



# Disturbance in Mesophotic Coral Ecosystems and Linkages to Conservation and Management

# 47

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## Abstract

Disturbances are a natural part of the ecology of reef ecosystems including mesophotic coral ecosystems (MCEs). Storms, thermal stress, and volcanism are all documented as direct or indirect impacts on MCEs and have been shaping these systems for millennia. In general, anthropogenic disturbances are increasingly challenging community resistance and resilience and, in some cases, altering community composition. Potential anthropogenic disturbances to MCEs include the effects of climate change (warming waters, extreme temperature fluctuations, sea level rise, and increased intensity and frequency of storms), ocean acidification, physical impacts (marine debris, anchoring, benthic infrastructure, and other mechanical disturbances), harvesting for fisheries and the aquarium trade, impacts from coastal development (turbidity and sedimentation), pollution, invasive species introduction, and increases in disease outbreaks. Many of these disturbances are shown to impact MCEs, with subsequent degradation occurring just as these systems are coming into increasing scientific and management focus. Thermal stress and ocean acidification are suggested to pose the greatest existential threat to MCEs, while many local disturbances are amenable to local management strategies. Increasing knowledge of the distribution and structure of MCEs is a critical first step in management.

## Keywords

Mesophotic coral ecosystems · Bleaching · Marine pollution · Ocean acidification · Fishing

## 47.1 Introduction

Disturbance is a fundamental process shaping ecological systems including mesophotic coral ecosystems (MCEs). MCEs show high degrees of heterogeneity in community structure, sometimes on reef-to-reef scales within a region. Where requisite conditions are favorable for coral reef development, it is expected that MCEs will be present from 30 to 150 m (Hinderstein et al. 2010). These ecosystems can be dominated by stony corals, octocorals, gorgonians, sponges, and macroalgae (Bridge et al. 2011; Baker et al. 2016; Smith et al. 2016c). In some cases, disturbance may limit stony coral abundance and contribute to heterogeneity in regional community structure (Nyström and Folke 2001). Disturbance was defined by Battisti et al. (2016) as an “interference” that causes populations and communities to fall below a state of equilibrium and, potentially, to begin an exponential rate of regrowth to equilibrium. In their view, stress decreases population or community growth rate, but does not involve a change from equilibrium. Here, we consider stress as a part of disturbance, since sufficient stress can ultimately decrease population sizes. This chapter is focused on three key questions. How disturbance impacts MCEs? Are MCEs more or less resilient to disturbance than shallow reefs and how does this affect their ability to persist in the Anthropocene?

Natural disturbances have been shaping modern MCEs since the stabilization of sea level some 7000 years before present and likely had a major influence on the distribution of populations, abundance of species, and community composition in many MCEs. Understanding natural and anthropogenic disturbances is key to predicting where MCEs are most abundant, well-developed, and connected to shallow-

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water systems. There are differences in disturbance regimes across regions (latitude and ocean basin) and within regions (Nyström and Folke 2001) suggesting that different MCEs are under different disturbance regimes (type, magnitude, and frequency). For example, low latitude regions outside the tropical storm belts, such as Curaçao in the Caribbean Sea and Papua New Guinea in the Western Pacific Ocean, have MCEs that experience a lower frequency and magnitude of hurricane/cyclone disturbance. Within a region affected by hurricanes or cyclones, some MCEs may be more sheltered than others. Furthermore, anthropogenic disturbances have been increasing and are altering community structures, usually at the expense of structure-forming species that provide important ecosystem services (Holstein et al. 2019). Understanding anthropogenic disturbances on MCEs and how they interact with natural disturbance regimes is fundamental to improving the management and conservation of MCEs (Nyström et al. 2000).

There is a common view that remoteness and depth have limited disturbance in MCEs, yet disturbances still impact these systems and are likely very important to their ecology. The effect of disturbance on ecological communities is a function of the absolute *magnitude* of the disturbance and the *resilience* of the community in terms of *resistance* to the disturbance and its potential for *recovery* following the disturbance (Holling 1973; Battisti et al. 2016). For example, mechanical disturbance from the swell caused by a passing tropical storm is attenuated with depth (lowered magnitude), but the effect on MCEs could be large if the community is composed of fragile plating forms susceptible to breakage (low resistance) and with slow growth rates that limit the return to pre-disturbance abundance (low recovery). Together, these three factors are important to consider when evaluating how disturbance shapes MCEs (Nyström et al. 2000).

## 47.2 Natural Disturbances Affecting MCEs

Disturbance is a natural part of the ecology of coral reef ecosystems (Connell 1978). While natural and anthropogenic disturbances are often treated separately, disturbances that are considered “natural” may be accentuated or attenuated by anthropogenic processes (Paine et al. 1998; Nyström et al. 2000). One fundamental question of natural disturbance is how it shapes and keeps communities from achieving a hypothetical equilibrium or climax community. In some cases, the disturbance occurs with a return frequency that is faster than the rate at which the community can recover based on its resilience (Nyström et al. 2000). In this case, a community in a given area is defined by disturbance and will always be some iteration of the climax community, potentially in an exponential growth phase (Battisti et al. 2016). An example is an MCE that has the potential to be a well-developed stony coral habitat but is found to be a hard-

bottom habitat with a low abundance of stony corals and higher relative cover of other sessile organisms (see Smith et al. 2016c). Such a community may be structured by mechanical disturbance that limits the formation of complex reef. On the other hand, more infrequent disturbance may maintain a heterogeneous mix of habitats across the seascape at various states of recovery, with the potential for some patches to be at or near climax communities. An example might be where MCEs across a given region exist along a continuum of well-developed reef to hardbottom, with the disturbance history determining the spatial distribution of the patches.

### 47.2.1 Storms, Surface Waves, and Swell

Storms, surface waves, and swell generate benthic turbulence that can negatively impact MCEs (Hubbard 1992; Kobluk and Lysenko 1992; Aronson et al. 1994; Harmelin-Vivien 1994; Bongaerts et al. 2013; White et al. 2013; Colin 2016). As a rule, the absolute magnitude of benthic turbulence for surface waves decreases with depth as the energy is dissipated through the water column (Woodley et al. 1981). However, this does not mean that they have a small impact on MCEs. In addition, under global warming, tropical storms are predicted to increase in intensity, with a greater occurrence of Category 4 and 5 storms (Knutson et al. 2015), meaning impacts to MCEs will also increase. Storms can increase the magnitude of benthic orbital velocities from surface waves and also generate strong unidirectional benthic currents through wind and density-driven transport of massive volumes of water. Both of these forms of turbulence can directly and indirectly influence stony corals and other sessile organisms.

Surface waves are attenuated with depth linearly, which buffers the relative magnitude of the mechanical forces. However, large storm systems and swell from distant sources can cause sufficiently large orbital velocities that impact MCEs directly. For example, a tropical storm generating realistic wave heights of 7 m and surface periods of 13 s (Lugo-Fernández and Gravois 2010) could generate oscillating benthic currents with speeds greater than  $1 \text{ m s}^{-1}$  to about 47 m depth (Groves 2016; Smith et al. 2016c). Such velocities could directly dislodge colonies (Baldock et al. 2014), and this effect might be accentuated where colony growth forms are fragile, such as the thin plating and foliose forms common in MCEs (Done 1983; Lesser et al. 2010; Madin and Connolly 2006; White et al. 2017). These impacts are likely to be most severe and spatially widespread in shallower MCE environments (Bongaerts et al. 2013; White et al. 2013; Smith et al. 2016c). For example, Kobluk and Lysenko (1992) showed corals and sponges buried under rubble, covered in sand, and dead or dying on upper MCEs (30–37 m depth) in Bonaire, Dutch Caribbean, from the pas-

sage of two tropical storms (see Table 1 in Bongaerts et al. 2010). Much less is known about unidirectional current impacts in MCEs. However, unidirectional current impacts might be large, as Hubbard (1992) showed unidirectional currents of  $2 \text{ m s}^{-1}$  at 18.5 m depth in Salt River Canyon, St. Croix, during Hurricane Hugo (Hubbard 1989).

The indirect impacts of storms and swell on stony corals and other sessile organisms in MCEs can be severe and may be transferred into deeper depths, such as the lower mesophotic zone (>60 m depth). Increased benthic orbital velocities can liberate benthic sediments, increasing turbidity or causing direct smothering of coral colonies (Hubbard 1992; Kobluk and Lysenko 1992). However, benthic currents can also cause sediment and debris flows into deeper water on high-angle seafloors, which can smother or dislodge sessile organisms (Harmelin-Vivien 1994; Colin 2016). Overturning of sediments may also contribute to temporary eutrophication, increasing growth of algal and microbial communities (D'Angelo and Wiedenmann 2014). Colony breakage and sediment contact also have the ability to stimulate transmissible coral disease (Brandt et al. 2013), amplifying the negative impacts of storms.

### 47.2.2 Thermal Stress: Upwelling and Downwelling

MCEs are typically positioned below the upper mixed layer (UML), a region of homogenous water temperature and other oceanographic properties from the surface to the first thermocline (Leichter and Miller 1999). Water below the UML associated with thermoclines can benefit corals, possibly by providing heterotrophic food subsidies (Leichter and Genovese 2006) and relief from warmer temperatures (Wall et al. 2015). However, these waters can also have characteristics that might be inimical to coral survival, such as high nutrients (Leichter et al. 2003) and low temperatures (Kahng and Kelley 2007). Also, in regions where surface productivity is high, such as eastern ocean basins, water below the UML can have very low oxygen concentrations (Smith et al. 2014) and reduced aragonite saturation state (Manzello 2010). Thus, processes that bring these deeper waters in contact with mesophotic corals could cause stress or disturbance by limiting growth or causing direct mortality. Periodic upwelling along the thermocline can push sub thermocline water onto MCEs (Lesser et al. 2009), acting as a regular disturbance if the sub thermocline water has inimical characteristics. While this has not been demonstrated in MCEs, the negative effects on reef development can be inferred from studies in shallow water where low temperatures caused by internal waves limit coral development (Schmidt et al. 2012). In the eastern tropical Pacific, well-developed MCEs are restricted to offshore areas where the UML is deep but are sparse or absent in other areas influ-

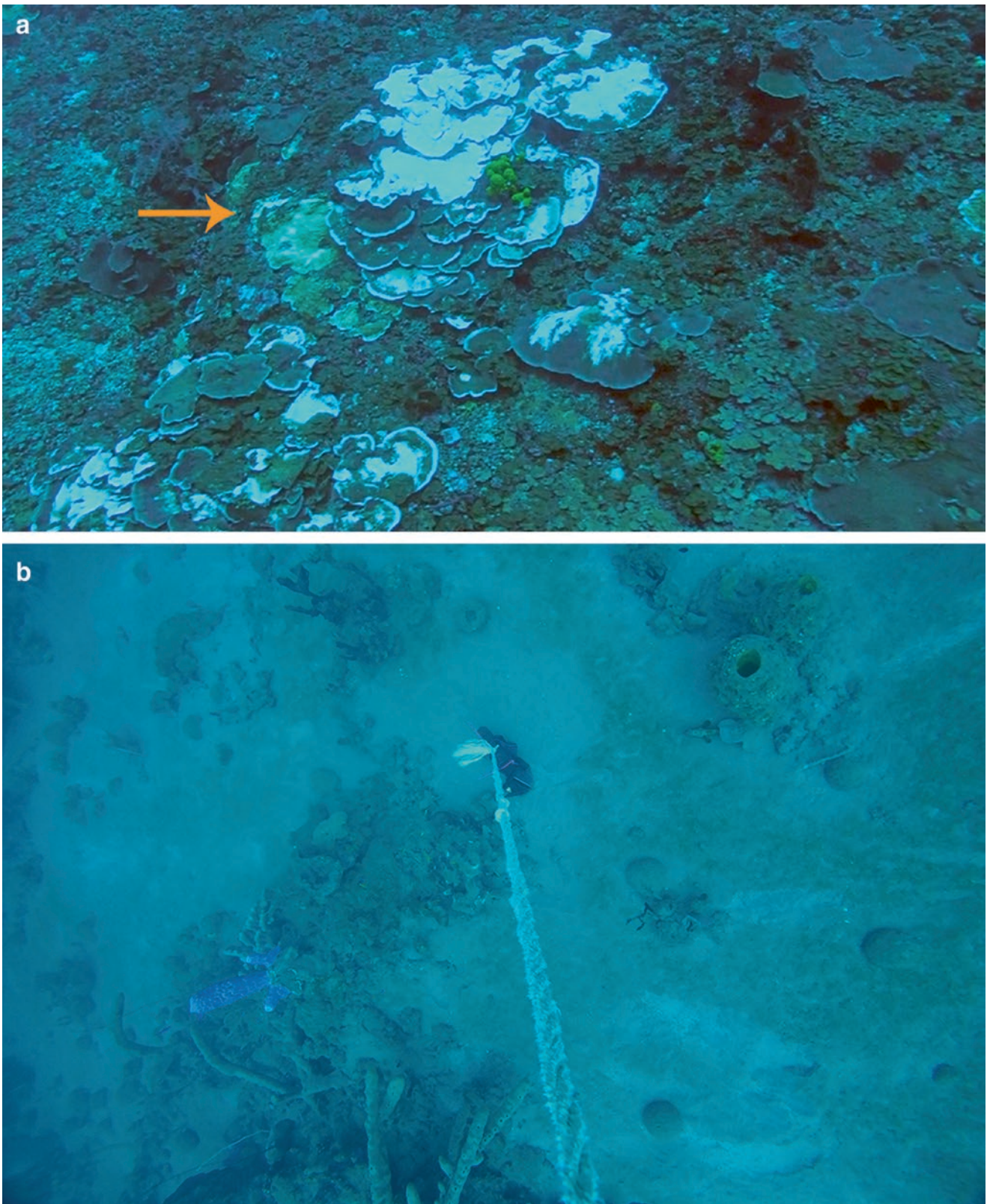
enced by water below the UML (Smith et al. 2017). Where deep water reaches the surface (e.g., the surface breaking of the  $20^\circ \text{C}$  isotherm) in continuous or seasonal upwelling areas, impacts on MCEs could be more severe. While the distribution of well-developed stony coral MCEs is still under-described, these habitats have not been reported from continuous and seasonal tropical upwelling areas where shallow-water coral reefs are present (e.g., the eastern tropical Pacific; Smith et al. 2017).

Downwelling of UML water onto MCEs can also act as a disturbance. Mesophotic corals that exist below the thermocline can have a lower bleaching threshold than shallow-water corals (Smith et al. 2016b). Thus, any deepening of the UML when sea surface temperatures are at their annual maximum could put mesophotic corals in water temperatures exceeding their bleaching thresholds. This happened in the US Virgin Islands in 2012, when a deepened UML exposed upper and lower mesophotic zone corals to anomalously warm sea surface temperatures and stimulated moderate bleaching (Fig. 47.1a; Smith et al. 2016b). Processes that cause a deepening of the UML include increased surface turbulence from storms or decreasing stratification caused by dense surface water, such as from high salinity.

### 47.2.3 Volcanism

Volcanism has the potential to disturb MCEs in a variety of direct and indirect ways. Lava flows and debris slides can cover MCEs causing direct damage from burial, breakage, and scouring (R. Pyle, pers. comm.) as has been shown in shallow-water coral reefs (Grigg and Maragos 1974; Tomascik et al. 1996). Ash deposition and smothering of corals have been particularly devastating to shallow-water corals surrounding active island volcanoes (Vroom and Zgliczynski 2011). However, corals growing on steeper slopes may be less impacted as ash retention is lower (Maniwavie et al. 2001). Thus, there may also be differences in impacts of ash deposition to low-angle (bank) and high-angle (slope and wall) MCEs. On the Caribbean island of Montserrat, recent volcanic activity appears to have deposited large quantities of ash on the low-angle mesophotic shelf (30–65 m) and may be contributing to depauperate MCEs (Fig. 47.1b; authors, unpub. data). Suspended ash can also cause severe increases in turbidity (Vroom and Zgliczynski 2011), which could be particularly harmful to light-limited MCEs. In addition, volcanism has a variety of indirect impacts such as the creation of unstable substrates that inhibit recovery (Tomascik et al. 1996) and promotion of species that compete with corals for space, possibly through iron enrichment (Schils 2012). Recovery to new or degraded substrata in shallow water can occur rapidly (~5 years) when coral diversity is high (e.g., Banda Islands, Indonesia; Tomascik et al. 1996) but may be delayed in less diverse





**Fig. 47.1** Natural disturbances affecting MCEs. (a) Bleached lower mesophotic corals (*Agaricia undata*) caused by a deepening UML and downwelling of warm surface water at 65 m depth, Ginsburg's Fringe, St. Thomas, US Virgin Islands, 21 February 2013. Orange arrow denotes recent mortality. (b) Volcanic sediments covering mesophotic depths off southeast Montserrat, British West Indies, 33.6 m depth, 20 July 2017. (Photo credits: (a) Tyler B. Smith and (b) Viktor Brandtneris)

systems under calm hydrological regimes (e.g., Hawai'i; Grigg and Maragos 1974). Recovery might be slow in MCEs where fast colonizing coral genera, such as *Acropora*, can be rare.

### 47.3 Anthropogenic Disturbances Affecting MCEs

MCEs are vulnerable to global and local anthropogenic disturbances. It has been suggested that MCEs may be refugia from many global and localized anthropogenic impacts (Bongaerts et al. 2010; Bridge et al. 2013; Bongaerts and Smith 2019). This buffering has both a depth and distance from shore component. However, some disturbances are depth-independent or increase with depth, and some MCEs are located close to shore putting them in contact with land-associated stressors (Appeldoorn et al. 2016). Further, as human pressure on coral reefs increase (Hughes et al. 2017), MCEs will be subject to more disturbances. The timing of increased disturbance will likely vary depending on ocean basin and the regional rates of warming, ocean acidification, and local human population growth. Thus, a general look at how different anthropogenic disturbances and stressors affect MCEs is warranted. The anthropogenic disturbances described herein we suggest are some of the most important for MCE ecology or are ubiquitous.

#### 47.3.1 Global Warming and Thermal Stress

Anthropogenic warming of the Earth's surface by the emission of greenhouse gases is increasing water temperatures around coral reefs (Heron et al. 2016). Periods of anomalously high temperatures during the warmest part of the year can stimulate coral bleaching (Figs. 47.1a and 47.2a, b) and mass mortalities and are considered one of the greatest existential threats to shallow-water coral reef ecosystems (Hoegh-Guldberg et al. 2007). For MCEs that are exposed to the UML during warm water temperature periods, their fate may be linked directly to shallow-water reefs. Since shallow-water corals and MCEs in this situation share similar temperature profiles, their thermal tolerance limits (bleaching thresholds) may be similar. Only factors that increase thermal tolerance might cause divergent stress responses, including heterotrophic subsidy (Grottoli et al. 2006; Anthony et al. 2007), high water flow (Nakamura and van Woesik 2001), and reduced light (Mumby et al. 2002). These factors may help ameliorate some thermal stress, but during extreme thermal tempera-

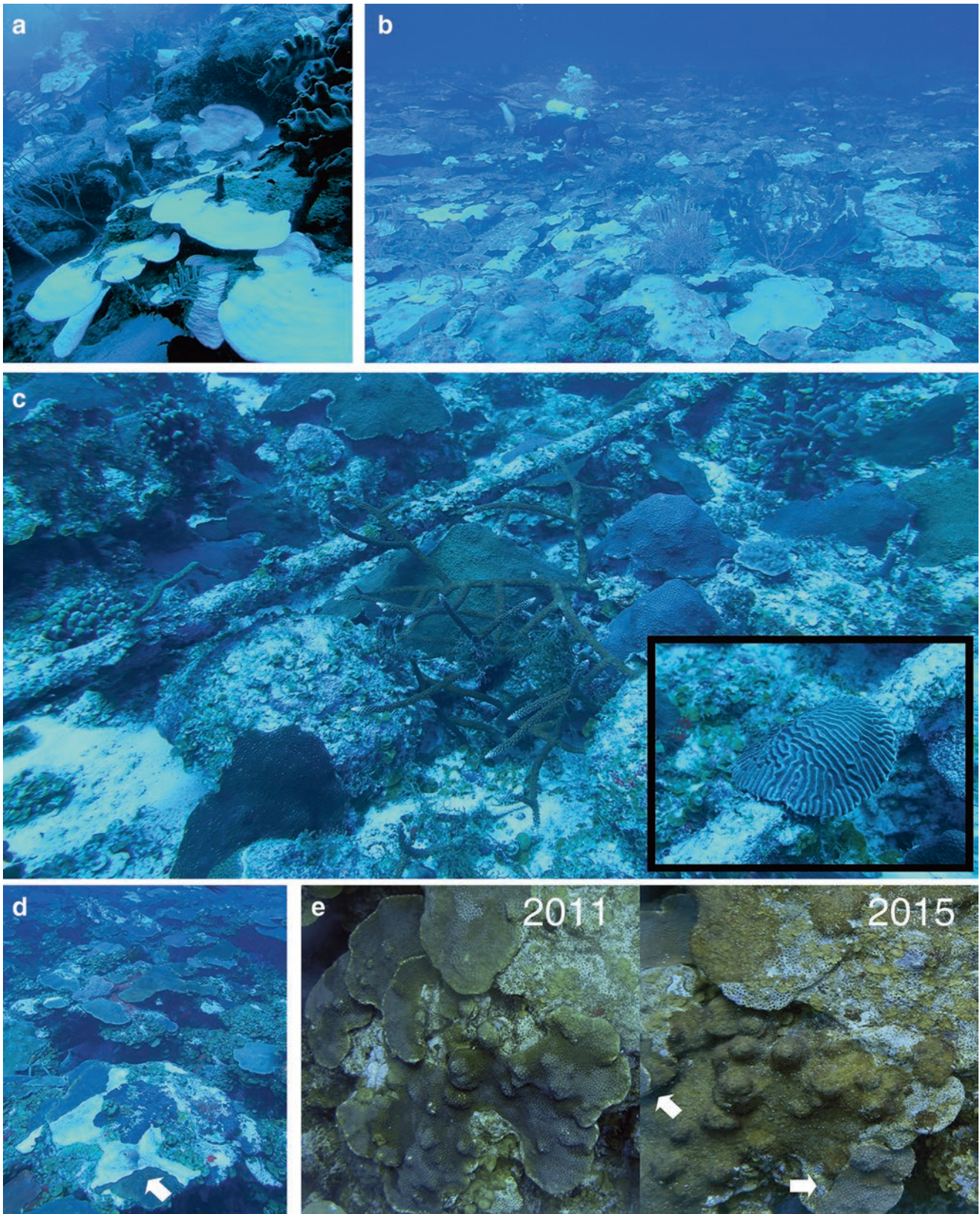
tures, these may be insufficient to prevent bleaching and coral mortality. In the US Virgin Islands, MCEs still bleached and suffered mortality despite the potential for heterotrophic subsidy, increased currents relative to shallow reefs, and decreased light intensity (Smith et al. 2016b; Fig. 47.2a, b).

Deeper light-dependent reefs, including MCEs, that are cooler than shallow reefs have been put forth as a potential refugia from human-induced climate change (Glynn 1996; Riegl and Piller 2003). However, it is not the relative difference of temperature between deep and shallow environments that determines if MCEs are refugia but maintenance of temperatures below stressful levels (e.g., +1 °C above the maximum monthly mean temperature; Smith et al. 2016b; Bongaerts and Smith 2019). The process(es) that moderate temperature may or may not be depth-dependent. Therefore, we suggest that most MCEs will become increasingly threatened by thermal disturbance as the Earth warms. If so, then thermal stress may be one of the most important anthropogenic disturbances affecting MCEs in the near future. In addition, basins with the highest rates of sea surface temperature warming will also be the areas predicted to have increasing occurrence of Category 4 and 5 cyclones by the end of the twenty-first century (Knutson et al. 2015). Thus, seawater warming will likely also increase storm impacts to coral reefs, compounding disturbances related directly to thermal stress.

#### 47.3.2 Ocean Acidification

Ocean acidification (OA) is a particularly broad threat facing all coral reef ecosystems (Hoegh-Guldberg et al. 2007). Research has not yet evaluated the specific effects on MCEs and hermatypic scleractinian corals. If similar to shallow-water reefs, as a result of OA, MCEs could see reductions in net community calcification (Albright et al. 2016), reductions in coral growth (Cerrano et al. 2013), and likely shifts to algae-dominated systems with a few resistant scleractinian taxa (Fabricius et al. 2011; Enochs et al. 2015). Studies at mesophotic Mediterranean vents (40 m depth) have shown shifts of sessile communities from calcifying (crustose coralline algae) to non-calcifying algae (kelps; Linares et al. 2015). Environmentally, waters at and below the thermocline can be enriched in carbon dioxide and organic acids and have lowered aragonite saturation states (Jiang et al. 2015). Thus, some MCEs may already be in conditions less favorable for maximum precipitation of aragonitic skeletons. It is not clear if changes in aragonite saturation state will occur more rapidly with depth and how OA might affect MCEs differently than shallow-water reefs.





**Fig. 47.2** Anthropogenic disturbances in MCEs from 30 to 40 m depth. (a) Thermal stress and bleaching on an upper mesophotic wall, Cane Bay, St. Croix, US Virgin Islands, 23 November 2005. (b) The early stages of bleaching of an upper mesophotic orbicellid bank, St. John, US Virgin Islands, 6 October 2005. (c) A cable laid across an upper mesophotic coral reef as part of benthic infrastructure, Sail Rock, St. Thomas, US Virgin Islands, 13 February 2017. Inset shows a settled stony coral colony of *Pseudodiploria strigosa* growing on the same cable. (d) A case of white plague disease affecting a colony of *Orbicella franksi* in an upper mesophotic reef, Hammerhead Shoal, St. Thomas, US Virgin Islands, 12 May 2017. A four-eye butterflyfish (*Chaetodon capistratus*) feeds on the disease margin noted by a white arrow. (e) The invasive algae *Ramicrusta* spp. growing a colony of *O. franksi*. The alga was not apparent on this colony in 2011 but appeared by 2014 and may have been responsible for coral partial mortality. It was overgrowing the margins of coral tissue in 2014 (arrows) and 2015 (not shown). (Photo credits: (a–c) Tyler B. Smith, (d) Viktor Brandtneris, and (e) Rosmin Ennis)



### 47.3.3 Pollution

Pollution from land and marine sources can directly and indirectly impact MCEs and cause disturbances. Sewage, toxins, and marine debris can be pumped or dumped directly into the marine environment or arrive as components of runoff from land.

*Waterborne Pollution* Reef corals and associated biota can be negatively impacted by nutrients derived from sewage and agriculture (Vega Thurber et al. 2013) and toxins from runoff, discharges, and port activities (Burke et al. 2011). Shifts between “normal” and perturbed microbial communities may also occur (Olson and Kellogg 2010).

MCEs may be buffered to some degree from pollution carried by runoff and deposited in the neritic marine environment because of their depth and distance from shore (Bridge et al. 2013). However, intentional point source discharges from municipal and industrial effluents may be specifically located at mesophotic depths. Since MCEs are often uncharted, deep effluents may be sited near them unintentionally. For instance, in North Sulawesi, Indonesia, a submarine tailings disposal pipeline from the Newmont Minahasa Raya gold mining operation discharged in 82 m depth about 900 m from shore, with the plume extending ~3 km beyond (Edinger 2012). The impacts on MCEs were not specifically studied, but tailings were found as shallow as 50 m depth in piles and in the reef at 20 m. The tailings contained mercury, arsenic, and antimony at elevated concentrations, and the mining operation resulted in fish kills, human health complaints, and the relocation of a nearby coastal village. Negative impacts to any MCEs present in the area must be inferred, but this study demonstrates the potential disturbance that can be caused by poorly sited effluents. It is likely that many MCEs have been damaged prior to characterization because of discharges placed at MCE depths (see Appeldoorn et al. 2016).

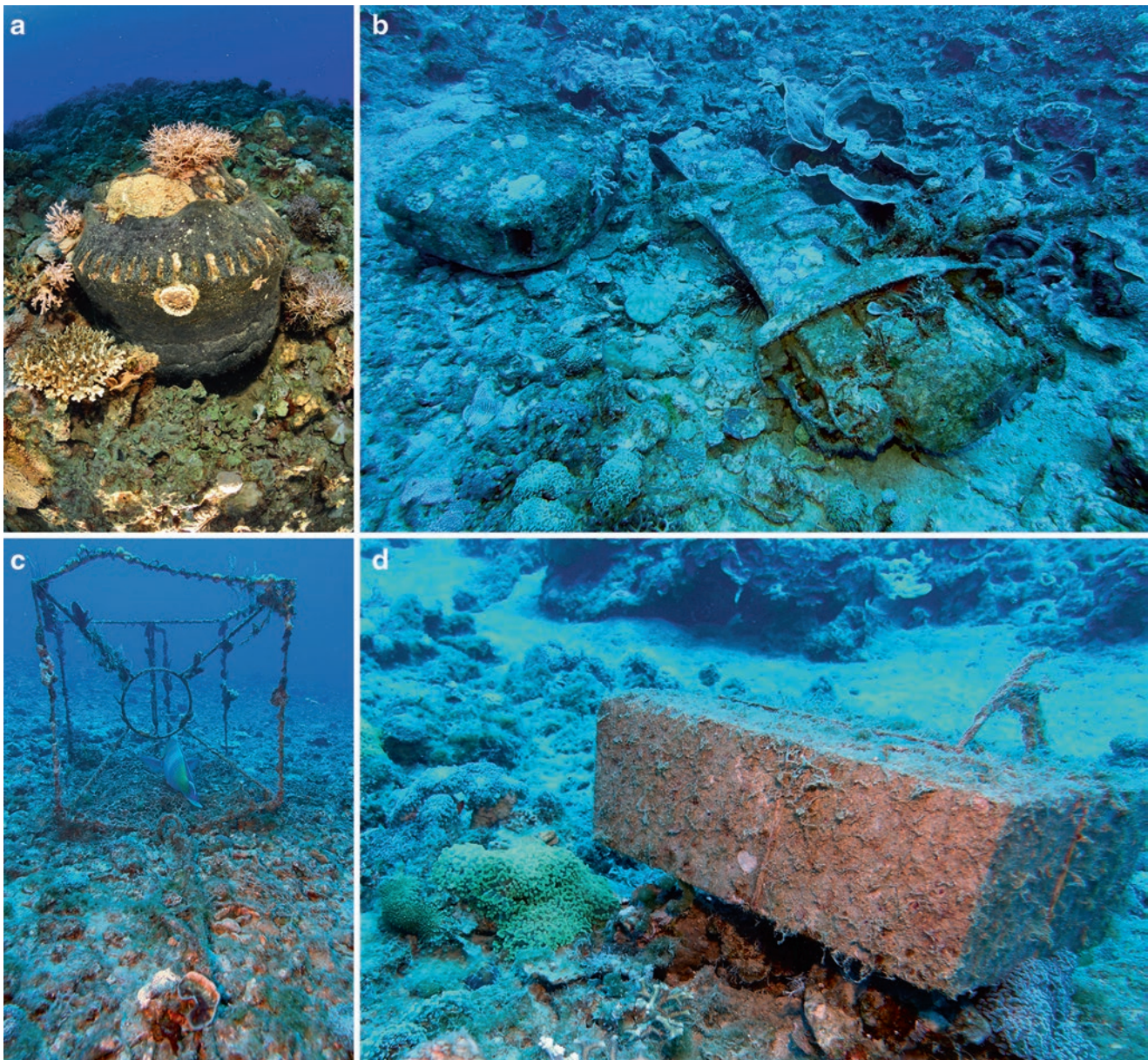
In addition, major accidental pollutant discharges and subsequent remediation techniques can impact MCEs. The 2010 Deepwater Horizon well oil spill and oil dispersant application in the northern Gulf of Mexico damaged gorgonian octocorals (Alcyonacea) in mesophotic depths (73 m) that were under the oil and dispersant slick for 10–60 days (Etoyner et al. 2016). Up to 50% of large gorgonians were affected within about 100 km of the well and were deemed unlikely to recover because of their continued degradation in health post-disturbance. Given negative impacts caused by oil on shallow-water scleractinian corals (Loya and Rinkevich 1980), scleractinians in MCEs could be similarly vulnerable.

*Marine Debris* MCEs near population centers can be impacted by marine debris by direct littering or disposal where people do not know that reefs are present or do not care or when materials are transported downslope and into MCE environments (Fig. 47.3a–d). The negative impacts of marine debris can come from physical injury, leaking of chemicals, and ingestion by organisms. Plastic debris can degrade in the marine environment to microplastics that negatively impact stony corals in a variety of ways and are becoming ubiquitous near large human populations and even in many remote areas of the Pacific (Lamb et al. 2018).

### 47.3.4 Sedimentation

Despite distance away from human activities, many MCEs are impacted naturally and anthropogenically by sedimentation, i.e., the deposition of sediments from the water column onto benthic surfaces. Sedimentation rates are artificially increased in the marine environment by a variety of means, including runoff from land, dredge dumping, and alterations to water flow that change natural sedimentation patterns. While sediment burial from any source can be detrimental to living coral tissue, terrigenous sediments have been found to be particularly harmful. Deposition of fine-grained (silt-clay fraction) sediments of terrestrial origin supports higher microbial activity and compacts on coral surfaces creating anoxic zones that lead to tissue death (Weber et al. 2006, 2012). MCE bank systems that are offshore see almost no sediment flux (Smith et al. 2008, 2010), and the flux is nearly all of marine origin (Weinstein et al. 2015). Therefore, these MCEs may not be impacted by sediment disturbance. On the other hand, in many natural steep slope systems, sediments control the geomorphology of reef construction, by creating sediment channels that transport biogenic and terrestrial sediments from the upper reef to off shelf (Hubbard 1986, 1989, 1992). In these environments, contact with terrestrial sediments may act as a disturbance.

MCEs adjacent to high islands or mountainous continental shelves may also be vulnerable to increased runoff of sediments. Appeldoorn et al. (2016) studied a site off Ponce, Puerto Rico, that was impacted by sediment runoff and dredge spoil dumping for port maintenance. Compared with a reference site, the authors found an increase of 16 times the sedimentation rate, with benthic sediment coverage that contained two to three times the terrigenous content and a higher proportion of fine-grained silt-clay sediments. In the impacted zone, there were no corals in MCE depths and sparse living benthic cover, whereas adjacent sites had stony corals in MCEs, suggesting that sedimentation had greatly impacted living benthic cover.



**Fig. 47.3** Marine debris in MCEs of Eilat, Israel, Red Sea. (a) Tire colonized by stony corals, 36 m depth, 9 November 2011. (b) An outboard boat motor, 42 m depth, 19 May 2015. (c) A lost fish trap, 46 m depth, 19 May 2015. (d) Cement block used as an anchor, 45 m depth, 19 May 2015. (Photo credits: Gal Eyal)

#### 47.3.5 Turbidity and Light Penetration

MCEs are generally light-limited systems (Lesser et al. 2009) and, thus, may be extremely vulnerable to reductions in light as a consequence of increased turbidity or rising sea level. At the deepest extent of their ranges, many stony coral species may be near their lower light limit, although many MCEs exhibit adaptations for efficient light capture (Kahng et al. 2010, 2012, 2019). Human activities that increase water column turbidity include sediment runoff and dredge dumping (suspended sediment) and increased nutrient pollution

that increases the abundance of phytoplankton and zooplankton (Furnas et al. 2005). Long periods where light penetration is decreased (higher attenuation coefficients) could lead to light limitation of phototrophic corals, with concomitant partial bleaching and mortality (Bessell-Browne et al. 2017). The light field at any depth is the sum of the attenuation properties of all of the water layers above it. Therefore, MCEs could be vulnerable to any small layer with a very high attenuation (e.g., a layer of turbid water associated with a muddy riverine discharge) or a small attenuation distributed across the whole water column (e.g., increased phytoplankton



concentrations throughout the UML). Light limitation as a disturbance in MCEs has not been well studied because time series of photosynthetically active radiation and spectral quality are challenging at MCE depths. However, this is likely to be a fruitful area of research, and setting light penetration standards for water quality could improve resource management where anthropogenic activities impact water clarity.

### 47.3.6 Benthic Infrastructure

Industrial infrastructure that is laid across the seafloor or built upon the seafloor could impact MCEs. In particular, cables and pipes used for energy, material, and data transfer are employed worldwide and in areas with MCEs. The initial emplacement and settling of cables could directly damage and kill habitat-forming corals and other sessile organisms, and maintenance activities where the cables are retrieved and replaced on the bottom could further these impacts. However, once settled and secure on the seafloor, cables can become part of the reef structure and are colonized by sessile organisms (Fig. 47.2c). In the US Virgin Islands, fiber optic and electrical cables are commonly laid across orbicellid coral banks in mesophotic depths (Fig. 47.2c), although greater care has been applied to installation of benthic infrastructure in recent years as the characterization of MCEs has increased. For example, a very large benthic mooring to support gas containership lightering was carefully sited in depths of 40 m south of St. Thomas, US Virgin Islands, by remotely operated vehicle (ROV) and technical divers to avoid living coral frameworks (authors, unpub. data).

### 47.3.7 Mechanical Disturbance

There is a great potential for MCEs to be damaged by mechanical disturbance, which causes the physical displacement and movement of corals. Since MCEs are underdescribed, their presence is poorly known to society, and activities such as anchoring in mesophotic depths may be considered non-detrimental. At the same time, many plating colony morphologies particularly common in MCEs are susceptible to breakage. Fishing gear (e.g., nets, traps, and lines) are commonly entangled and abandoned in MCEs (Fig. 47.4a–c). This debris can be detrimental to the reef, and it is also indicative of gear that regularly comes in contact with MCEs. In the US Virgin Islands, steel and rubberized wire Antillean fish traps are commonly deployed in mesophotic depths (Tobias 1997). A common strategy with mechanized trap haulers is to lay strings of five to ten traps tethered with floating polypropylene line. The line can become a bottom rake during storms, cutting and dislodging

sessile organisms (Fig. 47.4d), before it eventually settles or wraps on the bottom. In addition, coral cover was driven to nearly 0% by shrimp trawling on the azooxanthellate *Oculina* banks off the east coast of Florida, USA, at depths 60–100 m (Reed et al. 2007).

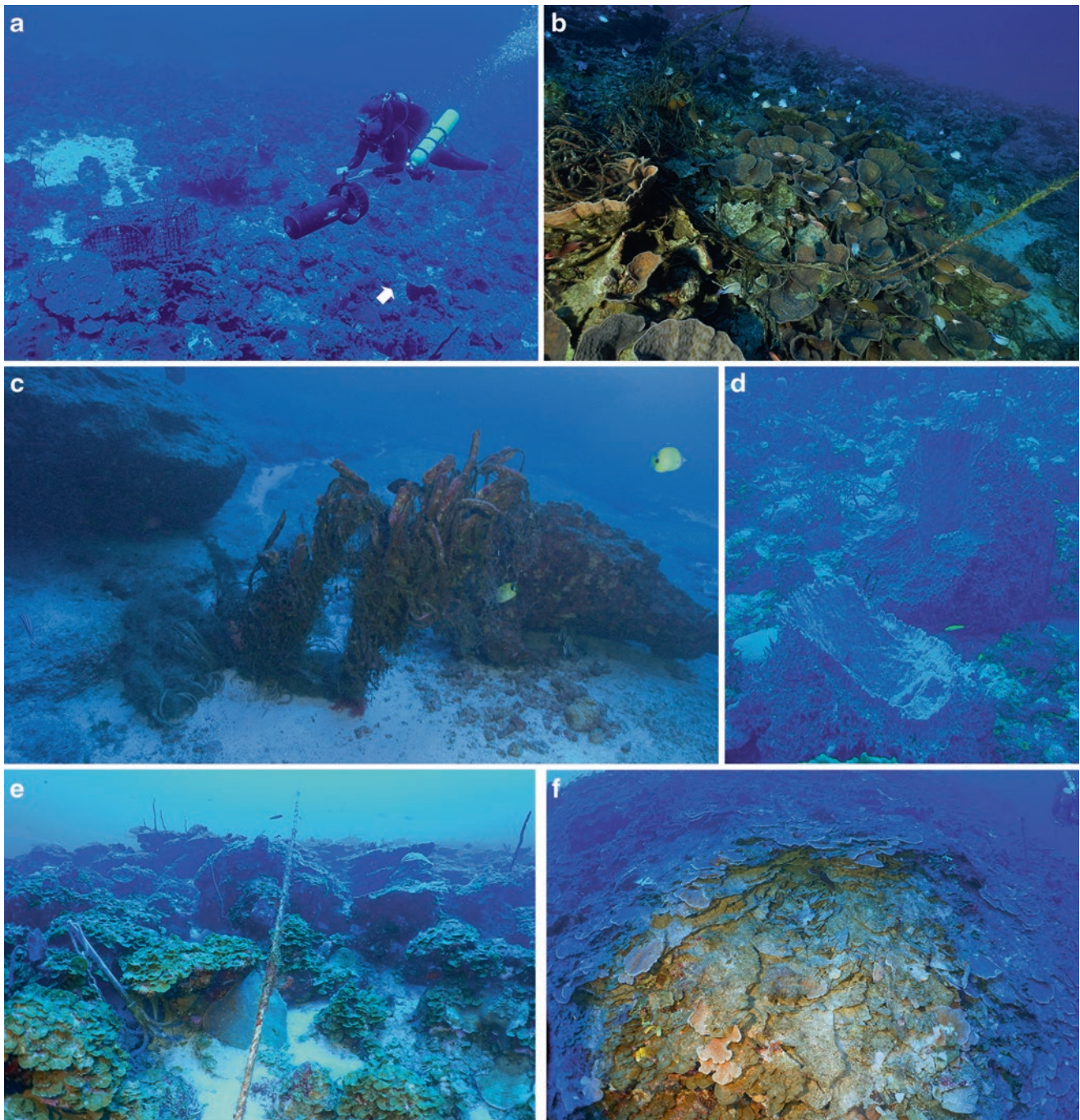
Anchoring can be particularly destructive in MCEs. Reef claw type anchors (Fig. 47.4e) are typically welded steel grapples used to hook and detach from hardbottom habitats, including coral reefs. In one example from the US Virgin Islands, a lower mesophotic zone coral monitoring site was reduced from 45% to 25% coral cover over 4 years (Fig. 47.5a) because of damage to the living *Agaricia undata* coral community and the underlying reef framework (Fig. 47.4f). The presence of a derelict anchor indicated the cause of destruction, and this type of anchoring may be common where fishermen anchor along mesophotic submarine edges to fish.

### 47.3.8 Fishing and Collection

Disturbance to food webs by the selective reduction or removal of organisms is commonly put forth as a leading issue in coral reef management (Jackson et al. 2001; Paddock et al. 2009; Edwards et al. 2014). Organisms can be removed by fishing for consumption, collection for the aquarium, medicinal, and curio trade, and inadvertent loss or outmigration from other activities or factors, such as introductions of predators and incidence of disease.

MCEs have been shown to provide a refuge from intensive fishing impacts and, thus, support higher abundance of fishes prized as food (Bejarano et al. 2014; Lindfield et al. 2015; Pinheiro et al. 2016; Kadison et al. 2017). This may limit the ecological impacts of fishing on MCE ecology in many cases. However, this does not mean that fishing is absent and unimportant as a disturbance in MCEs (Andradi-Brown et al. 2016). Fishes in MCEs are increasingly targeted, such as long lining on MCE slopes for large-bodied fishes and sharks (Sattar and Adam 2005), as commercially important reef fishes are overfished in shallow waters. In the northern US Virgin Islands, a commercial trap fishery targets shelf depths of 20–65 m for parrotfish (Scaridae), triggerfish (Balistidae), groupers (Serranidae), and snappers (Lutjanidae) (Kadison et al. 2017). In addition, transient fish spawning aggregations (Domeier and Colin 1997) are common in mesophotic ecosystems because they often occur along shelf edges where many fish aggregate for reproduction (Holstein et al. 2019). These areas are specifically targeted by fishers, resulting in reductions of large-bodied predatory fish, such a highly prized groupers and snappers, and increased fishing gear impacts to sessile organisms (Nemeth 2005).

Collection of organisms from MCEs for aquarium, curio, or medicinal purposes is poorly studied (Andradi-Brown et al. 2016). One exception is the comprehensive review of



**Fig. 47.4** Mechanical disturbance to MCEs caused by human activities. (a) A derelict Antillean fish trap and associated gear lines (arrow) on an upper mesophotic orbicellid bank reef, Grammanik Bank, St. Thomas, US Virgin Islands, 36 m depth, 5 May 2017. (b) Fishing trap lines and ropes wrapped in mesophotic coral *Mycedium* sp. at Eilat, Israel, 37 m depth, 16 January 2012. (c) Fishing nets wrapped on mesophotic hardbottom off Pearl and Hermes Reef, Northwestern Hawaiian Islands, in the Papahānaumokuākea Marine National Monument, 66 m depth, 14 September 2015. (d) Barrel sponges (*Xestospongia muta*) with shearing damage caused by nearby derelict Antillean trap string lines, St. Thomas, 25 m depth, 23 September 2008. This is not in MCE depths, but similar types of damage have been observed in the Virgin Islands at mesophotic depths (authors, pers. obs.). (e) Abandoned reef claw type anchor and associated polypropylene line in an upper mesophotic orbicellid bank, Hammerhead Shoal, St. Thomas, 40 m depth, 15 April 2017. (f) A 3-m wide cavity in the *Agaricia undata* reef framework caused by anchoring at Ginsburg's Fringe, St. Thomas, 65 m depth, 20 April 2017. Framework collapsed and living fragments are partially bleached. (Photo credits: (a, d) Tyler B. Smith, (b) Gal Eyal, (c) Robert K. Whitton, and (e, f) Viktor Brandtneris)



the “precious coral” jewelry trade of various structure-forming mesophotic and deep-water cnidarians by Tsounis et al. (2010). Their review clearly shows evidence of global overexploitation of red corals (Coralliidae) and black corals (Antipatharia). European red corals have been under exploitation for hundreds of years, with cases of collapsed fisheries driven by low population numbers (Boavida et al. 2016). Reductions in the abundance of these precious coral species may have impacts on fishes and invertebrates that are obligate or facultative associates that shelter in corals (Boland and Parrish 2005). An important observation of Grigg (2001) and Tsounis et al. (2010) is the increasing use of ROVs for collections of organisms at depth. With even greater miniaturization and reduction in cost of ROVs and better technical diving techniques, targeted harvesting of species in MCEs could become a much more important management issue in the next few decades. This may open up vulnerable species in MCEs to exploitation and upend previous notions of MCEs as fisheries/collection refugia.

One of the most common negative impacts of fishing shown for shallow-water ecosystems is the removal of benthic grazing fishes (Edwards et al. 2014) and invertebrates (Hughes 1994). These functional groups can maintain the reef in an overgrazed state favorable for settlement and growth of stony corals (Mumby et al. 2006). The importance of grazing has been far less studied in MCEs, but research has shown a general decline of the intensity of grazing and herbivores at mesophotic depths (Brokovich et al. 2010; García-Sais 2010; Bejarano et al. 2014; Weinstein et al. 2014; Fukunaga et al. 2016). However, grazers can play an important role in controlling MCE benthic structure in some cases. MCEs in the Caribbean have been shown to undergo a phase shift to higher macroalgal abundance that corresponded to a loss of invertebrate (Hughes 1994) and fish grazers (Lesser and Slattery 2011). If true, this indicates how trophic cascades can affect MCE ecology. Thus, grazing may be an important process on MCEs, despite a general decline in its magnitude with depth, and can be particularly sensitive to fishing, either through direct depletion of reef herbivores or trophic cascades.

### 47.3.9 Diseases

Stony corals are susceptible to diseases that appear to be increasing in frequency and impact on community structure (Porter et al. 2001; Harvell et al. 2002; Weil 2019). Some coral diseases are also showing the ability to transmit between colonies through direct contact (Brandt et al. 2013) and waterborne transmission (Clemens and Brandt 2015). While disease can reflect the signs of coral death due to environmental causes (Lesser et al. 2007), the ability of disease to transmit between colonies and undergo outbreaks of high

prevalence at the colony level indicates disease is a multiplier of environmental stress and disturbance.

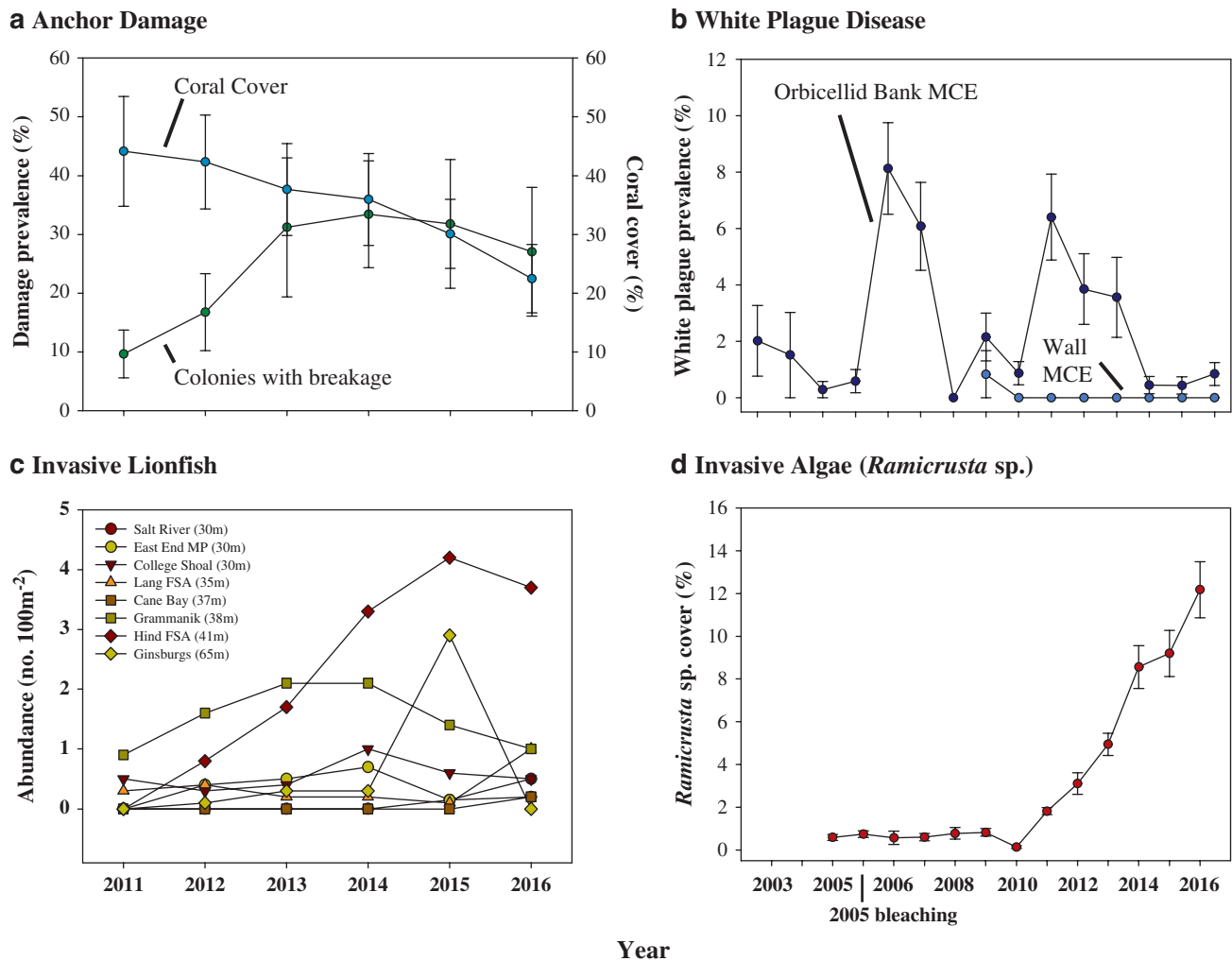
MCEs are not immune to disease disturbances. In the US Virgin Islands, *Orbicella* spp. dominated bank MCEs are very susceptible to outbreaks of white disease or other diseases (Figs. 47.2d and 47.5b; Smith et al. 2010). White diseases in MCEs follow an etiology of white plague disease and are capable of waterborne transmission to unaffected colonies in the lab (Clemens and Brandt 2015), affect multiple species of coral, and exhibit clustering among colonies in the field during outbreaks (M. Brandt, unpub. data). As in shallow coral reefs, these observations suggest that vectoring of undescribed disease-causing microbiota between colonies supports outbreaks. It has been suggested that disease disturbances in the USVI *Orbicella*-dominated MCEs, where diseases are more prevalent than in shallow water, are limiting resilience after disturbance and preventing recovery of coral cover following thermal disturbances (Smith et al. 2016b). It is not known if coral diseases are common in MCEs in the Pacific Ocean or lower MCEs (>65 m depth).

### 47.3.10 Invasive Species

Invasive species that are introduced to a novel biogeographic range or are native but released by ecological forces have been demonstrated to act as a disturbance in MCEs. These include invasive stony ahermatypic corals in the Atlantic and Pacific (*Tubastraea coccinea*, Precht et al. 2014; *Carijoa riisei*, Kahng and Grigg 2005), Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) in the Atlantic (Schofield 2009), and macroalgae, such as *Avrainvillea* sp. in Hawai'i (Spalding 2012) and *Ramicrosta* spp. in the US Caribbean.

One of the most striking results of an invasive species occurred after the introduction of the Indo-Pacific lionfish to the Atlantic Ocean (Schofield 2009). The two introduced lionfish species have had large impacts on the shallow-water fish fauna in some areas of the Caribbean (Albins 2015); they are common or even more abundant at mesophotic depths (Fig. 47.5c; Andradi-Brown et al. 2017) and are hypothesized to have caused large reductions in MCE fish biomass (Lesser and Slattery 2011). Predation on native fishes includes indirect effects on benthic composition through trophic cascades, such as the consumption of reef herbivores, declines in grazing, and a subsequent increase in macroalgae.

Introduced or invasive sessile organisms can also reside in and impact MCEs. For example, algae of the genus *Ramicrosta* (Peyssonneliaceae) have recently appeared in the Caribbean where they were absent or rare and have become successful space competitors. The algae are able to overtop edges of living stony corals and other benthic organisms, causing death of underlying tissue. They seem to be a



**Fig. 47.5** Data from long-term MCE monitoring sites showing impacts of mechanical disturbances, disease, invasive lionfish, and invasive algae in the US Virgin Islands. (a) Anchoring in a lower MCE (65 m), Ginsburg's Fringe, reduced the coral cover of a well-developed portion of the *Agaricia undata* reef from 45% to 25% cover in 4 years. Coral cover was lost to mechanical breakage of fragile plating colonies, recorded as the prevalence of colonies exhibiting breakage. Because coral morphology was oriented to capture light (horizontal plating), fragments that landed in orientations off this axis showed poor survival. (b) White diseases in dense orbicellid bank MCE have undergone periodic outbreaks at extremely high prevalence values. Two outbreaks in 2006 and 2011 were subsequent to regional thermal stress events the preceding year. MCE walls have much lower prevalence of white disease. (c) The abundance of the introduced and invasive Indo-Pacific lionfish (*Pterois volitans*) on mesophotic sites of the US Virgin Islands. MCE site assessments first recorded lionfish in 2011. (d) The invasive red encrusting alga *Ramicrusta* spp. has shown an exponential increase in cover in the College Shoal coral reef monitoring site. This alga is capable of direct overgrowth of living coral tissue. (All data from the US Virgin Islands Territorial Coral Reef Monitoring Program (Smith et al. 2016a))

poor substrate for the settlement of sexual and asexual propagules of other organisms and may, therefore, preempt space for recruitment (authors, unpub. data). Species of *Ramicrusta* are present in multiple locations in the Pacific Ocean (Dixon and Saunders 2013), but were not reported in the shallow waters of the Caribbean until recorded in 2009 at Discovery Bay, Jamaica (Pueschel and Saunders 2009). The genus has since been documented in Bonaire (Eckrich and Engel 2013), Puerto Rico (Ballantine et al. 2016), and the US Virgin Islands (Smith et al. 2016a). In the US Virgin Islands, the genus has been rapidly increasing in cover in one MCE study site (College Shoal; Figs. 47.2e and 47.5d). Although these

algae appear to be a new threat to MCEs in the Caribbean, it is unclear if they were introduced from the Indo-Pacific or are a natural part of the flora that was released from control by some other ecological change.

#### 47.4 Response of MCEs to Disturbance

Little is known about how MCEs respond to disturbance since there are few longitudinal monitoring studies of these communities and their response to disturbance (but see de Bakker et al. 2016; Smith et al. 2016b; White et al. 2017).



Future studies are needed to fill in this gap in knowledge; however, examining the ecology of MCEs will help to frame the potential impacts of disturbance. The responses of MCEs to disturbance will likely depend on their geomorphological setting and intrinsic characteristics of the community itself. In general, MCEs that are subject to multiple types of disturbances may have to deal with “compound perturbations,” which interact to lower resilience and stimulate ecosystem reorganization (Paine et al. 1998).

#### 47.4.1 Extrinsic Factors

The geomorphological setting of MCEs influences the natural formation and distribution of MCEs and their characteristic communities and also shapes their resistance and resilience to disturbance. A basic characteristic of MCEs is the angle of slope of the antecedent topography upon which they form. High-angle (wall and slope) and low-angle (bank) systems may have different propensities to resist disturbance. High-angle systems are susceptible to downslope movement of material, such as sediment and storm debris, from shallower benthic systems (Hubbard 1986, 1989, 1992). Natural movement of material downslope supports the creation of buttresses of living coral and channels that move sediment downslope and off shelf along the periphery of living coral. This characteristic could help in the face of increasing sedimentation from anthropogenic activities by also directing sediments away from living corals. However, corals that are dislodged by bioerosion or mechanical disturbances, such as storms and anchoring, may also be more likely to fall into channels or off shelf, with less likelihood of reattachment and clonal regrowth by asexual processes.

Low-angle systems, such as MCE banks, may be more vulnerable to deposition of materials from the water column, such as sediment, because there are fewer conduits to channel material away from living coral tissues. On the other hand, *Orbicella* bank communities in the US Virgin Islands are often formed on 0.5–2 m high pillars above the surrounding seafloor (Smith et al. 2010), which could partly reflect preferential coral survival on highs above sediment contact. MCE banks may also favor the retention of colonies dislodged by bioerosion and mechanical disturbance since they are less likely to be carried downslope (Smith et al. 2016c). Dislodged colonies in complex frameworks have been observed to live for up to a decade, even detached, in permanent transects on *Orbicella* banks of the US Virgin Islands (authors, unpub. data).

Oceanographic forces such as temperature, currents, and light shape many characteristics of MCEs, such as coral growth (Leichter and Genovese 2006; Lesser et al. 2010), coral caloric content (Brandtneris et al. 2016), and response to thermal stress (Smith et al. 2016b). Well-flushed environ-

ments, with stable light regimes, and moderate maximum and minimum temperatures are more likely to be supportive of coral growth and, hence, resilient. It is less clear how wave climates affect MCE resilience. MCE environments buffered from natural mechanical disturbance from depth or shelf geomorphology include deep lagoons and shelf faces oriented away from the dominant wave climate. Under wave disturbance regimes, these environments may avoid compound disturbance and be more likely to recover following other disturbances. However, some wave exposure that stimulates moderate benthic orbital currents could increase resilience by promoting flushing, heterotrophic food delivery, and supporting higher growth rates (Jokiel 1978).

#### 47.4.2 Intrinsic Factors

Intrinsic MCE community characteristics, shaped by the environment, can affect both resistance to and resilience after disturbances. These factors include colony morphology, growth rate, competitive hierarchies, susceptibility to disease, susceptibility to bioerosion, and rate of sexual and asexual reproduction. While an exhaustive treatment is outside the scope of this chapter, a few examples will help illustrate how intrinsic factors might affect resistance and resilience to disturbance.

Stony corals in deeper reef environments are often optimized to collect light by exhibiting a platy or flattened morphology (Done 1983). Some plating and flattened depth-specialist and depth-generalist corals have skeletal linear extension rates equaling shallow-water colonies (Kahng 2013; Bongaerts et al. 2015) but are thin and fragile. These corals may show low resistance to breakage but may be resilient through fast clonal regrowth of remnant pieces or fragments that resettle on suitable substrate and regrow. In addition, areas of the Indo-Pacific with high ecological redundancy in coral species and fast coral recruitment can recover rapidly. For example, White et al. (2017) showed that a decline in foliose *Pachyseris* spp. after cyclone damage on Okinawan MCEs (~30 m depth) opened up space that was colonized by coral species with arborescent, bushy, columnar, massive, and encrusting morphologies. This increased functional and species diversity of the reef. On the other hand, some depth-generalist coral species with massive morphology grow very slowly in mesophotic depths (linear extension) but can have very dense and hard skeletons (e.g., Caribbean orbicellids; Weinstein et al. 2016; Groves et al. 2018). These corals may be more resistant to breakage than fragile plating forms but also may have low recovery after a disturbance because of low growth rates that slow repair of partial colony mortality. In addition, MCEs composed of a diverse coral fauna may be more resistant to storm damage (White et al. 2013).

While understanding the relative resilience of MCEs compared with shallow systems is still in its infancy, longitudinal studies are needed to shed light on these ecological processes, much as they did for shallow reefs starting in the 1960s and 1970s. We suspect that different MCEs will have varying responses to disturbance similar to shallow coral reef communities.

## 47.5 Conservation and Management of MCEs: Out of Sight, Out of Mind

This chapter discusses known and suspected ways that MCEs are impacted by natural and anthropogenic disturbances and stresses. Conservation and management of MCEs depend on identifying threats, removing or ameliorating them, and supporting natural or assisted recovery after disturbances.

One of the greatest threats to MCEs is their lack of visibility to science and society. MCEs are understudied and poorly characterized ecosystems. The “out of sight, out of mind” issue is particularly pervasive, both from users of ocean resources who are not aware of impacts and because natural resource managers often do not consider MCEs in conservation plans. Where MCEs are well studied, it has been possible to increase management by expanding marine protected area boundaries to encompass MCEs. For instance, once Red Sea MCEs were characterized in Eilat, Israel, marine park boundaries were expanded to a depth of 80 m to ensure their inclusion (Bridge et al. 2013; Eyal et al. 2019). In US waters, federally managed areas were put in place based on the increasing awareness of the extent, development, and importance of MCEs to maintaining a refuge for fisheries species and fish spawning aggregations (e.g., the Hind Bank Marine Conservation District and the Grammanik Bank, St. Thomas, US Virgin Islands: Nemeth 2005; Smith et al. 2010, 2019; Pulley Ridge, Gulf of Mexico: Reed et al. 2019).

Technology is revolutionizing our understanding of MCEs (Locker et al. 2010). The increasing availability of sonar technologies, remote survey techniques, technical diving capabilities, geographic information systems, and modeling techniques is rapidly allowing the estimation of the abundance and structure of habitat-forming species in MCEs. Technologies, such as multibeam and side scan sonar, are producing georeferenced high-resolution meter to submeter scale resolution maps of MCE bathymetry and structure. Some open access remote sensing technologies, such as Google Earth, can also allow lower-resolution bathymetric profiles that can reveal the presence of large seafloor features, such as banks in the appropriate depths and areas to support well-developed MCEs. These data can be combined with observations of the occurrence or abundance of corals and other organisms to create spatial predictive maps of

species and community distribution (Bridge et al. 2012; Costa et al. 2012, 2017). In turn, these maps can become critical in management of MCE resources. Furthermore, technology is making direct observation of MCEs much more cost-effective; thus, there are fewer reasons not to include MCEs as explicit parts of environmental impact assessments for natural resource permitting.

Technology is also democratizing society’s ability to directly observe and interact with MCEs. An issue in the near future for management will be the possibility of technology-assisted resource extraction (e.g., market fish, precious corals, and aquarium trade) from MCEs (Grigg 2001; Tsounis et al. 2010). Since MCEs are often not explicitly incorporated into natural resource regulations and the distribution of organisms are poorly known, there is the possibility of species extirpations before management can catch up to changing resource extraction techniques.

### 47.5.1 Management Options for the Conservation of MCEs

*Global Warming, Thermal Stress, and Disease* Coral bleaching from thermal stress in MCEs will be an increasing problem in the coming decades as seawater temperatures continue to increase. While the ultimate anthropogenic causes of global warming cannot be addressed on a local scale, resource managers can take local action by identifying thermal refugia (West and Salm 2003) and reducing co-occurring stressors to support resilience (Carilli et al. 2009; but see Côté and Darling 2010). MCEs as refugia for stony corals and their potential to serve as brood stock to shallower disturbed reefs is a topic that is gaining research attention (Bongaerts et al. 2010). We advise caution in considering MCEs as a panacea for ailing reefs, as they may be much less important as refugia for scleractinian corals as previously hypothesized, and a focus on persistent areas that can avoid or absorb climate change disturbances may be more fruitful (Bongaerts and Smith 2019). Therefore, we recommend that persistence areas be identified and prioritized for protection.

*Light Penetration, Turbidity, and Sedimentation* Preservation of natural light climates in MCEs is an important area for management. Phototrophic corals living near their lower limit of light availability for photosynthesis may be very sensitive to light reductions. These corals may have very limited capacity for acclimating to lower light conditions or, if they are able, may need to make sacrifices in growth and reproduction to maintain a positive energy balance. Changes in light penetration through the water column above MCEs can be impacted by turbidity, which in turn reduces light avail-



ability and spectral quality to MCEs. Therefore, maintaining light penetration should be a prime consideration for management. For nearshore MCEs in areas with terrestrial runoff, management may focus on limiting discharges by enforcing upland regulations that encourage sediment and storm-water retention. This will also alleviate stress caused directly by sedimentation to coral surfaces. Mapping of MCEs will also be able to show areas with susceptible corals (e.g., plating forms) in areas also prone to sediment delivery. These areas may need more stringent protection of upland processes to limit sedimentation on downstream reefs. For offshore MCEs, limiting nutrient pollution that stimulates plankton blooms and decreases water column light penetration (Furnas et al. 2005) could be a focus of management.

*Pollution and Benthic Infrastructure* Preventing pollution impacts from planned discharges, such as submarine effluents, will require better mapping of MCE resources to avoid emplacing outflows in areas with coral development. Likewise, emplacement of other benthic infrastructure, such as cables and pipelines, would also benefit from better mapping of MCE resources. A positive step is simply recognizing the potential for coral reef presence in mesophotic depths and explicitly mandating environmental assessments to evaluate potential impacts when potentially destructive activities are proposed. In developed countries, access to habitat maps in mesophotic shelves of the exclusive economic zone has facilitated industrial projects.

*Marine Debris and Mechanical Disturbance* The issue of marine debris and mechanical disturbance (e.g., anchoring) often relates to the actions of a few individuals who lack the knowledge of MCE presence and the impacts caused by debris and bottom gear. Incorporating MCEs into outreach and education activities would help to raise awareness and reduce intentional dumping through positive community engagement. In addition, mapping and long-term monitoring programs can call attention to susceptible areas and demonstrate the negative effects of certain activities, which can be used in educational activities or increased regulation. Recognized MCEs that are protected in marine protected areas often have no-anchoring zones and prohibitions on bottom-tending fishing gear to avoid damage to benthic organisms (e.g., Eilat, Israel; Flower Gardens Banks, US Gulf of Mexico; Hind Bank Marine Conservation District, US Virgin Islands). In the USA, legal definition of Habitat Areas of Particular Concern has been used to focus attention and subsequent protection of stony corals from bottom gear in mesophotic depths at Pulley Ridge (Reed et al. 2019) and Oculina Banks (Reed et al. 2007).

*Fishing and Collection* Activities such as fishing that alter reef trophic structures are commonly managed through regulations on catch and the formation of marine protected areas. Similar actions could be taken for MCEs. However, additional research into MCE community ecology is needed to understand how important community components are to maintaining desirable ecological function, such as grazing, and the importance of these ecological functions to maintaining desirable benthic community structure, such as high coral cover. This information can be used to weigh the importance of specific management action (e.g., banning harvesting of parrotfishes), so that sparse management resources can be most effectively applied. In addition, where specific MCE species are targeted for collection (e.g., black corals), success has been found in managing populations through harvest limits and closed areas (Grigg 2001).

*Invasive Species* Management involving invasive species is no different than in shallow reefs. For introduced species, preventing introduction is paramount. After introduction, however, direct management in MCEs through targeted removals is limited, and this may make MCEs even more vulnerable to introduced species than shallow reefs. Technology, such as remote or robotic systems, may improve this capability in the future. For introduced species and native species that escape ecological control, more research is needed to determine their impacts on community function.

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## 47.6 Conclusions

MCEs are prone to natural and anthropogenic disturbances, and their future may depend on managing these disturbances. Shallow and intermediate depth reefs (0–30 m) share many of the same disturbances as MCEs. Even though the magnitudes of some disturbances are attenuated with depth, their impacts on MCEs may or may not diminish as this depends on the sensitivity of the ecosystem to such disturbances. For example, since some MCEs may be acclimated to conditions of lower turbulence and temperature relative to shallow reefs, they may also be more sensitive to any increase of these potential sources of disturbance. Thus, deviation of the disturbance from the mean conditions may be more important to assessing impacts than magnitude relative to shallow reefs.

In general, research is needed on the ecology of MCEs to understand the cumulative impacts of disturbance and the prospects of MCE persistence in an era of rapid global change. Long-term data are critical. This can include both sampling the same reef areas repeatedly and randomized

sampling over larger reef areas and types. Encapsulating the variety of MCE types in these assessments is important to understand how MCEs function across environmental and human impact regimes. In fact, starting with a baseline from many habitats might help avoid some of the myopic views that have plagued shallow-water long-term datasets. In shallow water, a historical (and logistically necessary) focus on a few coral reef sites amid the diversity of coral reefs has limited the ability to generalize about coral reef ecology and hindered formulating the most important management actions. Establishing long-term data collection, of course, requires dedicated resources. Hopefully, the increasing volume of MCE research will facilitate awareness of these systems and their importance to a society that will almost universally never see them first hand.

Conservation and management of MCEs will need to first solve the problem of their invisibility. Making people care about MCEs will require a focus on the ecosystem services that MCEs provide to society. This may come in the form of charismatic and commercially important species or valuable ecosystem functions, such as the potential replenishment of degraded shallow-water reefs. It is hoped that as science progresses, MCEs will be fully integrated into the ecological exploration of reef systems and that management will follow.

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