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Modelling the effects of climate change on a Caribbean coral reef food web

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ABSTRACT

Global climate change and local anthropogenic pressures are among the primary factors leading to the decline of functional biodiversity and critical habitats in coral reefs. Coral bleaching, the potential decreases in dissolved oxygen concentration (deoxygenation) and pH (acidification) in the oceans can induce severe changes in coral reef ecosystem biodiversity and functionality. The main objective of this study was to apply four Ecopath with Ecosim models of a Caribbean coral reef system to individually and collectively model the effects of coral bleaching on the trophic web, deoxygenation on fish, and acidification on calcifying organisms. These three sources of stress were used as forcing functions on several trophic groups depending on the model. The forcing functions were scaled according to the species' responses achieved in previously tested climate change marine models. For the bleaching model, a mediation function was also considered that represents the degree of coral reef protection on small and intermediate fish groups. The dynamic models were constructed from an extensive database of 171 reef fish species (abundance and biomass) and benthic communities from 13 coral reefs that were evenly distributed parallel to approximately 400 km of the Mexican Caribbean coast as well as fishery landings in this area. Simulations driven with these different forcing and mediation functions predicted different changes in the biomasses of fish and non-fish functional groups as well as the biomass of the functional groups of fished species. Coral bleaching and pH reduction caused a phase shift to a decrease in coral biomass and an increase in primary producer biomass. This shift produced a cascading decrease in the biomass of small and intermediate fish groups. Additionally, the fished functional group biomass increased with coral bleaching but decreased with the effects of decreased oxygen on fish and pH on calcifying organisms. The biomasses of certain macroinvertebrate functional groups were predicted to respond favourably to the combined effect of the sources of stress. However, when all the sources of stress were combined, we found a general decrease of biomass in fish, non-fish, and some commercially valuable fish and macroinvertebrate functional groups, suggesting that the combined effects of stress induced synergistic effects as a result of global climate change and overfishing, which can result in a potential loss of biodiversity and ecosystem services in coral reefs.

1. Introduction

Since the Anthropocene period, humans have altered the landscape in various ways. In the last two centuries, the air and ocean temperatures have increased as the ocean pH and dissolved oxygen levels have decreased (Sabine et al., 2004; Byrne et al., 2010; C.H. Ainsworth et al., 2011). These three sources of stress have been inducing changes in the intra- and inter-specific interactions, structure, dynamics, productivity, and biodiversity of coral reefs, which in turn significantly alter marine systems worldwide by interacting with anthropogenic stressors (e.g., overfishing, pollution, land use change and habitat loss; Calderon-Aguilera et al., 2012; Darling et al., 2013). Global warming is increasing surface layer stratification in the water column by reducing the supply of nutrients from the subsurface to surface waters, production and export of organic carbon, and subsurface oxygen utilisation rates (Keeling et al., 2010). In response to these climatic variations, aquatic organisms must modify their metabolic, reproductive, and developmental processes (IPCC, 2014).

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Of all marine ecosystems, coral reefs are among the most vulnerable to climate change. These ecosystems contain a variety of habitats, exhibit high environmental heterogeneity, and harbour highly complex biological and ecological processes. The increased temperatures and decreased dissolved oxygen and pH levels associated with pollution, coastal development (land-use change), and fisheries are alarmingly impacting reef ecosystems (Nyström et al., 2008; Madin et al., 2012).

Over the last 30 years, temperatures of 1–2 °C above the maximum recorded temperature have caused devastating effects worldwide (Johnson and Marshall, 2007). These temperatures have resulted in coral stress, bleaching, and death of corals (Baker et al., 2008; Brown, 1990; Hoegh-Guldberg, 1999; Douglas, 2003; Donner et al., 2005; McWilliams et al., 2005; Munday et al., 2008). Coral bleaching occurs when the symbiotic relationship between algae (zooxanthellae) and the host coral breaks down under certain environmental stresses (Baker et al., 2008). As a result, the host expels its zooxanthellae, consequently exposing its white calcium carbonate skeleton, and the affected coral colony becomes stark white or pale in colour (T.D. Ainsworth et al., 2011). Coral bleaching can be triggered and sustained under various environmental stresses. Anomalously warm water temperatures have been observed to be one of the major causes of mass coral bleaching worldwide (Munday et al., 2009; Eakin et al., 2010). Critical water temperatures (30–31 °C), duration extent (hours, days, or weeks) and event intensity (Berkelmans and Willis, 1999; Craig et al., 2001; Vargas-Angel et al., 2001; Berkelmans, 2002; Sammarco et al., 2006) are all known to affect coral bleaching (Berkelmans and Willis, 1999; Reaser et al., 2000; Eakin et al., 2010; Bastidas et al., 2012). Coral often dies after having been partially or totally bleached for long periods (Crabbe, 2008). Severe bleaching events exert dramatic long-term ecological and social impacts, including the loss of reef-building corals, changes in benthic habitats and, in some cases, decline in species abundance and richness of fish communities (Jones et al., 2004; Wilson et al., 2006). Even under favourable conditions, it can take decades for severely bleached reefs to fully recover (Wilkinson, 2008).

One associated source of temperature-related stress is the deoxygenation of ocean water. Fish and invertebrates are among the aquatic organisms most affected by deoxygenation because their physiological rates are determined by the dissolved oxygen concentration in water (Nilsson et al., 2010). Recent studies have noted that when the oxygen supply in water is low (deoxygenation), the vulnerability of fish to predation increases and their growth capacity is limited (Pörtner, 2010; C.H. Ainsworth et al., 2011; Sheridan and Bickford, 2011; Cheung et al., 2012).

Another source of stress is the change in ocean pH that results from increasing atmospheric carbon dioxide (CO_2) levels. Increased $CO_{2[atm]}$ levels exert worldwide effects on the chemical properties of oceans. The acidification of marine ecosystems has led to changes in biodiversity, trophic interactions, and essential ecosystem processes (Kleypas and Langdon, 2006; Riegl et al., 2009; C.H. Ainsworth et al., 2011). Increased CO_2 levels in water cause increased concentrations of carbonic acid (H_2CO_3), bicarbonate ion (HCO_3^-), and hydrogen ion (H^+), which leads to decreased carbonate (CO_3^{2-}) concentrations and a lowering of pH (Fabry et al., 2008; Doropoulos et al., 2012; Comeau et al., 2013). Certain global climate models have predicted a 0.3 pH unit reduction from 8.1 to 7.8 by the end of the 21st century (Caldeira and Wickett, 2005; Doney et al., 2009). It is estimated that concomitant with this drop in pH, the CO_2 reactivity with seawater will induce a 50% reduction in the availability of carbonate ions by the year 2065 (Cao and Caldeira, 2008). These ions are essential to organisms that produce shells and have exoskeletons that consist of calcium carbonate ($CaCO_3$), particularly corals, molluscs, echinoderms, foraminifera, and crustaceans (Langdon and Atkinson, 2005; Wisshak et al., 2012). The effects of acidification on calcifying organisms are well known (Guinotte et al., 2006; Anthony et al., 2011; Madin et al., 2012; Maier et al., 2012; Chan and Connolly, 2013). However, minimal information is available regarding the effects of acidification on non-calcifying organisms (e.g., fish). Recent studies that have examined the effects of acidification on the ethology and physiology of coral reef fish have observed that fish exposed to high levels of CO_2 exhibited deficiencies in the senses of smell, vision, and hearing (Munday et al., 2009; Dixson et al., 2010; Simpson et al., 2011; Ferrari et al., 2012a, 2012b; Mitchell et al., 2013).

Despite significant advances in the knowledge pertaining to the effects of climate change and anthropogenic change on marine ecosystems, gaps remain (Nicol et al., 2012), particularly regarding the overall effects of coral bleaching, deoxygenation, and acidification on the coral reef trophic web and the response of individual species to these sources of stress. Therefore, a better understanding of the impacts of multiple stressors on the structure and function of coral reef ecosystems is required. The main objective of this article is to evaluate the effects of climate change stressors on the trophic webs of a coral reef model within the Mesoamerican Reef System. To this end, we simulated four Ecopath with Ecosim (EwE) food web models by using forcing functions on temperature (coral bleaching), reduced concentrations of dissolved oxygen on fish communities (deoxygenation), reduced pH levels on calcifying organisms (acidification), and the combined effect of these three sources of stress throughout the trophic web and on certain commercially important species. In the coral bleaching model, we also mediated the structural protection that corals produce for small and intermediate fish species. Overall, the results were highly variable in single or combined models because of the multiple food web interactions in each model. There were important ecosystem shifts, as well as important biomass changes, in the fished and unfished group species depending on the model. Our work is an exploration of climate change and the modelling and simulation of coral reefs relevant to coastal conservation and management.

2. Materials and methods

2.1. Study area

Thirteen reefs distributed along the eastern coast of the Yucatan Peninsula were used to construct the north sector of the Mesoamerican Barrier Reef System (nsMBRS) trophic web (Fig. 1). These reefs form part of a semi-continuous fringing reef that runs closely and parallel to the coast beginning in Punta Nizuc in the Mexican state of Quintana Roo and connects in the south to the fringing reefs of Belize. This area is part of the MesoAmerican Reef System (MAR), one of the major biodiversity hotspots in the Caribbean Sea (for a complete description, see Arias-González, 1998; Núñez-Lara et al., 2005; Arias-González et al., 2008; Bozec et al., 2008; Hernández-Landa et al., 2014).

2.2. Ecopath with Ecosim models

Ecopath with Ecosim (EwE; Ecopath Research and Development Consortium, available at http://www.ecopath.org) was used to develop a simulation model from extensive information collected from the registries of 171 reef fish species (abundance and biomass) and benthic communities in 13 coral reef systems along the coast of Quintana Roo, Mexico. Ecopath with Ecosim 6.3 (EwE), which was used for model construction, is an approach to analysing and quantifying trophic flows within an ecosystem, which includes fisheries, and to evaluating specific ecosystem properties (http://www.ecopath.org) (Christensen and Pauly, 1992; Christensen et al., 2005, 2008). This system is based on earlier