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A framework for understanding climate change impacts on coral reef social–ecological systems

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Abstract Corals and coral-associated species are highly vulnerable to the emerging effects of global climate change. The widespread degradation of coral reefs, which will be accelerated by climate change, jeopardizes the goods and services that tropical nations derive from reef ecosystems. However, climate change impacts to reef social–ecological systems can also be bi-directional. For example, some climate impacts, such as storms and sea level rise, can directly impact societies, with repercussions for how they interact with the environment. This study identifies the multiple impact pathways within coral reef social–ecological systems arising from four key climatic drivers: increased sea surface temperature, severe tropical storms, sea level rise and ocean acidification. We develop a novel framework for investigating climate change impacts in social–ecological systems, which helps to highlight the diverse impacts that must be considered in order to develop a more complete understanding of the impacts of climate change, as well as developing appropriate management

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actions to mitigate climate change impacts on coral reef and people.

Keywords Social–ecological · Coral reef · Climate change · Multiple impacts

Introduction

Climate change has rapidly emerged as one of the major long-term threats to coral reefs (e.g. Hoegh-Guldberg et al. 2007; Hughes et al. 2003; McClanahan and Cinner 2012). Numerous studies have quantified the ecological impacts of disturbance on coral reefs and examined how projected increases in ocean temperature, acidity and the increasing frequency of high-intensity storm events will impact coral communities (De'ath et al. 2012), and reef-associated organisms, principally fishes (e.g. Wilson et al. 2006). These studies are important in understanding how climate change will impact on the sustainability and productivity of coral reef fisheries (Bell et al. 2013; Burrows et al. 2014; Cheung et al. 2010). Aside from fisheries impacts, little is known about how climate change may impact coral reef-dependent human societies and the major drivers and pathways through which this may operate (Carpenter et al. 2009; Daw et al. 2009).

Millions of people, primarily from developing countries, are heavily dependent on the goods and services provided by coral reefs (Teh et al. 2013). These goods and services include fisheries, tourism, coastal protection, habitat provision for valuable species and cultural values (Hicks 2011). An emerging literature has begun to explore the vulnerability of coastal societies to climate change impacts on marine fisheries and ecosystem health (Bell et al. 2013; Béné et al. 2012; Marshall and Marshall 2012). To date, most of these studies tend to take a uni-directional view of impact pathways (i.e. climate change impacts key aspects of the ecosystem, which in turn impacts society) (e.g. Allison et al. 2009; Cinner et al. 2012; MacNeil et al. 2010). However, climate change may not only interrupt the flow of goods and services to society, but may also alter how people interact with reefs, creating potential pathways from society to ecosystems (Butler and Oluoch-Kosura 2006; Cinner et al. 2011; Daw et al. 2009). Critically, coral reefs are linked social–ecological systems (Kittinger et al. 2012; Walker and Meyers 2004), meaning that the changes in the ecological domain may influence social dynamics and vice versa.

A major impediment to understanding the impacts that climate change will have on human societies dependent on coral reefs, and vice versa, is the limited consideration of multiple pathways through which impacts can manifest, especially indirect and bi-directional linkages among distinct components of social–ecological systems. Frameworks exist that reflect the interdependent nature of human–environment systems (e.g. Kittinger et al. 2012), but the majority of research on climate change and coral reefs is focused on unidirectional flow of both benefits and impacts from environment to people (e.g. Bell et al. 2013). Here, we contribute to expanding this emerging field of research in two important ways. First, we explicitly consider the multitude of pathways through which select climate drivers (e.g. increasing temperatures) will impact coral reefs and reef-dependent societies, exploring the existence of well-supported or hypothesized linkages across relevant components of the social–ecological system. Secondly, we also highlight key instances when the impact pathways are expected to be bi-directional (e.g. also flow from people to ecosystems). Our review of impact pathways focuses on four distinct climate drivers: (1) increasing sea surface temperature; (2) increasing frequency and/or intensity of storms; (3) sea level rise; and (4) ocean acidification. This is not to say other environmental changes (e.g. depth stratification and declines in vertical mixing, shifts in the position and strength of ocean currents, and changes in rainfall and freshwater input) will not have equally important or even greater impacts on coral reefs and reef-dependent societies. However, it is not our intention to comprehensively assess the multitude of impacts arising from sustained and ongoing climate change. Rather, we present key exemplars to provide a focus for understanding the existence of multiple impact pathways.

Potential impacts of climate change on coral reef ecosystems have been extensively reviewed (e.g. Hoegh-Guldberg et al. 2007; MacNeil et al. 2010; Pratchett et al. 2008; Wilson et al. 2006), as have (to a lesser extent) the flow-on effects to reef-dependent and coastal societies (e.g. Allison et al. 2009; Badjeck et al. 2010; Burke et al. 2011; Cinner et al. 2012; McClanahan and Cinner 2012). The novelty of this study is not only to understand impacts of climate change on coral reefs and reef-dependent societies, but explicitly recognize that societal responses may in turn impact on natural resources and the environment. Our approach was centred around five key components of the social–ecological system: (1) *Environment*, which includes aspects of habitat availability, water chemistry, primary productivity and the structural complexity of the benthic habitat; (2) *Population dynamics* of exploited or ecologically important organisms, including dispersal and intrinsic growth rates; (3) *Resource availability*, which includes abundance, richness, distribution and behaviour; (4) *Fisheries*, which includes aspects of yield, fishing effort and variability; and (5) *Societal well-being*, which includes livelihoods, human health and safety, infrastructure and cultural

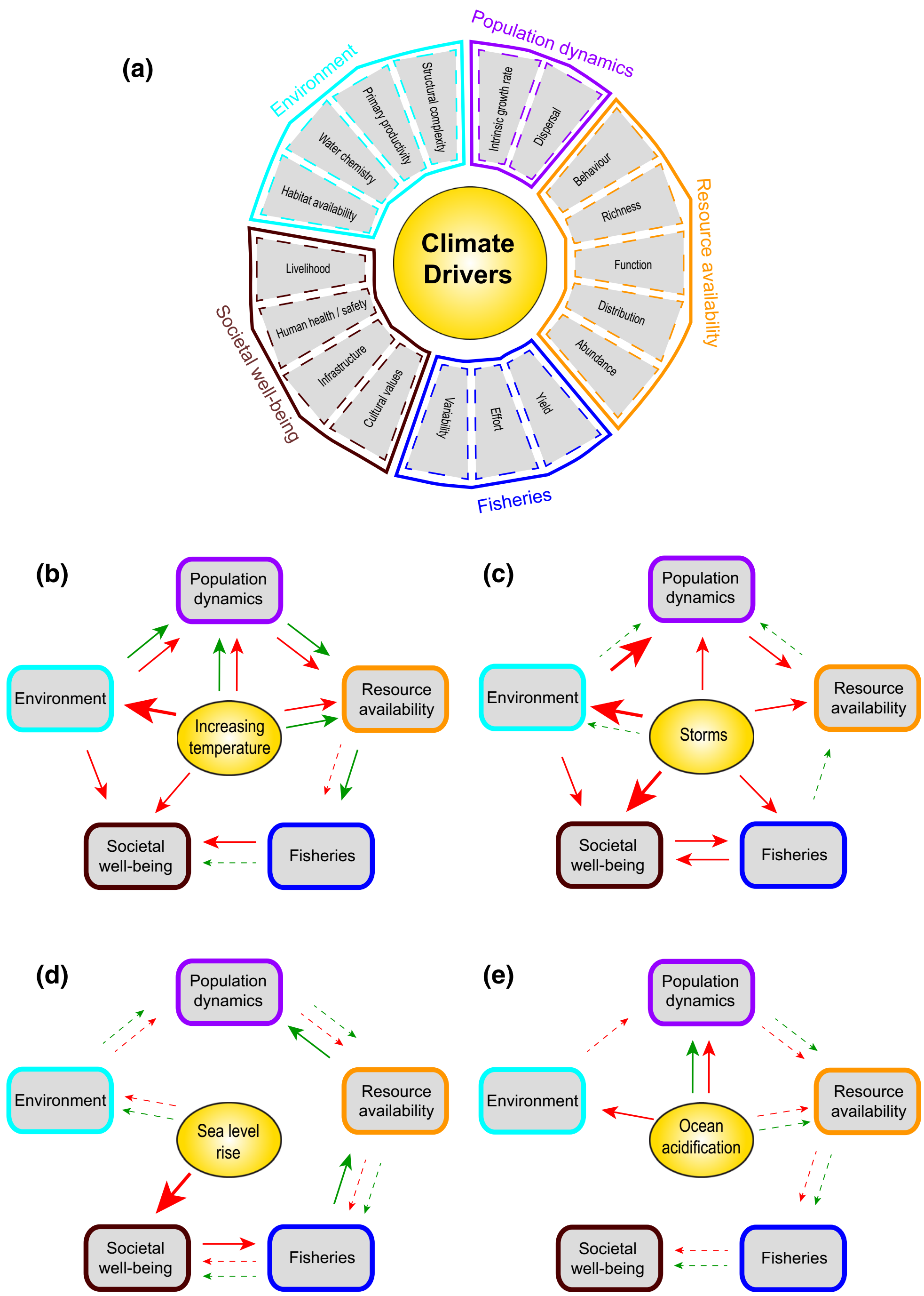

Fig. 1 Conceptual figure showing: **a** the five key components of the social–ecological system (developed based on expert opinion) used to guide consideration of multiple links and impact pathways, and the specific mechanistic bases of potential impacts considered for each component, and: **b**–**e** different impact pathways linking specific drivers to mechanisms of impact. Sea surface temperature (**b**) mainly affects environmental conditions like structural complexity availability of habitat and primary production. Storms (**c**) affect processes like settlement, and thereby availability of resources, fishing effort in stormy seas and fisher safety. Sea level rise (**d**) has significant direct impacts on societal well-being through coastal erosion and inundation, which could motivate fishers to exit the fishery leading to positive feedbacks on resource abundance, richness and ecological function. Ocean acidification (**e**) has weaker impacts through environmental conditions and processes relative to the other drivers by the end of the century, but acts as an important cumulative impact on, for example, habitat complexity and reproduction. *Red arrows* represent a potentially negative impact. *Green arrows* represent a potentially positive influence. The width of the *arrows* reflects the strength of the pathway, with *dotted arrows* representing weaker and less certain pathways, and *thick arrows* representing strong pathways with considerable certainty (color figure online)

values (Fig. 1a). These five components of the social–ecological system were developed based on expert opinion of the authors and are intended to be representative rather than comprehensive, providing an explicit focus for analyses of multiple links and impact pathways. For each of these components, we reviewed published studies to establish whether there are likely or documented impacts arising from each of the distinct climatic drivers (increasing temperature, storms, sea level rise and ocean acidification). Moreover, we reviewed evidence of bi-directional linkages between each successive pair of the five social–ecological components, thereby highlighting the multiple impact pathways through which climate change will impact coral reef social–ecological systems. Exploration of multiple links and impact pathways among the major social–ecological components was necessarily constrained to specific mechanisms by which impacts may become manifest, e.g. changes in the overall yield, effort or variability in yields for fisheries (Fig. 1a). These sub-components are broadly reflective of anticipated and wellstudied impacts, but are certainly not intended to capture the comprehensive range of potential impacts.

Sea surface temperatures (Fig. 1b)

Increasing atmospheric and ocean temperatures is the most pervasive effect of increasing concentrations of atmospheric greenhouse gases (Hartmann et al. 2013) with direct biological impacts (e.g. Hughes 2000; Walther et al. 2002). Sea surface temperature (SST) of the tropical oceans has warmed ~0.08 °C/decade over the period 1950–2011 (Lough 2012). Under relatively optimistic future greenhouse gas emission reductions, projected increases in SST range from ~0.5 to 1.5 °C by mid-century (Kirtman et al. 2013) and from ~0.7 to 2.5 °C by the end of the twenty-first century (Collins et al. 2013). Significant increases in thermal fluctuations, as well as higher frequency and duration of hot temperature extremes, are also projected (Collins et al. 2013; Walther et al. 2002).

Key impact pathways

The most apparent impact of ocean warming on coral reef ecosystems, to date, has been the recurrence of mass bleaching events (e.g. Donner et al. 2005) where ambient temperatures exceed the critical thermal limits of many coral species (Donner 2009). These bleaching events reduce coral fitness (Howells et al. 2013) and may cause widespread coral mortality (Eakin et al. 2010; McClanahan 2004). In 1998, for example, up to 90 % of habitat-forming corals were lost in many parts of the Indian Ocean (Graham et al. 2006). Extensive coral mortality results in large-scale changes to the reef environment, such as habitat loss and a collapse of the structural complexity of coral reef architecture (large red arrow between sea surface temperature and environment in Fig. 1b; Graham et al. 2006). In the absence of sufficient herbivores, these changes can further alter the environment through phase shifts to algal-dominated states (Hughes et al. 2010). Directional shifts in the structure of coral reef habitats further impact the population and community dynamics of reef-associated organisms, generally leading to declines in abundance and diversity of fish (e.g. Pratchett et al. 2011; Wilson et al. 2006), and other associated organisms (Stella et al. 2011).

Aside from climate-induced changes in habitat structure, ocean warming can also directly impact population dynamics such as the physiology, behaviour and fitness of reef-associated organisms. Tropical species, such as reef fishes tend to have very narrow thermal tolerances and also live very close to their upper thermal limits (e.g. Dillon et al. 2010; Donelson et al. 2010; Rummer et al. 2014; Tewksbury et al. 2008), making them extremely vulnerable to sustained increases in baseline temperature, as well as acute fluctuations in maximum temperatures (Munday et al. 2008). In responding to sustained and ongoing temperature increases, coral reef organisms may move to higher latitudes or increasing depths (Cheung et al. 2009). However, coral reef organisms (both fish and invertebrates) exposed to high temperatures may experience accelerated development (Figueiredo et al. 2014; Heyward and Negri 2010; McLeod et al. 2013; O'Connor et al. 2007), increased growth rates (e.g. Fulton et al. 2014; Munday et al. 2008), reduced body size (Daufresne et al. 2009), lower fecundity (McClanahan et al. 2009) and increased metabolic rates (Rummer et al. 2014). These changes may lead to reduced abundance and fitness of affected populations, as well as reduced connectivity among populations.

The sensitivity of reef-associated organisms to increasing temperatures and extreme hot weather events varies greatly, depending on specific thermal limits and local thermal history (Munday et al. 2012). Importantly, there are likely to be winners and losers (Graham et al. 2014; Pratchett et al. 2011). For example, not all reef fish species decline in abundance (at least in the short term) following bleaching-induced changes to reef habitats. Some species exhibit rapid and pronounced increases in abundance after bleaching (green arrows from environment, through population dynamics, and resource availability in Fig. 1b; Cinner et al. 2013; Pratchett et al. 2011). It is likely that some fishers will be able to take advantage of these changes to receive at least short-term increases in fish catch. For example, fishing gears that target herbivorous fishes may see short-term catch increases after a coral bleaching event (Cinner et al. 2013), but these may not carry through to an increase in income for the wider fishery (McClanahan et al. 2008). In the longer-term, temperature-induced changes to benthic habitat complexity and availability are expected to erode reef productivity and ultimately lead to reductions in fishery yields and fishers' livelihoods (Barange et al. 2014; Bell et al. 2013; Graham et al. 2007; Williamson et al. 2014). However, the empirical evidence of climate-induced changes upon resource availability, the fishery and associated societal well-being have yet to be conclusively demonstrated (indicated by dotted arrows between fishery and societal wellbeing in Fig. 1b; MacNeil et al. 2010). Importantly, this does not mean that climate change cannot impact societal well-being through this pathway. These changes are complex and difficult to detect (given the SST changes to date), and there is a paucity of research on reef fisheries attempting to disentangle these causal links (e.g. how temperature-induced changes to dispersal may impact the distribution and abundance of key target species).

The direct impacts of increased SST in tropical oceans can also affect human well-being and human health (red arrow directly from sea surface temperature to societal wellbeing in Fig. 1b). For example, increasing SST can result in increased phytoplankton blooms that are related to incidents of shellfish poisoning (Allison et al. 2009; Baschieri and Kovats 2010), toxic dinoflagellates such as *Gambierdiscus* spp. associated with ciguatera fish poisoning (Chateau-Degat et al. 2005; Tester et al. 2010), and conditions conducive to cholera outbreaks because the *Vibrio cholera*e bacterium thrives in warmer waters (Ceccarelli and Colwell 2014; Lipp et al. 2002). The socioeconomic impacts of human health-related incidents due to microbial outbreaks include health-related costs, loss of labour productivity, loss of a food source, loss of reef fish sales in both local and international markets, and changes to the social, cultural and traditional characteristics of fishing communities (Rongo and van Woesik 2012). These impacts affect the well-being of people directly, but also indirectly through a loss of tourism (Westmacott et al. 2000). In particular, the potential increase in production of harmful viruses and biotoxins could have severe implications for societies unprepared for their increased prevalence and range expansions (Hallegraeff 2010).

Severe tropical storms (Fig. 1c)

The effects of climate change (specifically, ocean warming) on the frequency and severity of tropical storms (e.g. cyclones and hurricanes) are complex (Haig et al. 2014; Klotzbach 2006; Landsea et al. 2006; Webster et al. 2005). Intuitively, increasing SST will increase energy and intensity of severe tropical storms, and consistent with this link, several recent analyses suggest that extreme wave heights have been increasing over the last decades (Elsner et al. 2008; Hoyos et al. 2006; Young et al. 2011). However, fluctuations in the frequency and intensity of tropical cyclones make it very difficult to detect clear long-term trends, especially during the period that there have been unequivocal increases in atmospheric temperature due to anthropogenic forcing (Knutson et al. 2010). Empirical data point to recent declines in the incidence of high-intensity tropical storms (Callaghan and Power 2011), yet the global incidence of high-intensity tropical storms (e.g. category 5 cyclones) is expected to increase with ocean warming (Knutson et al. 2010).

Key impact pathways

Severe storms can cause extensive physical damage to coral reef environments (thick red arrow between storms and environment in Fig. 1c; De'ath et al. 2012). For example, physical disturbance during intense storms fractures carbonate reef foundations (McAdoo et al. 2011; Nott and Hayne 2001), reducing live coral cover and structural complexity by 80–100 % (Harmelin-Vivien 1994). This physical damage also redistributes sediment and rubble, which increases water turbidity and can smother some reefs (McAdoo et al. 2011; Scoffin 1993; Vanwoesik et al. 1991; Woodley 1980). Storm impacts are correlated to frequency and/or intensity of events and, in general, negatively affect coral reef social–ecological systems. Yet, storm events can also facilitate windows of opportunity for renewal within ecological systems. For instance, intense storms have scoured algal-covered reefs, providing opportunities for corals to recruit (indicated by green arrow between storms and environment in Fig. 1c; Graham and Nash 2013).

The physical disturbance caused during and after storms also impacts population dynamics such as recruitment, settlement and survival of coral and fish larvae (Lassig 1983), which, in turn, reduce the abundance and diversity of species, with potential impacts to the fishery. Several studies have attempted to quantify changes to fish abundance following a storm, with inconsistent results. For example, Fenner (1991) found that fish populations were largely unaffected over 22 months following a severe storm in Mexico. Lassig (1983) found little effect on adult fishes, but high juvenile mortality and re-distribution of sub-adult fishes after 27 months post-storm on the Great Barrier Reef, Australia. Further, in a longer-term study, Halford et al. (2004) found that of 26 fish species analysed on the GBR, 23 decreased in abundance post-storm(s), with all but two species recovering to pre-disturbance levels after 10 years.

Storms can also directly affect aspects of resource availability (Fig. 1c). For instance, some fish species change their behaviour and movement patterns in storms (Heupel et al. 2003; Kawabata et al. 2010; Locascio and Mann 2005). These changes can in turn influence the catchability of fishes and/or reduce their availability to fishers, impacting fishery yields, incomes and adding to the inherent variability in a fishery (Tobin et al. 2010). For example, Marshall and Marshall (2012) reported reduced catches nine months after category 5 Cyclone Yasi on the Great Barrier Reef. Storms therefore have a mix of short- and long-term effects on resource availability. Where major structural changes occur on the reef environment, long-term effects are highly likely.

Severe storms can also directly impact social well-being, imposing significant risk to infrastructure, human health and safety. For instance, extreme surface waves produced by typhoons/cyclones can propel large parts of carbonate reef (e.g. 14 m waves moving 235-tonne boulders, Goto et al. 2011) to cause major damage to landing sites, boats and gear, with knock on effects to coastal livelihoods and incomes. In Antigua and Barbuda, damage and loss of fishing fleet assets resulted in an estimated decrease of 24 % in gross revenues (Mahon 2002). Damage to fishery infrastructure and reduced fleet capacity could also have flow-on effects that result in increased resource availability and population dynamics (indicated by green dotted arrows between fishery, resource availability and population dynamics in Fig. 1c; Baird et al. 2005). Damage to reefs from storms can also directly affect societal well-being because tourists may stop visiting certain reefs that have experienced severe storm damage, with flow-on effects to tourism-dependent livelihoods. Severe direct effects on aspects of societal well-being such as health, safety and the loss of life following extreme events can further cascade into chronic impacts on other household and community aspects of life (Blythe et al. 2013; Westlund et al. 2007).

In addition to direct mechanical damage, storms can lead to increases in rainfall, severe flooding, runoff and surface currents. These in turn can cause elevated catchment runoff (e.g. freshwater, sediment, nutrients and pollutants), enhanced coastal erosion and increases in marine sediment re-suspension which all result in declining coral and fish health (Cheal et al. 2013; Fabricius and Wolanski 2000; Goatley and Bellwood 2012; Mallela et al. 2007; Wenger et al. 2012, 2013, 2014), as well as potential habitat loss. Storm surges can directly impact societal well-being by lowering the availability and quality of limited freshwater sources of atoll nations (Bridges and McClatchey 2009). The microbial community in both the water column and surface biofilms is also altered by runoff and sedimentation, and while these shifts may be bio-indicators of change (Witt et al. 2012), they are also associated with a shift towards greater organism disease. These community shifts towards pathogenic microbial communities is linked to the emergence of disease in vertebrate and invertebrate hosts (Sandin 2009; Thurber et al. 2012) and also within human populations using reef resources (Burge et al. 2014). Negative feedbacks between run-off, ecosystem decline and human health will be further exacerbated in developing regions where wastewater treatment infrastructure is limited.

Sea level rise (Fig. 1d)

There is considerable uncertainty about the likely magnitude of sea level rise, in part due to the unpredictable nature and instability of key ice sheets. Sea level is currently rising at approximately 3.2 mm per year due to thermal expansion of the ocean and melting of land ice, and the rate of change is accelerating (Rhein et al. 2013). Continued melting of the polar ice sheets will increase sea level rise, by as much as 3–5 m by 2100 (Overpeck et al. 2006). Coral reef ecosystems are generally resilient to sea level fluctuations, and even rapid changes in the geological past (e.g. a 2- to 3-m jump with years to decades approximately 121,000 years ago) have had only minor impacts on the growth and development of reef assemblages (Blanchon et al. 2009). Increase in sea level does, however, pose a significant threat to the millions of people who inhabit coastal villages and cities (Overpeck et al. 2006).

Key impact pathways

Sea level rise is perhaps the most unique climate change driver in that it is not expected to have profound direct negative effect on coral reef environments because accretion rates of coral are generally sufficient to keep pace with sea level rise. In fact, coral reefs in some locations might benefit due to increased habitat availability (i.e. coral reefs growing upwards as coral recolonizes the tops of currently mature reefs, and as corals expand into areas currently too shallow for them to inhabit; dotted green arrows from sea level rise to environment in Fig. 1d). Humans may benefit from this increased habitat availability through increased primary productivity, resource availability, fishery yields and, ultimately, increased fisheries productivity. However, coral reef-associated species could be negatively affected by sea level rise if they depend on habitats that are not capable of vertical migration as the sea rises (e.g. coastal development may prevent mangrove forests or turtle nesting beaches from moving inland; dotted red arrows in Fig. 1d).

While there could be minor ecological benefits to coral reefs, sea level rise is expected to have direct negative impacts on societal well-being (thick red arrow in Fig. 1d). Rising seas, especially when combined with severe storm events, threaten coastal infrastructure. Damage to ports and docks could reduce fishing fleet capacity, creating negative impacts on livelihoods yet alleviating pressure on marine resources (red arrow between societal well-being and fishery, and slow on green arrows to resource availability and population dynamics in Fig. 1d; Adger et al. 2005). Many low-lying tropical islands are in peril, and whole nations may become uninhabitable, for example, atoll nations such as Kiribati (McCarthy et al. 2001). Climate change-induced migration has been linked to increased possibilities for violent conflict (e.g. in areas of in-migration) and is likely to have greater impacts upon poorer members of coastal societies (Reuveny 2007). While this form of migration, if planned strategically, also has potential benefits (e.g. income diversification) and can be viewed as an adaptive response to environmental conditions (Black et al. 2011), it is important to bear in mind that biophysical changes enter stratified social systems, meaning that impacts are experienced differentially due to class, castes, gender, profession, race, ethnicity, age and ability (Marino 2012). Sea level rise is likely to create variable social impacts in places like the Pacific where fishing strategies vary by cultural group, gender and habitat fished (coastal reef, lagoon and outer reef; Kronen and Vunisea 2009). The links between sea level rise, human migration and well-being are thus complex and context dependent (Black et al. 2011; Farbotko and Lazrus 2012).

Ocean acidification (Fig. 1e)

Increased atmospheric CO_2 is readily dissolved into the world's oceans, leading to marked changes in seawater chemistry (most notably declines in pH, carbonate ion concentrations and carbonate saturation state), commonly referred to as ocean acidification (Caldeira and Wickett 2003). Rapidly rising atmospheric partial pressure of carbon dioxide (pCO_2) over the last century has induced a lowering of oceanic pH by $\sim$0.1 units (from $\sim$8.25 to $\sim$8.14, Orr et al. 2005). Estimates of future atmospheric pCO_2 (Pörtner et al. 2014) suggest a further decrease of 0.3 pH units by the end of the century (Caldeira and Wickett 2003). These marked and sustained changes in seawater chemistry of oceanic waters (e.g. Doney et al. 2009) are raising concerns. However, seawater chemistry in near-shore environments (e.g. within the immediate vicinity of corals reefs) is highly variable, fluctuating over diurnal (due to respiration and photosynthesis of coral reef organisms), tidal and seasonal cycles, and daily extremes often exceed the projected levels of pCO_2 and pH to occur by the end of the century in open ocean waters (Albright et al. 2013; Guadayol et al. 2014; Hofmann et al. 2011; Shaw et al. 2013).

Key impact pathways

A wide range of coral reef organisms, from calcifying algae through to large piscivorous fishes, are affected by exposure to extreme levels of pCO_2 or reduced pH (De'ath et al. 2009; Munday et al. 2013; Pandolfi et al. 2011; Fig. 1e). For calcifying organisms, such as reef-building corals, the concern is that low levels of aragonite saturation will increase the energetic cost of calcification, thereby compromising skeletal growth and/or development (Doney et al. 2009). By 2050, sustained declines in aragonite saturation are expected to cause 10–50 % reduction in calcification rates of key reef-building corals relative to pre-industrial rates (Kleypas and Langdon 2006; Kleypas and Yates 2009; Langdon and Atkinson 2005). The decline in calcium carbonate production, coupled with an increase in calcium carbonate dissolution, may result in reduced cover of corals, coralline algae and other calcareous reef-building organisms, leading to marked declines in reef growth and topographic structure of reef habitats (red arrow between ocean acidification and environment in Fig. 1e). Although some coral species are able to internally buffer their pH (Dissard et al. 2012; McCulloch et al. 2012), a study on coral reefs exposed to volcanic CO_2 seeps in PNG showed a loss of many coral species, which resulted in reduced coral diversity and a shift to corals of low structural complexity and calcification rates (Fabricius et al. 2011). A loss in structural complexity (e.g. Graham et al. 2006; Wilson et al. 2006) and coral diversity (e.g. Messmer et al. 2011) is expected to have negative impacts on fish productivity (dotted red arrows between environment, population dynamics, resource availability and fishery in Fig. 1e).

Early life history stages of coral and fishes are also at high risk from ocean acidification (red arrow between ocean acidification and population dynamics in Fig. 1e). Exposure to reduced pH has been shown to affect development and suppress metamorphosis of some coral larvae species (e.g. Nakamura et al. 2011), but not fishes. Negative impacts on early life history biology are particularly significant for the maintenance of genetic diversity and for the re-establishment of corals after disturbances such as mass bleaching events.

For other reef organisms, such as fishes, ocean acidification may compromise sensory systems, impair behaviour (dotted arrows between ocean acidification and resource availability in Fig. 1e; Munday et al. 2014; Nilsson et al. 2012) and increase energetic costs to compensate tissue acidosis (Pörtner and Farrell 2008). Results from these studies suggest that fish exposed to near-future CO_2 levels exhibit impaired olfaction (e.g. distinguishing the smell of a predator; Dixson et al. 2010; Munday et al. 2009, 2014), decision-making and learning (Chivers et al. 2014; Domenici et al. 2012; Ferrari et al. 2012). Some fish even exhibit bolder behaviour and increased anxiety when exposed to elevated CO_2 (Hamilton et al. 2014; Munday et al. 2013, 2014). However, the effects of near-future CO_2 levels on physiological performance have been mixed. While some species appear to be negatively affected (Munday et al. 2009), other species exposed to elevated CO_2 exhibit either no change (Couturier et al. 2013; Yates and Halley 2006) or even exhibit enhanced scope for aerobic performance (dotted green arrows between ocean acidification and resource availability in Fig. 1e; Couturier et al. 2013; Munday et al. 2014; Rummer et al. 2013). Furthermore, studies have found that rearing fish under near-future CO_2 levels resulted in increases in reproduction and larger larvae and juveniles in comparison with control counterparts (Miller et al. 2012, 2013). Although current evidence suggests that coral reef fishes can maintain or even enhance the scope for aerobic metabolic performance under elevated CO_2, there is considerable variation among species' level responses to elevated CO_2 and ocean acidification, as reflected in studies on behaviour. Therefore, trade-offs likely exist among critical life history traits (e.g. behaviour and physiological performance) that are not yet well understood, but could result in serious implications for the replenishment of fish populations and patterns of population connectivity in coral reef ecosystems. Impact pathways through resource availability, fishery and societal well-being have not been conclusively demonstrated because ocean acidification processes will unfold over multi-decadal timescales.

Caveats and future considerations

Our attempts to highlight the multiple impact pathways through which climate change will affect coral reef social–ecological systems represent an important first step in synthesizing and guiding this emerging field of research, but has some shortcomings that could potentially be addressed as new research becomes available. Most notably, our synthesis focused on the direct impacts of four key climate drivers, but synergistic impacts, feedbacks and indirect impact pathways will likely potentially play an even more important role, and our appreciation of such impacts is currently very limited. Even among the direct impacts, there are major differences in the understanding and confidence surrounding impact pathways, partly attributable to differences in the timing of impacts (e.g. there are already impacts from SST and storms, whereas sea level rise and ocean acidification impacts will take time to emerge). As such, we fully expect that new impact pathways will emerge with ongoing research in this field. Even so, it is important to document the diverse impact pathways that are already apparent or understood, in order to develop a complete understanding of the impacts of climate change, as well as developing appropriate management actions to mitigate climate change impacts in coral reef social–ecological systems.

Documenting the impacts of interacting pathways will become increasingly critical as novel, unanticipated interactions emerge. For example, ocean acidification is likely to increase susceptibility of corals to the mechanical damage caused by storms because reductions in pH reduce coral skeleton density and strength (Hoegh-Guldberg et al. 2007; Madin et al. 2008). Decreases in calcification rates may also be exacerbated with associated increases in ocean temperature, as has already been observed for crustose coralline algae (Anthony et al. 2008; Martin and Gattuso 2009). However, to date, observational and experimental research on how synergies between key climate drivers affect coral reef systems is very limited (Ban et al. 2014). Consequently, our synthesis focused on each individual driver, rather than potential synergies among them. As more research on synergistic impacts becomes available, this will be a crucial area of research. Similarly, feedbacks between social and ecological dynamics can exacerbate the impacts of key climate drivers (Cinner et al. 2011). However, empirical and experimental research on how key climate drivers may create feedbacks in coral reef social–ecological is also limited (Nyström et al. 2012).

Some of the biggest impacts from climate change may be the indirect and unpredictable pathways on human responses, policies and changing market structures. Much of the uncertainty about the impacts of climate change on social–ecological systems arises due to the variability of human responses to change. In many instances, these linked dynamics have the potential to create both positive and negative feedbacks between social and ecological domains. For example, reduced fisheries yields associated with climate change (Cheung et al. 2009) may cause some fishers to exit the fishery (reducing fishing pressure, thus dampening environmental impacts), while other fishers may increase effort to supplement losses (potentially amplifying environmental impacts) (Cinner et al. 2011). Already in Mozambique, small-scale fishers have begun to fish into the open ocean in response to declining inshore catches resulting from overfishing; their un-motorized vessels are ill-equipped to cope with increasingly severe tropical storms leading, in the worst cases, to loss of lives (Blythe et al. 2013). At a larger scale, policy responses, motivated by a range of agendas from personal to political, will feedback into reef systems with differential impacts on individuals, groups and societies. In the Maldives, for example, climate change adaptation discourses are being used to legitimize unfavourable government resettlement programs, despite resistance from local people (Kothari 2014). Changing market structures, political unrest and demographic trends in coral reef-dependent societies will likely interact with key climate drivers to produce profound changes in the social–ecological system. Yet, to date, research on these types of impacts is extremely limited (Daw et al. 2009). Considerable research is required into the range of motivation and impacts of people's responses to climate change (Barnett and O'Neill 2010; Marino and Ribot 2012), and also how climate change will differentially impact cultures, geographies and segments of societies.

Conclusion

This study highlights a diversity of pathways in which sustained and ongoing climate change will impact coral reef ecosystems and reef-dependent societies. The relative importance of different linkages and major impact pathways varies according to the specific climate drivers being considered. For example, sea level rise is likely to only have strong direct impacts on societal well-being, but limited direct impacts on reef ecosystems. In contrast, ocean warming will have direct impacts to multiple components of coral reef ecosystems, with flow-on effects to societal well-being. Despite these important differences, existing research into impacts of climate change on coral reefs is highly biased towards one or two key pathways, which almost invariably ascribe major impacts on human societies to declines in overall fisheries yields (e.g. Cinner et al. 2012), largely ignoring broader understandings of climate impacts on societal well-being that are becoming established in other social–ecological systems (e.g. Adger et al. 2005) and the potential for bi-directionality. An important corollary of this is that that established links are as much a reflection of inherent bias in prior research, as they are indicative of major links and impact pathways.

By explicitly highlighting the specific pathways through which climate drivers can directly or indirectly influence ecosystems and societies, we hope to stimulate research into previously overlooked (or poorly understood), but potentially important pathways, to expedite a more comprehensive understanding of climate impacts on social–ecological systems associated with coral reefs. Most notably, there needs to be increased attention given to non-fisheries linkages between reef environments and reef-dependent societies. Notwithstanding emergence of even more diverse impact pathways, this will provide a more thorough and comprehensive understanding of the impacts of climate change, illustrating how impacts on coral reef environments can and will affect reef-dependent societies, and that societal responses may in turn impact on natural resources and the environment. This is fundamental in developing appropriate management actions to mitigate climate change impacts in coral reef social–ecological systems.

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