

Vulnerability of macroalgae of the Great Barrier Reef to climate change

Guillermo Diaz-Pulido ^{1,2} and Laurence J. McCook ^{3,4}, Anthony W.D. Larkum ⁵,
Heike K. Lotze ⁶, John A. Raven ⁷, Britta Schaffelke ⁸, Jennifer E. Smith ⁹ and
Robert S. Steneck ^{3,10}

1 Centre for Marine Studies, University of Queensland, St Lucia 4072, QLD, Australia. Phone: +61-0733653378; Email: g.diazpulido@uq.edu.au

2 Programa de Biología, Universidad del Magdalena, Santa Marta, Colombia

3 Pew Fellows Program in Marine Conservation

4 Great Barrier Reef Marine Park Authority, Research and Monitoring Coordination, PO Box 1379, Townsville QLD, Australia

5 School of Biological Sciences, University of Sydney, Sydney, New South Wales 2006, Australia,

6 Biology Department, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1

7 Plant Research Unit, University of Dundee at SCRI, Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, UK

8 Australian Institute of Marine Science, PMB 3, Townsville MC QLD 4810, Australia

9 National Center for Ecological Analysis and Synthesis, University of California, USA

10 School of Marine Sciences, University of Maine, Darling Marine Center, Walpole, USA

7.1 Introduction

7.1.1 Macroalgae of the Great Barrier Reef

Definition and scope

Macroalgae is a collective term used for seaweeds and other benthic marine algae that are generally visible to the naked eye. Larger macroalgae are also referred to as seaweeds. The macroalgae of the Great Barrier Reef (GBR) are a very diverse and complex assemblage of species and forms. They occupy a wide variety of habitats, including shallow and deep coral reefs, deep inter-reefal areas, sandy bottoms, seagrass beds, mangroves roots, and rocky intertidal zones.

Macroalgae broadly comprise species from three different phyla, Rhodophyta (red algae), Heterokontophyta (predominantly Phaeophyceae, the brown algae), and Chlorophyta (the green algae; Table 1). They are clearly distinguished from microalgae, which require a microscope to be observed (eg phytoplankton, benthic and pelagic diatoms, free-living dinoflagellates, cyanobacteria (blue-green algae)

and the symbiotic zooxanthellae that live within coral tissue). In some cases, benthic microalgae, such as some cyanobacteria and Chrysophyta, form large colonies that resemble thalli of macroalgae (Schaffelke et al. 2004, Ritson-Williams et al. 2005). Such colony-forming cyanobacteria are often common components of turf algal assemblages and, in this context, will be included in this chapter.

Taxonomic diversity

GBR macroalgae are an important component of Australia's marine plant biodiversity. The Australian Marine Algal Name Index lists 629 species (including varieties) recorded for the GBR (Cowan 2006), accounting for nearly 32% of the total number of algal species recorded for the continent (although the compilation for the GBR is based on very limited collections). GBR macroalgae are not only relatively diverse at the species level, but have complex and diverse evolutionary histories (Andersen et al. 1993, Van den Hoek et al. 1995), including more than 40 orders belonging to at least five phyla and two kingdoms (Prokaryota and Eukaryota; Table 7.1). In contrast, for example, hard corals includes only 1-2 orders.

Table 7.1 Systematic diversity of coral reef benthic macroalgae in comparison to hard corals

Taxonomic Group	Orders	Phyla
Benthic macroalgae	~40	5 <ul style="list-style-type: none"> ▪ Rhodophyta (red algae); ▪ Heterokontophyta (class Phaeophyceae: brown algae; Class Bacillariophyceae: diatoms); ▪ Chlorophyta (green algae); ▪ Chrysophyta (golden algae, especially the predominantly benthic class Pelagophyceae) ▪ Cyanophyta (blue-green algae, especially colonial cyanobacteria)
Hard corals	~2 Scleractinia Milleporina	1 Cnidaria

Assessing the vulnerability of benthic macroalgae is further complicated by the fact that the taxon 'algae' is an unnatural (and, some suggest, outdated) grouping that encompasses several distinct and diverse evolutionary lines (Table 7.1). Adl et al. (2005) suggest that 'algae' remains a useful functional term, denoting photosynthetic protists and their multicellular derivatives which are not embryophytes (higher plants), as well as cyanobacteria. However, they also show that the 'algae', like the 'protists', is not a formal taxon (and therefore should not be capitalised), nor a single, homogeneous group.

Functional form group diversity

Macroalgae are not only more diverse, but also more complex in functional morphology and ecological roles, than most other groups in coral reef ecosystems. In tropical habitats, macroalgae range from small, structurally simple, filamentous turfs, a few millimetres high, or heavily calcified crustose forms, to large leathery macrophytes, such as *Sargassum*, up to several metres tall (Table 7.2). Given this diversity, different macroalgae should be assumed to respond in qualitatively different ways to the stressors associated with climate change: they can not be considered as a uniform group.

In addition to taxonomic groups, macroalgae can be considered in terms of functional groupings, based on plant attributes and ecological characteristics (such as the form of the plant, size, toughness, photosynthetic ability and growth, grazing resistance, etc) (Littler et al. 1983a, Littler et al. 1983b, Steneck & Dethier 1994). The three main categories are i. algal turfs; ii. upright macroalgae (fleshy and calcified); and iii. crustose calcareous algae (Figure 7.1). Each category includes several "functional groups" (Table 7.2). This approach is considered more useful by ecologists, because it reflects both physiological traits and the role of algae in the ecosystem (Table 7.2; Section 7.1.2), whereas ecological roles are not well correlated with taxonomic groupings.

Table 7.2 Categories and functional groups of benthic algae present in the Great Barrier Reef, as used in this vulnerability assessment.

Algal categories		Functional groups	Examples of common genera in the GBR								
Algal turfs (< 10 mm height)		Microalgae Filamentous Juvenile stages of macroalgae	<i>Lyngbya, Chryscystis</i> <i>Cladophora, Polysiphonia</i>								
“Upright” macroalgae (> 10 mm height)	Fleshy (ie non-calcareous)	<table border="0"> <tr> <td rowspan="3">Foliose</td> <td>Membranous</td> <td rowspan="3"> <ul style="list-style-type: none"> <i>Ulva, Anadyomene</i> <i>Ventricaria, Dictyosphaeria</i> <i>Dictyota, Lobophora</i> </td> </tr> <tr> <td>Globose</td> </tr> <tr> <td>Corticated</td> </tr> <tr> <td>Terete Corticated</td> <td></td> <td><i>Laurencia, Acanthophora</i></td> </tr> </table>	Foliose	Membranous	<ul style="list-style-type: none"> <i>Ulva, Anadyomene</i> <i>Ventricaria, Dictyosphaeria</i> <i>Dictyota, Lobophora</i> 	Globose	Corticated	Terete Corticated		<i>Laurencia, Acanthophora</i>	
	Foliose	Membranous		<ul style="list-style-type: none"> <i>Ulva, Anadyomene</i> <i>Ventricaria, Dictyosphaeria</i> <i>Dictyota, Lobophora</i> 							
Globose											
Corticated											
Terete Corticated		<i>Laurencia, Acanthophora</i>									
Calcareous	Leathery Calcareous articulated	<i>Sargassum, Turbinaria</i> <i>Halimeda, Amphiroa</i>									
Crustose algae		Calcareous Crustose	<i>Porolithon, Peyssonnelia</i>								
		Non-calcareous Crustose	<i>Ralfsia, Cutleria</i>								

Note: As used in this chapter, the term crustose calcareous algae (CCA) includes all calcified algal crusts, including members of both the families Corallinaceae (ie non-geniculate coralline algae, called crustose coralline algae) and Peyssonneliaceae

Distributions and seasonal dynamics

GBR algal communities are highly variable, showing latitudinal, cross-shelf and within-reef variation in composition and abundance (Morrissey 1980, McCook et al. 2000). Cross-shelf differences in seaweed composition are especially pronounced. In contrast to inshore reefs, offshore reefs usually have low abundance of fleshy macroalgae, but high cover of crustose calcareous algae (CCA) and turf assemblages. Species of fleshy macroalgal genera such as the green algae *Caulerpa*, *Chlorodesmis*, and *Halimeda*, and the red algae *Laurencia*, *Spyridia*, *Galaxaura* and *Liagora* are often present on offshore reefs, but in low abundance (Rogers 1996). Brown algae are generally low in abundance, with the most common genera including *Padina*, *Dictyota*, *Turbinaria* and *Lobophora* (McCook 1996, McCook et al. 1997, Fabricius et al. 2005). CCA are abundant and diverse on offshore reefs and can contribute to reef formation (Scoffin & McLean 1978, Chisholm et al. 1990, Ringeltaube & Harvey 2000, Fabricius & De'ath 2001, Steneck and McCook unpubl.). Abundant taxa on offshore reefs include

Porolithon, *Neogoniolithon*, *Paragoniolithon*, and *Lithophyllum* species (Steneck Unpublished).

Inshore reefs usually have abundant and conspicuous macroalgal assemblages. In particular, the often extensive reef flats are dominated by dense and highly productive beds, up to 4 m tall, of large, fleshy brown seaweeds, predominantly *Sargassum*, as well as *Hormophysa*, *Turbinaria* and *Cystoseira* (all from the Order Fucales, the rockweeds) and a variety of larger red algae (Morrissey 1980, Price 1989, Martin-Smith 1993, Vuki & Price 1994, Schaffelke & Klumpp 1997, McCook et al. 1997).

Seaweeds are also abundant in some deepwater, inter-reefal areas of the northern part of the GBR. Large mounds formed from deposits of the green calcareous alga *Halimeda* are estimated to cover up to 2,000 km² in this region and may be up to 20 m high (Orme & Salama 1988, Marshall & Davies 1988, Drew & Abel 1988). These *Halimeda* meadows occur principally in the northern sections, at depths between 20 and 40 m, but are also found in the central and southern sections, where they have been found at depths down to 96 m (Drew & Abel 1988). The GBR apparently contains the most extensive beds of actively calcifying *Halimeda* in the world, although the real extent of such meadows is unknown. The extensive deep (30 to 45 m) meadows of *Halimeda* in the northern section of the GBR appear to be sustained by nutrients injected by tidal jets and localized upwelling events (Drew 1983, Wolanski et al. 1988).

In addition to this spatial variability, many GBR macroalgae are highly seasonal in their occurrence, growth and reproduction (Price 1989). Large seaweeds such as *Sargassum* are strongly seasonal, with peaks in biomass and reproduction during the summer and lowest biomass during the winter (Martin-Smith 1993, Vuki & Price 1994, Schaffelke & Klumpp 1997, Diaz-Pulido & McCook 2005). A large proportion of the GBR benthic algal species, especially red algae, grow most actively during the Australian autumn (March to May), winter (June to August), and spring (Price 1989). Extensive but ephemeral blooms of smaller, fleshy brown macroalgae, such as *Chnoospora* and *Hydroclathrus*, have been observed on

shallow reef flats predominantly during winter and early spring (Schaffelke & Klumpp 1997, Burgess 2006, GDP, LM, BS pers.obs.)).

The challenge: assessing the vulnerability of a group with diverse ecological roles

In this paper, we consider the vulnerability of benthic macroalgae to climate change in terms of the vulnerability of natural assemblages and distributions, rather than simply the overall abundance of the entire group. That is, if a turf algal assemblage undergoes a marked shift in species composition, but remains dominated by turf algae, that assemblage is nonetheless vulnerable.

Also critical to this assessment is recognition that different macroalgae have different ecological functions, contributing to both the maintenance of reef health, and to the degradation of reefs (section 7.1.2). Disturbances or stresses such as climate change may lead to an overall increase in total amount of macroalgae, but this may be detrimental to the ecosystem as a whole, and does not mean that macroalgae as a group are not vulnerable. Some taxa, groups or assemblages of algae may thrive, but others may decline markedly, in response to direct impacts, or indirectly if, for example, outcompeted by more successful algae. The outcome will be algal assemblages, and ecosystems, that are markedly different in terms of taxonomic composition, ecosystem function, and the relative and overall abundance of different taxa. In this scenario, the macroalgal flora of the GBR is clearly vulnerable.

Further, the different algal groups outlined above (Tables 7.1 and 7.2) are likely to respond to climate change stressors in distinct and different ways. However, whilst this is true for both taxonomic and functional groupings, assessing the vulnerability of taxonomic groups is unlikely to be relevant in terms of ecological outcomes, because the broader taxonomic groups (i.e. above Order) are not well correlated with ecological roles and functions.

For these reasons, we have assessed the vulnerability of GBR macroalgae based on the ecologically-derived functional categories identified in Table 7.2, as the

approach and level of detail most useful to environmental managers or researchers. Whilst there will clearly still be considerable variation within these categories, more detailed treatment is not warranted by the available information, and is beyond the scope of the present chapter.

7.1.2 Ecological roles of macroalgae in the Great Barrier Reef

Macroalgae have critical and complex roles on coral reefs of the GBR, including significant contributions to primary production, nitrogen fixation, construction and cementation of reef framework, facilitation of coral settlement, and creation of habitats for other reef species. Macroalgal colonisation and abundance have also been recognised as causes or, more importantly, consequences of coral reef degradation.

Contribution to primary production and carbon storage

A large proportion of the primary production (the formation of organic matter by plants through photosynthesis) on a coral reef is contributed by benthic algae, particularly by algal turfs (Gattuso et al. 1998). Available research from the GBR indicates that primary production by fleshy macroalgae and crustose algae is also important (Schaffelke & Klumpp 1997, Chisholm 2003). Planktonic microalgae and algal symbionts of scleractinian corals contribute to reef productivity to a lesser degree (Adey 1998). The organic matter produced enters the reef food web by several pathways. Many algae are directly consumed by herbivorous fishes, crabs, sea urchins and mesograzers, while dissolved organic carbon released by the algae into the water enters the microbial food web (Borowitzka & Larkum 1986). Some organic matter is exported as detritus by currents and tides to adjacent ecosystems such as seagrass meadows, mangroves and the deeper, inter-reefal sea floor. There is no published information on primary production of benthic algae in GBR habitats other than coral reefs.

Reefs dominated by fleshy macroalgae, such as inshore reefs and reef flats may play important roles as short-term sinks for atmospheric CO₂ (Gattuso et al. 1997, Adey 1998). However, the seasonal and disturbance-driven dynamics of algal

abundance and taxonomic composition in the GBR is likely to lead to distinct fluctuations in the metabolic performance (primary production and respiration; (Barnes 1988) and therefore in the amount of carbon being stored.

Nitrogen fixation and nutrient retention

Filamentous blue-green algae living in algal turf communities and on sandy bottoms fix significant amounts of atmospheric nitrogen to sustain their growth independent of dissolved nutrients (Jones et al. 1998, Heil et al. 2004). Because of the rapid growth rates of blue-green algae and intense grazing on turf communities, the organic nitrogen fixed in algal tissue rapidly enters the food web and becomes available for other primary producers (Hatcher 1988). Studies on the GBR have found high rates of nitrogen fixation, particularly on substrates exposed to fish grazing (Wilkinson & Sammarco 1983, Wilkinson et al. 1983, Larkum et al. 1988).

Reef construction and habitat formation

Many macroalgae make important contributions to the construction of reef framework by depositing calcium carbonate (CaCO_3). Crustose calcareous algae (eg *Porolithon* and *Peyssonnelia*) are significant framework builders and framework 'cementers' on coral reefs (Littler & Littler 1984, Chisholm 2000). CCA bind adjacent substrata and provide a calcified tissue barrier against erosion (Littler & Littler 1984). This process may be particularly important on reef crests on the GBR, where CCA may be the dominant benthic organisms, potentially contributing to reef cementation (Cribb 1973, Scoffin & McLean 1978, Chisholm et al. 1990). However, the contribution of coralline algae to reef cementation in the GBR (as opposed to cementation that is microbially mediated lithification) has not been quantified, although deposition of calcium carbonate may be high (Chisholm 2000). Geological formations of small CCA concretions (rhodoliths) have been shown to occur over wide areas in shallow and deep continental shelf waters in other parts of the world (Ballantine et al. 2000, Sagawa et al. 2001, Foster 2001) and this is likely to be true for Australia and the GBR (Foster 2001, Braithwaite et al. 2004). CCA are important in areas between 80 and 120 m depth, at the edge of

the continental platform in the southern GBR, where they form large frameworks, several meters high (Davies et al. 2004).

Upright calcareous algae, such as *Halimeda*, *Udotea*, *Amphiroa* and *Galaxaura* make important contributions to the production of marine sediments (Hillis-Colinvaux 1980, Drew 1983, Davies & Marshall 1985). The white sand of beaches and reef lagoons are largely composed of eroded calcium carbonate skeletons of these algae, as well as foraminiferans and corals. These sediments are important to reef accretion, filling spaces in the reef matrix or structure. Calcium carbonate is deposited as aragonite, calcite and high magnesium calcite in the algal tissues (Littler & Littler 1984). Calcification may be an adaptation which inhibits grazing (defensive mechanism) (Steneck & Watling 1982, Steneck 1982, 1983, 1986, 1988), resists wave damage, and provides mechanical support and protection from UV radiation (Littler & Littler 1984, Beach et al. 2006).

In habitats such as *Sargassum* and *Halimeda* beds, the macroalgae also provide the three-dimensional structure that defines the habitat (“habitat formers”), in the same way that trees create a forest. Many other organisms find shelter or food within the physical environment created by these algae, and some macroalgal beds may serve as important juvenile or nursery habitats for reef fish and invertebrates (e.g. Beck et al. 2003).

Facilitation of coral settlement

Crustose calcareous algae of the order Corallinales are suggested to induce settlement of coral larvae in the GBR (Heyward & Negri 1999). Recent experimental studies have suggested that the crustose coralline alga *Titanoderma prototypum* is one of the most preferred substrates for coral settlement, with larval settlement rates 15 times higher than on other CCA (Harrington et al. 2004). The implications of this process at the ecosystem level remain to be explored.

Reef degradation

Macroalgae also play critical roles in reef degradation, particularly in ecological phase shifts or gradual transitions, where abundant reef-building corals are replaced by abundant fleshy macroalgae (Done 1992, Hughes 1994, McCook 1999, Koop et al. 2001, McManus & Polsenberg 2004). Reductions in herbivory due to overfishing and increases in nutrient inputs have been shown to cause increases in fleshy macroalgal abundance, leading to coral overgrowth by algae and, ultimately, reef degradation (Steneck 1994, McCook 1999, Szmant 2002, McClanahan et al. 2002). Many disturbances, such as coral bleaching, crown-of-thorns starfish outbreaks, extreme low tides, outbreaks of coral diseases and storm damage (specifically tropical cyclones) often lead directly to coral mortality. The dead coral skeletons are then rapidly colonised by diverse algal communities (Price 1975, Johnson et al. 1995, Diaz-Pulido & McCook 2002, Halford et al. 2004). A reef community dominated by abundant, high biomass algal turfs or larger, fleshy macroalgae may lead to overgrowth, smothering and/or shading of corals, the exclusion of coral recruitment, and increases in pathogens, resulting in an alternate stable state, with decreased ecological, economic and aesthetic value (Hughes 1994, Tanner 1995, McCook et al. 2001, Nugues et al. 2004, Smith et al. 2006). A macroalgal-dominated state may be very persistent, especially if the initial stressors that led to coral mortality are still present, and either do not adversely affect the new macroalgal community or even have positive feedback effects.

7.1.3 Critical factors for survival of macroalgae

The distribution and abundance of macroalgae on coral reefs are determined by the resources they require (ie light, carbon dioxide, mineral nutrients, substrate), the effects of environmental factors (eg temperature, salinity, water movement), individual rates of recruitment, mortality and dispersal, and biological interactions such as competition and herbivory. All these aspects and their interactions are of particular importance under climate change scenarios since they are all likely to be altered. For instance, sea temperatures govern global biogeographic distributions of seaweeds and therefore any temperature change is expected to affect distribution ranges and seasonality of reef algae (Van den Hoek et al. 1990, Adey & Steneck 2001, Schils & Wilson 2006). Increased resources such as carbon

dioxide (CO₂) and nutrients may enhance growth rates but the accumulation of biomass will largely depend on the interactions with herbivores (McCook 1999). In this chapter we consider the impacts of changes in environmental conditions and resources including (1) ocean circulation, (2) sea water temperature, (3) ocean chemistry (sea surface CO₂ and the consequent increase in bicarbonate), (4) light and UV radiation, (5) sea level rise, (6) tropical storms, (7) rainfall and river flood plumes and (8) substrate availability.

7.2 Vulnerability of algal turfs, fleshy and crustose calcareous macroalgae to climate change

7.2.1 Changes in ocean circulation

7.2.1.1 Exposure - ocean circulation

Perhaps one of the least studied aspects of global climate change, there is only limited information about how ocean circulation might change under global climate scenarios (see Steinberg chapter 3 this volume). Algal turfs, upright macroalgae and CCA are likely to be considerably exposed to changes in ocean circulation, such as changes in water movement, temperature and quality (e.g., upwelling or dispersion of flood plumes). For example, a strengthening of the Hiri current may depresses the thermocline suppressing the ability of cooler deep waters to access the continental shelf (see Steinberg chapter 3 this volume), with potential impacts on macroalgal productivity. Cai et al. (2005) predict a strengthening of the Eastern Australian Current but the extent to which this will affect the GBR is not clear.

7.2.1.2 Sensitivity - ocean circulation

Algal dispersal is dependent on ocean currents and algal distributions and ecological functions (productivity, nitrogen fixation, etc) are sensitive to changes in water temperature and water quality (discussed in more detail below). There is potential for shifts in species composition, and these changes may be sudden or abrupt, depending on the nature of the circulation changes.

Upright algae, especially of the order Fucales (e.g. *Sargassum*), are less homogeneous in distribution (McCook et al. 1997) than turfs or CCA, and hence

may be more sensitive to changes in dispersal by water movements. For example, *Sargassum* spp. distributions are restricted to the inshore reefs and therefore changes in ocean circulation could affect populations of these algae.

Distributions of CCA depend on water flow, temperature, water quality and dispersal and are therefore sensitive to variation in such factors and processes (Littler & Doty 1975). (Steneck & Adey 1976, Johansen 1981, Adey & Steneck 2001)

7.2.1.3 Impacts - ocean circulation

Impacts of altered ocean circulation on turf algae and most upright macroalgae include potential changes in propagule dispersal and consequent changes in distribution patterns, including range expansions and the potential for of species introductions. However, baseline descriptions of the GBR algal flora are limited, especially for turfs. Thus impacts of changing ocean circulation are essentially impossible to assess.

Shifts in temperature and water quality are likely to result in altered distribution patterns (range extensions or contractions) and species composition of algal turfs (Schiel et al. 2004), and consequent changes in ecological functions such as productivity and nitrogen fixation. Increases in seawater temperature, associated with changes in ocean circulation, have been suggested to be causing range contractions of some species of macroalgae along the New South Wales coast (Millar 2007).

The distribution of beds of *Halimeda* (an upright calcified macroalga) in the northern GBR is known to be a consequence of specific oceanographic conditions (tidal jets), which may be dramatically altered by changes in oceanography (Steinberg chapter 3 this volume). However, these are deep-water beds fed by very deep ocean currents, potentially diminishing the impacts of decreases in carbonate saturation of surface ocean waters, relevant for shallow sites.

Changes in ocean circulation may cause shifts in habitat suitability for CCA, with

consequence changes in distributions, and species composition within habitats. This may have potential flow-on impacts on reef accretion and coral recolonisation after disturbances such as bleaching.

7.2.1.4 Adaptive capacity - ocean circulation

As groups, algal turfs, upright macroalgae and CCA are likely to adapt (i.e. adjust, *sensu* IPCC, see also glossary of terms) through shifts in relative abundance of functional groups and shifts in species composition and function. However, such shifts, particularly of turfs and upright macroalgae, are likely to have serious, negative impacts on the adaptive capacity of the reef system as they may inhibit the growth of other benthic organisms, particularly after disturbance.

7.2.1.5 Vulnerability and thresholds - ocean circulation

Baseline descriptions of turf and upright macroalgae flora of the GBR are limited, and uncertainties about projected changes of ocean circulation are high, and the consequences of specific changes are not clear. Therefore assessing the vulnerability of algae to changing ocean circulation is difficult, but estimated to be low to moderate for algal turfs and CCA, and moderate for upright macroalgae.

7.2.2 Changes in water temperature

7.2.2.1 Exposure - water temperature

Climate change models for the GBR indicate that the average annual sea surface temperatures on the GBR are projected to continue to warm over the coming century and could be between 1 and 3 °C warmer than present temperatures by 2100 (Lough chapter 2 this volume, (IPCC 2001)¹. Projections also show that extremes in sea surface temperature will shift towards warmer extremes and a reduction in the frequency of cold extremes (Lough chapter 2 this volume). Algal turfs, upright macroalgae and CCA from shallow and deep reef zones, from both inshore and offshore reefs will be exposed to changes in sea surface temperature. Intertidal and shallow water species of all three groups will experience higher

¹ Current monthly average temperatures in coastal GBR: ~20 to 29°C, extremes ~18 to 34°C (AIMS)

exposure during emersion and there is potential for interaction with increased desiccation stress.

7.2.2.2 Sensitivity - water temperature

Although there is no information about temperature tolerances of tropical turf algae or CCA species, studies of sub-tropical algae suggest tolerances are relatively wide. Temperature tolerances of tropical macroalgal species from elsewhere (non-GBR) indicate a wide range for survival of 8 to 35°C for subtidal species and -2 to 35°C for intertidal species, but many are unable to survive permanently at 35°C (or even 33°C; (Biebl 1962, Pakker et al. 1995). Pakker et al. (1995) also found that intertidal species are generally more tolerant to high temperatures than subtidal taxa. In the more severe climate scenarios, projected sea surface temperatures will exceed optima or thresholds for photosynthesis, growth and reproduction.

7.2.2.3 Impacts - water temperature

Potential impacts of increased sea surface temperature on algal turf, upright macroalgae and CCA species, include increased metabolism, increased production (Beardall et al. 1998), and changes in seasonality, growth and reproduction (Breeman 1990). Given the diversity of forms and species, potential for wide-spread direct mortality of turf algae is likely to be low but changes in composition of assemblages are likely.

Seasonal growth and reproduction of temperate upright algae is controlled by temperature and/or day length (Lüning 1993, 1994), and several studies indicate that this also applies to tropical macroalgae (Diaz-Pulido & Garzón-Ferreira 2002, Atweberhan et al. 2005a, 2005b). While seasonality has been observed in many GBR algae (Price 1989, Martin-Smith 1993, Rogers 1996) there is no specific information available on the environmental triggers. Without this knowledge we can only suggest that temperature-controlled life cycles may become un-synchronised under climate change, with potential catastrophic effects for individual species or food webs (see Sommer et al. 2007 for an example from temperate plankton).

The potential for wide-spread direct mortality of upright macroalgae is low due to assumed wide temperature tolerances (Pakker et al. 1995). For calcified upright algae there may be increased calcification (Littler & Littler 1984, Aguirre & Riding 2005). Community changes due to shifts in relative abundance of turf algae and upright macroalgae, and range expansions, are also likely to occur (Breeman 1990, Schiel et al. 2004).

For CCA, there is potential for a slight increase in calcification², but this may be greatly offset by the projected increase in ocean CO₂ and lower carbonate saturation state. Warmer temperatures may have significant indirect impacts on CCAs. For example, high temperatures favour microbial growth, which may increase the incidence of CCA diseases, such as the Coralline Lethal Orange Disease CLOD (Littler & Littler 1995), or the *Peyssonnelia* Yellow Band Disease PYBD. Both diseases have been observed more commonly during the warmer months, although the nature and impact of such diseases in the GBR are not known (Diaz-Pulido 2002).

Changes in sea temperature may increase the potential for a new suite of introduced macroalgal species to establish in GBR habitats (especially ports and other disturbed environments that receive introduced species from human activities such as shipping) because the changed environmental conditions could match their physiological tolerances (Schaffelke et al. 2006).

7.2.2.4 Adaptive capacity - water temperature

There is limited information available on the adaptive capacity of algal turfs, upright macroalgae and CCA to cope with increased sea surface temperatures. However, it is likely to be high for all three groups, due to their wide temperature tolerances and the short generation times of algae.

7.2.2.5 Vulnerability and thresholds - water temperature

²Temperate CCA show variable responses to rising temperature (Johansen 1981, King & Schramm 1982); information for tropical CCA is very limited (King & Schramm 1982).

The vulnerability of algal turfs as a complex is likely to be low but variable, due to the high diversity of turf species and the wide range of temperature tolerances (Pakker et al. 1995). For example, taxa such as *Ulva* (*Enteromorpha*) and *Cladophora* are eurithemal with large distributional ranges and are likely to be less vulnerable than species with more restricted distributions, such as many turfing red algae (eg see Price & Scott 1992). The vulnerability of upright macroalgae and CCA is likely to be low to moderate, given the expected high adaptive capacity, and wide temperature tolerances. The effects of higher temperatures on temperature-controlled algal life cycles are not understood.

The abundance of fleshy macroalgae and CCA has been negatively correlated with sea surface temperature on reefs of the Red Sea and the Caribbean, while algal turfs are positively correlated with temperature (Diaz-Pulido & Garzón-Ferreira 2002, Atweberhan et al. 2006). This may suggest a strong competitive advantage for turfing assemblages under increased temperatures scenarios. However, this pattern needs testing in the GBR.

7.2.3 Changes in ocean chemistry

7.2.3.1 Exposure - ocean acidification

Changes to ocean chemistry will increase bicarbonate ions (HCO_3^-) with a consequent decrease in pH and in carbonate concentration. With continued emissions of CO_2 , oceanic pH is projected to decrease by about 0.4 to 0.5 units by 2100 (a change from 8.2 to 7.8). Although all benthic macroalgae will be exposed, on reefs from shallow to deep, changes in pH, CO_2 and calcium carbonate saturation state will be particularly significant for crustose and upright calcareous macroalgae (Royal Society 2005). There is also potential for changes in the availability of nutrients under reduced pH (Royal Society 2005, Kleypas et al. 2006).

7.2.3.2 Sensitivity - ocean acidification

The sensitivity of all algal groups is expected to be complex due to interactions between the effects of pH and CO_2 enhancement of photosynthesis. Although there are no data specific to the GBR, a doubling of CO_2 produced a 52% increase

in growth of a temperate red algae (Kübler et al. 1999)³ and up to 130% in other species (Gao et al. 1993b)⁴. However, calcified algae are particularly sensitive to ocean acidification. For example, in the GBR, a decrease of pH from 8 to 7.5 reduced calcification dramatically for the alga *Halimeda tuna* (Borowitzka & Larkum 1976). Reduction of pH may also decrease calcification of *Amphiroa foliacea* from the GBR (Borowitzka 1981)⁵. Decreases in carbonate saturation state will also inhibit calcification for upright macroalgae and CCA. CCA are the algal group most likely to be affected by ocean acidification, as they are highly sensitive to reductions of saturation state. Very small changes in pH (from 8.1 to 7.8) reduced calcification by as much as 21% for a coral reef community that included CCA (Leclercq et al. 2000)⁶.

7.2.3.3 Impacts - ocean acidification

Impacts of changes in ocean chemistry will vary between functional form groups. Increased ocean CO₂ concentration may enhance rates of photosynthesis and growth (particularly for species with no mechanisms for concentrating carbon), although such increases may be limited by the availability of nutrients⁷ and by possible direct effects of acidification on photosynthesis. However, if nutrient availability increases, due to higher terrestrial inputs (see 7.2.7), there is a real possibility of synergistic increases in growth of turf algae (due to increased CO₂ and nutrients), further disturbing the balance between corals and turf algae. Changes in ocean chemistry may alter the availability of nutrients, and temperature increases tend to increase stratification and reduce mixing with nutrient-enriched waters (Royal Society 2005). The overall outcome for turf algae is difficult to predict. Increased ocean CO₂ may also increase carbon uptake by turf

³ Data for the temperate intertidal fleshy red macroalga *Lomentaria articulata* showed non-linear response (Kübler et al. 1999).

⁴ Data for two species of the red fleshy alga *Gracilaria* from Japan (Gao et al. 1993b).

⁵ One of the few experiments that have used macroalgae from the GBR (Borowitzka 1981). Effects of acidification in *Amphiroa* seem to be smaller than the effects on *Halimeda tuna*.

⁶ Leclercq et al. (2000) manipulated CO₂ in a coral reef community that included the CCA *Neogoniolithon* spp. and *Hydrolithon* and predicted a reduction of 21% in calcification by 2100 (when pH is expected to be 0.3 to 0.5 units lower than present).

⁷ Some studies have shown carbon limitation for planktonic microalgae (Royal Society 2005) and temperate fleshy macroalgae (Kübler et al. 1999, Raven et al. 2005), but there are few specific examples demonstrating carbon limitation of growth of turf algae or fleshy macroalgae from coral reefs (Enríquez & Rodríguez-Román 2006), including the GBR (Larkum et al. 2003).

algae, with a resultant increase in the release of dissolved organic carbon, as has been demonstrated for some microalgae (Riebesell 2004).

For fleshy upright macroalgae, impacts of increased CO₂ are likely to be similar to those for algal turfs, including enhanced rates of photosynthesis and growth, and increased carbon storage (Borowitzka & Larkum 1976, Gao et al. 1993b). Such increases may be regulated in part by water flow and nutrient availability (Enríquez & Rodríguez-Román 2006). There is potential for shifts from carbon-saturated to presently carbon limited species. Intertidal species are likely to respond less to increased CO₂, as they are generally carbon-saturated (Beardall et al. 1998).

Ocean acidification reduces calcification of seaweeds such as *Halimeda* (Borowitzka & Larkum 1976, De Beer & Larkum 2001), *Amphiroa* (Borowitzka 1981, Langdon et al. 2000)⁸ and *Corallina pilulifera* (Gao et al. 1993a). Increased CO₂ may enhance photosynthesis in such upright, calcified algae, but these effects will be offset against those of decreased calcification as result of decreased carbonate saturation state; again the overall outcome is difficult to predict. Acidification may also increase the susceptibility of algae to grazing and erosion, and may lead to a reduction in sand production, significant loss of habitat (e.g. *Halimeda* banks), and shifts from calcifying to non-calcifying algae (Beardall et al. 1998, Kleypas et al. 1999, Royal Society 2005, Kleypas et al. 2006).

The impacts of increased CO₂ on CCA may include not only reduced calcification but may ultimately include dissolution of calcified skeletons (Royal Society 2005, Orr et al. 2005, Kleypas et al. 2006). Coralline algae calcify with high magnesium calcite which is metabolically more costly than aragonite, the form used by *Halimeda* and most other tropical calcified organisms including corals (Littler & Littler 1984). CCA algae are sensitive to water temperature and carbonate saturation state as a prime regulator of their growth rate. Recent models suggest a reduction in calcification of 21% for a coral reef community (including two species of CCA) by 2100 (when pH is expected to be 0.3 to 0.5 units lower than present;

⁸(Langdon et al. 2000) found a 24-42% decrease in calcification for the predicted change in CO₂ between 1880 and 2065 in a coral reef mesocosms dominated by upright calcified algae *Amphiroa* spp.

(Leclercq et al. 2000). It is worth emphasising that these predictions should be interpreted cautiously, as they are based on very few studies, which have included mainly temperate CCA species (Leclercq et al. 2000) and there are no published studies of the effects of acidification for tropical CCA. It is also clear, on the basis of studies of the natural abundance of boron isotopes, the pH of seawater in coral reefs, that there have been preindustrial to modern interdecadal variations in reef-water pH (Pelejero et al. 2005, Kleypas et al. 2006). Further, there are potentially complex interactions between calcification, rising temperature and increasing nutrients, and there is strong evidence (in articulated calcareous algae and corals) that calcification rates are enhanced by photosynthesis, with a mean light: dark ratio of about 3 (Gattuso et al. 1999, Kleypas et al. 2006).

Increased CO₂ may enhance rates of photosynthesis in CCA, as in turfs and upright macroalgae, although increases may be limited by the availability of nutrients and water flow. High pressure of CO₂ negatively affected net photosynthesis of epilithic algal communities dominated by the crustose calcareous alga *Hydrolithon (Porolithon) onkodes* (Tribollet et al. 2006). Recruitment of CCA may also be reduced with elevated pCO₂ (Agegian 1985). Weaker crusts may be more susceptible to grazing, erosion or diseases. These impacts may generate shifts from calcifying crusts to non-calcifying algae with potential impacts on reef cementation and stability. Loss of CCA may reduce settlement cues for coral larvae, in turn causing a serious reduction in the overall resilience of reef ecosystems.

CCA may play a role on cementing reef structures together. Thus a negative effect of increased surface water carbon dioxide and attendant decreased carbonate and pH on CCA is likely to have a negative impact on reef stability. However, the effects that will occur are difficult to forecast without more knowledge.

7.2.3.4 Adaptive capacity - ocean acidification

There is no information on the potential for adaptation of algal turfs, upright macroalgae or CCA to ocean acidification. The adaptive capacity of CCA in particular is critical to reef structures, but is likely to be low, given that calcification

is purely a physico-chemically mediated process. Calcified algae can alter their physical and chemical environment for calcification in confined spaces (within the cell wall and intercellular spaces). However, significant adaptation would also require the capacity to influence dissolution of pre-existing parts of the skeleton that abut directly with the surrounding medium. There may be some potential for adaptation by CCA and calcified upright algae by secreting less soluble skeletons (eg lower content of magnesium calcite in calcitic skeletons) as found in the articulated calcareous alga *Amphiroa* (Corallinales) from the Caribbean (Stanley et al. 2002). Coralline algae (Order Corallinales) radiated to nearly modern levels of diversity during the Eocene (Steneck 1983) when the World was much warmer and had higher CO₂ than at present (Sluijs et al. 2006, Moran et al. 2006), so adaptation may be possible but in ways we do not yet understand (Royal Society 2005). Crustose algae as a group are likely to persist in the GBR, but at significantly reduced abundances, and with ecologically significant shifts in species composition, distribution and function. Given their apparent importance to coral recruitment, such changes are likely to significantly reduce the adaptive capacity of the ecosystem as a whole.

7.2.3.5 Vulnerability and thresholds - ocean acidification

Overall, the vulnerability of algal turfs and un-calcified upright macroalgae to ocean acidification is low to moderate, depending on the balance between enhanced production, and the effects of decreased pH on growth, nutrient availability and water mixing. Vulnerability of calcareous upright and crustose algae is high, with potential for habitat loss and a reduction in the production of calcareous sand.

7.2.4 Changes in light and ultraviolet radiation

7.2.4.1 Exposure - light and ultraviolet radiation

Ultraviolet (UV) radiation is likely to continue to increase, due to the effects of ozone depletion (Lough chapter 2 this volume), and UV levels are already high in tropical regions (Vincent & Roy 1993). Although no significant increasing trends have been observed in the GBR to date, UV penetration is highly dependent on water clarity suggesting that GBR inshore algae will be less exposed to UV

radiation than algae further offshore, and algae in intertidal and shallow water habitats more than deeper algal assemblages. UVB radiation is more harmful to marine organisms than UVA.

7.2.4.2 Sensitivity - light and UV

Intertidal and shallow water algal turf and CCA species appear generally less sensitive than deeper species, apparently reflecting adaptation to high light/light UV-B levels, through the accumulation of UV-B screening compounds (Larkum & Wood 1993). Upright macroalgae with thick thalli (plant body) are less sensitive to UV radiation than those with thin thalli, a pattern which applies to differences between species, individuals (old versus young) and thallus parts (Dring et al. 1996, Lotze et al. 2002, Gomez et al. 2005). Macroalgal embryos and early life history stages are more sensitive than juveniles and adults (Henry & Van Alstyne 2004). Experimental data for temperate algae have shown that even small doses and short exposure times (eg 2h) of UV radiation will often reduce photosynthesis, growth and reproduction of turf algae, upright macroalgae and CCA (Lotze et al. 2002, Banares et al. 2002, Hoffman et al. 2003, Roleda et al. 2005, Wiencke et al. 2006). However there are no published data for GBR algae.

7.2.4.3 Impacts - light and UV

There are very few experimental studies documenting impacts of UV radiation on tropical algal turfs, upright macroalgae or CCA; although the effects are likely to be comparable, most relevant studies are from temperate and polar regions. The most common impacts include direct damage to the photosynthetic apparatus (Beardall et al. 1998, Garbary et al. 2004), DNA (Franklin & Forster 1997, Van De Poll et al. 2003), reproductive tissues (Beardall et al. 1998), and reduction of nutrient uptake (Doehler et al. 1995). There are documented cases of changes in algal secondary metabolites which may consequently alter herbivore consumption (Cronin & Hay 1996), with important implications for algal dynamics and interactions. All these effects may lead to community changes, due to shifts in relative abundance (Vincent & Roy 1993, Dawson & Dennison 1996, Lotze et al. 2002) but the potential for wide-spread direct mortality seems low. Tropical algae are likely to have higher UV tolerances than temperate macroalgae because they

have evolved in naturally high UV environment.

7.2.4.4 Adaptive capacity - light and UV

Available evidence suggests some potential for algal turf and upright macroalgae species to adapt to high levels of UV radiation, but there is limited information available for CCA. Higher exposure leads to higher levels of UV absorbing compounds in turf and upright macroalgae (carotenoids, mycosporine-like amino acids) (Beach & Smith 1996). Higher UV exposure may also cause shifts in assemblage composition to species with a high capacity to produce UV absorbing compounds, or to species that have a broader complement of such compounds (Beach & Smith 1996). Red macroalgae appear to have higher levels of UV absorbing compounds than green and brown macroalgae, potentially giving red algae greater adaptive capacity (Beach et al. 1997). The presence of phlorotannins in some brown algae may provide some protection against UV radiation (Henry & Van Alstyne 2004). Adaptive capacity apparently increases during succession, apparently because spores are more susceptible than sporophytes to UV damage⁹. Some calcareous upright algae, such as the temperate calcareous alga *Corallina officinalis*, have the potential to adapt to high levels of UV radiation (Haeder et al. 2003) because calcium carbonate acts as a broadband reflector (Littler 1976, Beach et al. 2006) and may confer some tolerance in CCA.

7.2.4.5 Vulnerability and thresholds - light and UV

The vulnerability of algal turfs and upright macroalgae as a whole is moderate since there is a potential for adaptation to increased UV radiation and the impacts are likely to be restricted to shallow assemblages. The vulnerability of CCA as a group is likely to be low to moderate.

7.2.5 Sea level rise

7.2.5.1 Exposure - sea level rise

Sea level rise due to thermal expansion of the oceans and the melting of glaciers

⁹ Experiments with coral reef macroalgae and diatoms (Santas et al. 1998a, 1998b).

and ice sheets is occurring at a rate of 1 to 2 mm per year. By 2100, the global sea level is projected to be 310 ± 30 mm higher than in 1990 (Lough chapter 2 this volume). Inundation of land due to sea level rise will increase available substrate for colonisation by macroalgae in shallow coastal habitats. On the other hand, subtidal areas, especially on platform reefs, may exceed depth limits for survival of certain species, especially for shallow-water algal turfs, upright macroalgae and CCA.

7.2.5.2 Sensitivity - sea level rise

Intertidal species of algal turfs, upright macroalgae and CCA are likely to expand in area in response to sea level rise due to colonisation of newly available substrate. Within all three algal groups, different taxa will have very different colonisation and dispersal potentials, resulting in highly variable responses to the increase in available substrate with sea level rise.

7.2.5.3 Impacts - sea level rise

The potential impacts of sea level rise on algal turfs, macroalgae and CCA include increased colonisation and abundance of turf algae in shallow habitats and shifts in the placement of the intertidal zone and associated species (Harley et al. 2006). Reduced light levels at deeper depths may shift the distribution of deeper water species. Some reef species, such as reef-crest CCA, may lose habitat due to 'drowning' of reefs.

7.2.5.4 Adaptive capacity - sea level rise

Under the assumed scenario of a sea level rise that is slow relative to the life spans of most algal turfs, upright macroalgae and CCA, rapid colonisation and growth rates are likely to confer high adaptive capacities, assuming light levels and substrate availability are suitable.

7.2.5.5 Vulnerability and thresholds - sea level rise

Vulnerability of algal turfs, upright macroalgae and CCA to rise in sea level is low. High colonisation, growth and reproduction rates will, together with high biodiversity of turf species, reduce the vulnerability of all macroalgal groups to sea

level rise.

7.2.6 Physical disturbance – tropical storms

7.2.6.1 Exposure – tropical storms

The intensity of tropical cyclones is projected to increase in the future, although there is uncertainty as to whether their frequency will increase (Lough chapter 2 this volume). The exposure of algal turfs, upright macroalgae and CCA to tropical cyclones is related to their proximity to storms, both spatially and temporally. Shallow algal turfs, macroalgae and CCA assemblages are more likely to be exposed to the physical forces and wave energy of cyclones than deeper assemblages. Since conditions suitable for cyclone development in the GBR occur from November through May, algal assemblages growing during this season will be more exposed. For example, the main growth and reproductive season of canopy-forming Fucales (e.g. *Sargassum*) is during this period, making them highly exposed. Algal turfs, upright macroalgae and CCA are also likely to be exposed to increased nutrients, re-suspension of sediments and increased water flow associated with cyclones (see section 7.2.7), but the most important effect is likely to result from increased substrate due to damage to corals (see section 7.2.8).

7.2.6.2 Sensitivity - tropical storms

The small size of turfing and CCA species, their creeping or crustose habits, well developed anchoring systems (holdfasts), and rapid growth rates and reproduction, will presumably minimise their sensitivity to direct impacts of physical disturbance. However, increased coral mortality from cyclones is likely to generate large increases in algal turfs.

Shallow water macroalgal flora will be more sensitive than deeper assemblages. Sensitivity will also depend on thallus morphology and holdfast/anchoring characteristics. For example, large upright seaweeds such as *Sargassum* will be more sensitive to increased wave surge than shorter, low-lying species, so the sensitivity of upright macroalgae as a group is highly variable. Again, storms, and consequent coral mortality, are likely to have marked, indirect effects on upright

algae by increasing substrate availability

7.2.6.3 Impacts - tropical storms

Direct damage by tropical cyclones to algal turfs is likely to be minimal, given their small size; potential impacts on algal turfs include short-term increases in algal productivity and growth due to increases in nutrient availability, from terrestrial runoff (in the case of inshore reefs) or released from storm-disturbed sediments (see section 7.2.7). Russ and McCook (1999) showed a dramatic increase in algal productivity following a cyclone in the central GBR, apparently due to local increases in nitrogen and phosphorus, which are rapidly taken up by algal turf species. Increases in the biomass of algal turfs may occur if herbivory is reduced. Perhaps the major impact of storms on algal turfs will be due to colonisation of damaged or dead coral. Algal turfs rapidly colonise newly available substrate in a successional sequence, beginning with benthic diatoms, rapidly followed by more complex morphologies (Diaz-Pulido and McCook 2002, Halford et al. 2004; see also section 7.2.8).

Impacts of tropical cyclones on upright macroalgae vary, depending on habitats and species. Physical wave energy will reduce abundance by dislodging and removing shallow water species, particularly of delicate forms¹⁰ but would increase propagation and dispersal for some species (Vroom et al. 2005). Importantly however, the large seaweed *Sargassum*, whilst vulnerable to physical removal, has a spectacular capacity to regrow from minute fragments of holdfast tissue (Umar et al. 1998). Newly available substrate, nutrient and sediment loading may increase the abundance of some fleshy macroalgae. Such impacts may produce shifts in species composition, with some macroalgae becoming rare while others bloom (eg *Ulva*).

Negative impacts have not been documented for CCA, and this group of algae may also benefit from storms through increases in available substrate due to coral mortality and removal of competing turf and fleshy algae. Potential negative impacts include sediment deposition after storms, and fragmentation, giving rise to living rubble or “rhodoliths”, although these effects have not been documented

from the GBR.

7.2.6.4 Adaptive capacity - tropical storms

The adaptive capacity of algal turfs and some CCA to impacts of tropical cyclones is likely to be high. Turf species have high growth and turnover rates, and rapid replacement of early colonizers may result in pre-disturbance algal composition being achieved before the next storm. Some slower growing CCA may not recover quickly but, at larger spatial scales, are likely to derive some protection from their morphology.

The adaptive capacity of upright macroalgae is unknown but is likely to be variable and species specific. Some species will regrow from holdfasts or attachment points (*Lobophora*, *Sargassum*: Umar et al. 1998), others will regrow from storm-generated fragments (*Dictyota*) (Vroom et al. 2005), but some species may not recover until spores or gametes settle (Santelices 1990). Rapid recovery in those species with an adaptive holdfast may confer competitive advantages. Two years after cyclone Fran in 1995, *Sargassum* populations had still not fully recovered, whereas populations of other species (eg *Lobophora*) did not suffer major damage from the cyclone (Rogers 1997). In contrast, recovery of a macroalgal community in a coral reef off Puerto Rico was considered to be complete within one year of the disturbance (Ballantine 1984).

7.2.6.5 Vulnerability and thresholds - tropical storms

Vulnerability of algal turfs and CCA to tropical cyclones is likely to be low, although experimental information is limited. The turfing morphology and creeping habit of algal turf species, and the high growth and reproduction rates may provide mechanisms for rapid recovery after disturbances. High growth and reproduction rates of some CCA are likely to provide mechanisms for rapid recovery after disturbances. The vulnerability of upright macroalgae is likely to be low but highly variable and taxon-specific.

¹⁰ See Rogers (1996, 1997) for examples of cyclone damage on fleshy macroalgal communities in Heron Island.

7.2.7 Rainfall and river flood plumes

7.2.7.1 Exposure – terrestrial inputs

Regional rainfall and river flow show high inter-annual and decadal variability and currently there is no information about long-term trends towards more freshwater entering the GBR lagoon. However, the intensity of extreme rainfall events might increase as a consequence of climate change. Higher rainfall will produce large freshwater plumes and associated fine suspended sediments, nutrients and other pollutants such as herbicides. Flood plumes already occasionally reach reefs up to 50 km from major river mouths (Devlin & Brodie 2005). Exposure of algal turfs, upright macroalgae and CCA to rainfall and river flood plumes will be most pronounced at GBR inshore reefs, particularly during the summer monsoon from December to March, and will depend on the extent and severity of changes in runoff patterns.

7.2.7.2 Sensitivity - terrestrial inputs

Sensitivity of algal turfs and upright macroalgae to terrestrial inputs is moderate to high, complex and variable. Variability in sensitivity will be considerable, due to the species diversity of algal turfs and upright macroalgae, and the complexity of terrestrial inputs: for example, runoff may increase both nutrient supply, enhancing some species, and herbicides (inhibition). Thresholds are likely in competitive balances and in the balance between algal growth and herbivore consumption. The sensitivity of CCA is probably high, as they are sensitive to sediment deposition, eutrophication, pesticides and freshwater. Sensitivity to light reduction varies among CCA species. Competitive interactions and the balance between growth of CCA and their consumption by herbivores are also likely to show thresholds.

7.2.7.3 Impacts - terrestrial inputs

Impacts of terrestrial inputs on the ecology of algal turfs are considerable and variable, although, there are few examples from the GBR. Nutrient increases from flood plumes may enhance algal growth, resulting in increased productivity of the whole reef ecosystem (Russ & McCook 1999). The expression of enhanced growth as increased biomass will depend on the capacity of herbivores to absorb

extra production. Sediment deposition may reduce growth of some algal species due to hypoxia, light reduction, pesticide inhibition and salinity effects. However, in some reef habitats, algal turf height and biomass are positively related to sediment deposition (Purcell 2000, Purcell & Bellwood 2001). Impacts also include competitive shifts¹¹, resulting in changes to species composition, loss of diversity, and changes in ecological functions. For example, a shift in species composition of blue-green algal assemblages from nitrogen-fixing to non-nitrogen fixing species may alter rates of nitrogen fixation. Such shifts may alter chemical microhabitats for coral recruitment.

Runoff may also have indirect effects on algal turfs. While sediment deposition and trapping may be deleterious to some algal turfs, it is likely to be more deleterious to corals or other groups of algae, resulting in changes to overall abundance (McCook 1999, Fabricius 2005). Indirect effects may also result from enhanced nutrients, which inhibit coral growth and reproduction (Ward & Harrison 2000, Koop et al. 2001, Fabricius 2005) and from more turbid waters, which are less suitable for herbivorous fish recruitment (Williams 1982, Williams et al. 1986). Such indirect effects generally lead to increased relative dominance of algal turfs.

Nutrient increases from flood plumes are likely to enhance macroalgal growth and potentially abundance (Hatcher & Larkum 1983, Littler & Littler 1985, Lapointe 1997, Schaffelke & Klumpp 1998, Schaffelke 1999, Smith et al. 2001, Schaffelke et al. 2005). Expression of enhanced growth as increased biomass will depend on the capacity of herbivores to consume the extra production (Russ & McCook 1999, Jompa & McCook 2002, Diaz-Pulido & McCook 2003). However, growth and reproduction may also be reduced, due to epiphyte overgrowth, light reduction, effects of herbicides and reduced salinity and possible nutrient “overload” (GBR examples: (Schaffelke et al. 2005, Diaz-Pulido & McCook 2005); temperate examples: (Bergström et al. 2003). Sediment deposition (hypoxia) may reduce macroalgal recruitment (Umar et al. 1998, Eriksson & Johansson 2003, Isæus et al. 2004, 2005). These processes may result in shifts in species composition to

¹¹ Eg Nutrients: nitrogen fixing cyanobacteria affected by N and P balances; *Cladophora* tolerant to freshwater exposure; freshwater carries silicic acid, which may favour diatom blooms (Dodds & Gudder 1992, Valiela et al. 1997, Anderson et al. 2002).

shorter-lived 'weedy' species, loss of diversity, and carbon and nutrient retention, due to competitive shifts between species and groups (Fabricius et al. 2005)¹². Negative impacts on corals are likely to lead to increased substrate availability for all algal groups.

Potential impacts on CCA include reductions in abundance and diversity, and shifts in composition, eg to more shade tolerant but slow-growing species¹³. Such changes are likely to lead to reductions in ecological functions, eg reef cementing and facilitation of coral settlement. There is potential for complex interactions between algal turfs, sediments, herbivores and the abundance of CCA (eg Steneck 1997 for the Caribbean).

7.2.7.4 Adaptive capacity - terrestrial inputs

The capacity to adapt to increased rainfall and river flood plumes is high for turfs as an assemblage, due to the potential for shifts in relative species composition, flexibility in nutrient processing, but will depend on herbivore consumption. However, the ecological roles of algal turfs may have less capacity to adapt. For example, increased biomass of turfs and subsequent sediment trapping will limit coral recruitment.

The adaptive capacity of upright macroalgae to terrestrial inputs is probably moderate to high, and positive effects are expected. However, this adaptation is likely to involve shifts in composition, involving losses or shifts in diversity and ecological roles. Shifts in species composition of upright macroalgal communities will reflect adaptive capacity of individual species to different salinity, nutrient, herbicide and sediment conditions.

¹² Also temperate studies suggest perennial, upright algae are less sensitive than simpler, ephemeral algae, evidence for shifts in species composition (Lotze et al. 1999, 2000, 2001, Lotze & Worm 2002), loss of diversity (Worm et al. 2002), reduced carbon storage and nutrient retention in community (Worm et al. 2000).

¹³ Correlation studies suggest runoff has impacts on species composition (Fabricius & De'ath 2001). Experimental studies have demonstrated negative effects of sediments and diuron [a herbicide regularly found in low concentrations in GBR coastal waters (Shaw & Mueller 2005)], on CCA (Björk et al. 1995, Steneck 1997, Harrington et al. 2005).

There is a lack of empirical data on the adaptive capacity of CCA to terrestrial inputs, but it is likely to be low due to slow growth rates of some species and competition from turfs and upright macroalgae. Evidence of low abundance and diversity in areas affected by high runoff supports this (Fabricius and De'ath 2001).

7.2.7.5 Vulnerability and thresholds - terrestrial inputs

Algal turfs and upright macroalgae, particularly from inshore reefs, are moderately to highly vulnerable to terrestrial inputs. Physiological and ecological impacts of runoff of terrestrial nutrients, sediments and pollutants are likely to be species-specific, leading to changes in species composition. CCA are highly sensitive to terrestrial inputs, are likely to have low adaptive capacity and therefore are highly vulnerable to increased inputs of terrestrial material.

7.2.8 Increased substrate availability due to coral mortality

7.2.8.1 Exposure - Increased substrate availability due to coral mortality

Exposure of algal turfs, upright macroalgae and CCA to increased substrate availability due to coral mortality is considerable. Widespread coral mortality is extremely very likely, due to mass coral bleaching, and other directly or indirectly climate change-related causes of mortality (see Hoegh-Guldberg et al., chapter 10).

7.2.8.2 Sensitivity - Increased substrate availability due to coral mortality

Algal turfs are extremely responsive to increased substrate availability (Diaz-Pulido & McCook 2002, 2004). There is considerable potential for thresholds, due to rapid colonisation of new substrate and positive feedbacks. Upright macroalgae are also very likely to benefit from newly available substrate, but their response may be moderated by competition with the faster colonising turf algae and by herbivory. Some CCA are rapid colonisers of any bare space, whereas others will be strongly dependent on low levels of competition with algal turfs and significant herbivore impacts. There is considerable potential for thresholds, due to rapid colonisation of available substrate and the potential for saturation of herbivore consumption capacity. For a given algal growth rate, increased area of algae may

result in growth rates that overwhelm the capacity of a given herbivore population to control upright macroalgal abundance (Williams et al. 2001).

7.2.8.3 Impacts - Increased substrate availability due to coral mortality

Among the impacts of increased substrate availability due to coral mortality is a massive increase in the area and abundance of turf algae and upright macroalgae (examples from the GBR: (Diaz-Pulido & McCook 2002, 2004), pers obs for 2006 bleaching; non-GBR: (Hughes 1994, Ostrander et al. 2000, McClanahan et al. 2001, Aronson & Precht 2006). Turf algae are rapid colonisers of dead and injured corals (Price 1975, Done 1992, Diaz-Pulido & McCook 2002, Halford et al. 2004). Turf areas may undergo succession towards more upright macroalgae, because turf algae provide a more suitable substrate for macroalgae than live coral (Diaz-Pulido & McCook 2002, 2004). The extent of this replacement will depend strongly on levels of herbivory and other factors such as nutrient availability.

Increases in macroalgal colonisation will increase coral – algal competition, inhibit coral recruitment and recovery, reducing overall reef resilience and stabilising phase shifts from dominance by corals to dominance by turf and upright macroalgae (Birkeland 1977, Jompa 2001, Birrell et al. 2005). Many of the climate change stressors will increase the competitiveness of turf algae over CCA, leading to further inhibition of coral recruitment. This may generate positive feed-back effects for turfs and, subsequently for upright macroalgae, especially if herbivory is low. There is also potential for positive feedback through algal derived increases in dissolved organic carbon, which damages coral health and may inhibit coral recovery (Smith et al. 2006). Shifts are also likely in species composition and ecological functions of turf and upright algae (eg primary production, nutrient fixation), along with changes in habitat creation¹⁴ and herbivore palatability.

7.2.8.4 Adaptive capacity - Increased substrate availability due to coral mortality

Algal turfs and upright algae (based on limited knowledge for the latter group) are likely to increase in abundance but species composition of assemblages is likely to

shift to more 'weedy' species. The capacity of the ecosystem to adjust to these changes is limited and uncertain, and will depend on other aspects of resilience of the system, such as eutrophication and herbivore abundance. The resilience of the ecosystem is likely to be significantly reduced by upright algal assemblages. Abundant herbivores may prevent this dominance, allowing persistence of crustose forms, with long-term benefits to ecosystem recovery and adaptation.

There is no information on the adaptive capacity of CCA to increased substrate availability and the subsequent succession of algal assemblages, but, given the important ecological roles of CCA, this is likely to be critical to longer-term adaptive capacity and resilience of the ecosystem.

7.2.8.5 Vulnerability and thresholds - Increased substrate availability due to coral mortality

Algal turfs, upright macroalgae and CCA as groups will benefit from increases in substrate availability due to coral mortality. However, in the long term, the natural composition of algal turfs and CCA may be highly vulnerable, due to competitive shifts, to preferential feeding by herbivores, and potentially significant loss of functional diversity. These changes are likely to have major impacts on the ecosystem vulnerability as a whole. Ultimately the response of each algal functional group to increased substrate availability will depend upon the overall characteristics of the given location.

7.3 Linkages and Summary

7.3.1 Linkages and summary of major vulnerabilities to climate change

Assessing the vulnerability to climate change of any group of benthic algae of the GBR is severely hampered by the general dearth of eco-physiological studies, either from the GBR, or from tropical regions more generally. Further, climate change will affect algae not only directly (eg physiological effects of increased sea-temperatures) but also indirectly. For example, climate change impacts on corals or herbivores will have major effects on the area and biomass of algae. For these

¹⁴ Beds of upright algae such as *Sargassum*, provide important habitat structure in extensive areas of shallow inshore GBR (e.g. Martin-Smith 1994); *Halimeda* beds form extensive habitats in several

reasons, the following treatment is based not only on the available information from the GBR and other tropical regions, but also on inferences drawn from better studied temperate species, and from expert opinion. The complexity and lack of information mean that even loose predictions are not realistic, and we aim instead to outline potential scenarios for consideration.

Turf algae

Algal turf assemblages are ubiquitous and particularly diverse in coral reefs. On shallow reefs of the GBR, a single square centimetre may contain more than 20 species of benthic algae (Diaz-Pulido & McCook 2002). This high species diversity complicates any interpretation of the impacts of climate change on algal turfs, particularly when looking at impacts at large spatial and temporal scales. Even more than for the upright macroalgae and CCA, the assessment of vulnerability for algal turfs of the GBR is seriously hampered by a lack of information on the taxonomy, species composition, diversity, and spatial and temporal dynamics of this group of macroalgae.

Algal turfs are likely to be affected by both direct and indirect climate stressors. The vulnerability of algal turfs to direct impacts is highly variable, ranging from low to moderate, and in some situations, some stressors are likely to have positive effects on some species (Table 7.3, 7.4). For example, if terrestrial runoff of nutrients increases as a result of climate change, this may enhance productivity and growth of some taxa or individuals. This may, in turn, cause shifts in competitive balance, resulting in shifts in species composition of the turf assemblage to more 'weedy' taxa. Similarly, increases in temperature and CO₂ may initially benefit species with wide temperature tolerances (Breeman 1990) and carbon-limited species, inducing species shifts with unknown consequences. Increased UVB radiation may reduce photosynthesis of some species in shallow waters, while other taxa may gain a competitive advantage from such increases (e.g. species that produce high levels of UV absorbing compounds such as mycosporine-like amino acids, provided there is adequate nitrogen availability).

inter-reefal areas of the GBR (Coles et al. 2003),

Thus, impacts on individual species are likely to be variable and complex (Figure 7.2), but will most likely generate shifts in species composition.

Despite the lack of studies on the adaptive capacity of algal turfs to global climate change, it seems probable that the adaptation potential of turfs, as an assemblage, will be moderate to high. Turf species have high rates of colonisation, growth, and reproduction, and are quite resilient to disturbances (Littler et al. 1983a, Steneck & Dethier 1994). For example, more frequent cyclones may disturb a turf assemblage, initially shifting community structure to stages dominated by early colonisers such as benthic diatoms (Delesalle et al. 1993, GDP pers obs). However, this early stage is rapidly replaced by filamentous forms characteristic of 'typical' algal turfs (ie they have a strategy of 'recovery' sensu Steneck 1988, Steneck & Dethier 1994). At a temporal scale of weeks to months, physical disturbances may not lead to major overall impacts on the turf assemblage, but may result in shifts in species composition, depending on magnitude and duration of disturbance. This constitutes ecological adjustment, in the sense that turf algae are likely to persist, but the specific combination of turf species is likely to be quite vulnerable within a location.

Significant interactions between stressors, and changed competitive relationships with other functional groups of algae, are also likely. Such interactions might lead to large shifts in species composition with little potential for adaptation within particular habitats. For instance, increased frequency of cyclones may reduce the abundance of canopy forming *Sargassum* (which is fertile during the cyclone season) with long lasting consequence for the understory turf assemblage. Rapid and prolonged exposure of the understory to high light may lead to photoinhibition causing decreased productivity and growth, and in the longer term leading to a shift to more light-tolerant taxa. There are no reported cases of extinctions of turf algal species, although the flora is not well known and difficult to study on the scale of the GBR. Nonetheless, we consider climate stressors are unlikely to lead to extinction of turf species.

The direct effects of climate stressors on algal turfs are likely to be strongly regulated by interactions between substrate availability, herbivore grazing and

nutrient supply. Increasing sea temperatures are expected to cause massive coral mortality (Hoegh-Guldberg et al. chapter 10 this volume, Hoegh-Guldberg 1999), followed by extensive algal colonisation of dead coral substrata, resulting in marked increases in cover and biomass of algal turfs (Diaz-Pulido & McCook 2002). Climate change impacts on herbivore populations, both invertebrates (urchins, molluscs, crustaceans) and vertebrates (fishes, marine turtles) will have profound consequences for the composition and abundance of turfs. The proposed impacts of climate change on herbivore abundance include increased food availability (due to algal overgrowth of dead coral; Robertson 1991) but ultimately a decrease in abundance due to the loss of coral habitat and shelter (due to coral mortality and breakage; Mundy et al. chapter 12 this volume). The former impact is a consequence of algal abundance, not a cause: that is, increased herbivore abundance can only moderate, but not negate the increased algal abundance. The effects of habitat-loss on herbivores are likely to be greater and longer term than any food-driven increases, resulting in net decreases in algal consumption. This may contribute to feedback effects, as algal abundance inhibits recruitment and recovery of corals (McCook 1999).

Healthy populations of herbivores will reduce the risks of runoff impacts on algal turfs, and minimise the chances of shifts from communities dominated by healthy productive turf assemblages to less desirable communities (Hughes et al. 2007). Loss of herbivores has been shown to cause self-shading and a decline in mass specific productivity (Carpenter 1985a, Carpenter 1985b, Carpenter 1986). It is also important to recognise that, if significant shifts in composition of turfs do occur, this may be assumed to result in changes in the ecological roles and effects of the turfs on the ecosystem as a whole. Thus, for example, trophic and nutrient dynamics may change, or an over-abundance of unpalatable or toxic algae may inhibit coral recruitment, in effect stabilising declines in coral populations. Studies from the GBR have shown that interactions between benthic algae (especially turf algae), corals, nutrients and herbivores is complex (Koop et al. 2001, also Jompa & McCook 2002, Diaz-Pulido & McCook 2003, Hughes et al. 2007), so predicting the effects of global climate change on each of these factors (and others), and their interactions, will require considerable care.

There is also a significant risk that, even without declines in herbivore populations, massive increases in the area of algae may sufficiently increase total algal production, such that it exceeds the capacity of existing herbivores to consume it. Such saturation of herbivore consumption will in effect release algal abundance from herbivore control (eg Williams et al. 2001; McCook pers. obs.), potentially reducing the suitability of habitat for herbivores. Further, under such circumstances, herbivores may feed preferentially on palatable species, such as *Polysiphonia* and *Sphacelaria*. This may lead to a positive feedback, increasing the relative abundance of unpalatable and/or toxic taxa, such as cyanobacteria or larger, fleshy macroalgae with chemical deterrents, with a potential further loss of functional diversity.

However, the vulnerability of algal turfs to such indirect effects is difficult to assess, given our poor understanding of the long-term impacts of coral disturbances on the dynamics of algal species (the result of a lack of detailed long-term monitoring of algal communities). In simple terms, algal turfs as a group will strongly benefit from increases in substrate availability due to coral mortality. In the long term, however, the natural composition of algal turfs may be highly vulnerable, due to competitive shifts, and to preferential feeding by herbivores.

We conclude that the vulnerability of algal turfs to climate change is highly variable and unpredictable, and the lack of information severely reduces the ability of making accurate predictions. Nonetheless, we suggest that turfs as a group have the potential to adapt (ie adjust) to the changing environment, provided herbivore populations remain adequate. However, shifts in species composition of turf assemblages are likely. The consequences of these shifts for the ecological roles of algal turfs, and hence for the vulnerability of the ecosystem are difficult to predict, but may well be more extreme than postulated above. More serious than the vulnerability of turfs as a group is the vulnerability of reefs to shifts from corals to turfs (as has already happened in the Caribbean). The adaptive capacity of algal turfs makes them a threat to corals and, hence, increase the vulnerability of the reef system as a whole.

Upright algae (fleshy and calcified)

Upright algae in the GBR occur in a wide range of habitats, but predominantly in shallow (to ~ 20 m depth) or intertidal waters (Price 1990; the notable exception being the deep-water *Halimeda* beds). The diversity of the algal flora of the deep GBR lagoon floor is currently being explored (Skelton pers comm), but there is little ecological information available. Shallow water habitats are likely to be exposed to a range of climate change stressors, including more storms and associated terrestrial run-off, higher temperatures and UV radiation.

There are currently no studies demonstrating the effects of changing climate on GBR upright macroalgae. We suggest that some climate change stressors will have positive effects on productivity, growth, reproduction and abundance of upright macroalgae (Table 7.3, 7.4). These include sea level rise (in coastal areas without artificial structures such as sea walls), temperature and increased CO₂ availability (although the latter two are likely to be detrimental to calcified algae). These stressors would positively interact with the expected higher availability of substrate for algal colonisation, caused by climate-related coral mortality and rises in sea level (Hoegh-Guldberg et al. chapter 10 and Fabricius et al. chapter 17 this volume, Nordemar et al. in prep, Figure 7.3). Other climate derived stressors, such as storms, increased terrestrial run-off, UV radiation, and changed circulation patterns, will have variable or no effects, depending on the species' biology and ecology.

As for turf algae, we do not expect climate change to cause serious direct mortality of macroalgal species or communities, but rather to lead to significant changes in benthic community composition. This would be mainly through direct effects such as changes to productivity, growth and reproduction. Even slight changes in temperature, or other factors, are likely to lead to species (or ecotype)-specific changes in optimal production, distribution, and possibly the seasonal timing of growth and reproduction; these changes may generate shifts in competitive relationships, in turn causing transitions in community composition (Breeman 1990, Harley et al. 2006). Southward immigration of species and/or ecotypes is likely, especially in the southern GBR. Interactions between climate change stressors probable but poorly understood. For example, in temperate algal

species, UV tolerance was higher at higher temperatures, up to a species-specific threshold (Hoffman et al. 2003).

These direct effects are likely to be intensified by indirect effects of climate change on other organisms that interact with upright algae, such as herbivores, and competitors, especially corals (McCook et al. 2001, Lirman 2001, Lotze & Worm 2002, Schiel et al. 2004). Any climate change stressor that has detrimental effects on coral health will indirectly benefit most upright macroalgae. Macroalgal biomass may reduce coral growth, reproductive output and recruitment (Birkeland 1977, Tanner 1995, McCook et al. 2001, Lirman 2001, Jompa & McCook 2002, Fabricius 2005). Saturation of algal consumption by herbivores may accentuate such changes (Williams et al. 2001), stabilising macroalgal dominance. Further feedback effects may include selective over-grazing of unpalatable algae, and loss of coral habitat for herbivores.

It is likely that GBR upright algae may adapt to several stressors, such as increasing temperature and UV radiation, given their assumed existing tolerance. . At the ecosystem level however, such adaptation is likely to enhance, rather than reduce phase-shifts (Nyström et al. 2000, Bellwood et al. 2004, McCook et al, this chapter). The species diversity of GBR macroalgae is poorly described and the genetic diversity undescribed, but it is possible that high diversity, and/or functional redundancy, may provide some insurance against community transitions caused by climate change (Harrington et al. 1999 for plants and insects, Reusch et al. 2005 for seagrasses)

We conclude that, as a group, fleshy upright macroalgae in the GBR are likely to benefit from many of the environmental changes brought about by climate change. Adapted species may find more space to colonise and may grow better due to more optimal temperatures, nutrient and dissolved inorganic carbon availability, provided they are not disturbed by increasing storm intensity or frequency. However, future macroalgal communities are likely to change in composition as less adapted species are excluded and biological interactions change. Higher biomass and altered species composition of fleshy upright algae on coral reefs

may change competitive interactions with corals and lead to impairment of coral recruitment, which would indirectly further reduce coral resilience (McCook et al. 2001, McCook et al. this volume). In habitats other than coral reefs, the interactions of upright macroalgae with other major ecosystem builders (eg seagrasses) are less well understood and cannot be predicted with any certainty.

In contrast, calcified upright macroalgae are likely to be adversely affected by climate change. Higher temperature, nutrient and CO₂ availability and associated acidification of the tropical sea will affect calcification, outweighing any positive effects on algal productivity. Disturbance of these very important components of the GBR ecosystem is likely to lead to serious cascading effects, such as loss of unique habitats (e.g. Halimeda banks, Drew & Abel 1983, Phipps et al. 1985, Marshall & Davies 1988) and decreased production of calcareous sediments.

Crustose calcareous (calcified) algae

Assessing vulnerability for CCA is, as for turf and upright macroalgae, a difficult task due to the taxonomic heterogeneity, variety of life histories and ecological roles within the group. Thin, 'weedy' CCA have high growth rates and rapid colonisation and are therefore likely to respond differently to climate changes compared to thick, slow-growing CCA. CCA are exposed to a variety of climate stressors, but our analyses suggest that changes in ocean chemistry through acidification and increasing runoff are likely to be the most harmful.

The vulnerability of CCA to the impacts of some climate stressors is probably low. Increased frequency and intensity of storms will have little effect, given the hard, calcareous nature of these algae. The shallow CCA flora is also quite well adapted to high UV-radiation and it has been recently suggested that calcification may provide extra protection to increasing UV radiation (Beach et al. 2006). The impacts of increasing substrate availability due to coral mortality are difficult to predict, given the lack of long-term monitoring of the dynamics of this group. Cover of CCA, particularly the 'weedy' species, may increase with increasing substrate availability due to coral mortality, but this will be moderated by competition with other algal groups, less affected by acidification. Direct impacts of rising sea

temperature on the abundance of CCA are not known but are likely to be minor. However, rising temperatures may have significant, indirect negative impacts, such as enhancing diseases. Increases in disease among many groups of calcified organisms (CCA, corals, sea urchins and lobsters) but not in other groups (e.g. fishes, Ward & Lafferty 2004) may reflect cumulative impacts from a range of stressors, such as temperature, UV radiation and CO₂.

In contrast, CCA are highly vulnerable to the direct impacts of increasing atmospheric and hence sea surface CO₂ and the consequent slight increase in bicarbonate, and decrease in pH and in carbonate concentration (Figure 7.4).

Increasing runoff may have varied effects on CCA, and their vulnerability will depend on the location on the continental shelf. Inshore CCA are highly exposed, due to the proximity to the source, and moderately vulnerable to increased nutrients, compared to the offshore CCA flora. Longer-term impacts of runoff will depend strongly on competition with turfs and macroalgae, in turn also influenced by herbivore abundance.

The overall potential for adaptation of CCA to global climate change is unknown. It is likely that CCA will adapt to increasing impacts of storms, sea level rise and increasing UV-radiation. However, the potential for adaptation to acidification is likely to be low. Crustose algae as a group are likely to persist in the GBR, but at significantly reduced abundances, and with ecologically significant shifts in species composition, distribution and function. Given their apparent importance to coral recruitment, such changes are likely to significantly reduce the adaptive capacity of the ecosystem as a whole.

7.4 Recommendations

7.4.1 Potential management responses

As with all climate change impacts, the most powerful, and cost-effective, management strategy is to minimise the extent of the impacts, by abatement of greenhouse gas emissions. Although obvious, and beyond the scope of marine park managers, it is important to emphasise, especially as it is common to all

climate change impacts. Measures which reduce the impacts of increased CO₂ concentrations and therefore ocean acidification are probably particularly important, given the vulnerability of CCA to acidification, and the potential significance of CCA to overall ecosystem resilience.

Management responses to enhance resilience of natural macroalgal populations on the Great Barrier Reef will essentially overlap with those that protect coral populations and enhance general ecosystem resilience. To protect the natural abundance and composition of macroalgae, it is crucial to protect populations of herbivores, and to minimise terrestrial runoff and other sources of nutrient, sediment or toxicant pollution. These measures will not only benefit corals directly but reduce the feedback impacts of increased abundance and changes in algal community composition. Similarly, any measures that serve to minimise the extent and severity of coral mortality events will also reduce the extent of algal colonisation, and vulnerability to subsequent shifts in community structure.

Finally, there is clearly a need for more information on the potential nature and extent of climate change impacts on tropical algal assemblages. Whilst this is generally true for all groups, the taxonomic and ecological diversity of the algae, and the lack of knowledge regarding the composition, physiology and ecology of algal assemblages is markedly greater than that for other major groups of benthic organisms in the GBR.

7.4.2 Further research

There is a general need for more information about almost all aspects of climate change effects on most types of algae. However, several areas are likely to be particularly important in recognising and assessing emerging impacts, or to be more significant for the GBR ecosystem as a whole. Given the likely importance of shifts in community composition, there is a strong need for better baseline descriptions of current species distribution and abundance patterns of all macroalgal groups along the whole GBR, including groups, such as the turf algae and CCA, which are difficult to identify in the field. Without such descriptions we are unlikely to detect or understand many community shifts.

Given the important roles CCA play on reefs, and the potentially dramatic effects of acidification on calcification by CCA, research on the impacts of CO₂ and ocean acidification on CCA is urgently needed, as are studies of other stressors on CCA. Similarly, the few studies on *Halimeda* species and other upright calcifying algae suggest that calcification will be inhibited, and further studies are needed.

Finally, better understanding of the ecological interactions between algae, coral populations and herbivores (mainly fish), under climate change scenarios is required. There is a need for experimental studies under climate change conditions (eg high temperature, low pH) to predict future algal colonisation and succession after coral mortality, and the effects of different algal assemblages on coral recruitment. Similarly, we cannot assume that the critical influence of herbivorous fishes on coral-algal interactions will be the same under changed climate conditions. A strong understanding of how coral-algal-herbivore interactions will change under climate change scenarios will be critical to future efforts to manage for resilience of the Great Barrier Reef, and of tropical habitats generally.

Bibliography

- Adey WH (1998) Coral reefs: algal structured and mediated ecosystems in shallow, turbulent, alkaline waters. *Journal of Phycology* 34:393-406
- Adey WH, Steneck RS (2001) Thermogeography over time creates biogeographic regions: A temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *Journal of Phycology* 37:677-698
- Adl SM, Simpson AGB, Farmer MA, Anderson RA, Anderson OR, Barta JR, Bowser SS, Brugerole G, Fensome RA, Fredericq S, James TY, Karpov S, Kugrens P, Krug J, Lane CE, Lewis LA, Lodge J, Lynn DH, Mann DG, McCourt RM, Mendoza L, Moestrup R, Mozley-Standridge SE, Nerad TA, Shearer CA, Smirnov AY, Spiegel FW, Taylor MFRJ (2005) The new higher level classification of eukaryotes with emphasis on the taxonomy of protists. *Journal of Eukaryotic Microbiology* 52:399-451
- Agegian CR (1985) The biogeochemical ecology of *Porolithon gardineri* (Foslie). Ph.D. Dissertation. University of Hawaii.
- Aguirre J, Riding R (2005) Dasycladalean algal biodiversity compared with global variations in temperature and sea level over the Past 350 Myr. *Palaios* 20:581–588
- Andersen RA, Saunders GW, Paskind MP, Sexton JP (1993) Ultrastructure and 18S rRNA gene sequence for *Pelagomonas calceolata* gen. et sp. nov. and the description of a new algal class, the Pelagophyceae classis nov. *Journal of Phycology* 29:701-715
- Anderson DM, Glibert PM, Burkholder JM (2002) Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25:704-726
- Aronson RB, Precht WF (2006) Conservation, precaution, and Caribbean reefs. *Coral Reefs* DOI 10.1007/s00338-006-0122-9:
- Ateweberhan M, Bruggemann JH, Breeman AM (2005a) Seasonal dynamics of *Sargassum ilicifolium* (Phaeophyta) on a shallow reef flat in the southern Red Sea (Eritrea). *Marine Ecology Progress Series* 292:159-271
- Ateweberhan M, Bruggemann JH, Breeman AM (2005b) Seasonal patterns of biomass, growth and reproduction in *Dictyota cervicornis* and

- Stoechospermum polypodioides* (Dictyotales, Phaeophyta) on a shallow reef flat in the southern Red Sea (Eritrea). *Botanica Marina* 48:8-17
- Ateweberhan M, Bruggemann JH, Breeman AM (2006) Effects of extreme seasonality on community structure and functional group dynamics of coral reef algae in the southern Red Sea (Eritrea). *Coral Reefs* 25:391-406
- Ballantine DL (1984) Hurricane-induced mass mortalities to a tropical subtidal algal community and subsequent recoveries. *Marine Ecology Progress Series* 20:75-83
- Ballantine DL, Bowden-Kerby A, Aponte NE (2000) *Cruoriella* rhodoliths from shallow-water back reef environments in La Parguera, Puerto Rico (Caribbean Sea). *Coral Reefs* 19:75-81
- Banares E, Altamirano M, Figueroa FL, Flores-Moya A (2002) Influence of Uv radiation on growth of sporelings of three non-geniculate coralline red algae from southern Iberian Peninsula. *Phycological Research* 50:23-30
- Barnes DJ (1988) Seasonality in community productivity and calcification at Davies Reefs, Central Great Barrier Reef. *Proceedings of the Sixth International Coral Reef Symposium, Townsville* 2:521-527
- Beach KS, Borgeas HB, Nishimura NJ, Smith CM (1997) In vivo absorbance spectra and the ecophysiology of reef macroalgae. *Coral Reefs* 16:21-28
- Beach KS, Borgeas HB, Smith CM (2006) Ecophysiological implications of the measurement of transmittance and reflectance of tropical macroalgae. *Phycologia* 45:450-3457
- Beach KS, Smith CM (1996) Ecophysiology of tropical rhodophytes. I. Microscale acclimation in pigmentation. *Journal of Phycology* 32:701-710
- Beardall J, Beer S, Raven JA (1998) Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Botanica Marina* 41:113-123
- Beck MW, Heck KLJ, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern BS, Hays CG, Hoshino K, Minello TJ, Orth RJ, Sheridan PF, Weinstein MP (2003) The role of nearshore ecosystems as fish and shellfish nurseries. *Issues in Ecology* 11:1-12
- Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. *Nature* 429:827-833
- Bergström L, Berger R, Kautsk L (2003) Negative direct effects of nutrient

- enrichment on the establishment of *Fucus vesiculosus* in the Baltic Sea. European Journal of Phycology 38:41-46
- Biebl R (1962) Temperaturreistenz tropischer Meeresalgen (Verglichen mit jener von Algen temperierten Meeresgebieten). Botanica Marina 4:241-254
- Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proceedings, Third International Coral Reef Symposium, Miami 1:15-21.
- Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. Marine Pollution Bulletin 51:40-414
- Björk M, Mohammed SM, Björklund M, Semesi A (1995) Coralline algae, important coral-reef builders threatened by pollution. Ambio 24:502-505
- Borowitzka LJ, Larkum AWD (1986) Reef algae. Oceanus 29:49-54
- Borowitzka MA (1981) Photosynthesis and calcification in the articulated coralline red algae *Amphiroa anceps* and *Amphiroa foliacea*. Marine Biology 62:17-24
- Borowitzka MA, Larkum AWD (1976) Calcification in the green alga *Halimeda*. III. - The sources of inorganic carbon for photosynthesis and calcification and a model of the mechanism of calcification. Journal of Experimental Botany 27:879-893
- Braithwaite CJ, Dalmaso H, Gilmour MA, Harkness DD, Henderson GM, Kay RLF, Kroon D, Montaggioni LF, Wilson PA (2004) The Great Barrier Reef: The chronological record from a new borehole. Journal of Sedimentary Research 74:298-310
- Breeman AM (1990) Expected effects of changing seawater temperatures on the geographic distribution on seaweed species. Beukema JJ, Wolff WJ, Brouns M (Expected effects of climate change on marine coastal ecosystems. Kluwer Academic Publishers, The Netherlands, p 69-76
- Burgess SC (2006) Algal blooms on coral reefs with low anthropogenic impact in the Great Barrier Reef. Coral Reefs 25:390
- Cai W, Shi G, Cowan T, Bi D, Ribbe J (2005) The response of the Southern Annular Mode, the East Australian Current, and the southern mid-latitude ocean circulation to global warming. Geophysical Research Letters 32:L23706, doi:10.1029/2005GL024701
- Carpenter RC (1985a) Relationships between primary production and irradiance in coral reef algal communities. Limnology and Oceanography 30:784-793

- Carpenter RC (1985b) Sea urchin mass-mortality: Effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. Proceedings of the Fifth International Coral Reef Congress, Tahiti 4:53-60
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecological Monographs 54:345-363
- Chisholm JRM (2000) Calcification by crustose coralline algae on the northern Great Barrier Reef, Australia. Limnology and Oceanography 45:1476-1484
- Chisholm JRM (2003) Primary productivity of reef-building crustose coralline algae. Limnology and Oceanography 48:1376-1387
- Chisholm JRM, Collingwood JM, Gill EF (1990) A novel *in situ* respirometer for investigating photosynthesis and calcification in crustose coralline algae. Journal of Experimental Marine Biology and Ecology 141:15-29
- Coles R, McKenzie L, Campbell S (2003) The seagrasses of Eastern Australia. Green EP, Frederick TS (eds) World Atlas of Seagrasses. UNEP World Conservation Monitoring Centre. University of California Press, Berkeley, p 119-133
- Cowan RA (2006) Australian Marine Algal Name Index: A database of the taxonomy, nomenclature and distribution of Australian marine macroalgae. Murdoch University and Australian Biological Resources Study, <http://dseweb.murdoch.edu.au/wise/>
- Cribb AB (1973) The algae of the Great Barrier Reef. Jones, Endean (Biology and geology of coral reefs: Biology 1. Academic, New York, p 47-75
- Cronin G, Hay ME (1996) Susceptibility to herbivores depends on recent history of both the plant and animal. Ecology 77:1531-1543
- Davies PJ, Braga JC, Lund M, Webster JM (2004) Holocene deep water algal buildups on the eastern Australian shelf. Palaios 19:598-609
- Davies PJ, Marshall JF (1985) *Halimeda* bioherms - low energy reefs, northern Great Barrier Reef. Proceedings of the Fifth International Coral Reef Congress, Tahiti 1:1-7
- Dawson SP, Dennison WC (1996) Effects of ultraviolet and photosynthetically active radiation on five seagrass species. Marine Biology 125:629-638
- De Beer D, Larkum AWD (2001) Photosynthesis and calcification in the calcifying algae *Halimeda discoidea* studied with microsensors. Plant Cell and

Environment 24:1209-1217

- Delesalle B, Pichon M, Frankignoulle M, Gattuso JP (1993) Effects of a cyclone on coral reef phytoplankton biomass, primary production and composition (Moorea Island, French Polynesia). *Journal of Plankton Research* 15:1413-1423
- Devlin M, Brodie J (2005) Terrestrial discharge into the Great Barrier Reef Lagoon: nutrient behaviour in coastal waters. *Marine Pollution Bulletin* 51:9-22
- Diaz-Pulido G (2002) Microbial degradation of the crustose alga *Peyssonnelia* spp. on reefs of the Caribbean and Great Barrier Reef. *Proceedings of the Ninth International Coral Reef Symposium, Bali* 1:1257-1260
- Diaz-Pulido G, Garzón-Ferreira J (2002) Seasonality in algal assemblages on upwelling-influenced coral reefs in the Colombian Caribbean. *Botanica Marina* 45:284–292
- Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. *Marine Ecology Progress Series* 232:115-128
- Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral reef seaweeds. *Ecology* 84:2026-2033
- Diaz-Pulido G, McCook LJ (2004) Effects of live coral, epilithic algal communities and substrate type on algal recruitment. *Coral Reefs* 23:225-233
- Diaz-Pulido G, McCook LJ (2005) Effects of nutrient enhancement of the fecundity of a coral reef macroalga. *Journal of Experimental Marine Biology and Ecology* 317:13-24
- Dodds WK, Gudder DA (1992) The ecology of *Cladophora*. *Journal of Phycology* 28:415-427
- Doehler G, Hagmeier E, David C (1995) Effects of solar and artificial Uv irradiation on pigments and assimilation of ^{15}N ammonium and ^{15}N nitrate by macroalgae. *Journal of Photochemistry and Photobiology B Biology* 30:179-187
- Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* 247:121-132
- Drew EA (1983) *Halimeda* biomass, growth rates and sediment generation on reefs in the central Great Barrier Reef Province. *Coral Reefs* 2:101-110
- Drew EA, Abel KM (1983) Growth of *Halimeda* in reefal and inter-reefal environments. In: Baker JT, Carter RM, Sammarco PW, Stark KP (eds)

- Proceedings: Inaugural Great Barrier Reef Conference, Townsville. James Cook University Press, Townsville, Australia, p 299-304
- Drew EA, Abel KM (1988) Studies on *Halimeda* I. The distribution and species composition of *Halimeda* meadows throughout the Great Barrier Reef Province. *Coral Reefs* 6:195-205
- Dring MJ, Makarov V, Schoschina E, Lorenz M, Luening K (1996) Influence of ultraviolet-radiation on chlorophyll fluorescence and growth in different life-history stages of three species of *Laminaria* (Phaeophyta). *Marine Biology* 126:183-191
- Enríquez S, Rodríguez-Román A (2006) Effect of water flow on the photosynthesis of three marine macrophytes from a fringing-reef lagoon. *Marine Ecology Progress Series* 323:119–132
- Eriksson BK, Johansson G (2003) Sedimentation reduces recruitment success of *Fucus vesiculosus* (Phaeophyceae) in the Baltic Sea. *European Journal of Phycology* 38:217-222
- Eriksson BK, Johansson G (2005) Effects of sedimentation on macroalgae: species-specific responses are related to reproductive traits. *Oecologia* 143:438-448
- Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis. *Marine Pollution Bulletin* 50:125-146
- Fabricius KE, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs* 19:303-309
- Fabricius KE, De'ath G, McCook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin* 51:384-398
- Foster MS (2001) Rhodoliths: Between rocks and soft places. *Journal of Phycology* 37:659-667
- Franklin LA, Forster RM (1997) The changing irradiance environment: consequences for marine macrophyte physiology, productivity and ecology. *European Journal of Phycology* 32:207-232
- Gao K, Aruga Y, Asada K, Ishihara T, Akano T, Kiyohara M (1993a) Calcification in the articulated coralline alga *Corallina pilulifera*, with special reference to the effect of elevated CO₂ concentration. *Marine Biology* 117:129-132

- Gao K, Aruga Y, Asada K, Kiyohara M (1993b) Influence of enhanced CO₂ on growth and photosynthesis of the red algae *Gracilaria* sp. and *G. chilensis*. *Journal of Applied Phycology* 5:563-571
- Garbary DJ, Kim KY, Hoffman J (2004) Cytological damage to the red alga *Griffithsia pacifica* from ultraviolet radiation. *Hydrobiologia* 512:165-170
- Gattuso JP, Allemand D, Frankignoulle M (1999) Photosynthesis and calcification at cellular, organismal and community levels in coral reefs: a review of interactions and control by carbonate chemistry. *American Zoologist* 39:160-183
- Gattuso JP, Frankignoulle M, Wollast R (1998) Carbon and carbonate metabolism in coastal aquatic ecosystems. *Annual Review of Ecology and Systematics* 29:405-434
- Gattuso JP, Payri CE, Pichon M, Delesalle B, Frankignoulle M (1997) Primary production, calcification, and air-sea CO₂ fluxes of a macroalgal-dominated coral reef community (Moorea, French Polynesia). *Journal of Phycology* 33:729-738
- Gibbs SJ, Bown PR, Sessa JA, Bralower TJ, Wilson PA (2006) Nannoplankton extinction and origination across the Paleocene-Eocene Thermal Maximum. *Science* 314:1770-1773
- Gomez I, Ulloa N, Oróstegui M (2005) Morpho-functional patterns of photosynthesis and Uv sensitivity in the kelp *Lessonia nigrescens* (Laminariales, Phaeophyta). *Marine Biology* 148:231-240
- Haeder DP, Lebert M, Helbling EW (2003) Effects of solar radiation on the Patagonian Rhodophyte *Corallina officinalis* (L.). *Photosynthesis Research* 78:119-132
- Halford A, Cheal AJ, Ryan D, Williams DM (2004) Resilience to large-scale disturbance in coral and fish assemblages on the Great Barrier Reef. *Ecology* 85:1892-1905
- Harley CDG, Hughes AAR, Hultgrem KM, Miner BG, Sote CJB, Thornber CS, Rodriguez LF, Tomanek L, Williams SL (2006) The impacts of climate change in coastal marine systems. *Ecology Letters* 9:228-241
- Harrington L, Fabricius KE, De'ath G, Negri AP (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. *Ecology* 85:3428-3437

- Harrington L, Fabricius KE, Eaglesham G, Negri A (2005) Synergistic effects of diuron and sedimentation on photosynthesis and survival of crustose coralline algae. *Marine Pollution Bulletin* 51:415-427
- Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. *Trends in Ecology & Evolution* 14:146-150
- Hatcher BG (1988) Coral reef primary productivity: a beggar's banquet. *Trends in Ecology & Evolution* 3:106-111
- Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. *Journal of Experimental Marine Biology and Ecology* 69:61-84
- Heil CA, Chaston K, Jones A, Bird P, Longstaff B, Costanzo S, Dennison WC (2004) Benthic microalgae in coral reef sediments of the southern Great Barrier Reef, Australia. *Coral Reefs* 336-343
- Henry BE, Van Alstyne KL (2004) Effects of UV radiation on growth and phlorotannins in *Fucus gardneri* (Phaeophyceae) juveniles and embryos. *Journal of Phycology* 40:527-533
- Heyward AJ, Negri AP (1999) Natural inducers of coral larval metamorphosis. *Coral Reefs* 18:273-279
- Hillis-Colinvaux L (1980) Ecology and taxonomy of *Halimeda*: primary producers of coral reefs. *Advances in Marine Biology* 17:1-327
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research* 50:839–866
- Hoffman JR, Hansen LJ, Klinger T (2003) Interactions between UV radiation and temperature limit inferences from single-factor experiments. *Journal of Phycology* 39:268-272
- Hughes TP (1994) Catastrophes, phase-shifts and large-scale degradation of a Caribbean coral reef. *Science* 265:1547-1551
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook LJ, Moltschanowskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17:1-6
- IPCC (2001) Technical summary of the Working Group I report. IPCC Third Assessment Report.
- Isæus M, Malm T, Persson S, Svensson A (2004) Effects of filamentous algae and

- sediment on recruitment and survival of *Fucus serratus* (Phaeophyceae) juveniles in the eutrophic Baltic Sea. *European Journal of Phycology* 39:301-307
- Johansen HW (1981) *Coralline algae: A first synthesis*. CRC Press, Boca Raton, Florida
- Johnson CR, Klumpp DW, Field J, Bradbury R (1995) Carbon flux on coral reefs: effects of large shifts in community structure. *Marine Ecology Progress Series* 126:123-143
- Jompa J (2001) Interactions between macroalgae and scleractinian corals in the context of reef degradation. School of Marine Biology and Aquaculture, James Cook University, Townsville
- Jompa J, McCook LJ (2002) The effects of nutrients and herbivory on competition between a hard coral (*Porites cylindrica*) and a brown alga (*Lobophora variegata*). *Limnology and Oceanography* 47:527-534
- Jones RJ, Hoegh-Guldberg O, Larkum AWD, Schreiber U (1998) Temperature induced bleaching of corals begins with impairment of dark metabolism in zooxanthellae. *Plant Cell and Environment* 21:1219-1230
- King RJ, Schramm W (1982) Calcification in the maerl coralline alga *Phymatolithon calcareum*: effects of salinity and temperature. *Marine Biology* 70:197-204
- Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric CO₂ on coral reefs. *Science* 284:118-120
- Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine CL, Robbins LL (2006) Impacts of ocean acidification on coral reefs and other marine calcifiers: A guide for future research. NSF, NOAA, and the U.S. Geological Survey, St. Petersburg, FL
- Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison WC, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neil J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D (2001) ENCORE: The effect of nutrient enrichment on coral reefs. 2. Synthesis of results and conclusions. *Marine Pollution Bulletin* 42:91-120
- Kübler JE, Johnston AM, Raven JA (1999) The effects of reduced and elevated

- CO₂ and O₂ on the seaweed *Lomentaria articulata*. *Plant Cell and Environment* 22:1303-1310
- Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. *Global Biogeochemical Cycles* 14:639-654
- Lapointe BE (1997) Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography* 42:1119-1131
- Larkum AWD, Kennedy IR, Muller WJ (1988) Nitrogen fixation on a coral reef. *Marine Biology* 98:143-155
- Larkum AWD, Koch E-MW, Kuehl M (2003) Diffusive boundary layers and photosynthesis of the epilithic algal community of coral reefs. *Marine Biology*
- Larkum AWD, Wood WF (1993) The effects of UV-B radiation on photosynthesis and respiration of phytoplankton, benthic macroalgae and seagrasses. *Photosynthesis Research* 36:17-23
- Leclercq N, Gattuso J-P, Jaubert J (2000) CO₂ partial pressure controls the calcification rate of a coral community. *Global Change Biology* 6:329-334
- Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. *Coral Reefs* 19:392-399
- Littler MM (1976) Calcification and its role among macroalgae. *Micronesica*
- Littler MM, Doty MS (1975) Ecological components structuring the seaward edges of tropical Pacific reefs: the distribution, communities and productivity of *Porolithon*. *Journal of Ecology* 63:117-129
- Littler MM, Littler DS (1984) Models of tropical reef biogenesis: the contribution of algae. *Progress in Phycological Research* 3:323-364
- Littler MM, Littler DS (1985) Factors controlling relative dominance of primary producers on biotic reefs. *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 4:35-39
- Littler MM, Littler DS (1995) Impact of CLOD pathogen on Pacific coral reefs. *Science* 267:1356-1360
- Littler MM, Littler DS, Taylor PR (1983a) Evolutionary strategies in a tropical barrier reef system: Functional-form groups of marine macroalgae. *Journal of Phycology* 19:229-237

- Littler MM, Taylor PR, Littler DS (1983b) Algal resistance to herbivory on a Caribbean barrier reef. *Coral Reefs* 2:111-118
- Lotze HK, Schramm W, Schories D, Worm B (1999) Control of macroalgal blooms at early developmental stages: *Pilayella littoralis* versus *Enteromorpha* spp. *Oecologia* 119:46-54
- Lotze HK, Worm B (2002) Complex interactions of climatic and ecological controls on macroalgal recruitment. *Limnology and Oceanography* 47:1734-1741
- Lotze HK, Worm B, Molis M, Wahl M (2002) Effects of UV radiation and consumers on recruitment and succession of a marine macrobenthic community. *Marine Ecology Progress Series* 243:57-66
- Lotze HK, Worm B, Sommer U (2000) Propagule banks, herbivory and nutrient supply control population development and dominance patterns in macroalgal blooms. *Oikos* 89:46-58
- Lotze HK, Worm B, Sommer U (2001) Strong bottom-up and top down control of early stages of macroalgae. *Limnology and Oceanography* 46:749-757
- Lüning K (1993) Environmental and internal control of seasonal growth in seaweeds. *Hydrobiologia* 260 / 261:1-14
- Lüning K (1994) When do algae grow? *European Journal of Phycology* 29:61-67
- Marshall JF, Davies PJ (1988) *Halimeda* bioherms of the northern Great Barrier Reef. *Coral Reefs* 6:139-148
- Martin-Smith KM (1993) The phenology of four species of *Sargassum* at Magnetic Island, Australia. *Botanica Marina* 36:327-334
- Martin-Smith KM (1994) Short-term dynamics of tropical macroalgal epifauna: patterns and processes in recolonisation of *Sargassum fissifolium*. *Marine Ecology Progress Series* 110:177-185
- McClanahan TR, Muthiga NA, Mangi S (2001) Coral and algal changes after the 1998 coral bleaching: interaction with reef management and herbivores on Kenyan reefs. *Coral Reefs* 19:380-391
- McClanahan TR, Polunin NVC, Done TJ (2002) Ecological states and the resilience of coral reefs. *Conservation Ecology* 6:18 (online)
- McCook LJ (1996) Effects of herbivores and water quality on *Sargassum* distribution on the central Great Barrier Reef: cross-shelf transplants. *Marine Ecology Progress Series* 139:179-192
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific

- issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18:357-367
- McCook LJ, De'ath G, Price IR, Diaz-Pulido G, and Jompa J (2000) Macroalgal resources of the Great Barrier Reef: taxonomy, distributions and abundances on coral reefs. Report to the Great Barrier Reef Marine Park Authority, Townsville
- McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400-417
- McCook LJ, Price IR, Klumpp DW (1997) Macroalgae on the GBR: causes or consequences, indicators or models of reef degradation? Proceedings of the Eighth International Coral Reef Symposium, Panama 2:1851-1856
- McManus JW, Polsenberg JF (2004) Coral –algal phase shifts on coral reefs: ecological and environmental aspects. *Progress in Oceanography* 60:263-279
- Millar AJK (2007) The Flindersian and Peronian Provinces. *Algae of Australia Series. Algae of Australia: Introduction. Australian Biological Resources Study / CSIRO Publishing, in press*
- Moran K, Backman J, Brinkhuis H, Clemens SC, Cronin T, Dickens GR, Eynaud F, Gattacceca J, Jakobsson M, Jordan RW, Kaminski M, King J, Koc N, Krylov A, Martinez N, Matthiessen J, McInroy D, Moore TC, Onodera J, O'Regan M, Pälike H, Rea B, Rio D, Sakamoto T, Smith DC, Stein R, St John K, Suto I, Suzuki N, Takahashi K, Watanabe M, Yamamoto M, Farrell J, Frank M, Kubik P, Jokat W, Kristoffersen Y (2006) The Cenozoic paleoenvironment of the Arctic Ocean. *Nature* 441:601-605
- Morrissey J (1980) Community structure and zonation of macroalgae and hermatypic corals on a fringing reef flat of Magnetic Island (Queensland, Australia). *Aquatic Botany* 8:91-139
- Nugues MM, Smith GW, Hoodonk RJv, Seabra MI, Bak RPM (2004) Algal contact as a trigger for coral disease. *Ecology Letters* 7:919–923
- Nyström M, Folke C, Moberg F (2000) Coral reef disturbances and resilience in a human-dominated environment. *Trends in Ecology & Evolution* 15:413-417
- Orme GR, Salama MS (1988) Form and seismic stratigraphy of *Halimeda* banks in part of the northern Great Barrier Reef Province. *Coral Reefs* 6:131-137
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A,

- Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner G-K, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer L, Slater RD, Totterdell IJ, Weirig M-F, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437:681-686
- Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP (2000) Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. *Proceedings of the National Academy of Sciences of the United States of America* 97:5297-5302
- Pakker H, Breeman AM, Prud'homme van Reine WF, Van den Hoek C (1995) A comparative study of temperature responses of Caribbean seaweeds from different biogeographic groups. *Journal of Phycology* 31:499-527
- Pelejero C, Calvo EVA, Mcculloch MT, Marshall JF, Gagan MK, Lough JM, Opdyke BN (2005) Preindustrial to modern interdecadal variability in coral reef pH. *Science* 309:2204-2202
- Phipps CVG, Davies PJ, Hopley D (1985) The morphology of *Halimeda* banks behind the Great Barrier Reef east of Cooktown, QLD . *Proceedings of the Fifth International Coral Reef Congress, Tahiti* 27-30
- Price IR (1975) The development of algae on the skeletons of reef-building corals. In: Anon. (ed) *Crown-of-thorns starfish seminar proceedings*. Australian Government Publishing Service, Canberra, p 181-191
- Price IR (1989) Seaweed phenology in a tropical Australian locality (Townsville, North Queensland). *Botanica Marina* 32:399-406
- Price IR (1990) Marine plant life. In: Clayton MN, King RJ (eds.) *Biology of marine plants*. Longman Cheshire, Melbourne, p 5-24
- Price IR, Scott FJ (1992) The turf algal flora of the Great Barrier Reef: Part I. Rhodophyta. James Cook University of North Queensland, Townsville
- Purcell SW (2000) Association of epilithic algae with sediment distribution on a windward reef in the northern Great Barrier Reef, Australia. *Bulletin of Marine Science* 66:199-214
- Purcell SW, Bellwood DR (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. *Coral Reefs* 20:117-125
- Raven JA, Ball LA, Beardall J, Giordano M, Maberly SC (2005) Algae lacking carbon-concentrating mechanisms. *Canadian Journal of Botany* 879-890:

- Reusch TBH, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences* 102:2826-2831
- Riebesell U (2004) Effects of CO₂ enrichment on marine phytoplankton. *Journal of Oceanography* 60:719-729
- Ringeltaube P, Harvey A (2000) Non-geniculate coralline algae (Corallinales, Rhodophyta) on Heron reef, Great Barrier Reef (Australia). *Botanica Marina* 43:431-454
- Ritson-Williams R, Paul VJ, Bonito V (2005) Marine benthic cyanobacteria overgrow coral reef organisms. *Coral Reefs* 24:629
- Robertson DR (1991) Increase in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicate food limitation. *Marine Biology* 111:437-444
- Rogers RW (1996) Spatial, seasonal and secular patterns in the cover of green algae on Heron reef flat, Great Barrier Reef, Australia. *Botanica Marina* 39:415-419
- Rogers RW (1997) Brown algae on Heron reef flat, Great Barrier Reef, Australia: spatial, seasonal and secular variation in cover. *Botanica Marina* 40:113-117
- Roleda MY, Wiencke C, Hanelt D, Van De Poll WH, Gruber A (2005) Sensitivity of Laminariales zoospores from Helgoland (North Sea) to ultraviolet and photosynthetically active radiation: Implications for depth distribution and seasonal reproduction. *Plant Cell and Environment* 28:466-479
- Royal Society (2005) Ocean acidification due to increasing atmospheric carbon dioxide. The Royal Society, London
- Russ GR, McCook LJ (1999) Potential effects of a cyclone on benthic algal production and yield to grazers on coral reefs across the central Great Barrier Reef. *Journal of Experimental Marine Biology and Ecology* 235:237-254
- Sagawa N, Nakamori T, Iryu Y (2001) Pleistocene reef development in the southwest Ryukyu Islands, Japan. *Palaeogeography Palaeoclimatology Palaeoecology* 175:303-323
- Santas R, Korda A, Lianou C, Santas. P. (1998a) Community responses to Uv radiation. I. Enhanced UvB effects on biomass and community structure of filamentous algal assemblages growing in a coral reef mesocosm. *Marine Biology* 131:153-162

- Santas R, Santas P, Lianou C, Korda A (1998b) Community responses to Uv radiation. II. Effects of solar UvB on field-grown diatom assemblages of the Caribbean. *Marine Biology* 131:163-171
- Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds. *Oceanography and Marine Biology: An Annual Review* 28:177-276
- Schaffelke B (1999) Short-nutrient pulses as tools to assess responses of coral reef macroalgae to enhanced nutrient availability. *Marine Ecology Progress Series* 182:305-310
- Schaffelke B, Heimann K, Marshall PA, Ayling AM (2004) Blooms of *Chrysocestis fragilis* on the Great Barrier Reef. *Coral Reefs* 23:514
- Schaffelke B, Hewitt CL, Smith JE (2006) Introduced macroalgae - a growing concern. *Journal of Applied Phycology* 18:529-541
- Schaffelke B, Klumpp DW (1997) Biomass and productivity of tropical macroalgae on three nearshore fringing reefs in the central Great Barrier Reef, Australia. *Botanica Marina* 40:373-383
- Schaffelke B, Klumpp DW (1998) Nutrient-limited growth of the coral reef macroalga *Sargassum baccularia* and experimental growth enhancement by nutrient addition in continuous flow culture. *Marine Ecology Progress Series* 164:199-211
- Schaffelke B, Mellors J, Duke NC (2005) Water quality in the Great Barrier Reef region: responses of mangrove, seagrass and macroalgal communities. *Marine Pollution Bulletin* 51:279-296
- Schiel DR, Steinbeck JR, Foster MS (2004) Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology* 85:1833-18339
- Schils T, Wilson SC (2006) Temperature thresholds as a biogeographic barrier in northern Indian Ocean macroalgae. *Journal of Phycology* 42:749-756
- Scoffin TP, McLean RF (1978) Exposed limestones of the northern province of the Great Barrier Reef. *Philosophical Transactions of the Royal Society of London. Series A, Mathematical and Physical Sciences* 291:119-138
- Shaw M, Mueller JF (2005) Preliminary evaluation of the occurrence of herbicides and PAHs in the Wet Tropics region of the Great Barrier Reef, Australia, using passive samplers. *Marine Pollution Bulletin* 51:876-881
- Sluijs A, Schouten S, Pagani M, Woltering M, Brinkhuis H, Damste JSS, Dickens

- GR, Huber M, Reichert G-J, Stein R, Matthiessen J, Lourens LJ, Pedentchouk N, Backman J, Moran K, Clemens S, Cronin T, Eynaud R, Gattacceca J, Jakobsson M, Jordan R, Kaminski M, King J, Koc N, Martinez N, McInroy D, Moore Jr TC, O'Regan M, Onodera J, Pa'like H, Rea B, Rio D, Sakamoto T, Smith DC, St John KEK, Suto I, Suzuki N, Takahashi K, Watanabe M, Yamamoto M (2006) Subtropical Arctic Ocean temperatures during the Palaeocene/Eocene thermal maximum. *Nature* 441:610-613
- Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe induced coral mortality. *Ecology Letters* 9:835-845
- Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332-342
- Sommer U, Aberle N, Engel A, Hansen T, Lengfellner K, Sandow M, Wohlers J, Zöllner E, Riebesell U (2007) An indoor mesocosm system to study the effect of climate change on the late winter and spring succession of Baltic Sea phyto- and zooplankton. *Oecologia* 150:655-667
- Stanley SM, Ries JB, Hardie LA (2002) Low-magnesium calcite produced by coralline algae in sea-water of Late Cretaceous composition. *Proceedings of the National Academy of Sciences* 99:15323-15326
- Steneck RS (1982) A limpet-coralline alga association: adaptations and defenses between a selective herbivore and its prey. *Ecology*
- Steneck RS (1983) Escalating herbivory and resulting adaptive trends in calcareous algae. *Paleobiology* 9:45-63
- Steneck RS (1986) The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annual Review of Ecology and Systematics* 7:273-303
- Steneck RS (1988) Herbivory on coral reefs: a synthesis. *Proceedings of the Sixth International Coral Reef Symposium, Townsville* 1:37-49
- Steneck RS (1994) Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978-1988). Ginsburg RN (Comp) *Proc. Colloquium on Global Aspects of Coral Reefs: Health, Hazards, and History*. Univ. Miami, Miami, p 220-226
- Steneck RS (1997) Crustose corallines, other algal functional groups, herbivores and sediments: complex interactions along reef productivity gradients.

- Proceedings of the Eighth International Coral Reef Symposium, Panama
1:695-700
- Steneck RS (Unpublished) An artificial key to the common crustose coralline algae of the Great Barrier Reef.
- Steneck RS, Adey WH (1976) The role of environment in control of morphology in *Lithophyllum congestum*, a Caribbean algal ridge builder. *Botanica Marina* 19:197-215.
- Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69:476-498
- Steneck RS, Watling L (1982) Feeding capabilities and limitations of herbivorous molluscs: a functional group approach. *Marine Biology* 68:299-319
- Szmant AM (2002) Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries* 25:743-766
- Tanner JE (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. *Journal of Experimental Marine Biology and Ecology* 190:151-168
- Tribollet A, Atkinson MJ, Langdon C (2006) Effects of elevated p CO₂ on epilithic and endolithic metabolism of reef carbonates. *Global Change Biology* 12:2200-2208
- Umar MJ, McCook LJ, Price IR (1998) Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs* 17:169-177
- Valiela I, McClelland J, Hauxwell J, Behr PJ, Hersh D, Foreman K (1997) Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. *Limnology and Oceanography* 42:1105-1118
- Van De Poll WH, Bischof KAI, Buma AGJ, Breeman AM (2003) Habitat related variation in UV tolerance of tropical marine red macrophytes is not temperature dependent. *Physiologia Plantarum* 118:74-83
- Van den Hoek C, Mann DG, Jahns HM (1995) *Algae: An introduction to Phycology*. Cambridge University Press, Cambridge
- Van den Hoek C, Stam WT, Breeman AM (1990) The geographic distribution of seaweed species in relation to temperature: Present and past. Beukema JJ, Wolff WJ, Brouns M (eds) *Expected effects of climate change on marine coastal ecosystems*. Kluwer Academic Publishers, The Netherlands, p 55-67
- Vincent WF, Roy S (1993) Solar ultraviolet-B radiation and aquatic primary

- production: damage, protection and recovery. *Environmental Reviews* 1:1-12
- Vroom P, Walters L, Beach K, Coyer J, Smith J, Abgrall MJ, Byron D, Deangelis K, Konar B, Liss J, Okano R, Roberts C, Herren L, Woo M, Smith C (2005) Hurricane-induced propagation and rapid regrowth of the weedy brown alga *Dictyota* in the Florida Keys. *Florida Scientist* 68:161-174
- Vuki VC, Price IR (1994) Seasonal changes in the *Sargassum* populations on a fringing coral reef, Magnetic Island, Great Barrier Reef region, Australia. *Aquatic Botany* 48:153-166
- Ward JR, Lafferty KD (2004) The elusive baseline of marine disease: are diseases in ocean ecosystems increasing? *PloS Biology* 2:542-547
- Ward S, Harrison P (2000) Changes in gametogenesis and fecundity of acroporid corals that were exposed to elevated nitrogen and phosphorus during the ENCORE experiment. *Journal of Experimental Marine Biology and Ecology* 246:179-221
- Wiencke C, Roleda MY, Gruber A, Clayton MN, Bischof KAI (2006) Susceptibility of zoospores to Uv radiation determines upper depth distribution limit of Arctic kelps: Evidence through field experiments. *Journal of Ecology* 94:455-463
- Wilkinson CR, Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. II. Nitrogen fixation. *Marine Ecology Progress Series* 13:15-19
- Wilkinson CR, Williams DM, Sammarco PW, Hogg RW, Trott LA (1983) Relationships between fish grazing and nitrogen fixation rates on reefs across the central Great Barrier Reef. *Proceedings of the Inaugural Great Barrier Reef Conference, Townsville* 375-375
- Williams DM (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1:35-43
- Williams DM, Russ GR, Doherty PJ (1986) Reef fish: large-scale distribution and recruitment. *Oceanus* 29:76-82
- Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187-196
- Wolanski E, Drew E, Abel KM, O'Brien J (1988) Tidal jets, nutrient upwelling and their influence on the productivity of the alga *Halimeda* in the ribbon reefs, Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 26:169-201

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature* 417:848-851

Worm B, Lotze HK, Sommer U (2000) Coastal food web structure, carbon storage, and nitrogen retention regulated by consumer pressure and nutrients loading. *Limnology and Oceanography* 45:339-349

Table 3: Generalised predictions of the characteristics of future GBR algal communities affected by climate change, based on the vulnerability assessments, and comparison to present day characteristics (note that predictions are very uncertain, and likely to vary considerably with conditions).

Present	Future
Habitat characteristics	
<p>Dynamic communities, infrequent disturbance leads to decrease of coral cover and subsequent recovery;</p> <p>Substrate availability dynamic due to infrequent and local disturbance;</p> <p>Some inshore reefs with sustained low coral cover;</p>	<p>Frequent and chronic disturbance leads to low coral cover, especially in shallow water.</p> <p>Higher substrate availability for algal colonisation over longer periods of time and larger spatial scales</p>
<p>High herbivore abundance, sufficient to control macroalgal biomass (except for inshore reefs with high standing stocks of macroalgae)</p>	<p>Low herbivory due to low habitat complexity and turbid water, insufficient to control macroalgal biomass</p>
Characteristics of algal communities and species	
<p>Patchwork of algal communities, controlled by herbivory, substrate and nutrient availability.</p> <p>Generally higher algal biomass inshore</p>	<p>Generally higher algal cover, high biomass in areas with low herbivory</p> <p>Southward expansion of distribution ranges</p>
<p>Mix of canopy-forming, understory, turfing and encrusting species inshore, mainly turf and CCA offshore</p>	<p>Short, low-lying species (turf and short upright macroalgae inshore), turf and some CCA offshore</p>
<p>Mix of calcified and un-calcified species (more un-calcified inshore)</p>	<p>Un-calcified dominate</p> <p>Low CCA everywhere, weak</p>

<p>Low CCA inshore, high CCA offshore</p>	<p>skeletons</p>
<p>Mix of species with perennial, annual and ephemeral life cycles, likely controlled by seasonal triggers</p> <p>Inshore: summer-growing and reproducing Fucales form canopies; understory of turfs and diverse green and red algae; sporadic spring blooms of brown algae</p> <p>Offshore: turf, CCA, <i>Halimeda</i>, low macroalgal abundance, no distinct seasonality, local ephemeral blooms of greens, cyanobacteria or <i>Chrysozystis</i></p>	<p>Species with ephemeral life cycles prevail, dominance of fast-growing weedy species that recover and colonise quickly after disturbance, algal blooms after substrate release</p>
<p>Mix of species with different:</p> <p>Temperature tolerances (some occur only as winter annuals)</p> <p>UV tolerances and light requirements (variation along inshore/offshore, within-canopy and depth gradients)</p> <p>Nutrient requirements (variation along inshore/offshore gradients; species with higher nutrient requirement generally inshore, apart from some <i>Halimeda</i> species)</p>	<p>Communities dominated by species with:</p> <p>High temperature tolerance or generalists, loss or southward shift of winter annuals</p> <p>High UV tolerance and broad light requirements (strong fluctuations in water column light attenuation due to more intense floods and storms alternating with extended drought conditions)</p> <p>High nutrient demand, ephemerals, bloom-forming species (variable nutrient availability due to alternation of floods and storms with extended</p>

	droughts)
--	-----------

Table 4. Summary of the responses of macroalgae of the Great Barrier Reef to global climate change. Upward arrows represent a beneficial effect, downward arrows a detrimental effect (eg due to indirect impacts or impacts at the level of the community), dash a neutral effect for algae. The table is based on the vulnerability assessments and inherently speculative.

Climate Stressor	Algal turfs	Upright macroalgae	Crustose calcareous algae
Change in Ocean circulation	↑↓	↑↓	↑↓
Increase water temperature	↑↓	↑↓	↑↓
Increase CO ₂ & acidification	↑↑↓	↑↑↓ (fleshy) ↓↓ (calcified)	↑↓↓
Light & UV	↑↓↓	↑↓↓	↑↓
Sea level rise	↑↑↓	↑↑↓	↑↑↓
Tropical storms	↑↑	↑↓	↑-
Terrestrial inputs	↑↓	↑↓↓	↑↓↓
Increased substrate availability	↑↑↓	↑↑↓	↑↓↓

Figure legends

7.1. General model of the impacts of global climate change on macroalgae of the Great Barrier Reef and likely outcomes

7.2. Global climate change impacts on algal turfs.

7.3. Global climate change impacts on upright macroalgae.

7.4. Global climate change impacts on crustose calcareous algae.