

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-reef 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 7.1). Macroalgae 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^{172,158}. 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 GBR⁴¹, accounting for nearly 32 percent of the total number of algal species recorded for the continent (although the compilation for the GBR is based on very limited collections). In addition to being relatively diverse at the species level, GBR macroalgae have complex and diverse evolutionary histories^{6,200}, including more than 40 orders belonging to at least five phyla (Table 7.1) and two kingdoms (Prokaryota and Eukaryota). In contrast, for example, hard corals include only one to two orders.

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

Taxonomic group	Orders	Phyla	
Benthic	~40	5	
macroalgae		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	1	
	Scleractinia	Cnidaria	
	Milleporina		

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. Adl et al.³ 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 'algae', like '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 than most other groups in coral reef habitats, they are also more complex, in functional morphology and ecological roles. 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 cannot 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)^{117,118,191}. The three main categories are: i) algal turfs, ii) upright macroalgae (fleshy and calcified), and iii) crustose calcareous algae. 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, 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 (less than 10 mm height)		Microalgae Filamentous Juvenile stages of macroalgae		Lyngbya, Chrysocystis Cladophora, Polysiphonia
'Upright' macroalgae (greater than 10 mm height)	Fleshy (ie non- calcareous)	Foliose - Terete Co	Membranous Globose Corticated orticated	Ulva, Anadyomene Ventricaria, Dictyosphaeria Dictyota, Lobophora Laurencia, Acanthophora Sargassum, Turbinaria
Crustose algae	Calcareous	Calcareous articulated Calcareous Crustose Non-calcareous Crustose		Halimeda, Amphiroa Porolithon, Peyssonnelia Ralfsia, Cutleria

Distributions and seasonal dynamics

GBR algal communities are highly variable, showing latitudinal, cross-shelf and within-reef variation in composition and abundance^{139,134}. 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)^a 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 abundance¹⁶⁰. Brown algae are generally low in abundance, with the most common genera including *Padina*, *Dictyota*, *Turbinaria* and *Lobophora*^{131,133,67}. CCA are abundant and diverse on offshore reefs and can contribute to reef formation^{177,39,157,66} (Steneck and McCook unpublished data). Abundant taxa on offshore reefs include *Porolithon*, *Neogoniolithon*, *Paragoniolithon*, and *Lithophyllum* species (Steneck unpublished data).

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 four metres 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^{139,149,127,203,170,133}.

Seaweeds are also abundant in some deep-water, inter-reef 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 2000 km² in this region and may be up to 20 metres high^{142,126,61}. These *Halimeda* meadows occur principally in northern sections of the GBR, at depths between 20 and 40 metres, but they are also found in the central and southern sections, where they have been found at depths down to 96 metres⁶¹. 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 meadows of *Halimeda* in the northern section of the GBR (at depths between 30 and 45 metres) appear to be sustained by nutrients injected by tidal jets and localised upwelling events^{59,212}.

In addition to this spatial variability, many GBR macroalgae are highly seasonal in their occurrence, growth and reproduction¹⁴⁹. Large seaweeds such as *Sargassum* are strongly seasonal, with peaks in biomass and reproduction during the summer and lowest biomass during the winter^{127,203,170,55}. A large proportion of the GBR benthic algal species, especially red algae, grow most actively during the Australian autumn (March to May), winter dry season (June to August), and spring¹⁴⁹. 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^{170,32}.

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.

a 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.

Also critical to this assessment is recognition that different macroalgae have different ecological functions, contributing both to the maintenance of reef health, and to the degradation of reefs (see 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, out-competed by more successful algae. The outcome will be algal assemblages, and ecosystems, that are markedly different in terms of taxonomic composition, 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, while 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 (ie 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. While 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 making 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.

7.1.2.1 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 turfs⁷⁴. Available research from the GBR indicates that primary production by fleshy macroalgae and crustose algae is also important^{170,38}. Planktonic microalgae and algal symbionts of scleractinian corals contribute to reef productivity to a lesser degree¹. 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 web²⁹. Some organic matter is exported as detritus by currents and tides to adjacent habitats such as seagrass meadows, mangroves and the deeper, inter-reef 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 carbon dioxide (CO₂)^{73,1}. However, the seasonal and disturbance-driven dynamics of algal abundance and taxonomic composition in the GBR are likely to lead to distinct fluctuations in the metabolic performance (primary production and respiration¹⁵ and therefore in the amount of carbon being stored).

7.1.2.2 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^{99,85}. Due to 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 producers⁸³. Studies on the GBR have found high rates of nitrogen fixation, particularly on substrates exposed to fish grazing^{207,208,108}.

7.1.2.3 Reef construction and habitat formation

Many macroalgae make important contributions to the construction of reef framework by depositing calcium carbonate (CaCO₃). Crustose calcareous algae (eg *Porolithon* and *Peyssonnelia*) are significant framework builders and framework 'cementers' on coral reefs^{114,37}. CCA bind adjacent substrata and provide a calcified tissue barrier against erosion¹¹⁴. 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^{42,177,39}. 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 high³⁷. 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^{13,165,68} and this is likely to be true for Australia and the GBR^{68,30}. CCA are important in areas at depths between 80 and 120 metres, at the edge of the continental platform in the southern GBR, where they form large frameworks, several meters high⁴⁵.

Upright calcareous algae, such as *Halimeda, Udotea, Amphiroa* and *Galaxaura,* make important contributions to the production of marine sediments^{88,60,44}. The white sand of beaches and reef lagoons is 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 tissues¹¹⁴. Calcification may be an adaptation that inhibits grazing (defensive mechanis)¹ ^{92,184,185,186,187}, resists wave damage, and provides mechanical support and protection from ultraviolet (UV) radiation^{114,18}.

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 (eq Beck et al.²⁰).

7.1.2.4 Facilitation of coral settlement

Crustose calcareous algae of the order Corallinales are suggested to induce settlement of coral larvae in the GBR⁸⁷. 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 CCA⁸¹. The implications of this process at the ecosystem level remain to be explored.

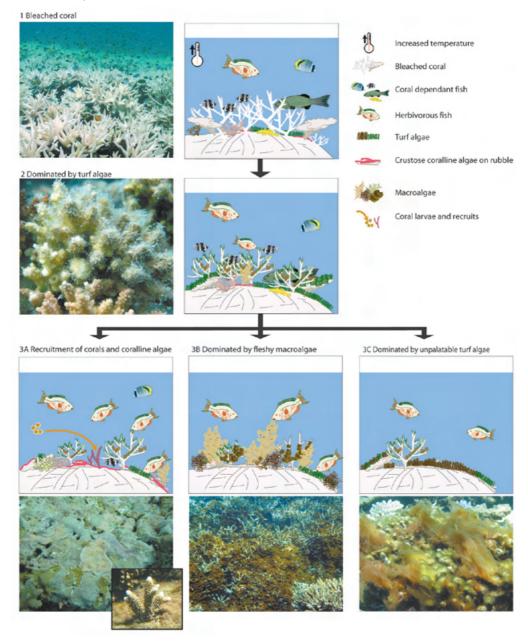
7.1.2.5 Reef degradation

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^{58,91,132,103,136}. 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^{188,132,193,130}. 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^{148,96,52,78}. 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^{91,194,135,140,181}. 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 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 (Figure 7.1). 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^{199,2,176}. Increased resources such as carbon dioxide (CO₂) and nutrients may enhance growth rates but the accumulation of biomass will largely depend on interactions with herbivores¹³². In this chapter we consider the impacts of changes in environmental conditions and resources including: i) ocean circulation, ii) seawater temperature, iii) ocean chemistry (sea surface CO₂ and the consequent increase in bicarbonate), iv) light and UV radiation, v) sea level rise, vi) tropical storms, vii) rainfall and river flood plumes, and viii) substrate availability.

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



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 (Steinberg chapter 3). 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 (eq upwelling or dispersion of flood plumes). For example, a strengthening of the Hiri Current may depress the thermocline, suppressing the ability of cooler deep waters to access the continental shelf (see Steinberg chapter 3) with potential impacts on macroalgal productivity. Cai et al.³³ 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 (eq productivity, nitrogen fixation) are sensitive to changes in water temperature and water quality (see section 7.1.2.3). 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 (eg Sargassum), are less homogeneous in distribution¹³³ 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 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^{113,190,95,2}.

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 species introductions. However, baseline descriptions of 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 turfs¹⁷⁵, 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 coast¹³⁷.

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). However, these are deep-water beds fed by 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 consequent 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 (ie adjust, sensu IPCC, see 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 reefs 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, uncertainties about projected changes in ocean circulation are high, and the consequences of specific changes are not clear. Assessing the vulnerability of algae to changing ocean circulation, therefore, is difficult, but vulnerability is 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 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^{6,93} (Lough chapter 2). 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). 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 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 subtropical 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^{23,145}. Pakker et al.¹⁴⁵) also found that intertidal species are generally more tolerant to high temperatures than are 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 production¹⁹, and changes in seasonality, growth and

b Current monthly average temperatures in coastal GBR: approximately 20 to 29°C, with extremes approximately 18 to 34°C (Australian Institute of Marine Science).

reproduction³¹. Given the diversity of forms and species, potential for widespread 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^{124,125}, and several studies indicate that this also applies to tropical macroalgae^{51,9,10}. While seasonality has been observed in many GBR algae^{149,127,160}, there is no specific information available on the environmental triggers that may be involved. Without this knowledge, we can only suggest that temperature-controlled life cycles may become unsynchronised under climate change, with potentially catastrophic effects for individual species or food webs (see Sommer et al.¹⁸² for an example from temperate plankton).

The potential for widespread direct mortality of upright macroalgae is low, due to assumed wide temperature tolerances¹⁴⁵. For calcified upright algae, there may be increased calcification^{114,5}. Community changes due to shifts in relative abundance of turf algae and upright macroalgae, and range expansions, are also likely to occur^{31,175}.

For CCA, there is potential for a slight increase in calcification^c 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)¹¹⁶, or the *Peyssonnelia* Yellow Band Disease (PYBD)⁵⁰. Both diseases have been observed more commonly during the warmer months, although the nature and impact of such diseases in the GBR are not known⁵⁰.

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 tolerances¹⁷⁴.

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

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 tolerances¹⁴⁵. For example, taxa such as *Ulva* (Enteromorpha) and Cladophora are eurythermal with large distributional ranges and are likely to be less vulnerable than species with more restricted distributions, such as many turfing red algae (see Price and Scott¹⁵¹). The vulnerability of upright macroalgae and CCA is likely to be low to moderate, given their expected high adaptive capacity, and wide temperature tolerances. The effects of higher temperatures on temperature-controlled algal life cycles are not understood.

Temperate CCA show variable responses to rising temperature95,100; information for tropical CCA is very limited100.

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^{51, 11}. This may suggest a strong competitive advantage for turfing assemblages under increased temperatures scenarios. However, this pattern requires 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 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; Lough chapter 2). 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 macroalgae¹⁶³. There is also potential for changes in the availability of nutrients under reduced pH^{163,102}.

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 CO₂ enhancement of photosynthesis. Although there are no data specific to the GBR, a doubling of CO₂ produced an increase in growth of 52 percent in a temperate red algae^{d,104} and up to 130 percent in other species^{e,71}. However, calcified algae are particularly sensitive to ocean acidification. For example, in the GBR, a decrease in pH from 8 to 7.5 reduced calcification dramatically for the alga *Halimeda tuna*²⁸. Reduction of pH may also decrease calcification of *Amphiroa foliacea* from the GBR^{27f}. 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. Minor changes in pH (from 8.1 to 7.8) reduced calcification by as much as 21 percent for a coral reef community that included CCA^{g110}.

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 nutrients^h and by possible direct effects of acidification on photosynthesis. However, if nutrient availability increases, due to higher terrestrial inputs (see section 7.2.7), there is a possibility of synergistic increases in growth of turf algae (due to increased CO₂ and nutrients), further disturbing

d Data for the temperate intertidal fleshy red macroalga Lomentaria articulata showed nonlinear response 104.

e Data for two species of the red fleshy alga Gracilaria from \textit{Japan}^{71} .

f One of the few experiments that have used macroalgae from the GBR²⁷. Effects of acidification in *Amphiroa* seem to be smaller than the effects on *Halimeda tuna*.

g Leclerq et al. 110 manipulated CO $_2$ in a coral reef community that included the CCA *Neogoniolithon* spp. and *Hydrolithon* and predicted a reduction of 21 percent in calcification by 2100 (when pH is expected to be 0.4 to 0.5 units lower than at present).

h Some studies have shown carbon limitation for planktonic microalgae¹⁶³ and temperate fleshy macroalgae^{104,154}, but there are few specific examples demonstrating carbon limitation of growth of turf algae or fleshy macroalgae from coral reefs⁶³, including the GBR¹⁰⁹.

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 nutrientenriched waters¹⁶³. The overall outcome for turf algae is difficult to predict. Increased ocean CO₂ may also increase carbon uptake by turf algae, with a resultant increase in the release of dissolved organic carbon, as has been demonstrated for some microalgae¹⁵⁶.

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^{28,71}. Such increases may be regulated in part by water flow and nutrient availability⁶³. 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 saturated¹⁹.

Ocean acidification reduces calcification of seaweeds such as Halimeda^{28,47}, Amphiroa^{1,27,105} and Corallina pilulifera70. Increased CO2 may enhance photosynthesis in such upright, calcified algae, but these effects will be offset against those of decreased calcification as a 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 (eq Halimeda banks), and shifts from calcifying to non-calcifying algae^{19,101,163,102}.

The impacts of increased CO₂ on CCA may include not only reduced calcification, but may ultimately include dissolution of calcified skeletons^{163,143,102}. 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 corals¹¹⁴. CCA 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 percent for a coral reef community (including two species of CCA) by 2100 (when pH is expected to be 0.4 to 0.5 units lower than present¹¹⁰). 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 species¹⁰⁵, 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 and the pH of sea water in coral reefs, that there have been pre-industrial to modern interdecadal variations in reef-water pH146,102. 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-to-dark ratio of about three^{75,102}.

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. Net photosynthesis of epilithic algal communities dominated by the crustose calcareous alga Hydrolithon (Porolithon) onkodes was negatively affected by high pressure of CO₂¹⁹⁵. Recruitment of CCA may also be reduced with elevated CO24. 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.

Langdon et al.¹⁰⁵ found a 24 to 42 percent decrease in calcification for the predicted change in CO₂ between 1880 and 2065 in coral reef mesocosms dominated by upright calcified algae Amphiroa spp.

CCA may play a role in cementing reef structures together. Thus, a negative effect on CCA of increased surface water carbon dioxide, and attendant decreased carbonate and pH, 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 Caribbean¹⁸³. Coralline algae (order Corallinales) radiated to nearly modern levels of diversity during the Eocene¹⁸⁵ when the world was much warmer and had higher CO₂ than at present^{179,138}, so adaptation may be possible but in ways we do not yet understand¹⁶³. 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 uncalcified 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), and UV levels are already high in tropical regions²⁰¹. 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 ultraviolet radiation

Intertidal and shallow-water algal turf and CCA species appear generally less sensitive than deeper species, apparently reflecting adaptation to high light/light UVB levels, through the accumulation of UVB-screening compounds¹⁰⁸. 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^{62,123,76}. Macroalgal embryos and early life history stages are more sensitive than juveniles and adults⁸⁶. Experimental data for temperate algae have shown that even small doses and short exposure times (eg two hours) of UV radiation will

often reduce photosynthesis, growth and reproduction of turf algae, upright macroalgae and CCA^{123, 4,90,162,206}. However, there are no published data for GBR algae.

7.2.4.3 Impacts – light and ultraviolet radiation

There are few experimental studies documenting impacts of UV radiation on tropical algal turfs, upright macroalgae or CCA; most relevant studies are from temperate and polar regions. However, the effects of UV radiation are likely to be comparable. The most common impacts include direct damage to the photosynthetic apparatus^{19,72}, DNA^{69,198}, reproductive tissues¹⁹, and reduction of nutrient uptake⁵⁷. There are documented cases of changes in algal secondary metabolites that may consequently alter herbivore consumption⁴³, with important implications for algal dynamics and interactions. All these effects may lead to community changes, due to shifts in relative abundance^{201,46,123}, but the potential for widespread direct mortality seems low. Tropical algae are likely to have higher UV tolerances than temperate macroalgae because they have evolved in a naturally high UV environment.

7.2.4.4 Adaptive capacity – light and ultraviolet radiation

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, mycosporinelike amino acids)16. 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 16. Red macroalgae appear to have higher levels of UV-absorbing compounds than green and brown macroalgae, potentially giving red algae greater adaptive capacity¹⁷. The presence of phlorotannins in some brown algae may provide some protection against UV radiation86. Adaptive capacity apparently increases during succession, apparently because spores are more susceptible than sporophytes to UV damage¹. Some calcareous upright algae, such as the temperate calcareous alga Corallina officinalis, have the potential to adapt to high levels of UV radiation⁷⁷ because calcium carbonate acts as a broadband reflector^{112,18} and may confer some tolerance in CCA.

7.2.4.5 Vulnerability and thresholds – light and ultraviolet radiation

The vulnerability of algal turfs and upright macroalgae as a whole is moderate since there is potential for adaptation to increased UV radiation and the impacts are likely to be restricted to shallow-water 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 and ice sheets is occurring at a rate of one to two millimetres per year. By 2100, the global sea level is projected to be 310 \pm 30 mm higher than in 1990 (Lough chapter 2). 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.

Experiments with coral reef macroalgae and diatoms^{166,167}.

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 species⁷⁹. 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 rates of colonisation, growth and reproduction 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). The exposure of algal turfs, upright macroalgae and CCA to tropical cyclones is related to their proximity to storms, both spatially and temporally. Shallow-water 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 (eg *Sargassum*) is during this period, making them highly exposed. Algal turfs, upright macroalgae and CCA are also likely to be exposed to increased nutrients, resuspension of sediments and increased water flow associated with cyclones (section 7.2.7), but the most important effect is likely to result from increased substrate due to damage to corals (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 or 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 (section 7.2.7). Russ and McCook¹⁶⁴ 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^{52,78} (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 forms,^k but would increase propagation and dispersal for some species²⁰². Importantly, however, the large seaweed Sargassum, while vulnerable to physical removal, has a spectacular capacity to regrow from minute fragments of holdfast tissue¹⁹⁶. 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 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 colonisers 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.¹⁹⁶), others will regrow from storm-generated fragments (*Dictyota*)²⁰², but some species may not

See Rogers^{160,161} for examples of cyclone damage on fleshy macroalgal communities at Heron Island.

recover until spores or gametes settle¹⁶⁸. 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 cyclone¹⁶¹. In contrast, recovery of a macroalgal community in a coral reef off Puerto Rico was considered complete within one year of the disturbance¹².

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 their 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.

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 fresh water 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 mouths⁴⁹. 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 fresh water. 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 reef¹⁶⁴. 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^{152,153}. Impacts also include competitive shifts¹, 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 nitrogenfixing 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^{132,65}. Indirect effects may also result from enhanced nutrients, which inhibit coral growth and reproduction^{204,103,67}, and from more turbid waters, which are less suitable for herbivorous fish recruitment^{2090,210}. 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 abunda nce84,115,106,171,169,180,173. Expression of enhanced growth as increased biomass will depend on the capacity of herbivores to consume the extra production^{164, 98, 53}. 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.¹⁷³, Diaz-Pulido and McCook⁵⁵); temperate examples: (Bergström et al.²²). Sediment deposition (hypoxia) may reduce macroalgal recruitment^{196, 64, 94}. These processes may result in shifts in species composition to shorter-lived 'weedy' species, loss of diversity, and carbon and nutrient retention, due to competitive shifts between species and groups⁶⁷. Also, temperate studies suggest perennial, upright algae are less sensitive than simpler, ephemeral algae, and suggest evidence for shifts in species composition^{120,121, 122,119}, loss of diversity²¹⁴, reduced carbon storage and nutrient retention in community²¹³. 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, for example, to more shade-tolerant but slow-growing species^m. Such changes are likely to lead to reductions in ecological functions, for example, reef cementing and facilitation of coral settlement. There is potential for complex interactions between algal turfs, sediments, herbivores and the abundance of CCA based on information from the Caribbean (eg Steneck¹⁸⁹).

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, and 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.

For example, nutrients: nitrogen-fixing cyanobacteria affected by N and P balances; Cladophora tolerant to freshwater exposure; fresh water carries silicic acid, which may favour diatom blooms^{56,197,6}.

m Correlation studies suggest runoff has impacts on species composition⁶⁶. Experimental studies have demonstrated negative effects of sediments and diuron [a herbicide regularly found in low concentrations in GBR coastal waters¹⁷⁸], on CCA^{26, 189, 82}.

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.

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. This is supported by evidence of low abundance and diversity in areas affected by high runoff⁶⁶.

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 likely, due to mass coral bleaching and other causes of mortality directly or indirectly related to climate change (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^{52,54}. 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 abundance²¹¹.

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 and McCook^{52,54}; pers obs for 2006 bleaching); non-GBR: (Hughes⁹¹, Ostrander et al.¹⁴⁴, McClanahan et al.¹²⁹, Aronson and Precht⁸). Turf algae are rapid colonisers of dead and injured corals^{148,58,52,78}. Turf areas may undergo succession towards more upright macroalgae, because turf algae provide a more suitable substrate for macroalgae than live coral^{52,54}. 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 and inhibit coral recruitment and recovery, reducing overall reef resilience and stabilising phase shifts from dominance by corals to dominance by turf and upright macroalgae^{24,97,25}. 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 feedback 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 recovery¹⁸¹. 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 creationⁿ 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 ecosystem, 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 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 reasons, the

n Beds of upright algae such as Sargassum provide important habitat structure in extensive areas of the shallow inshore GBR (eg Martin-Smith¹²⁸); Halimeda beds form extensive habitats in several inter-reef areas of the GBR⁴⁰.

following treatment is based not only on the information available 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.

7.3.1.1 Turf algae

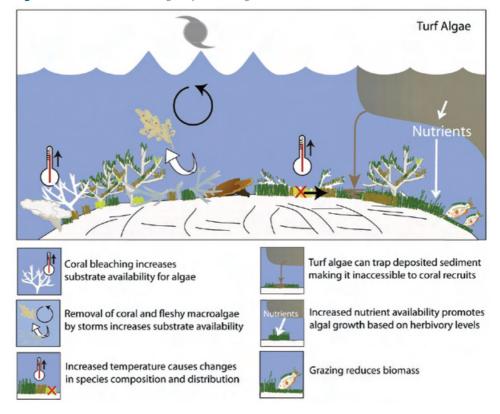
Algal turf assemblages are ubiquitous and particularly diverse in coral reefs. On shallow reefs of the GBR, a single square centimetre may contain more than 20 species of benthic algae⁵². This high species diversity complicates any interpretation of the impacts of climate change on algal turfs, particularly when looking at impacts at large spatial and temporal scales. Even more than for 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 (Tables 7.3 and 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 tolerances³¹ 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 (eg species that produce high levels of UV-absorbing compounds such as mycosporine-like amino acids, provided there is adequate nitrogen availability). 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^{117,191}. For example, more-frequent cyclones may disturb a turf assemblage, initially shifting community structure to stages dominated by early colonisers such as benthic diatoms⁴⁸. However, this early stage is rapidly replaced by filamentous forms characteristic of 'typical' algal turfs (ie they have a strategy of 'recovery' sensu^{187,191}). 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 consequences for the understorey turf assemblage. Rapid and prolonged exposure of the understorey to high light may lead to photoinhibition, causing decreased productivity and growth

Figure 7.2 Global climate change impacts on algal turfs



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 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 mortality⁸⁹ (Hoegh-Guldberg et al. chapter 10), followed by extensive algal colonisation of dead coral substrata, resulting in marked increases in cover and biomass of algal turfs⁵². 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 coral¹⁵⁹) but ultimately a decrease in abundance due to the loss of coral habitat and shelter (due to coral mortality and breakage; see Munday et al. chapter 12). The former impact is a consequence of algal abundance, not a cause: that is, increased herbivore abundance can only moderate, but not negate, 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 corals¹³².

Table 7.3 Generalised predictions of the characteristics of future GBR algal communities affected by climate change, based on vulnerability assessments, and comparison to present-day characteristics*

Present	Future			
Habitat characteristics				
 Dynamic communities, infrequent disturbance leads to decrease of coral cover and subsequent recovery Substrate availability dynamic due to infrequent and local disturbance Some inshore reefs with sustained low coral cover 	 Frequent and chronic disturbance leads to low coral cover, especially in shallow water Higher substrate availability for algal colonisation over longer periods of time and larger spatial scales 			
High herbivore abundance, sufficient to control macroalgal biomass (except for inshore reefs with high standing stocks of macroalgae)	Low herbivory due to low habitat complexity and turbid water, insufficient to control macroalgal biomass			
Characteristics of algal communities and species				
 Patchwork of algal communities, controlled by herbivory, substrate and nutrient availability Generally higher algal biomass inshore 	 Generally higher algal cover, high biomass in areas with low herbivory Southward expansion of distribution ranges 			
Mix of canopy-forming, understorey, turfing and encrusting species inshore; mainly turf and CCA offshore	Short, low-lying species (turf and short upright macroalgae inshore), turf and some CCA offshore			
Mix of calcified and uncalcified species (more uncalcified inshore) Low CCA inshore, high CCA offshore	Uncalcified dominate Low CCA everywhere, weak skeletons			
 Mix of species with perennial, annual and ephemeral life cycles, likely controlled by seasonal triggers Inshore: Fucales growing and reproducing in summer form canopies; understorey of turfs and diverse green and red algae; sporadic spring blooms of brown algae Offshore: turf, CCA, Halimeda, low macroalgal abundance, no distinct seasonality, local ephemeral blooms of greens, cyanobacteria or Chrysocystis 	Species with ephemeral life cycles prevail, dominance of fast-growing weedy species that recover and colonise quickly after disturbance, algal blooms after substrate release			

Present	Future
 Mix of species with different: temperature tolerances (some occur only as winter annuals) UV tolerances and light requirements (variation along inshore/offshore, within-canopy and depth gradients) nutrient requirements (variation along inshore/offshore gradients; species with higher nutrient requirement generally inshore, apart from some <i>Halimeda</i> species) 	Communities dominated by species with: High temperature tolerance or generalists, loss or southward shift of winter annuals 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) High nutrient demand, ephemerals, bloomforming species (variable nutrient availability due to alternation of floods and storms with extended droughts)

^{*} Note: Predictions are very uncertain, and likely to vary considerably with conditions.

Table 7.4 Summary of the responses of macroalgae of the Great Barrier Reef to global climate change*

Climate stressor	Algal turfs	Upright macroalgae	Crustose calcareous algae
Change in ocean circulation	$\uparrow\downarrow$	$\uparrow\downarrow$	$\uparrow\downarrow$
Increased water temperature	$\uparrow \downarrow$	↑↓	$\uparrow\downarrow$
Increased CO ₂ and acidification	$\uparrow\uparrow\downarrow$	↑↑↓ (fleshy) ↓↓ (calcified)	↑↓↓
Light and UV	$\uparrow\downarrow\downarrow$	$\uparrow\downarrow\downarrow$	$\uparrow\downarrow$
Sea level rise	$\uparrow \uparrow \downarrow$	$\uparrow \uparrow \downarrow$	$\uparrow \uparrow \downarrow$
Tropical storms	$\uparrow \uparrow$	$\uparrow\downarrow$	↑_
Terrestrial inputs	↑↓	$\uparrow\downarrow\downarrow$	$\uparrow\downarrow\downarrow$
Increased substrate availability	↑↑↓	↑↑↓	↑↓↓

Upward arrow (↑) represents a beneficial effect. Downward arrow (↓) represents a detrimental effect (eg due to indirect impacts or impacts at the level of the community). Dash (-) represents a neutral effect for algae.

^{*} Note: The table is based on vulnerability assessments and is inherently speculative.

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 communities⁹². Loss of herbivores has been shown to cause self-shading and a decline in mass-specific productivity^{34,35,36}. 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 overabundance 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 are complex^{103,92,98,53}, 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.²¹¹, McCook unpublished data), 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 lack of information severely reduces the ability to make 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 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, increases the vulnerability of coral reefs as a whole.

7.3.1.2 Upright algae (fleshy and calcified)

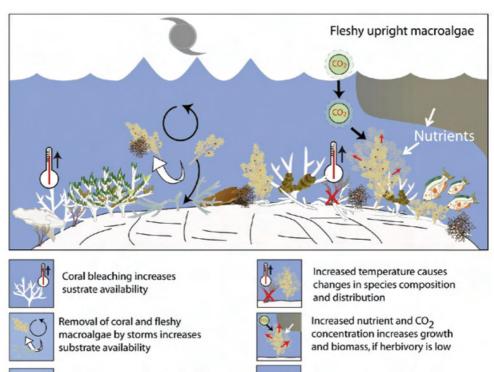
Upright algae in the GBR occur in a wide range of habitats, but predominantly in shallow (to approximately 20 metres depth) or intertidal waters; the notable exception being the deep-water Halimeda beds. The diversity of the algal flora of the deep GBR lagoon floor is currently being explored (Skelton 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 runoff, 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 (Tables 7.3 and 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, Figure 7.3). Other climate-derived stressors, such as storms, increased terrestrial runoff, 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

Figure 7.3 Global climate change impacts on upright macroalgae

Recruitment onto new substrate



Grazing may reduce biomass

and reproduction. These changes may generate shifts in competitive relationships, in turn causing transitions in community composition^{31,79}. Southward immigration of species or ecotypes is likely, especially in the southern GBR. Interactions between climate change stressors are probable but poorly understood. For example, in temperate algal species, UV tolerance was higher at higher temperatures, up to a species-specific threshold⁹⁰.

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^{135,111,119,175}. 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^{24,194,134,111,98,67}. Saturation of algal consumption by herbivores may accentuate such changes²¹¹, stabilising macroalgal dominance. Further feedback effects may include selective overgrazing 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 (McCook et al. chapter 4;^{141, 21}). 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.⁸⁰ for plants and insects, Reusch et al.¹⁵⁵ 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 and 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. chapter 4;135). 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 CO_2 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 (eq *Halimeda* banks^{60,147,126}) and decreased production of calcareous sediments.

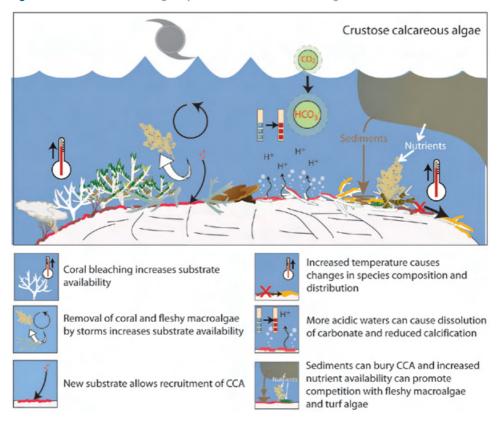
7.3.1.3 Crustose calcareous (calcified) algae

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 with 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-water CCA flora is also quite well adapted to high UV radiation, and it has been recently suggested that calcification may provide extra protection against increasing UV radiation¹⁸. 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 (eg fishes²⁰⁵) 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).

Figure 7.4 Global climate change impacts on crustose calcareous algae



Increasing runoff may have varied effects on CCA, and their vulnerability will depend on their location on the continental shelf. Inshore CCA are highly exposed, due to their proximity to the source, and moderately vulnerable to increased nutrients, compared with 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, greenhouse gas emissions are important to emphasise, especially as they are common to all climate change impacts. Measures that reduce the impacts of increased $\rm CO_2$ 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 minimise terrestrial runoff and other sources of nutrient, sediment or toxicant pollution. These measures will not only benefit corals directly but will also 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. While 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 turf algae and CCA, that are difficult to identify in the field. Without such descriptions, we are unlikely to detect or understand many community shifts.

Given the important roles that 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.

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