17 CARIBBEAN CORAL REEFS

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CLASSIFICATION

International: Coral reefs mainly fall within two major biogeographic regions: the tropical Indo-Pacific realms and the tropical Atlantic. Almost all of the latter are found within the Tropical Northwestern Atlantic ecological province of Spalding et al. (2007), sometimes referred to as the Wider Caribbean, and occur within all nine of its ecoregions (Burke and Maidens 2004). The only other coral reefs in the Tropical Atlantic realm are found off the coast of Brazil, and although these have considerable biogeographic affinities to the wider Caribbean region they are also marked by lower diversity, distinct faunal communities and somewhat different reef morphology (Leão et al. 2003). IUCN Habitats Classification Scheme (Version 3.0): 9. Marine Neritic / 9.8 Coral Reef

ECOSYSTEM DESCRIPTION

Characteristic native biota

Coral reefs are physical structures that have been built up, and continue to grow over decadal timescales, as a result of the accumulation of calcium carbonate laid down by hermatypic corals and other organisms (Spalding 2001). The Caribbean coral reefs are primarily fringing reefs and bank barrier reefs (Figre. 1) separated from island and mainland shorelines by reef flats, shallow waters or slightly deeper lagoons (Alevizon 2010). There are only a very small number of oceanic reefs and atolls surrounded by very deep water. Most of these reefs lack an algal ridge on the seaward crest, unlike many reefs of the Indo-Pacific region. Instead windward crests are, or were, dominated by Acropora palmata, a large branching coral (Bruckner & Bruckner 2006; Alevizon 2010), or in its absence, octocorals, sponges and algae (Dudgeon et al. 2010).

Figure S17. 1. Fringing coral reef off the east coast of The Bahamas (Google Earth).

Caribbean reefs include about 65 - 75 species of hermatypic (reef-building) coral (mostly Scleractinia). Many of these are endemic to the region due to the long isolation of the West Atlantic from the east Pacific Ocean since the formation of the Panamanian isthmus. Widespread hermatypic genera include
Acropora, Montastrea Porites Agaricia Diploria, Colpophylia, Meandrina, Mycetophyllia, Dendrogyra as well as the non-Scleractinian fire corals Millepora spp. Many of these corals have distinct growth forms – notably branching, massive, sheet-like and leafy forms. Others show remarkable variation even within the same species (Goreau 1959; Spalding 2004; Alevizon 2010; CARMABI 2012; CARMABI Foundation 2012).

Different coral species are associated with different water conditions (Goreau & Goreau 1973). For example, Acropora palmata is primarily on the reef crest and fore reef at 0-5 m depth, while A. cervicornis occurs at depths of 5-15 m on exposed reefs, as well as shallower areas at 1-10 m depth on more protected reefs, where it may co-occur with Montastrea annularis (Bruckner & Bruckner 2006). Caribbean coral reefs are also distinguished by an abundance of octocorals (e.g. Eunicea, Gorgonia, Plexaura, Muricea spp.) and sponges that grow from the hard coral base and contribute to the diversity and structural complexity of the reef. Other prominent invertebrate groups include crustacea, mollusca and holothuria, including Diadema antillarum, a key algal herbivore.

Figure S17. 2. Caribbean coral reef with (a) staghorn coral, Diploria strigosa, (b) Elkhorn coral Acropora palmata, (c) Pillar coral Dendrogyra cylindrus, and (d) soft corals (Photos: Mark Spalding).

Approximately 500 - 700 species of fish are associated with Caribbean coral reefs (Figure 2). These include grunts (Haemulidae), snappers (Lutjanidae) groupers (Serranidae), angelfish (Pomacanthidae), butterflyfish (Chaetodontidae), damselfish (Pomacentridae), jawfish (Opistognathus spp.), parrotfish (Scaridae), wrasses (Labridae) and surgeonfish (Acanthuridae). About 80% and coral and fish species occur within the Bahamas portion of the ecosystem distribution. The Caribbean Monk Seal (Monachus
tropicalis) was an apex predator of fish in Caribbean reef systems until its extinction in the mid-late twentieth century due to overexploitation (Le Boef et al. 1986; Jackson et al. 2001). Marine turtles, notably green and hawksbill are still found, but have probably lost their role as keystone species due to overexploitation (Jackson et al. 1997; McClanahan, 2006).

Figure S17. 3. Characteristic fish of Caribbean coral reefs: (a) Red Hind, (b) Banded Butterflyfish, (c) Queen Parrotfish, and (d) Stoplight parrotfish; and (e) sea urchin Diadema sp. (Photos: Mark Spalding).
Abiotic environment
Caribbean coral reefs occur in warm, shallow (rarely >60 m depth), clear, relatively nutrient-poor, open coastal waters, where sea temperatures vary between 17-34°C and salinity is 30-38 ppt. By contrast turbid coastal waters, estuaries, deltas and deep oceans are not suitable for coral reef development, and there are no reefs, for example, in the vicinity of the Mississippi delta.

Distribution
The Tropical Northwestern Atlantic province (Spalding et al. 2007) stretches between latitudes of about 10–30° N and longitudes of about 60–95° W, including the Caribbean Sea, Gulf of Mexico, Florida Keys, The Bahamas, Cuba, Antilles and Venezuelan coast, with an outlier at Bermuda (Figure S17). The latest global reef map estimates some 26,000 km² of reefs in the Caribbean, or about 10% of the global total (Burke et al 2011).

![Figure S17. 4. Distribution of Caribbean coral reefs (excluding reefs off the southeast coast of Costa Rica and Panama). Source: Global distribution of coral reefs, United Nations Environment Program - World Conservation Monitoring Centre (Andréfouët et al. 2005) [http://www.arcgis.com/home/webmap/viewer.html?useExisting=1].](image)

Key processes and interactions
Most reef corals are colonial organisms, with individual coral polyps forming a communal skeleton. Most species form endosymbiotic relationships with dinoflagellates (Symbiodinium spp.), which assimilate solar energy and nutrients, providing more than 95% of the metabolic requirements of the coral host. Scleractinian corals develop their skeletons by extracting dissolved carbonate ions from seawater and depositing it as aragonite crystals. The obligate endosymbiosis and calcification processes that underpin the survival, growth and reproduction of individual corals, are highly dependent on environmental conditions including ambient temperature, turbidity, pH and carbonate concentration of seawater (Hoegh-Guldberg 1999; Hoegh-Guldberg et al. 2007).

Individual coral polyps reproduce asexually to enable colony growth. While asexual reproduction is important for growth and regeneration of individual colonies, establishment of new colonies relies on sexual reproduction, which occurs by simultaneous spawning (release of gametes) over one to several
nights per year around a full moon. The fertilised zygotes settle on a range of hard substrates including red (coralline) algae and other corals, and once established, undergo asexual reproduction. Colonies of different species co-occurring within a reef community have different characteristic growth forms, creating a complex spatial architecture (rugosity) that provides shelter and breeding sites for a high diversity of fish and a wide range of marine invertebrates including sponges, crustacea, polychaete worms, holothurians, etc. (Alvarez-Filip et al. 2009).

Many Caribbean coral reefs are impacted by irregular disturbance from storms and outbreaks of disease or predators, which interrupt more prolonged periods of reef building (e.g. Woodley et al. 1981; Aronson & Precht 2001). The recovery of reefs after these events often involves a transitory phase of algal dominance which, under other conditions is kept in check by herbivores, notably parrotfish and the urchin Diadema antillarum. The algal phase may be prolonged or established more permanently by local and regional factors that increase growth of algae relative to that of coral. These include eutrophication due to increased runoff from developed coastal catchments and reduced herbivory due to overfishing or herbivore diseases (Fabricius 2005, Hughes, 1994; Hughes et al 2007). Diseases have also had a tremendous impact on certain Caribbean corals, including two of the major reef-building corals (Acropora palmata and A. cervicornis) and while susceptibility to disease does appear to be heightened by other stressors, the widespread prevalence of disease, even in areas where other perturbations are minimal suggests that this is an independent impact which is also affecting whole ecosystem persistence in the region (Sutherland et al. 2011; Weil and Rogers 2011).

In addition to the above factors, reef-scale dynamics are influenced by interactions with global climate through three main processes (Figure 5). Firstly, rising temperatures, or more specifically increased duration and intensity of high-temperature anomalies, increase the frequency of coral dieback events. These 'bleaching' events are caused by disintegration of obligatory endosymbiosis between corals and dinoflagellates (Hoegh-Guldberg 1999; van Oppen and Lough 2008) and a bleaching response is typically triggered when temperatures exceed summer maxima by 1-2°C for 3-4 weeks. Consequently, for analysis of bleaching events, thermal anomalies are defined by a 1°C elevated temperature threshold. Under mild or short periods of thermal stress, corals may survive and recover their symbiont but typically show reduced calcification, growth and fecundity for an extended period. They may also be more susceptible to disease (Bruno et al. 2007). Bleaching and mortality become progressively more severe as thermal anomalies intensify and lengthen (Hoegh-Guldberg 1999), although there is some evidence that past exposure to thermal anomalies may confer partial resilience to subsequent events (Donner & Potere 2007; Ateweberhan & McClanahan 2010; Guest et al. 2012). Secondly, as atmospheric concentrations of CO2 increase, approximately 25% is taken up by the ocean and reacts with water to reduce pH. As ocean acidification progresses, the seawater concentration of carbonate ions is reduced as they react with free hydrogen ions, and this in turn reduces aragonite formation, calcification and growth rates of coral and coralline algae (Hoegh-Guldberg et al. 2007). A third potential mechanism affecting the dynamics of Caribbean coral reefs is through changes in frequencies of storms (Woodley et al. 1981; Robbins et al. 2011), as this influences the balance between rates of reef depletion and building, as well as turbidity of coastal waters.

Overall, some of the above processes affect the frequency and severity of coral mortality events on reefs, while others affect rates of growth and recruitment, and hence rates of reef regeneration and recolonisation. Several of these processes may interact at a range of scales to mediate reef persistence and rates of expansion or decline (Wilson et al. 2006). For example, there is evidence that warm sea temperature anomalies can drive disease outbreaks where coral cover is high (Bruno et al. 2007). A cause-effect process model proposed by Hoegh-Guldberg et al. (2007) shows the mechanisms of reef dynamics in relation to warming, acidification and some of the regional and local-scale processes discussed above (Figure 5).
Fig. 3. Ecological feedback processes on a coral reef showing pathways of disturbance caused by climate change. Impact points associated with ocean acidification (e.g., reduced reef rugosity, coralline algae) are indicated by the blue arrows, and impact points from global warming (e.g., bleached and dead corals) by the red arrows. Boxes joined by red arrows denote that the first factor has a negative (decreasing) influence on the box indicated. Green arrows denote positive (increasing) relationships. Over time, the levels of factors in hexagonal boxes will increase, whereas those in rectangular boxes will decline. Boxes with dashed lines are amenable to local management intervention.

Figure S17. 5. Cause-effect process model for coral reefs with a focus on warming and acidification (from Hoegh-Guldberg et al. 2007). Other important processes include sedimentation, eutrophication and overfishing (see text).

Threatening processes

The principal threats to Caribbean coral reefs include diseases, pollution, bleaching, ocean acidification, increased storm frequencies and overfishing. These factors have compounding effects on reef dynamics, for example; as pollution reduces the ability of reefs to recover from disease epidemics or storm damage; or as severe storms increase sedimentation and turbidity from runoff.

Caribbean coral reefs are vulnerable to sedimentation and eutrophication of coastal waters from onshore agricultural, urban and industrial land uses (Rogers 1990; Boyer & Jones 2002; Fabricius 2005). Many are fringing reefs and hence exposed to runoff from coastlines, of which some have very high human population densities (e.g. Florida, Haiti). By 2010 43 million lived within 30 km of a coral reef (Burke et al. 2011). Consequently, 25% of Caribbean coral reefs are currently threatened by coastal development, including sewage discharge, urban runoff, construction and tourist development. Overuse associated with heavy tourist activity within the Caribbean region also poses threats from physical damage incidental to recreational boating, fishing, diving and snorkeling, in addition to degradation of water quality.

Diseases of coral and algal herbivores have had a major impact on Caribbean coral reefs in recent decades, with an outbreak of White Band Disease associated with a precipitous decline in abundance of Acropora palmata in the 1980s, and few reefs showing evidence of subsequent recovery (Aronson & Precht 2001). A subsequent outbreak of Yellow Band Disease substantially reduced the abundance of Montastrea spp. from the mid 1990s, especially across the southern Caribbean (Gil-Agudelo et al. 2004; Bruckner & Bruckner 2006). Diseases may also threaten coral reefs indirectly. In 1983 and 1984, for example, there was Caribbean-wide die-off of the sea urchin Diadema antillarum. Prior to this date, overharvesting of many herbivorous fish had left this one urchin species as the only remaining significant algal grazer on many reefs (Lessios 1988). A substantial increase in algal abundance followed. While the algal response was not sustained in all areas, the urchin populations have not recovered (Schutte et al. 2010).
Extensive bleaching events occurred in Caribbean coral reefs following sea temperature anomalies in 1998 (Aronson et al. 2000) and in late 2005 (Donner et al. 2007; Wilkinson & Souter 2008), especially in the southern portion of the ecosystem distribution. Other large bleaching events were recorded in 1987, 1990 and 1995 (McWilliams et al. 2005). The frequency and severity of bleaching events is projected to increase under climate change (Hoegh-Guldberg et al. 2007).

Periodic hurricanes cause substantial physical damage to Caribbean coral reefs (e.g. Stoddart 1963; Woodley et al. 1981). There is some evidence that the frequency of hurricanes may have increased since 1995 (Robbins et al. 2011). Although this is consistent with climate change projections for rising sea surface temperatures, the trend was primarily due to an increase in the number of weak, short-duration storms (Landsea et al. 2010) and it is difficult to disentangle climate-related trends from multi-decade variability (Knutson et al. 2008; Bender et al. 2010). Although trends in hurricane frequency and intensity are uncertain, reductions in inter-storm recovery time, if they occur, may compound the impacts of other threats (Hoegh-Guldberg et al. 2007).

Ocean acidification has been shown empirically to reduce calcification rates of corals and coralline algae (Langdon et al. 2003), although the precise geochemical mechanism is uncertain (Kleypas & Yates 2009). The effects may be expressed as reduced rates of coral growth (linear extension) or reduced density of coral skeletons (Cooper et al. 2008). In the Caribbean region, aragonite saturation, which is related to calcification rates, is projected to decline from 4.0 - 4.2 under pre-industrial CO₂ levels (280ppm) to 3.0 - 3.2 under elevated CO₂ levels of 550 ppm (Hoegh-Guldberg et al. 2007).

Trophic cascades initiated by overfishing are likely responsible for some of the observed changes in Caribbean reef fish assemblages (Dustan 1999; Paddock et al. 2009). Overexploitation of herbivorous fish also increases the competitive advantage of algae over coral. Historic declines in large herbivorous fish in the Caribbean lead to dependence on urchins for control of algal dominance, and may have been precursors of changes in coral and algal communities when disease caused collapse of urchin populations (Jackson et al. 2001). Burke et al (2011) estimated that almost 70% of Caribbean coral reefs are currently threatened by overfishing. Extinction of the Caribbean Monk seal and loss of its trophic function is also thought to have had a dramatic effect on reef fish assemblages (McClenachan and Cooper 2008).

Ecosystem collapse

For criteria A and B, ecosystem collapse was assumed to occur when the mapped distribution of Caribbean coral reefs declined to zero. As coral is the main structural element of the reef, we identified coral cover as a suitable variable for assessing disruption to biotic processes and interactions under criterion D. We assumed that collapse will occur when live coral cover declines to 0-5% throughout the ecosystem.

ASSESSMENT

Summary

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Criterion A

Current decline:

One widely cited statistic suggests that some 20% of coral reefs have been lost to human impacts in recent years (Wilkinson 2004), however there are no robust statistics to justify this estimate. One of the greatest challenges to measuring declines in terms of spatial extent arises from the definition of the
Keith et al. (2013). Scientific foundations for an IUCN Red List of Ecosystems. PLoS ONE Supplementary material
doi:10.1371/journal.pone.0062111.s002

ecosystem – most authors agree that reefs are large physical structures with a living veneer including an
important component of live coral cover, but that reefs are long-lived, slow-growing and subject to
natural fluctuations. By definition, then, the loss of a coral reef is not clearly measurable, and this is
exacerbated by most mapping efforts (e.g. Andréfouët et al. 2006) which tend to focus on the physical
structures which are built by corals, but which remain robust following coral death.

Improvements in remote sensing technology are increasing the possibility of measuring fine resolution
changes in reef habitat, and Palandro et al (2008) provide a useful, field-tested, example of change in
the Florida Keys. In a number of test locations they showed that coral dominated substrate declined
from 19% in 1984 to 7.6% in 2002, a reduction of 61% (3.4%/year) over 18 years. Such changes are in
many ways more relevant to Criterion A than the more commonly measured coral cover (see below),
but most definitions would include the other habitat classes they measured (bare sand, seagrass and
non-Scleractinian hardbottom) as part of the reef ecosystem and hence that these data reflect a shift of
dominance rather than loss of reef. The authors also caution against generalising their results to other
regions, which so far lack similar analyses (Palandro et al. 2008).

The status of the ecosystem is therefore Data Deficient under criterion A1. While these data are
unsuitable to support overall estimates of change in distribution of the ecosystem, changes in coral
cover are relevant to biotic interactions within reefs and are assessed under criterion C below.

Future decline: No projections are currently available for future reef distribution. Consequently, the
status of the ecosystem is Data Deficient under criterion A3.

Historical decline: Estimates of changes in reef distribution exist only for localised areas (e.g. Duering
1901), and given their limited temporal resolution it is difficult to distinguish declines from natural
fluctuations in reef distribution. The status of the ecosystem is therefore Data Deficient under criterion
A3.

Criterion B
Spatial data from the Millenium coral reef mapping project (Andréfouët et al. 2006) were used to assess
the distribution of Caribbean coral reefs under criterion B. The total mapped area of coral in the
Caribbean is estimated to be 21,000 to 26,000 km² (Andréfouët et al. 2006; Burke et al. 2011).

Extent of occurrence: A minimum convex polygon enclosing mapped coral reefs of the Caribbean
region has an area of at least 7.37 million km². Even with the outlying reefs of Bermuda excluded, the
estimated extent of occurrence greatly exceeds the thresholds for threatened status (c. 6 million km²).
The status of the ecosystem under criterion B1 is therefore Least Concern.

Area of occurrence: Caribbean coral reefs occupy approximately 10,000 10 × 10 km grid cells,
including more than 2,000 that contain more than 1 km² of reef. Once again, then, the status of the
ecosystem is Least Concern under criteria B2 because the estimated area of occurrence greatly
exceeds the thresholds for threatened status.

Number of locations: There are likely to be many thousands of individual reefs and locally interacting
reef systems across the Caribbean. Based on recent past declines, these reefs are threatened by a suite
of threats operating over a range of scales from local to global. Local impacts such as overfishing and
pollution occur independently on individual or small-scale groups of reefs. By contrast disease
outbreaks and bleaching events are widely occurring, and it is difficult to define or determine how
independent such events may be across the region. Although these processes have generated strong
region-wide declines in coral cover, there is substantial variation between different reefs with some
maintaining stable coral cover or undergoing only minor declines over the same period that other
undergo large declines (Schutte et al. 2010) and this is almost certainly linked to the interaction of local
modifiers. It is thus impossible to determine any exact number of independent locations at which reefs
may be considered to be impacted from these combined stressors, although it is clearly much greater than five.

Future global change, both from warming and from ocean acidification (Kleypas and Yates 2009) is likely to increase the relative importance of regional threats to a level where they drive ecosystem collapse independently of more localised threats. At this point it may be relevant to consider these processes alone as the 'most serious plausible threats', and because of their broad scale of impact it may become relevant to consider the much broader spatial scale of their operation as defining much larger locations of threat. Future scenarios for ocean acidification, for example, suggest that there will be a strong cline of change in pH across the wider Caribbean, with more dramatic impacts along the coast of Central America, and much lower rates of change in the Greater Antilles (Cao and Caldeira 2008; Burke and others 2011). Under this interpretation, the ecosystem possibly occupies one to three locations, with reefs in the central portion of the distribution likely to maintain higher aragonite saturation for longer than the southern Caribbean, Gulf and Florida-Bahamas areas. Although aragonite saturation will decline markedly as atmospheric CO₂ increases, this process is projected to occur over the next 50-100 years, and the resulting declines in coral reefs may involve further lags of uncertain duration. As a consequence of this process, it is therefore doubtful that the ecosystem is capable of collapse or becoming Critically Endangered within a very short time period (e.g. the next 20 years). The status of the ecosystem is therefore likely to be Least Concern under criteria B3.

Criterion C

Environmental degradation of Caribbean coral reefs may occur through sedimentation and pollution (e.g. eutrophication), changes in the frequency and severity of ocean thermal anomalies associated with bleaching events and changes in ocean aragonite saturation due to acidification (Figure 5). All three processes were examined in the application of criterion C.

Sedimentation and pollution are generally localised and have only been quantified at a few locations (e.g. Rogers 1990; Fabricius 2005). However, an extensive spatial analysis of threats posed by coastal development, catchment-based sedimentation and pollution, marine-based pollution and damage, and overfishing has been carried out under the Reefs At Risk project (Burke and Maidaens 2004; Burke et al. 2011). For each mapped grid cell (500 × 500 m) across the Caribbean reef ecosystem, each of these threats was ranked high, medium or low based on a number of spatial metrics. The ranks were integrated into an overall local threat index, "integrated local threat", by summing ordinal scores assigned to the threat levels (high, medium, low) across all four local threat types within each cell (Burke et al. 2011). These were further integrated with a thermal stress threat index to produce "integrated local threat plus thermal stress index". The analysis suggests that 92% of Caribbean coral reef extent is under at least a medium level of threat, 55% is under at least a high level of threat, while about 25% is under a very high level of threat (Burke et al. 2011). Changes in the extent and intensity of these threats were also assessed over a 10-year period 2001 - 2011 (Burke et al. 2011), however the assessment is limited by the aggregated construction of the index and this limited period of assessment.

Increasing summer sea surface temperature anomalies are a major degradation process influencing coral reef dynamics (Figure 5). Remote monitoring of sea surface temperatures has recently been established in the Caribbean (Hayes & Goreau 2008; Cerdeira-Estrada & López-Saldaña 2011). Mean (+±se) sea surface temperatures (SST) at reef locations across the Caribbean increased by 0.66±0.06°C between 1982 and 2003, with the western Caribbean warming more rapidly than the east (based on mean of regressions in Hayes & Goreau 2008). Summer anomalies in SST, which are more closely related to bleaching events than mean SSTs, also increased in the region during 1983 to 2000 relative to a 1961-1990 base period (McWilliams et al. 2005). Burke et al. (2011) reported that 55% of Caribbean coral reefs were located in areas where water temperatures were warm enough to cause bleaching on at least one occasion since 1998. A further analysis of thermal stress anomalies related to bleaching in the Caribbean between 1985 and 2005 showed that maximum annual numbers of anomalies occurred in 2005 in the eastern Caribbean and in 1998 in the west (Selig et al. 2010). Based on sea surface
temperature data and bleaching records averaged across all sampled Caribbean sites, McWilliams et al. (2005) showed that an increase of 0.1°C in summer SST anomalies was associated with 35% and 42% increases in the geographic extent and intensity of coral bleaching, respectively. By extrapolation of their regression models, they predicted maximum bleaching extent (i.e., 100% of coral-bearing cells) and maximum bleaching intensity (100% of coral colonies) when regional SST anomalies reach 0.97–0.98°C and 0.80–0.85°C, respectively (McWilliams et al. 2005). These changes in SST anomalies are slightly below the most conservative forecasted temperature increases projected to occur between 1990 and 2100 (McClean & Tysbain 2001). There is some limited evidence of partial adaptation by at least some corals to rising temperatures (Maynard et al. 2008; Jones et al. 2008; LaJeunesse et al. 2009; Ateweberhan & McClanahan 2010; Donner 2011), and thus although there is a consensus that this will not be sufficient for reefs to withstand the projected future change it makes it even more challenging to estimate what levels may become critical to continued coral survival.

Ocean acidification is a salient process influencing ecosystem dynamics (Figure 5), and effects are related to aragonite saturation. Aragonite saturation has been monitored at four stations in the Greater Caribbean region since 1988 and show a constant rate of decline reflecting acidification over that period (Friedrich et al. 2012). In addition, a coupled carbon cycle - climate model enables projection of aragonite saturation back to pre-industrial times and forward to year 2100 (Friedrich et al. 2012). Simulations suggest that anthropogenic effects on ocean acidification became detectable around 1850-1875 and after initial acceleration, became constant by about the mid 1960s. However, the noise around acidification impact is likely to be large at species, community and regional levels due to compensatory responses and non-linear relationships (Ries et al. 2010; Anthony et al. 2011).

The data from all three proxies and their associated assumptions for environmental degradation are currently under review. At the time of writing, the status of the ecosystem under criteria C1, C2 and C3 was assigned to Not Evaluated.

Criterion D

Based on salient processes within the ecosystem, coral recruitment and growth are central to ecosystem dynamics (Figure 5). Consequently, coral cover is widely regarded as a critical measure of habitat loss and degradation, given the key role that corals play in facilitating the entire reef ecosystem (Bruno & Selig 2007). More broadly, disruption of biotic interactions within Caribbean coral reefs are expressed as changes in coral cover, reef architecture and loss of fish diversity. To compare alternative choices of biotic variables, all three processes were assessed below using criterion D.

Current decline: Two meta-analyses have been carried out to estimate changes in coral cover (% of seafloor covered by live scleratinian corals) in the Caribbean region during recent decades (Gardner et al. 2003; Schutte et al. 2010).

Gardner et al. (2003) analysed data from 263 sites from 65 separate studies across the Caribbean and found that coral cover declined from an estimated 54±10% cover in 1977 to 9±1% cover in 2001, a decline of 83% (range 77-88%) over 24 years. However, few surveys were obtained for early years and may not have accurately estimated coral cover. Schutte & Bruno (2009) were able to obtain data from 3777 sites on 1962 reefs recorded between 1971 and 2006. These included a majority of sites that were surveyed only once and a smaller number (376) repeat-surveyed in two or more years. Based on this larger data set, Schutte et al. (2010) estimated that coral cover declined from 32±10.5% in 1971 to 13±1.5% in 2006, representing a reduction of 59% (range 33-75%) over 35 years (Schutte et al. 2010). Based on the repeat monitoring sites only, the estimate was in the upper part of this range (74% decline over 34 years). Both studies recorded the most precipitous declines in coral cover during the 1980s, coincident with major coral disease epidemics and bleaching events, from which reefs have generally failed to recover. Both studies also show a broad consistency across subregions, although there is some variability in declines between time periods and reefs. Neither study covered the entire 50-year period required for assessing criterion D. Although trends are uncertain prior to the 1970s, declines appear to
have continued for more than a century and possibly much longer (Pandolfi et al. 2003). The level of coral cover at which reefs are unable to support their characteristic native biota is uncertain, but likely to be greater than zero. For this assessment, it was assumed that collapse will occur at 0-5% coral cover. Using Schutte's et al. best estimates of coral cover decline, the relative severity of disruption to biotic interactions was estimated to be $100 \times (32-13)/(32-5) = 70\%$, or 59\% if collapse is assumed to occur at 0% coral cover. Using uncertainty bounds around Schutte's et al. best estimates of decline in coral cover produces estimates of relative severity as low as $100 \times (21.5-14.5)/(21.5-0) = 33\%$ and as high as $100 \times (42.5-14.5)/(42.5-5) = 85\%$. As these estimates of relative severity are based on samples throughout the distribution of the ecosystem, the disruption to biotic interactions was assumed to have occurred over 100\% of the extent of the ecosystem. The status of the ecosystem under criterion D1 is therefore Endangered (plausible range Vulnerable - Critically Endangered).

While the overall cover of coral is declining, the architecture of the reef structures is becoming more simplified. Alvarez-Filip et al. (2009) carried out a meta-analysis of studies that quantified the surface rugosity at 464 sites on 200 reefs between 1969 and 2008. Rugosity was assessed using an index that scales to one for a flat surface and takes values around three for the most architecturally complex reefs. They found a decline in rugosity index from 2.4 in 1969 to 1.2 in 2008, a 50% decline over 39 years. The temporal pattern of decline included a period between 1985 and 1997 when rugosity remained stable. Declines prior to 1985 were apparently driven by outbreaks of coral disease, while those after 1997 were apparently driven by a series of thermal anomalies, associated bleaching and storms (Alvarez-Filip et al. 2009).

Reductions in reef fish community diversity and biomass, linked to unsustainable fishing practices can be traced back over extended periods of centuries in many areas of the Caribbean (Hughes 1994; Jackson 1997; Wing & Wing 2001; Hughes et al. 2003). Further evidence of the altered state of fish populations region-wide comes from the dramatic changes resulting from local fisheries closures. More recently, reductions in coral cover and reef rugosity have apparently led to further declines in diversity of reef fish (Bohnsack 2000; Halpern 2003; Mahon & Mascia 2003; Mumby & Harborne 2010).

Paddack et al. (2009) analysed a time series of reef fish density from 318 sites across the distribution of Caribbean coral reefs during the period 1955-2007. For all species combined, densities were essentially stable from 1955 until a period of increase in 1981-1985, followed by continuing declines over 1996-2000 and 2001-2007, particularly in three trophic groups of fish: herbivores, invertivores and generalist carnivores. Overall, however, the recent declines compensated the earlier increase so that the mean rate of change over the 52 year period was not statistically different from zero. The increase in the 1980s coincided with mass mortality of the algal herbivore urchin Diadema antillarum, which may have delayed the onset of decline (Paddack et al. 2009). Paddack et al. (2009) suggest a degradation debt, in which trends in fish populations lag considerably behind changes in coral cover and rugosity, with declines in herbivorous fish potentially contributing to positive feedbacks by increasing algal dominance over coral.

The historical impacts of overfishing in the Caribbean appear to have taken place much greater than 50 years ago. Meanwhile, apparent lags in fish population densities make this a less suitable response variable for assessing disruptions to biotic interactions than coral cover and reef rugosity.

The estimates of relative severity and extent of declines in reef rugosity are within the range of values estimated for decline in coral cover: relative severity 33-85\% over 100\% of the extent of the ecosystem. Based on these estimates, the status of the ecosystem is Endangered (plausible range Vulnerable - Critically Endangered) under criterion D1.

Future declines: No projections are available for disruption to biotic interactions in Caribbean coral reefs over the next 50 years. The status of the ecosystem is therefore Data Deficient under criterion D2.
Historic declines: Historic levels of coral cover in the Caribbean are uncertain. Bruno & Selig (2007) suggest that historic (100-1000 years ago) average coral cover in the Indo-Pacific was probably 50%. If a similar cover of coral occurred historically in the Caribbean, then a present-day mean estimate of 13±1% coral cover (Schutte et al. 2010) suggests a decline with relative severity of 100 × (50-11.5)/(50-0) = 71% to 100 × (50-14.5)/(50-5) = 88%. An alternative analysis presented by Pandolfi et al. (2003) based on a semi-quantitative index of reef degradation integrated across seven groups of biota, including corals and fish. Caribbean coral reefs span index values of 52 to 78, where 0 represents pristine condition and 100 represents ecological extinction. Standardising these changes to a 1750 baseline (equating to the ‘colonial occupation’ period of Pandolfi et al. 2003), produces an estimated relative severity of biotic decline approximately 65%. Both estimates are applicable across 100% of the extent of the ecosystem.

The two estimates of relative severity are remarkably concordant. The estimate derived from Pandolfi’s degradation index is possibly lower due to averaging across some biotic groups that are less sensitive to threats than corals. Brino & Selig (2007) argue that coral cover is a critical measure of habitat loss and degradation, given the key role that corals play in facilitating the entire reef ecosystem, hence the relative severity of decline was assumed to be 71-88%. Based on this approach, the status of the ecosystem is Endangered under criterion D3.

Criterion E

No quantitative analysis has been carried out to assess the risk of ecosystem collapse for Coastal sandstone upland swamps. The status of the ecosystem is therefore Data Deficient under criterion E.

REFERENCES


