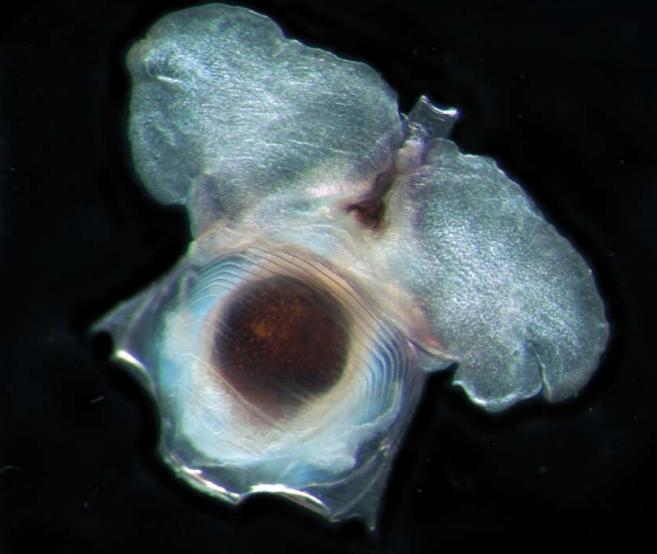
# Part II: Species and species groups

# Chapter 6

Vulnerability of Great Barrier Reef plankton to climate change

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The pteropod Cavolinia longirostris is threatened by acidification of Great Barrier Reef waters. Image courtesy of Russ Hopcroft, University of Alaska, Fairbanks (c) 2007

#### **6.1 Introduction**

Published observations of plankton within the Great Barrier Reef (GBR) date back to Captain Cook's northward passage through the lagoon, when he reported extensive 'blooms' of unknown origin. His ship log entry for August 28 1770 reads:

The sea in many places is here cover'd with a kind of brown scum, such as sailors generally call spawn; upon our first seeing it, it alarm'd us thinking that we were amongst Shoals, but we found the same depth of water where it was as in other places. Neither Mr Banks nor Dr Solander could tell what it was although they had of it to examine.

These were undoubtedly blooms of *Trichodesmium*<sup>8</sup>. However, it was not until the Great Barrier Reef Expedition of 1928 to 1929 that the first and only significant study of plankton in the region was undertaken<sup>74,100,29</sup>. Unfortunately, since then, there has been little emphasis placed on documenting and understanding the biodiversity and processes within plankton communities of the GBR.

Our approach here is to examine potential ways that climate change may alter plankton communities of the GBR in the future, focusing on the physical mechanisms that currently drive plankton productivity and composition. Many of the oceanographic and climatic features of the western Coral Sea and GBR region and the ways in which they may be influenced by climate change are detailed in Steinberg (see chapter 3). Smaller members of the plankton such as the viruses and bacteria are covered by Webster and Hill (see chapter 5). Key reef-associated organisms with planktonic life stages such as crown-of-thorns starfish, corals, fish and jellyfish, as well as the ecosystem-level responses such as their recruitment and patch connectivity, will be covered by Kingsford and Welch (see chapter 18). Since there are no long time series of plankton data for waters of the GBR for assessing climate-related trends and their drivers, and few detailed studies in the laboratory or in the field, this review necessarily draws on relevant knowledge from other ecosystems, tropical where possible, and others when required.

#### 6.1.1 Plankton

Plankton is a generic term describing organisms that have limited locomotive ability relative to the water bodies in which they live. A variety of organisms live in the plankton, ranging in size from viruses (femtoplankton) to large jellyfish (megazooplankton). Table 6.1 shows size classes of plankton in aquatic ecosystems, with some of their important members in GBR waters mentioned in the text.

Tropical plankton communities are highly diverse, containing organisms from almost all kingdoms, phyla and families. These organisms use their environment, its resources, and each other, in a wide variety of ways. The most common way to classify planktonic organisms is on the basis of size, which affects sinking, light utilisation, mobility and trophic status. Organisms with particular functional roles in the ecosystem (eg grazers and nitrogen-fixers) occur in a number of size classes, though in general primary producers tend to be smaller than grazers, which tend to be smaller than predators.

**Table 6.1** Size classes of plankton in aquatic ecosystems<sup>67</sup>. Sizes are reported in  $\mu$ m (micrometres) and mm (millimetres)

Size class	Size range	Representative organisms	Functional groupings
Femtoplankton	Less than 0.2 µm	Viruses	Parasites
Picoplankton	0.2 to 2 μm	Archaea, bacteria, cyanobacteria (eg <i>Synechococcus</i> ), Prochlorophytes (eg <i>Prochlorococcus</i> )	Primary producers, saprophytic heterotrophs, nitrogen-fixers
Nanoplankton	2 to 20 μm	Cyanobacteria, diatoms, flagellates (autotrophic, heterotrophic)	Primary producers, grazers, predators, nitrogen-fixers
Microplankton	20 to 200 μm	Ciliates (including foraminifera), coccolithophores, diatoms, dinoflagellates, copepod juveniles	Primary producers, grazers, predators
Mesoplankton	0.2 to 20 mm	Amphipods, appendicularians, chaetognaths, copepods, cyanobacteria (eg <i>Trichodesmium</i> colonies), thaliaceans (doliolids and salps)	Primary producers, grazers, predators, nitrogen-fixers
Macroplankton	20 to 200 mm	Euphausiids, heteropods, jellyfish, larval fish, mysids, pteropods (eg <i>Cavolinia longirostris</i> ), solitary salps	Grazers, predators
Megaplankton	Greater than 200 mm	Jellyfish, colonial salps	Grazers, predators, primary producers

This chapter focuses on the best studied plankton, primarily the phytoplankton and mesozooplankton. Key groups within the phytoplankton that we discuss are the cyanobacteria, dinoflagellates and diatoms. Within the mesozooplankton, we concentrate on the copepods, because this has been the most studied group and they are numerically the most abundant. Copepods constitute 63 percent of mesozooplankton abundance on tropical continental shelves<sup>72</sup>, and somewhat more, about 80 percent, in the waters of the GBR<sup>70</sup>.

## 6.1.1.1 Biodiversity

Phytoplankton communities in the GBR ecosystem are diverse and cosmopolitan in character, comprising a mixture of oceanic forms with global pan-tropical distributions, and assemblages of diatoms and dinoflagellates<sup>109</sup> found in coastal and upwelling regions worldwide. There are no known phytoplankton species endemic to the GBR. A three-year survey of the microphytoplankton in the 1970s produced a species list of 220 diatoms and 176 dinoflagellates<sup>93</sup>. The colonial nitrogen-fixing cyanobacterium *Trichodesmium* episodically accounted for a significant proportion of the microphytoplankton in lagoon samples, with abundances inversely correlated with those of diatoms<sup>92</sup>.

Recent studies using size fractionation of phytoplankton communities show that phytoplankton biomass and productivity are dominated by picoplankton-sized organisms, such as the phototrophic cyanobacteria *Synechococcus* (approximately 1 to 2 micrometres) and *Prochlorococcus* (approximately 0.6 micrometres<sup>36,19,20,21</sup>. Both of these genera are present as genetically identifiable, physiologically adapted strains<sup>82,45</sup> rather than as morphologically identifiable species.

Zooplankton communities in GBR waters are similar to those of other tropical or subtropical coasts, and may include endemic species in bays and estuaries<sup>78,79</sup>. Copepods are the most speciose group of zooplankton in the GBR (Table 6.2). The most comprehensive species list for the zooplankton of the GBR is from a study nearly 80 years ago, where Farran<sup>29</sup> identified 193 species of pelagic copepods. However, such early plankton studies used nets with mesh sizes greater than 200 micrometres, as widely recommended for northern temperate plankton, but which miss the numerically dominant and smaller (less than 200 micrometres) copepod species in GBR waters (eg *Parvocalanus crassirostris*, *Oithona attenuata* and *O. nana*). Based on collections with nets of finer mesh, McKinnon et al.<sup>81</sup> added a further 11 species of small copepods.

**Table 6.2** Meso- and macrozooplankton biodiversity recorded by the Great Barrier Reef Expedition of 1928 to 1929

Taxon	Number of species
Siphonophora <sup>110</sup>	32
Doliolida <sup>100</sup>	3
Salpida <sup>100</sup>	6
Appendicularia <sup>100</sup>	8
Pteropoda (Thecosomata and Gymnosomata) <sup>100</sup>	15
Heteropoda <sup>100</sup>	3
Mysidiacea <sup>108</sup>	23
Euphausiacea <sup>108</sup>	14
Copepoda <sup>29</sup>	193
Chaetognatha <sup>17</sup>	12

Reef-associated zooplankton assemblages comprise a mixture of open-water and demersal or emergent species, such as amphipods, cumaceans, decapods, mysids, ostracods and polychaete worms<sup>107,111</sup>. Larger zooplankton, such as the pteropods *Creseis* spp. and *Cavolinia longirostris*, are also present, and are particularly abundant in December and January respectively<sup>100</sup>. Salps (Thaliacea) can occur sporadically in great abundance<sup>100</sup>.

#### 6.1.1.2 Distribution across the GBR

Phytoplankton studies spanning the width of the GBR ecosystem have demonstrated a strong onshore–offshore gradient. Communities in nearshore waters are morre frequently dominated by diatoms<sup>93</sup> because of more consistent nutrient inputs and greater nutrient availability from adjacent terrestrial sources and shallow sediments. Diatom-dominated assemblages within GBR waters are therefore

diagnostic of enhanced or persistent nutrient inputs into a region. Diatoms achieve dominance after disturbances, for brief periods at least, because they have faster intrinsic growth rates<sup>32</sup> than picoplanktonic cyanobacteria<sup>34</sup>. The difference in response times between the flagellate grazers of picoplankton (days) and the metazoan grazers of microplankton diatoms (weeks) also contributes to the persistence of diatom blooms. By contrast, communities in oligotrophic (low nutrient) outer-shelf and oceanic waters are dominated by picoplankton-sized unicellular cyanobacteria (*Synechococcus*) and prochlorophytes (*Prochlorococcus*), together with nitrogen-fixing cyanobacterial rafts of *Trichodesmium* and characteristic assemblages of open-ocean dinoflagellates<sup>92, 93, 20, 21</sup>.

Mesozooplankton communities also show cross-shelf patterns, with distinct inshore and offshore assemblages<sup>103,115,80</sup>. Inshore and estuarine zooplankton communities, where temperatures can seasonally exceed 30°C, are dominated by small copepods<sup>81</sup>. Most (62%) of the mesozooplankton biomass is comprised of organisms less than 350 micrometres in size, and regional differences in zooplankton community composition are very small, at least within the inshore community<sup>81</sup>.

These marked cross-shelf changes in plankton composition are a result of gradients in the physicochemical properties of water. These gradients are determined by the dynamic balance between terrestrial inputs of nutrients, water movements alongshore, and oceanic exchanges. The cross-shelf extent of terrestrial influence is governed by bathymetry, the limited cross-shelf extension of river plumes, and the magnitude of a northward-flowing, wind-driven coastal current. As a result, nearshore waters are insulated to some degree from mixing with inter-reef waters on the outer shelf<sup>64,73</sup>. A variety of indicators show that the direct effects of runoff from the land are restricted to the nearshore zone 10 to 20 km in width<sup>41,68,104</sup>. Conversely, at the seaward end of the gradient, upwelled intrusions of the Coral Sea thermocline episodically inject nutrient-rich water onto the outer shelf<sup>5,38</sup>. On occasion, large intrusions of Coral Sea water can extend almost the full width of the GBR lagoon<sup>38</sup>.

#### 6.1.2 The role of plankton in the GBR

Phytoplankton account for approximately half the global primary production, and consequently play a major role in cycling of atmospheric carbon dioxide (CO<sub>2</sub>). They are also the major primary producers in the GBR ecosystem<sup>37</sup>. Approximately 70 percent of the estimated 2.2 x 10<sup>5</sup> tonnes of carbon (C) fixed daily by primary producers in the GBR shelf ecosystem originates from phytoplankton production (58 x10<sup>7</sup> tonnes C per year) and, of this, two-thirds is fixed by picoplankton<sup>38</sup>.

Micro- and mesozooplankton are the basis of food webs supporting oceanic and many coastal fisheries. Plankton and suspended non-living organic particles directly support a wide variety of suspension-feeding organisms and planktivorous fish on coral reefs. In addition, most benthic macroalgae, invertebrates and fish have a planktonic life stage that is dispersed by currents.

Plankton inhabit and dominate (both numerically and by mass) the largest habitat within the GBR, the pelagic ecosystem. Within the GBR, which has an area-weighted average water depth of 36 metres, this ecosystem has a total water volume of over 7200 km<sup>3</sup>. By contrast, coral reefs comprise about 6 percent of the area within the GBR Marine Park<sup>69</sup>.

#### 6.1.2.1 Production and energy flow

GBR waters are characterised by rapid rates of phytoplankton growth, pelagic grazing and remineralisation<sup>40</sup>. *In situ* growth rates for the dominant phytoplankton species range from approximately one to several doublings per day. Fast growth results in a high demand for nutrients and, given the low ambient concentrations of dissolved nitrogen and phosphorus, rapid cycling occurs. Ammonium cycling times range from hours to a few days, and phosphate and nitrate cycling times are typically less than a few days<sup>40</sup>. The cyanobacterium *Trichodesmium* plays an important role in the ecosystem by fixing significant quantities of atmospheric nitrogen. One estimate of new nitrogen fixation suggests that the contribution of *Trichodesmium* is at least of the same order as that entering via riverine discharge<sup>12</sup>.

Despite the relatively high rate of primary production, mesozooplankton in GBR waters appear to be food limited<sup>70,77,80,81</sup>. Grazing experiments indicate that essentially all picoplankton biomass production and 62 percent of the nanoplankton production are consumed daily by microzooplankton. Approximately 30 percent of the production by nano- and microphytoplankton is grazed by mesozooplankton<sup>97</sup>. The balance of pelagic production either is respired within the water column, or settles to the ocean floor. Furnas et al.<sup>39</sup> estimated that 25 to 100 percent of particulates in the water column fall to the ocean floor each day, and must therefore be an important driver of benthic ecosystems. Assuming a primary production rate of 0.67 grams C per metre squared per day<sup>40</sup> and copepod production of 8.5 milligrams C per metre squared per day<sup>81</sup>, the transfer efficiency between these trophic levels is only 1 percent, supporting the hypothesis that microbial food chains (ie the microbial loop) dominate waters of the GBR.

Some indication of the importance of mesozooplankton in the GBR can be gained by calculating the flux of organic matter through this compartment from both *in situ* production and import of biomass. Based on a rate of copepod production in shallow inshore regions of the GBR of approximately 8.5 milligrams C per metre squared per day<sup>81</sup>, we calculate that *in situ* copepod production in the entire GBR is greater than 630,000 tonnes C per year. Though copepods are the most important group numerically, other types of zooplankton that have received less attention are likely to add significantly to pelagic production. For example, appendicularians grow faster than any other multicellular organisms<sup>57</sup> and can be almost as abundant as copepods in GBR waters, although there are no estimates of their production in the region.

There is also likely to be a significant import of oceanic plankton into the GBR from the Coral Sea. Brinkman et al. 15 estimated oceanic inflow into the GBR of 0.58 Sv (1 Sv = 1,000,000 cubic metres per second). Assuming an average biomass of 100 milligrams per cubic metre (wet weight of zooplankton greater than 200 micrometres) in the Coral Sea $^{70}$ , this would equate to an annual import of 1.83 million tonnes wet weight, equivalent to 110,000 tonnes C.

#### 6.1.2.2 Pelagic-benthic linkages

Plankton are an important food resource for many components of the GBR ecosystem. Soft corals have been shown to graze picoplankton carried onto coral reefs<sup>28</sup>, and scleractinian corals are effective zooplankton feeders<sup>105</sup>. Planktivores make up the largest trophic guild of fishes living at shallow depths

on the faces of GBR coral reefs<sup>114</sup>, both by weight and by number. Reef-associated planktivorous fish are a diverse group that differ in their degree of dependence on plankton or suspended particulate matter for food, and partition their feeding activity into different reef zones<sup>51</sup>. These fishes remove most of the mesozooplankton from the water prior to it impinging on the reef face. In open waters, megafauna such as manta rays, whale sharks and some species of turtles are also dependent on plankton for food.

Though the contribution of particulate food to reef ecosystems is poorly quantified at larger scales, there have been some attempts to quantify the contribution of plankton and suspended particulate material to individual reefs. Fabricius and Dommisse<sup>27</sup> measured depletion rates of suspended particulate material in tidal channels at the Palm Islands and estimated a carbon removal rate by soft corals of approximately 900 grams C per metre squared per year, similar to estimates made in the Red Sea by Yahel et al.<sup>116</sup>. These studies suggest that soft corals remove an order of magnitude more organic matter from the overlying water than hard coral-dominated reef flats. In turbid coastal waters, some hard corals are able to compensate for low light levels by increasing heterotrophic feeding activity<sup>6</sup>. Holzman et al.<sup>56</sup> showed that actively swimming zooplankton avoid the benthic boundary layer (approximately 1.5 metres thick) of Red Sea coral reefs, below which there is high plankton predation by fishes<sup>84</sup>. Hamner et al.<sup>51</sup> estimated that the flux of zooplankton to 'the wall of mouths' on the face of Davies Reef (central GBR) was 0.5 kilograms per metre per day. At specific locations, the interaction of strong currents and bottom topography may act to greatly amplify the contribution of zooplankton to coral reefs via trophic focusing<sup>43</sup>.

An important component of the pelagic environment that is receiving greater recognition as a significant food resource for coral reefs and other habitats is marine snow. Marine snow is the assemblage of largely organic particles or aggregates that are visible to the naked eye (generally greater than 0.5 mm). Marine snow is formed by aggregation of organic material from a variety of sources including polysaccharides from diatoms<sup>65</sup> and discarded appendicular houses<sup>1</sup>. Aggregates are a rich substrate for the growth of micro-organisms, which in turn are concentrated and available to larger-particle consumers such as mesozooplankton, macroplankton and fish. These large particles or aggregates facilitate the settling of organic material onto coral reefs. The extent and importance of this trophic link between pelagic production and the reefs of the GBR ecosystem are yet to be adequately quantified.

#### 6.1.3 Critical factors regulating plankton communities

The abundance and growth of planktonic organisms are directly influenced by several climate stressors that will respond to climate change. These include water temperature, ocean chemistry, light, ultraviolet radiation (UVR) and nutrient enrichment. We believe, however, that the direct impact of these climate stressors on plankton species and communities will be overshadowed by the indirect influence of climate change on oceanographic processes that affect the mixing and advection of water masses. We have a limited understanding of how climate change will affect light, nutrient enrichment, mixing and advection of water masses at local and regional scales. Therefore, in assessing these factors, a range of scenarios is considered.

#### 6.1.3.1 Temperature

All plankton are poikilothermic and thus are directly influenced by water temperature<sup>26</sup>. More broadly, studies in other regions of the world have shown that plankton growth and development<sup>60,46,66</sup>, abundance<sup>95</sup>, distribution<sup>9</sup>, and timing of blooms<sup>24</sup> are all influenced by temperature. However, these studies were conducted in temperate regions with marked seasonal temperature changes and thus should be applied with some caution to tropical regions.

## 6.1.3.2 Ocean chemistry

Over the last 200 years, oceans have absorbed 50 percent of the anthropogenic CO<sub>2</sub> injected into the atmosphere, causing chemical changes that increase the proportion of dissolved CO<sub>2</sub>, lower pH (approximately 0.1 pH units) and decrease the saturation state of carbonate minerals (calcite, aragonite) in the water<sup>99</sup>. Effects of ocean acidification and increased carbonate dissolution will be greatest for plankton species with calcified (calcium carbonate) shells, plates or scales. These organisms include coccolithophorids, foraminifera, molluscs, echinoderms, and some crustaceans. For these organisms, sea water has to be saturated with carbonate to ensure that, once formed, their calcium carbonate structures do not redissolve. Acidification reduces the carbonate saturation of sea water, making calcification more difficult and dissolving structures already formed.

All phytoplankton obtain dissolved  $CO_2$  by passive diffusion, but this can lead to carbon limitation at times of rapid demand. To increase the efficiency of  $CO_2$  utilisation, many types of phytoplankton have evolved  $CO_2$ -concentrating mechanisms to actively transport and accumulate inorganic carbon<sup>44,10</sup>. An increase in dissolved  $CO_2$  may well increase the proportion of species that are only capable of passive diffusion of  $CO_2$ .

Increases in dissolved  $\mathrm{CO}_2$  can also change the nutritional composition of phytoplankton, such as decreasing the carbon to nitrogen ratio and increasing carbon to phosphorus and nitrogen to phosphorus ratios<sup>11</sup>. Additionally, the proportion of unsaturated fatty acids can decrease, as well as the patterns of macromolecular synthesis. This may have a flow-on effect on growth and reproduction of zooplankton, and increase the production of marine snow, hence affecting nutrient and carbon cycling.

#### 6.1.3.3 Light and ultraviolet radiation

Many copepod species are sensitive to changing ambient light levels. Light is the most important cue for zooplankton diel vertical migration and emergence, and has been implicated as a cue in the copepod swarming behaviour that occurs on GBR coral reefs<sup>50</sup>. For example, *Oithona oculata* forms small swarms around coral heads, whereas larger *Acartia australis* swarms form around coral heads and blanket the bottom of reef lagoons<sup>76</sup>. In late summer, *Centropages orsinii* can also form swarms in the deeper parts of reef lagoons. Although the mechanism behind the formation of zooplankton swarms is not well understood, we do know that light is an important determinant of copepod aggregations<sup>18,4</sup>.

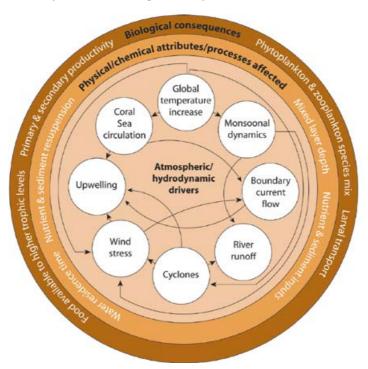
Diel migration patterns in GBR holoplankton communities appear to be weak, though studies to date on vertical migration of GBR zooplankton are equivocal<sup>30,81</sup>. In contrast, emergent zooplankton are a striking feature of the night time plankton within coral reefs<sup>102,2,107</sup>. Even small differences in light, such as occur on moonlit versus non-moonlit nights, can cause changes in the composition of emergent zooplankton assemblages<sup>3</sup>.

The highly energetic ultraviolet radiation (UVR) component of sunlight penetrates the surface layers of the ocean and may have detrimental effects on plankton. In the last quarter of the 20th century, there has been an increase in UVR reaching the surface of the earth due to thinning of the protective ozone layer by anthropogenic ozone-depleting substances such as chlorofluorocarbons, halons and hydrochlorofluorocarbons<sup>22</sup>. Since the implementation of the Montreal Protocol in September 1987 to reduce emissions of such substances, stratospheric ozone levels have stabilised. Most climate models show that the ozone layer will recover and thicken throughout the 21st century<sup>22</sup>, and presumably UVR will also decline<sup>25</sup>, although there remains uncertainty in the timing of the ozone thickening because of the complexity of atmospheric chemical processes<sup>62</sup>.

#### 6.1.3.4 Nutrient enrichment

Large-scale oceanographic and atmospheric drivers that influence nutrient input and mixing processes include: (i) circulation patterns, (ii) rainfall and the coupled runoff of sediment and nutrients, (iii) frequency and intensity of shelf-break intrusions and topographic upwelling, (iv) frequency and intensity of cyclonic disturbance, (v) wind stress and its effects on sediment resuspension, vertical mixing and coastal current dynamics. These atmospheric and hydrodynamic processes interact in complex ways (Figure 6.1), influencing the physical and chemical attributes of the water column that regulate food web structure, productivity, and dispersal of plankton communities.

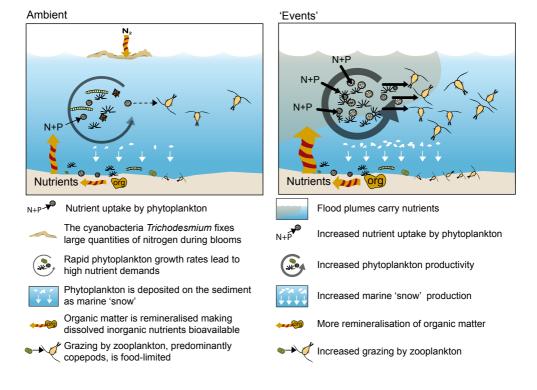
**Figure 6.1** Complex interrelationships between atmospheric and hydrodynamic drivers, effects on physical and chemical processes, and biological consequences



Global warming affects several atmospheric and oceanographic processes including the Coral Sea circulation, monsoonal dynamics, wind stress and cyclones, all of which change the physico-chemical environment of the GBR with impacts on food web structure and function.

Phytoplankton productivity, biomass and community composition in the GBR lagoon are most strongly influenced by event-driven processes affecting the input or availability of nutrients (Figure 6.2). These processes include terrestrial freshwater runoff<sup>33</sup>, rainfall<sup>38</sup>, sediment resuspension following cyclones<sup>74,112</sup>, upwelling from the Coral Sea thermocline<sup>5,38</sup> and lateral exchanges of oligotrophic surface water from the Coral Sea<sup>15</sup>. Nutrient input events occur episodically throughout the year, but they occur most often during the summer wet season. Phytoplankton communities developing after such events are characterised by assemblages of fast-growing diatoms<sup>92,31,32,35</sup>. For example, a large diatom-dominated phytoplankton bloom throughout the central GBR followed Cyclone Winifred in 1986<sup>31</sup>. Liston<sup>70</sup> observed increases in zooplankton biomass, particularly of herbivorous copepods, after Cyclone Charlie in 1989, and McKinnon and Thorrold<sup>80</sup> reported significant increases in copepod biomass and production rates in the Burdekin River flood plume. Climate change factors that influence the frequency, intensity or duration of the wet season and its associated nutrient inputs will therefore have a significant effect on the composition and productivity of phytoplankton communities.

**Figure 6.2** Effects of a nutrient enrichment event, using a flood plume example, on plankton abundance, composition and production of marine snow



In terms of large-scale oceanographic processes, climate-driven changes to the intensity of the South Equatorial Current, which flows westward across the Coral Sea, will directly affect the strength and volume of the southward-flowing East Australian Current (EAC) and the northward-flowing Hiri Current. Changes in the intensity of the EAC, in particular, directly affect the strength of the southward-flowing residual current through the southern half of the GBR. This in turn influences inter-reef mixing and dispersal and water residence times within the lagoon. The strength of the EAC influences the intensity and frequency of shelf-break upwelling along the southern half of the GBR through geostrophic adjustments in the thermocline depth along the continental slope.

The frequency and size of upwelling events in the central GBR are dependent upon interactions between regional wind stress (strong south-easterly, calm or northerly) and the depth of the Coral Sea thermocline which is in part, determined by the strength of the EAC. Seasonal wind stress patterns are influenced by the dynamics of the northern Australian monsoon and interannual ENSO dynamics. Upwelling is likely to be more frequent when there is a stronger monsoon (more prevalent northerly winds) or during La Niña periods and weaker during stronger SE trade winds. Furnas and Mitchell<sup>35</sup> describe midshelf blooms of cells greater than 10 micrometers in size, mainly diatoms, in water advected sufficiently inshore to have a residence time of about one week. These pulses of production by large phytoplankton cells result in more efficient energy transfer to higher trophic levels and increased secondary production. Wind stress from the south-easterly trade winds is also the primary driver for the northward-flowing coastal current along the entire GBR. This current and the shear zone between it and the southward-flowing residual current are partly responsible for the retention of terrestrial materials near the coastline. Finally, strong winds over the GBR also cause resuspension of bottom sediments in depths less than 20 metres. Resuspension is a source of nutrients to coastal plankton, but also increases turbidity and results in a decrease in photosynthetic depth.

Changes in the intensity and duration of the summer monsoon will influence the quantity of freshwater inputs to the GBR, either directly as rainfall or indirectly as terrestrial runoff. The volume of terrestrial runoff and its source within the GBR catchment, in turn, have a direct effect upon the quantity of sediment and nutrients entering the GBR. During periods of heavy runoff, the inshore plankton community can extend out as far as the midshelf reefs<sup>103</sup>. McKinnon and Thorrold<sup>80</sup> were able to detect an increase in secondary production (as copepod egg production) subsequent to a flood event, and an elevation in zooplankton biomass that lasted two months after the event.

Cyclones produce large regional (10³ to 10⁴ km²) disturbances with enhanced nutrient inputs, mineralisation and plankton production. Liston<sup>70</sup> found that both nutrients and chlorophyll concentrations increased in Bowling Green Bay subsequent to a cyclone. However, the strongest signal was observed in zooplankton abundance and biomass, which showed a fourfold increase two weeks later. Such event-driven pulses in production may have significant implications for food availability for planktivorous fish, larval fish and invertebrate larvae, especially if these events coincide with spawning events.

Our understanding of how plankton communities of the GBR will respond to this complex array of atmospheric and hydrodynamic drivers can be summarised in Figure 6.3. Other factors, including acidification, UVR and cloudiness are considered in section 6.2. We envisage the plankton community as a continuum of states, ranging from those dominated by picoplankton, *Trichodesmium* and gelatinous zooplankton (pelagic tunicates), to those dominated by diatoms and crustacean zooplankton (copepods). Even this is simplistic, as many states may exist at the same time in different

parts of the GBR. Local or regional nutrient enrichment is the key determinant of the state of the plankton community; elevated nutrient conditions lead to short and efficient food webs dominated by copepods that are high-quality food resources for planktivorous fish, corals and ultimately piscivorous fish, seabirds and mammals, whereas low nutrient conditions lead to a long and inefficient food web that supports a far lower biomass of higher trophic levels.

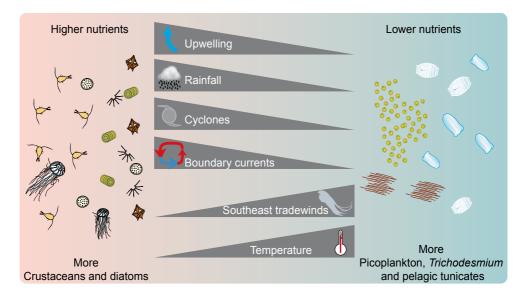


Figure 6.3 How physical drivers and stressors regulate plankton community interactions and dynamics<sup>a</sup>

## **6.2 Vulnerability**

Planktonic organisms all have short life cycles: hours to days for phytoplankton, seven to ten days for copepods, and weeks to months for macrozooplankton<sup>52</sup>. In the warm and typically sunny waters of the GBR, the entire phytoplankton community essentially turns over on a daily basis. Dominant copepod species have generation times in the order of a week or two. This means that plankton organisms and communities respond quickly to changes in their physical environment and, as such, are sentinels of environmental change that respond more rapidly than longer-lived animals such as fish, birds and mammals. It also means that the impact of climate change on event-scale processes will be particularly important.

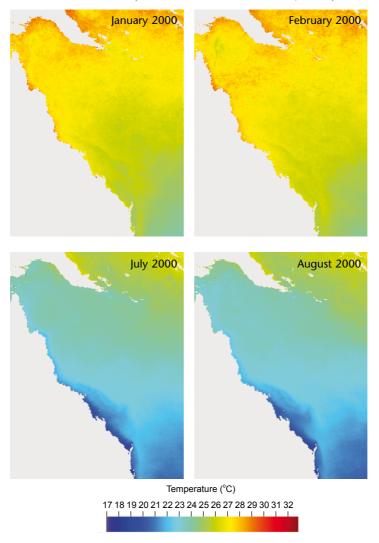
a Acidification, UVR and cloudiness are considered in section 6.2.

## 6.2.1 Changes in water temperature

## 6.2.1.1 Exposure – water temperature

Exposure of plankton to increased water temperatures is unavoidable. The GBR currently exhibits considerable variation in temperature (Figure 6.4), both seasonally and over its 15 degrees of latitudinal extent from Torres Strait (9° S) to Lady Elliott Island (24° S). Although the water column is generally well mixed, vertical temperature differences can exceed 5°C during intrusion events from the Coral Sea<sup>38</sup>. Consequently, direct effects of small temperature changes on plankton will likely be minimal given the temperature range already encountered within the waters of the GBR.

Figure 6.4 Variation in sea surface temperature on the Great Barrier Reef (Courtesy Mike Mahoney, AIMS)



#### 6.2.1.2 Sensitivity – water temperature

Culture studies<sup>106</sup> indicate that species with tropical and subtropical distributions have growth temperature ranges that encompass the temperature range in the GBR at the present and the range likely in the near future (ie warming by 1 to 2°C), but with optima less than 30°C. In most cases, however, these experiments have been carried out with temperate strains, so potential regional adaptations to warmer temperatures are not apparent. Optimal growth for the dominant picophytoplankton species *Synechococcus* and *Prochlorococcus* in the GBR was found to be between 20 and 30°C<sup>34</sup>. Studies of *Synechococcus* and *Prochlorococcus* in the Atlantic Ocean have shown that *Synechococcus* growth peaked at 28°C, while *Prochlorococcus* peaked at 24°C<sup>83</sup>.

Growth rates of copepods are faster at warmer temperatures<sup>60</sup>, although this is not always achieved in the GBR because of food limitation. The Q<sub>10</sub> of copepods is approximately 3 (ie a 10°C change in temperature results in a threefold change in physiological rates such as growth). Small inshore copepods such as *Parvocalanus crassirostris*, *Oithona attenuata* and *O. nana* occur in estuaries where maximum summer water temperatures exceed 30°C<sup>79</sup>. *P. crassirostris* thrives at these temperatures, with growth rates to 1.2 per day at 29°C in the Caribbean<sup>57</sup>. Available evidence indicates that copepod growth and egg-production rates in waters of the GBR exhibit little seasonal variation and are primarily regulated by food availability rather than temperature<sup>70,80,77,81</sup>. However, generation times of the common coastal copepod *Acrocalanus gibber* decrease by 25 percent with a 5°C rise in temperature<sup>77</sup>. In addition, copepod body length typically declines with increasing temperature, though differences in condition (dependent upon food supply) often obscure a causative relationship between weight and temperature<sup>77</sup>.

#### 6.2.1.3 Impacts – water temperature

As individual plankton species have their own thermal optimum and limits for growth, warming will have differential effects on the growth of individual species. Changes in temperature are more likely to directly affect metabolic processes (growth, respiration) rather than overall community biomass, particularly if plankton communities are resource limited (nutrients, food), and overall productivity may not change greatly. There may also be an enhancement of stratification due to the increase in temperature in the GBR, which will favour picoplankton, *Trichodesmium* and pelagic tunicates. Change in phytoplankton community composition and productivity will have flow-on effects to the productivity of zooplankton grazers.

#### 6.2.1.4 Adaptive capacity – water temperature

Most tropical plankton species have relatively broad temperature ranges relative to daily and annual temperature fluctuations in the GBR. While the warmest temperatures encountered in the GBR lagoon and adjacent estuarine waters are above the published optimal growth temperatures for many species, these species can still survive and grow. Our understanding of temperature responses based on laboratory studies is constrained by the fact that individual species often have substantial strain variation. Therefore, there may be undescribed strains with higher thermal optima, improving the ability of individual species to adapt to change<sup>42,13,101</sup>. It is unknown whether individual species in local plankton populations have higher thermal optima than those used in experimental studies, but a changing environment would select for individuals and species better able to grow and survive under changing conditions.

There is some evidence however, that not all species are able to genetically adapt quickly enough to tolerate the projected oceanic warming rate. In such cases, species with preferences for warm water have expanded their ranges towards the poles, and species with cooler-water preferences have retracted to higher latitudes<sup>9</sup>. Despite many plankton species having a fairly catholic distribution throughout the GBR, it is likely that there will be some southward movement of tropical species, with a concomitant range contraction of subtropical species at the northern extent of their range in the southern GBR. For example, the highly venomous box jellyfish (*Chironex fleckeri*) is at the southern limit of its range in North Queensland and may expand its range further south as waters warm.

Warming may also result in earlier periods of peak abundance. This has been observed for many terrestrial groups including the earlier flowering of daffodils and the earlier arrival of migratory birds<sup>90,98</sup>. No work has been done on the timing of maximum plankton abundance in the GBR, but observations from temperate waters may provide some clues despite the much greater seasonality at such high latitudes. In the North Sea, temperature thresholds cue spawning and influence the development of larval stages<sup>24,46,66</sup>. Larvae of echinoderms, lamellibranchs, fish, and decapods are temporary members of the plankton (meroplankton) and their timing is sensitive to temperature<sup>24,46</sup>. Data from the North Atlantic have shown that the timing of peak abundance for these larvae is more than a month earlier now than 50 years ago<sup>24</sup>. If echinoderm larvae in the GBR respond similarly, peak larval abundances of crown-of-thorns starfish could appear earlier in the year. Warming could also lead to the earlier production of meroplanktonic larvae such as medusa stages of box jellyfish (*Chironex fleckeri*).

#### 6.2.1.5 Vulnerability and thresholds – water temperature

Plankton are vulnerable to ocean warming, as they inhabit the GBR waters throughout their life, they are poikilothermic and have short generation times. Worldwide no plankton species are known to have become extinct, but the possibility of extinctions cannot be discounted. Individual plankton species can persist as cryptic populations (below the threshold of detection by sampling methods). The greatest effect of temperature on plankton in the GBR is likely to be on species composition and metabolic fluxes.

## 6.2.2 Changes in ocean chemistry

## 6.2.2.1 Exposure – ocean acidification and increased dissolved CO<sub>2</sub>

Plankton cannot escape exposure to changes in ocean chemistry, such as increased dissolved  ${\rm CO}_2$  and ocean acidification.

#### 6.2.2.2 Sensitivity – ocean acidification

Plankton groups with calcium carbonate structures will be sensitive to ocean acidification, though it is possible that physiological stress as a result of acidification may occur in a broader range of organisms. Calcified plankton differ in their susceptibility to acidification depending on whether the crystalline form of their calcium carbonate is calcite or aragonite. Calcite has a higher stability (is less soluble) than aragonite, making it less susceptible to dissolution. Coccolithophores (calcifying phytoplankton), foraminifera (protist plankton), and non-pteropod molluscs produce calcite, the more stable form of

calcium carbonate. Coccolithophorids show reduced calcite production and an increased proportion of malformed liths at increased CO<sub>2</sub> concentrations<sup>96</sup>. Pteropods are the most sensitive planktonic group because their shell is composed of aragonite, which will be subject to increased dissolution under more acidic conditions<sup>88</sup>.

#### 6.2.2.3 Impacts - ocean acidification and increased dissolved CO<sub>2</sub>

The direct effect of ocean acidification on calcifying zooplankton will be to partially dissolve their shells, increasing shell maintenance costs and reducing growth. Foraminifera contribute a significant proportion of the sediments in sandy regions of the GBR. Acidification will deform the calcite scales of coccolithophorids, but this group of phytoplankton occurs only sporadically on the GBR and is found more frequently in the Coral Sea (Furnas, unpublished data), although the coccolithophorid community there is diverse<sup>49</sup>.

Pteropods and heteropods are relatively uncommon members of GBR zooplankton assemblages, though the pteropod *Cavolinia longirostris* can form aggregations in summer<sup>100</sup>. *C. longirostris* is likely to be the plankton organism most sensitive to climate-induced change in pH.

Declining pH may also alter the growth rates of photosynthetic organisms. In particular, changes in pH will affect nutrient uptake kinetics, altering rates of growth and photosynthesis. Changes may also occur in phytoplankton cell composition, which could affect their nutritional value for higher trophic levels.

Phytoplankton species lacking carbon-concentrating mechanisms may well increase in dominance under higher concentrations of dissolved  $CO_2$ . However, the proportion of these species in tropical waters is unknown, but some coccolithophores are able to increase photosynthetic rate in response to elevated  $CO_2$ .

#### 6.2.2.4 Adaptive capacity – ocean acidification

Within the next several centuries, first the aragonite and then the calcite saturation state of GBR waters may decline below levels needed for shell formation and maintenance in calcifying plankton organisms. Orr et al. 88 suggested that pteropods would not be able to adapt quickly enough to live in undersaturated conditions. Undersaturation of aragonite and calcite in sea water is likely to be more acute at higher latitudes and then move toward the equator. Therefore, there is unlikely to be a refuge for these species further south as temperatures warm.

## 6.2.2.5 Vulnerability and thresholds - ocean acidification

Pteropods, with their aragonite shells, are highly vulnerable, while coccolithophorids, foraminifera and some crustaceans, with their calcite shells and liths, are less vulnerable. Pteropods are likely to decline and may eventually disappear in response to ocean acidification on the GBR. No quantitative work on thresholds has been conducted, but experiments on the pteropod *Clio pyrimidata* at 788 parts per million CO<sub>2</sub> for 48 hours<sup>88</sup> and the coccolithophores *Emiliania huxleyi* and *Gephyrocapsa oceanica* at 780 to 850 parts per million<sup>96</sup> led to shell and lith deterioration respectively. These experiments were both conducted at CO<sub>2</sub> levels approximating those that are likely to exist around the year 2100 under a business-as-usual scenario of greenhouse gas emissions.

## 6.2.3 Changes in light and ultraviolet radiation

## 6.2.3.1 Exposure – light and ultraviolet radiation

Plankton that inhabit the euphotic zone (greater than 1% of surface light) are sensitive to changes in light and ultraviolet radiation (UVR). The exposure of plankton to light and UVR is dependent upon surface light conditions, dissolved coloured substances and particulate matter in the water column<sup>85</sup>.

## 6.2.3.2 Sensitivity - light and ultraviolet radiation

Changes in light intensity affect phytoplankton growth. Many species of zooplankton will also be sensitive to changes in light, as they exhibit swarming and vertical migration behaviours.

Many neustonic copepods (residing close to the surface) such as the Pontellidae have pigments to reduce damage caused by UVR. Some copepod species on the GBR contain carotenoid pigments with UVR-absorbing properties<sup>7</sup>. Temporary members of the zooplankton that reside close to the sea surface (eq eggs and larvae of fish) can be sensitive to UVR and are likely to receive higher doses.

## 6.2.3.3 Impacts - light and ultraviolet radiation

Persistent levels of cloud cover reduce light levels and thus primary production, with concomitant declines in secondary production and food for higher trophic levels. In addition, as light is also the cue for both swarming and vertical migration, any changes in the light field will impact these zooplankton behaviours.

UVR impacts the growth, mobility and cellular stoichiometry and the relative dominance of many phytoplanktonic organisms. Tropical regions like the GBR naturally receive high UVR doses. Studies have found that UVR affects nitrogen uptake and thus the growth and productivity of important phytoplankton species<sup>23</sup>. UVR negatively influences several physiological processes and cellular structures of phytoplankton including photosynthesis, cell motility and orientation, algal life span, and DNA machinery<sup>54,55,71</sup>. These effects compromise the ability of phytoplankton to adapt to changing environmental conditions<sup>47,48</sup>. They also result in changes in cellular elemental stoichiometry including increased cellular carbon content, decreased chlorophyll a content, and less frequent cell division resulting in increased cell size54.

Irradiation of the copepod Acartia clausi with high doses of UVR resulted in curtailed adult survival and reduced fecundity<sup>61</sup>. A 20 percent increase in UVR resulted in the death of eight percent of anchovy larvae<sup>59</sup>. UVR can also damage eggs and larvae of copepods, crabs, and fish<sup>25</sup>.

UVR can cause changes in community structure because small cells are more prone to deleterious effects of UVR than large cells, and have comparatively high metabolic costs to screen out damaging UVR<sup>91</sup>. Changes in the cellular elemental stoichiometry of phytoplankton caused by UVR often decrease the nutritional value of phytoplankton. Negative effects of such altered food quality can propagate to zooplankton<sup>63</sup>. Further, UVR lowers copepod fecundity, increases naupliar mortality and affects vertical distribution61,14.

#### 6.2.3.4 Adaptive capacity – light and ultraviolet radiation

Some phytoplankton may partially acclimate to or repair UVR damage, although this involves metabolic costs that reduce the energy available for cell growth and division. Mycosporine-like amino acids confer protection against UVR damage in some taxa<sup>11</sup>. Many UVR-tolerant species produce dense surface blooms, some of which are toxic; leading to the possibility that increased UVR may increase the incidence of toxic surface blooms.

## 6.2.3.5 Vulnerability and thresholds – light and ultraviolet radiation

We suggest that the overall vulnerability of plankton to changes in the light and UVR regime is relatively low; moreover, UVR is likely to decline in the longer term. The tropics are naturally high-light and high-UVR environments. At this time, there has been insufficient research to report thresholds of vulnerability for tropical species.

#### 6.2.4 Nutrient enrichment

#### 6.2.4.1 Exposure

Changing nutrient inputs to the water column of the GBR will affect planktonic species and communities.

## 6.2.4.2 Sensitivity - nutrient enrichment

All phytoplankton species are affected by nutrient enrichment processes to some degree. Diatoms are likely to be particularly responsive to changes in nutrient availability. Zooplankton are not directly affected by nutrient enrichment.

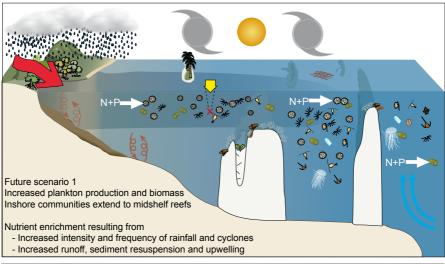
#### 6.2.4.3 Impacts - nutrient enrichment

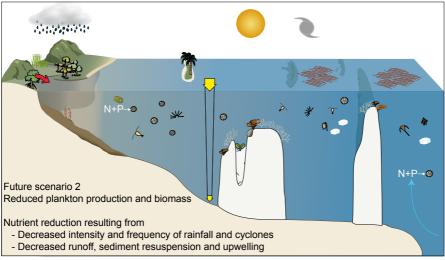
Changes in oceanographic and weather processes, which affect nutrient inputs to the GBR ecosystem (eg upwelling, runoff and resuspension), will have direct influences on plankton abundance, community structure, and production and thereby affect higher trophic levels (Figure 6.3).

There are likely to be changes in the abundance of phytoplankton, with lower nutrient conditions leading to less plankton, and enhanced nutrient conditions resulting in greater plankton abundance (Figure 6.5). The cyanobacterium *Trichodesmium* is either toxic or of poor nutritional quality to most copepods – only some pelagic harpacticoids graze *Trichodesmium*<sup>86,87</sup>. Phytoplankton and zooplankton community structure will also change, with picoplankton and the nitrogen-fixing cyanobacterium *Trichodesmium* likely to be more important if nutrient input processes decline (Figure 6.5). As a result, under low nutrient conditions, small non-crustacean zooplankton and gelatinous filter-feeding groups (salps, doliolids, appendicularia) will be more prominent, while enhanced nutrient conditions may favour larger crustacean zooplankton. Under nutrient enrichment, diatoms are likely to increase, leading to more crustacean zooplankton and carnivorous medusae and ctenophores.

Oceanographic processes, which affect residual current strengths on the GBR shelf, will also affect the longshore mixing and dispersal of plankton organisms or life stages and residence times within the GBR system. Climate-driven changes in the relative balance between wind stress and the southward residual current in the southern half of the GBR will influence the cross-shelf extent of coastal plankton assemblages.

Figure 6.5 Future scenarios under two different nutrient enrichment regimes





#### Community composition

Picoplankton (eg Prochlorococcus)

Diatom-dominated community

Dinoflagellate-dominated community

Trichodesmium (cyanobacteria) blooms

Zooplankton



Medusae and ctenophores

#### Drivers



Cyclones and rainfall



Sediment resuspension



Nutrient-rich runoff



Upwelling Nutrient uptake (nitrogen and phosphorus)



Light penetration/extinction

#### 6.2.4.4 Adaptive capacity – nutrient enrichment

The plankton community will adjust to changes in nutrient inputs and availability by changing its composition. The relative abundance of Picophytoplankton, *Trichodesmium* and gelatinous zooplankton is likely to increase under a low nutrient regime, while diatoms and large zooplankton are likely to be more important under a high nutrient regime.

#### 6.2.4.5 Vulnerability and thresholds - nutrient enrichment

The plankton community is affected by changes in the degree of nutrient enrichment. Whether this constitutes vulnerability is open to debate. The concept of a threshold may not apply in this situation. We consider there is a continuum between the two end-member states (Figure 6.5).

# 6.3 Linkages with other ecosystem components

Altered phytoplankton and zooplankton abundance, composition, productivity and timing of occurrence will have a cascading effect on higher trophic levels of the GBR. Any decline (or increase) in overall abundance, growth and trophic efficiency of phytoplankton and zooplankton communities is likely to lead to the decline (or increase) in higher trophic levels. Larvae of almost all fishes feed on copepod nauplii at first feeding<sup>58</sup>, and therefore variations in the timing and extent of copepod reproduction could influence patterns of recruitment of fishes and economically important invertebrates, especially those with a long larval life, such as crayfish. This will be discussed more fully in Kingsford and Welch (see chapter 18). Synchronous and infrequent events in plankton (eg coral spawning) may be affected by changes in the magnitude and timing of primary and secondary productivity, and changes in the predators present. Changes in runoff regime may affect the life cycles of stingers and productivity of the coastal zone where they feed.

Pteropods contribute to the diet of carnivorous zooplankton, myctophids and other zooplanktivorous fish, and a reduction in pteropods may have ramifications higher up the pelagic food web. Over long timescales, the calcite-producing foraminifera are likely to be negatively impacted by reduced pH.

#### 6.3.1 Constraints to adaptation

Smaller plankton species have shorter life cycles and hence presumably greater scope for genetic recombination. They are therefore more likely to adapt physiologically than larger plankton. However, predation rather than physiological stress is the principal source of mortality in plankton organisms. Local oceanographic factors determine the movement of water across natural climatic gradients much larger than those that we expect from climate change alone. Plankton organisms are therefore more likely to be carried into and out of the GBR ecosystem before any significant adaptation could occur. If adaptation does occur, it will most likely be through regional-scale selection of genotypes more closely attuned to warmer temperatures and shorter generation times.

#### 6.3.2 Interactions between stressors

At large scales, atmospheric and hydrodynamic variables interact to produce a complex temporal and spatial pattern of nutrient enrichment (Figure 6.1). At local scales, the predictive value of temperature as a stressor is often overridden by concurrent resource limitation. In the GBR ecosystem, phytoplankton growth rates are more dependent upon nutrient availability than temperature (Furnas unpublished data). In estuarine ecosystems, which are less likely to be nutrient limited, models based on biomass, photic depth and incident irradiance outperform models based on temperature alone<sup>16</sup>. Similarly for zooplankton, growth rates are related more to food availability than temperature.

Another interaction between stressors is between UVR and the depth of the mixed layer. A decrease in the depth of the mixed surface layer, coupled with an increase in turbulence, increases exposure of phytoplankton to UVR and the chance of algal cells receiving harmful doses<sup>63,53</sup>. UVR can also interact with nutrient availability, as enhanced UVR can increase the availability of essential macronutrients via increased photochemical dissolution of organics, thus enhancing phytoplankton growth<sup>94,89,113</sup>.

#### 6.3.3 Threats to resilience

The plankton community as a whole is resilient to changes in climate-related stressors such as large-scale nutrient enrichment, temperature, acidification, UVR and winds. Plankton groups that are not favoured by the prevailing conditions will be restricted to certain favourable environments in space and time, and the plankton community is able to reorganise to maintain key functions and processes. The continuum between different states summarised in Figure 6.3 has different trophic efficiencies; the ability of communities dominated by picoplankton and pelagic tunicates to provide food for higher trophic levels is limited in comparison with communities dominated by diatom and large zooplankton.

# 6.4 Summary and recommendations

#### 6.4.1 Major vulnerabilities to climate change

Apart from some estuarine copepods, there are no known endemic species of holoplankton in the GBR ecosystem. There is a low probability of extinction risk; no plankton species worldwide are considered to have become extinct, although many plankton species are cryptic, difficult to identify, or undescribed, and almost none have any regular assessment of their status. Therefore, as individual plankton taxa may not be particularly vulnerable (the pteropod *Cavolinia* is an exception) and there is also insufficient information for any individual taxa to assess potential vulnerabilities, we have taken a functional group approach. Table 6.3 summarises findings on the vulnerability of plankton functional groups from section 6.2. The column order of the stressors reflects our judgment of the perceived vulnerability of plankton and ecosystem consequences to each stressor, namely nutrient enrichment, temperature, ocean chemistry, and light and UVR.

We consider that the most likely changes in plankton communities will be a consequence of alterations in atmospheric and oceanographic variables that drive nutrient enrichment processes, and that changes in other stressors will probably have a smaller secondary impact on plankton and the ecosystems they support.

Table 6.3 Summary of vulnerability of plankton to climate change. The column order of the stressors reflects our judgment of the perceived vulnerability of plankton to each stressor, with nutrient enrichment being the most important and light/UVR the least.

			Stressors	
	Nutrient enrichment (upwelling, winds, rainfall, cyclones)	Temperature	Ocean chemistry	Light and UVR
Exposure	<ul> <li>Phytoplankton spend their entire life cycle in GBR waters so will be exposed to and directly responsive to changes in nutrient enrichment processes.</li> </ul>	Plankton spend their entire life cycle in GBR waters so will be exposed to increased regional temperature.	<ul> <li>Plankton spend their entire life cycle in GBR waters so will be exposed to acidification as a result of increased dissolved CO<sub>2</sub>.</li> </ul>	Plankton spend their entire life cycle in near- surface GBR waters so will be exposed to changes in light and UVR.
Sensitivity	All phytoplankton species would be responsive to some degree, but diatoms are particularly responsive to changes in nutrient conditions.  Increase in dissolved organic matter (DOM) from runoff may locally favour dinoflagellates and heterotrophic protists over diatoms.	Species-specific effects, with some having wide and others narrow temperature tolerances.     Short generation times make plankton particularly sensitive.     Substantial response of rate processes such as growth.     Copepod growth in GBR more related to phytoplankton abundance	<ul> <li>Those with aragonite shells such as pteropods will be most sensitive and adversely affected.</li> <li>Those with calcite shells such as coccolithophores, foraminiferans, some molluscs &amp; crustacean larvae will be affected, but to a lesser degree.</li> <li>Other plankton groups not affected directly</li> </ul>	Photosynthesising organisms (phytoplankton) will be directly affected by light availability.     Zooplankton that exhibit swarming and diel vertical migration behaviours will be sensitive.     Species without photoprotective devices and living in or near surface layers will be most sensitive to UVR.

Table 6.3 (continued)

			Stressors	
	Nutrient enrichment (upwelling, winds, rainfall, cyclones)	Temperature	Ocean chemistry	Light and UVR
Impacts	<ul> <li>Change in phytoplankton community structure (see Fig. 6.2), with dominance of picoplankton and <i>Trichodesmium</i> if nutrient availability declines, and more diatoms if nutrient availability increases</li> <li>Change in primary productivity (see Fig. 6.2), with lower production rates if nutrients decline, and higher rates if nutrients increase.</li> <li>Zooplankton will respond indirectly, via their trophic linkage with phytoplankton.</li> <li>Change in zooplankton community structure (see Fig. 6.2), with increased dominance of small crustacean zooplankton if nutrients decline, and more medusae and ctenophores if nutrients increase.</li> <li>Change in secondary productivity (see Fig. 6.2), with lower production rates if nutrients increases.</li> <li>Declines/increases in primary and secondary production will lead to depressed/enhanced marine snow sedimentation.</li> </ul>	Change in primary and secondary production. Change in community structure (see Fig. 6.2), with more picoplankton, Trichodesmium and small zooplankton. Most copepod species decrease in body size with warming. Phenology of spawning and production of larvae	Dissolution of shells     Disappearance/ reduction of species	<ul> <li>Change in primary production, with a decline if cloud cover increases (light decreases).</li> <li>Change in zooplankton swarming patterns, with more swarming if clouds were to decline (light increases)</li> <li>Change in zooplankton emergence, with amphipods, cumaceans, mysids, and ostracods emerging more frequently if cloud cover was to decline (light increases).</li> <li>Change in community structure, particularly size.</li> <li>Cell mutation</li> <li>Increased cell death</li> <li>UVR can affect nutrient availability and uptake in phytoplankton.</li> </ul>

Table 6.3 (continued)

			Stressors	
	Nutrient enrichment (upwelling, winds, rainfall, cyclones)	Temperature	Ocean chemistry	Light and UVR
Adaptive capacity	<ul> <li>Nature of change in community structure is adaptive.</li> <li>Restriction of plankton groups to certain favourable environments in space and time</li> </ul>	<ul> <li>Change to strains of a species that may be better adapted</li> <li>Change in distribution</li> <li>Change in timing of life history events</li> </ul>	None known, but physio- logical buffering possible	Changed pigment content in phytoplankton cells Change in vertical structure of phytoplankton Zooplankton exposed to more intense UVR can augment their pigment content.
Vulnerability and thresh- olds	<ul> <li>Plankton community is not highly vulnerable, with a continuous response rather than a threshold due to the complexity of response and number of plankton species.</li> </ul>	Plankton community     directly affected, with     a continuum response     rather than a threshold     due to the complexity of     response and number of     plankton species.	<ul> <li>Pteropods highly vulnerable; other molluscs, coccoliths, foraminifera and some crustaceans less vulnerable; and other plankton not directly vulnerable.</li> <li>No threshold work</li> </ul>	• Phytoplankton productivity is highly vulnerable to changes in light availability, as are some zooplankton, but thresholds unknown.

Table 6.3 (continued)

			Stressors	
	Nutrient enrichment (upwelling, winds, rainfall, cyclones)	Temperature	Ocean chemistry	Light and UVR
Linkages and Interactions	<ul> <li>Climate impacts on plankton cascading to higher trophic levels</li> <li>Reduced trophic efficiency within the plankton if picoplankton dominate</li> <li>Decreased food quality and quantity for higher trophic levels if picoplankton dominate</li> <li>Decline in abundance of higher trophic levels if picoplankton dominate</li> <li>Changes in food availability for benthic detritivores if picoplankton dominate</li> </ul>	Possible consequences for higher trophic levels     Reduced trophic efficiency within the plankton     Decreased food quality and quantity for higher trophic levels     Decline in abundance of higher trophic levels	Consequences for higher trophic levels unknown but may be relatively minor     Over long times scales, decreased amount of sedimentation of foraminifera shells     Decreased rate of sedimentation (reduced density of shells that carry attached organic matter to depth)	Possible consequences for higher trophic levels     Change in primary production most critical, with effects cascading to higher trophic levels     Consequences for higher trophic levels unknown but may be relatively minor

#### 6.4.2 Potential management responses

As most of the climate change impacts on plankton are driven by large-scale oceanographic, weather and climate processes, few local management responses are possible. Further, because of the enhanced levels of CO<sub>2</sub> in the atmosphere and rates of fossil fuel burning, the process of ocean acidification is irreversible over the next several centuries. The only practical way to ameliorate these effects is to reduce CO<sub>2</sub> emissions to the atmosphere. This requires a global solution.

Ocean acidification will have direct consequences on some plankton groups. Broad-scale addition of chemicals to the ocean to re-equilibrate the pH is not practical, and it will take thousands of years for ocean chemistry to return to a condition similar to that of pre-industrial times<sup>99</sup>.

Perhaps the only action likely to succeed at the regional scale would be the reduction of terrestrial runoff of sediment, nutrients and chemical pollutants through widespread changes in land use practices within the GBR catchment. This would help maintain the structure and functioning of existing plankton communities in the GBR lagoon. Efforts to make such changes are now under way through the Reef Water Quality Protection Plan.

#### 6.4.3 Further research

The lack of information on the state of GBR plankton communities currently hinders policymakers from being able to fully address the impacts of climate change on the GBR. This is a consequence of the lack of long-term (multi-decadal) plankton datasets in the region. The longest dataset for a crude system variable such as plankton biomass (eg chlorophyll a) commenced in 1989, covering coastal waters between Cape Tribulation and Cape Grafton. During this period, there has been a slight, nonlinear decrease of 30 percent in chlorophyll, although there is no clear evidence that this change is climate driven. Much of the impact of climate change in plankton systems elsewhere has not been apparent from such bulk indices but from species-specific changes in distribution, timing of life-cycle events or in changes of rate processes.

As part of an overall environmental monitoring program for the GBR, consideration should be given to the inclusion of one or more plankton monitoring sites (perhaps based at island research stations) to track long-term changes in plankton biomass and community structure, particularly for those few forms (eg pteropods) that are at particular risk from ocean acidification.

Species-specific sampling of plankton over larger areas is more difficult. Ocean colour satellites provide information on bulk indices such as surface chlorophyll, but no species-specific information on phytoplankton or zooplankton. One possibility is to use the continuous plankton recorder, a robust yet cost-effective device for capturing phyto- and zooplankton that is towed behind commercial vessels. A route is beginning in 2007 from Brisbane to Fiji, but none is currently planned closer to the GBR.

Most of the climate-influenced changes in GBR plankton communities will result from changes in atmospheric and oceanographic variables that drive transport, mixing and nutrient input processes.

Fortunately, many of the critical environmental variables underpinning these processes such as water temperature, cloud cover, solar radiation, UVR and wind stress are already routinely collected as part of the research and monitoring of the GBR (eg Australian Institute of Marine Science weather stations and Transports of the East Australian Current System moorings) and need to be continued.

In terms of critical research foci in the future, we can highlight two areas. First, we have insufficient knowledge of the role of marine snow as a linkage between pelagic and coral reef ecosystems. Studies so far have provided tantalising glimpses into this linkage but much remains to be discovered. Second, in this review we have identified that nutrient input processes are critical to understanding future climate change impacts on the GBR. The big unknown is the direction of these processes – whether inputs are going to increase or decrease and whether the spatial and temporal pattern of inputs will change. Hydrodynamic and geochemical modelling efforts focused on the intensity of the boundary currents bordering the GBR and in the Coral Sea (East Australian Current and Hiri Current) as well as upwelling dynamics and riverine runoff are pivotal to answering these questions. Only with nutrient-phytoplankton–zooplankton models embedded within these hydrodynamic models will we be able to understand and forecast the response of the plankton community and thus higher trophic levels.

## References

- Alldredge AL (1976) Discarded appendicularian houses as sources of food, surface habitats, and particulate organic matter in planktonic environments. Limnology and Oceanography 21, 14–23.
- 2 Alldredge AL and King JM (1977) Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Marine Biology 41, 317–333.
- 3 Alldredge AL and King JM (1980) Effects of moonlight on the vertical migration patterns of demersal zooplankton. Journal of Experimental Marine Biology and Ecology 44, 133–156.
- 4 Ambler JW (2002) Zooplankton swarms: characteristics, proximal cues and proposed advantages. *Hydrobiologia* 480, 155–164.
- 5 Andrews JC and Gentien P (1982) Upwelling as a source of nutrients for the Great Barrier Reef ecosystems: A solution to Darwin's question? *Marine Ecology Progress Series* 8, 257–269.
- 6 Anthony KRN and Fabricius KE (2000) Shifting roles of autotrophy and heterotrophy in coral energetics under varying turbidity. Journal of Experimental Marine Biology and Ecology 252, 221–253.
- Bandaranayake WM and Gentien P (1982) Carotenoids of Temora turbinata, Centropages furcatus, Undinula vulgaris and Euchaeta russelli. Comparative Biochemistry and Physiology 72B, 409–414.
- 8 Beaglehole JC (ed) (1955) The Journals of Captain James Cook on his voyages of discovery. Vol. 1. The voyage of the Endeavour 1768–1771. Cambridge University Press, Cambridge, pp. 404–405.
- Beaugrand G, Reid PC, Ibanez F, Lindley JA and Edwards M (2002) Reorganisation of North Atlantic marine copepod biodiversity and climate. Science 296, 1692–1694.
- 10 Beardall J and Raven JA (2004) The potential effects of global climate change on microalgal photosynthesis, growth and ecology. *Phycologia* 43, 26–40.
- 11 Beardall J and Stojkovic S (2006) Microalgae under global environmental change: Implications for growth and productivity, populations and trophic flow. *ScienceAsia* 21, supplement 1, 1–10.
- 12 Bell PRF, Elmetri I and Uwins P (1999) Nitrogen fixation by *Trichodesmium* spp. In the Central and Northern Great Barrier Reef Lagoon: Relative importance of the fixed-nitrogen load. *Marine Ecology Progress Series* 186, 119–126.
- 13 Bolch CJS, Blackburn SI, Hallegraeff GM and Vaillancourt RE (1999) Genetic variation among strains of the toxic dinoflagellate *Gymnodinium catenatum* (Dinophyceae). *Journal of Phycology* 35, 356–367.
- 14 Bollens SM and Frost BW (1990) UV Light and Vertical Distribution of the Marine Planktonic Copepod Acartia hudsonica Pinhey. Journal of Experimental Marine Biology and Ecology 137, 89–93.
- 15 Brinkman R, Wolanski E, Deleersnijder E, McAllister F and Skirving W (2001) Oceanic inflow from the Coral Sea into the Great Barrier Reef. Estuarine, Coastal and Shelf Science 54, 655–668.
- 16 Brush MJ, Brawley JW, Nixon SW and Kremer JN (2002) Modelling phytoplankton production: problems with the Eppley curve and an empirical alternative. *Marine Ecology Progress Series* 238, 31–45.
- 17 Burfield ST (1950) Chaetognatha. Great Barrier Reef Expedition (1928–29). Scientific Reports 5, 459–473.
- 18 Buskey EJ, Peterson JO and Ambler JW (1995) The role of photoreception in the swarming behavior of the copepod Dioithona oculata. Marine and Freshwater Behavioural Physiology 26, 273–285.
- 19 Crosbie ND and Furnas M (1999) Abundance and distribution of photosynthetic prokaryotic picoplankton in shelf waters of the Great Barrier Reef, Australia. Bulletin de l'Institut océanographique, Monaco no. spécial 19, 377–385.
- 20 Crosbie ND and Furnas MJ (2001a) Net growth rates of picocyanobacteria and nano-/ microphytoplankton inhabiting shelf waters of the central (17° S) and southern (20° S) Great Barrier Reef. Aquatic Microbial Ecology 24, 209–224.
- 21 Crosbie ND and Furnas MJ (2001b) Abundance, distribution and flow-cytometric characterization of picophytoprokaryote populations in central (17° S) and southern (20° S) shelf waters of the Great Barrier Reef. Journal of Plankton Research 23, 809–828.
- 22 de Jager D, Manning M and Kuijpers L (2005) Safeguarding the Ozone Layer and the Global Climate System: Issues Related to Hydrofluorocarbons and Perfluorocarbons. IPCC/TEAP Special Report. Summary for Policymakers and Technical Summary. (http://arch.rivm.nl/env/int/ipcc/pages\_media/SROC-final/srocspmts\_en.pdf)
- 23 Döhler G (1994) UV effects on the nitrogen metabolism of marine phytoplankton and adaptation to UV radiation, In: R Biggs and M Joyner (eds) Stratospheric Ozone Depletion/UV-B Radiation in the Biosphere NATO ASI Series. Vol. 18 (Springer-Verlag, Berlin), 163–174.
- 24 Edwards M and Richardson AJ (2004) The impact of climate change on the phenology of the plankton community and trophic mismatch. *Nature* 430, 881–884.
- 25 El-Sayed SZ, van Dijken GL and Gonzalez-Rodas G (1996) Effects of ultraviolet radiation on marine ecosystems. International Journal of Environmental Studies 512, 199–216.

- 26 Eppley RW (1972) Temperature and phytoplankton growth in the sea. Fishery Bulletin 70, 1063–1085.
- 27 Fabricius KE and Dommisse M (2000) Depletion of suspended particulate matter over coastal reef communities dominated by zooxanthellate soft corals. Marine Ecology Progress Series 196, 157–167.
- 28 Fabricius KE, Benayahu Y and Genin A (1995) Herbivory in asymbiotic soft corals. Science 268, 90–92.
- 29 Farran GP (1936) Copepoda. Great Barrier Reef Expedition (1928–29) Scientific Reports 5, 73–142.
- 30 Farran GP (1949) The seasonal and vertical distribution of the copepods. Great Barrier Reef Expedition. Scientific Reports 2, 291–312.
- 31 Furnas MJ (1989) Cyclonic disturbance and a phytoplankton bloom in a tropical shelf ecosystem. In: K Okaichi, DM Anderson and T Nemoto (eds) *Red Tides: Environmental Science and Toxicology*, Elsevier, New York.
- 32 Furnas MJ (1991) Net *in situ* growth rates of phytoplankton in an oligotrophic, tropical shelf ecosystem. *Limnology* and Oceanography 36, 13–29.
- 33 Furnas MJ (2003) Catchments and Corals: Terrestrial Runoff to the Great Barrier Reef. Australian Institute of Marine Science and CRC Reef Research, Townsville.
- 34 Furnas MJ and Crosbie ND (1999) In situ growth dynamics of the photosynthetic prokaryotic picoplankters Synechococcus and Prochlorococcus. Bulletin de l'Institut Oceanographique, Monaco, Marine Cyanobacteria supplement, 387–417.
- 35 Furnas MJ and Mitchell AW (1986) Phytoplankton dynamics in the central Great Barrier Reef I. Seasonal changes in biomass and community structure and their relation to intrusive activity. Continental Shelf Research 6, 363–384.
- 36 Furnas MJ and Mitchell AW (1987) Phytoplankton dynamics in the central Great Barrier Reef II. Primary production. Continental Shelf Research 7, 1049–1062.
- 37 Furnas MJ and Mitchell AW (1989) Shelf-scale estimates of phytoplankton primary production in the Great Barrier Reef. *Proceedings of the 6<sup>th</sup> International Coral Reef Symposium 2*, 557–582.
- 38 Furnas MJ and Mitchell AW (1996) Biological Oceanography of the Great Barrier Reef. In: Anon (ed) Proceedings: The Great Barrier Reef. Science, Use and Management. Townsville, 25–29 November 1996. 1, 75–87. Great Barrier Reef. Marine Park Authority, Townsville.
- 39 Furnas MJ, Mitchell AW and Skuza M (1995) Nitrogen and phosphorus budgets for the central Great Barrier Reef. Research Publication No. 36, Great Barrier Reef Marine Park Authority, Townsville.
- 40 Furnas MJ, Mitchell A, Skuza M and Brodie J (2005) In the other 90%: phytoplankton response to enhanced nutrient availability in the Great Barrier Reef Lagoon. Marine Pollution Bulletin 51, 253–265.
- 41 Gagan MK, Sandstrom MW and Chivas AR (1987) Restricted terrestrial carbon input to the continental shelf during cyclone Winifred: implications for terrestrial runoff to the Great Barrier Reef province. *Coral Reefs* 6, 113–119.
- 42 Gallagher JC (1980) Population genetics of Skeletonema costatum (Bacillariophyceae) in Narragansett Bay. Journal of Phycology 16, 464–474.
- 43 Genin A (2004) Bio-physical coupling in the formation of zooplankton and fish aggregations over abrupt topographies. *Journal of Marine Systems* 50, 3–20.
- 44 Giordano M, Beardall J and Raven JA (2005) CO<sub>2</sub> concentrating mechanisms in algae: mechanism, environmental modulation, and evolution. *Annual Review of Plant Biology* 56, 99–131.
- 45 Giovanni S (2004) Evolutionary biology: oceans of bacteria. *Nature* 430, 515–516.
- 46 Greve W, Reiners F, Nast J and Hoffmann S (2004) Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004: lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. *Helgoland Marine Research* 58, 274–288.
- 47 Häder D and Häder MA (1989) Effects of solar UV-B irradiation on photomovement and motility in photosynthetic and colorless flagellates. *Environmental and Experimental Botany* 29, 273–282.
- 48 Häder D and Liu SL (1990) Effects of artificial and solar UV-B radiation on the gravitactic orientation of the dinoflagellate Peridinium gatunense. FEMS Microbiology and Ecology 73, 331–338.
- 49 Hallegraeff GM (1984) Coccolithophorids (calcareous nanoplankton) from Australian waters. *Botanica Marina* 27, 229–247.
- 50 Hamner WM and Carleton JH (1979) Copepod swarms: Attributes and role in coral reef ecosystems. *Limnology and Oceanography* 24, 1–14.
- 51 Hamner WM, Jones MS, Carleton JH, Hauri IR and Williams DM (1988) Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. *Bulletin of Marine Science* 42, 459–479.
- 52 Hays GC, Richardson AJ and Robinson C (2005) Climate change and plankton. *Trends in Ecology and Evolution* 20, 337–344.

- 53 Hernando MP and Ferreyra GA (2005) The effects of UV radiation on photosynthesis in an Antarctic diatom (Thalassiosira sp.): Does vertical mixing matter? Journal of Experimental Marine Biology and Ecology 325, 35–45.
- 54 Hessen D, de Lange HJ and van Donk E (1997) UV-induced changes in phytoplankton cells and its effects on grazers. Freshwater Biology 38, 513–524.
- 55 Hogue VE, Wilkerson FP and Dugdale RC (2005) Ultraviolet-B radiation effects on natural phytoplankton assemblages of central San Francisco Bay. Estuaries 28, 190–203.
- 56 Holzman R, Reidenbach MA, Monismith SG, Koseff JR and Genin A (2005) Near-bottom depletion of zooplankton over a coral reef II: relationships with zooplankton swimming ability. *Coral Reefs* 24, 87–94.
- 57 Hopcroft RR and Roff JC (1995) Zooplankton growth rates: extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *Journal of Plankton Research* 17, 205–220.
- 58 Hunter JR (1981) Feeding ecology and predation of marine fish larvae. In: R Lasker (ed) Marine fish larvae. morphology, ecology and relation to fisheries. University of Washington Press Seattle and London. pp: 33–77.
- 59 Hunter JR, Kaupp SE and Taylor JH (1982) Assessment of effects of UV radiation on marine fish larvae. In: J Calkins (ed) *The Role of Solar Ultraviolet Radiation in Marine Ecosystems*. Plenum, New York.
- 60 Huntley M and Lopez MDG (1992) Temperature-dependent production of marine copepods: a global synthesis. American Naturalist 140, 201–242.
- 61 Karanas JJ, Worrest RC and Van Dyke H (1981) Impact of UV-B Radiation on the Fecundity of the Copepod *Acartia clausi. Marine Biology* 65, 125–133.
- 62 Kelfkens G, Bregman A, de Gruijl FR; van der Leun JC, Piquet A, van Oijen T, Gieskes WWC, van Loveren H, Velders GJM, Martens P and Slaper H (2002) Ozone layer climate change interactions. Influence on UV levels and UV related effects. Report No. 410200112, ISBN: 90 5851 079 4.
- 63 Keller AA, Hargraves P, Jeon H, Klein-MacPhee G, Klos E, Oviatt C and Zhang J (1997) Effects of ultraviolet-B enhancement on marine trophic levels in a stratified coastal system. *Marine Biology* 130, 277–287.
- 64 King B and Wolanski E (1992) Coastal dynamics along a rugged coastline. In: D Prandle (ed) *Dynamics and exchanges in estuaries and the coastal zone*. Springer Verlag, New York pp. 577–598.
- 65 Kiørboe T, Andersen KP and Dam HG (1990) Coagulation efficiency and aggregate formation in marine phytoplankton. *Marine Biology* 107, 235–245.
- 66 Kirby RR, Beaugrand G, Lindley JA, Richardson AJ, Edwards M and Reid PC (2007) Climate effects and benthic-pelagic coupling in the North Sea. Marine Ecology Progress Series 330, 31–38.
- 67 Lalli CM and Parsons TR (1997) Biological oceanography: an introduction. Butterworth Heinemann, Oxford, England.
- 68 Lambeck A and Woolfe KJ (2000) Composition and textural variability along the 10 m isobath, Great Barrier Reef: evidence for pervasive northward sediment transport. *Australian Journal of Earth Science* 47, 327–355.
- 69 Lewis A (2001) Great Barrier Reef Depth and Elevation Model: GBRDEM. CRC Reef Research Technical Report No. 33, CRC Reef Research, Townsville.
- 70 Liston PW (1990) Spatial variability and covariability of chlorophyll and zooplankton on the Great Barrier Reef. Ph.D dissertation, James Cook University of North Queensland, Townsville.
- 71 Litchman E and Neale PJ (2005) UV effects on photosynthesis and acclimation of an estuarine diatom and cryptomonad. Marine Ecology Progress Series 300, 53–62.
- 72 Longhurst AR (1985) The structure and evolution of plankton communities. Progress in Oceanography 15, 1–35.
- 73 Luick JL, Mason L, Hardy T and Furnas M (2007) Circulation in the Great Barrier Reef lagoon using numerical tracers and in situ data. *Continental Shelf Research* 27, 757-778.
- 74 Marshall SM (1933) The production of microplankton in the Great Barrier Reef region. *Great Barrier Reef Expedition* (1928–29). Scientific Reports 2, 111–157.
- 75 McKenzie RL, Björn LO, Bais A and Ilyasd M (2003) Changes in biologically active ultraviolet radiation reaching the Earth's surface. *Photochemical and Photobiological Sciences* 2, 5–15.
- 76 McKinnon AD (1991) Community composition of reef associated copepods in the lagoon of Davies Reef, Great Barrier Reef, Australia. Proceedings of the Fourth International Conference on Copepoda; Bulletin of the Plankton Society of Japan, Special Volume 467–478.
- 77 McKinnon AD (1996) Growth and development in the subtropical copepod *Acrocalanus gibber. Limnology and Oceanography* 41, 1438–1447.
- 78 McKinnon AD (2000) Two new species of *Oithona* (Copepoda: Cyclopoida) from mangrove waters of North Queensland, Australia. *Plankton Biology and Ecology* 47, 100–113.
- 79 McKinnon AD and Klumpp DW (1998) Mangrove zooplankton of North Queensland, Australia I. Plankton community structure and environment. *Hydrobiologia* 362, 127–143.

- 80 McKinnon AD and Thorrold SR (1993) Zooplankton community structure and copepod egg production in coastal waters of the central Great Barrier Reef lagoon. *Journal of Plankton Research* 15, 1387–1411.
- 81 McKinnon AD, Duggan S and De'ath G (2005) Mesozooplankton dynamics in inshore waters of the Great Barrier Reef. Estuarine, Coastal and Shelf Science 63, 497-511.
- 82 Moore LR, Goericke R and Chisholm SW (1995) Comparative physiology of *Synechococcus* and *Prochlorococcus*: influence of light and temperature on growth, pigments, fluorescence and absorptive properties. *Marine Ecology Progress Series* 116, 259–275.
- 83 Moore LR, Rocap G and Chisholm SW (1998) Physiology and molecular phylogeny of coexisting *Prochlorococcus* ecotypes. *Nature* 393, 464–467.
- 84 Motro R, Ayalon I and Genin A (2005) Near-bottom depletion of zooplankton over a coral reef III: vertical gradient of predation pressure. *Coral Reefs* 24, 95–98.
- 85 Neale PJ, Davis RF and Cullen, JJ (1998) Interactive effects of ozone depletion and vertical mixing on photosynthesis of Antarctic phytoplankton. *Nature* 92, 585–589.
- 86 O'Neil JM (1995) Interaction of pelagic harpacticoid copepods and the colonial marine cyanobacterium Trichodesmium spp. PhD thesis, University of Maryland, Baltimore.
- 87 O'Neil JM, and Roman MR (1994) Grazing of the pelagic harpacticoid copepods *Macrosetella, Miracia* and *Oculosetella*, on the colonial cyanobacterium *Trichodesmium* spp. from the Caribbean. *Hydrobiologia* 292–293, 235–240.
- 88 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 GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y and Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- 89 Palenik B, Price NM and Morel FMM (1991) Potential effects of UV-B on the chemical environment of marine organisms: a review. Environmental Pollution 70, 117–130.
- 90 Parmesan C and Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.
- 91 Raven JA, Finkel ZV and Irwin AJ (2005) Picophytoplankton: bottom-up and top-down controls on ecology and evolution. *Vie et Milieu* 55, 209–215.
- 92 Revelante N and Gilmartin M (1982) Dynamics of phytoplankton in the Great Barrier Reef Lagoon. *Journal of Plankton Research* 4, 47–76.
- 93 Revelante N, Williams WT and Bunt JS (1982) Temporal and spatial distribution of diatoms, dinoflagellates and Trichodesmium in waters of the Great Barrier Reef. Journal of Experimental Marine Biology and Ecology 63, 27–45.
- 94 Rich HW and Morel FMM (1990) Availability of well-defined iron colloids to the marine diatom *Thalassiosira* weissflogii. Limnology and Oceanography 35, 652–662.
- 95 Richardson AJ and Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305, 1609–1612.
- 96 Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE and Morel FMM (2000) Reduced calcification in marine plankton in response to increased atmospheric CO<sub>2</sub>. *Nature* 407, 634–637.
- 97 Roman MR, Furnas MJ and Mullin MM (1990) Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Marine Biology 105, 73–82.
- 98 Root TL, Price JT, Hall KR, Schneider SH, Rosenzweigk C and Pounds JA (2003) Fingerprints of climate change on wild animals and plants. Nature 421, 57–60.
- 99 Royal Society (2005) Ocean acidification due to increasing atmospheric carbon dioxide.
- 100 Russell FS (1935) The zooplankton: IV. The occurrence and seasonal distribution of the Tunicata, Mollusca and Coelenterata (Siphonophora). *Great Barrier Reef Expedition* (1928–29). Scientific Reports 2, 203–276.
- 101 Rynearson TA and Armbrust EV (2004) Genetic differentiation among populations of the planktonic marine diatom Ditylum brightwellii (Bacillariophyceae). Journal of Phycology 40, 34–43.
- 102 Sale PF, McWilliam PS and Anderson DT (1976) Composition of the near-reef zooplankton at Heron Reef, Great Barrier Reef. Marine Biology 34, 59–66.
- 103 Sammarco PW and Crenshaw H (1984) Plankton community dynamics of the central Great Barrier Reef Lagoon: Analysis of data from Ikeda et al. *Marine Biology* 82, 167–180.
- 104 Sandstrom MW (1988) Aliphatic hydrocarbons in surface sediments from the North Queensland coast and Great Barrier Reef: effects of tropical cyclone Winifred. Organic Geochemistry 12, 445–454.
- 105 Sebens KP (1997) Adaptive responses to water flow: morphology, energetics, and distribution of reef corals. Proceedings of the 8th International Coral Reef Symposium 2, 1053–1058.

- 106 Smayda TJ (1976) Phytoplankton processes in mid-Atlantic nearshore and shelf waters and energy-related activities.
  In: B Manowitz (ed) Effects of Energy-Related Activities on the Atlantic Continental Shelf. Brookhaven National Laboratory Report No. 50484, pp. 70–95.
- 107 Smith DF, Bulleid NC, Campbell R, Higgins HW, Rowe F, Tranter DJ and Tranter H (1979) Marine food-web analysis: an experimental study of demersal zooplankton using isotopically labelled prey species. *Marine Biology* 54, 49–59.
- 108 Tattersall WM (1936) Mysidacea and Euphausiacea. *Great Barrier Reef Expedition (1928–29)*. Scientific Reports 5, 143–176.
- 109 Tomas CR (1997) Identifying Marine Phytoplankton. Academic Press, New York.
- 110 Totton AK (1932) Siphonophora. Great Barrier Reef Expedition (1928-29). Scientific Reports 4, 317-374.
- 111 Tranter DJ, Bulleid NC, Campbell R, Higgins HW, Rowe F, Tranter HA and Smith DF (1981) Nocturnal movements of phototactic zooplankton in shallow waters. *Marine Biology* 61, 317–326.
- 112 Ullman WJ and Sandstrom MW (1987) Dissolved nutrient fluxes from the nearshore sediments of Bowling Green Bay, central Great Barrier Reef Lagoon (Australia). Estuarine, Coastal and Shelf Science 24, 289–303.
- 113 Wängberg SA, Garde K, Gustavson K and Selmer JS (1999) Effects of UV-B radiation on marine phytoplankton communities. *Journal of Plankton Research* 21, 147–166.
- 114 Williams DM and Hatcher Al (1983) Structure of fish communities on outer slopes of inshore, middle-shelf and outer shelf reefs of the Great Barrier Reef. Marine Ecology Progress Series 10, 239–50.
- 115 Williams DM, Dixon P and English S (1988) Cross-shelf distribution of copepods and fish larvae in the central Great Barrier Reef. *Marine Biology* 99, 577–589.
- 116 Yahel G, Post AF, Fabricius K, Marie D, Vaulot D and Genin A (1998) Phytoplankton distribution and grazing near coral reefs. *Limnology and Oceanography* 43, 551–563.