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Ecological and socioeconomic strategies to sustain Caribbean coral reefs in a high-CO_2 world

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ABSTRACT

The Caribbean and Western Atlantic region hosts one of the world's most diverse geopolitical regions and a unique marine biota distinct from tropical seas in the Pacific and Indian Oceans. While this region varies in human population density, GDP and wealth, coral reefs, and their associated ecosystem services, are central to people's livelihoods. Unfortunately, the region's reefs have experienced extensive degradation over the last several decades. This degradation has been attributed to a combination of disease, overfishing, and multiple pressures from other human activities. Furthermore, the Caribbean region has experienced rapid ocean warming and acidification as a result of climate change that will continue and accelerate throughout the 21st century. It is evident that these changes will pose increasing threats to Caribbean reefs unless imminent actions are taken at the local, regional and global scale. Active management is required to sustain Caribbean reefs and increase their resilience to recover from acute stress events. Here, we propose local and regional solutions to halt and reverse Caribbean coral reef degradation under ongoing ocean warming and acidification. Because the Caribbean has already experienced high coral reef degradation, we suggest that this region may be suitable for more aggressive interventions that might not be suitable for other regions. Solutions with direct ecological benefits highlighted here build on existing knowledge of factors that can contribute to reef restoration and increased resilience in the Caribbean: (1) management of water quality, (2) reduction of unsustainable fishing practices, (3) application of ecological engineering, and (4) implementing marine spatial planning. Complementary socioeconomic and governance solutions include: (1) increasing communication and leveraging resources through the establishment of a regional reef secretariat, (2) incorporating reef health and sustainability goals into the blue economy plans for the region, and (3) initiating a reef labeling program to incentivize corporate partnerships for reef restoration and protection to sustain overall reef health in the region.

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Contents

1. Introduction

The objective of this article is to provide recommendations regarding potential local and regional solutions that could halt and reverse the degradation of Caribbean coral reefs in the context of a future warmer and less alkaline ocean, i.e., ocean acidification. We first provide a brief background on the recent history and current status of Caribbean reefs (Section 1.1), and review the past, present and future changes in seawater carbonate chemistry in this region (1.2). Then, we present critical ecological (2.1) and socioeconomic (2.2) solutions that could assist in reversing the degradation of coral reefs in this region, and where applicable, provide case studies of past or present success stories. Although local and regional actions can make a significant difference for local reef health on short and intermediate timescales, it is important to recognize that the long-term threat of anthropogenic ocean acidification can only be addressed by development of international agreements on CO_2 stabilization pathways (IPCC, 2013).

1.1. Background

The Caribbean and West Atlantic region is politically, culturally and economically diverse. Roughly 44 countries and territories are represented in this region, ranging in size from small islands, such as Montserrat and Bermuda, to large countries associated with major continents, for example, Venezuela and the U.S. (Fig. 1). Coastal population densities, individual average wealth, and national GDPs are diverse across countries (Table 1). Regardless of these differences, however, coral reefs and the marine environment are central to many people's livelihoods in Caribbean nations. Some of the human benefits or ecological services that coral reefs provide include nutritional resources for both local residents and tourists, an attraction for tourist-based economies, and physical protection from storm-driven waves (Moberg and Folke, 1999). The economic benefits of coral reef ecosystem services are significant, as is exemplified by the estimated US$1.09 billion per year they provide to Puerto Rico alone (Brander and van Beukering, 2013). In general, the extent and quality of ecosystem services provided by coral reefs, and their economic benefits to local communities, are strongly linked to the "health" of the reef ecosystem (Moberg and Folke, 1999; UN Environment, 2018; Woodhead et al., 2019). While reefs are recognized for their ecosystem services to coastal human populations, reef services and economic benefits have been in decline in the Caribbean over the last few decades, mainly as a direct result of human activities, but potentially magnified by high ecological sensitivity resulting from its unique biogeography (Jackson and O'Dea, 2013) and accelerating climate change.

The Caribbean Sea is comprised of five major basins with an average depth of ∼4400 m (Fig. 1; Gallegos, 1996). It has a unique biota that is distinct from tropical seas in the Pacific and Indian Oceans (Jackson et al., 2014) due to a lack of natural connectivity with these areas. This biological isolation resulted from the emergence of the Isthmus of Panama around 3 million years ago (Jackson and O'Dea, 2013). As a consequence, the Caribbean marine biota has low taxonomic diversity and minimal ecological redundancy (i.e., the ability of species to serve the same function when species are lost) relative to other tropical seas (McWilliam et al., 2018). This makes it especially challenging for reefs to recover from acute mortality events caused by, for example, thermal bleaching and disease outbreaks. The biological isolation may also magnify Caribbean reef vulnerability to introduced pathogens and non-native species, compared to less isolated coral reef regions (Jackson et al., 2014). Although these reefs have persisted in isolation for more than 3 million years, their inherent fragility has likely contributed to major declines in recent decades under increased human pressures leading to highly degraded Caribbean reefs (e.g., Hughes, 1994; Lugo et al., 2000; Pandolfi et al., 2003; Bellwood et al., 2004; Aronson and Precht, 2006; Burke et al., 2011; Huntington et al., 2011).

Even though some Caribbean reefs have managed to maintain stable coral cover, the Caribbean-wide region has lost 60%–80% of its coral cover since the 1970s (Gardner et al., 2003; Jackson et al., 2014). The region-wide decline has been attributed to a combination of disease, overfishing of herbivores, and an additional range of pressures resulting from human activities (Jackson et al., 2014). In the mid-1970s, white band disease affected acroporids, which were major coral reef builders in the region (Gladfelter, 1982; Aronson and Precht, 2001; Kline and Vollmer, 2011). In the early 1980s mass mortality of the sea urchin *Diadema*, an important grazer of macroalgae on the reef, occurred owing to an unidentified pathogen (Lessios et al., 1984; Hughes et al., 1985). The severe reduction of *Diadema*, combined with a diminished herbivorous fish population due to unsustainable fishing practices, allowed fleshy algae to become increasingly dominant at the expense of corals (Hughes, 1994). Various human activities affecting water quality provided nutrients to support the growth and increasing abundance of macroalgae on reefs, further contributing to the decline in reef health. In many instances these processes have triggered ecological phase shifts in which

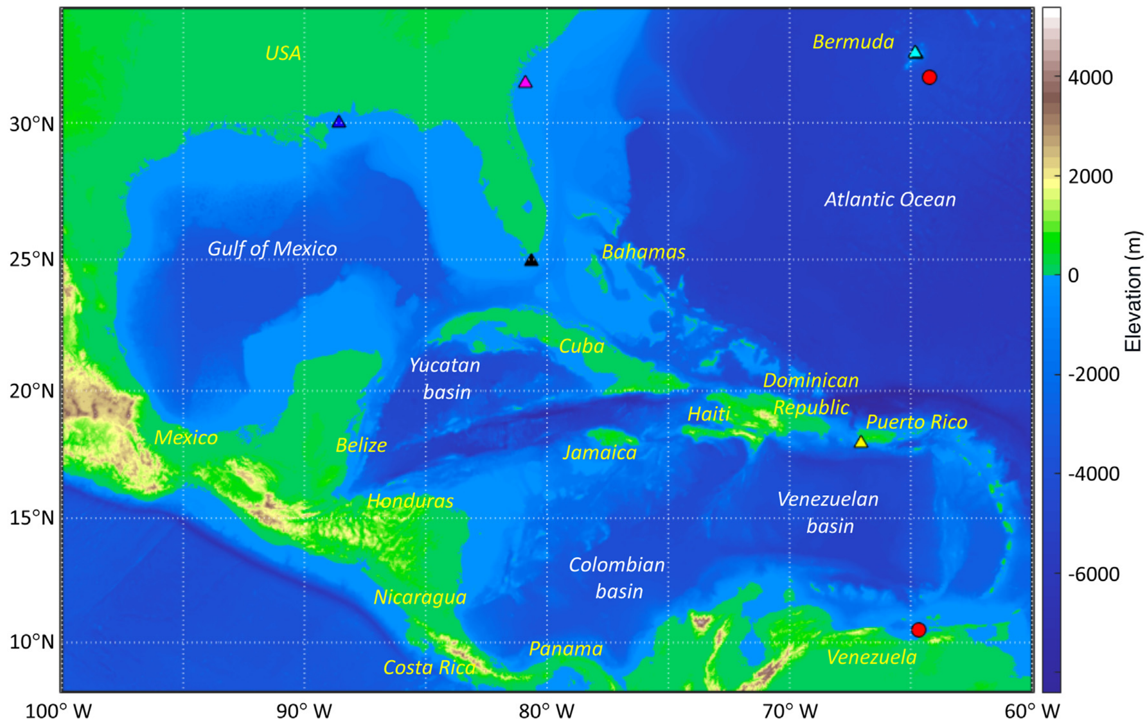

Fig. 1. Overview map of the Caribbean and West Atlantic region. Red symbols illustrate locations of oceanic time-series observations of seawater physics, chemistry and biology at the Bermuda Atlantic Time-series Study (BATS; 31.6°N 64.2°W) and the CARIACO Ocean time-series (10.5°N 64.7°W). Triangles represent locations of near-shore seawater CO_2 monitoring with color coding corresponding to the data in Fig. 3c (Sutton et al., 2019) . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Demographic data for some Caribbean nations and territories.
Source: World Bank, World Development Indicators database (http://databank.worldbank.org/data/source/world-development-indicators; accessed July 25, 2018).

	Population density (people per sq. km of land area) [World Bank]	GDP (current US$) [World Bank]	Population, total [World Bank]	GDP per capita (US$) (calculated)
Antigua and Barbuda	232	1,532,397,556	102,012	15,022
Aruba	585	–	105,264	–
Bahamas	40	12,162,100,000	395,361	30,762
Barbados	665	4,796,845,981	285,719	16,789
British Virgin Islands	208	–	31,196	–
Cayman Islands	257	–	61,559	–
Cuba	110	–	11,484,636	–
Curacao	363	–	161,014	–
Dominica	99	562,540,741	73,925	7,609
Dominican Republic	223	75,931,656,815	10,766,998	7,052
Grenada	317	1,118,816,679	107,825	10,376
Haiti	398	8,408,150,518	10,981,229	765
Jamaica	267	14,768,134,912	2,890,299	5,109
Puerto Rico	376	–	3,337,177	–
Sint Maarten (Dutch part)	1209	–	41,109	–
St. Kitts and Nevis	213	945,854,481	55,345	17,090
St. Lucia	293	1,712,306,556	178,844	9,574
St. Martin (French part)	591	–	32,125	–
St. Vincent and the Grenadines	282	789,629,630	109,897	7,185
Trinidad and Tobago	267	22,104,775,828	1,369,125	16,145
Turks and Caicos Islands	37	–	35,446	–
Virgin Islands (U.S.)	307	–	107,268	–

coral-dominated reefs have gradually given way to macroalgal dominance or other communities where corals are less abundant (Gardner et al., 2003; Bruno et al., 2009; Mumby, 2009).

In addition to a shift from coral to algal dominance across many Caribbean reefs in recent decades, the community structure of remaining coral populations has been altered (Green et al., 2008; Alvarez-Filip et al., 2011). In many areas, declines in branching Acroporids, and important reef-builders such as *Orbicella* sp., have led to a loss in architectural complexity of the reef framework (Alvarez-Filip et al., 2009, 2013). These changes have been accompanied by a relative increase in the abundance of slower growing, domed, plated and encrusting species (e.g., *Agaricia* sp. and *Porites asteroides*) that have not historically been important reef builders over geological time scales that keep up with sea level rise (Precht and Miller, 2006; Green et al., 2008; Perry et al., 2015). Reef-scale carbonate budgets indicate that this transition to communities characterized by non-framework builders with slower calcification rates are associated with overall declines in calcium carbonate ($CaCO_3$) production and a loss of the reef growth potential (Perry et al., 2015).

Caribbean coral reefs continue to face significant threats from acute issues, such as diminished local water quality, disease, and intensive fishing pressure. However, these local factors coincide with increasing global pressures associated with climate change, including ocean warming (Antuna-Marrero et al., 2016; Taylor and Stephenson, 2017), intensified hurricanes (Knutson et al., 2010), and ocean acidification (e.g., Hoegh-Guldberg et al., 2007; Kleypas and Yates, 2009; Andersson and Gledhill, 2013; Melendez and Salisbury, 2017).

1.2. Ocean acidification in the Caribbean and West Atlantic

Since the industrial revolution, the oceans have taken up approximately 40% of the CO_2 released to the atmosphere from burning of fossil fuels and cement production (Sabine et al., 2004; Gruber et al., 2019). In the Caribbean, this uptake of CO_2 has resulted in increased surface seawater pCO_2 and lowered pH and aragonite saturation state (Ω_{ar}) (Fig. 2). In some areas, surface seawater Ω_{ar} has decreased in excess of 40%. This makes the Caribbean basin one of the fastest changing chemical environments under ocean acidification. As a result, conditions there have become increasingly less favorable for biological $CaCO_3$ production (Fig. 2). The changes in seawater chemistry with ocean acidification are well documented based on long-term monitoring in the Sargasso Sea since 1988 (Bermuda Atlantic Time-series Study, BATS; e.g., Bates, 2007) and in the Cariaco basin since 1995 (CARIACO Ocean time-series; e.g., Astor et al., 2013) (Fig. 1). Seawater pCO_2 has increased by 1.69 ± 0.11 and 2.95 ± 0.43 μatm yr^{-1} and pH decreased by 0.0017 ± 0.0001 and 0.0025 ± 0.0004 units yr^{-1} at these two locations, respectively. These changes follow those anticipated based on rising atmospheric CO_2 (Fig. 3; Bates et al., 2014). However, detecting this small anthropogenic CO_2 trend on reefs and in coastal waters of the Caribbean is elusive because of high natural variability and limited duration of measurements (Fig. 3; Sutton et al., 2019). Shallow reef seawater chemistry is more variable than oceanic conditions owing to strong, local influences from biology (metabolism influencing daily CO_2 dynamics), hydrodynamics, geomorphology and land inputs (Andersson and Mackenzie, 2012; Duarte et al., 2013; Fig. 3). In fact, local, contemporaneous factors such as eutrophication and organic matter input can be the main drivers of acidification of reef waters or exacerbating the long-term effect of rising atmospheric CO_2 (Box I; Cyronak et al., 2014). Consequently, local management efforts addressing water quality can assist in lowering global acidification effects at the reef scale, as the local and global acidification impacts combine and are intrinsically coupled (Andersson, 2015).

While Caribbean waters are mostly still favorable for biological $CaCO_3$ production, higher pCO_2, and lower pH and Ω_{ar} have been shown to reduce calcification rates in corals and other marine calcifiers (Chan and Connolly, 2013; Kroeker et al., 2013). These ocean chemistry changes have also shown to enhance the loss of $CaCO_3$ from reefs by increased carbonate dissolution (Andersson and Gledhill, 2013; Eyre et al., 2018). Further, the ability of physical processes, such as waves and storms, and biological organisms to erode the weakened $CaCO_3$ reef framework has also been enhanced under a lowering of pH and Ω_{ar} (e.g., Manzello et al., 2008; Tribollet et al., 2009; Wisshak et al., 2012). Nonetheless, it is currently unclear what role ocean acidification and the changes in chemistry of Caribbean waters have played in inhibiting the resistance and recovery of these reefs following the observed degradation during the past several decades.

Under current global socioeconomic conditions, future model projections for the wider Caribbean suggest that average (± standard error) sea surface temperature could increase by 1.76 ± 0.39 °C during the 21st century (2000–2099; Antuna-Marrero et al., 2016), but with different warming trends in summer and winter (Angeles et al., 2007; Antuna-Marrero et al., 2016). Average surface seawater pH and Ω_{ar} could decrease by 58% and 32%, respectively, relative to conditions observed in 2015 (Melendez and Salisbury, 2017). These estimates certainly carry some level of uncertainty and will not be uniform throughout the region, and the biological implications of the projected changes are not fully known. However, it is evident that both ocean warming and acidification will pose increasing threats to the ability of Caribbean reefs to sustain themselves and recover from future

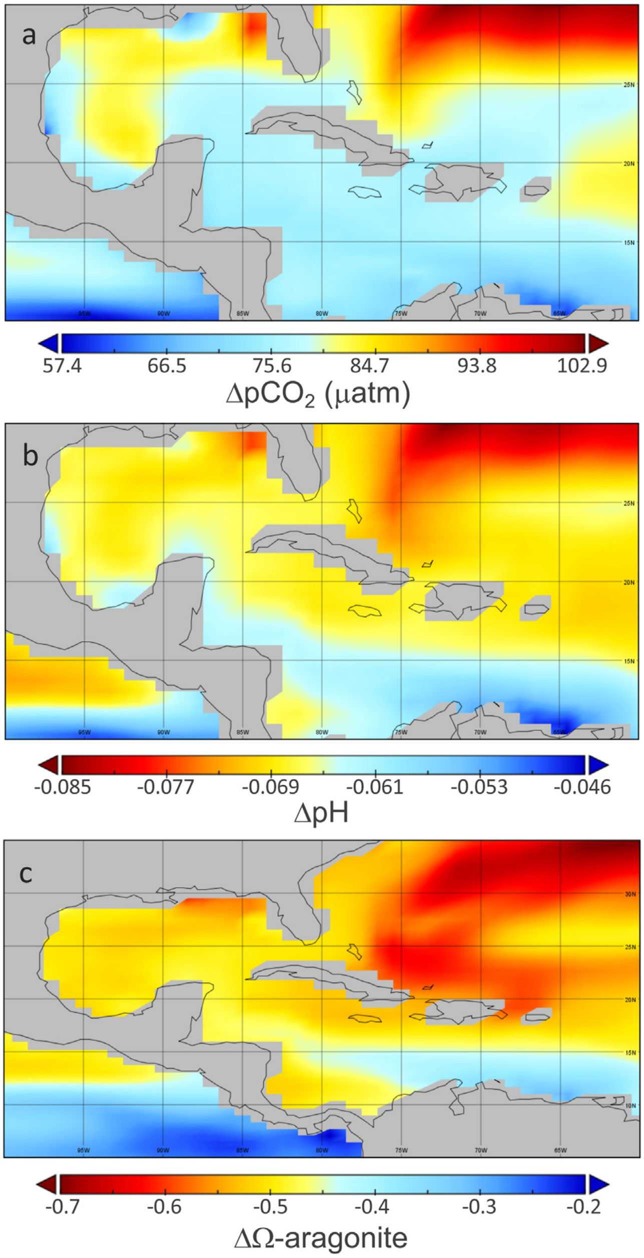

Fig. 2. Calculated changes (Δ) in (a) surface seawater pCO_2, (b) pH and (c) aragonite saturation state (Ω_{ar}) in the Caribbean-wide region between 1863 and 2003 based on NOAA GFDL model output. Red colors represent areas that have experienced large changes in pCO_2, pH and Ω_{ar} whereas blue colors represent areas that have experienced smaller changes . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

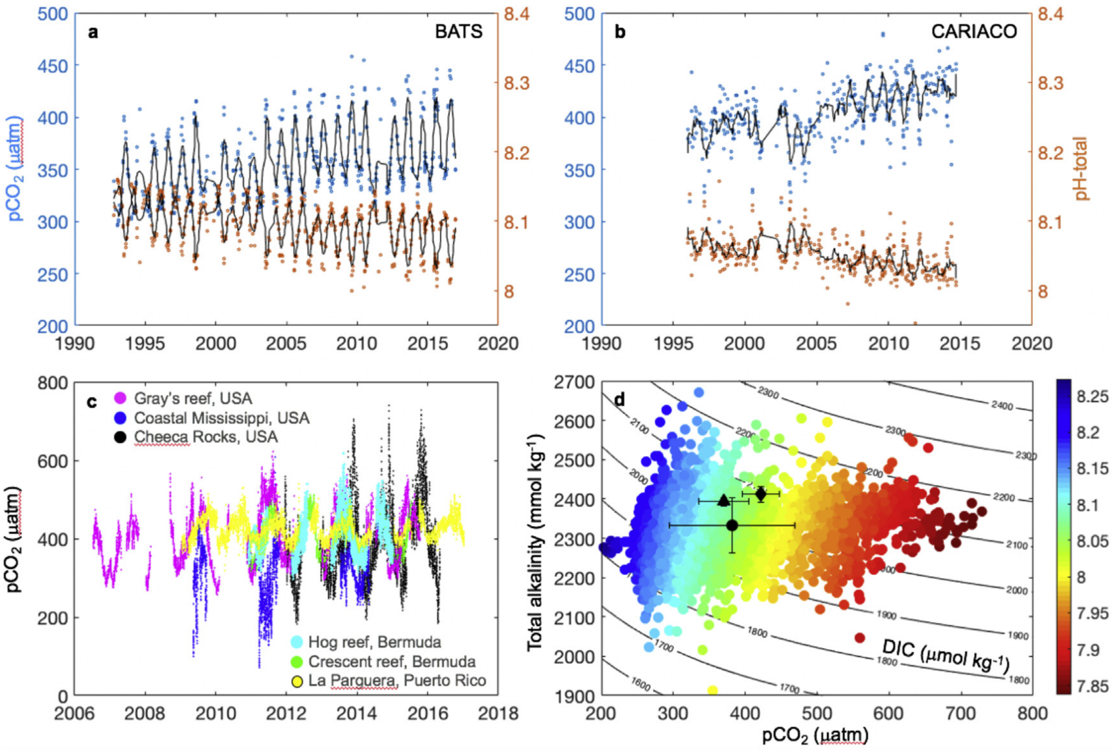

Fig. 3. Direct observations of increasing seawater pCO$_2$ (µatm; blue symbols) and decreasing pH (orange symbols) at (a) the Bermuda Atlantic Time-series Study (BATS) and, (b) the CARIACO Ocean time-series based on data publicly available at http://bats.bios.edu/bats-data/ and http://imars.marine.usf.edu/cariaco, respectively. The black lines represent the moving mean. (c) Surface seawater pCO$_2$ (µatm) at six different near-shore and/or coral reef locations (Fig. 1; Sutton et al., 2019; https://www.nodc.noaa.gov/ocads/oceans/Moorings/ndp097.html). (d) Multivariate relationships between seawater total alkalinity (µmol kg^{-1}), pCO$_2$ (µatm), dissolved inorganic carbon (DIC; µmol kg^{-1}), and pH (colors). Colored data points represent individual measurements from the Cheeca Rocks coral reef in Florida between 2012 to 2016 (Sutton et al., 2019). The average of these data (±1 sd) is shown by the black circle whereas average data from BATS and CARIACO (2010 to last measurement in panels (a) and (b) are shown by the black triangle and black diamond, respectively . (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

acute stress events unless imminent actions are taken at both the local, regional and global scale.

1.3. Strategy moving forward

There is no clear evidence of atmospheric CO$_2$ stabilization in the imminent future. Thus, the ecological and socioeconomic solutions discussed in this article are oriented toward reversing the observed downward trajectory of Caribbean coral reef conditions, and ensuring these reefs continue to provide ecosystem services through increased resistance and resilience in a future high-CO$_2$ world. Given the observed phase shift and severe degradation that have already transpired in many Caribbean coral reefs, we suggest that these reefs have achieved a certain level of resilience and that this region may prove more receptive to aggressive interventions that might be unsuitable for other regions. Active and well-developed restoration programs are already underway on many reefs in the Caribbean, including the establishment of coral nurseries at several sites (Fig. 4; e.g., Johnson et al., 2011; Young et al., 2012; Lirman and Schopmeyer, 2016). However, current restoration knowledge will have to be taken to the next level to prepare reefs to withstand changing conditions under rapid global climate change (e.g., van Oppen et al., 2015; Anthony et al., 2017; National Academies of Sciences, Engineering, and Medicine, 2019. Such improved restoration technologies and methods developed to sustain the wider Caribbean reefs could provide best practice guidance and a way forward for many other coral reef regions that are only now considering more active management approaches. A recent report by the National Academies of Sciences, Engineering, and Medicine (2019) reviews the range of potential intervention techniques in detail including feasibility, limitations and risks.

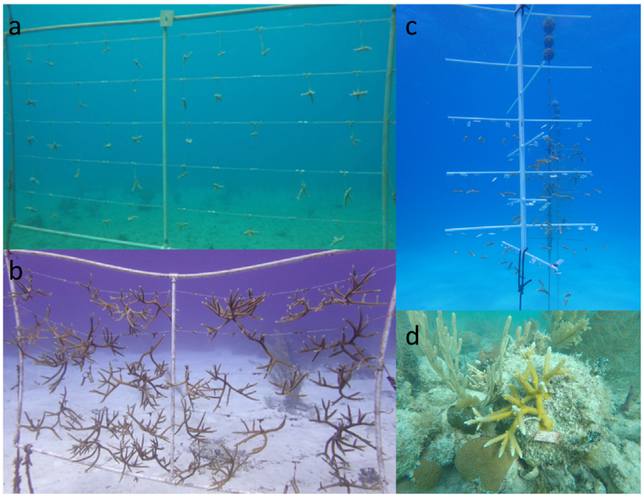

Fig. 4. Examples of coral nurseries in the Caribbean. (A) Vertical frame nursery in the Cayman Islands in the summers of 2016 and, (B) 2017 showing significant growth over a 12 month period (Maneval, 2018; see also: https://www.youtube.com/watch?v=x1ijUVWDNh4&feature=youtu.be). (C) Coral Restoration Foundation's Nursery in Florida and (D) outplanted coral on the reef (Photo credit: K.Lohr and J.Patterson).

External input of organic material to coastal environments inevitably results in microbial decomposition of some fraction of this material either in the water column, at the seafloor or in the sediments. At every depth, decomposition of organic material produces CO_2 and consumes oxygen, the former leading to lower seawater pH and Ω_{ar}. Depending on the specific setting (i.e., depth, geomorphology, and hydrodynamics) as well as the amount and reactivity of the organic material, oxygen availability may reach hypoxic or even anoxic conditions while seawater pH and Ω_{ar} may reach levels that are corrosive to calcareous structures (i.e., $\Omega_{ar} < 1$). Eutrophication, the addition of excess nutrients, may initially stimulate phytoplankton blooms in the water column that lower CO_2 and elevate oxygen, but once this material settles to the benthos, the reverse will occur with potential negative consequences for sessile benthic organisms like reef-building corals (Cai et al., 2011; Drupp et al., 2011).

Box I. Effect of organic matter loading and eutrophication on seawater chemistry.

2. Recommended strategies to sustain Caribbean coral reefs

2.1. Solutions with direct ecological benefits

The solutions presented in this section build on existing knowledge of the drivers that have degraded reefs in the wider Caribbean region. They represent interventions that may reverse decline in reef systems and contribute to enhanced reef persistence and resilience under ocean warming and acidification. The proposed solutions have direct ecological benefits, but require accompanying socioeconomic and political support and decisions. These solutions are presented in four categories: (1) manage land-based and near-shore water fluxes and quality, (2) reduce unsustainable fishing practices, (3) apply ecological engineering and, (4) implement marine spatial planning.

2.1.1. Manage land-based and near-shore water fluxes and quality

Data on underwater visibility produced by the historically largest monitoring program in the Caribbean CARICOMP (Caribbean Coastal Marine Productivity network; 1985–2007) indicate widespread decreases in water transparency from poor water quality (Chollett et al., 2017). Declining water quality is perceived as a serious threat to the reefs in the Caribbean and Western Atlantic, and may be a key driver of their degradation (Jackson et al., 2014). Land-based sources of pollution include the input of contaminants directly or indirectly into river/lagoon systems which drain into the coastal environment. These sources include agricultural runoff of nutrients, pesticides and herbicides, as well as industrial and municipal wastewater disposal. Nearshore sources of pollution also include wastewater from cruise ships and leaking of antifouling chemicals from watercraft (Box II; Burke et al., 2011; Owen et al., 2003). The deleterious effects of these sources of pollution and associated declining water quality on reef building corals and the organisms that depend on them are complex, and have been reviewed previously (Box II; e.g., Fabricius, 2005; Fabricius et al., 2005). Although the sources and impacts of coastal pollution can be diverse and location specific, improving and maintaining water quality is a key step in improving and sustaining Caribbean reefs. Enhancing water quality would allow coral reefs to continue providing ecosystem services, and enhance resilience to ocean warming and acidification. Nutrient input and municipal wastewater have particular relevance to ocean acidification, as organic matter and nutrient enhanced phytoplankton blooms accelerate microbial respiration rates, increasing CO_2 and decreasing pH in the benthic bottom layer (Box I; e.g., Cai et al., 2011). Thus, reduced loading of inorganic nutrients and organic matter favors better water quality, which can raise seawater Ω_{ar} and promote calcification and reduce $CaCO_3$ dissolution (Andersson, 2015; Eyre et al., 2018).

Three interventions would support solutions for improved water quality on reefs in this region:

(1) reduce the point sources and inputs of pollution (prevention), including waste water effluent treatment, and regulation of compounds harmful to the marine environment,
(2) introduce natural barriers or filters (run interference), which includes spatial planning and land use practice that promote the maintenance or establishment of natural barrier systems (e.g. mangroves) between the land-based sources of pollution and the reef,
(3) redirect or divert pollutants away from reef ecosystems, preferably to treatment facilities, either industrial or natural.

2.1.2. Reduce unsustainable fishing practices

The second major driver of reef decline in the wider Caribbean region is widespread unsustainable and destructive fishing practices (Sala et al., 2001; Myers and Ottensmeyer, 2005; Ward-Paige et al., 2010). Unsustainable fishing can directly undermine reef resilience, while best management practices could enhance fish stocks. The removal of herbivorous fish and apex predators may alter ecosystem balance, promoting macroalgal growth on reefs, particularly in areas where the abundance of other herbivores (e.g., sea urchins) is already low. This will be increasingly important in a high-CO_2 world as some macroalgae benefit from higher CO_2 while calcifying organisms will be at a disadvantage under such conditions (Enochs et al., 2015). To support sustainable fishing, it is necessary to identify and protect key habitats where spawning and reproduction of fish and invertebrates are important (Sadovy and Domeier, 2005; Russell et al., 2012; Nagelkerken et al., 2012). In addition, there should be consideration of new stock enhancement by lowering pressure on pre-reproductive fish (Nagelkerken et al., 2012). Fishing practices vary widely throughout the Caribbean and recommended best practices can be based on regional success stories of sustainability, many of which are linked to Marine Management Areas (MMAs), including Marine Protected Areas (MPAs) to provide a source for new recruitment (Box III).

The solutions for enhancing reef fish stocks include:

(1) develop a hierarchy of fishing rights for stakeholders,
(2) replicate successful MMA/MPA management considering additional stressors are forthcoming,
(3) enhance opportunities to build stocks by protecting a subset of juveniles, apex predators and protecting spawning and nursery areas,
(4) remove destructive practices that negatively impact reef accretion.

2.1.3. Explore and test new ecological engineering approaches

Ecological engineering is defined as the design of sustainable ecosystems that integrate human society with its natural environment for the benefit of both (Mitsch and Jorgensen, 1989; Mitsch, 2012). In the context of Caribbean and Western Atlantic coral reefs, the ecological engineering approaches presented here place a special emphasis on reef restoration, as many reefs in this region are presently in a highly degraded and altered state. We propose two complementary approaches: (1) coral gardening and sexual propagation integrating assisted

Antifouling compounds are widely used on boat hulls to limit the growth of sessile invertebrates and algae. These compounds include herbicides that inhibit photosynthesis; such as the compound Iragrol 1051. In 1995, analysis of water samples taken from a number of inshore sites and harbors around the island of Bermuda in the Western Atlantic indicated high levels of Irgarol (Readman, 1996; Connelly et al., 2001). This sparked fears that leaching of Irgarol from boat hulls was a threat to Bermuda's inshore environment, particularly the endosymbiotic algae found in most reef building corals. In response, the Bermuda Government (Ministry of the Environment) funded a series of toxicological studies at the Bermuda Biological Station for Research that demonstrated that Irgarol presented a threat to coral photosynthesis and a potential threat to coral reef health around the island (Owen et al., 2003). On July 1, 2005, Irgarol- and diuron-based antifouling paints were banned in Bermuda by amendment to the Bermuda Statutory Instrument BR 20/1989 Fisheries (Anti-Fouling Paints Prohibition) Regulations 1989.

Box II. Case study: Banning antifouling chemicals to protect Bermuda's coral reefs.

In 1995, the Cabo Pulmo National Park was created at the southern end of the Baja California Peninsula in the Gulf of California with the purpose of protecting its coral reefs (Bonilla, 1997). One third (35%) of the national park was officially designated as a no-take area, but through actions by the local community, most of the park has effectively been established as a no-take area (Aburto-Oropeza et al., 2011). In a comparison of fish surveys conducted between 1999 (Sala et al., 2002) and 2009 (Aburto-Oropeza et al., 2011), fish biomass increased by 463%, top predators increased by >1000%, and the fish species richness increased from 15 to 25 species per survey transect. The observed increase in fish biomass is the largest increase reported for a marine protected area over a 10-year period. This extraordinary response was attributed to the large size of the reserve, its intact coral reefs, inclusion of critical spawning areas, and natural high productivity in this part of the Gulf of California (Aburto-Oropeza et al., 2011). The success of the development, management, and enforcement of the Cabo Pulmo marine reserve has been largely attributed to the leadership and active involvement of the local community.

Box III. Case study: Cabo Pulmo National Park and no-take marine reserve.

evolution and (2) selective harvesting. These approaches integrate both active and passive methods of reef restoration (as defined by Albright and Cooley, 2019; see also National Academies of Sciences, Engineering, and Medicine, 2019). Active methods require direct human involvement (e.g., outplanting corals) and passive methods involve enhancing naturally-occurring processes (larval settlement). All approaches require research to assess their effectiveness and wider effects before implementation. There is also a need to engage other disciplines (e.g., architects, engineers, biotechnologists) to foster innovative ideas and elucidate potential ecological engineering approaches that are sustainable and have no impact on the broader marine community.

(1) *Coral gardening and sexual propagation (integrating assisted evolution).* The Caribbean and Western Atlantic has a long history of coral reef restoration with earlier efforts initially focused on repairing the 3D structure of reefs following physical disturbances such as ship groundings on the Florida Keys reef tract (Precht, 2006). These physical engineering projects aimed to repair reef structure in order to enhance the eventual settlement and growth of new coral recruits, or to provide new reef structure for the transplantation of corals from other areas (Zimmer, 2006). Coral gardening, pioneered by Rinkevich (1995) involves the growth of coral colonies in nurseries and their subsequent outplanting (transplantation) on the reef (Fig. 4; Box IV). Cultivation of corals in a nursery involves a relatively small stock of corals propagated by asexual reproduction (fragmentation) which are grown in land-based aquaria or designated areas in the marine environment (Lirman and Schopmeyer, 2016). Mariculture techniques of corals have improved in recent years to maximize coral survivorship and productivity (Johnson et al., 2011). While coral gardening utilizes fragmentation (asexual) propagation, recent initiatives have sought to increase the genetic diversity and resistance of coral stocks by developing sexual propagation techniques. This is achieved by fertilizing field-collected gametes in the laboratory, rearing them to adults and outplanting them on the reef (Chamberland et al., 2015, 2016; see also http://www.secore.org). Provided adequate coral stocks can be reared and made available in nurseries, coral gardening and sexual propagation approaches have the advantages of restoring coral populations to the reef more rapidly than natural settlement and avoids transplantation of corals from wild environments (i.e., "robbing Peter to pay Paul") (Lirman and Schopmeyer, 2016).

The Caribbean and Western Atlantic has a growing infrastructure of coral gardening projects with the potential to contribute to coral reef restoration projects on an ecologically meaningful scale. In a recent review, Lirman and Schopmeyer (2016) report that there are >150 programs in >20 countries that now use the gardening method. The increasing availability of these programs present opportunities to integrate new technologies that may enhance long-term survivorship and reproductive success of outplanted corals on reefs under restoration. Notably coral nurseries and outplanting programs could integrate "assisted evolution" approaches that are currently in development (Box V; e.g., van Oppen et al., 2015; National Academies of Sciences, Engineering, and Medicine, 2019). These programs may involve the inoculation of corals with stress resistant symbiotic algae or microbial communities (Peixoto et al., 2017). The nursery phase of coral gardening or sexual propagation may provide the ideal circumstances to apply and experiment with these techniques, particularly where environmental conditions may be manipulated, such as in land-based coral culture facilities (Lirman and Schopmeyer, 2016). For reef restoration, consideration should be given to the ecological role of the coral species to be reared in nurseries and outplanted in coral gardening and sexual propagation programs. For example, certain species are major contributors to the reef framework and are thus important to reef accretion rates, e.g., those belonging to the *Orbicella* species complex and branched *Acropora* species (Perry et al., 2015). These species also contribute to the architectural complexity of the reef which is an important factor underlying reef biodiversity (Alvarez-Filip et al., 2011). Furthermore, restoration practices should consider how the choice of coral species used for outplanting may affect the long-term biodiversity of the coral assemblage and the reef in general (Drury and Lirman, 2017). Importantly, coral restoration projects must also take into account genetic diversity among outplanted corals, as populations with lower genetic diversity tend to be more vulnerable to disease and are slower to adapt to environmental change (Baums, 2008). Finally, outplanting of corals onto the reef may be supplemented by physical engineering approaches to stabilize reef foundation and improve reef rugosity to enhance settlement and growth of juvenile corals. Positioning of coral outplants on the reef should also take in to account physical aspects of the reef, e.g. depth, current speeds and exposure to storm damage as a way to promote calcification rates and long-term reef growth potential (Perry et al., 2013).

Overall, the Caribbean and Western Atlantic is potentially a key region where significant advances in the integration of assisted evolution techniques with coral gardening and sexual propagation can be made due to the relatively high number of existing nurseries and outplanting programs in the region. There are many examples of where coral nurseries are in relatively close proximity to universities and research institutes (e.g. coral nurseries in Florida) where scientific expertise and equipment are available. However, it should be emphasized that while human-assisted evolution approaches are widely used in other contexts (e.g. for terrestrial plants), these techniques are in an experimental phase for corals and much remains to be learned before their full application to coral reef restoration.

(2) *Selective harvesting to enhance coral settlement and resilience.* Selective harvesting involves the design of fishing practices that promote reef resilience in an effort to reverse ecological phase shifts. For example, on a macroalgal-dominated reef, selective fishing would target the predators of reef herbivores to increase herbivore numbers to reduce algal cover. In addition, direct harvesting of macroalgae by humans could lower algal competition with corals on the reef (Ceccarelli et al., 2018; Neilson et al., 2018). Another example of selective harvesting is to target fish or invertebrate species that bioerode reefs to enhance reef accretion. In recent decades, bioerosion rates of Caribbean reefs have declined in concert with lower reef accretion rates. However, bioerosion is predicted to become a more important control on reef growth potential and should be taken into account when considering ecological engineering approaches to sustain reefs in the future (Perry et al., 2014). In all cases, trophic cascades are complex and difficult to predict, and selective harvesting approaches should be restricted to specific locations and situations, and should be carefully investigated before implementation (Salomon et al., 2010).

Two primary solutions were identified where ecological engineering could potentially enhance restoration efforts:

(1) strategic reef restoration using coral gardening and sexual propagation of corals, while exploring and testing the potential benefits of human-assisted evolution,
(2) selective harvesting approaches to enhance coral settlement and overall reef ecosystem resilience.

2.1.4. Spatial planning

Marine spatial planning (MSP) is an essential aspect of environmental management that mitigates stress on reef systems and ensures the long-term success of reef restoration (Harvey et al., 2018). MSP involves designation of marine protected areas (MPAs), supports key ecosystem services, and separates conflicting uses of marine resources by zoning. For example, coastal waters can be zoned for different activities, such as conservation, food security and livelihoods (Agardy et al., 2011; Sale et al., 2014). If sufficient understanding of local ecology, habitats and hydrology is available, MSP can be tailored to enhance reef recovery and to promote reef resilience based on multiple environmental factors. For example, design of reef restoration initiatives can use information on thermal patterns to plan for reserve networks that maximize the probability of persistence of the reef system (Chollett and Mumby, 2013; Chollett et al., 2014). Information on water quality and carbonate chemistry at local and regional scales may indicate potential refugia from ocean acidification (Manzello et al., 2012; Page et al., 2018). Connectivity between habitats should also be considered in MSP to promote gene flow via larval transport and recruitment of corals, other invertebrates and fish at restoration sites (Hughes and Tanner, 2000; Ayre and Hughes, 2004). Connectivity should be promoted to enhance gene flow between environmentally variable habitats, for example, inshore reefs and mangroves where more environmentally tolerant genotypes of coral have been found (e.g., Oliver and Palumbi, 2011), to maximize genetic diversity and environmental tolerance.

2.2. Socioeconomic and governance solutions

To maximize the impact and support the application of solutions with direct ecological benefits, it is critical to simultaneously implement a range of socioeconomic and governance solutions that consider climate change coupled with preexisting human impacts (Hughes et al., 2003). A number of actions could be taken to align funding and economic forces to better support coral reef management, protection, and restoration in the face of ocean warming and acidification. Specifically, we propose three key actions: (1) establish a secretariat for coordinated reef restoration investments, (2) develop blue economy principles that protect coral reefs, and (3) initiate a reef stewardship and labeling program (Boxes VII and VIII).

2.2.1. Establish a secretariat for coordinated reef investments

In an effort to promote better coordination of international and regional funds that are being deployed within the region, and to maximize the return (Kark et al., 2009), we envision a small secretariat that could reside within an existing regional, international organization such as CARICOM. This would have to be developed *de novo*; some thought has already been given to CARICOM's potential role in fisheries management (Chakalall et al., 1998), but the organization has not focused primarily on coral reefs to date. Other potential coordinating bodies include the International Coral Reef Initiative (ICRI) or the Caribbean Challenge Initiative (CCI), but other organizations may also be suitable. The goal of the secretariat would be to increase communication and coordination amongst international governmental, non-governmental, and funding organizations with the aim to manage, protect, and restore coral reefs of the wider Caribbean region to enhance long-term sustainability and ecosystem services to local communities. Establishing an international entity typically requires overcoming political and social obstacles, sometimes within individual nations (Grip, 2017), but the secretariat proposed here would be intended to offer improved effectiveness and better outcomes for investments (Kark et al., 2009) across the entire Caribbean region. This program could provide an attractive platform for funder engagement, while also attracting coral reef conservation professionals by serving as a funding portal. The secretariat would have the added benefit in that it would create a community of practice for inter-disciplinary and across-sector knowledge sharing in the region.

2.2.2. Develop blue economy principles for reef sustainability in region

Principles for a sustainable blue economy have already been developed by entities such as the WWF, UN Environment, the Prince of Wales' International Sustainability Unit (ISU), and specifically for the Caribbean region by the World Bank (e.g., Patil et al., 2016). Recent efforts have started to focus on those business sectors that directly benefit from and potentially impact coral reef resources including tourism, commercial fisheries and coastal

Since 2010, SECORE International (USA, Germany), the Carmabi Marine Research Station (Curaçao), and the University of Amsterdam (Netherlands) have been developing techniques to rear large numbers of *Acropora palmata* by sexual propagation so they could eventually be outplanted to degraded reefs throughout the Caribbean. In 2011, male and female gametes of *A. palmata* were caught in the wild and fertilized in the laboratory to generate large numbers of genetically distinct-individual colonies. These colonies were cultured for a year before outplanting on the reef. Seven out of nine outplanted colonies survived and continued to grow *in situ* reaching a size of 30–40 cm diameter and 20–30 cm height after four years. In September, 2015, two colonies were observed releasing gametes. This was the first time that an endangered Caribbean *Acropora* species was raised from larvae and grown to sexual maturity in the field. The relatively short time until onset of spawning (≤4 yr) observed for *A. palmata* suggests that recovery of degraded coral populations by enhancing natural recruitment rates may be realistic if outplanted colonies are able to rapidly contribute to the natural pool of larvae (Chamberland et al., 2015, 2016).

Box IV. Case study: Coral sexual propagation for reef restoration in Curaçao.

Assisted evolution involves the acceleration of natural evolutionary processes to enhance certain traits, such as the tolerance to environmental stress. In the context of coral gardening and sexual propagation, the ultimate aim of assisted evolution would be to produce coral colonies for outplanting that display improved fitness and greater capacity to contribute to reef restoration. Assisted evolution approaches include the identification of stress resistant coral genotypes and selective breeding of corals from extreme environments. Assisted evolution may also include preconditioning (environmental hardening) of corals at juvenile and adult stages to certain environmental regimes to promote environmental resistance by acclimatization and/or epigenetic progresses (e.g., to low seawater pH) (Liew et al., 2018). Approaches also include the active modification of the community composition of coral-associated microbes (eukaryotic and prokaryotic) and laboratory evolution of the algal endosymbionts of corals to enhance stress tolerance (van Oppen et al., 2015).

Box V. Assisted evolution.

development (UN Environment, 2018). A recent assessment of the Mesoamerican reef (Belize, Guatemala, Honduras, Mexico) showed that the current economic returns to these three sectors alone were US$6.2 billion per year. In a scenario of continued reef degradation from 3.7% to 1.6% coral cover, these returns could decrease by US$3 billion per year by 2030 opposed to an increase to US$10.2 billion per year if the coral cover increased to ∼14% during this time period (UN Environment, 2018). It is evident from this analysis that investments aimed at improving reef health, are likely to generate positive net returns for these sectors into the future. This connection between reef health and economic returns is gaining recognition and driving new partnerships between multiple stakeholders aimed at improving reef health (Box VI). We propose a coral-specific plan be established (e.g., by WWF, ICRI and ISU [or similar entities]) that recognizes the importance of future blue growth with a commitment to net positive improvement in coral reef ecosystem health. This plan should include increased investment in reef management and restoration activities (reviewed herein) that supports reef function and health in planning to provide long-term ecosystem services from reefs (Hughes et al., 2003).

2.2.3. Initiate a Reef Stewardship and Eco-Labeling Program

Many people who care deeply about coral reefs may unwittingly participate in or support economic activities that are detrimental to coral reef health. For instance, when diver tourists choose a hotel or restaurant they likely have no idea whether these businesses follow best practices regarding coral reef health. Is the *fish du jour* a critical reef inhabitant? Does the hotel manage its wastewater properly? Coral reef-dependent businesses and those businesses that potentially impact coral reef health could be incentivized to take concrete steps to improve their environmental and sustainability practices, and thus reef health, if they were positively rewarded with an eco-label that reflected their contributions and steps taken to protect reefs (Box VII; e.g., Sasidharan et al., 2002). Relevant sectors that might be positively influenced by a coral reef stewardship label could include the hotel and cruise ship industries, restaurants, dive shops and liveaboards that cater to the dive industry, airlines and energy companies operating in coral reef areas, and others. Efforts to develop sustainable standards for tourism are ongoing through entities such as the Caribbean Tourism Organization (CTO), the Caribbean Alliance for Sustainable Tourism (CAST), the cruise ship industry, and others, but it is imperative that standards and certifications are assessed by independent entities.

Eco-labeling serves to make sustainability commitments more transparent to consumers, signaling overall better resource health than in unlabeled resources (Gutiérrez et al., 2012). Eco-labels such as the well-recognized Marine Stewardship Council (MSC) Fisheries Certification are not without controversy, however, as critics argue they fail to provide consistently comprehensive protections for the species in question (e.g., Jacquet et al., 2010). Nevertheless, a thoughtfully constructed voluntary stewardship labeling program, managed by a transparent third party (e.g., similar to the Blue Flag certification; Box VIII), could be developed for Caribbean reef ecosystems. The label would reflect direct investment, the adoption of best practices, or other concrete, regionally appropriate actions directly linked to coral reef resilience and health in the face of climate change.

Three socioeconomic and governance solutions were identified that could enhance reef health and restoration efforts in the region:

1. increase the communication and potential to leverage resources through the establishment of a regional reef secretariat,
2. incorporate reef health and sustainability issues into the blue economy plans of the region,
3. initiate a coral reef eco-labeling program that provides positive rewards for corporations becoming partners in reef restoration and sustaining overall coral health in the region.

3. Summary and conclusions

The coral reefs of the Caribbean and Western Atlantic Region have suffered extreme damage and degradation over the last

STI strives to minimize negative impacts of tourism while maximizing the benefits to local communities and the environment. They work with multiple partners (governments, companies, NGOs and local communities) to find a balance between economic development and protection of natural and cultural assets. One focus area of STI targets oceans and coral reefs, and several initiatives with partners in the Caribbean aim to foster sustainable tourism, slow the decline of coral reef health, and conserve marine habitats (https://sustainabletravel.org/our-work/oceans-reefs/). Some of these initiatives include partnerships with the Mesoamerican Reef Tourism Initiative (MARTI), Sustainable Destinations Alliance For The Americas and The Heart of St. Kitts Foundation.

Box VI. Case Study: Sustainable Travel International (STI).

Some of the world's most popular surf locations are located in some of the most pristine and vulnerable coral reef locations that are threatened by both local and global environmental change. Surf travel to remote places is often associated with a high carbon footprint contributing to climate change. While poor planning, development, and operation of surf resorts can have strong direct negative impacts on the local environment, culture and heritage, the STOKE program attempts to mitigate these impacts. The idea of the STOKE certification program is that both operators and clients contribute to environmentally sustainable practices. It offers operators a clear and structured path to implement best practices based on an extensive list of criteria. These consider sustainability management, conservations of resources, environmental impact and many more. Similarly, clients can identify and choose operators who embody sustainability based on their level of certification (https://www.stokecertified.com/).

Box VII. Case Study: STOKE sustainability certification program for surf resorts.

The Blue Flag is a voluntary eco-label focused on beaches, marinas and boating tourism operators with a global reach. They have developed a set of criteria based on environmental, educational, safety- and access-related properties that need to be fulfilled in order to qualify for the certification. As an example, the environmental criteria for Blue Flag certified beaches are focused on educating recreational users about the environment and local ecosystems, train personnel and tourist service providers about best practices, fulfill certain water quality standards with regular water quality testing and reporting, and monitor nearby sensitive habitats such as coral reefs. This monitoring program is required to be conducted in consultation with an expert organization. For boating tourism operators, general requirements have been developed for all operators, while additional criteria depend on whether the activity involves diving, whale watching, fishing, etc. (https://www.blueflag.global).

Box VIII. Case Study: Blue Flag certification.

few decades. Nevertheless, these coral ecosystems have achieved a certain level of resilience and opportunities to enhance reef resistance to current and future impacts provide hope for the future. The persistence of coral reef ecosystems are critical to the culture and economics of human communities in the region and innovative solutions are needed to counteract losses in coral reef function and ecosystem services. Because of the fundamental dependence on reef ecosystems, and the poor ecological condition of many coral reefs in the region, there are few downsides to innovative ecological, social and economic approaches to improving reef health. We highlight four categories of solutions that could be implemented immediately to enhance coral reef health now and into the future throughout the Caribbean and Western Atlantic Region. These include: (1) manage land-based and near-shore water fluxes and quality, (2) reduce unsustainable fishing practices, (3) develop and evaluate ecological engineering and, (4) implement marine spatial planning. Furthermore, from a socioeconomic and governance perspective, we propose to (1) establish a Caribbean secretariat for coordinated reef restoration investments, (2) develop blue economy principles for coral reefs, and (3) initiate a reef eco-labeling program. Implementing these strategies will improve the ecological and human well-being of the Caribbean region and could make the region a testbed for novel approaches that could benefit coral reefs and people worldwide. Although the proposed actions can make a significant difference for local reef health on short and intermediate timescales, it is important to recognize that this should occur in parallel with the development of international agreements on CO_2 stabilization pathways to ensure the long-term sustainability of global coral reef ecosystems under the threat of a rapidly changing climate and ocean acidification.

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Declaration of competing interest

None.

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