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> CARIBBEAN MARINE CLIMATE CHANGE REPORT CARD: SCIENCE REVIEW 2017 Science Review 2017: pp 83-114.

Impacts of Climate Change on Fish and Shellfish in the Coastal and Marine Environments of Caribbean Small Island Developing States (SIDS)

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EXECUTIVE SUMMARY

The commercially important fish and shellfish of Caribbean SIDS have been considered in four groups based on environment and following the typical division of fishery groups used in this region.

There is a dearth of research and long-term datasets on the impacts of climate change on Caribbean marine environments and the important fishery resources. Most research to date has been outside of the Caribbean and has examined the impacts of one or two stressors in short-term *ex situ* experiments which are unlikely to accurately reflect the true complexity of long-term *in situ* impacts of climate change in the region. There is a need to consider the combined effects of climate change stressors (direct and indirect) on both individuals and ecosystems, together with the synergistic effects of other chronic anthropogenic stressors in the region.

We consider the reef-associated shallow shelf group to be the most vulnerable of the four fishery groups given: 1) the already apparent negative climate change impacts on their critical habitats; 2) the overexploited state of most reef-associated fishery stocks; 3) the already degraded state of their nearshore habitats as a result of other anthropogenic activities; and 4) their biphasic life history, requiring the ability to settle in specific benthic nursery habitat from a pelagic early life stage.

We consider the most resilient group, over the short-term, to be the oceanic pelagic species that generally show fewer negative responses to the climate change stressors given that they: 1) are highly mobile with generally good acid-base regulation; 2) have an entirely pelagic lifecycle; 3) have less vulnerable reproductive strategies (i.e. they have extended spawning seasons and over broad areas); and 4) are generally exposed to fewer or less severe anthropogenic stressors.

This summary is provided with the following important caveat: "Any attempt to report on what has already happened to fish and shellfish resources in the Caribbean, based on direct evidence, will be strongly biased by the fact that there is a lack of monitoring and directed research examining fish and shellfish species-level impacts of climate change in this region. As such, any conclusions drawn from direct evidence alone will likely misrepresent the true nature and extent of the climate change impacts on the coastal and marine fish and shellfish resources within the Caribbean to date."

What is Already Happening?

With regard to ocean acidification (OA) there has been a recorded decrease in the Caribbean basin in the pH of seawater accompanied by a sustained decrease in the aragonite saturation state over the period 1988 – 2012. More widespread





United Kingdom Hydrographic Office

[Version 0.6]).



ocean acidification data, derived from satellites, and showing

high resolution spatialpatterns is still under experimental development (see NOAA's Ocean Acidification Product Suite

With regard to sea surface temperature (SST) there is

measured evidence across the entire Caribbean Sea (albeit

National Oceanography Centre NATURAL ENVIRONMENT RESEARCH COUNCIL spatially variable) during the latter part of the last century and the early part of this century of: an overall increase in SST; an increase in the frequency of occurrence of anomalous 'hotspots'(greater than 1 °C above mean monthly maximum SST); an increase in the occurrence of periods of deleterious 'heating stress'(greater than 8 degree heating weeks); and an increase in the frequency of category 4 and 5 hurricanes.

To date there is no direct evidence of reduced calcification by Caribbean fish or shellfish, although there is scant anecdotal evidence that some Pedro Bank fishers perceive queen conch shells are becoming more brittle. There is also no published evidence of the insidious impacts of high pCO_2 (hypercapnia) in the commercially important fish and shellfish resources of the region, although laboratory studies are currently underway for queen conch in Mexico.

It is clear that warmer SSTs must be having a direct impact on Caribbean fish and shellfish metabolism since they are poikilothermic ectotherms ('cold blooded'). This impact is likely to be largely negative, given that many species are already likely to be close to their critical maximum temperature and minimum oxygen thresholds, at least during the summer months. Changing temperatures will have already impacted species' phenologies and ELH development times with the likely result of less successful recruitment (population replenishment). However, again there are no studies that have examined likely changes in, for example: metabolic rate, growth, development of ELH stages, phenologies, or mortality from anoxia in Caribbean species from any of the commercially important groups in the wild, over time-scales long enough to detect change that can be attributed to climate-induced changes in SST.

However, increasing SSTs and associated changes have had measurable negative impacts across the Caribbean on the essential habitats of fish and shellfish, especially coral reefs since the 1980s, through mass coral bleaching and mortality events, increased incidences of coral and other invertebrate diseases, and greater physical destruction. These climate change stressors have exacerbated the on-going chronic degradation of these habitats from other anthropogenic stressors including deteriorating water quality (from land-based activities along the coast and within watersheds), physical destruction (from coastal development and marine construction), and chronic over-harvesting. The evidence is clear in the changing composition of the foundational reef species, the decline in live coral cover and architectural complexity (rugosity) of reef structural framework; as well as in the loss of mangrove and seagrass habitat. There is also evidence of climate-induced reductions in the seasonal coastal upwelling off Venezuela coupled with a reduction in phytoplankton productivity and a change in the dominant phytoplankton species in the southern Caribbean Sea. Similarly, climate-induced changes to SST and global winds have been associated with the recent mass influxes of pelagic sargassum into the Caribbean Sea.

The impact of OA on essential habitats is less well studied than SST, but there is laboratory evidence, for at least some Caribbean coral species, of significant negative impacts on successful sexual reproduction and settlement success,

resulting in a reduction in the resilience of coral communities. For mangroves and seagrasses in the Caribbean, the impacts of climate change have not been determined separately from those of other anthropogenic stressors, although the latter are considered to have been more important to date.

The indirect impacts of the climate-induced changes to essential habitats (including the open ocean) on the fish and shellfish resources have not been widely monitored or reported, and are indeed difficult to separate from the whole gamut of changes occurring within these habitats that have been largely caused by other anthropogenic stressors. However, there are several studies providing evidence. Decline in live coral cover, caused largely by temperature-induced mass coral bleaching, has already been linked to declines in reef fish in Cuba. Declines in herbivorous reef fish biomass across the Caribbean have been attributed to increases in SST. Likewise, substantial Caribbeanwide declines over the period 1955-2007 in the density of three broadly different functional groups of reef fish (herbivores, planktivores and carnivores) have been attributed to sustained decline in the health of essential habitats. This has also been demonstrated in the Bahamas, with a decline in fish size and abundance with loss of reef architecture. The decline in manaroves across the Caribbean has also been linked with a decline in Caribbean fishery species, and declining seagrass habitat has been blamed for the decline in gueen conch stocks in several countries. With regard to the open ocean, the climateinduced reduction in phytoplankton productivity in the southern Caribbean has been linked to the collapse of sardine populations there. Further, there is substantial anecdotal evidence that the mass influxes of pelagic sargassum into the Caribbean over the last few years has impacted the availability and/or size of commercially important pelagic species including flyingfish and dolphinfish, as well as species within the reef-associated shallow shelf group. The variable stock dynamics of spiny lobsters has also been linked to climate-induced changes in the North Atlantic Oscillation.

What Could Happen?

The complex and varied impacts of climate change on commercially important Caribbean fish and shellfish expected to occur during this century have been described and referenced in detail in the Full Review presented in Section 1 and the Supplementary Information presented at the end of this document. Most of these expectations are drawn from studies conducted outside of this region but in similar tropical marine habitats or on closely related species. Here we simply provide a very brief summary of some of the main findings.

There will be few if any 'winners' with regard to the commercially important fish and shellfish resources as climate change progresses in this region.

Essential habitats, especially coral reefs, and to a slightly lesser extent, mangroves and sea grasses, will continue to degrade under increasing SST (largely through recurrent mass coral bleaching and mortality events) and the associated increases in climate variability and storm intensity, under intensifying OA and sea level rise (SLR). As such, coral reefs will continue to lose live coral cover, structural complexity, and the ability to support the enormous biodiversity that makes up the reef community, directly (and indirectly) supporting a large number of commercially important fish and shellfish species. Coral reef communities are therefore expected to lose resilience and ultimately to show negative accretion (erosion) of the reef structural framework. Mangroves and sea grasses that are currently protected by reef barriers will likely be lost as reefs erode and sea level continues to rise. Mangroves will become increasingly impacted by SLR, and in SIDS where there is little opportunity to migrate landwards, these habitats will be lost. Since mangroves and seagrasses are obligatory nursery habitats for some species, and for others provide adult habitat or greatly enhanced reef productivity, their loss will result in declining carrying capacity of coastal environments to support reef-associated fish and shellfish populations.

Decline in the health of essential coastal habitats will result in decline in biomass of reef-associated shallow shelf species; those associated with estuarine environments (many of the shrimp and groundfish species); the deep-slope species whose juveniles rely on reefs; and will also impact the offshore pelagic species whose diets depend, at least in part, on pelagic ELH stages of reef-associated species.

Continuing physical, chemical and biological changes to the open ocean environment, expected under climate change this century, especially increasing OA and SST, changes to mesoscale currents, and changes in phytoplankton productivity will have very wide-ranging impacts on all fish and shellfish species within the Caribbean, given that all have pelagic ELH stages. Distribution and survival of ELH stages are expected to decline with faster development times under increasing SST and physiological impairment under increasing OA. Those species requiring settlement to critical benthic habitats will be particularly affected by changes in surface currents, and impairment of their ability to recognize settlement cues. Increased occurrence of toxic algal blooms will be detrimental particularly to coastal species, whereas pelagic sargassum blooms are likely to have mixed effects, perhaps enhancing the recruitment success of some pelagic and coastal species, decreasing the catchability of flyingfishes, and damaging essential coastal habitats when mass strandings of the weed occur.

Range shifts expected in most marine species, as they seek to re-align their distribution to match their physiological tolerances, will likely see a reduction (or at worst local extinction) in most commercially important species in the Caribbean as they shift polewards. Immigration of new species seeking to shift their range is not expected in the Caribbean under climate change.

Confidence Assessment

What is already happening



observations / models) modelled)

Medium/low level agreement based on already observed changes to nearshore and ocean environments within the Caribbean and published evidence of impacts of these changes on related species, mostly from other tropical regions.

What could happen in the future



Low/low level agreement based on: 1) the extreme complexity of the combined effects of multiple climate change stressors about which there is little information, 2) the large variation in responses among and within species and life history stages, 3) lack of agreement amongst studies on the response trajectories of similar taxonomic groups to climate changes, and 4) the general lack of understanding of the synergistic effects of overexploitation and habitat degradation in addition to climate change impacts.

Knowledge Gaps

Species-specific studies of increasing SST and OA on queen conch and spiny lobster are necessary to improve predictions of climate change on two of the region's most economically valuable fishery species. There is a need to assess the difference in resilience to climate change between heavily exploited versus protected reef fish stocks to provide better guidance on the appropriate management tools and strategies (including marine reserves) needed for climate change adaptation.

There is also a need to assess the extent to which sea surface currents will change under climate change and thereby impact marine population connectivity patterns, to improve decisionmaking with regard to marine protected area networks; potential changes to locations of shared stocks; and the timing and frequency of sargassum influxes.

Socio-economic Impacts

Climate change impacts on commercially important fish and shellfish will have a wide array of social and economic implications in Caribbean SIDS including impacts on: (1) the consumptive use value to the fisheries sector, resulting in decreased food security and livelihood and employment of those working in the fisheries sector *inter alia*; (2) the non-consumptive use value of fish and shellfish to the recreational diving (SCUBA and snorkelling) sector as well as other underwater viewing activities (e.g. glass-bottomed boats and recreational submarines) resulting in substantive losses in potential revenues; and 3) the non-market values of fish and shellfish in providing supporting and regulating ecosystem services with significant implications.

1) Consumptive direct use values (Fisheries sector)

The direct and indirect socio-economic impacts of climateinduced changes to the availability (abundance and distribution) of commercially important fish and shellfish to the fishery sector in the Caribbean SIDS are covered in a fishery-specific chapter (see Monnereau & Oxenford, 2017 this volume). The main points regarding this issue, are summarised here:

Decreasing abundance of reef-associated fishes, expected to be the hardest hit by climate change initially, will have the greatest socio-economic impacts on the harvest and postharvest sectors in coastal communities where these reef fish species are primarily harvested by traps, spears, nets and handlines, and sold to local consumers.

The SIDS most severely impacted will be those where reefassociated fisheries are the most important, such as Antigua & Barbuda, Belize, Jamaica, and St Vincent & the Grenadines.

Projected increases in ciguatera poisoning will also affect trade in reef-associated and some deep-slope fishes and will impact on the health of local communities, the main consumers of these fish species.

Changes in availability of high-value species (spiny lobster, conch, shrimp) will have particular impact on harvesters (both small-scale and semi-industrial) and will negatively affect export trade volumes and foreign currency revenue generation.

SIDS countries likely to be most severely impacted by declines in these high-value shellfishes are those with significant export fisheries, such as Guyana (shrimp), Belize and Jamaica (conch, spiny lobster).

Changes in the productivity and distribution of oceanic pelagic species, such as dolphinfish, tuna, and tuna-like species, are likely to result in reduced abundance and catchability, as stocks are predicted to move northwards and beyond the limited reach of small-scale fleets at least within the southern SIDS.

In the short-term, pelagic fishers will most likely have to fish longer or travel further to maintain catch rates, or rely on moored FADS to aggregate fishes. The former will have both financial and safety implications for fishers.

Smaller catches of pelagic species and associated increased ex-vessel prices will have significant impact on the harvest and the post-harvest sector, especially as it is these species that generally support the greatest value-added processing.

Possible changes in the migration patterns and distribution of transboundary oceanic pelagic species will also have implications for regional policy and shared management plans, and for fishing quota allocation and access agreements.

Possible changes in the distribution patterns of ELH stages of demersal species and/or changes in their distribution ranges has implications for population connectivity of species across the Caribbean and for the designation of effective networks of Marine Protected Areas (MPAs).

SIDS most likely to be impacted by declines in pelagic species and processing opportunities will include Dominica and St Lucia where pelagic fish species are particularly important.

Decreases in the profitability of fishing will negatively affect the willingness of investors and the attractiveness of investing in the harvest and post-harvest processing sectors.

Over the longer-term as reef resources become increasingly degraded and over-exploited and pelagic species less available, fisherfolk may have to abandon fishing and look for scarce alternative employment opportunities. This will likely require government incentives and training programmes to retool fishers. Alternatively, the sector may adapt by switching from small-scale to medium-sized boats, resulting in higher capital investment and maintenance costs as well as higher potential losses in cases of extreme-weather events.

Reductions in fish and shellfish fishery yields in Caribbean SIDS can be expected to have significant socio-economic impacts on fisherfolk (fishers and other actors in the fish market chain) and their dependents. It will also have implications at the level of national governments for: domestic productivity in the fishing sector; food security and food sovereignty (and by implication on the food import bill); export trade and foreign currency earnings.

Reducing abundance of fish and shellfish resources will also exacerbate conflict, not only intra-fisheries conflict amongst fishers competing for the same limited resource, including commercial versus recreational fishers, but also between the fisheries sector (consumptive users) and other nonconsumptive users (e.g. recreational divers). The latter will be especially acute for reef fishes.

2) Non-consumptive direct use values (recreational use)

Fish and shellfish resources have significant non-consumptive use value to the recreational diving (SCUBA and snorkelling) sector as well as other underwater viewing activities (e.g. glassbottomed boats and recreational submarines), Again, Caribbean studies specifically focusing on these values for the commercially important fish and shellfish resources (rather than the entire coral reef community) under climate change are scarce (see Mumby et al., 2014). However, a recent study by Gill et al. (2015) examined the value of the reef fish resource to the recreational SCUBA diving industry across seven different coastal communities in three Caribbean countries and, using a choice experiment and willingness-to-pay model, they assessed how this value might be altered by changes in reef fish attributes (size and density) that could be expected under future climate change. The results indicated that relatively small (5-10%) future declines in the abundance of reef fishes, and particularly in the number of large fishes observed on recreational dives, will result in significant reductions in diver consumer surplus. For example, these losses ranged from US\$ 1.2 million in St Kitts & Nevis to 7.9 million per year in the Bay Islands, Honduras for reductions in the current abundance of fish seen on recreational dives. Aggregate annual losses for a reduction in the number of largesized fish viewed on recreational dives varied from US\$ 1.2 million in Barbados to 11 million in the Bay Islands (Gill et al., 2015). Furthermore, these loss values would likely be considerably more substantial, if the aesthetic value of reef fish to the much larger number of recreational snorkellers and other boaters viewing reef fish at these sites were to be included.

In some countries, there is considerable value attached to recreational diving/snorkelling on iconic reef fish species aggregations such as sharks and rays. Examples include famous dive/snorkelling sites such as Shark Ray Alley in Hol Chan Marine Reserve, Belize; Stingray City in Grand Cayman; and a mixed species spawning aggregation site at Gladden Spit, Belize where divers pay considerable sums to view the spawning snappers and groupers and the whale sharks that are attracted to the site during spawning events (see Heyman *et al.*, 2010 and references therein).

3) Non-market ecosystem service values:

Caribbean fish and shellfish provide a number of important ecosystem services which are acknowledged, but have not had monetary values attached to them (see Mumby *et al.*, 2014 for reef fish). These include both regulating services that help to control climate (e.g. carbon sequestration) and supporting services that help to maintain ecosystem functioning (e.g. nutrient cycling, biodiversity, grazing etc.).

With regard to regulating services, recent attention has been given to the global value of marine vertebrates in sequestering carbon (dubbed 'blue carbon' or 'fish carbon') and therefore helping to reduce climate change impacts (Lutze & Martin, 2014).

With regard to supporting services, fish and shellfish are known to provide essential nutrient cycling services within coral reef communities, where retention and efficient recycling of nutrients are critical to sustaining reef productivity in typically low nutrient (oligotrophic) environments. Likewise, many species (e.g. grunts, parrotfishes, spiny lobsters, queen conchs, octopuses) are important in transport and dispersal of nutrients among associated ecosystems (e.g. coral reefs, mangroves and seagrasses) through diurnal movements, seasonal spawning and ontogenic movement among migrations, them. Furthermore, reef fishes support oceanic pelagic food webs through export of ELH stages (pelagic larvae and juveniles) that provide an important component of the diets of many commercially important large oceanic pelagic fishes (Heileman et al. 2008).

Recent attention has also been focused on the commercially important parrotfishes and surgeonfishes in the Caribbean as keystone grazers or reef health engineers, critical for maintaining the balance between coral and macroalgae on the region's reefs (Adam *et al.*, 2015).

The current socio-economic values of these regulating and supporting ecosystem services and how they will change as the region's fish and shellfish decline under climate change remain unknown.

Full Review

1. INTRODUCTION

In this review we first set the context by: 1) providing a very brief overview of Caribbean marine biogeography; 2) defining the key groups of commercially important fish and shellfish that support the main fisheries of the Caribbean SIDS; and 3) outlining the climate change stressors of greatest relevance to Caribbean fish and shellfish resources.

Given the highly technical nature of the impacts on the biology and ecology of fish and shellfish, we then go on to explain first the direct physiological changes that will occur under climate change, drawing on the physics and chemistry of each stressor to explain observed and expected changes to the physiology and resultant development and behaviour fish and shellfish. In this regard we focus on tropical species of relevance to the Caribbean. We then examine the indirect impacts that are likely as a result of climate-induced changes to essential habitats of fish and shellfish, focusing on the coastal habitats (coral reefs, mangroves and seagrasses) and the open ocean ecosystem. This section should link directly to the separate chapters specifically dealing with coral reefs (McField, 2017) and mangroves (Wilson, 2017), and as such the relevant information on changes to essential habitats is provided here as concise summaries only, in a supplementary information section.

Having described the scientific details of climate change impacts to fish and shellfish, we then examine this from the perspective of commercially important fisheries in the Caribbean SIDS that relates directly to the chapter on impacts to the fishery sector (Monnereau and Oxenford, 2017). We do this by summarising what we believe to be the most important impacts of climate change over this century, on each of the four main fishery species groups separately. This summary draws on information available in the published literature from conspecifics and related taxa and from laboratory and field studies, mostly outside of the Caribbean, together with information on the biophysical characteristics of the Caribbean Sea and our knowledge of the broad exploitation status of commercially important stocks. Wherever possible we have attempted to point out the impacts that have already happened, and those which are likely to happen in the near-future. However, this is constrained by a lack of Caribbean studies, meaning that impacts that are likely to have already happened, have not been monitored or reported. As such, any attempt to report on what has already happened, based on direct evidence, will be strongly biased and likely provide a false sense of security that the Caribbean is somehow faring better than other locations that have been better studied.

1.1. Aspects of Caribbean Marine Biogeography

The Caribbean Sea holds the highest density of marine species within the Atlantic and is recognized as a global-scale hotspot for marine biodiversity (Roberts et al., 2002). This semi-enclosed, tropical sea (extending from 10-22°N latitude) also exhibits relatively high levels of endemism, being estimated to be as much as 45% for fish and 26% for molluscs (Miloslavich et al., 2010). Whilst high species richness is a feature of tropical latitudes, it is enhanced in this region by the considerable spatial heterogeneity of physical and chemical environments and variety of coastal and oceanic habitats found here (e.g. Sullivan Sealy & Bustamante, 1999; Spalding et al., 2007; Chollett et al., 2012; Rice et al., 2016). However, it is also considered to be a region of low marine productivity, thus 'posing a considerable challenge to maintaining sustainable fisheries' (Die & Rodriguez Casariego, 2016: 1). Furthermore, significant declines in Caribbean marine biodiversity have been noted in the recent global integrated marine assessment, with overexploitation and environmental degradation listed as the key drivers of this decline to date (Rice et al., 2016).

1.2. Defining the Commercially Important Fish and Shellfish

The fish and shellfish resources of commercial importance to capture fisheries in the Caribbean are highly diverse. This is the result of the underlying biogeographic heterogeneity and high biodiversity of the region, and reflected in the large variety of non-specific gear (e.g. fish traps, nets, spears, lines) generally used by the small-scale artisanal and semi-industrial fisheries of the region (FAO, 1993; Salas *et al.*, 2011). There are over 1,100 fish and shellfish species of interest to fisheries documented in this region (Carpenter, 2002). As an example, the US Caribbean Fishery Management Council lists 93 shallow reef fish species alone in their shallow-water reef fish fishery management plan¹ as being commonly caught by the commercial reef fishery. The wide range of non-reef species landed by individual countries, although often grouped, is also evident from the FAO global fishery statistics database²).

In this review, for ease of comparison with much of the literature on CARICOM fisheries and for informing the review of impacts on the fisheries sector, we examine the impacts of climate change on each of the four main groupings of commercially important species generally considered to typify the CARICOM region, especially the small island developing states (SIDS) of Antigua & Barbuda, Belize, Dominica, Grenada, Guyana, Jamaica, Saint Lucia, and Saint Vincent & Grenadines. These species groups are categorized by the environment (broad habitat types) in which they are found. The 'reef-associated shallow shelf group' includes a large number of essentially benthic or site-attached species such as the reef fishes (e.g. shallow-water snappers, groupers, parrotfishes, grunts, squirrelfishes, triggerfishes, surgeonfishes inter alia) and shellfishes (mainly conch and spiny lobster), and nearshore, schooling pelagic fishes (jacks, sardines, pilchards, ballyhoo, mackerels, small tunas, etc.). This group of species is characterized by a reliance on coral reefs and associated ecosystems (seagrass meadows, mangroves, sand flats, algal hard grounds and reef rubble) which are typical of the shallow, clear-water, shelf areas of the insular Caribbean and Caribbean coastlines of Belize and other Central American countries. The 'deep slope group' includes a number of essentially benthic species that live, at least as adults, in deep (>100 m) rocky or rubble areas well below the typical depth of actively growing euphotic coral reefs (i.e. < 50 m) usually along the shelf edge or deep banks, and includes mostly finfishes such as deep-water snappers (e.g. red, queen, vermilion, silk, blackfin), deep-water groupers (e.g. red, black, yellowfin, yellowmouth) and others such as amberjacks, etc. The 'shrimp and groundfish group' generally refers to a number of benthic species of shellfishes, i.e. penaeid shrimps/prawns (seabob, white belly shrimp, southern pink shrimp, southern brown shrimp, southern white shrimp, red spotted prawn) and finfishes (e.g. weakfishes such as

¹<u>http://www.caribbeanfmc.com/fmp_reef_fish.html</u>

² <u>http://www.fao.org/fishery/statistics/global-capture-production/query/en</u>

bangamary and Guyana sea trout; croakers such as butterfish; and sea catfish) which rely on shallow, muddy or sandy continental shelf areas and associated estuaries and mangroves typical of **the** Caribbean coastlines of Guyana and other South American countries. The '**oceanic pelagics group**' includes the more offshore, open water, highly migratory, epipelagic (surface) species (e.g. flyingfish, dolphinfish, wahoo) and large subsurface species (e.g. billfishes, large tunas, sharks) which occur throughout the Atlantic and Caribbean Sea in offshore, open water.

1.3. Climate Change Stressors of Greatest Significance to Marine Fishery Resources

Recent substantive reviews that have examined the impact of climate change globally on marine ecosystems include Brierley & Kingsford (2009), Hoegh-Guldberg & Bruno (2010), Doney et al. (2012) and those of the Working Group II (WGII) of the fifth assessment report (AR5) of the Intergovernmental Panel on Climate Change (IPCC) (ocean systems: Pörtner et al., 2014; Hoegh-Guldberg et al., 2014; coastal systems: Wong et al. 2014). There have been a few reviews that have considered the potential climate change impacts specifically on Caribbean marine resources supporting fisheries (e.g. Cambers et al., 2008 examine coastal and marine biodiversity; Simpson et al., 2009 give coral reefs some coverage; and Lum Kong, 2002; Mahon, 2002; Nurse, 2009; 2011; and Martínez Arroyo et al., 2011 consider fisheries). All have highlighted the dearth of research on actual observed impacts of climate change on marine resources specifically within this region.

The climate change parameters on which we particularly focus in this review include those known to have the greatest impact on fish and shellfish, i.e. increasing sea surface temperature (SST) and ocean acidification (OA). We also consider sea level rise (SLR) and increased variability of extreme weather events (e.g. storms, precipitation anomalies) mostly in relation to their impacts on critical fish and shellfish habitats. We use published information on changes that have already occurred and that are predicted to occur in these climate parameters as summarised by the most recent assessment (AR5) of the (IPCC) released as a series of technical documents during 2013-14³. Wherever possible, we are also guided by on-going efforts to downscale the global climate change models to smaller regional scales that focus on the Caribbean (e.g. see Simpson et al., 2009; Taylor et al., 2012a for review; Hall et al., 2012; Nurse & Charlery, 2016) and by summaries that focus on the plight of SIDS (e.g. Pulwarty et al., 2010; Carabine & Dupar, 2014).

These climate change stressors are likely to have numerous inter-related impacts on commercially important species in the Caribbean, through (1) direct effects on their physiology and life processes (e.g. respiration, growth and development rate,

reproduction, longevity); and (2) indirect effects arising from significant impacts to essential benthic habitats effecting living space, refuge and predator-prey relationships, to name a few; and from physical and biological oceanographic changes effecting survival, dispersal and settlement of early life history stages, and migration and distribution ranges of adults, *inter alia*. These direct and indirect impacts on different life stages and processes by different climate change stressors are examined in the following sections, focusing on the Caribbean or at least on Caribbean species wherever relevant studies are available. Lastly, we attempt to summarise the climate change impacts for each of the four main commercially important species groupings (i.e. reef associated shallow shelf, deep slope, shrimp and groundfish, and oceanic pelagics) based on what we can deduce from this literature review.

2. DIRECT PHYSIOLOGICAL IMPACTS

2.1. Ocean Acidification (OA)

Elevated atmospheric carbon dioxide (CO₂), the main driver of climate change, results in an increased uptake of CO₂ at the ocean's surface, manifesting as higher partial pressure of CO₂ (pCO₂) in the ocean and leading to a decline in seawater pH and a change in the relative concentrations of carbonate, bicarbonate and hydrogen ions and decreasing carbonate/aragonite saturation state. This occurs because the increased numbers of hydrogen ions. The outcome of these relatively complex chemical processes in seawater is referred to generally as 'ocean acidification' (OA) (Doney, 2010).

The most recent IPCC AR5 report provides several greenhouse gas emission trajectories based on representative concentration pathways (RCPs) by the year 2100, which range from low (RCP2.6) resulting in carbon dioxide equivalent (CO₂ eq) concentrations of around 430 - 480 ppm to high (RCP8.5) resulting in CO₂ eq concentrations of more than 1000 ppm.

These changes, when considered as the acidity of seawater, are given in pH units. The average ocean pH is estimated to have declined by 0.1 units over the last 250 years, but is projected to show a much more rapid decline in the coming years, dropping by a further 0.1 - 0.35 units by the end of this century under current (AR5) CO₂ emission trajectories (Collins *et al.*, 2013). In the Caribbean basin, a recorded decrease in the pH of seawater has followed the global trend and has been accompanied by a sustained decrease in the aragonite saturation state over the period 1988 – 2012, albeit seasonally and spatially variable (Mumby *et al.*, 2014).

³ see <u>http://www.ipcc.ch/report/ar5/</u>

The increase in ocean pCO_2 and altered relative concentration of ions readily diffuses into the bodies of many water-breathing marine organisms through their gills and/or relatively porous body walls, in turn causing hypercapnia and pH disturbances in extra- and intra-cellular spaces throughout their bodies and directly or indirectly influencing cells and their inherent processes and functions, including the calcium carbonate saturation state in the fluids at calcification sites.

Attention was initially placed on the impacts of OA on calcifying organisms, but more recent work has uncovered a large number of other pervasive physiological impacts across a range of tissues affecting non-calcifying organisms. These impacts are summarised in the following subsections.

2.1.1. Reduced calcification

The changes in sea water chemistry under increased atmospheric CO₂ are complex, but have the potential to profoundly affect the ability of calcifying organisms to build calcium carbonate shells and exoskeletons. As the pH decreases, it will become increasingly difficult (energetically costly) for calcifying tissues to function, as they will need to actively pump out increasing numbers of hydrogen ions in order to utilise the carbonate ions (Wittmann & Pörtner, 2013). The resultant impacts on a variety of calcifying organisms is still under investigation, with quite different responses being reported for different taxa of importance to fisheries and at different latitudes (e.g. Ries et al., 2009; see Wittmann & Pörtner, 2013 for meta-analysis). Not only will many commercially important calcifiers (shellfish) be negatively impacted, but also the major planktonic calcifiers (e.g. coccolithophores, foraminifera, pteropods) and a host of other meroplankton calcifiers (which include the larval stages of many benthic invertebrates). The impacts on these planktonic members which, to date, have been poorly studied, are expected to have profound effects on ocean food webs and indeed the entire ocean carbon budget (Kleypas et al., 2006).

2.1.2. Impaired neurosensory function and metabolism

Elevated *p*CO₂ causes a host of physiological changes (in addition to declining calcification rates) in fish and other waterbreathing organisms, resulting from a failure of their acid-base and ion regulation mechanisms, and the consequent acidosis of blood and other tissues (see recent reviews and meta-analyses of impacts on: a range of marine taxa - Wittmann & Pörtner, 2013; fishes - Heuer & Grosell, 2014; early life history of fishes - Llopiz *et al.*, 2014; and lobsters - Briones-Fourzan & Lozano-Alverez; 2015). These authors list a large number of somewhat surprising sensitivities to present-day and near-future CO₂ levels resulting from this failure in some organisms to compensate for acid-base changes in ocean chemistry. Among these are significant impacts to neurosensory function through alteration of GABA-A neurotransmitters (Nilsson *et al.*, 2012; Wittmann & Pörtner, 2013; Chivers *et al.*, 2014) which in turn result in a widerange of behavioural changes. Impacts can also include: changes in mitochondrial function resulting in depressed metabolism; reduced function of blood oxygen transport; changes in gene expression leading to changes in protein synthesis which can affect cellular and organism growth; and increased otolith deposition resulting in larger otoliths, which itself may result in changes to hearing sensitivity and orientation (see Llopiz *et al.*, 2016).

2.1.3. Combined impacts of OA

Wittmann & Pörtner (2013) undertook the most comprehensive meta-analysis of published data to date, covering 153 species from a range of taxa. They examined the sensitivity of each species to a range of *p*CO₂ values relevant to IPCC predictions, across five groups: corals, echinoderms, molluscs, crustaceans and fishes. They used a wide array of indicators of physiological performance as criteria to judge sensitivity to OA exposure such as: standard metabolic rate; aerobic scope; growth; morphology; calcification; maintenance of acid-base balance; immune response; fertilization; sperm motility; developmental time; changes in gene expression; and behavioural changes; and included information on different life history stages where available.

From this analysis, they were able to reveal the relative sensitivity of the five taxa and to conclude that, overall, corals, echinoderms and molluscs were the most impacted. These taxa generally tend to be sessile, have relatively low metabolic rates, poor capacity to compensate for acid-base disturbances, and heavy skeletal structures/shells of aragonite or calcite. A significant number of species examined in these taxa is negatively affected even at the lowest levels of pCO_2 tested (500 – 650 µatm) and more than half are negatively affected by levels predicted for the year 2100 (851 - 1,370 µatm) in the RCP8.5 scenario.

Wittmann & Pörtner (2013) conclude that the crustacean group (lobsters, shrimps, crabs), which generally build lighter exoskeletons and are more active than corals, echinoderms and molluscs will fare better under increasing OA (perhaps because of more efficient pH regulation), with the majority of species not being negatively affected until pCO_2 levels exceed 2,086 µatm. However, they also note that almost one third of the crustacean species examined will be negatively affected at lower levels of pCO_2 that can be expected before the year 2100.

With regard to fishes, the results are less clear. As Wittmann & Pörtner (2013) point out, fishes are motile with relatively high metabolic rates and are generally (at least as adults) excellent osmotic and acid-base regulators and have lightweight endoskeletons. As such, they could be expected to cope relatively well with increasing OA. The authors note, however, that their meta-analysis was biased by the fact that the fishes were not from across all climate zones, nor over the long timescales that were available for the invertebrate group. They

noted that the majority of studies were of tropical reef fishes and or early life stages which appear to be highly sensitive to even small increases in pCO_2 (see also Llopiz *et al.*, 2014; Heuer & Grosell, 2014). Another meta-analysis was published in the same year by Kroeker *et al.* (2013), looking at 10 major taxonomic groups, but fewer indices. They considered the impact of OA on survival, calcification, growth, photosynthesis and abundance. Results were broadly similar to the Wittmann & Pörtner (2013) study, with the greatest negative impacts for calcifying algae, corals, coccolithophores, molluscs and echinoderms; no conclusive responses for crustaceans and only growth data for fish, which showed no significant response.

2.2. Sea Surface Temperature (SST)

The Caribbean Sea has warmed by approximately 1.5° C over the last century (Palanisamy *et al.*, 2012) and is expected to warm further by an average of 1.4° C by the years 2081–2100 compared to 1986–2005 levels (Nurse *et al.*, 2014). The actual rise, will of course, depend on which of the projected global emissions scenarios is most closely followed, with average increases in atmospheric temperature projected to be between $0.5 - 0.9^{\circ}$ C by 2100 for the lowest carbon emissions scenario (RCP2.6) and in excess of 4 °C under RCP8.5 (Carabine & Dupar, 2014).

Regional downscaling of SST across the Caribbean indicates that the current spatial heterogeneity, whereby a seasonal warm pool expands out from the Western Caribbean each spring/summer and retracts each fall/winter, will be replaced during this century by two warm pools centred over the Western and Eastern Caribbean that will merge, blanketing the entire region (Nurse & Charlery, 2016). They also note that the small annual range in SST will continue to decrease from a current average of 3.3 °C to just 2.3 °C by the end of the century, indicating that the traditional seasonal 'warm' and 'cool' periods will become less differentiated over the coming decades.

Rising temperatures will have major implications for the structure and functioning of all marine ecosystems (Llopiz *et al.*, 2014). Since fish and shellfish are poikilothermic ectotherms, rising temperatures will result in exponential increases to their metabolisms, leading to higher rates for most physiological processes including: respiration, growth and reproduction *inter alia* (Doney *et al.*, 2012). This could mean higher growth rates and greater stock productivity (provided there is adequate food) for some polar and temperate species, but, for species whose physiological thermal optimum is exceeded, growth and productivity will be reduced.

2.2.1. Sub-optimal or lethal effects

Tropical species will be at greatest risk, given that they are adapted to a relatively stable thermal regime with a narrow temperature range, and the fact that many species already live near their upper thermal limits (Rummer *et al.*, 2013). For these species, reduced growth and reduced fitness will be the outcome

of increasing SST (see Pratchett et al., 2015 and references therein). Early life history (ELH) stages may be particularly sensitive to temperature, although this aspect has not been well studied to date (Llopiz et al., 2014). Rising temperature is known to increase both the hatch rate and development time of eggs and larvae, thereby shortening their pelagic larval duration (PLD) (i.e. the time they spend drifting and dispersing in the plankton). Although this reduces the amount of time they remain highly vulnerable to predation, as Llopiz et al. (2014) point out, increased activity resulting from increased temperature could increase the encounter rate with predators and thus offset any increase in survivorship associated with higher SST. They also note that water viscosity decreases with rising temperature, and that this is likely to promote exponential increases in maneuverability of the tiny prey of larval fish, making them more difficult to catch and compromising larval fish feeding.

Furthermore, as metabolism goes up and O_2 availability diminishes (due to its decreased solubility in warmer water), respiratory distress will result, with many ramifications for decreased performance and increased mortality (Pörtner & Farrell, 2008). Increased biological oxygen demand is particularly significant at night, especially in shallow eutrophic environments, when phytoplankton and macroalgal communities stop photosynthesizing but continue respiration, and the result can be mass asphyxiation of the less mobile vertebrates and invertebrates. Fish and crustaceans are particularly sensitive to low oxygen levels (hypoxia) compared with other taxa (Keeling *et al.*, 2010).

2.2.2. Altered phenologies and population connectivity

Precise timing of life history processes is critical to the survival of many organisms, including fish and shellfish, which have evolved to align their phenologies to seasonal environmental events and to the phenologies of other organisms to maximize their survivorship. For marine species, this precise timing is especially important for the survival of their vulnerable ELH stages (Llopiz et al., 2014). Warmer SSTs are likely to induce significant changes to the timing, duration and locations of spawning in marine species. Of particular concern are changes in the spatio-temporal dynamics of spawning in species that aggregate to spawn in a very specific location for a very short period of time, thereby requiring very precise spawning cues (Petitgas et al., 2013). Furthermore, Lett et al. (2010) used biophysical modelling to show that a decrease in the PLD, caused by an increase in water temperature (within the range currently expected under climate change), would likely reduce average larval dispersal distance and result in an increased contribution of self-recruitment to the population renewal process, altering the existing connectivity patterns among populations. They also showed that a change in the timing of reproduction, caused by increased temperatures, could result in completely different dispersal patterns, since meso-scale currents often have seasonal patterns to their strength and

direction. These changes could therefore have a fundamental impact on the sustainability, connectivity and genetic structure of future populations.

2.2.3. Spread of diseases

There is some evidence that marine diseases will proliferate as waters warm through increasing the ranges and/or virulence of disease agents and/or by compromising the immune systems of heat-stressed organisms (Harvell *et al.*, 2002; 2007), although this remains under debate and does not appear to be the case for all taxonomic groups (Ward & Lafferty, 2004; Burge *et al.*, 2014).

2.2.4. Ecosystem effects

The complexities of predicting the impacts of climate change on marine fish resources over the longer term are enormous and are highlighted by the studies reviewed here. Direct impacts on individuals translate to population-level and community-level changes, which in turn alter predator-prey dynamics and entire marine food webs, causing ecosystem-level effects. Furthermore, species ranges will shift as they align their distribution to match their physiological tolerances under changing environmental conditions. For many species, this means shifts to higher latitudes with substantial declines in tropical species where many are already living close to their maximum temperature and/or minimum oxygen levels.

2.3. Evidence of Direct Impacts Relevant to Commercially Important Caribbean Species

2.3.1. Finfishes

2.3.1.1. Reef and deep slope fishes

There is a large body of recent work on the impacts of elevated SST and pCO_2 specific to coral reef fishes (see reviews by Llopiz *et al.*, 2014; Heuer & Grosell, 2014; Pratchett *et al.*, 2015; Hoey *et al.*, 2016). In summary, research to date suggests that ocean warming and acidification is already having and will continue to have substantive direct effects on physiology, behaviour, abundance, distribution, and composition of tropical coral reef fishes, including those that move to deeper water as adults (deep slope species). This body of work is summarized by impact in the following paragraphs.

Behaviour: High pCO₂ has been shown to result in impairment of a diverse suite of sensory and behavioural abilities in reef fishes which affect habitat selection and timing of settlement to coral reef habitats (Devine *et al.*, 2012). Further, reduced responses to sensory cues, altered activity levels and impaired decision-making is impacting predator-prey interactions in the pelagic larval stages of reef fishes (even at near-future atmospheric concentrations of CO₂ around 650 ppm) and has serious implications for larval survival and subsequent recruitment to benthic juvenile populations (Munday *et al.*, 2010), thus affecting population renewal. For example, pioneering laboratory and field studies on two species of Indo-Pacific reef fishes (clownfish and damselfish) have clearly demonstrated that the diminished olfactory detection of predators by their larvae, results in reduced avoidance behaviour and increased mortality due to predation (Ferrari *et al.*, 2011; Munday *et al.*, 2016). The physiological impacts of high *p*CO₂ have also been shown to be exacerbated in reef fishes by increased SST (Hoey *et al.*, 2016).

Reproduction: Reproduction appears to be highly sensitive to temperature (in at least some reef fishes examined so far), with reduced pairing, lower fecundity and smaller eggs and larvae being produced, or even a complete cessation of spawning, when they are exposed to climate change-relevant increases (i.e. $1.5 - 3 \,^{\circ}$ C) in ambient temperature (Pratchett *et al.*, 2015). Failure of annual recruitment has already been recorded in some coral reef fishes in the central Pacific and attributed to anomalously high temperatures **associated** with El Niňo conditions (Lo-Yat *et al.*, 2011, cited by Pratchett *et al.*, 2015).

Temperature is also an important spawning cue, such that changes to STTs will have far-reaching effects on spawning behaviour. An area of much needed research is the impact on the aggregating reef fish species such as many of the groupers and snappers, whereby as much as 80% of a population's spawning occurs in a highly specific location and over a very short period of time (Petitgas *et al.*, 2013). So far, modelled scenarios for the spawning aggregations of Nassau grouper in the Caribbean predict an overall decrease in spawning activity throughout its range, a shift in the spawning season, and a northward shift in the geographic range where spawning aggregations occur (Erisman & Asch, 2014).

Growth: Munday *et al.*, (2008) examined the impact of increasing water temperature $(26 - 31^{\circ}C)$ on the spiny chromis damselfish, a common Pacific reef fish, and reported that growth rates of all life stages declined with increasing temperatures, implying that capacity for growth would be severely limited at temperatures expected to become the norm in the near future under climate change.

Disease: Although eliciting no known symptoms in reef fish carriers, the incidences of ciguatera fish poisoning in humans after consumption of ciguatoxic reef fish is expected to change in the Caribbean under increasing SSTs that will affect the abundance and distribution of the dinoflagellates producing ciguatoxins (Kibler *et al.*, 2015) (see case study).

2.3.1.2. Estuarine fishes

Information on the direct impacts of climate change on estuarydependent fishes (and shrimps) of importance to fisheries of the Caribbean SIDS is negligible (Meynecke *et al.*, 2006; cited by Ayub, 2010) and apparent in this review. However, since the species of greatest importance to fisheries rely on offshore marine benthic areas as adults and on shallow estuarine habitats as juvenile nursery areas, they are likely to be better adapted to significant changes in salinity, temperature, and hypercapnia than many other species living in more stable habitats, and may therefore have greater resilience to projected near-future changes in these parameters.

2.3.1.3. Open-water pelagic fishes

Our understanding of how OA will impact pelagic open-water fish species has lagged behind that of reefs and their associated species, although there has been recent progress on pelagic species relevant to the Western Central Atlantic and Caribbean (see Hobday et al., 2013; Muhling et al., 2015). All of the Atlantic tunas, swordfish and other billfishes are known to spawn within the Caribbean Sea and/or the Gulf of Mexico (GoM), and water temperature is of great physiological importance to these highly migratory species, but their spawning strategies and temperate tolerances are species-specific (see Muhling et al., 2015 for review). As such the impact of changes in SST on migration, spawning, larval survival and recruitment will potentially differ among species, and will likely be most critical for the temperate bluefin tuna (not of commercial importance to Caribbean SIDS), which has the narrowest spawning period and area, located only within the GoM (Muhling et al. 2011). On the other hand, warming SSTs will be less detrimental, at least in the near-future for species such as the smaller and more widely dispersed skipjack tuna (Muhling et al., 2015). Interestingly, size (which is determined by both age and sex) also has a bearing on temperature tolerance in the large pelagic species. For example, the ability of tunas and billfishes to tolerate warm waters decreases with age and size, whilst their ability to tolerate cold water may increase, illustrating the complexities of discerning temperature effects on these highly migratory species (Muhling et al., 2015).

Most studies indicate that mobile adult fish generally have good acid-base regulation and will be less impacted by OA than their ELH stages. Based on research documenting the impacts of OA on the early life history stages of reef fish (LLopiz et al., 2014), it is reasonable to assume that oceanic pelagic species eggs and larvae will be similarly affected by hypercapnic suppression of metabolism, acid-balance disturbances, interference with a ubiguitous neurotransmitter resulting in behavioural changes, reduced size and sub-lethal effects on developmental stages, inter alia. However, the very limited research in this area for tropical oceanic pelagic species (most of the work has been on the temperate bluefin tuna), so far demonstrates considerable variation in responses both across and within species. For example, Bromhead et al. (2015) examined the effects of OA on yellowfin tuna eggs and larvae at current and relatively extreme pCO_2 levels predicted in some spawning areas by 2100 (< 2,500 µatm), and other high values (5,000 and 10,000 µatm). Their results were somewhat inconclusive, only finding a reduction in larval growth at the level predicted for 2100 in one of two trials and other impacts occurring only at extreme levels expected well beyond the next two centuries. A study examining the impact of OA on the early life history stages of dolphinfish raised for 21

days under current and near-future pCO₂ (350, 770 and 1460 µatm) also detected minimal sensitivity, showing no significant negative effects on hatch rate, size, development or larval swimming ability, although there was some evidence of oversized otolith development (Bignami et al. 2014). In contrast, Pimentel et al. (2014) did detect some OA impacts in dolphinfish larvae incubated at 1,600 µatm pCO2. These included reduced oxygen consumption rate, by as much as 17 %, and reduced swimming duration and orientation frequency by 50% and 62.5 %, respectively. Based on these results, Pimentel et al. (2014) posited that these hypercapnia-driven metabolic and locomotory challenges may potentially influence recruitment and dispersal success in dolphinfish, whereas Bignami et al. (2014) were cautiously optimistic that dolphinfish would cope with near-future OA conditions. With regard to flyingfish, there have been no climate change-focussed studies, but Oxenford et al., (1994) reported a significant positive relationship between flyingfish (Hirundichthys affinis) pelagic larval/juvenile growth and SST for samples collected at sea in the eastern Caribbean. They reported higher growth rates where SSTs were higher and for juveniles hatched in warmer months (April - July; mean SST 28.2 °C) than in cooler months (December to March; mean SST 27.5 °C).

2.3.2. Shellfishes

2.3.2.1. Lobsters

The impact of climate change on lobsters has recently been summarized by Briones-Fourzan et al. (2015) and, not surprisingly, includes many of the direct impacts seen in reef fishes such as changes to: growth rates; sizes at maturity; timing of reproductive processes; duration of larval development; timing and level of settlement; post-settlement mortality; behavioural ecology; and spatial distribution of stocks. Many of the species studied to date have been temperate species and may not be relevant to the commercially important Caribbean spiny lobster. However, the Western rock lobster in Australia (in the same genus as Caribbean spiny lobster) has been experiencing very low settlement levels of post-larvae since 2006 and this has been linked to higher SSTs resulting in earlier seasonal spawning and a potential mismatch with other environmental factors that ensure the return of post-larvae several months later (de Lestang et al., 2015). Further, Caputi et al. (2010) identified increasing water temperatures over the last few decades as the key driver in decreasing size at sexual maturity and in the size of adult lobsters migrating from shallow to deep water. In addition, de Lestang et al. (2012) reported that the pre-adult migration is also influenced by the strength of local currents, which are likely to be influenced over the long-term by climate change.

2.3.2.2. Conch

Although, to our knowledge, there are no published studies on the direct impacts of climate change on Caribbean queen conch, a review of their current status by NMFS-NOAA (2012) suggests that two aspects of climate change (ocean acidification and increasing SST) pose the greatest threats. They suggest that conch will either expend more energy building their protective shells or their shells will become weaker and the animals more vulnerable to predation. There is already anecdotal evidence that at least some older fishers from Pedro Bank, Jamaica, perceive that queen conch shells are becoming more brittle (Allen, unpublished data⁴). Davis (2000) reported the optimum temperature range for embryo and larval development of gueen conch in the laboratory was 20-32 °C, suggesting minimal impact of near-future SSTs on the early developmental stages of conch. More recently, however, unpublished data from laboratory experiments in Mexico (Aldana Aranda, presented at 69th GCFI meeting, Nov. 2016) indicate that near-future (by 2100) changes in ambient water temperature from 28-31 °C in concert with a decrease in water acidity from pH 8.1-7.6 results in a 15% decrease in conch larvae survival; a 50% reduction in the calcification of aragonite to the larval shell; and an increase in the development rate of veliger larvae, resulting in a faster time to reach competence (ability to settle to the benthos) resulting in a 30% shorter PLD. This would likely result in fewer larvae surviving, and a shorter PLD would impact larval dispersal and/or settlement success and thus ultimately affect recruitment to the fishable-sized adult populations. Furthermore, the importance of annual temperature profiles in determining queen conch reproductive strategy has also been demonstrated in a Caribbean-wide study (Aldana Aranda et al., 2014). They report significant differences in the timing and intensity of reproductively active stages between gueen conch from western and eastern sites of the Caribbean, with continuous and low levels of reproduction by the population throughout the year in the west and a discrete and intense reproductive period in the eastern Caribbean.

A study by Ries et al., (2009) examined the effects of 60-day treatments under current and elevated pCO₂ (409, 606, 903 and 2856 ppm) across a number of species from a wide range of taxa including the Florida fighting conch. They reported a 'thresholdnegative response' with little or no change under intermediate pCO₂ and a decline in net calcification rate and even a net dissolution at the highest levels of pCO_2 for this conch species. Studies on another species from the conch genus (humpbacked conch) in the GBR have indicated that near-future SST (33 °C) and pCO_2 (955–987 µatm) does not appear to impact the aerobic scope (respiratory capacity) of young adults, even during the rigorous lurching movement characteristic of conch and used to escape predation (Lefevre et al., 2015). However, Watson et al. (2014) report that elevated pCO_2 (961 μ atm) significantly reduces this escape response by impairing the decision-making process (neurotransmission) in the same way as reported for several reef fishes (see Munday et al., 2010). Shirayama and Thornton (2005) studied another Indo-Pacific conch species (strawberry conch) under increased atmospheric CO₂ (560 ppm) and reported significant reductions in shell height and wet weight of juvenile conch kept in these conditions for several months ex They concluded that both tissue physiology and situ. calcification rates were impacted by the higher pCO_2 and noted that the impacts would likely be even more severe in situ due to further increases in pCO_2 that occur in shallow environments during the hours of darkness when many other organisms are also respiring and no photosynthesis is taking place. Fields (2013), studying the same species of strawberry conch, found impacts of high CO_2 (950 ppm) on their predator-prey behaviour. This author reported that the strawberry conchs exhibited an increased rate of self-righting in the high CO₂ conditions, but, as reported for the humpbacked conch by Watson et al. (2014), it lowered their ability to assess predator (cone shell) presence and to escape efficiently.

2.3.2.3. Shrimps

We could find no studies of direct impacts of climate change on penaeid shrimps in the Caribbean. However, their life cycle involves adults spawning in offshore marine areas and the pelagic larvae and post-larvae entering brackish estuaries where they remain as juveniles. Since estuarine organisms routinely encounter significant fluctuations in dissolved O₂, CO₂ and pH both diurnally and seasonally, the changes associated with nearfuture climate change may not be detrimental. However, research in the GoM on penaeid shrimp has suggested that increased levels of these stressors, particularly hypoxia, hypercapnia and low pH combined, can negatively affect the immune system, placing shrimps at higher risk from opportunistic pathogens (Mikulski et al., 2000). Reis et al., (2009) included one species of tropical penaeid shrimp (eastern king prawn) from the Great Barrier Reef (GBR) in their study of tolerance to elevated pCO₂ and determined that they showed a 'positive response' with net calcification rate increasing linearly with increasing CO₂ levels. They attributed this to an ability to utilise bicarbonate (as opposed to carbonate) ions in the calcification process. They also noted that shrimp have a relatively thick epicuticle over their exoskeletons, providing a protective organic layer against dissolution by surrounding acidic seawater. Interestingly, a recent study by Taylor et al. (2015) of a distantly related cleaner shrimp also found increased calcification under short-term exposure to elevated CO₂ but they determined that although the exoskeleton was heavier, it was less flexible and more brittle meaning that it is more likely to fracture during sudden movements such as in predator defence or sudden escape response.

https://www.pacificclimatechange.net/sites/default/files/doc uments/Session%201%20Allen.pdf

3. INDIRECT IMPACTS THROUGH CHANGES TO ESSENTIAL HABITATS

Apart from the substantial direct physiological impacts of climate change on commercially important fish and shellfish, a further important concern will be the indirect impacts of changes to their essential habitats including the wider ocean ecosystem that will be driven by climate change. These are summarized in the following sections.

3.1. Degradation of Essential Coastal Habitats

Coral reefs have received a great deal of attention and a brief review of the reported impacts of climate change on Caribbean coral reefs is given in the supplementary information (S1). In summary, degradation of coral reefs globally, driven by climate change (especially SST resulting in mass coral bleaching and associated mortality; and larger more damaging storms), and often exacerbated by chronic local anthropogenic stressors (especially overfishing and poor water quality) is manifesting in numerous ways and has been extensively researched over the last few decades (e.g. Hughes *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007; Pandolfi *et al.*, 2011; Salvat, 2015).

In the Caribbean, degradation of coral reefs has included a substantial, but varied, reduction in live coral cover (Gardner *et al.*, 2003, Jackson *et al.*, 2014), loss of coral reef species (Newman *et al.*, 2015), changes in the dominant substrate cover species assemblages, including in some cases a complete phase shift to algal dominated reef communities (e.g. Hughes *et al.*, 2007), and probably of greatest significance: the loss of reef architectural complexity (physical 3-dimensional structure) as reported across the Caribbean region by Alvarez-Filip *et al.* (2009).

Recent work is also beginning to uncover direct physiological impacts and indirect environmental impacts of high pCO_2 on the reproduction, early life history stages, settlement success and survivorship of corals (the foundation species for reefs), including at least some Caribbean coral species (see Albright, 2011a for review). These authors note that whilst further studies are clearly needed in this area, information to date indicates that direct impacts include: depressed sperm motility; reduced fertilization success; increased larval respiration rates; and decreased tissue growth and calcification of newly settled coral larvae. They also note that indirect impacts include changes to substrate conditions that do not favour coral settlement, resulting in reduced coral larval supply and depressed coral recruitment, which will likely further compromise coral reef resilience, or the ability of reefs to recover from future disturbance.

Mangroves, seagrasses and other reef associated habitats have, in general, received much less attention in the Caribbean although it is acknowledged that mangrove and seagrass habitats are also declining across the region (CARSEA, 2007; Cambers *et al.*, 2008; Mumby *et al.*, 2014; van Tussenbroek *et* al., 2014). A brief summary of climate change impacts on these ecosystems, with a focus on Caribbean studies, is given in the supplementary information (S2 and S3). With regard to mangroves (S2), the general consensus appears to be that Caribbean mangroves have so far been degraded primarily by anthropogenic stressors other than climate change (primarily land reclamation and petroleum pollution) although SLR is considered to be an important potential threat for the future sustainability of mangrove ecosystems, especially fringe mangroves along developed or developing coastlines in the Caribbean. This will be exacerbated where mangroves rely on the protection of coral reefs to attenuate wave action, since corals are likely to be significantly affected by other climate change parameters, especially SST. With regard to seagrasses (S3), there is no reported evidence of increased or decreased productivity within the region's seagrass habitats as a direct result of climate change impacts. Other anthropogenic activities resulting in sedimentation, eutrophication and physical damage, inter alia, have been implicated in the reported declines to date (van Tussenbroek et al., 2014), with the latest potential threat being a recent rapid invasion of seagrass meadows across much of the eastern Caribbean by a non-native seagrass species from the Red Sea and western Indian Ocean (Willette et al., 2014; van Tussenbroek et al., 2016).

The state of estuarine environments within the Caribbean has received very little attention compared with coral reefs. Although not specific to the Caribbean, the degradation of estuaries to date has been largely driven by overexploitation (of fish and shellfish populations), destruction of aquatic plants (including seagrasses and mangroves) and pollution and eutrophication via terrestrially-sourced nutrient runoff (Lotze et al., 2006). Climateinduced warming will undoubtedly exacerbate the hypoxic conditions caused by eutrophication in estuaries and coastal waters and will favour anaerobic microbes and development of harmful algal blooms (Pörtner et al., 2014). This in turn causes additional stress to euryhaline fishes dependent on estuarine environments (e.g. Steidinger, 2009; cited in Linardich et al., in prep.). However, as Carter et al. (2014) and FAO (2016) point out, climate change induced SLR will result in displacement of brackish and fresh water in tidal estuaries and coastal swamps; whilst changes in precipitation and/or storm activity (intensity and occurrence) will alter salinity regimes and sediment loads within estuaries. These will, in turn, further impact the health and extent of essential marsh, mangrove and seagrass habitats within estuaries.

3.2. Alteration of Open-Ocean Ecosystems

Climate change has not only altered physical and chemical properties of seawater through increased atmospheric temperature and CO₂, but has fundamentally altered the physical, chemical and biological characteristics of ocean environments affecting marine ecosystem processes and services, with the most striking effects occurring or expected to

occur in polar and tropical latitudes (Hoegh-Guldberg & Bruno, 2010; Doney et al. 2012; Poloczanska et al. 2013; Bijima et al., 2013; Pörtner et al., 2014; Hoegh-Guldberg et al., 2014). For example, the distribution and abundance of phytoplankton communities, as well as their phenology and productivity, are changing in response to warming, acidifying and stratifying oceans, with cascading impacts on secondary producers through to the highest trophic levels (Hoegh-Guldberg & Bruno, 2010). There have been measurable decreases in global ocean productivity over the last few decades and this is altering marine food web dynamics (Hoegh-Guldberg & Bruno, 2010; Doney et al., 2012; Hoegh-Guldberg et al., 2014). Another important consequence of warming and increased stratification is an expansion and shoaling of the oceans' oxygen minimum zones, where O₂ levels are too low to support many water-breathing macrofauna (Keeling et al., 2010).

Climate warming also affects the pattern and strength of regional winds which in turn affect ocean circulation, mesoscale currents and upwelling (Doney *et al.*, 2012). Furthermore, changes in ocean density have the potential to impact large-scale ocean circulation (Hoegh-Guldberg *et al.*, 2014). Cowen & Sponaugle (2009), in a review of larval dispersal and marine population connectivity, reported that projected changes in the speed and direction of major currents (coupled with decreased PLDs from increased SST) has the high potential to disrupt existing marine larval dispersal pathways and thus affect population replenishment and patterns of population connectivity.

There is a general paucity of published information specifically on climate-induced ocean ecosystem changes within the Caribbean region, due largely to the sparse availability of observational datasets, although the PRECIS-Caribbean Initiative, inter alia, has allowed valuable down-scaling of global climate projection models for the region (see Campbell et al., 2011; Taylor et al., 2012a; Hall et al., 2012; Nurse & Charlery, 2016). However, a study by Taylor et al. (2012b) reveals substantial ecosystem-level changes in the southern Caribbean Sea in response to global climate change, detected by monthly observations measured at the 'carbon retention in a coloured ocean' (CARIACO) time-series station off Venezuela from 1996-2010. In this study, the authors reveal that the poleward expansion of the large-scale atmospheric Hadley circulation cell over the tropics, which controls the behaviour of the Intertropical Convergence Zone (ITCZ) and the North Atlantic Oscillation (NAO), has in turn affected the strength of the North Atlantic Trade Winds, resulting in decadal-scale increases in SST, intensified open-water stratification and reduced seasonal upwelling of deep nutrient-rich waters along the Venezuelan shelf edge. They link this to substantial declines over the same period in net primary production, and change in the dominant phytoplankton species composition in the southern Caribbean Sea, with significant impacts on the ocean food web and collapse of planktivorous sardine populations. Given the evidence of these changes in the southern Caribbean, it is reasonable to assume, that the complex surface currents within the entire Caribbean Sea that are influenced by both the North and South Atlantic Equatorial Currents and driven by the seasonally variable Trade Winds and complex geomorphology (see Smith et al., 2002 for overview), will also be substantially altered by climate change.

Climate-induced changes to ocean currents, together with ocean warming and eutrophication (from increased land-based sources of nutrient loading), have been implicated in the recent increased frequency and severity of marine algal blooms ('green tides') occurring around the globe (Smetacek & Zingone, 2013). In this regard the recent mass influxes of pelagic sargassum seaweed into the Caribbean Sea from the tropical Atlantic, starting in 2011 (Franks et al., 2012; 2015; Gower et al. 2013) have indeed been associated with changes in climate and equatorial ocean dynamics (Franks et al., 2016). This presents a number of potential positive and negative impacts for commercially important fish and fisheries in the region (see Case Study). Although still under debate (see Havens, 2015), it has also been suggested that the seasonal occurrence of harmful algal blooms (often referred to as 'red tides') will also become more frequent with increased eutrophication, and warming waters under climate change (e.g. Hallegraeff, 2010), which will have serious implications for the health of fish and shellfish, as well as humans (Fleming et al., 2011). Other factors such as iron-rich Sahara dust influx to the Caribbean Sea are also thought to play a major role in causing red tides (Walsh et al., 2006) and these too may become more frequent with climate variability and increasing desertification.

3.3. Evidence Relevant to Commercially Important Caribbean Species

Degradation of coastal (coral reefs, mangroves, seagrasses and estuaries) and ocean habitats driven in part by climate change, will influence the fish and shellfish species which are variously reliant on these essential habitats for critical resources including food, shelter, nursery habitat and adult living space. Although there has been a burgeoning number of studies examining these impacts over the last decade, there has been much less research specific to the Caribbean.

3.3.1. Finfishes

A review and meta-analysis by Wilson *et al.* (2006) reported on the effects of a decline in coral cover (> 10% loss) caused by acute disturbances (storms, coral bleaching, crown of thorns starfish) on reef fishes. Although responses were not consistent across the multiple fish species examined, some general patterns of response emerged for Indo-Pacific reef communities and included: 62% of fish species examined declined in abundance within three years of a disturbance, whilst a minority of species increased slightly in abundance; the diversity of fish communities declined in proportion to the loss of coral; species richness of fish communities declined when the coral loss was > 20%; and disturbances that caused an immediate loss of reef structural complexity (e.g. storms) had the greatest impact on fish species of all trophic levels, but especially on small-bodied individuals (i.e. small species and juveniles of larger species), suggesting greater long-term consequences than currently documented.

Other subsequent studies have added to the body of knowledge from the Indo-Pacific, and include Bellwood et al., (2006) who reported no long-term decrease in diversity, richness or abundance of a multispecies cryptobenthic assemblage of shortlived fishes in response to significant coral loss in the 1998 bleaching event in the GBR. However, they noted a significant, and apparently stable, shift in the species composition of this assemblage, and posited that this pattern may in fact be repeated across other longer lived species given time. A followup study confirmed that it may take decades or more, for recovery of long-lived fish species to begin after an acute disturbance, and that coral reef fish assemblages may never recover to their previous composition even after the return of corals to their former abundance (Bellwood et al. 2012). Cheal et al., (2008) examined responses of 22 reef fish species to coral declines across numerous reefs in the GBR. They concluded that fish diversity rarely decreased, but reported major changes in species composition of fish communities, involving declines in coral-dependent fishes and other species with no clear dependence on coral, and increases in abundance of large herbivores. Further, they reported that the magnitude of these changes was correlated with the magnitude of coral decline, but that the proportion of species that increased or decreased in abundance, varied considerably among reefs (Cheal et al., 2008). Similar findings were reported by Wilson et al. (2009) looking at 210 fish species across 10 disturbed reefs in the GBR. Another study in the Seychelles showed that bleaching-related loss of live coral cover impacted corallivores and planktivores over the short-term, with striking reductions in the abundance of these fishes following a major bleaching event (Graham et al., 2007). These authors also reported a longer-term response whereby the relative abundance of small sized-fish declined, whilst larger ones increased. They attributed this to a longer-term reduction in reef structural complexity following the mass bleaching event, which would have reduced refuge for small fish and allowed better foraging and therefore better growth for larger predatory fish. However, they predicted an impending recruitment failure to the commercially important reef fish stock as a result of this loss of juveniles (Graham et al. 2007). A recent analysis by Pratchett et al. (2014) concludes that the ongoing and sustained degradation of coral reef ecosystems that is resulting in changes to the abundance and species composition of reef fish assemblages will inevitably result in the loss of critical ecosystem goods and services provided by coral reef fishes, including their maintenance of coral-dominated communities and support of coral reef fisheries.

In the Caribbean, studies examining the impacts of reef degradation on fishes have been limited, but draw broadly similar conclusions, although some differences are evident. We suggest that Caribbean reefs and their fish communities are likely to be more easily and dramatically impacted by climate change, given the fact that they have much lower species biodiversity and resilience than Indo-Pacific systems (see Roff & Mumby 2012).

Claro et al., (2007) reported a significant decrease in reef fish density and biomass in the Cuban Sabana-Camagüey Archipelago, as a result of a drastic reduction in coral cover and subsequent overgrowth by macroalgae caused by several climate-induced coral bleaching events. Mora (2008), using Atlantic and Gulf Rapid Reef Assessment (AGRRA) data from 322 reefs across 13 Caribbean countries reported that human activities (agriculture, coastal development, overfishing) and climate change had created independent responses in coral reef fishes (as well as corals and macroalgae) across the region. His results clearly showed a negative relationship between temperature and herbivorous fish biomass, which he attributed to a previously reported thermophysiological constraint, which suggests that digestion of macroalgae may be restricted at higher temperatures. In a meta-analysis of Caribbean data sets from 20 countries, spanning the period 1955 - 2007, and covering 318 reefs and 273 fish species Paddack et al. (2009) reported significant declines in fish densities over the last decade of between 2.7 and 6% per year for three of six trophic groups (i.e. herbivores, invertivores and generalist carnivores). They concluded that these declines did not appear to be driven by fishing pressure, nor correlated directly with the substantial declines in coral cover across the Caribbean, but were likely a response to sustained habitat degradation over this period.

A recent study by Rogers et al. (2014) used a size spectrum food web model linking the vulnerability of prey to predation based on their size and the structural complexity of the reef. Using data from The Bahamas they were able to demonstrate that for Caribbean reefs, there is a significant overall loss in reef fish size and abundance with loss of reef architecture, with an estimated 3-fold reduction in commercial reef fish biomass when transitioning from a high- to a low-complexity reef. This was further corroborated by Newman et al. (2015) examining the importance of reef habitat structural complexity in three marine reserves across the Caribbean (Bonaire, St Vincent and the Grenadines, and Puerto Rico). They concluded that on-going reductions in reef architectural complexity in Caribbean reefs will lead to the extirpation of some species and a reduction in most species, and that the few 'winners' will be small non-fisheries species such as wrasses, blennies and damselfishes. They also concluded that predictable shifts in fish community composition that will affect essential ecosystem processes on the reef are likely to occur (Newman et al., 2015).

With regard to declines in coral-associated ecosystems (e.g. mangroves, seagrasses), Ellison & Farnsworth (1996) noted that

the Caribbean region's fisheries were declining at a similar rate to the regional decline in mangroves, and attributed this to the fact that most commercially important fish and shellfish species use mangroves as nurseries or refugia. Mumby et al. (2004) (further refined in Mumby et al., 2006) clearly demonstrated that Caribbean mangroves strongly influence fish community structure and productivity on neighbouring reefs, being very important as an intermediate nursery habitat for many reef fish species, substantially increasing survivorship of these young juveniles prior to their recruitment to adult habitats in reefs. Using a series of study sites in Belize, they were able to quantify the importance of mangroves, even in the presence of alternative nursery habitats, and reported that the biomass of commercially important species (e.g. striped parrotfish, several grunt species and schoolmaster snappers) was more than double when adult reef habitat is connected to mangroves. They also noted that rainbow parrotfish, the largest herbivorous fish in the Caribbean, has an obligatory dependence on mangroves such that it is only found on reefs with associated mangroves and has become locally extinct where mangroves have been removed. Other studies in the Caribbean have identified many commercially important reef fish species that are heavily dependent on mangrove and seagrass nurseries (Nagelkerken et al., 2002; Nagelkerken, 2009; and references therein). Many studies have also examined diel movements of reef fishes and decapods (including spiny lobsters) between reefs and adjoining seagrass and rubble habitats (Nagelkerken et al., 2000a, 2000b; see Krumme, 2009 for review). Mumby et al. (2004) reiterated the conclusion of Nagelkerken et al. (2002) and others that mangrove depletion in the Caribbean is likely to have severe deleterious consequences for coastal ecosystem function, fisheries productivity and resilience of many reefs. Ontogenic habitat shifts in many commercially important species also serve to highlight the important links between offshore areas, reefs, seagrasses and mangroves in the Caribbean (see Haywood & Kenyon, 2009 for review). For example, Verweij et al. (2008) studying the association of yellowtail snapper population on the reef with seagrass nursery habitats in Curacao calculated that 98% of the yellowtail snapper reef population consisted of immigrants that had passed through seagrass nurseries.

We can find no published information specifically linking degradation of Caribbean estuarine environments to changes in commercially important finfish species whose ontogeny relies on euryhaline estuaries as nursery areas and soft-bottom nearshore or deep offshore areas as adult habitat (e.g. weakfish [bangamary, Guyana seatrout], croakers [butterfish], and sea catfish). However, Martínez Arroyoy *et al.* (2011) noted that, in the Gulf of Mexico, the distribution of croakers and brown shrimp in estuaries is significantly affected by seasonal hypoxic zones occurring with seasonal increases in SST, suggesting that climate change-induced rise in SST would have significant effects on the distribution and mortality of these commercially important species.

The distribution, migration routes and locations of foraging aggregations of the major pelagic species (dolphinfish, tunas, mackerels, sailfish, swordfish, and the marlins) are known to be highly sensitive to surface currents, SST and to the location of oceanic features (e.g. frontal systems, convergences, vortices, thermocline, mixed layer). For example, yellowfin tuna aggregate along thermal fronts (see Martínez Arroyo et al., 2011). Climate-induced changes in large scale ocean currents together with increasing SSTs are likely to cause shifts in the size and distribution of oceanic pelagic fish stocks of commercial importance, with implications for change in the EEZs in which they occur (Bell et al., 2013). As such there will be winners and losers, with the countries of the Caribbean standing to lose over the longer term, as pelagic populations move poleward. Also of relevance to the oceanic pelagic species is the expected decline in the biomass of reef-associated species, whose pelagic larvae and juvenile phases make up an important part of the diet of many oceanic pelagic species in the Caribbean (e.g. dolphinfish, billfishes, swordfish, yellowfin tuna, skipjack tuna, albacore, dolphinfish: see Heileman et al., 2008 and references therein; blackfin tuna: Headley et al., 2009). A further change in the ocean environment of relevance to oceanic pelagics is the increased ocean temperature stratification and reduced oxygen content in the upper layers, which has already been implicated in significant vertical compression of suitably oxygenated habitat for some of the large highly migratory pelagic fish species such as billfishes and tunas in the tropical northeast Atlantic Ocean (Prince et al., 2010; Stramma et al., 2012). These authors report that the oxygen minimum zone, representing a lower hypoxic habitat boundary for high oxygen-demand tropical pelagic billfishes and tunas is rising, resulting in increased densities of the large pelagic fish species in the mixed surface layer. They also report that the decrease in depth of the oxygen minimum layer in the tropical northeast Atlantic between 1960-2010 has amounted to an astounding loss of habitat of approximately 15% per year, and they concluded that the expected further habitat compression under future climate change would threaten the sustainability of the pelagic fisheries that these species support.

The recent mass influxes of sargassum into the Caribbean, considered to be, in part, another climate-induced change to the pelagic environment in this region (Franks *et al.*, 2016) is also having a number of impacts on pelagic and reef-associated species (see Case Study), although as yet unpublished (but see Ramlogan *et al.* in press). The commercially important flyingfish are using the sargassum as spawning substrate, perhaps with a positive effect on population abundance, given that floating substrates are considered a possible limiting factor controlling the size of the eastern Caribbean flyingfish stock (Hunte *et al.*, 2007). However, it is also possible that the distribution of the flyingfish population may be altered by this change in spawning substrate, taking fish away from traditional fishing grounds. The sargassum has also been bringing large numbers of small young dolphinfish into the eastern Caribbean in the late summer, ahead

of the normal migration of larger fish into the region. This indicates a change in the normal annual/ontogenic migration of this species. Other reef-associated species (jacks, pufferfish, ballyhoo etc.) have been observed to be recruiting in unusually large numbers in high sargassum years, implying that the pelagic larval stages of many species may have greater survival rates when associated with the shelter of sargassum mats.

3.3.2. Shellfishes

There are fewer studies on the impacts of climate-induced changes to essential habitats of taxa other than fish, including commercially important shellfish, although many of the same patterns of impact are likely to occur. In the Caribbean, Newman *et al.* (2015) examined several reef taxa, including the arthropod group (lobsters, shrimps, crabs) and concluded that abundance of large corals, reef complexity and size of gorgonians were key reef characteristics that influenced the species richness of the arthropods. By implication, changes in these reef characteristics, which are already occurring with climate change, will result in changes to arthropod species richness.

Specific to the Caribbean spiny lobster, Ehrhardt et al. (2011) highlighted the negative effects of losing critical nursery habitat (mangroves, seagrasses and algal hard ground) and adult refuge (corals and sponges) in the Caribbean since the 1980s, especially as a result of increased severity of hurricanes and mass coral bleaching events. Likewise, loss of critical nursery and adult habitat such as seagrass, will have impacts on sustainability of conch populations (Appeldoorn et al., 2011). For example, loss of preferred adult habitat (seagrass) has been blamed for the decline in conch stocks in several Caribbean countries (see NMFS-NOAA, 2012 and references therein). Loss of adjacent mangrove, seagrass and reef habitats will impact optimal foraging strategies (i.e. diel migrations between habitats) of lobsters and juvenile shrimp (Krumme, 2009). Likewise, increasing levels of hypoxia that are expected in Caribbean estuarine environments will decrease the suitability of these habitats for juvenile commercially important penaeid shrimps and increase incidences of abiotic mortality (Martínez Arroyo et al., 2011).

The long pelagic larval stage of lobsters, particularly spiny lobsters (6-12 months) makes them particularly vulnerable to climate variability, with open-water environmental conditions having a significant effect on their advection (dispersal), development, growth and survival (Phillips *et al.*, 2000; cited by Caputi *et al.*, 2013). A study by Chavez & García-Córdova (2012) examined spiny lobster landings data reported across 25 Caribbean countries from 1950-2007 in relation to several climate indices including the NAO (North Atlantic Oscillation), ACI (Atmospheric Circulation Index of the North Atlantic) and the AFI (Atmospheric Forcing Index) and found them to be highly correlated. From this, they infer that climate change appears to be having a significant effect on the stock dynamics of the pan-

Caribbean spiny lobster population, but they did not offer any further explanation of the potential mechanisms.

A recent modeling study of the PaV1 virus, which is pathogenic (usually lethal) primarily to juvenile Caribbean spiny lobsters and likely dispersed via pelagic larval stages, demonstrates how any climate-induced changes in the hydrology of the Caribbean Sea could significantly affect the spread of the disease (Kough *et al.*, 2015) with significant implications for this commercially valuable, pan Caribbean species. Furthermore, another recent study (Lozano-Álvarez, *et al.* 2015) has hypothesised, on the basis of just two infected postlarvae (out of 239 sampled) that pelagic sargassum may be an environmental reservoir for the PaV1 virus.

4. OBSERVED AND EXPECTED IMPACTS ON MAIN FISHERY SPECIES GROUPS

A review of available literature published since Nurse (2011) has confirmed what he and others reported, at the time, as a dearth of studies on the impacts of climate change on fishery species specific to this region, perhaps with the exception of coral reef fishes. In light of this, where we have been unable to find any relevant studies within the region, we have considered the broad biological and ecological characteristics of each of the four main species groups that may be impacted by one or more aspects of climate change and made inferences wherever possible, based on climate change impacts reported for similar species and their ecosystems elsewhere.

As such, in this section, we have considered the information available in the published literature from conspecifics and related taxa and from laboratory and field studies, mostly outside of the Caribbean, together with information on the biophysical characteristics of the Caribbean Sea and knowledge of the broad exploitation status of commercially important stocks to summarise what we believe to be the most important impacts of climate change on the four main fishery species groups during this century.

4.1. Reef-Associated Shallow Shelf Group

The most obvious impacts of climate change on this diverse multispecies group of fish and shellfish are indirect and result from the significant impacts (already witnessed in the Caribbean) on their essential benthic habitats, especially coral reefs and, to a lesser extent, mangrove wetlands and seagrass meadows. Degradation of these habitats, driven in part by climate change, influences the reef-associated fish and shellfish species which are variously reliant on these habitats for critical resources, including food, shelter, nursery habitat and adult living space. It is important to note that the impacts of climate change on these essential habitats are exacerbating decades of degradation that have already occurred in the region as a result of other chronic and acute anthropogenic stressors such as coastal development, agriculture, pollution (resulting in poor water quality) and overfishing (resulting in loss of functional groups and services to habitats), which have increased their vulnerability to climate change through loss of biodiversity and ecosystem resilience, loss of habitats' carrying capacity, and depressed standing stocks of commercially important fish and shellfish.

Changes to the seasonal timing, speed and direction of Caribbean regional surface water currents will have, as yet unknown, consequences for the dispersal and survivorship of early life history stages, since almost all of the commercially important fish and shellfish species in this grouping have a biphasic life history. This means that they have a pelagic early life stage (usually as eggs and always as larvae) being dispersed by ocean currents and then they metamorphose and settle into benthic juvenile and adult habitats. This is also complicated by temperature-induced changes in species' phenology (such as timing of spawning events and release of larvae) and decreased pelagic larval duration (PLD). This will be especially apparent for those species with naturally long PLDs (from weeks to months) like conch and lobster, as opposed to some reef fish and urchins with PLDs of just a few days. The only exceptions to the bi-phasic life history in this broad grouping are the small pelagic fish species that do not settle into benthic habitats as adults, but do, however, remain reliant on these nearshore habitats for food.

The less obvious but direct physiological impacts, which are likely to occur or have already occurred, given the evidence from conspecifics and other related taxa in laboratory studies on reefs elsewhere, have yet to be confirmed for commercially important Caribbean reef-associated fish and shellfish. However, these physiological impacts may ultimately be the most severe of the future climate change impacts, given that they have insidious cellular and tissue-level impacts that affect life processes, and will ultimately translate into changes in community structure and ecosystem function.

As conditions become less optimal, marine populations would typically move, and there is already considerable evidence elsewhere of poleward movement of species, or movement to greater depths, as temperatures have increased. In the case of this group, physically constrained by the semi-enclosed nature of the Caribbean Sea, and heavily reliant on shallow-water habitats that have taken 100s to 1000s of years to develop, the prospect of movement poleward or to deeper water is unlikely. The consequence for most of these commercially important species is likely to be one of diminishing health, productivity and overall abundance as environmental conditions continue to move towards sub-optimal or become completely unsuitable.

There will of course be considerable species-specific variability, as well as spatial variability (driven by differences in current and past environmental experience; and exploitation status) in response to the different climate change stressors. However, overall, the most vulnerable species within this group are likely to be those that have all or several of the following traits: heavily calcified shells, long PLDs, poor acid-balance mechanisms, highly reef-attached as adults, and short reproductive periods (especially those reliant on highly specific spawning aggregation sites).

In summary, the impacts of climate change on this group, although species-diverse, are almost undoubtedly the most serious of the four commercially important fishery groups in the Caribbean. The reliance of this group on highly vulnerable and already damaged shallow coastal habitats and the severely overexploited status of many of the Caribbean's nearshore marine fishery stocks puts them at the greatest disadvantage for withstanding climate change stressors.

4.2. Deep Slope Group

Much less is known about this group of species and their essential habitats than the shallow reef-associated taxa. Although not reliant on shallow reefs and other associated shallow shelf habitats as adults, it is known that the newly settled larvae and juveniles of many of the deep water grouper and snapper species use these shallow habitats as nursery areas, and the adults may use reefs as spawning aggregation sites. As such, degradation of reefs, mangroves and seagrasses will also impact this group, likely reducing the recruitment success to adult populations.

As with the reef-associated group, these species have bi-phasic life cycles and thus their eggs and larvae would be similarly vulnerable to changes in ocean currents and surface water temperatures, potentially affecting the dispersal of their early life history stages and ultimately the settlement success and survival of their young recruits.

There is also no reason to assume that the early life stages of this group would be any less affected by the direct and pernicious physiological impacts of rising SST and increasing pCO_2 than other fish and invertebrate species already examined, including an impairment of appropriate responses to settlement cues. However, perhaps the surviving adults will be less affected by increased SSTs since they are not reliant of shallow coral reefs and associated habitats and thus, unlike the shallow reef-attached species, they could potentially move to deeper water than they currently inhabit.

However, in general, these large deeper water species tend to grow more slowly, mature at a greater age and live longer than their shallow reef counterparts. These life history traits make them more vulnerable to overexploitation, and several of these commercially important species are already considered under the IUCN Red List to be 'Vulnerable' (yellowedge, snowy and yellowmouth groupers; vermilion, cubera and northern red snappers) or even 'Critcally Endangered' (black grouper) within the Wider Caribbean (Linardich *et al.*, in prep). In summary, the impacts of climate change on this group have received little or no specific attention, but, considering their biological characteristics and current exploitation status, they are likely to be similar, or perhaps slightly less severe, than those on the shallow reef-associated group. The fact that the species in this group tend to be longer lived than their shallower relatives, means, however, that the impacts of climate change on stock biomass and abundance will likely be delayed, but any recovery will also take longer.

4.3. Shrimp and Groundfish Group

The finfish and shellfish (shrimp) species in this group mostly rely on estuarine nursery areas, including mangroves and seagrasses, and offshore deeper soft bottom areas as adults. Although much less studied in the Caribbean than some of the other groups, they too are known to have bi-phasic life cycles with a free-floating pelagic early life stage and a benthic adult stage. This means that they will share the same potential threats posed to early life stages as all of the other fishery groups, i.e. shorter PLDs and changing currents impacting successful dispersal and delivery of new recruits to suitable estuarine settlement habitats and nursery grow-out areas for population replenishment. The early life stages will also be vulnerable to the myriad of potential effects of high pCO_{2} , elevated SST and declining carbonate saturation states (the latter likely to impact shrimps), as discussed in detail for the reef-associated shallow shelf group. Further, estuarine areas, especially those with high or increasing nutrient and sediment loads (which could be driven in part by climate change-induced high-volume precipitation events) will be particularly prone to developing hypoxic, or even anoxic, conditions under increasing SST, to which juvenile shrimps and croakers are known to be particularly susceptible. The persistence of mangroves and seagrasses in these estuarine environments is also under threat of climate change, particularly from SLR, presenting further vulnerabilities for this group in terms of degradation of juvenile habitat. However, like the deep slope group, the adult habitats will likely be less impacted by climate change and adults could probably move to deeper offshore soft-bottom habitats.

4.4. Oceanic Pelagic Group

The oceanic pelagic group comprising large highly migratory species (billfishes, large tunas) as well as smaller, more regionally migrating species (flyingfish, dolphinfish, wahoo, small tunas) is the only group in which none of the members have biphasic life cycles, but remain in pelagic environments for their entire lives as eggs, larvae, juveniles and adults. They also generally have extended spawning periods, being multiple batch spawners, and have relatively broad spawning areas that are not well defined and/or poorly known in the literature.

Of all the groups, we propose that this one will be the least affected, in the short term, by climate change. Although not well studied, it would seem that the early life stages are perhaps less affected by hypercapnia and increasing SST than some of the other species groups and are not reliant on finding and settling in benthic coastal habitats, perhaps making them less vulnerable to changes in PLD and dispersal routes that may take them away from appropriate settlement habitats, and from impairment of auditory and olfactory function required to recognize settlement cues. Further, the open ocean environment will experience much less extreme ranges in hypoxia, pH and SST than shallow nearshore areas and will be less affected by additional landbased anthropogenic stressors that exacerbate climate change stressors. Furthermore, the recent sargassum influxes, if they continue, may boost productivity in many of the pelagic species that can benefit from increased shelter opportunity as larvae and small juveniles, and from aggregation of prey items as adults. For flyingfish in particular, sargassum may alleviate what is believed to be a spawning substrate bottleneck for the eastern Caribbean stock. Lastly, at least for the regional migratory species, the stocks are generally not overexploited and will therefore be more resilient to future change.

Citation

Please cite this document as:

Oxenford, H.A. and Monnereau, I. (2017) Impacts of Climate Change on Fish and Shellfish in the Coastal and Marine Environments of Caribbean Small Island Developing States (SIDS), Caribbean Marine Climate Change Report Card: Science Review 2017, pp 83-114.

The views expressed in this review paper do not represent the Commonwealth Marine Economies Programme, individual partner organisations or the Foreign and Commonwealth Office.

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Supplementary Information

S1. Coral Reefs

The effects of climate change on Caribbean reefs have received considerable attention and have recently been summarized by Mumby *et al.* (2014).

Coral bleaching: Increasing SST is already having a devastating impact on many of the Caribbean's coral reefs largely through mass coral bleaching events, especially in 2005 and 2010 (Wilkinson & Souter, 2008; Oxenford et al., 2010; Eakin et al., 2010; Brathwaite, 2012; Jackson et al., 2014; Oxenford and Vallés, 2016). Mass coral bleaching occurs when SST rises just 1°C or more above the normal summer maximum temperature and persists for several weeks. The stress to corals is generally measured as 'degree heating weeks' (DHW) and values in excess of eight weeks are associated with high levels of bleaching-related coral mortality (Liu et al., 2006), with bleaching and mortality response becoming more severe the higher the heating stress above the threshold (Eakin et al., 2010). Extreme bleaching events kill corals outright, while less extreme events can weaken corals, affecting their reproductive potential, reducing growth and calcification, and leaving them vulnerable to disease (Mumby et al., 2014). There are considerable differences in the warming trends across the Caribbean (Chollett et al., 2012, Nurse & Charlery, 2016) which will presumably affect the rate at which reefs become degraded through bleaching. Furthermore, there is some evidence of localised refuges from bleaching in the Caribbean (see Oxenford & Vallés 2016 and references therein). Predictions of when mass bleaching events are likely to become annual in the Caribbean have been reported by Van Hooidonk et al., (2015) and although there is some variation across the region, they report that most reefs will suffer annual bleaching by 2045-50. As such, temperature induced bleaching events will probably become the key driver of reef decline in the near future.

Coral disease: Warming SST has also been linked to increases in outbreaks and prevalence of coral diseases (Ruiz-Moreno et al., 2012), resulting in further decline of live coral. Coral and other marine diseases have certainly played a significant role in shaping the reef communities within the Caribbean over the last few decades of increasing SST inter alia (Weil, 2004; Cambers et al., 2008; Jackson et al., 2014), resulting in the Caribbean being dubbed a 'disease hot spot' (Weil, 2004). Of particular note were two widespread virulent epizootics in the 1980s that changed the structure and morphology of most shallow water coral communities in the Caribbean (Weil, 2004). The first was a region-wide die-off of the Diadema sea urchin, a keystone reef grazer (Lessios et al., 1984). The second was the white band coral disease event that killed the vast majority of acroporid corals (foundational reef builders) across the Caribbean (Gladfelter, 1982).

Calcification rate: The impact of ocean acidification on reefs is less well studied than other aspects of climate change such as rising SST, but there is general consensus that coral calcification rates will decline as the pH and resultant aragonite saturation levels decline, leading to weaker skeletons and less reef building, and ultimately to increased bioerosion and dissolution of the existing reef framework (Andersson & Gledhill, 2013). As vet there is little evidence of reduced coral calcification due to OA within the Caribbean (see Carricart-Ganivet et al., 2012), although a consistent decline in aragonite saturation state has been recorded for the Greater Caribbean (Gledhill et al., 2008; Mumby et al. 2014). However, laboratory experiments on an important Caribbean reef-building coral (Siderastrea siderea) have demonstrated impacts on calcification rates and coral skeleton morphology at pCO₂ levels predicted by 2100 (Horvath et al., 2016). These authors also noted that reduction in calcification rates were particularly severe when experiments were run at levels of pCO2 and SST predicted by the year 2100 (i.e. 32°C / 940ppm). It is also worth noting that 10% live coral cover has been identified as a likely threshold below which Caribbean coral reefs will switch from net growth to net erosion (Perry et al., 2013).

Reproduction and settlement success: A relatively new area of study is the impact of OA on reproduction, early life history stages, and settlement of corals (see Albright, 2011a for a review). Several studies have examined the impacts on Caribbean reef building corals. For example, Albright et al. (2010) reported that fertilization, settlement and growth of coral spats were all negatively impacted by increasing pCO_{2} , and concluded that the cumulative impact of OA on fertilization and settlement success of the Caribbean reef building coral, Acropora palmata, is an estimated 52% and 73% reduction in the number of larval settlers on the reef under pCO_2 conditions projected for the middle (560 µatm) and the end (800 µatm) of this century, respectively. Albright & Langdon (2011) reported reduced metabolism in the larvae of another Caribbean coral, Porites astreoides and suggested that it could translate into decreased larval fitness, motility, and the ability of larvae to regulate their vertical position in the water column thereby limiting dispersal and settlement rates. They also showed that as pH declines it causes changes in the epilithic algal community of settlement substrates such that taxa known to facilitate larval settlement of some coral species, acting as a settlement cue (e.g. encrusting coralline algae) were replaced by alternate algal and diatom species, which reduced settlement by the Caribbean astreoides coral. Furthermore, acidification-induced Ρ. reductions in post-metamorphic calcification and/or growth has already been reported for four Caribbean corals: Porites astreoides (Albright & Langdon, 2011), Acropora palmata (Albright et al., 2010), Agaricia agaricites (Albright, 2011b) and Favia fragum (de Putron et al., 2011).

Coral competitors: Whilst corals will clearly be losers, some important space competitors are likely to benefit from aspects of

climate change. For example, a recent paper on reef-associated turf algae from the Great Barrier Reef has indicated that increased turf algae growth under high CO₂ will aid the overall expansion and growth of fleshy macroalgae in coral reef ecosystems (Ober *et al.*, 2016).

Sea level rise: An increasing rate of sea level rise will likely result in the deeper coral reefs (which have less light and therefore slower rates of net accretion) being unable to keep pace with the change and therefore eventually ceasing to grow and becoming relic (or 'drowned') reefs with low productivity. For coastlines where shallow reefs have been degraded by other stressors, the rates of coastal erosion are likely to increase with increasing sea level and this will exacerbate poor water quality (high sediment and nutrient loads) and sediment smothering of reefs reducing their live coral cover and rugosity (3D framework) and therefore the quality and quantity of living spaces.

Storms: The increased intensity of North Atlantic hurricanes that has been recorded since the 1970s is predicted to continue in this region, fuelled by warming SST (IPCC 2013). Gardner *et al.* (2005) examined the impact of this trend on Caribbean reefs and pointed to the significant physical damage and loss of corals and the large amount of time needed for recovery, especially given the synergistic impacts of other anthropogenic stressors. Storm-related flash flood events also exacerbate the poor water quality of nearshore reefs.

In summary, Mumby *et al.* (2014) conclude that the impact of climate change on Caribbean corals in the future is likely to be particularly negative given the considerable stressors from other anthropogenic impacts (e.g. overfishing, deteriorating water quality) to which they are chronically exposed (Burke & Maidens, 2004), and the ongoing trend (albeit regionally variable) of reef decline (see Gardner *et al.*, 2003; Jackson *et al.* 2014).

S2. Mangroves

McLoed & Salm (2006) and Gilman *et al.* (2008) reviewed climate change threats to mangroves globally, listing SLR, extreme weather events and changes to precipitation, increased temperatures and atmospheric CO₂, ocean circulation and adjacent ecosystem responses as highly relevant. The impact of climate change on mangroves in the insular Caribbean was reviewed by Cambers *et al.* (2008).

Rates of change: Studies examining the long term changes in Caribbean mangroves are relatively scarce and conclusions on the potential impacts of climate change on these ecosystems are still being debated. Ellison & Farnsworth (1996) examined past and current trends and made predictions for the future of Caribbean mangroves. They reported net losses in mangroves over the decade 1980-1990 ranging from an average of 1.7% per year for mainland Caribbean and a 0.2% annual loss for the insular Caribbean, stating that this was due mainly to land reclamation for urban, industrial and tourism development. A more recent study by Cherrington *et al.* (2010), focusing on rates

of change in Belize's extensive mangrove system from the late 1980s to 2010 found that net losses have averaged just 0.07% per year over this period, and have been attributed to clearing for development, rather than any negative impacts of climate change.

Sea level rise: Gilman *et al.* (2008) noted that although climate change has been a relatively small threat to mangroves globally over the last few decades compared with other anthropogenic stressors, SLR in particular, is likely to be a significant factor in future loss of mangrove habitats world-wide. They concluded that most mangroves have slower sedimentation and accretion rates than predicted SLR and will therefore not be able to keep pace with rising water. Most affected will be those areas where mangroves are facing a net lowering of sediments and limited area for landward migration, such as the Pacific Islands (Gilman *et al.*, 2008).

In the Caribbean, Ellison & Farnsworth (1996) noted that changing weather patterns and increases in sea level are likely to have profound effects on mangrove growth and survival although the exact nature of the impacts on Caribbean mangrove mortality and community structure is still being debated. They note that studies of mangrove peat in Bermuda and Grand Cayman have indicated landward movement or die-off of fringing mangroves under past SLR and suggest that modern development will severely constrain this type of range shift in the future. Ellison and Farnsworth (1996) further note that up to 35% of Caribbean fringe mangrove could be negatively affected by SLR in the near future, while riverine mangrove systems, with high rates of sedimentation are expected to fare better. McKee et al. (2007) examined mangroves that dominate the coastlines of islands off Belize, Honduras and Panama and concluded that these systems can adjust to SLR through biotic controls of soil elevation such as the contribution of mangrove roots to peat formation and sediment trapping (mineral accretion) and concluded that riverine mangroves would be buffered against SLR by mineral accretion. Cambers et al. (2008) concluded that SLR would likely be the climate change stressor with the greatest impact on mangroves in the insular Caribbean, but the severity of the impacts would be highly site-specific given the variation in geomorphology and hydrology of the coastlines. They did note however, that the small islands with limited flat coastal land would likely be the most negatively impacted, with loss of species diversity and even loss of mangrove swamps altogether in places where retreat inland would not be possible. They also noted that seawater intrusion from SLR, and/or extended periods of drought could increase salinity and reduce seedling growth and survival as well as impact their photosynthetic capacity.

Rising temperatures: In Caribbean mangroves, Ellison & Farnsworth (1996) suggested that leaf drop and significant tree mortality was unlikely to occur until air temperatures exceeded 38 °C. They noted that other temperature related impacts such as soil warming (resulting in increased respiration, peat

decomposition and increased release of methane and hydrogen sulphide gases) have not been explored.

*Elevated pCO*₂: Ellison & Farnsworth (1996) suggested that higher levels of atmospheric CO₂ are expected to enhance growth through increased photosynthetic rates and water-use efficiency. Farnsworth *et al.* (1996) have demonstrated greater photosynthetic rates, stem elongation, meristem and leaf production, stem lignification and aerial root production in red mangroves when grown artificially at double the ambient atmospheric CO₂ concentrations. They also noted earlier maturation. However, Ellison & Farnsworth (1996) noted that growth enhancement of mangroves expected to result from increasing atmospheric CO₂ is unlikely to compensate for the negative effects of concomitant rises in sea level in Caribbean mangroves.

Degradation of supporting ecosystems: McLoed & Salm (2006) and Cambers *et al.* (2008) both emphasized the indirect impact on mangroves through the degradation of protective coral reef barriers, themselves impacted by climate change related bleaching events.

S3. Seagrasses

Like coral reefs and mangroves, seagrasses are among the most threatened of marine ecosystems across the globe, but much less studied than their counterparts (Orth *et al.*, 2006). The effects of climate change on seagrasses are only just beginning to be studied (Koch *et al.*, 2013; West *et al.*, 2016) and so far have not focussed on tropical species. Bjork *et al.* (2008) reviewed the range of disturbances to seagrass systems and summarized potential climate change impacts. These included: increased atmospheric CO_2 ; OA; rise in SST; changes in irradiance; storm damage; and sediment anoxia, and are summarized here with other relevant literature.

Rates of change: A global assessment by Waycott *et al.* (2009), although acknowledged to be of relatively low resolution and to include both temperate and tropical systems, indicated accelerating losses in seagrass habitat, of around 7% per year since the 1990s, thus equaling or exceeding reported loss rates for corals and mangroves. Like mangroves, the losses of seagrass habitats to date have largely been driven by anthropogenic stressors other than climate change, primarily deterioration in water quality (nutrient and sediment loading) from coastal development and to a lesser extent, physical damage (marine construction, land reclamation, vessel damage), aquaculture and disease (Short *et al.*, 2011).

In the Caribbean, Cambers *et al.* (2008) report considerable degradation of seagrass habitats from: land-based sources of high nutrient and sediment loading; physical damage by marine dredging and construction, boat traffic and hurricanes; and overexploitation of fish and turtles disrupting grazing pressure, but they note that climate change is considered an emerging threat for Caribbean seagrasses, about which little is known.

Long-term monitoring of seagrasses by the CARICOMP monitoring network found that most study sites across the Caribbean basin showed a decline in seagrass health between 1993 and 2007, but concluded that although the causes were varied, none were attributed to climate change (van Tussenbroek *et al.*, 2014).

*Elevated pCO*₂: As is the case with mangroves, increasing CO_2 could potentially increase seagrass productivity by boosting photosynthesis, but experimental evidence over the long-term remains inconclusive (Bjork et al., 2008). They note, however, that antagonistic to this outcome, could be the enhanced growth of epiphytic algae on the seagrass leaves, resulting in shading and reduced photosynthesis. They also point out that another potential benefit to seagrasses from elevated CO₂ is increased seawater acidity. This could counteract the seawater alkalinity that occurs in dense seagrass meadows and which leads to decreased inorganic carbon uptake and reduced photosynthesis, thereby leading to increased productivity in dense seagrass meadows (Bjork et al., 2008).

Rising temperatures: Increased SST will likely result in shifting distributions and species composition in seagrass communities, and changes to patterns of sexual reproduction, growth rates, metabolism and the carbon balance in seagrasses (Bjork *et al.*, 2008). If photosynthesis is reduced, this will in turn reduce the amount of oxygen transported to the roots, a requirement for growth in the typically anoxic (low oxygen) sediments. Higher temperatures will exacerbate sediment anoxia and encourage the buildup of sulphides which are themselves toxic to seagrasses.

Storms: Increased severity of tropical storms will result in greater physical damage to seagrass meadows and increased levels of sedimentation (Bjork et al., 2008).

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