to 40 m depth (de Bakker et al. 2016). However, most of the surveyed substrate across mesophotic depths is covered by sediment (Bongaerts et al. 2013, 2015b), which probably limits the formation of mesophotic reef communities (Bak 1977). Sediment beds are interrupted by patches of hard substrate harboring sparse communities of corals, although these communities can become locally dominant (Fig. 9.4). Toward deeper parts of the mesophotic zone, light-dependent corals are gradually replaced by azooxanthellate corals, stylasterids, and sponges, as well as coralline-, turf- and macroalgae (Bak 1975; van den Hoek et al. 1978).

Unpublished data collected in 2015 by the Waitt Institute and the University of the Virgin Islands (Fig. 9.1) provides a first impression of the spatial variation in coral cover for the MCEs of Curaçao. This data covers 26 sites along the leeward coast and the easternmost third of the windward coast, where mesophotic communities potentially occur. Results highlight that MCEs potentially cover large areas of the reef slopes surrounding Curaçao and that some communities are relatively well developed. Several locations exhibited coral cover above 8%, particularly in the upper mesophotic (30–60 m). Coral cover becomes low or absent at lower mesophotic depths



Fig. 9.4 Diver hovering over mesophotic *Agaricia* beds on the leeward shore of Bonaire (Karpata) at 40 m depth. (Photo credit: ©Pim Bongaerts, can be reused under the CC BY license-NC 4.0)

(>60 m), with only 2 out of the 26 surveyed locations showing coral cover >2%. Recent reports of up to 100% coral cover on a leeward location between depths of 70 and 85 m (Hoeksema et al. 2017a), however, highlight the need for extensive surveys to be undertaken to capture the patchy distribution of MCEs. This is particularly relevant for Bonaire, for which the available information on mesophotic coral cover is still scarce (Becking and Meesters 2014). Interestingly, recent AUV-based surveys described in Trembanis et al. (2017) have generated yet unpublished detailed data, with unprecedented spatial resolution on substrate cover for the leeward coast of Bonaire (see Fig. 9.2 with two examples of available datasets). Overall, mesophotic coral cover along this coast decreases with depth for all sites combined, with 7.7% at 25–50 m, 5.1% at 50–75 m, 5.2% at 75–100 m, and 4.7% at 100–125 m depth (Trembanis unpubl. data). This data and the acoustic class maps generated (Fig. 9.2) clearly show that developed MCEs exist as rather patchy occurrences reaching high percentages of coral cover locally.

9.4 Biodiversity

9.4.1 Macroalgae

The MCEs of Bonaire and Curaçao are dominated by *Lobophora*, which has been increasing in abundance in recent decades (de Ruyter van Steveninck and Breeman 1987), and other macroalgae such as *Halimeda*, *Dictyota*, or *Sargassum* (van den Hoek et al. 1978; Nugues and Bak 2008). Algal abundance is generally low when compared to other locations in the Caribbean, likely a result of grazing by a relatively well-developed herbivore community (Waitt Institute 2017). Spatial variation in algal abundance has been registered for the MCEs of Bonaire and Curaçao over the last few decades (de Bakker et al. 2017).

9.4.2 Anthozoans

Of the 65 species of scleractinian corals currently recognized for Bonaire and Curaçao (IUCN 2011), approximately 25 species are found in the upper mesophotic zone (30–60 m), down to approximately 7 at 80–90 m depth (Bongaerts et al. 2015a, b; Vermeij and Bak 2003). Coral communities on Bonaire's and Curaçao's MCEs are typically dominated by agariciids (Goreau and Goreau 1973; Bak et al. 2005; Bongaerts et al. 2013), which are efficient at capturing light in low-light environments (Titlyanov 1981). In particular, the depth-generalist *Agaricia lamarcki* and deep-specialist *A. grahamae* (Bongaerts et al. 2010, 2013) comprise a substantial proportion of hard substrate communities at upper mesophotic depths (30–60 m depth). Other species common in the shallows that also occur down to 80 m depth

are *Stephanocoenia intersepta*, *Montastraea cavernosa*, *Madracis pharensis*, and *Madracis senaria* (Bak 1975; Vermeij and Bak 2003; Bongaerts et al. 2013).

While the upper mesophotic zone supports many coral species found on shallow reefs that could be considered depth generalists (Bak 1977; Bongaerts et al. 2010), communities occurring deeper (>60 m) in the mesophotic zone (Fig. 9.4) consist predominantly of deep-water specialists such as *A. grahamae* and *A. undata* (Bongaerts et al. 2015b), although they can locally be outnumbered by other species such as *Madracis pharensis* (Bongaerts et al. 2015b). *Madracis formosa* and *Scolymia cubensis* are among other deep specialists that can be relatively abundant throughout the upper and lower mesophotic but never become dominant (Bak 1977; Bongaerts et al. 2010). Colonies of *A. grahamae/undata* can occupy up to 100% of the benthos in some locations in depths of 70–85 m (Hoeksema et al. 2017a). Such domination by corals at these depths has only rarely been observed elsewhere, such as at 70–90 m in Hawai'i (Kahng and Maragos 2006) and at Myrmidon Reef in the Great Barrier Reef (Hopley et al. 2007). At these depths, calcareous red algae often cover the underside of plating *A. grahamae*, resulting in a dark brown color at the center of the colony in comparison to a light brown toward the colony's edges (Hoeksema et al. 2017a). Solitary corals, although less conspicuous than their colonial counterparts, are also an important component of the mesophotic coral fauna. Species reported include *Caryophyllia* sp., *Balanophyllia* sp. or *Desmophyllum* sp., and *Phacelocyanthus flos*, which can establish extensive monospecific groups at 50–80 m (Vermeij et al. 2003; Becking and Meesters 2014).

9.4.3 Sponges

The sponge fauna of the MCEs of Bonaire and Curaçao is representative of mesophotic sponge assemblages in the Caribbean and generally dominated by glass sponges in the class Hexactinellida, as well as demosponge orders Astrophorida, Haplosclerida, and Halichondrida (Pomponi et al. 2001). This community had been relatively well surveyed by the end of the twentieth century via a submersible and SCUBA diving cruise by the Harbor Branch Oceanographic Institute (Reed and Pomponi 2001). However, a recent survey covering only four submersible dives off Bonaire and Curaçao to depths of 100–240 m found 13 species new to science out of a total of 31 species (van Soest et al. 2014), highlighting the need for further surveys in the region. Overall, the mesophotic sponge community of Bonaire and Curaçao is composed of members of the genera *Characella*, *Geodia*, *Caminus*, *Discodermia*, and *Pachastrella* (order Astrophorida); *Theonella*, *Corallistes*, *Aciculites*, *Gastrophanelia*, *Daedalopelta*, *Neopelta*, and *Leiodermatium* (order Lithistida); *Hamacantha*, *Antho*, and

Clathria (order Poecilosclerida); *Phakellia*, *Spongosorites*, *Topsentia*, and *Parahigginsia* (order Halichondrida); *Agelas* (order Agelasida); *Siphonodictyon*, *Neopetrosia*, and *Calyx* (order Haplosclerida); *Aplysilla* (order Dendroceratida); *Dactylocalyx*, *Cyrtaulon*, and *Verrucocoeloidea* (order Hexactinellida); and *Plakinastrella* (order Homosclerophorida) (Pomponi et al. 2001; van Soest et al. 2014). Interestingly, the MCE community shows little species overlap with the shallow-water community present in the same locations but a remarkable overlap with mesophotic sponge assemblages in other Caribbean regions (van Soest et al. 2014). This finding provides evidence that depth and habitat strongly influence the composition of sponge assemblages in the Caribbean.

9.4.4 Fishes

The establishment of Substation Curaçao, which operates the *Curasub* submersible, in 2010, has resulted in the mesophotic fish fauna off Curaçao being among the best known in

the world. Researchers with the Smithsonian Institution's Deep Reef Observation Project (DROP) have conducted over 100 dives on the *Curasub* to depths between ~40 and 300 m off Curaçao since 2011, as well as additional dives off Bonaire in 2013 and 2017. These efforts have resulted in the description of 13 new species of mesophotic or deeper cryptobenthic fishes (Fig. 9.5) and the discovery of at least 15 additional species currently awaiting description (Baldwin and Robertson 2013, 2014, 2015; Baldwin and Johnson 2014; Baldwin et al. 2016a, b; Tornabene et al. 2016a, b; Tornabene and Baldwin 2017).

The large number of new species discovered in a well-known vertebrate taxon highlights the substantial knowledge gap associated with deep-reef biodiversity and the need for focused exploratory research on deep reefs of the Caribbean and beyond. Data on fish assemblages also support the recognition of a unique faunal assemblage below the mesophotic, but above the deep aphotic zone, recently named the "rariphotic", which comprises species with evolutionary affinities to mesophotic and shallower faunas vs. deep-sea taxa (Baldwin et al. 2018). Recent phylogenetic analysis dis-

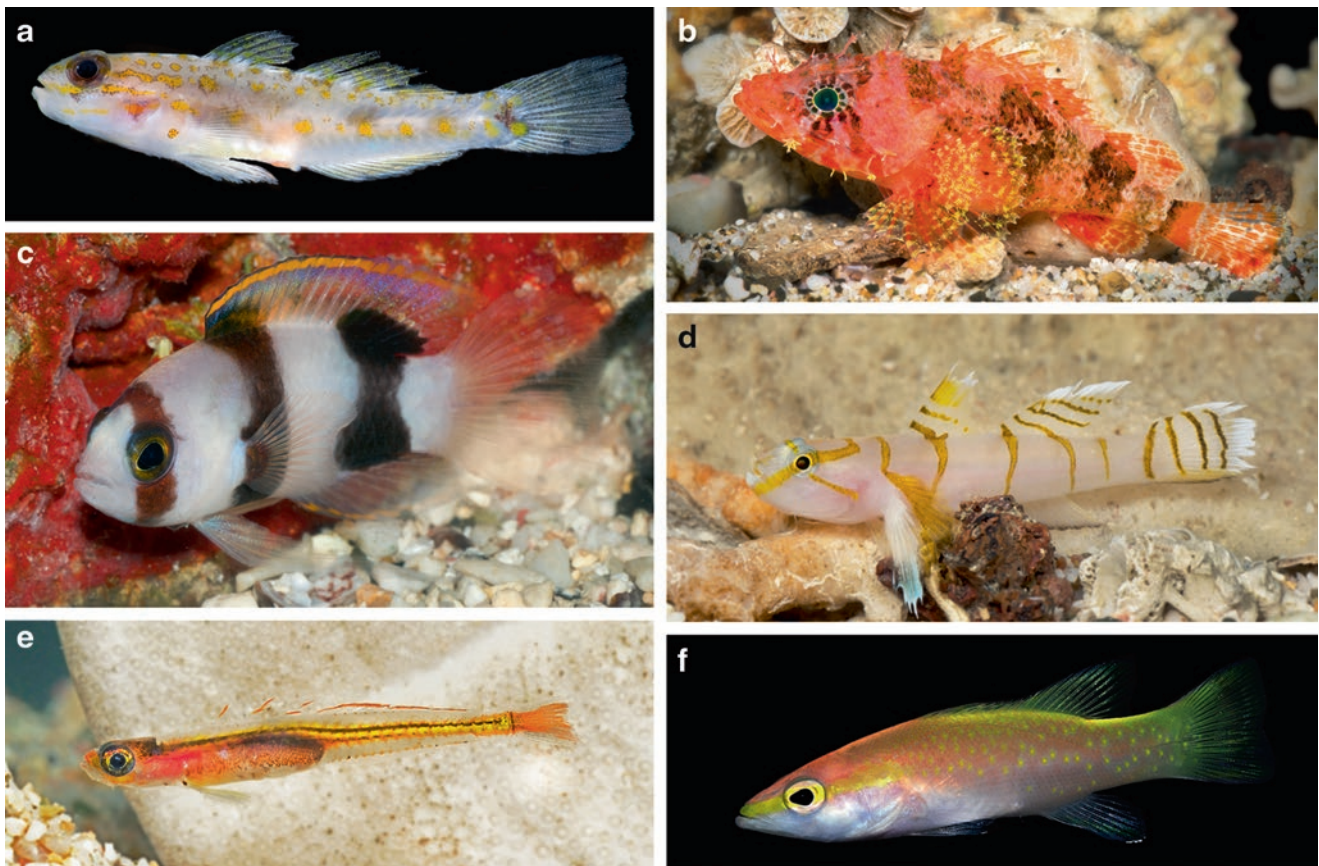


Fig. 9.5 Recently described species of cryptobenthic fishes discovered on MCEs off Bonaire and Curaçao using the *Curasub*. (a) *Coryphopterus curasub* (image from Baldwin and Robertson 2013); (b) *Scorpaenodes barrybrowni* (image from Baldwin et al. 2016a); (c) *Lipogramma levinsoni*; (d) *Psilotris laurae* (image from Tornabene et al. 2016a); (e) *Palatogobius incendius* (image from Tornabene and Baldwin 2017); (f) *Liopropoma olneyi* (image from Baldwin and Johnson 2014). (Photo credits: (a) Carole C. Baldwin, (c) Ross Robertson, and (b, d–f) ©Barry B. Brown; All images can be reused under the CC BY license)

covered that not only are some deep-reef goby species related to shallow-reef taxa but also represent recent (10–14 mya) evolutionary offshoots of shallow-reef lineages that have subsequently undergone radiation on deep reefs (Tornabene et al. 2016b). Understanding the evolution of deep-reef faunal communities will require similar phylogenetic efforts among other fish, invertebrate, and algal taxa. In addition to the Gobiidae, common mesophotic fish families off Curaçao include the Serranidae, Pomacentridae, Grammatidae, and Haemulidae. Invasive lionfish, *Pterois* sp., are also common inhabitants of mesophotic depths off Bonaire and Curaçao. Furthermore, MCEs appear to offer a refuge for invasive lionfish populations from culling-based control programs, which are mostly based at <30 m (Andradi-Brown et al. 2017). Tornabene and Baldwin (2017) documented the first record of lionfish preying on unknown biodiversity: a new species of *Palatogobius* goby, a tiny fish that schools in large numbers off Curaçao at depths of ~120 to 150 m.

Recent surveys of the fish fauna off Dominica and St. Eustatius conducted aboard the *Curasub* will enable comparisons among multiple Caribbean sites. Preliminary analysis of observation and catch data indicates that while much of the mesophotic fish fauna off Bonaire and Curaçao is widespread throughout the Caribbean, some cryptobenthic species may have much more restricted geographical distributions (Baldwin and Robertson 2013; Baldwin et al. 2016b). Results from underwater visual censuses conducted with mixed-gas, rebreather technology off Curaçao show differences in density, biomass, and richness of reef fish communities between upper (45–80 m) and lower (45–130 m) mesophotic reefs (Pinheiro et al. 2016). In particular, MCEs supported lower overall fish biomass than shallow reefs but a higher proportion of macro-carnivores and mobile invertebrate feeders (Pinheiro et al. 2016). All of the available data to date on Caribbean mesophotic fish communities suggest that depth and habitat are likely important drivers of fish diversity.

9.4.5 Other Biotic Components

Alongside recent discoveries of new species and hidden genetic diversity of sponges, fishes, and corals, knowledge of other taxonomic groups has also increased as a result of scientific exploration aboard the *Curasub*. Examples are the discovery of at least two new species of deep-living mollusks from 130 to 315 m depth (Harasewych 2014; Harasewych and Temkin 2015), several new genera of micropagurid hermit crabs (Lemaitre et al. 2017), and the second recorded species of echinoid-associated deep-water shrimp (Fransen 2014). Even though the Caribbean region is relatively well studied, much biodiversity remains to be discovered, particularly in mesophotic depths (Hoeksema et al. 2017b). Documenting the diversity and deciphering the function of

microbial communities within MCEs is a topic of growing interest, due to the role microbes are known to play in mediating ecosystem processes such as nutrient cycling. Over the last decade, studies on the microbial ecology of MCEs based on the reefs of Bonaire and Curaçao, focusing on both eukaryotic (Frade et al. 2008b; Bongaerts et al. 2015a) and prokaryotic symbionts of corals (Glasl et al. 2017), have been at the forefront of this research.

9.5 Ecology

Abiotic gradients in seawater temperature, water movement, and light attenuation have been quantified for only a few mesophotic locations along the south coast of Curaçao (Vermeij and Bak 2002, 2003; Bak et al. 2005; Frade et al. 2008b; Bongaerts et al. 2015b). This data paucity limits the capacity to make robust generalizations regarding environmental conditions on MCEs around the two islands. Once again, this stresses the need to further characterize the coastal oceanography of the islands and how this relates to the local distribution of MCEs. Nonetheless, these records provide valuable insight regarding the environmental conditions and their effects on ecological processes on MCEs.

Downwelling light (photosynthetically active radiation) decreases exponentially with depth at an attenuation coefficient (K_d) of 0.06–0.07 m^{-1} (Vermeij and Bak 2002; Frade et al. 2008b). Consequently, light irradiance declines to ~0.18 to 0.45% of surface irradiance at 90 m, the maximum depth at which zooxanthellate corals are generally observed on Curaçaoan reefs (Bongaerts et al. 2015b). Light availability at the lower limit of coral distribution on MCEs in Curaçao is therefore somewhat higher than the lowest values at which corals are known to survive in other locations (e.g., 0.007% of surface irradiance measured in Hawai'i; (Kahng et al. 2010), although *M. cavernosa* has been observed at 136 m (Mark Vermeij, pers. obs.). These records challenge the hypothesis that light is the only factor determining the lower limit of MCEs (Kahng et al. 2010) and suggest that other environmental factors such as temperature, substrate availability, food availability, and/or sedimentation (Bak 1977; Sheppard 1982) probably also limit the development of coral communities at depth.

Mean seawater temperatures for Curaçao (Fig. 9.6) vary less than 0.3 °C between 10, 25, and 40 m (27.6–27.9 °C) but decline linearly by 0.84 °C per 10 m depth increase between 40 and 100 m (Bongaerts et al. 2015b). Temperatures in the lower mesophotic (80–120 m) are substantially lower (~2 to 6 °C) than in shallow depths (10–40 m). For example, the annual mean temperature at 100 m depth is 22.8 °C, 5 °C lower than at 10–40 m (27.6–26.9 °C). Seasonal variation is also apparent, with seawater temperatures lowest between January and April and warmest from September to November (Bak et al. 2005; Frade et al. 2008b; Bongaerts et al. 2015b).

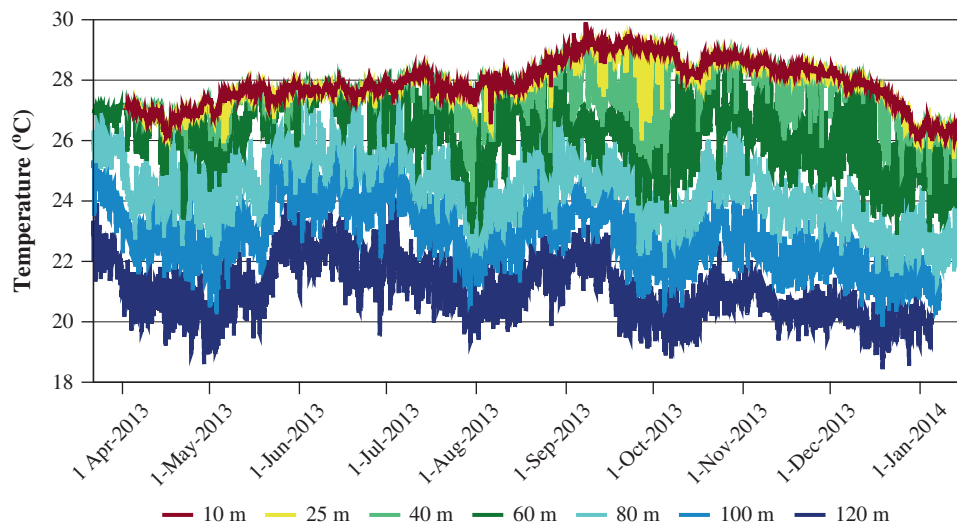


Fig. 9.6 Long-term temperature records registered at the leeward shore of Curaçao (Seaquarium reef) from mid-March 2013 to mid-January 2014 at depths ranging from 10 to 120 m. (Data published in Bongaerts et al. 2015b)

There are striking differences in the temperature gradient from 10 to 60 m throughout the year (Fig. 9.6), due to the upwelling system forcing the vertical structure of the water column in the region (Rueda-Roa 2012; Varela et al. 2015). In the spring (April–June), the relative subsidence of the upwelling system (Rueda-Roa 2012) results in a relatively small difference in temperature between the upper mesophotic zone and shallow reefs (Fig. 9.6). During the warmer half of the year (from August onward), as surface water warms up, stratification of the water column takes place. This culminates in the steepest depth-temperature gradient during late summer (>8 °C difference from surface to lower mesophotic in October), after which horizontal stratification in the upper mesophotic zone is gradually dissolved, and temperature differences between these depths are reduced (Bak et al. 2005). The winter months (December–April) are marked by decreasing temperatures coinciding with the upwelling season in the southern Caribbean (Varela et al. 2015). Rapid and frequent cold-water influxes which extend to upper mesophotic depths (40 m) are superimposed on this seasonal variation throughout the year. The time scales involved in these up- and downward movements of the thermocline correspond to those often associated with breaking internal waves, such as those described around Bonaire (Leichter et al. 2006). These cause drops of 1–3 °C within time intervals of 10–30 min leading to regular exposure to temperatures ~ 22 °C at upper mesophotic depths (Bongaerts et al. 2015b). Such a transient upwelling of sub-thermocline water masses would likely represent an important source of dissolved inorganic nutrients, zooplankton, and suspended particles but could also have negative effects on MCEs. Unusually low temperatures at upper mesophotic depths such as those reported here have been linked to deep-water bleaching of *Agaricia* colonies in Curaçao (Bak et al. 2005;

Nugues and Bak 2008) and Bonaire (Kobluk and Lysenko 1994), resulting in subsequent mortality of large numbers of *Agaricia* colonies. These observations demonstrate that occasional cold-water exposure can contribute to shaping mesophotic reef communities, leading to the hypothesis that temperature may play a stronger role than previously recognized in determining the lower depth limits of coral assemblages in Curaçao (Bongaerts et al. 2015b), either via a long-term control of coral community development or a short-term control through episodic cold-water anomalies (Kahng 2012).

Research on the drivers of genetic variation among coral populations across large depth gradients on Curaçao reefs has led to some insights as to whether (and to what degree) MCEs and shallow reef communities are connected genetically. In general, mesophotic communities show strong genetic differentiation among depths in both coral hosts and photosymbionts. Findings indicate limited connectivity between shallow and mesophotic habitats (Frade et al. 2008b; Bongaerts et al. 2015a), as well as between upper and lower mesophotic reefs (Bongaerts et al. 2015b). One clear conclusion from this research on Curaçao MCEs is that, rather than a marginal extension of the upper mesophotic reef community, the lower mesophotic represents a specialized community that warrants specific attention from science and management (Bongaerts et al. 2015b).

9.6 Threats and Conservation Issues

MCEs around Bonaire and Curaçao are located relatively close to shore (50–300 m) and are therefore influenced by coastal activities. Although reefs off Bonaire and Curaçao are often considered among the least degraded in the

Caribbean (Jackson et al. 2014), they have nonetheless experienced a chronic decline in water quality, the overexploitation of fish populations, unsustainable coastal development, and industrial waste issues (Siung-Chang 1997; Jackson et al. 2014). The negative effects of coastal activities on coral reefs are relatively less pronounced in areas free of coastal development than elsewhere along the coast (de Bakker et al. 2016). Local stressors, such as industrial pollution and overfishing, are particularly problematic around densely populated areas (Bak et al. 2005; Nugues and Bak 2008; de Bakker et al. 2016). Population centers on Bonaire and Curaçao are concentrated around the central, southwestern-facing leeward side of the islands, where most beach and tourism-related development occurs. However, the two islands present quite distinct scenarios due to quite distinct anthropogenic pressures and somewhat diverging environmental policies over the last 30–40 years.

The reefs around Bonaire were designated as a marine park, the BNMP, in 1979, and effective management began in 1991. The BNMP extends from the high-tide mark down to 60 m in depth, covering a substantial part of the MCEs surrounding the island. Furthermore, five sites of the international Ramsar Convention on Wetlands are recognized on the island, all of which include coastal sections bordered by more or less developed reef formations (Steneck et al. 2015). Bonaire currently depends substantially on sustainable tourism and diving visitors (TEEB Caribbean Netherlands 2001). Although remaining among the healthiest and most resilient in the Caribbean (IUCN 2011; Steneck et al. 2015), Bonairean reefs are still threatened by coastal development and artificial beach construction, as well as inappropriate sewage treatment facilities. There are population explosions of damselfish due to overfishing of predatory fish species, as well as an unprecedentedly high abundance of organisms overgrowing coral such as the colonial ascidian *Trididemnum* sp. and the brown algae *Lobophora* sp. (IUCN 2011), which directly threaten mesophotic coral communities. While *Trididemnum* has aggressively invaded Bonaire's shallow reefs (Sommer et al. 2010; Debrot et al. 2011) and spread down to the upper mesophotic zone (Bak et al. 1981), *Lobophora* has become increasingly dominant since the 1980s between 35 and 60 m throughout Bonaire (Vermeij 2011; de Bakker et al. 2017). The high availability of ammonium (NH_4^+) in Bonaire's coastal waters (Slijkerman et al. 2014) that results from the local salt industry (Lapointe and Mallin 2011), as well as the high NH_4^+ uptake capacity recently demonstrated by *Lobophora variegata* (den Haan et al. 2016), has been proposed as likely explanation for the dominance of *Lobophora* on upper mesophotic reefs in Bonaire (Vermeij 2011). Still, concrete evidence for a causal relationship implicating Bonaire's salt industry is lacking. Although Bonaire does not experience the intense fishing pressure that is common throughout the Caribbean,

predator populations continue to decline, and it is relevant to note that large groupers are absent from most of the island's reefs (Steneck et al. 2015).

While only 50% larger in area, Curaçao has an eight times larger human population than Bonaire (United Nations 2015) and relies more heavily on non-sustainable coastal development practices to support its economy (Waitt Institute 2017). An oil refinery has operated on the island for over a century, and the reefs are overfished as a result of uncontrolled past use of spear guns and gill nets and high general fishing pressure (van't Hof et al. 1995; Waitt Institute 2017). By the 1980s, there was already a marked difference in grouper populations between the reefs of Curaçao and Bonaire, with a lower abundance and smaller size of fish reported for Curaçao (LeLoup and van der Mark 1984). Activities related to coastal development, such as sewage discharge and (historic) industrial pollution, added to the decline of Curaçao's reefs. Sedimentation caused by coastal development and the maintenance of artificial beaches along the leeward coast of Curaçao has caused chronic stress to corals (Nagelkerken 2006; Waitt Institute 2017), in addition to acute stresses such as sediment "waterfalls" that can affect the mesophotic zone (Bongaerts et al. 2015b). Despite these impacts, reefs occur in a broad range of ecological states on Curaçao, ranging from degraded to those considered among the best in the Caribbean (Jackson et al. 2014; de Bakker et al. 2016). The more well-preserved reefs occur in the remote areas, such as "Oostpunt," the easternmost part of the island (Jackson et al. 2014). In 2013, four Ramsar sites were designated, of which three specifically protect the island's nearshore reefs.

Until the last decade, mesophotic coral communities on Bonaire and Curaçao were thought to have remained relatively stable since the early 1970s (Bak et al. 2005). However, a recent study has shown that communities in the upper mesophotic zone (30–40 m depth) have also suffered some degree of degradation, causing a decrease in coral cover over the last 40 years from 33 and 23% to 12 and 9.5% at 30 and 40 m depth, respectively (de Bakker et al. 2016, 2017). Coral loss in the mesophotic zone was primarily due to loss of agariciid species and was concomitant with a shift toward benthic cyanobacterial mats down to at least 40 m from the late 1990s (de Bakker et al. 2017). The increased presence of cyanobacterial mats on sandy bottoms is also reported for the deep slopes of Bonaire at depths of 45–90 m (Becking and Meesters 2014). These observations led to the debate around the direction of reef community shifts such as the ones reported for Curaçao from coral and crustose coralline algae toward turf- and macroalgae (Vermeij et al. 2010).

Currently, no targeted form of protection covers the lower MCEs (>60 m) of Bonaire and Curaçao. The plate-like coral colonies that dominate the lower mesophotic are highly susceptible to sedimentation and prone to direct physical disturbances (Bongaerts et al. 2015b; Hoeksema et al. 2017b). Catastrophic sedimentation, together with cold-water coral

bleaching, is among the potential major sources of coral mortality that can disrupt space monopolization of the mesophotic reef by agariciids (Bak et al. 2005). Although findings from a recent study on the growth rates of lower mesophotic agariciid communities have shown some potential for recovery following damage (Bongaerts et al. 2015b), these communities are already under threat. Recent dives aboard submersibles, both in Bonaire and Curaçao, have reported on relatively large amounts of human debris present on MCEs, ranging from car tires, discarded glass bottles, and cans to fishing anchors and lines (Becking and Meesters 2014; Debrot et al. 2014; Bongaerts et al. 2015b; Hoeksema et al. 2017b). Adequate protections should be provided to these hidden coral reefs as a means to protect their structural complexity and associated biodiversity, including the ecological and economic services they provide to the islands of Bonaire and Curaçao.

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