

## CLIMATE CHANGE AND AUSTRALIAN MARINE LIFE

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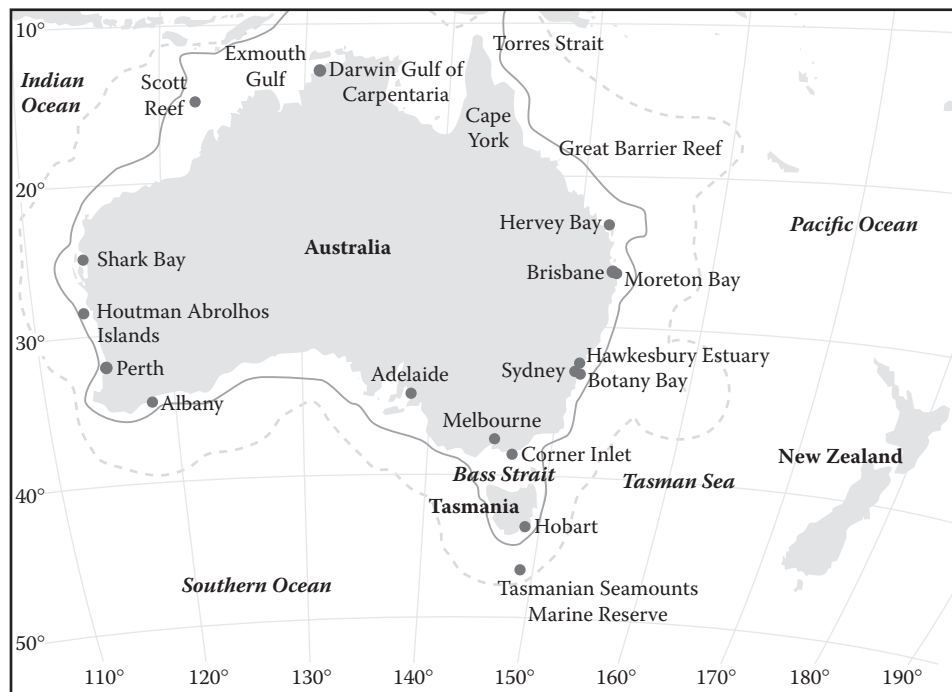
**Abstract** Australia's marine life is highly diverse and endemic. Here we describe projections of climate change in Australian waters and examine from the literature likely impacts of these changes on Australian marine biodiversity. For the Australian region, climate model simulations project oceanic warming, an increase in ocean stratification and decrease in mixing depth, a strengthening of the East Australian Current, increased ocean acidification, a rise in sea level, alterations in cloud cover and ozone levels altering the levels of solar radiation reaching the ocean surface, and altered storm and rainfall regimes. Evidence of climate change impacts on biological systems are generally scarce in Australia compared to the Northern Hemisphere. The poor observational records in Australia are attributed to a lack of studies of climate impacts on natural systems and species at regional or national scales. However, there are notable exceptions such as widespread bleaching of corals on the Great Barrier Reef and poleward shifts in temperate fish populations. Biological changes are likely to be considerable and to have economic and broad ecological consequences, especially in climate-change 'hot spots' such as the Tasman Sea and the Great Barrier Reef.

### Introduction

The global climate is changing and is projected to continue changing at a rapid rate for the next 100 yr (IPCC 2001, 2007). Average global temperatures have risen by  $0.6 \pm 0.2^\circ\text{C}$  over the twentieth century and this warming is likely to have been greater than for any other century in the last millennium. The 1990s were the warmest decade globally of the past century; and the present decade may be warmest yet (Hansen et al. 2006). Most of the warming observed during the last 50 yr is attributable to anthropogenic forcing by greenhouse gas emissions (Karoly & Stott 2006). The increase in global temperature is likely to be accompanied by alterations in patterns and strength of winds and ocean currents, atmospheric and ocean stratification, a rise in sea levels, acidification of the oceans and changes in rainfall, storm patterns and intensity. Evidence is mounting that the

changing climate is already impacting terrestrial, marine and freshwater ecosystems (Hoegh-Guldberg 1999, Walther et al. 2002, Parmesan & Yohe 2003, Root et al. 2003, Walther et al. 2005). Species' distributions are shifting poleward (Parmesan et al. 1999, Thomas & Lennon 1999, Beaupre et al. 2002, Hickling et al. 2006), plants are flowering earlier and growing seasons are lengthening (Edwards & Richardson 2004, Wolfe et al. 2005, Linderholm 2006, Schwartz et al. 2006) and timing of peak breeding and migrations of animals are altering (Both et al. 2004, Lehikoinen et al. 2004, Weishampel et al. 2004, Jónzén et al. 2006, Menzel et al. 2006). Most of this evidence, however, is from the Northern Hemisphere, with few examples from the Southern Hemisphere and only a handful from Australia (Chambers 2006). The lack of observations in Australia is attributed to a lack of studies of climate impacts on natural systems and species at regional or national scales. Further, the extent of historical biological datasets in Australia is largely unknown, many are held by small organisations or by individuals and the value of these datasets may not be recognised (Chambers 2006).

Because of the unique geological, oceanographic and biological characteristics of Australia, conclusions from climate impact studies in the Northern Hemisphere are not easily transferable to Australian systems. Including fringing islands, Australia has a coastline of almost 60,000 km (Figure 1) that spans from southern temperate waters of Tasmania and Victoria (~45°S) to northern tropical waters of Cape York, Queensland (~10°S). Australia is truly a maritime country with over 90% of the population living within 120 km of the coast. Most of Australia's population of 20 million live in the southeast with the west and north coasts being sparsely populated. Around 40% of Australia's population live in the cities of Sydney and Melbourne alone (Australian Bureau of Statistics 2006).



**Figure 1** (See also Colour Figure 1 in the insert following page 344.) Map of Australia indicating the locations discussed in the text. The 200 nm EEZ for Australia is marked by the dashed line, and the 200 m depth contour by the solid line.

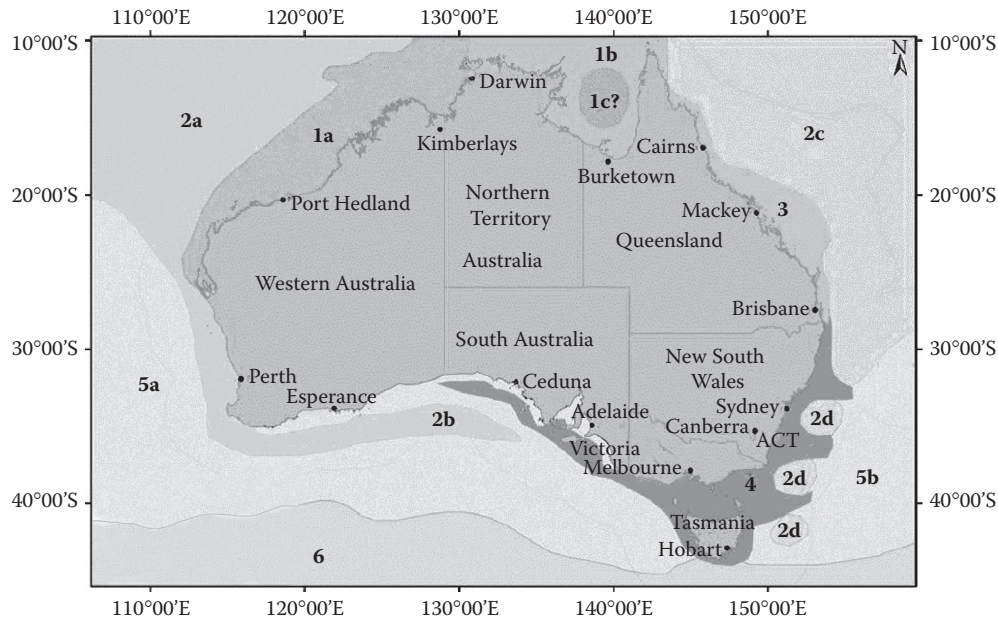
## CLIMATE CHANGE AND AUSTRALIAN MARINE LIFE

Australia has sovereign rights over ~8.1 million km<sup>2</sup> of ocean and this area generates considerable economic wealth estimated as \$A52 billion per year or about 8% of gross domestic product (CSIRO 2006). Fisheries and aquaculture are important industries in Australia, both economically (gross value over \$A2.5 billion) and socially. Marine life and ecosystems also provide invaluable services including coastal defence, nutrient recycling and greenhouse gas regulation valued globally at \$US 22 trillion (\$A27 trillion) per annum (Costanza et al. 1997). The annual economic values of Australian marine biomes have been estimated: open ocean \$A464.7 billion, seagrass/algal beds \$A175.1 billion, coral reefs \$A53.5 billion, shelf system \$A597.9 billion and tidal marsh/mangroves \$A39.1 billion (Blackwell 2005). This assessment assumes Australian marine ecosystems are unstressed so actual values may be lower for degraded systems. Compared to other countries, relatively little is known about the biology and ecology of Australia's maritime realm, mainly due to the inaccessibility and remoteness of much of the coast as highlighted by the discovery of living stromatolites (representing the one of the oldest known forms of life on Earth) in Western Australia in the 1950s (Logan 1961).

Australia is unique among continents in that both the west and east coasts are bounded by major poleward-flowing warm currents (Figure 2), which have considerable influence on marine flora and fauna. The East Australian Current (EAC) originates in the Coral Sea and flows southward before separating from the continental margin to flow northeast and eastward into the Tasman Sea (Ridgway & Godfrey 1997, Ridgway & Dunn 2003). Eddies spawned by the EAC continue southward into the Tasman Sea bringing episodic incursions of warm water to temperate eastern Australia and Tasmanian waters (Ridgway & Godfrey 1997). The Leeuwin Current flows southward along the Western Australian coast and continues eastward into and across the Great Australian Bight reaching the west of Tasmania in austral winter (Ridgway & Condie 2004). The influence of these currents is evident from the occurrence of tropical fauna and flora in southern Australian waters at normally temperate latitudes (Maxwell & Cresswell 1981, Wells 1985, Dunlop & Wooller 1990, O'Hara & Poore 2000, Griffiths 2003). The importance of these major currents in structuring marine communities can be seen in the biogeographic distributions of many species, functional



**Figure 2** Major currents and circulation patterns around Australia. The continent is bounded by the Pacific Ocean to the east, the Indian Ocean to the west and the Southern Ocean to the south. Figure courtesy of S. Condie/CSIRO.



**Figure 3** (See also Colour Figure 3 in the insert.) Phytoplankton provinces around Australia. In northern shelf waters westwards from Torres Strait tropical diatom species dominate, with slight regional differences in relative abundances and absolute biomass (1a-c). The shallow waters of the Great Barrier Reef region (3) are dominated by fast-growing nano-sized diatoms. The deeper waters of the Indian Ocean and the Coral Sea are characterised by a tropical oceanic flora (2a and 2c, respectively) that is dominated by dinoflagellates and follows the Leeuwin Current (2b) and the East Australia Current and its eddies (2d). South-eastern coastal waters harbour a temperate phytoplankton flora (4) with seasonal succession of different diatom and dinoflagellate communities. Waters south of the tropical and temperate phytoplankton provinces are characterised by an oceanic transition flora (5a,b) that communicates to the subantarctic phytoplankton province (6) and is highly variable in extent. The phytoplankton provinces are associated with surface water masses and the zooplankton fauna likely shows a similar pattern (Figure prepared by G.M. Hallegraeff for CSIRO and National Oceans Office).

groups and communities. For example, there is broad agreement between phytoplankton community distributions and water masses (Figure 3).

Australian waters are generally nutrient poor (oligotrophic), particularly with respect to nitrate and phosphate because the boundary currents are largely of tropical and subtropical origins and there is little input from terrestrial sources. In general, Australia has a low average annual rainfall and this rainfall is highly variable. Much of the interior is desert and in the west the aridity extends to the coast. Monsoonal rains fall in the tropical north during the wet season (December to March) with cyclones common at this time, but there is little or no rainfall during the rest of the year. Australian soil is generally low in nutrients and this, together with the high variability in rainfall, results in little terrestrial nutrient input into the surrounding sea. The generally oligotrophic status of Australian marine waters contrasts with many mid-latitude productive coastal areas around the world. This distinction is particularly strong on the western coast of Australia where the Leeuwin Current replaces the upwelling systems produced by the highly productive eastern boundary currents characteristic of all other major ocean basins.

The impact of changing productivity on marine oligotrophic systems is largely unknown; they may not be as resilient to stress and disturbance, including climate change, as more productive

systems that commonly experience considerable interannual variability. Changes in the terrestrial climate also impact Australia's marine ecosystems to a greater degree than other parts of the world, so it may not be possible to generalise easily from knowledge elsewhere. Aeolian dust input may be an important regulator of coastal primary production. In regions south of Tasmania, where macronutrient concentrations are always high, iron availability influences growth, biomass and composition of phytoplankton (Sedwick et al. 1999, Boyd et al. 2000). In the macronutrient-limited regions more typical of the waters around continental Australia, the atmospheric supply of iron may stimulate nitrogen-fixing phytoplankton, which have a higher iron requirement than other phytoplankton and therefore influence phytoplankton community composition (Jickells et al. 2005). Climate-induced changes in wind or rainfall may thus have disproportionately large consequences for waters around Australia.

Climate change will influence physiology, abundance, distribution and phenology of species both directly and indirectly, although impacts will usually become most apparent at an ecosystem level. Given the intrinsic complexity of ecosystems and the uncertainties in future climate projections, predicting consequences for biodiversity is difficult and highly speculative. Response rates will depend on the magnitude of changes and on longevity of the species involved in a particular system. Plankton systems will therefore respond quickly (Hays et al. 2005), whereas a lag might generally be expected in responses of long-lived species. The ability for adaptation to change will also vary among species but the rapid rate of present climate change coupled with high exploitation and destruction or alteration of habitats will compromise the resilience of many populations and ecosystems (Travis 2002). Strategies for adaptation and mitigation of climate change impacts must begin with the identification of ecosystems or populations that are most vulnerable to change and those most vulnerable to other anthropogenic stressors.

In this review, we address the potential impacts of climate variability and climate change on Australian marine life from the intertidal zone through pelagic waters and into the deep sea. We provide a synopsis of climate change projections for Australia of key climate variables known to regulate marine ecosystems from the only IPCC (Intergovernmental Panel of Climate Change) climate system model constructed in the Southern Hemisphere, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Mk3.5 model. Our focus is on the critical variables that regulate processes in marine ecosystems, namely, temperature, winds, currents, solar radiation, mixed-layer depth and stratification, pH and calcium carbonate saturation state, storms and precipitation, and sea level. We review the expected impacts on species and communities of changes in each of these variables based on laboratory, modelling and field work and concentrate on biological groups found in three broad ecosystems: coastal, pelagic and offshore benthic.

### **Australian marine biodiversity**

Australia has highly diverse and unique marine flora and fauna, ranging from spectacular coral reefs in the tropics to giant kelp forests in Tasmanian waters. The biodiversity of tropical Australia is high because it is a continuation of the Indo-Pacific biodiversity hot spot, but much of this fauna is threatened by overharvesting and unregulated development in this region including countries to the north of Australia. The species diversity of seagrasses and mangroves is among the world's highest, particularly in tropical Australia (Walker & Prince 1987, Kirkman 1997, Walker et al. 1999). Temperate Australian waters contain high numbers of endemic organisms due to their long history of geographic isolation from other temperate regions (Poore 2001). Australian waters also harbour species and ecosystems that are of international importance. The best-known example is the Great Barrier Reef, which is the world's largest World Heritage Area and extends some 2100 km along the coast of northeast Australia.



Although Australian temperate waters have lower species diversity than the northern tropical waters, they harbour much higher numbers of endemic species (Poore 2001). Approximately 85% of fish species, 90% of echinoderm species and 95% of mollusc species in these southern waters are endemic (Poore 2001). This high endemism is also documented in Australia's temperate macroalgae (Bolton 1996, Phillips 2001). High endemism along the southern coastline is partly the result of low dispersal abilities of species and the presence of ecological barriers to dispersal along the southern coastal waters such as a sharp temperature gradient near the cessation of the Leeuwin Current and the absence of near-shore rocky reefs in the centre of the Great Australian Bight and at other locations along the southern Australian coastline.

Australia's fish fauna is extremely diverse and endemic by world standards due to a high diversity of tropical and temperate habitats and due to the geographic isolation of the temperate regions. Pelagic fish found around Australia include iconic species such as tuna, billfish (swordfish and marlin) and sharks. The continental shelf waters off southern Queensland have been identified as a biodiversity hot-spot for large pelagic fishes (Worm et al. 2003). In contrast to the pattern elsewhere, this Australian pelagic fish hot spot is located in an area of high catch rates and fishing effort (Campbell & Hobday 2003). Valuable fisheries exist, despite the generally low productivity of Australian marine waters; these include the Northern Prawn Fishery, the Southern Bluefin Tuna Fishery, the Eastern Tuna and Billfish Fishery and the Western Rock Lobster Fishery. Small pelagic species, such as sardines, jack mackerel, redbait and squid are captured in lower-value but high-volume coastal fisheries operating from a number of Australian ports. For many of these, there are well-known correlations between environmental factors and the productivity of the fishery. For example, the size of the Western Rock Lobster *Panulirus cygnus* Fishery, which is Australia's most important single-species fishery and the world's largest rock lobster fishery, varies in a predictable manner with the strength of the Leeuwin Current (Caputi et al. 2001). Similarly, size of banana prawn *Penaeus merguensis* catches in some areas of northern Australia is correlated with wet season rainfall (Staples et al. 1982, Vance et al. 1985). These variables are likely to change as climate changes.

Further offshore, cold-water corals are found on seamounts and the continental rise, particularly within the Tasmanian Seamounts Marine Reserve. Cold-water corals are hot spots for biodiversity, comparable to shallow tropical coral reefs, although little is known of their ecology, population dynamics or distribution in Australian waters. Over 850 macro- and megafaunal species were recently found on seamounts in the Tasman and southeast Coral Seas, of which 29–34% were potential endemics or new to science (Richer de Forges et al. 2000, Williams et al. 2006).

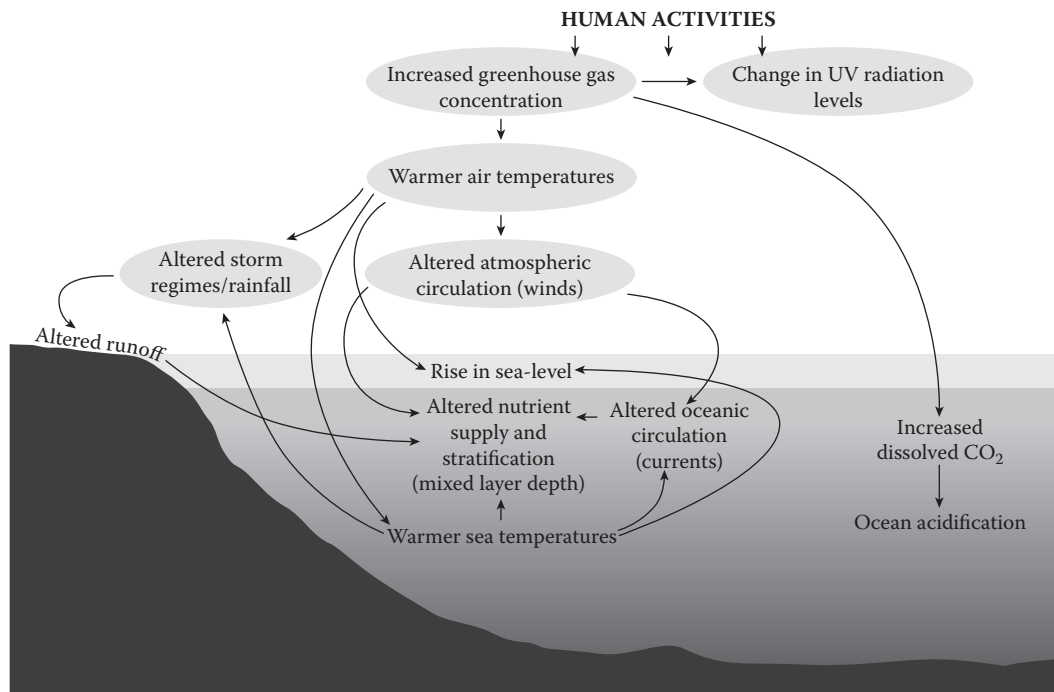
Globally significant populations of many other groups occur in Australia including populations of marine turtles, marine mammals and seabirds. Six of the seven living species of marine turtle forage and breed in Australian tropical waters. Marine turtles home to their natal area to breed and large rookeries used by tens to hundreds of thousands of turtles occur along the northern Australian coastline and the southern Great Barrier Reef area (Marsh et al. 2001). The flatback turtle *Natator depressus* nest only on Australian beaches so can be considered endemic to Australia. The dugong *Dugong dugon* forages on seagrasses in tropical Australasian waters. This species is highly threatened in much of its range and a large proportion of global dugong stock is believed to be in Moreton Bay in eastern Australia and Shark Bay in Western Australia (Marsh et al. 2001). Australian fur seals *Arctocephalus pusillus doriferus*, the world's fourth rarest seal species, and the endemic Australian sea lion *Neophoca cinerea*, one of the most endangered pinnipeds in the world, breed at sites along the southern coast of Australia. These non-migratory pinniped species remain in southern Australian waters for their entire lives. Around 45 species of whales, dolphins and porpoises are found in Australian waters including large baleen whales such as the southern right whale *Eubalaena australis* and the humpback whale *Megaptera novaeangliae*, which migrate from their Southern Ocean feeding grounds to temperate waters around the southern parts of Africa, South America and Australia and to the tropical waters of the Pacific to breed.

A diverse seabird fauna breeds on mainland and island coastlines around Australia; for example the Houtman Abrolhos Islands on the west coast are an important nesting area for Australian seabirds in terms of biomass and species diversity (Ross et al. 2001). One of the largest documented colonies of crested terns *Sterna bergii* globally (13,000–15,000 nesting pairs) occurs in the Gulf of Carpentaria in Australia's tropical north (Walker 1992). Planktivorous seabirds occur in high numbers in Australia's southern temperate waters. For example an estimated 23 million short-tailed shearwaters *Puffinus tenuirostris* nest in southeast Australia (Ross et al. 2001).

### Climate change projections for Australia

A number of climate models have been used to investigate the response of the ocean-atmosphere system to increased levels of greenhouse gases and aerosols (Cubasch et al. 2001). This review examines aspects of climate simulations that are relevant to determining how marine ecosystems will respond to global climate change. In general, climate model simulations using future greenhouse gas emission scenarios project oceanic warming, an increase in oceanic stratification and alteration of mixing depth, changes in circulation, increased pH and rise in sea level, alterations in cloud cover and ozone levels and thus solar radiation reaching the ocean surface and altered storm and rainfall regimes (Figure 4). It is very likely that such changes will cause considerable alterations in marine biological communities (Bopp et al. 2001, Boyd & Doney 2002, Sarmiento et al. 2004).

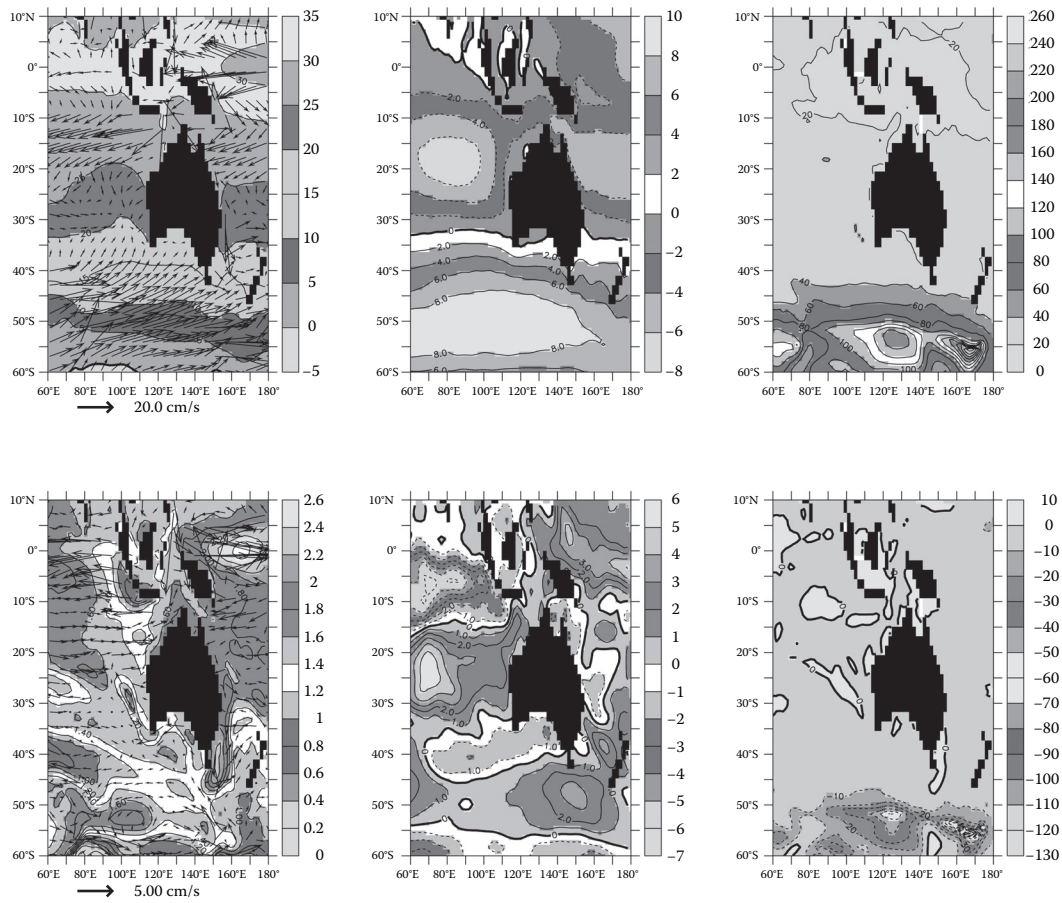
We use future climate projections over the next century from the CSIRO Mk3.5 climate model (hereafter called the CSIRO climate model; Appendix 1) using the IS92a future emissions scenario, often referred to as the 'business-as-usual' scenario. Although there are subtle differences between the CSIRO climate model and other international models, many of the general trends in these fields are similar and we use the CSIRO climate model to suggest the magnitude of the projected changes in the set of variables that follow.



**Figure 4** Important physical and chemical changes in the atmosphere and oceans as a result of climate change.

*Ocean temperature*

Waters around Australia are projected to warm by 1–2°C by the 2030s and 2–3°C by the 2070s (Figure 5). The CSIRO climate model projects the greatest warming off southeast Australia and this is the area of greatest warming this century in the entire Southern Hemisphere. This Tasman Sea warming is associated with systematic changes in the surface currents on the east coast of Australia; including a strengthening of the EAC and increased southward flow as far south as Tasmania (Figure 5). This feature is present in all IPCC climate model simulations, with only the magnitude of the change differing among models. Changes in currents leading to the Tasman Sea warming observed to date is driven by a southward migration of the high-latitude westerly wind belt south of Australia, and this is expected to continue in the future (Cai et al. 2005, Cai 2006).



**Figure 5** (See also Colour Figure 5 in the insert.) Simulated annual means of SST (°C) with annual mean surface currents (cm/s) (left), annual mean zonal winds (m/s) (middle), and mixed layer depth (m) (right). In the middle panels, westerly wind direction is denoted by positive sign, easterly wind direction by negative sign. Top row: 1990s, bottom row: difference between 1990s and 2070s.



*Winds*

Under global warming scenarios, the southeasterly trade winds strengthen east of northern Australia, but weaken to the west of the continent (Figure 5). Westerly winds in southern Australian waters will weaken. In the Australian coastal region, downwelling will prevail due to the dominating winds and density structure of the upper ocean. Increasing wind intensity may suppress localised upwelling in the northeast. However, decreasing wind intensity in southern waters may facilitate localised upwelling there.

*Ocean currents*

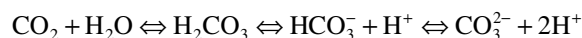
Surface currents on the east coast will show a systematic change (Figure 5) including EAC strengthening and increased southward flow as far south as Tasmania. On the west coast there will be no obvious strengthening of the Leeuwin Current. In the south, the Great Australian Bight region will experience more westward transport as global temperatures rise. Along the northwest and northeast coasts there will be an increase in the northward flow.

*Mixed-layer depth and stratification*

The Australian coastal region is generally a downwelling region due to prevailing winds and density structure of the ocean. In oligotrophic marine regions of Australia, the dominant mechanism of nutrient supply to the upper ocean is winter convective mixing due to cooling of surface waters. Under these conditions the seasonal evolution of the mixed-layer depth and density differences between this layer and the water below play an important role in the supply of nutrients to the upper ocean. Surface ocean warming will stabilise the upper ocean and reduce the supply of nutrients to the surface. The CSIRO climate model simulations project a decline in the annual mean mixed-layer depth by the 2070s (Figure 5).

*CO<sub>2</sub>, pH and calcium carbonate saturation state*

Over the last 200 years, oceans have absorbed 40–50% of the anthropogenic CO<sub>2</sub> released into the atmosphere (Raven et al. 2005). Rising atmospheric CO<sub>2</sub> concentrations via fossil fuel emissions will lead to enhanced oceanic CO<sub>2</sub> as the ocean re-equilibrates with the perturbed atmosphere (McNeil et al. 2003). Elevated CO<sub>2</sub> in the upper ocean will alter the chemical speciation of the oceanic carbon system. As CO<sub>2</sub> enters the ocean it undergoes the following equilibrium reactions:



Two important parameters of the oceanic carbon system are the pH and the calcium carbonate (CaCO<sub>3</sub>) saturation state of sea water ( $\Omega$ ).  $\Omega$  expresses the stability of the two different forms of CaCO<sub>3</sub> (calcite and aragonite) in sea water.

Increasing CO<sub>2</sub> concentration in the surface ocean via uptake of anthropogenic CO<sub>2</sub> will have two effects. First, it decreases the surface ocean carbonate ion concentration (CO<sub>3</sub><sup>2-</sup>) and decreases  $\Omega$ . Using an ocean-only model forced with atmospheric CO<sub>2</sub> projections (IS92a), Kleypas et al. (1999) predicted a 40% reduction in aragonite saturation ( $\Omega_{\text{arag}}$ ) by 2100. Laboratory experiments

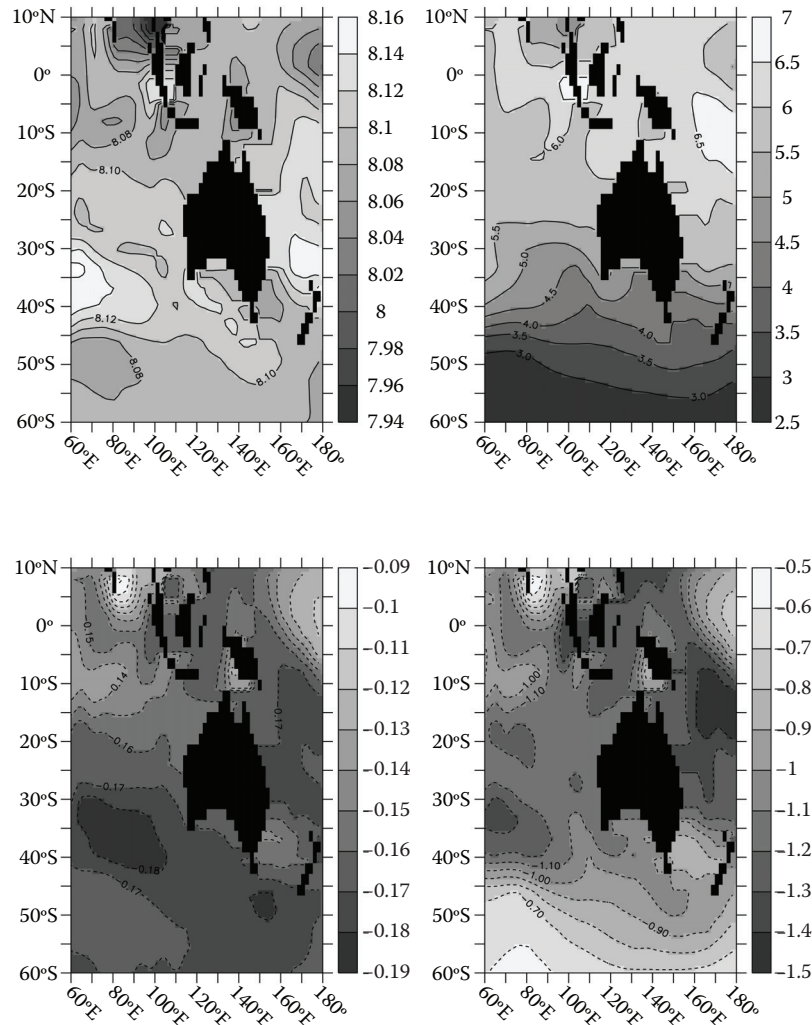
have shown that some species of corals and calcifying plankton (Gattuso et al. 1998, Langdon et al. 2000, Orr et al. 2005) are highly sensitive to changes in  $\Omega$ , which has led to the hypothesis of large decreases in future calcification rates under elevated atmospheric  $\text{CO}_2$  (Kleypas et al. 1999). Second, when  $\text{CO}_2$  dissolves in water it forms a weak acid ( $\text{H}_2\text{CO}_3$ ) that dissociates to bicarbonate, generating hydrogen ions ( $\text{H}^+$ ), which makes the ocean more acidic (pH decreases). Using an ocean-only model forced with atmospheric  $\text{CO}_2$  projections (IS92a), Caldeira & Wickett (2003) predicted a pH drop of 0.4 units by the year 2100 and a further decline of 0.7 by the year 2300. They argued that the oceanic absorption of anthropogenic  $\text{CO}_2$  over the next several centuries may result in a pH decrease greater than inferred from the geological record over the past 300 million years, with the possible exception of those resulting from rare, extreme events such as meteor impacts.

Changes in surface pH and in  $\Omega_{\text{arag}}$  reflect changes in the speciation of carbon within the ocean and are a function of temperature, salinity, alkalinity and dissolved inorganic carbon concentrations. McNeil & Matear (2006) showed that climate change does not alter the projected change in surface pH. The projected pH decrease is controlled by the future levels of atmospheric  $\text{CO}_2$ . However, the decline in  $\Omega_{\text{arag}}$  due to rising  $\text{CO}_2$  levels in the ocean is slightly reduced (~15%) because of the increase in  $\Omega_{\text{arag}}$  due to the increase in surface temperature. For the Australian region, the pH and  $\Omega_{\text{arag}}$  for the 1990s are shown along with the corresponding change in these values relative to 1990s (Figure 6). We see significant declines in these parameters but with the greatest declines occurring off northeast Australia. A major unknown in this region is whether any dissolution of the tropical coral reefs would buffer the pH decreases. Because of the enhanced levels of  $\text{CO}_2$  in the atmosphere and rates of fossil fuel burning, the process of ocean acidification is essentially irreversible over the next century. It will take thousands of years for ocean chemistry to return to a condition similar to that of preindustrial times.

### *Solar radiation*

Highly energetic ultraviolet radiation (UVR) penetrates the ocean surface and is known to have detrimental effects on marine organisms. UVR penetration to the earth's surface increased during the last quarter of the twentieth century as stratospheric ozone was depleted by chlorofluorocarbons (CFCs), halons, hydrochlorofluorocarbons and other compounds. Stratospheric ozone levels appear to have stabilised, however, due to the 1989 implementation of the Montreal Protocol designed to phase out the production of CFCs and other compounds that deplete the ozone layer (de Jager et al. 2005).

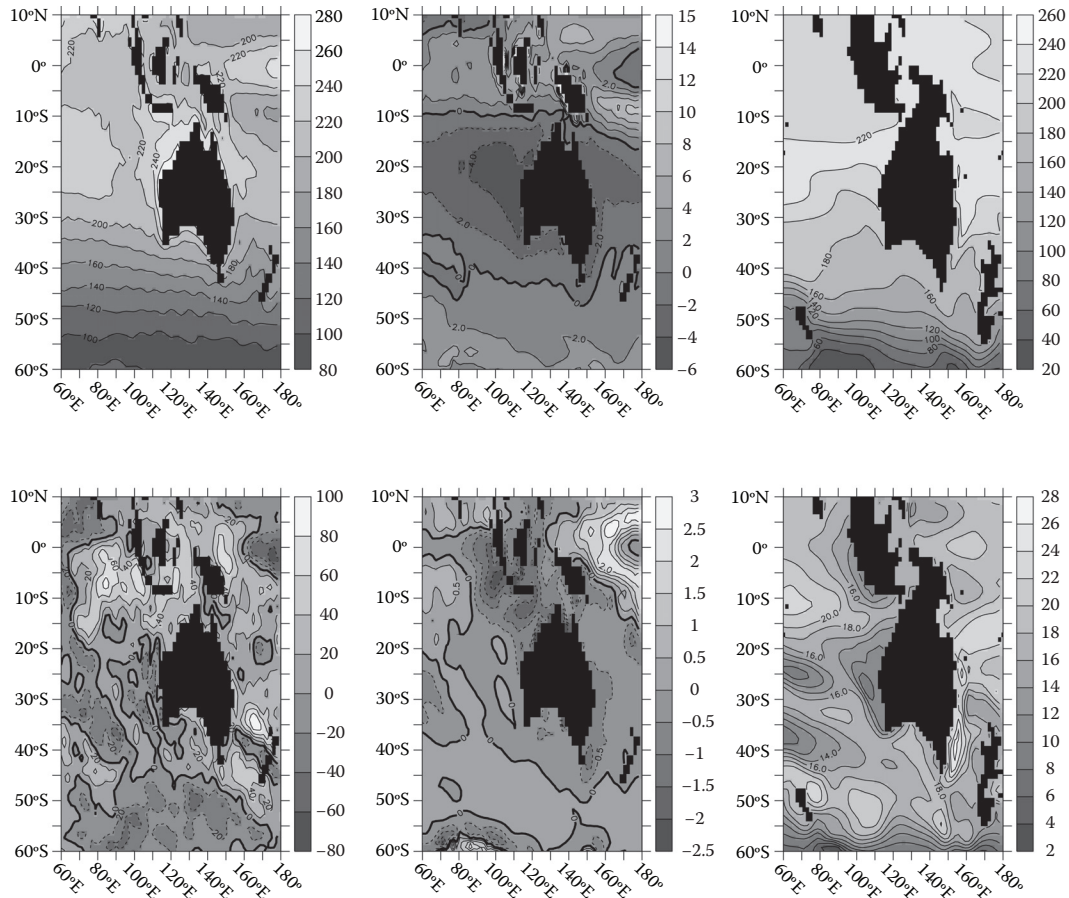
Most climate models predict that the ozone layer will recover and thicken throughout the twenty-first century (de Jager et al. 2005), so UVR penetration should decline (McKenzie et al. 2003). However, these predictions are somewhat uncertain, especially in the timing of the rethickening, due to uncertainties in projections of greenhouse gas emissions and degradation and due to the complex ways that chemical, radiative and dynamic processes will affect stratospheric ozone. For example, chemical reactions of some greenhouse gases (such as methane) can reduce total ozone in the stratosphere but the level of methane emissions is difficult to predict. Climate change will also affect UVR penetration indirectly by influencing other factors such as aerosols, clouds and snow cover. Aerosols can scatter more than 50% of the UV-B — the biologically important component of UVR — and aerosols increased in the atmosphere during most of the twentieth century, although they have shown declines since 1990 (Schiermeier 2005). Clouds can attenuate 15–30% of the UV-B, and cloud reflectance measured by satellite has shown a long-term increase in some regions of the world (McKenzie et al. 2003). All these factors introduce considerable uncertainty in future levels of UVR at the ocean surface, and it has been suggested that climate warming will slow the recovery of the ozone layer by up to 20 yr (Kelfkens et al. 2002).



**Figure 6** (See also Colour Figure 6 in the insert.) Simulated annual means of pH (left) and aragonite saturation state (right). Top row: 1990s, bottom row: difference between 1990s and 2070s.

### *Precipitation and storms*

Changes in the amount or timing of rainfall and the associated river runoff affect the salinity regimes of estuaries and adjacent coastal waters, while in comparison salinity is relatively constant throughout the year in most oceanic waters. Despite the high uncertainty of rainfall projections in Australia, there is a tendency for decreased rainfall over most of Australia and over the oceans in climate model simulations (Figure 7). This general reduction in rainfall may be offset by an increase in the frequency of intense storms (Emanuel 2005, Webster et al. 2005), which will increase rainfall intensity and the associated runoff of freshwater and suspended sediments. In northern Australia, tropical cyclones are important extreme rainfall events. A recent study under 3 times the baseline levels of CO<sub>2</sub> conditions based on levels prior to the industrial revolution in the mid-1800s, projected a 56% increase in the number of simulated tropical cyclones over northeastern Australia with peak winds greater than 30 ms<sup>-1</sup> (Walsh et al. 2004). However, the behaviour of tropical cyclones under



**Figure 7** (See also Colour Figure 7 in the insert.) Simulated annual means of downward solar radiation at the ocean surface ( $\text{W/m}^2$ ) (left), precipitation minus evaporation ( $\text{mm/d}$ ) (middle), and sea-level height anomaly due to upper ocean stratification relative to 2000 m (cm) (right). Top row: 1990s, bottom row: difference between 1990s and 2070s.

global warming is uncertain because they are not currently well resolved by global or regional climate models (Pittock et al. 1996, Walsh & Pittock 1998).

### *Sea level*

Rising sea level around Australia will flood existing coastal environments and alter their marine habitats. With global warming, the CSIRO climate model projects a doubling in the rate of sea-level rise from the observed  $1.44 \text{ mm yr}^{-1}$  for the twentieth century (Church et al. 2001). By the 2080s, sea level is projected to rise by  $0.06\text{--}0.74 \text{ m}$  above the 1990 value (Gregory et al. 2001). These projections take into account both the mean global projections from the IPCC scenarios and the non-uniform spatial distributions of sea-level change related to thermal expansion produced by the climate simulations. However, they do not include vertical land movement, which can be locally important. Sea-level rise projected by the CSIRO model for just the thermal expansion shows an increase in the entire Australian region but with large spatial variability (Figure 7). The variability in sea-level rise reflects how the excess heating of the planet due to global warming is stored in

the oceans, and this large variability is supported by reconstructed sea-level estimates from the past decade (Willis et al. 2003). Therefore, over this century the local impact of sea-level rise may substantially deviate from the global averaged value. For the Australian region, much greater sea-level rise is projected on the east coast than the west coast due to the increased southward penetration of the warm EAC, which causes water here to expand more than in other regions.

### Climate impacts on Australian marine life

In this section we describe the impacts of climate variables on marine life in coastal, pelagic and offshore benthic systems. We consider the climate variables that have greatest impact on structuring marine communities within these systems and for which projections over the next 100 yr are available from global climate models. Where applicable, we review impacts on physiology, distributions and abundance, and phenology of marine organisms. Studies of climate impacts from both field and experimental research from Australia are discussed and supplemented with studies and observations from international research. Results of this section are summarised in Table 1.

#### *Ocean temperature*

Elevated water temperatures stress plants and animals already near the upper limits of their optimal temperature range, slowing growth and impairing reproductive capacity (Philippart et al. 2003, Roessig et al. 2004, Helmuth et al. 2005, Keser et al. 2005). This is because most biological processes have an optimal temperature range and outside this range physiological efficiency declines.

#### *Coastal systems*

*Physiology* Extreme temperatures, both warm and cool, if severe or prolonged can lead to irreparable damage and death of coastal organisms as well as photosynthetic inhibition in marine plants (Bruhn & Gerard 1996, Ralph 1998, Davenport & Davenport 2005, Campbell et al. 2006). Large diebacks of marine fauna and flora in the intertidal and shallow subtidal occur on very hot days particularly when these coincide with low tides during the middle of the day (Tsuchiya 1983, Perez et al. 2000). Such a situation may have been responsible for the major dieback of seagrass beds in southern Australia during early 1993 when over 12,000 hectares were lost (Seddon et al. 2000).

Probably the most widely publicised mass mortalities induced by warmer-than-average temperatures are those resulting from tropical coral reef bleaching events (Hoegh-Guldberg 1999). During bleaching events, the symbiosis between the coral and the unicellular algae (dinoflagellates from the genus *Symbiodinium*) that live within the coral tissues disintegrates. Bleached corals may recover their symbiotic populations of *Symbiodinium* in the weeks and months after a bleaching event if the conditions triggering the event are mild and short-lived, but mortality has reached 100% in bleached corals when stressful conditions have persisted for days to weeks. Recent warming throughout tropical oceans has led to repeated coral bleaching events, not seen anywhere in the world before 1979, affecting hundreds to thousands of square kilometres of coral reefs in almost every region of the world where coral reefs occur. In the most severe global episode of mass coral bleaching (1998), 16% of corals that were surveyed before that event had died by the end of the year (Hoegh-Guldberg 1999, Knowlton 2001).

Mass bleaching events over large sections of the Great Barrier Reef have occurred six times during the past 30 years: in 1983, 1987, 1991, 1998, 2002 and 2006. Mortality rates in this region were relatively low however, primarily because warming on the Great Barrier Reef was less severe than in other parts of Australia and the world. For example, in 1998 a very warm pool of water sat



**Table 1** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
Increasing temperature	Seagrasses and mangroves	Poleward shift in species ranges and a shift in abundance toward species tolerant of warmer waters	Seagrass distributional limits linked to temperature <sup>1</sup>	
		Earlier flowering and fruiting	Flowering of seagrasses in temperate Australia linked to water temperature <sup>2</sup>	
	Seagrass	Increased frequency and intensity of large-scale diebacks with increase in frequency and intensity of extreme temperatures	Southern Australia early 1993 (>12,000 hectares) <sup>3</sup>	
	Rocky shore, fauna and macroalgae	Poleward shift in species ranges and a shift in abundance toward species tolerant of warmer waters		Rocky shores in Europe, United States and South America over past 50 yr <sup>4</sup>
		Increased frequency and intensity of large-scale diebacks with increase in frequency and intensity of extreme temperatures	Diebacks in Tasmania and South Australia hot days <sup>5</sup>	European and Japanese coasts <sup>6</sup>
	Kelp communities	Contraction of kelp ranges, declines in abundance, local extinctions, particularly in Tasmania	Decline of kelp in Tasmanian waters over past 50 yr <sup>7</sup>	Loss of kelp in east Pacific following El Niño <sup>8</sup>
	Phytoplankton	Poleward shift in species ranges and a shift in abundance toward warm-water species	Southward extension of a coccolithophore and a dinoflagellate in southeast Australia <sup>9</sup>	Poleward shift in North Atlantic <sup>10</sup>
		A decline where warming enhances stratification		North Atlantic <sup>11</sup>
		Earlier appearance of plankton in summer in temperate waters		North Sea <sup>12</sup>
		Increase in frequency and intensity of harmful and nuisance blooms		Norwegian coast <sup>13</sup>
	Zooplankton	Poleward shift in species ranges and a shift in abundance toward warm-water species		Large poleward range shifts (>1000 km) in North Atlantic <sup>14</sup>
		A decline where warming enhances stratification		North Atlantic <sup>15</sup>

## CLIMATE CHANGE AND AUSTRALIAN MARINE LIFE

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
		Earlier appearance of zooplankton in summer in temperate waters		North Sea <sup>16</sup>
	Coral reefs	Increase in frequency and severity of coral bleaching and mortality	Six severe bleaching events in past 30 yr (Great Barrier Reef, Ningaloo Reef) <sup>17</sup>	Coral reefs globally <sup>18</sup>
		Increase in local extinctions of coral-associated fauna with bleaching events		Coral reefs globally <sup>19</sup>
	Demersal and pelagic fish	Poleward shift in species ranges and a shift in abundance toward species tolerant of warmer waters	Tasmanian fish distributions shifting south with increase in fish that prefer warmer waters <sup>20</sup>	North Atlantic fish shifting northward <sup>21</sup>
		Earlier dates of mean migration and spawning in temperate and subtropical species		Earlier migrations in northeast Atlantic fish <sup>22</sup>
	Seabirds and wetland birds	Poleward shifts in species ranges and a shift in abundance toward species tolerant of warmer waters	Southward shift of seabird distributions in Western Australia and increase in abundance <sup>23</sup>	
		Earlier arrival in migratory species in temperate and subtropical regions	Southern Australian wetland birds <sup>24</sup>	Terrestrial, wetland and seabirds globally <sup>25</sup>
		Earlier nesting and laying and protracted breeding seasons in temperate and subtropical species	Western and southern Australian seabirds <sup>26</sup>	
	Marine turtles and mammals	Poleward shift in species foraging ranges		Northward shift of cetaceans and turtles in northeast Atlantic <sup>27</sup>
		Earlier breeding		Earlier nesting in marine turtles in United States <sup>28</sup>
		Skewing of turtle sex ratios toward females		Experimental and modelling evidence that warmer temperatures produce more females <sup>29</sup>

*(continued on next page)*

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
Alteration of winds	Phyto- and zooplankton	Increased productivity where wind mixing is enhanced and a reduction where wind strength declines	Production pulses correlated with peaks in wind oscillation in Tasmanian shelf waters <sup>30</sup>	Decreased production in central North Pacific during low-wind regimes <sup>31</sup>
	Coastal fish	Recruitment strength linked to wind strength	Rocky reef fish <sup>32</sup>	
	Seabirds	Reduction of breeding success with prolonged periods of strong winds	Breeding colonies on Great Barrier Reef <sup>33</sup>	
Alteration of currents including strengthening of EAC	Seagrasses & mangroves	Local extinctions of cold-water species in southeastern Australia with increased flow of EAC, appearance of tropical species further south on east coast	Seagrass distributional limits further south on west coast than east coast due to influence of warm-water Leeuwin Current <sup>34</sup>	
	Rocky shore, fauna and macroalgae	Local extinctions of cold-water species in southeastern Australia with increased flow of EAC, appearance of tropical species further south on east coast	Tropical species already found at temperate latitudes on east coast <sup>35</sup>	
	Kelp communities	Local extinctions of cold-water species in southeastern Australia with increased flow of EAC, appearance of tropical species further south on east coast	Expansion of long-spined urchin to Tasmania facilitated by larval transport by EAC <sup>36</sup>	
	Phyto- and zooplankton	Poleward extension of warm currents will transport tropical plankton more southward	High abundance of a tropical coccolithophore off southeast Australia <sup>37</sup>	
Decline in mixed-layer depth/increasing stratification	Phyto- and zooplankton	Decrease in abundance		Phytoplankton productivity in central North Pacific declines as mixed-layer depth decreases <sup>38</sup>
Increased CO <sub>2</sub> and decrease in pH and aragonite saturation state	Mangroves	Increase in productivity with rising atmospheric CO <sub>2</sub>		Experimental evidence <sup>39</sup>

# CLIMATE CHANGE AND AUSTRALIAN MARINE LIFE

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
Possible increase in UV	Seagrasses	Increase in productivity with increase dissolved CO <sub>2</sub> and deepening of depth limits		Experimental evidence <sup>40</sup>
	Rocky shore, fauna and macroalgae	Impaired growth in calcifying fauna and macroalgae and increase in mortality of early life stages		Experimental evidence <sup>41</sup>
	Phytoplankton	Changes in growth and community composition; long-term decline in abundance and distribution of calcifying species		Experimental evidence <sup>42</sup>
	Zooplankton	Impaired growth in calcifying species, particularly pteropods; midterm decline in abundance and distribution		Experimental evidence <sup>43</sup>
	Coral reefs	Impaired growth rates and possible dissolution		Experimental and modelling evidence <sup>44</sup>
	Cold-water corals	High threat of impaired growth rates and possible dissolution		Evidence from modelling work <sup>45</sup>
	Seagrasses	Reduction of growth rates and biomass in UV-sensitive species		Experimental evidence <sup>46</sup>
	Mangroves	Reduction of growth rates and biomass in UV-sensitive species		Experimental evidence <sup>47</sup>
	Rocky shore fauna and macroalgae	Increase mortality of early life stages and reduction of growth rates in UV-sensitive species		Experimental evidence <sup>48</sup>
	Kelp and subtidal macroalgae	Increase mortality of early life stages		Experimental evidence <sup>49</sup>
	Phytoplankton	Reduction of growth rates and biomass in UV-sensitive species and of nutritional value to zooplankton		Evidence from field and laboratory experiments <sup>50</sup>
		Changes in community composition		
	Zooplankton	Increased mortality of early life stages and reduction of growth rates in UV-sensitive species		Evidence from laboratory experiments <sup>51</sup>
	Coral reefs	Increase in mortality during bleaching events through synergistic effects with temperature		Evidence from laboratory experiments <sup>52</sup>

(continued on next page)

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
Increase in frequency or intensity of severe storms and extreme rainfall events and a decrease in average rainfall	Demersal and pelagic fish	Increase mortality of early life stages and reduction of growth rates		Evidence from laboratory experiments <sup>53</sup>
		Damage to epidermis and ocular components in pelagic species and increased mortality in egg and larval stages in shallow water and upper ocean		Evidence from laboratory experiments <sup>54</sup>
	Mangroves	Shifts in community abundance as coastal salinity regimes are altered and nutrient and sediment loading changes	Increase in mangrove area in southeast Australia may be indirectly linked to changes in rainfall although changes in land use likely to be overriding factor <sup>55</sup>	
	Seagrasses	Destruction of seagrass beds	Loss of >1000 km <sup>2</sup> in Harvey Bay after severe storms and flooding <sup>56</sup>	Large-scale destruction in United States after cyclones <sup>57</sup>
	Kelp communities and subtidal macroalgae	Shifts in community abundance and increased local mass mortality events associated with storms and flood events	Switch from canopy-forming macroalgae to turf-forming algae in South Australia linked to enhanced nutrient supply from coastal runoff <sup>58</sup>	Range shifts of macroalgae in New Zealand and California associated with storms and wave exposure <sup>59</sup>
	Benthic macrofauna	Shifts in community abundance and increased local mass mortality events associated with storms and flood events	Mass mortality of grazing urchins after freshwater pulse <sup>60</sup>	Field experiments revealed shift in community composition with increased sedimentation <sup>61</sup>
	Coral reefs	Alteration of peak timing of life cycle events	High rainfall may decrease salinity in estuaries so triggering prawn emigration in northern Australia <sup>62</sup>	High rainfall may decrease salinity in estuaries so triggering prawn emigration in the United States <sup>63</sup>
		Mass mortality events associated with storms and flood events	Mass mortality of corals on Great Barrier Reef after cyclones and flood events <sup>64</sup>	Mass mortality of corals in Caribbean after cyclones <sup>65</sup>



# CLIMATE CHANGE AND AUSTRALIAN MARINE LIFE

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

Expected change in climate	Species group/natural system	Expected climate impact in Australia	Observations in Australia	Observations elsewhere or experimental evidence
Rise in sea level	Phytoplankton	Community structure influenced by rainfall regime and runoff	Lower coral diversity on Great Barrier Reef in wet tropics <sup>66</sup>	Evidence from field experiment and time series <sup>67</sup>
		Diatoms may decline with decreasing average runoff and nutrient input while dino-flagellates (including harmful algae) may profit from storm-associated runoff and humic substances in coastal waters		
	Marine turtles and mammals	Increased mortality events	High mortalities of turtles and seal pups associated with cyclones and storms <sup>68</sup>	
	Mangroves	Alteration of hydrological or tidal regimes leads to mortality of mangroves		Mangroves in Africa and Asia <sup>69</sup>
	Seagrass	Mangrove retreat with rising sea level Reduction in growth of seagrass and distributional shifts		Caribbean <sup>70</sup> 50 cm rise in sea level expected to result in 30–40% reduction of seagrass growth <sup>71</sup>
	Seabirds	Loss of breeding sites for species that nest on low-lying coastal areas through increased flooding and erosion		Evidence from modelling work <sup>72</sup>
	Marine turtles and mammals	Loss of breeding and haul-out sites for species through increased flooding and erosion		50 cm rise in sea level expected to lead to a 32% loss of turtle nesting beaches in the Caribbean <sup>73</sup>

Notes: <sup>1</sup>Walker & Prince 1987; <sup>2</sup>West & Larkum 1979, Cambridge & Hocking 1997, Inglis & Smith 1998; <sup>3</sup>Seddon et al. 2000; <sup>4</sup>Barry et al. 1995, Southward et al. 1995, Sagarin et al. 1999, Zacherl et al. 2003, Mieszkowska et al. 2005, Rivadeneira & Fernandez 2005, Simkanin et al. 2005, Smith et al. 2006; <sup>5</sup>Valentine & Johnson 2004, Womersley & Edwards 1958; <sup>6</sup>Tsuchiya 1983, Perez et al. 2000; <sup>7</sup>Edyvane 2003, Edgar et al. 2005; <sup>8</sup>Dayton & Tegner 1984, Zimmerman & Robertson 1985, Dayton et al. 1998, 1999, Adey & Steneck 2001; <sup>9</sup>Blackburn & Creswell 1993, Blackburn 2005, G. Hallegraeff pers. com.; <sup>10</sup>M. Edwards 2005; <sup>11</sup>Richardson & Schoeman 2004; <sup>12</sup>Edwards & Richardson 2004; <sup>13</sup>Edwards et al. 2006; <sup>14</sup>Beaugrand et al. 2002, Bonnet et al. 2005; <sup>15</sup>Richardson & Schoeman 2004; <sup>16</sup>Greve et al. 2004, Edwards & Richardson 2004, Kirby et al. 2007; <sup>17</sup>Hoegh-Guldberg 1999, Wilkinson 2004; <sup>18</sup>Hoegh-Guldberg 1999, Knowlton 2001; <sup>19</sup>Dulvy et al. 2003; <sup>20</sup>Welsford & Lyle 2003, P. Last pers. com.; <sup>21</sup>Beare et al. 2004, Byrkjedal et al. 2004, Perry et al. 2005, (continued on next page)

**Table 1 (continued)** Expected and observed impacts of climate change on Australian marine life and field or experimental evidence from outside Australia

*Notes (continued):* Rose 2005a, 2005b; <sup>22</sup>Sims et al. 2001; <sup>23</sup>Dunlop & Wooller 1986, Dunlop et al. 2001, Bancroft et al. 2004; <sup>24</sup>Beaumont et al. 2006; <sup>25</sup>Mason 1995, Crick et al. 1997, Archaux 2003, Both et al. 2004, Lehtikoinen et al. 2004, Both et al. 2005, Marra et al. 2005, Jonzén et al. 2006, Moller et al. 2006; <sup>26</sup>Dunlop & Wooller 1986, Chambers 2004; <sup>27</sup>Robinson et al. 2005, MacLeod et al. 2005, McMahon & Hays 2006; <sup>28</sup>Weishampel et al. 2004; <sup>29</sup>Yntema & Mrosovsky 1982, Godfrey et al. 1999, Booth & Astill 2001, Glen & Mrosovsky 2004; <sup>30</sup>Harris et al. 1991; <sup>31</sup>Polovina et al. 1994; <sup>32</sup>Thresher et al. 1989; <sup>33</sup>King et al. 1992; <sup>34</sup>Walker & Prince 1987; <sup>35</sup>Griffiths 2003; <sup>36</sup>Johnson et al. 2005; <sup>37</sup>Blackburn & Cresswell 1993, Blackburn 2005; <sup>38</sup>Venrick et al. 1987, Polovina et al. 1994, 1995; <sup>39</sup>Polovina et al. 1995, Roemmich & McGowan 1995, Farnsworth et al. 1996, Ainsworth & Long 2005; <sup>40</sup>Invers et al. 1997, 2002, Zimmerman et al. 1997; <sup>41</sup>Gao et al. 1993, Kurihara et al. 2004, Michaelidis et al. 2005, Berge et al. 2006; <sup>42</sup>Riebesell et al. 2000, Antia et al. 2001, Tortell et al. 2002, Engel et al. 2005; <sup>43</sup>Orr et al. 2005; <sup>44</sup>See Hoegh-Guldberg 2004; <sup>45</sup>Guinotte et al. 2006, Raven et al. 2005; <sup>46</sup>Dawson & Dennison 1996; <sup>47</sup>Moorthy & Kathiresan 1997, 1998; <sup>48</sup>Graham 1996, Rijstenbil et al. 2000, Cordi et al. 2001, Lesser et al. 2003, Przeslawski et al. 2004, 2005, Bonaventura et al. 2006; <sup>49</sup>Graham 1996, Bischof et al. 1998, Swanson & Druehl 2000, Wiencke et al. 2006; <sup>50</sup>Behrenfeld et al. 1993, Keller et al. 1997, Wilhelm et al. 1997, Wängberg et al. 1999, Garde & Cailliau 2000, Barbieri et al. 2002, Litchman & Neale 2005; <sup>51</sup>Karanas et al. 1979, Damkaer & Dey 1983; <sup>52</sup>Lesser 1996, 1997, Baruch et al. 2005, Drohan et al. 2005; <sup>53</sup>Shick et al. 1996, Wellington & Fitt 2003; <sup>54</sup>Hunter et al. 1982, Keller et al. 1997, Zagarese & Williamson 2001, Markkula et al. 2005; <sup>55</sup>Saintilan & Williams 1999, Harty 2004, Rogers et al. 2006; <sup>56</sup>Preen et al. 1995; <sup>57</sup>Thomas et al. 1961; <sup>58</sup>Gorgula & Connell 2004; <sup>59</sup>Graham 1997, Cole et al. 2001; <sup>60</sup>Andrew 1991; <sup>61</sup>Norkko et al. 2002, Thrush et al. 2003a, 2003b, Lohrer et al. 2004; <sup>62</sup>Staples 1980, Vance et al. 1985, Staples & Vance 1986, Vance et al. 1998; <sup>63</sup>Zein-Eldin & Renaud 1986; <sup>64</sup>Alongi & Robertson 1995, Alongi & MacKinnon 2005; <sup>65</sup>Porter & Meier 1992, Gardner et al. 2005; <sup>66</sup>De Vantier et al. 2006; <sup>67</sup>Carlsson et al. 1995, Goffart et al. 2002; <sup>68</sup>Limpus & Reed 1985, Pemberton & Gale 2004; <sup>69</sup>Blasco et al. 1996; <sup>70</sup>Ellison 1993, Parkinson et al. 1994; <sup>71</sup>Short & Neckles 1999; <sup>72</sup>Galbraith et al. 2002, Smart & Gill 2003; <sup>73</sup>Fish et al. 2005.

above Scott Reef off northwest Australia for several months, resulting in an almost total bleaching of these offshore reefs and mortality of corals down to 30 m depth. The recovery of Scott Reef has been very slow (Wilkinson 2004).

By the middle of this century, temperature thresholds for coral bleaching will be exceeded every year in Australia if sea temperatures increase as projected by global climate models (Hoegh-Guldberg 1999). Based on the current responses of corals, it is estimated that an increase of 2°C in tropical and subtropical Australia would result in annual bleaching and quite possibly regular, large-scale mortalities (Hoegh-Guldberg 1999, 2004, Lough 2000). A geographic analysis of risk to the Great Barrier Reef associated with these changes in sea temperature indicated that the projected succession of devastating mass coral bleaching events will severely compromise the ability of reefs to recover, no matter where they are found along the Queensland coastline (Done et al. 2003). This analysis indicated that deterioration of coral populations is likely in most of the scenarios examined and this is reinforced by findings from other studies (Hoegh-Guldberg 1999, Donner et al. 2005).

For large, mobile animals that may be transient visitors to coastal waters, oceanic warming may impact particular life stages such as juveniles or embryos. For example, gender in all turtles is determined by ambient nest temperatures during embryonic development (Mrosovsky et al. 1992, Godfrey et al. 1999, Hewavisenthi & Parmenter 2002a). Small changes in temperature close to the pivotal temperature at which a 50:50 sex ratio is produced (~29°C for marine turtles) skew the sex ratio of hatchlings, with warmer temperatures producing more females (Yntema & Mrosovsky 1982, Godfrey et al. 1999, Booth & Astill 2001, Glen & Mrosovsky 2004). Many nesting beaches around the world, including most Australian beaches, already have a strong female bias (Limpus

1992, Loop et al. 1995, Godfrey et al. 1996, Binckley et al. 1998, Hewavisenthi & Parmenter 2002b, Hays et al. 2003, Glen & Mrosovsky 2004) so if temperatures rise, the proportion of eggs developing as males may be further reduced. However, light-coloured (thus cooler) beaches within nesting regions produce more males (Hays et al. 2003). In Queensland beaches on offshore coral cays and islands have lighter-coloured sand than mainland beaches, thus maintaining sex ratios (Environment Australia 1998). Therefore if temperatures warm on these beaches, the gross skewing in sex bias may have serious implications for local breeding population persistence.

On a global scale outbreaks of disease have increased over the last three decades in many marine groups including corals, echinoderms, mammals, molluscs and turtles (Ward & Lafferty 2004). Causes for increases in diseases of many groups remain uncertain, although temperature is one factor that has been implicated in corals, molluscs and turtles (Harvell et al. 2002). Previously unseen diseases have also emerged in new areas through shifts in distribution of hosts or pathogens, many of these shifts are in response to climate change (Harvell et al. 1999). A consequence of climate-mediated physiological stress is that host resistance to pathogens or parasites can be compromised (Scheibling & Hennigar 1997, Garrabou et al. 2001, Lee et al. 2001, Harvell et al. 2002, Mouritsen et al. 2005). Temperature-induced disease outbreaks in corals on the Great Barrier Reef have occurred at the same time as bleaching events, resulting in increased coral mortality rates (Jones et al. 2004). A large-scale mortality of greenlip abalone, *Haliotis laevis*, along the south Australian coast in 1985 and 1986 due to infection by *Perkinsus* parasites may have been aggravated by warmer water temperatures predisposing the abalone to this disease (Goggin & Lester 1995). Population declines due to temperature-related disease susceptibility have also been reported in several Californian abalone species through both observational and experimental studies (Davis et al. 1996, Vilchis et al. 2005).

Fibropapillomatosis, a disease that causes tumours, is now common in green turtles *Chelonia mydas* and olive ridley turtles *Lepidochelys olivacea* (Adnyana et al. 1997, Jones 2004). This disease was first documented in the 1930s and was rare until the early 1980s but has since reached epidemic proportions in many turtle populations worldwide (Jones 2004). The prevalence of the tumours in young turtles suggests prolonged exposure to anthropogenic pollutants may be responsible (Adnyana et al. 1997, Herbst et al. 2004, Jones 2004, Ene et al. 2005, Foley et al. 2005). However, the increase of this disease in recent decades coincides with rapidly rising temperatures so it may also be indirectly related to climate change (Robinson et al. 2005).

*Distribution and abundance* Temperature influences the abundance and distribution of coastal marine life such as macroalgae, seagrasses and molluscs (McMillan 1984, Walker & Prince 1987, Jernakoff et al. 1996, Steneck et al. 2002, Hiscock et al. 2004). Fluctuations in species abundances and community composition have been linked to variations in temperature (Southward et al. 1995, Tegner et al. 1996, Dayton et al. 1999, Grove et al. 2002, M.S. Edwards 2004, Schiel et al. 2004, Smith et al. 2006). Shifts in species distributions associated with ocean warming are documented from rocky shores in Europe, the United States and South America (Barry et al. 1995, Sagarin et al. 1999, Zacherl et al. 2003, Mieszkowska et al. 2005, Rivadeneira & Fernandez 2005, Simkanin et al. 2005). For example, a recent comprehensive resurvey of rocky intertidal shores around the United Kingdom found range extensions in the northern (high-latitude) limits of some warm-water species over the past 50 yr and a retraction in the southern limits of fewer cold-water species although rates of recession were not as fast as rates of advancement in warm-water species (Mieszkowska et al. 2005). The high levels of endemism along Australia's southern coastline could increase vulnerability to temperature increases compared to temperate rocky shores elsewhere; many endemic species may have more stringent temperature limits and so may be particularly susceptible to warming (Beardall et al. 1998).

There are interactive effects between the impacts of warming and availability of nutrients on distribution and abundance of macroalgae. Declines of giant kelp forest communities in Tasmanian coastal waters have been associated with thermal and nutrient stress (Edyvane 2003, Edgar et al. 2005). *Macrocystis* kelp forests in Australia are found predominantly in the southeast where water conditions are cool and relatively nutrient rich. There has been a considerable decline in Tasmanian kelp forests over the past 50 yr associated with rising temperatures (Edyvane 2003). Further, an unusual dieback of the shallow sublittoral brown macroalga *Phyllospora comosa* along the east coast of Tasmania in 2001 has also been attributed to above-average seawater temperatures coupled with nutrient stress (Valentine & Johnson 2004). If the EAC strengthens as projected by climate models, warm, nutrient-poor water will impinge more frequently on Tasmanian giant kelp communities, potentially leading to local extinction and a shift of macroalgal communities to understory-dominated forms (Kennelly 1987a,b, Dayton et al. 1999).

Globally, mangrove distribution is generally constrained by the 20°C winter sea isotherm; there are a few exceptions, such as the more southerly distribution of mangroves in eastern Australia (Duke 1992). It has been suggested that this distribution is the result of small-scale extensions of warmer currents, such as the EAC, or that the southern populations are a relict representing refuges of more poleward distributions in the past (Duke 1992). As mangrove species show considerable variation in their sensitivity to temperature, species composition of mangrove forests will alter as temperatures rise and species distributions are expected to shift poleward (Field 1995).

Evidence suggests that some benthic and demersal fish species may be able to move as oceans warm, regardless of whether there is a shift in associated habitats such as coral reefs, kelp forests or rocky reef communities. Certain fishes associated with coral reefs appear to be able to populate reefs that do not have corals, as shown by the appearance of coral reef fishes in southern New South Wales and Victoria during the summer (Hoegh-Guldberg 2004). These fishes recruit into coastal areas and grow for several months, disappearing when cold conditions return. Many coral reef fish may be able to move southward as oceans warm, although obligate corallivorous species would presumably be missing (Hoegh-Guldberg 2004). This has already been observed in other parts of the world such as California, where the composition of near-shore rocky reef fish communities shifted in dominance from cold-water northern species to warm-water southern species as temperatures warmed (Holbrook et al. 1997). However, coral bleaching has already led to local extinctions of a few coral-associated fish (Dulvy et al. 2003) and doubtless many more could disappear as coral bleaching episodes increase.

Other mobile groups such as seabirds and marine mammals may be able to rapidly shift their distributions with climate change, although many are restricted to coastal habitats during breeding seasons. Warmer waters may allow marine turtles and dugongs to extend their foraging distributions in Australian inshore waters further south. However, green turtles *Chelonia mydas* and dugongs *Dugong dugon* selectively feed on seagrasses while hawksbill turtles *Eretmochelys imbricata* forage on coral reefs, so their ability to shift distributions are likely to be limited by changes in the distribution of their food sources.

Range expansions have already been observed in seabird species along the west coast of Australia, with tropical species extending their breeding and foraging ranges southward (Dunlop & Wooller 1986, Dunlop et al. 2001). The recent growth of nesting colonies of wedge-tailed shearwaters *Puffinus pacificus* in southwestern Australia may be due to a southerly movement from more northerly colonies as temperatures rise (Bancroft et al. 2004). Wedge-tailed shearwaters are found only over waters with surface temperatures exceeding 20°C (Surman & Wooller 2000). The population of Australasian gannets *Morus serrator* that breed in southeast Australia has increased by approximately 6% per year since 1980, with new breeding sites being established as nesting space becomes limited (Bunce et al. 2002). This increase appears to be associated with a long-term

warming trend and a concurrent increase in the abundance of small pelagic prey fish, principally pilchards *Sardinops sagax*.

**Phenology** Water temperature and day length are the principal triggers or correlates for the timing of biological events such as breeding or migration in marine animals and flowering and seed germination in marine plants (Parmesan & Yohe 2003). Synchrony in reproduction of widely distributed seagrass beds and mangroves (Clarke & Myerscough 1991, Inglis & Smith 1998, Diaz-Almela et al. 2006) suggests control by these environmental variables. Such synchronies of biological events in distant populations may be regulated by a large-scale independent factor such as temperature or day length. Regular flowering of the seagrass *Posidonia australis* occurs between April and June in southwestern Australia, probably induced by a seasonal decline in water temperatures (West & Larkum 1979, Cambridge & Hocking 1997). However, further north in Shark Bay *P. australis* meadows do not flower every year (Larkum 1976). Widespread flowering *P. australis* is also rare off central New South Wales on the east coast (Walker et al. 1988). Shark Bay and central New South Wales are near the northern limits for this temperate seagrass species so the threshold decline in water temperature required to trigger flowering may begin to occur less frequently. As a warming of coastal waters is projected, particularly off southeast Australia, episodes of flowering of *P. australis* may become even rarer in northern meadows. The deposition of seed banks after flowering is an important process that allows seagrass beds to recover rapidly from catastrophic disturbances such as storms or floods (Preen et al. 1995).

Temperature has also been correlated with the timing of mass spawning in tropical reef corals on the Great Barrier Reef (Babcock et al. 1986) and on the tropical west coast (Simpson 1991). However, the physiological and evolutionary mechanisms that underlie the timing of reproduction in corals and in most marine invertebrates are far from clear; thus it is difficult to speculate on the consequences of any change in the timing of spawning.

There is global evidence that climate change is influencing the phenology of larger marine fauna. Marine turtles in Florida in the United States are nesting earlier in response to warmer ocean temperatures (Weishampel et al. 2004). Warmer waters also reduce the interval length between the multiple clutches laid within a nesting season (Sato et al. 1998, Hays et al. 2002). Not all adult turtles will breed each year, but the relative numbers arriving annually at widely separated rookeries in Australia and the Indo-Pacific are similar, suggesting large-scale environmental forcing on reproductive success (Limpus & Nicholls 1988, Chaloupka 2001). Variation in winter sea-surface temperature anomalies partly explains interesting intervals of a Costa Rican population of green turtles *Chelonia mydas*, with 2-yr remigration probabilities increasing in warmer years (Solow et al. 2002). In Australia, interannual fluctuations in numbers of green turtles nesting at rookeries within the Great Barrier Reef are positively correlated with the Southern Oscillation Index, also with a 2-yr lag (Limpus & Nicholls 1988). Modelling studies suggest breeding intervals (time between nesting years) are determined by resource provisioning on adult feeding grounds and the 2-yr lag represents the time required for physiological provisioning for reproduction and migration (Hays 2000, Rivalan et al. 2005). Green turtles are herbivorous so are likely to be tightly coupled to productivity in coastal waters (Broderick et al. 2001).

Mean egg-laying dates of many terrestrial bird species around the world have advanced considerably in response to increasing temperatures (Archaux 2003, Both et al. 2004, 2005, Moller et al. 2006). Migratory species are arriving earlier and leaving later (Mason 1995, Crick et al. 1997, Lehikoinen et al. 2004, Marra et al. 2005, Jonzén et al. 2006). Most evidence is from the Northern Hemisphere, but a similar pattern has recently been found in Australian migratory wetland birds such as the curlew sandpiper *Calidris ferruginea* and the double-banded plover *Charadrius bicinctus* (Beaumont et al. 2006). It is assumed that such changes are also occurring in Australian seabirds. Protracted breeding seasons observed in seabird species in Western Australia are likely to be a



response to changing climate (Dunlop & Wooller 1986, Chambers et al. 2005). Breeding success of little penguins *Eudyptula minor* in Bass Strait is correlated with sea temperatures and mean laying dates are earlier in warmer years (Chambers 2004).

#### *Pelagic systems*

**Physiology** All plankton are poikilothermic and thus physiological rate processes and rates of overall growth are highly sensitive to temperature (Eppley 1972, Peters 1983, Huntley & Lopez 1992), with many plankton having a  $Q_{10}$  between 2 and 3 (i.e., a doubling to tripling in the speed of rate processes for a 10°C temperature rise). Species have a thermal optimum where growth is maximal and thermal limits beyond which net growth ceases or becomes negative. Basal metabolic losses increase with increasing temperature so that zooplankton fitness and, subsequently, abundance and distribution may be adversely affected. Little information is available on temperature ranges for Australian plankton, and in most cases experiments have been carried out with temperate plankton strains. Culture studies do give some indication (e.g., Smayda 1976) and suggest that species with tropical and subtropical distributions have growth optima <30°C. Optimal growth for the dominant picophytoplankton species *Synechococcus* and *Prochlorococcus* in the Great Barrier Reef is in the range 20–30°C (Furnas & Crosbie 1999), and in the Atlantic Ocean growth of *Synechococcus* peaks at 28°C and growth of *Prochlorococcus* at a cooler temperature of 24°C (Moore et al. 1995). As individual plankton strains have their own thermal optimum and limits for growth, warming will have differential effects on the growth of individual species and changes in phytoplankton and zooplankton community composition.

Although direct effects of temperature changes are fundamentally important to plankton rate processes, indirect effects are also critical to plankton growth rates because zooplankton grow at temperature-dependent maximal rates only when they are food saturated (Kleppel et al. 1996, Hirst & Lampitt 1998, Richardson & Verheye 1998). Available evidence from tropical Australia indicates that copepod growth and egg production rates are regulated primarily by food availability rather than temperature (McKinnon & Thorrold 1993, McKinnon 1996, McKinnon & Ayukai 1996, McKinnon et al. 2005). For example, generation times of the common coastal tropical copepod *Acrocalanus gibber* decreased by 25% with a 5°C rise in temperature because of food limitation (McKinnon 1996). Therefore, zooplankton growth rates appear to be severely food limited in the warm, oligotrophic waters of tropical Australia (McKinnon & Duggan 2001, 2003). Climate impacts on nutrient enrichment processes are thus likely to be at least as important in Australia as local and direct temperature effects.

Temperature also has an effect on the body size of individual species of zooplankton. Copepod body length typically decreases with increasing temperature (McKinnon 1996). Effects of temperature on upper trophic levels may be strongly mediated by zooplankton size, which is a key determinant of food quality for planktivorous fish. Warming of ocean waters will impact the physiology or morphology of demersal and pelagic fish populations directly and indirectly, but too little is known to speculate how these might be driven by climate change. Warming temperatures will affect all life stages of these fish but egg and larval stages may be the most sensitive.

**Distribution and abundance** Plankton respond rapidly to ocean warming and have exhibited some of the largest range shifts of any marine group (Hays et al. 2005). Members of the warm temperate copepod communities in the northeast Atlantic have moved more than 1000 km poleward over the last 50 yr (Beaugrand et al. 2002, Bonnet et al. 2005), although this may be more associated with changing currents than warming. Concurrently, cooler water copepod assemblages have retracted further toward the North Pole. It is likely that similar expansions have also occurred in warm

temperate and tropical dinoflagellates in the North Atlantic (M. Edwards 2004). Unfortunately, plankton observations are rare in Australian waters. The only examples of plankton range extensions are for the coccolithophorid *Gephyrocapsa oceanica* and the dinoflagellate *Noctiluca scintillans*. Since the early 1990s this species has begun to appear in high densities off southeastern Australia, with the likely cause being warmer sea temperatures (Blackburn & Cresswell 1993, Blackburn 2005, G. Hallegraeff personal communication). Range expansions of other plankton species may have considerable social and economic consequences. The box jellyfish *Chironex fleckerii* is currently at the southern limit of its range on North Queensland beaches where it causes problems for bathers during summer; it may also expand its range further south as waters warm.

It is well recognised that sea temperature is a principal determinant of fish species abundance and distribution (Lehodey et al. 1997, Roessig et al. 2004, Perry et al. 2005), biomass (Ware 1995, O'Brien et al. 2000, Drinkwater 2005), and other critical life-history and physiological processes (Burkett et al. 2001). Poleward shifts in distribution over the last century have been documented for fish in the North Atlantic and the North Sea (Beare et al. 2004, Byrkjedal et al. 2004, Perry et al. 2005, Rose 2005a,b), but observations from Australian waters are again few. Changes in the distribution of large pelagic fishes, such as tunas and billfish, have been observed in response to climate variability both seasonally (Zagaglia & Stech 2004) and interannually in terms of El Niño Southern Oscillation (ENSO) (Lehodey 2001) and Rossby waves (White et al. 2004). Seasonal distributions may be impacted if the timing of expansion or contraction of currents, such as the Leeuwin or EAC, alters. For example, southern bluefin tuna *Thunnus maccoyii* are restricted to the cooler waters south of the EAC and range further north when the current contracts up the New South Wales coast (Majkowski et al. 1981). This response to climate variation has allowed real-time spatial management to be used to restrict catches of southern bluefin tuna by non-quota holders in the east coast fishery by restricting access to ocean regions believed to contain southern bluefin tuna habitat (Hobday & Hartmann 2006). The seasonal presence of these fish along the east coast of Australia may be reduced further if Tasman Sea warming continues. Preliminary analyses indicate that changes may have already occurred, with fewer fish moving to the east coast in the Austral winter (Polacheck et al. 2006).

Species from intermediate trophic levels (such as sardines and anchovies) are also crucial to maintenance of biodiversity in the pelagic realm. These are particularly sensitive to climate impacts based on studies elsewhere in the world (Chavez et al. 2003). A rare example from Australia is the replacement in eastern Tasmania of cold-water jack mackerel *Trachurus declivis* with warm-water redbait *Emmelichthys nitidus* from the EAC (Welsford & Lyle 2003), consistent with a warming trend on the east coast of Australia and Tasmania.

Most species of marine turtles (except flatback turtles) move between coastal habitats and open oceans, being distributed in waters generally warmer than 15–20°C (Davenport 1997), although leatherbacks and loggerheads do penetrate into colder waters. Large leatherbacks are reported from waters as cool as 8°C but juvenile leatherbacks (<100 cm carapace length) are rarely found in waters <26°C (Eckert 2002). Reports from the Northern Hemisphere indicate that turtle populations may already be responding to warmer temperatures. Most sightings of marine turtles in U.K. waters over the past century are from the last 40 yr and sightings are increasing, suggesting a poleward shift or expansion in distributions but may also be a result of better reporting (Robinson et al. 2005, McMahon & Hays 2006). Global ranges of marine mammals are often related to water temperature (Learmonth et al. 2006). However, climate-induced changes in prey availability will strongly influence distributions of marine mammals. A recent increase of warm-water cetaceans recorded in the northeast Atlantic is likely to be the result of northward expansions linked to shifts of lower trophic levels in response to warming temperatures (MacLeod et al. 2005).

*Phenology* There are insufficient data to assess changes in timing of plankton blooms in Australia, but overseas studies show that timing is sensitive to climate warming and this can have effects that resonate to higher trophic levels. In the plankton ecosystem of the North Sea, the timing of taxa associated with low turbulent conditions in summer advanced with warming of 0.9°C from 1958 to 2002, with meroplankton moving forward by 27 days, dinoflagellates by 23 days, diatoms by 22 days, copepods by 10 days and non-copepod holozooplankton by 10 days (Edwards & Richardson 2004). These changes in phenology were greater than those observed in terrestrial communities (Root et al. 2003). Some groups such as dinoflagellates may not only be responding physiologically to temperature, but may also react to temperature indirectly through earlier onset or intensity of stratification. Others such as meroplankton are temperature sensitive because they are dependent on temperature to stimulate physiological developments and larval release (Kirby et al. 2007). Important gelatinous meroplankton species that may display such tendencies include the medusa stages of box jellyfish and the small highly poisonous Irukandji jellyfish, which has stings that can be fatal to bathers. Only one species, *Carukia barnesi*, has been demonstrated to cause Irukandji syndrome but at least six other, mostly undescribed, species may also be responsible in Australian waters (Barnes 1964, Gershwin 2005, Little et al. 2006).

Although many plankton species are responding to climate warming, the magnitude of the response differs throughout the community, having profound implications for the assembly, structure and functioning of the pelagic communities and the entire pelagic ecosystem (Edwards & Richardson 2004). The different extent to which functional groups are moving forward in time in response to warming (e.g., phytoplankton responding more than zooplankton) may lead to a mismatch between successive trophic levels and a change in the synchrony of timing between primary, secondary and tertiary production. Efficient transfer of marine primary and secondary production to higher trophic levels such as commercially important fish species is largely dependent on the temporal synchrony between successive trophic production peaks in temperate systems (Cushing 1990). Thus, marine trophodynamics may have already been radically altered by ocean warming and the extent to which this is happening in Australian temperate waters is unknown.

Phenology of migrations and spawning of many other marine species is also expected to alter. For example, squid *Loligo forbesi* in the northeast Atlantic migrate to inshore spawning grounds earlier in warmer years (Sims et al. 2001) while flounder *Platichthys flesus* migrate later (Sims et al. 2004).

#### *Offshore benthic systems*

*Physiology* Cold-water corals have been recorded from all the oceans and differ from shallow, tropical, reef-forming species in that they lack symbiotic algae and are found at depths of several hundred metres below sea level. Cold-water corals are restricted largely to temperatures between 4°C and 12°C (Roberts et al. 2003, Roberts et al. 2006). As these corals have evolved to be adapted to this narrow yet stable temperature range, any rapid warming or cooling of temperatures is likely to impact negatively on coral physiology. For example, rising temperatures will influence their calcification rates, physiology and biochemistry.

*Distribution and abundance* Much of the relationship between temperature and benthic and demersal fish populations is likely to be a consequence of temperature-related productivity in pelagic layers of the ocean, in addition to physiological dependencies. This relationship between temperature and fish production and distribution is apparent over the decadal timescale where oceanographic (temperature and productivity) regime shifts regulate zooplankton biomass, fisheries catches and seabird abundances (Beamish et al. 1997, Mantua et al. 1997, McGowan et al. 1998, Beamish et al. 1999, Koslow et al. 2002).

Range shifts of benthic and demersal fish species have already been observed in response to warming of Australian waters. Most of these observations are from eastern or southeastern Australia,

although some such changes have been observed in Western Australia and it is not known whether these differences are a reflection of differences in observation effort. Distributions of at least 36 species of Tasmanian marine fish have shifted poleward during the last decade (P. Last, personal communication, CSIRO). Many of these are warm temperate reef species historically distributed adjacent to the coast of New South Wales that have now become established south of Bass Strait. Still others have shifted their ranges further south along the Tasmanian coast.

*Phenology* The benthic larval component of the zooplankton has shown large shifts in timing compared with the holozooplankton in Northern Hemisphere temperate waters (Edwards & Richardson 2004, Greve et al. 2004). Evidence from the North Sea has shown that larvae of benthic echinoderms are now appearing in the plankton about 6 wk earlier than 50 yr ago in response to warmer temperatures. If Australian benthic systems responded similarly, peak larval abundances of crown-of-thorns starfish could appear much earlier in the year, perhaps before the presence of their normal predators (a potential positive feedback) or before wet season pulses in nutrients originating from early wet season rains (a negative feedback).

### *Winds*

Marine systems are influenced by wind fields, which drive major surface currents, and by episodic wind events ranging in strength from low to extreme. In shallow waters, these wind events create hydrodynamic disturbance whereas in deeper waters, wind fields and events contribute to hydrodynamic regimes that affect upwelling and hence productivity at different spatial and temporal scales and across different trophic levels (Harris et al. 1991).

### *Coastal systems*

*Physiology* Hydrodynamic stress will affect growth forms and morphological adaptations of plants and animals (Denny & Gaylord 1996). For example, variation in the morphology of the kelp *Ecklonia radiata* along the southern Australian coastline is related to wave exposure, longitude, plant density and temperature at each site (Fowler-Walker et al. 2005, 2006). At sites with high wave exposure, plants have longer stipes and smaller surface areas so are better adapted to cope with high-energy water movement. Phenotypic responses to hydrodynamic stress are frequently a trade-off between reducing mechanical damage and risk of dislodgement and obtaining nutrients/food (Sebens 2002, Marchinko & Palmer 2003, Stewart & Carpenter 2003, Li & Denny 2004).

Populations cannot respond indefinitely to hydrodynamic stress so there are limits to the degree of plasticity in morphological characteristics in response to the environment. Barnacles on Northern Hemisphere exposed shores tend to have shorter cirri than those on sheltered shores (Arsenault et al. 2001, Marchinko & Palmer 2003, Li & Denny 2004, Chan & Hung 2005) but above a threshold current velocity barnacles cease to respond plastically to flow (Li & Denny 2004). Intertidal snails tend to have thicker and/or larger shells on shores with high wave exposure (Frid & Fordham 1994, Boulding et al. 1999). However, intertidal snails along the coast of southern Australia show no differences in morphology with wave exposure, and it is hypothesised that the generally homogeneous and wave-exposed nature of Australia's southern coastline may have favoured generalist traits (Prowse & Pile 2005). Fauna and flora of Australia's exposed southern coastline may be adapted to cope with high variability in wave exposure.

*Distribution and abundance* Intertidal and shallow-water animal and plant communities are structured by wave exposure and local current velocity so species tolerant of high-energy hydrodynamic forces dominate at high wave-exposed sites (Edgar et al. 1997, Coates 1998, Fonseca & Bell 1998, Goldberg & Kendrick 2004, Fulton et al. 2005, Jonsson et al. 2006). An increase in wind strength

may increase wave exposure and may result in a considerable reduction in algal and seagrass production or a shift in community composition in areas that are affected (Kendall et al. 2004, Cruz-Palacios & van Tussenbroek 2005).

A general weakening of those winds is expected to hinder recruitment for coastal marine populations. Strong relationships between wind strength and recruitment have been shown, including in a coastal rocky reef fish (*Heteroclinus* sp.) for which enhanced settlement followed wind-driven productivity boosts (Thresher et al. 1989). Prolonged periods of strong winds have impacted the breeding success of the sooty tern *Sterna fuscata* and common noddy *Anous stolidus* in the Great Barrier Reef region with large-scale desertion of nests and starvation of chicks (King et al. 1992). Environmental conditions associated with strong winds may have led to a reduction in prey availability or a reduction in the foraging success of adults. Nests were also lost through inundation by waves and shoreline erosion (King et al. 1992).

*Phenology* Winds and waves have the potential to affect timing of the reproduction of algae. For example species of *Fucus* in the North Atlantic release spores only under calm conditions at low tide at certain times of the year (Brawley 1992, Serrão et al. 1996, Brawley et al. 1999). It is not clear whether this is an absolute condition for reproduction, or whether it is simply periods of relative calm that are required. It is also unknown whether any Australian species of marine plants have similar requirements for reproduction. It has also been suggested that the timing of mass spawning in tropical reef corals is related to seasonal wind and current fields, coinciding with times of the year when calm conditions are likely to occur (Babcock et al. 1994). It is thought that the fertilisation success of coral populations may be the ultimate factor responsible for this pattern (Oliver & Babcock 1992), so any change in the seasonal wind pattern may affect reproduction and recruitment. If climate change decouples factors such as seasonal wind patterns and seasonal temperature cues that may be important for mass spawning corals then the reproductive success of these species may be reduced.

#### *Pelagic systems*

*Distribution and abundance* Wind is one of the driving forces of currents and vertical mixing in the water column. Wind therefore affects mixing depth and intensity and may thus be seen as a proxy for mixing depth, mixing intensity, and light and nutrient supply to the surface layer. Climate models consistently project a poleward shift in the zonal winds that normally cross the southern part of Australia, and these projections are consistent with recent changes in the Antarctic Oscillation Index (Gillett & Thompson 2003; also see Jones & Widmann 2004). The projected general weakening of those winds following this shift may reduce recruitment to marine fish populations. Strong relationships between wind strength and recruitment exist for some species, such as the commercially exploited blue grenadier *Macruronus novaezelandiae* in outer continental shelf waters (Thresher et al. 1992). In southeastern Australia, Harris et al. (1992) found evidence that reduced production of the jack mackerel *Trachurus declivis* off Tasmania resulted from decreased wind stress and subsequent decreases in large zooplankton.

#### *Offshore benthic systems*

*Distribution and abundance* The variability in the annual frequency of strong zonal westerly winds has been related to catch rates and recruitment variability in several southeastern demersal fisheries (Harris et al. 1988). The collapse of the gemfish fishery *Rexea solandri* in that region was likely a consequence of the combination of weak recruitment due to declining winds and overfishing (Thresher et al. 1996). A variety of southeastern shelf teleosts exhibit a decadal-scale recruitment cycle, in several cases directly linked to regional wind fields (Thresher 2002, Jenkins 2005).



*Ocean currents*

Currents and ocean circulation systems strongly affect dispersal, migration and geographic distribution of species and therefore have implications for the connectivity of marine systems. Southward-moving currents such as the EAC and Leeuwin Current interact with southern coastal and offshore waters, influencing temperature and regional productivity (Harris et al. 1987, Ridgeway & Dunn 2003, Ridgeway & Condie 2004).

*Coastal systems*

*Distribution and abundance* Many marine plants and animals rely on water movement for dispersal, particularly for early life stages. Distributional patterns of marine populations often reflect connectivity of marine systems. Evidence is mounting that despite the potential for long-distance dispersal, actual dispersal distances for coastal fauna may be constrained by behavioural mechanisms such as vertical migration. Typical larval dispersal distances for coral reef fish in the Caribbean are on a scale of 10–100 km, with dispersal distances strongly determined by active movement of larvae (Cowen et al. 2006). Some coastal invertebrates have very short larval durations which will restrict dispersal distance (McShane et al. 1988, Sammarco & Andrews 1988, Davis & Butler 1989, Stoner 1992). Further, the viability of larvae and plant propagules may diminish over time. For example, propagules of the mangrove *Avicennia marina* may only be able to establish successfully within the first 4–5 days of dropping (de Lange & de Lange 1994). The southern limit of this species in New Zealand appears to be controlled by limited transport by coastal drift and lack of suitable habitat within the dispersal range of existing populations, rather than by climatic factors (de Lange & de Lange 1994).

The most southerly mangroves globally are found at Corner Inlet in Victoria (de Lange & de Lange 1994). These may be relict populations from when favourable climate extended further south than at present. Projected global warming and strengthening of the EAC may facilitate further southerly expansion of mangrove species. Alternatively, this southerly limit may be set (and restricted) by eastward water movement through the Bass Strait (de Lange & de Lange 1994). Southward water movement through the Bass Strait by wind-induced drift is slow and is insufficient to transport the propagules to Tasmania within the 5-day period for viable establishment (de Lange & de Lange 1994, Clarke et al. 2001). Therefore, even if temperatures in Tasmania become warm enough to support *Avicennia* populations (conventional wisdom is that latitudinal range edges of mangroves are determined mainly by freezing temperatures) they are unlikely to become established there. Currents thus act as a barrier as well as an aid to dispersal for many marine organisms and therefore determine adult abundances as well as distributional limits (Gaylord & Gaines 2000). Incidentally, this means that a key consequence of future climate change will be influences on current patterns, often on a small scale and therefore dependent on fine-scale variations in weather and current patterns, which are still difficult to predict.

In addition to affecting the range of species distributions, a change in the strength of currents may alter the overall strength of recruitment. One of the best examples of this comes from the correlation between the strength of the Leeuwin Current and recruitment of the western rock lobster *Panulirus cygnus*. The strength of the Leeuwin Current is highly correlated with ENSO and in El Niño years when the current is weak, rock lobster recruitment is also weak (Caputi et al. 2001). The mechanism underlying this is not well understood, but it is clearly more complex than simply a range extension and may be related to temperature or cross-shelf transport, mixing and productivity driven by the Leeuwin (Griffin et al. 2001).

The establishment of long-spined sea urchins *Centrostephanus rodgersii* in Tasmania in the 1960s has been attributed to larval transport from northern populations by the EAC (Johnson et al. 2005). Populations have since expanded in Tasmania and have resulted in the elimination of

macroalgae in some areas through intense grazing pressure. A reduction in the density of rock lobster *Janus edwardsii* and abalone *Haliotis rubra* in areas devoid of macroalgae has serious implications for fisheries targeting these species. It must be assumed that any major shift or strengthening of wind fields and major currents may have profound implications for Australian coastal organisms.

#### *Pelagic systems*

*Distribution and abundance* Transport by large ocean currents plays a major role in the movements of marine turtle hatchlings and early juveniles to ocean pelagic nursery habitats where young turtles remain for a number of years exploiting biologically rich environments linked to current systems and convergence zones (Carr 1987, Witherington 2002, Ferraroli et al. 2004). Juvenile and adult turtles undertake extensive migrations; juvenile loggerheads originating from Australian populations have been identified from feeding grounds off Baja California, representing a journey that crosses the entire Pacific Ocean aided by the North Pacific Current (Bowen et al. 1995). Adult loggerheads and leatherbacks forage at fronts and eddies and are associated with major currents (Ferraroli et al. 2004, Polovina et al. 2004). Turtles have also been tracked swimming against prevailing currents as well as with currents so may only use current flows opportunistically to facilitate transport (Luschi et al. 2003, Polovina et al. 2004). Alteration of major current systems will impact the navigational abilities of marine turtles and deflect turtle movements (Luschi et al. 2003, Robinson et al. 2005).

#### *Offshore benthic systems*

*Distribution and abundance* Cold-water corals are found in areas of fast currents and this is evident on Australian seamounts where corals occur in distinct depth zones (Koslow et al. 2001). Alteration of currents may make areas unfavourable for coral growth and, given the low growth rate, colonisation of newly available areas with optimal environmental conditions may be slow and may take many decades before a viable population size is reached. Fast flow may also be necessary for larval supply or retention to establish or maintain populations (Genin et al. 1986). Changes in local current regimes could alter the 'stepping stone' function of seamount chains, whereby the biology on distant seamounts is linked by intermediate ones, and have a considerable impact on coral distribution (Roberts et al. 2003). Survival of cold-water corals appears to be controlled by oceanographic conditions. Chemical analysis of deep-water corals off southern Australia has indicated a long-term deep cooling that commenced in the mid-eighteenth century and is a result of enhanced poleward flow of the warm EAC as it interacts with the colder subsurface countercurrents (Thresher et al. 2004). This strengthening of the EAC is predicted to continue as the global climate warms (Cai et al. 2005, Cai 2006) with considerable impacts for ocean circulation and marine biodiversity, including cold-water coral ecosystems.

#### *Mixed-layer depth and stratification*

Mixing depth and mixing intensity in the surface ocean and the associated stratification are key factors for the production of phytoplankton and of higher trophic levels because they fundamentally affect the supply of nutrients (from below) and light (from above), and sinking losses of phytoplankton (Mitchell & Holm-Hansen 1991, Huisman & Weissing 1995, Diehl 2002) and because consumer biomass is positively related to the productivity of their food (Grover 1997).

*Pelagic systems*

*Distribution and abundance* Experimental manipulation of mixing depth has demonstrated the positive impact of decreasing mixing depth (increasing light supply) on the biomass of temperate phyto- and mesozooplankton when nutrients are relatively abundant (Kunz 2005). Flagellates profited from shallower mixing and the heterotroph-to-autotroph (mesozooplankton-to-phytoplankton) biomass ratio was higher at low mixing depth. Variability of mixing depth and change in stratification in several ocean regions since the 1950s provide striking examples of potential impacts on pelagic communities. In the central and subarctic North Pacific Ocean, large variability in plankton primary and secondary production has been linked to a decadal-scale climate change event between the mid-1970s and the late 1980s and associated changes in the depth of the winter and spring mixed layers (Venrick et al. 1987, Polovina et al. 1995, Hayward 1997). These impacts on lower trophic levels appear to have propagated to higher trophic levels with pelagic larvae, including squid, salmon and flying fishes with different mechanisms operating in different regions (Polovina et al. 1994, 1995). In the northwest Hawaiian Islands (situated in the North Pacific subtropical gyre), chlorophyll concentration and primary production were positively related to deepening of the mixed layer due to increased nutrient supply (Venrick et al. 1987, Polovina et al. 1995) while in the subarctic Gulf of Alaska copepod abundance and, likely, primary production were positively related to shallowing of the mixed layer due to increased light availability (Polovina et al. 1995). In the Northern California current, a decrease in macrozooplankton biomass by 80% since 1951 has been related to reduced nutrient transport across the thermocline due to warmer sea-surface temperatures and increased stratification (Roemmich & McGowan 1995). In the North Atlantic, large-scale northward shifts in the distribution of warm-water phyto- and zooplankton and changes in the abundance of plankton between 1958 and 2002 have been related to increasing water column stratification (Richardson & Schoeman 2004, Hays et al. 2005, Edwards et al. 2006).

With the projected enhancement of stratification around most of continental Australia nutrient transport to the surface layer will be reduced over vast areas of the pelagic zone. Most Australian waters are therefore likely to become more depauperate in nutrients with repercussions for production and biomass of most pelagic (and benthic) food webs. Cyanobacteria, flagellates and dinoflagellates (including nuisance and harmful algal bloom species) may increase in abundance where vertical mixing decreases and the 'microbial loop' may be favoured over the relatively more productive 'classic' food web in affected areas. The productive temperate pelagic province may shrink considerably in area and potentially become restricted to west of Tasmania by 2100. In tropical surface waters where increasing stratification lifts the oxycline, the abundance of pelagic apex predators, such as skipjack and yellowfin tuna may decline.

*Phenology* In the North Atlantic, earlier timing of dinoflagellate blooms in spring is partly attributed to earlier and enhanced stratification (Edwards & Richardson 2004, Richardson & Schoeman 2004). In Tasmanian waters, zonal westerly winds stimulate deeper and/or stronger vertical mixing and affect the timing and duration of phytoplankton blooms (Harris et al. 1988).

*Offshore benthic systems*

*Distribution and abundance* Deep seafloor habitats, with the exception of hydrothermal vents and cold seeps, are typically areas of low productivity, relying on the flux of detritus from surface waters which is partially regulated by mixed layer depth. Despite this, species diversity can locally be very high (Snelgrove & Smith 2002). Seamounts, with topographically enhanced currents are areas of high productivity (e.g., Koslow 1997) but are still sensitive to the flux of organic matter from surface waters, albeit over a wider area than that of the seamount itself. This coupling to

surface productivity may mean the deep sea is particularly susceptible to climate change (Glover & Smith 2003). If surface productivity is reduced as climate warms then the reduction in organic carbon flux to the sea floor will lead to a reduction in benthic biomass.

### *CO<sub>2</sub>, pH and calcium carbonate saturation state*

Changes to the atmospheric concentration of CO<sub>2</sub> and hence carbonate ions represents a serious threat to calcifying organisms such as corals, pteropods and coccolithophores (Raven et al. 2005), especially as calcification of most organisms appears linearly related to the carbonate ion concentration (Langdon et al. 2000). The level of calcification is significant in that it represents concentrations at which organisms such as tropical reef-building corals no longer calcify. Marine organisms differ in their susceptibility to acidification depending on whether the crystalline form of their calcium carbonate is calcite (calcifying phytoplankton, foraminiferans) or aragonite (pteropods, corals). Calcite is less soluble than aragonite, making it less susceptible to pH changes. Other effects of increased CO<sub>2</sub> on the physiology of marine flora and fauna are less well understood. Experiments to determine the likely response of marine organisms to pH changes have explored large changes in pH (>1.0) under laboratory conditions (Kikkawa et al. 2003, Pedersen & Hansen 2003a,b, Pörtner et al. 2004, Engel et al. 2005) but little is known on what the gradual long-term effects of pH lowering will be on marine organisms.

### *Coastal systems*

*Physiology* Marine plants vary in their degree of immersion in water, from mangroves that generally have their foliage and flowers above the water to macroalgae and seagrasses that are either fully submerged or submerged for part of the tidal cycle. Land plants, including mangroves, capture CO<sub>2</sub> primarily by diffusion so that increasing atmospheric CO<sub>2</sub> generally hastens photosynthesis, productivity and growth (Ainsworth & Long 2005). Seagrasses, although submerged, are of terrestrial origin and so rely primarily on dissolved CO<sub>2</sub>; thus they are photosynthetically inefficient in sea water (Invers et al. 1997, 2002, Short & Neckles 1999). By contrast, most marine phytoplankton and macroalgae have mechanisms that actively concentrate and take up inorganic carbon as CO<sub>2</sub>, bicarbonate ions (HCO<sub>3</sub><sup>-</sup>) or both, so changes in dissolved CO<sub>2</sub> have less effect on their rates of photosynthesis (Giordano et al. 2005). Carbon-concentrating mechanisms are not as common in benthic photosynthetic organisms (Giordano et al. 2005).

Mangrove growth may be stimulated as CO<sub>2</sub> levels increase. Seedlings of *Rhizophora mangle* grown under double ambient CO<sub>2</sub> for a year exhibited increases in growth and photosynthetic rate (Farnsworth et al. 1996). The young plants also became reproductive a year earlier than in the field, so elevated CO<sub>2</sub> may accelerate maturation as well as growth (Farnsworth et al. 1996). However, the long-term response of mature mangrove forests to elevated CO<sub>2</sub> is unknown. A widespread thickening of terrestrial vegetation observed in parts of Australia may be induced by recent climate change although is more likely the result of changes in land use (Bowman et al. 2001, Australian Greenhouse Office 2003).

Australian coastal waters are generally low in phosphate and nitrate but as seagrasses are rooted, they can take up these essential nutrients from the sediment. Therefore, seagrasses are primarily carbon limited. An increase in atmospheric CO<sub>2</sub> will result in a higher proportion of dissolved CO<sub>2</sub> in the oceans, potentially increasing seagrass biomass, deepening of seagrass depth limits and enhancing of the role of seagrass beds in carbon and nutrient cycles (Zimmerman et al. 1997, Invers et al. 2002). Intertidal macroalgae, which generally use bicarbonate when submerged, may only benefit from elevated CO<sub>2</sub> during aerial exposure (Farnsworth et al. 1996, Beardall et al. 1998, Gao et al. 1999, Zou & Gao 2002, 2005).

Coral reefs represent a balance between calcification and erosion, with 90% of what is laid down by calcifiers being removed by erosion. Ocean acidification could tip the balance from net calcification to erosion. If atmospheric CO<sub>2</sub> levels reach 500 ppm, projected to occur by the end of this century, then coral viability will be severely compromised (Hoegh-Guldberg 2004). At low carbonate ion concentrations (<200 µmol kg<sup>-1</sup>), calcification of corals and many other calcifying organisms effectively becomes zero. The actual seriousness and time frame of these changes have yet to be properly assessed.

There has been some debate about the significance of the threat of ocean acidification to the long-term viability of coral reefs (see McNeil et al. 2004 vs. Kleypas et al. 2005). Changes in calcification rates over recent centuries estimated from cores from long-lived corals such as *Porites* on the Great Barrier Reef show evidence of an increase in calcification rates over the 50 yr prior to 1982 (Lough & Barnes 2000). Calcification rates were highly correlated with average sea temperature, with an annual average increase in calcification of 0.3 g cm<sup>-2</sup> yr<sup>-1</sup> for each degree of ocean warming. Lough and Barnes (2000) suggested the increase in calcification was probably due to the 0.25°C warming of sea temperature on the Great Barrier Reef over the last 50 yr. Although calcification does increase with temperature, it does not increase indefinitely; several studies have shown that it increases up to the summer sea-temperature maximum, but declines rapidly at warmer temperatures. Interactions between temperature and decreasing pH are still largely unknown but are likely to be considerable given, for example, the linkages between metabolic rate (which is temperature sensitive) and calcification. Most authors have concluded that the combination of the two pressures on calcifying organisms such as corals will be largely negative and synergistic (Hoegh-Guldberg 2004).

Acidification may be expected to increase physiological stress on other calcifiers. Metabolic efficiency and growth rates of bivalves and other molluscs will be impaired (Michaelidis et al. 2005, Berge et al. 2006). Experiments have also shown that under lowered pH conditions the fertilisation rate of eggs of intertidal echinoderms declined and larvae were severely malformed (Kurihara et al. 2004).

*Distribution and abundance* Macroalgae take up primarily bicarbonate ions for photosynthesis. As only a small proportional change in bicarbonate concentration will occur as atmospheric CO<sub>2</sub> levels rise, little enhancement of growth is expected (Beardall et al. 1998). However, increased acidification of the oceans may have severe consequences for coralline algae (Gao et al. 1993) therefore enhancing competitive advantages of non-calcifying species over calcifying species (Gao et al. 1993, Beardall et al. 1998).

Potential range shifts in tropical corals with warming may be restricted by the future latitudinal gradient in the carbonate saturation state of sea water (Figure 6). The undersaturation of aragonite and calcite in sea water is likely to be more acute and happen earlier further south in the Southern Hemisphere and then move northward (Orr et al. 2005). This means that corals will not be able to move further south into cooler waters in response to warming seas because these waters are likely to be undersaturated in calcium carbonate. The additional problem of reduced light levels at higher latitudes is also probably an important limit in this respect.

#### *Pelagic systems*

*Physiology* Seawater pH affects phytoplankton via several processes. pH is an important determinant of the growth rate of phytoplankton species, with some growing consistently well over a wide range of pH and the growth rate of others varying considerably over a pH range of 7.5–8.5 (Hinga 2002). Both temperate and tropical coccolithophorids show reduced calcite production and an increased proportion of malformed liths at decreased pH (Riebesell et al. 2000, Engel et al. 2005).



Declining pH may also alter the growth rates of photosynthetic organisms; in particular changes in pH will affect the kinetics of the uptake of nutrients. Nitrification in marine bacteria is negatively affected below a pH of ~8. Because nitrification is an important pathway of nitrate supply to phytoplankton, nitrate availability for phytoplankton is likely to be reduced at pH <8.0, with consequences for phytoplankton community composition and productivity (Huesemann et al. 2002). Decreasing pH has also been found to increase the availability of potentially toxic trace elements such as copper, which may affect phytoplankton survival (Kester 1986). Changes may also occur in cell composition, which could affect the nutritional value of the microorganisms to the animals that feed on them.

As phytoplankton have carbon-concentrating mechanisms, photosynthesis is generally not carbon limited, even at present CO<sub>2</sub> levels. In almost all phytoplankton species, doubling CO<sub>2</sub> concentration only increases photosynthesis by <10% (Beardall & Raven 2004, Schippers et al. 2004, Giordano et al. 2005). The small number of studies that have investigated effects of CO<sub>2</sub> on phytoplankton community composition suggested that elevated CO<sub>2</sub> concentrations favour diatoms over flagellates and coccolithophores (Antia et al. 2001, Tortell et al. 2002).

The physiology of larger animals such as fish and squid are likely to be influenced by increasing CO<sub>2</sub> levels in the oceans, which influences tissue acid-base regulation and thus metabolism. Squid are acutely sensitive to even small changes in ambient CO<sub>2</sub> due to their high metabolic oxygen demand for locomotion (jet propulsion) and a strong relationship between O<sub>2</sub> binding in the blood and pH (see Pörtner et al. 2004). Pelagic fish generally have lower metabolic rates and some venous oxygen reserve so are only moderately sensitive to changes in ambient CO<sub>2</sub>. The projected increases in CO<sub>2</sub> are below lethal threshold levels; synergistic effects of warmer temperatures and increased CO<sub>2</sub> may influence growth and reproduction in large pelagic fauna.

*Distribution and abundance* The direct effect of ocean acidification on calcifying zooplankton will be to increase shell maintenance costs and reduce growth. Pteropods with their aragonite shells are particularly vulnerable to ocean acidification (Orr et al. 2005). In the Southern Ocean, shelled pteropods are prominent components of the food web contributing to the diet of carnivorous zooplankton, myctophid and other fishes, and baleen whales, as well as forming the entire diet of gymnosome molluscs. Pteropods can also account for the majority of the annual export flux of both carbonate and organic carbon in the Southern Ocean. Shells from live pteropods dissolve rapidly when placed in water undersaturated with aragonite, similar to the levels that are likely to exist in 2100. If pteropods cannot grow their protective shell, then their populations are likely to decline and their range will contract toward lower-latitude surface waters that remain supersaturated in aragonite. In Australian waters, pteropods are relatively rare but can be locally common. For example, the pteropod *Cavolinia longirostris* can form dense aggregations on the Great Barrier Reef during summer (Russell & Colman 1935), occurring in such large numbers that their shells wash up on beaches (D. McKinnon, personal communication).

#### *Offshore benthic systems*

*Distribution and abundance* Decreases in ocean pH will directly impact offshore soft sediment organisms that rely on calcium carbonate structures such as molluscs and foraminiferans. Changes in pH will also impact benthic organisms by influencing the composition of sediment as a large fraction in Australia is calcium carbonate in origin. For example, foraminiferan remains constitute most of the sediments in sandy regions of the Great Barrier Reef and a decline in the abundances of pelagic and benthic foraminiferans is likely to reduce the sedimentation of their skeletons to the sea bottom (McKinnon et al. in press).

The global distribution of cold-water corals is influenced by seawater carbonate chemistry with a clear relationship between the occurrence of cold-water scleractinian corals and depth of the



aragonite saturation horizon (Guinotte et al. 2006). The aragonite saturation horizon represents the limit between the upper saturated and the deeper undersaturated waters; calcium carbonate can form above the horizon but dissolves below it (Raven et al. 2005). As atmospheric CO<sub>2</sub> levels increase, the depth of the aragonite saturation horizon will rise closer to the ocean surface and the entire Southern Ocean water column could become undersaturated by 2100 (Caldeira & Wickett 2005, Orr et al. 2005). Cold-water corals are thus likely to be much more vulnerable to changes in ocean chemistry than shallow tropical reef-building corals (Raven et al. 2005). Over the next 100 years, the predicted decrease in the aragonite saturation horizon in the oceans will result in only 30% of known deep-sea coral reefs and mounds remaining in supersaturated waters compared to the present-day figure of >95% (Guinotte et al. 2006). Ocean waters south of Australia may become inhospitable for cold-water corals below a few hundred metres. The shallowest pinnacles in the Tasmanian Seamounts Marine Reserve peak at about 600 m below the surface so cold-water corals on these seamounts could simply disappear, along with their multitude of associated organisms.

### *Solar radiation*

Future changes in UVR are difficult to predict (see p. 416) but in the following sections we discuss the potential impacts of heightened UVR, while recognising that the possibility of ozone recovery is becoming more likely. The extent to which UVR affects marine organisms will depend on factors such as aerosol concentrations, cloud cover and the concentration of dissolved and particulate matter in the water column (Jerlov & Steeman-Nielsen 1974, Smith & Baker 1979, Erga et al. 2005).

### *Coastal systems*

*Physiology* UVR damages DNA and causes photo-oxidative stress in plants and animals (Setlow & Setlow 1962). In the aquatic environment, UVR effects should be most intense near the water surface. Sessile species, such as intertidal fauna and corals, do not have the capacity to avoid UVR through evasive movements and so can be exposed to powerful solar irradiances, particularly in tropical waters (see Shick et al. 1996). Tropical reef corals with their symbiotic zooxanthellae need to be exposed to sunlight for photosynthesis, so they are adapted for a high-UVR environment. However, an increase in UV light may exacerbate the simultaneous stress of warmer temperatures on corals and thus contribute to coral bleaching (Lesser 1996, 1997, Baruch et al. 2005, Drohan et al. 2005). Sublethal effects of UVR include depressed calcification and skeletal growth in corals (see Shick et al. 1996).

Increased UVR reduces plant photosynthetic efficiency and biomass (Dawson & Dennison 1996, El-Sayed et al. 1996, Moorthy & Kathiresan 1997, 1998). Excessive UVR can induce photoinhibition in dinoflagellates, macroalgae, seagrasses, and the symbiotic zooxanthellae of tropical corals and sea anemones, with tolerances varying among species and life stages (Dawson & Dennison 1996, Graham 1996, Bischof et al. 1998, Häder et al. 1998; also see Shick et al. 1996). For example, net photosynthesis of the mangrove *Rhizophora apiculata* seedlings increased by 45% for a 10% increase in UVR but a 59% decrease in net photosynthesis occurred with a 40% increase in UVR (Moorthy & Kathiresan 1997). Many tropical species may already be near their upper limits of UVR tolerance so any further increase may reduce the ability of vulnerable species to persist near the water surface, thus leading to a shift in community composition (Häder et al. 1998).

Egg and larval stages of many marine invertebrates and fish are highly susceptible to UV damage, particularly those that are pelagic (Lesser et al. 2003, Wellington & Fitt 2003, Przeslawski et al. 2004, 2005, Bonaventura et al. 2006). Increased UVR is known to have a deleterious effect on some adult fish, damaging ocular components and the epidermis, depressing the immune system,

and allowing invasion of pathogens (Zagarese & Williamson 2001, Markkula et al. 2005). Some coral reef fishes that are exposed to intense irradiance are able to sequester UV-absorbing compounds from prey and thus are less vulnerable to UV increases (Zamzow 2004).

*Distribution and abundance* Intertidal and subtidal algae and seagrasses will generally be susceptible to changes in solar irradiance. Upper depth limits of many species in these groups may deepen or grow shallower with increased or decreased levels of UVR, respectively (Dawson & Dennison 1996). Early life stages may be more susceptible to UVR than mature plants, thus regulating depth limits of adults (Graham 1996, Rijstenbil et al. 2000, Swanson & Druehl 2000, Cordi et al. 2001). For example, the upper depth limit of some kelp species is determined by susceptibility of their zoospores to UVR (Swanson & Druehl 2000, Wiencke et al. 2006) or early post-settlement stages (gametophytes or embryonic sporophytes) to photosynthetically active radiation (Graham 1996). Plants produce UV-absorbing compounds found predominantly in the epidermis and there is some capacity for adaptation in certain species. Levels of UVR-blocking pigment in certain tropical seagrasses increase when plants are grown at higher irradiance (Abal et al. 1994, Detres et al. 2001).

Unlike sessile plants and animals, mobile fauna can shift distributions or retreat to refugia during periods of high solar radiation. One example is that the settlement of coral larvae is influenced by UVR levels (Kuffner 2001, Gleason et al. 2006), so these larvae may have some choice in settlement locations. How alteration of solar radiation patterns will affect behavioural responses of other marine animals is, however, generally difficult to predict. Visual systems of some shallow-water fishes use UV wavelengths and allow con-specific communication during breeding, shoaling or territorial behaviour (Losey et al. 1999, 2003, Garcia & de Perera 2002, Losey 2003, Siebeck 2004, Modarressie et al. 2006). It is assumed there is large plasticity in behavioural responses so at least some populations may adapt rapidly.

Interspecific variability in the capacity of marine plants and animals to adapt to UVR changes (Hanelt et al. 1997, Choo et al. 2005) may lead to shifts in shallow-water and coral reef community structure if solar irradiance changes. Effects on communities should be most pronounced where there is a strong differential sensitivity to UVR between species or where protection against UVR is metabolically expensive or juvenile stages are found near the water surface (Wahl et al. 2004).

#### *Pelagic systems*

*Physiology* In phytoplankton, UVR can negatively impact several physiological processes and cellular structures, including photosynthesis, carbon and nutrient uptake, the ratio of polyunsaturated to saturated fatty acids, cell motility and orientation, the DNA, and life-span (Behrenfeld et al. 1993, Goes et al. 1994, Hessen et al. 1997, Wilhelm et al. 1997, Garde & Cailliau 2000, Hogue et al. 2005, Litchman & Neale 2005). These effects not only reduce phytoplankton growth, production and biomass (Worrest et al. 1978, Döhler 1994, Hessen et al. 1997, Keller et al. 1997, Wängberg et al. 1999) but also compromise the ability of phytoplankton to adapt to changing environmental conditions and respond to possibly hazardous situations (Häder & Häder 1989, Häder & Liu 1990). Although some phytoplankton are capable of acclimating to UVR via increased pigmentation or capability to repair damaged DNA, this inevitably involves metabolic costs reducing the energy that would otherwise be available for cell growth and division (Häder et al. 1998, Garde & Cailliau 2000). Increases in the cellular carbon-to-nutrient ratio and cell size reduce the nutritional value of phytoplankton for grazers. Negative effects of altered food quality are known to propagate to higher trophic levels and have been related to reductions in the abundance of copepod nauplii in experimental mesocosms (Hessen et al. 1997, Keller et al. 1997).

UVR may positively affect bacteria and phytoplankton production because it increases the photolysis of dissolved organic carbon and colloids thereby increasing the availability of essential

plant macro- and micronutrients from such compounds (Rich & Morel 1990, Palenik et al. 1991, Wängberg et al. 1999).

There have been relatively few studies on the effects of UVR on marine zooplankton, in comparison with studies on phytoplankton. UVR is also known to damage various life stages of zooplankton such as copepods and shrimp, as well as eggs and larvae of crabs and fish that are temporary members of the plankton (Hunter et al. 1982, Damkaer & Dey 1983, El-Sayed et al. 1996, Kouwenberg et al. 1999a,b). In copepods, UVR has been found to lower fecundity, increase mortality and affect the sex ratio (Karanas et al. 1979, 1981, Bollens & Frost 1990). Because UVR can have deleterious consequences for those organisms that lack photoprotective mechanisms, many of the permanent members of the neustonic copepod community which are common in Australia's warmer waters have pigments to reduce such damage. The effects of UVR radiation on fish eggs or larvae have rarely been investigated (see Zagarese & Williamson 2001). The few existing studies found deleterious effects of UVR in clear waters and confirm the importance of dissolved organic carbon in ameliorating those effects (Hunter et al. 1982, Keller et al. 1997, Zagarese & Williamson 2001).

*Distribution and abundance* The degree of water column stratification crucially affects the exposure to UVR of those plankton that do not migrate vertically. Shallowing of the mixed surface layer and more energetic turbulence both increase plankton exposure to UVR and, therefore, their chance to receive harmful doses (Keller et al. 1997, Garde & Cailliau 2000, Barbieri et al. 2002, Hernando & Ferreyra 2005). Differential sensitivities of individual plankton taxa are thus likely to cause or have caused shifts in community structure or even ecosystem integrity, depending on the magnitude of changes in UVR. It is questionable to what extent the observed short-term effects of UVR on individual organisms can be used to estimate long-term ecosystem response (Häder et al. 1998).

### *Precipitation and storms*

A 70-yr drying trend has occurred along the eastern seaboard of the Australian mainland (Australian Greenhouse Office 2003), and this has reduced vegetation and destabilised sediment in coastal watersheds. Following intense storms in temperate Australia and monsoonal rains in tropical Australia, runoff from rivers tends to carry high sediment loads. The increasing frequency of intense storms as a result of climate change (Emanuel 2005, Webster et al. 2005) is likely to increase extreme rainfall events, hence altering runoff of freshwater and suspended sediment loads. There are clearly numerous indirect impacts associated with changes in freshwater flux in addition to the direct potential for fresh water to have physiological effects on marine organisms.

### *Coastal systems*

*Physiology* Changes in rainfall patterns, and associated changes in watershed geomorphological dynamics, will affect the dynamics of coastal marine ecosystems through the physiological effects of large-scale flooding, fluctuations in salinity, and increases in turbidity and nutrients on resident organisms such as mangroves and wetland flora. Mangroves are adapted for coastal areas with waterlogged and often anoxic soils but their tolerance of salinity stress varies among species. As salinity levels increase, mangroves are faced with increasing salt levels in the tissues (see Field 1995). A 'zonation' of mangrove species can generally be observed going from the sea to the land or upriver from the mouth of estuaries reflecting the ecophysiological response of the plants along these and other environmental gradients and disturbance regimes (Ellison & Farnsworth 1993). Rainfall directly influences the salinity of the intertidal waters and sediments but also influences salinity through freshwater runoff from the land and freshwater seepage into the soil (Twilley & Chen 1998).

Hydrology of mangroves is complex; tidal inundation, rainfall, groundwater seepage and evaporation all influence soil salinity and have a profound effect on mangrove growth. Hydrology model simulations of mangrove systems in southwest Florida have demonstrated that mangroves in the upper intertidal are particularly sensitive to reductions in rainfall, even though these are areas with minor freshwater input (Twilley & Chen 1998). Animals and plants living in the upper intertidal are generally near the upper limits of environmental tolerance limits so small alterations in climate may have a greater impact on upper shore organisms than in the lower intertidal. For example, seedlings of the mangrove *Rhizophora apiculata* grew more rapidly in the lower intertidal than those in the upper intertidal, presumably reflecting the additional stresses in the upper intertidal (Kathiresan et al. 1996).

Freshwater runoff can increase sediment loading of coastal waters thus imposing metabolic costs on corals and other organisms that can potentially reduce growth or lead to mortality in severe cases (see Fabricius 2005). Other effects of sediment on corals can occur at early life-history stages. Sediment has been shown to reduce coral fertilisation (Gilmour 1999), as well as settlement (Babcock and Davies 1991) and post-settlement survival of recruits (Babcock and Smith 2002). Pollutants that are carried with flood waters are also known to have detrimental effects on the early life-history stages of corals. For example the herbicide diuron, commonly used in catchments adjacent to the Great Barrier Reef, inhibits coral metamorphosis and settlement (Negri et al. 2005).

*Distribution and abundance* Mangroves are considered highly susceptible to alteration in rainfall abundance or frequency. In southeast Australia mangroves are expanding as they migrate into saltmarsh areas (Saintilan & Williams 1999, Harty & Cheng 2003, Harty 2004, Rogers et al. 2006). At Botany Bay, New South Wales, mangrove area increased by 32.8% between 1956 and 1996 while saltmarsh coverage decreased by 78.7% (Evans & Williams 2001). Although no single factor is responsible, it has been suggested that increased rainfall associated with climate change has reduced salinity levels within salt marshes thereby allowing mangroves to migrate and outcompete saltmarsh plants (Harty & Cheng 2003, Harty 2004, Rogers et al. 2006). However, hydrodynamic modification related to urban and rural development is likely to be the overriding factor driving mangrove expansion in the present climate.

Freshwater influx not only reduces the salinity of coastal waters but also enhances the stratification of the water column thereby decreasing nutrient resupply from below. Flood events are associated with an increase in productivity as nutrients are washed into the sea (McKinnon et al. in press). While diatoms seem to be negatively affected by increases in river discharge, dinoflagellates have been observed to profit from the increase in stratification and availability of humic substances associated with riverine freshwater input (Carlsson et al. 1995, Goffart et al. 2002, Edwards et al. 2006). Irrespective of the direction of change, modifications in rainwater runoff and accompanying changes in salinity and resource supply should therefore affect the composition and, potentially, the productivity of the phytoplankton community in coastal waters. River discharge is also a primary shaper of soft-bottom coastal communities, particularly in tropical areas where smaller watersheds produce more sediment (Rhoads et al. 1985, Milliman 1991, Alongi & Robertson 1995, Hall 2002).

Coral reefs are well known to be susceptible to fresh water as well as the effects of turbidity and sedimentation that vary with coastal weather patterns. Numerous examples of coral communities being killed off or adversely affected purely as a result of extreme rainfall events have been reported (Endean 1973, Rogers 1990, Alongi & Robertson 1995, Wilkinson 1999, Alongi & McKinnon 2005, Fabricius 2005). Increases in rainfall, or extreme rainfall events, can increase upland erosion and sediment transport considerably, thus severely impacting estuarine and near-shore coastal ecosystems, especially along coastlines where development and other human land uses have degraded the integrity of watersheds (Norkko et al. 2002, Thrush et al. 2003a,b, 2004,

2005, Lohrer et al. 2004). This is of particular concern for the Great Barrier Reef (Devlin & Brodie 2005).

Flood events are also associated with an increase in productivity as nutrients are washed into the sea. These nutrients may also lead to undesirable effects, for example, producing ideal conditions for the larvae of species such as the crown-of-thorns starfish. Recently long-term trends of increasing nutrients and phytoplankton concentrations in the coastal waters of the Great Barrier Reef have been shown, and these have been linked to recurring outbreaks of these starfish on the reef (Brodie et al. 2005). These factors in combination appear to have resulted in large-scale trends in coral diversity and abundance patterns on the Great Barrier Reef. Coastal areas in the so-called wet tropics, characterised by higher rainfall, greater runoff, and the most intensive agriculture, have generally lower coral diversity and lower coral cover than those adjacent to dryer coastal areas (De Vantier et al. 2006).

Light penetration is an important factor limiting the distribution of marine macroalgae, both in Australia (Kennelly 1989) and elsewhere (Reed & Foster 1984, Deysher & Dean 1986, Dayton et al. 1999, Spalding et al. 2003). Increases in turbidity associated with greater rainfall, coastal development or other human activities would thus be expected to degrade macroalgal communities by generally decreasing the light penetration, so reducing depth ranges (Vadas & Steneck 1988; also see review in Okey et al. 2004). Increases in turbidity can give competitive advantage to shade-tolerant flora and non-photosynthetic organisms (Keough & Butler 1995). The ability of kelp to compete with algal turfs may be reduced by coastal runoff. Turfs may benefit from the interaction between sediment and nutrients (Gorgula & Connell 2004).

Cyclones and storms can be highly destructive by uprooting coastal plants, killing coastal animals, and destabilising and eroding coastlines. These natural disturbance regimes may be important in maintaining biodiversity in coastal ecosystems; however an increased frequency or intensity of storms may reduce the resilience of coastal ecosystems (Dayton et al. 1992, Graham 1997, Carruthers et al. 2002, Fourqurean & Rutten 2004). Impacts on coral reefs can be severe; the Category 4 Hurricane Andrew (Porter & Meier 1992) in Florida and other parts of the Caribbean substantially damaged corals through intense wave impacts. Cyclones in Australia and elsewhere have caused large-scale loss of algal cover and seagrass beds and devastation of mangroves and coral reefs (Dayton et al. 1992, Preen et al. 1995, Rothlisberg et al. 1998, Gardner et al. 2005). Recovery after these events can be relatively quick, but prolonged increases in the frequency or intensity of storms and cyclones may increase the likelihood of severe perturbations and lead to pronounced changes in biodiversity and community structure. Cyclones and storms also kill marine animals such as turtles and seabirds and destroy breeding and feeding habitat (Limpus & Reed 1985). Destruction by cyclones is considered a major threat for breeding colonies of northern birds such as the lesser noddie *Anous tenuirostris melanops* and the sooty tern *Sterna fuscata* (King et al. 1992, Garnett & Crowley 2000).

Storms also exert considerable damage in temperate ecosystems, for example through removal of habitat-forming kelps and associated fauna, and influence community structure (Dayton & Tegner 1989). For example, the large fucoid alga (*Carpophyllum flexuosum*) is characteristic of calm conditions and is now common in areas of northeastern New Zealand where it was once virtually absent (Cole et al. 2001). This range expansion coincides with a significant decrease in storm frequency and intensity in this part of New Zealand over the past 30 yr related to decadal-scale climate variation (de Lange & Gibb 2000). Pinnipeds and seabirds nesting along Australia's southern shores are vulnerable to storm-induced mortality. Pup mortality in Australian fur seals is strongly influenced by summer storms, particularly in low-lying colonies (Pemberton & Gales 2004).

*Phenology* The tropical wet season strongly influences life cycles of fauna and flora such as the flowering and fruiting patterns of trees and shrubs (Friedel et al. 1993, Bach 2002, Keatley et al.



2002, Boulter et al. 2006) including mangroves (Ochieng & Erftemeijer 2002, Tyagi 2004). The wet season also stimulates breeding in insects (Kemp 2001) and birds (Garnett & Crowley 2000, Whitehead & Saalfeld 2000).

Tropical rainfall may also trigger behavioural changes in estuarine animals such as banana prawns, *Penaeus merguensis*. In common with many commercially important species of penaeid prawns, these have a life cycle that involves migrations between nursery areas in mangrove-lined creeks and estuaries and offshore coastal waters. Rainfall is highly correlated with offshore commercial catches of banana prawns in southern areas of the Gulf of Carpentaria (Vance et al. 1985). It is thought high rainfall leads to a decrease in salinity of estuarine waters, which triggers an increased emigration of prawns (Staples 1980, Staples & Vance 1986, Vance et al. 1998). This salinity trigger has been noted in other parts of the world (see Zein-Eldin & Renaud 1986).

#### *Pelagic systems*

*Physiology* Because coastal regions may receive considerable freshwater input, coastal phytoplankton is subject to more variation in salinity than oceanic phytoplankton. In general phytoplankton species are adapted for ambient salinity so coastal species such as *Skeletonema costatum* thrive over a wide range of salinities while offshore species grow well only within narrow salinity ranges. In addition, estuarine and coastal species exhibit optimal growth at low and intermediate salinities while offshore species thrive at high salinities (Brand 1984, McQuoid 2005, Thessen et al. 2005).

### *Sea level*

#### *Coastal systems*

*Physiology* Different mangrove species are adapted for different tidal inundation regimes as apparent in the zonation patterns of coastal mangroves. Rising sea level will alter the tidal inundation regime experienced by mangroves and presumably increase environmental stress on individual plants. For example, laboratory experiments have shown increased tidal inundation reduced growth and photosynthetic rates in *Rhizophora mangle* seedlings (Ellison & Farnsworth 1997). At any particular site, the mangrove community is highly specialised for local environmental conditions so minor variations in hydrological or tidal regimes can result in high mortality (Blasco et al. 1996).

*Distribution and abundance* Coastal marine habitats will be vulnerable to changes in sea level (Short & Neckles 1999). The increase in water depth and consequent reduction in light availability to the sea bed will impact subtidal marine plants and tropical corals. At any given location, the location of maximum depth limits will shift, depending on topography, directly affecting distributions and abundance. For example, it is estimated that a 50-cm increase in sea level could result in a 30–40% reduction in growth of *Zostera marina*, a widespread Northern Hemisphere seagrass (Short & Neckles 1999). In many places, the shoreward shift of plants and animals will be impeded by coastal development.

Sea-level rise will also alter the magnitude of local tidal ranges, depending on interactions with coastal topography. An increase or decrease in tidal range will directly impact the 'zonation' of macroalgae and fauna in the intertidal and subtidal. An increase in tidal range will exacerbate effects of changing water depth on subtidal plant communities, resulting in a loss of biomass in deeper waters whereas a decrease in tidal range will reduce exposure stress at shallower depths (Short & Neckles 1999).

Mangroves typically occur on low-profile, low-energy coastlines and are ecologically restricted to saline intertidal environments so are considered particularly susceptible to rapid changes in sea



level (Woodroffe 1992, Ellison 1993, Parkinson et al. 1994, Field 1995). Mangrove areas around Australia with small tidal regimes such as Shark Bay and the Exmouth Gulf are likely to be inundated by the projected rise in sea level (see Hughes 2003). When sea levels rise, as projected over the next century, shorelines will move landward but if sedimentation is more rapid than sea-level rise, shorelines may actually move seaward. Mangroves trap suspended sediments, for example a field study in a mangrove swamp in Cairns found 80% of suspended sediment brought in from coastal waters at spring flood tide was trapped in the mangroves, resulting in a rise of the substratum of 1 mm per year and presumably reducing turbidity in coastal waters (Furukawa et al. 1997).

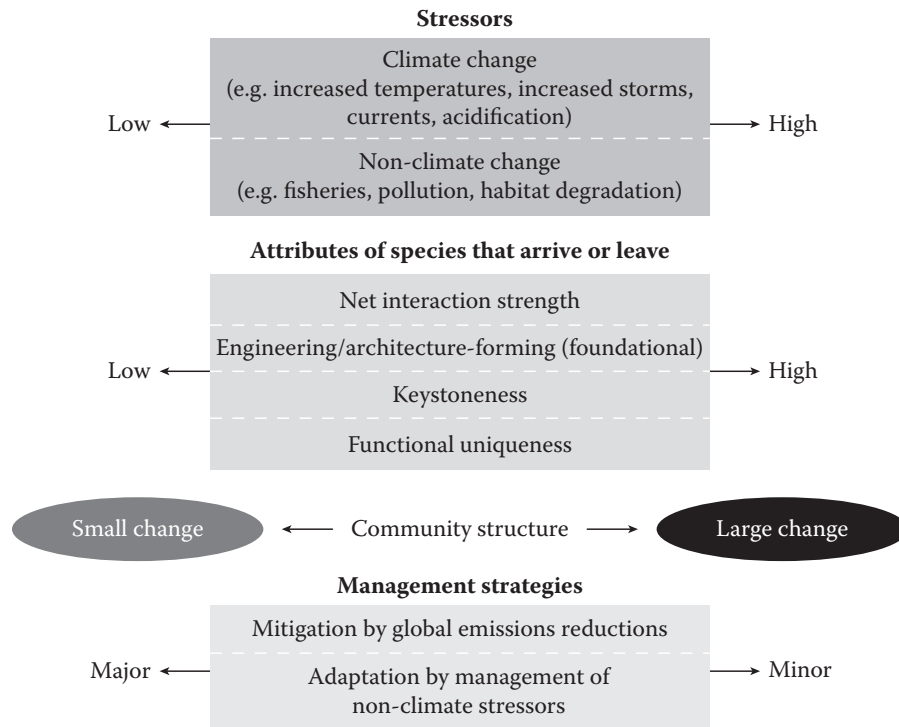
If sediment accretion rates in mangroves are equal to or exceed sea-level rise then mangroves will persist. The ability to accrete sediments will depend on the availability of suspended sediments in coastal waters so in areas where suspended sediment load is low, mangroves may not be able to track rising sea levels (Ellison & Stoddart 1991, Parkinson et al. 1994). Modelling studies of the response of tropical Australian estuaries to sea-level rise reveal differing responses depending on hydrodynamics and channel morphology; in some estuaries mangroves will expand while in others mangroves will retreat (Wolanski & Chappell 1996). Mangroves growing on carbonate settings or low islands may be strongly threatened by sea-level rise over the next century (Ellison & Stoddart 1991, Ellison 1993).

Rising sea level is also a threat to bird species that nest on low-lying coastal areas as valuable breeding sites are flooded or eroded (Galbraith et al. 2002). Examples are the little kingfisher *Alcedo pusilla pusilla* and spangled drongo *Dicrurus bracteatus carbonarius* nesting on low-lying islands in the Torres Strait and the lesser noddy *Anous tenuirostris melanops* that nests in mangroves (Garnett & Crowley 2000). Marine turtle breeding beaches will be impacted by sea-level rise. For example, 32% of current beach area on the island of Bonaire in the Caribbean could be lost if the sea level rises by 50 cm and the loss of potential turtle nesting habitat may be even higher particularly where land directly behind the beach system is developed (Fish et al. 2005). Pinniped haul-out sites for breeding and nurseries may also be reduced or eliminated by sea-level rise (Learmonth et al. 2006).

### Community impacts

Climate impacts on particular species or groups do not occur in isolation and can result in extensive cascading effects and complex interactions (Figure 8). Climatic impacts on a few leverage species, such as species considered foundation species or ecosystem engineers, may result in sweeping community-level changes (Coleman & Williams 2002). Foundation species such as corals support a diverse range of fauna and flora by providing complex architectures of living habitat while ecosystem engineers increase habitat complexity either morphologically or behaviourally. Species that are functionally unique play a distinct role, so loss of these species tends to result in severe impacts on the ecosystem (Fonseca & Ganade 2001). Others such as phytoplankton and zooplankton are found in great numbers and are the base of trophic webs. Most of these groups are primary or secondary producers and therefore support higher trophic levels such as pelagic and demersal fishes, seabirds, turtles and marine mammals. Keystone species have a disproportionate structuring effect on biological communities (large interaction strength relative to their own abundance or biomass), and they are often vulnerable to local extinction due to their small numbers or biomass.

Models and analytical tools provide the capability to estimate climate change impacts in terms of diversity, community composition and species interactions in the context of both direct and indirect effects. Relatively little modelling work has been done on Australian marine species and communities, and there has been no large-scale investigation on the potential impacts of climate change on the diverse and unique fauna of the region. Corals of the Great Barrier Reef are the only group that has been investigated extensively in terms of potential impacts of climate change.



**Figure 8** Species attributes, types of stressors and management strategies that influence the magnitude of climate change impacts on the structure and function of biological communities. Low levels of particular attributes of the species that invade an area or become locally extinct lead to minimal changes, as do low levels of climate and non-climate stressors that a community is exposed to. High levels of those attributes and stressors lead to large community changes. Major implementation of management strategies can reduce community impacts, whereas minor implementation in the context of major stressors can lead to large community changes.

### Non-climate stressors

Climate change is not the only stressor to impact ecosystems, either at present or into the future. Anthropogenic stressors, such as fishing, pollution, coastal development and exotic pests, will all decrease the resilience of marine life and ecosystems. Systems that are already highly stressed may be particularly vulnerable to further perturbations such as those induced by climate change (Hughes & Connell 1999, Steneck et al. 2002, Hughes et al. 2003). Most non-climate stressors can be managed faster than climate change by altering policy and management practices on national and regional scales.

Although Australian fisheries are relatively small by international standards due to the generally oligotrophic waters, considerable tonnage is still extracted and many species and groups are overexploited or at high risk. Fisheries can have major impacts on marine systems through removal of large predators, substantial by-catch of non-target species and habitat destruction by dredges and trawls. Australian fisheries include various commercial (Caton & McLaughlin 2004), recreational and indigenous fisheries (Henry & Lyle 2003). Commercial fisheries harvest more than 130,000 tonnes of fish, squid and crustaceans annually, mostly from coastal, continental shelf and upper continental slope waters. Of 74 Australian stocks considered in 2004, 17 were overfished, 17 were not overfished and 40 were of uncertain status (Caton & McLaughlin 2004), but such

statistics can underestimate the damage to non-target biota and habitat structure. Recreational fishers also remove a sizeable biomass of fish and crustaceans (>30,000 tonnes annually) from coastal and estuarine waters (Lyle et al. 2003).

Virtually all of Australia's population and industries are situated along the coastal fringe or rivers that drain into the sea, and so the effects of pollution and coastal development on marine species or ecosystems can be severe (Kirkman 1997, Duke et al. 2005, Votier et al. 2005). Modification of structure and function of coastal watersheds by agriculture, urban development, and deforestation can lead to considerable increases in erosion and nutrient runoff. Habitat modification and destruction through coastal development or activities such as dredging will all impact marine habitats such as estuaries, mangroves, seagrass beds and kelp forests. These habitats are integral features of marine ecosystems that provide a variety of critical ecosystem services such as nursery grounds, primary production and adult habitats for whole suites of marine organisms.

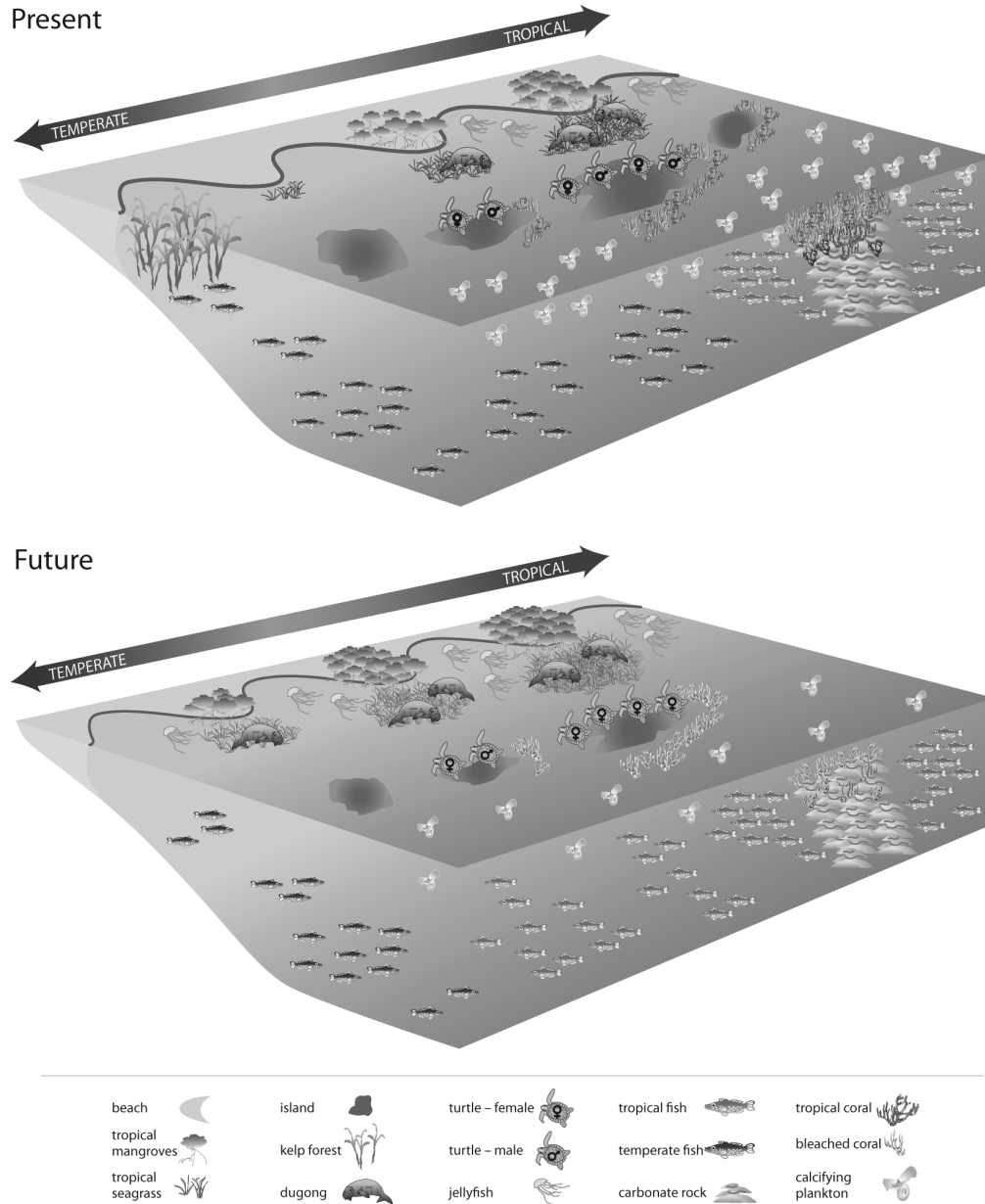
Introduced species can also have severe consequences for marine ecosystems. For example in 1995 and 1998/1999, mass mortalities linked to exotic pathogens probably introduced from aquaculture feed spread rapidly throughout the Australian population of the sardine *Sardinops sagax* (Gaughan 2001, Ward et al. 2001). These mortality events represent two of the most extensive mass mortality events recorded for marine organisms (Gaughan 2001).

Biological communities have adapted to various levels of natural disturbance and variability over evolutionary timescales. Shifts in these disturbance regimes increase stress to these systems and decrease the overall resilience of the system to other disturbances. However, the resilience principle also implies that reductions of the stressors that humans can control may partially ameliorate increasing climate change impacts (Figure 8). Thus easing the impacts of fisheries, pollution, habitat destruction and other non-climate anthropogenic-induced stressors on marine ecosystems may partly mitigate climate change impacts. Although immediate and conscientious international diplomacy to reduce greenhouse gas emissions is a critical mitigation strategy for addressing the long-term impacts of climate changes, adaptive and integrated management systems that focus on fisheries and pollution on regional levels are just as critical because these can address the near-term inevitable changes that will act synergistically with climate change to threaten Australia's marine life.

## Summary

Rising temperatures will have a major influence on species distributions, although population responses will be modified by climate-induced changes in competitive ability, dispersive capacity and behaviour of organisms. However, a general shift in species distributions toward higher latitudes is expected and is already occurring in many parts of the world (Parmesan et al. 1999, Thomas & Lennon 1999, Beaugrand et al. 2002, Parmesan & Yohe 2003, Hickling et al. 2006). In Australian coastal waters, this shift may be facilitated by the major southward-flowing surface currents, particularly given the projected enhancement of the EAC. A concurrent alteration in phenology is expected, with longer growing seasons for marine plants (e.g., seagrasses) and earlier breeding seasons of marine animals. Higher sea level will alter coastline and island hydrography and topography, with potential loss of nesting or breeding areas for seabirds, turtles and seals. Acidification may become a major threat to tropical coral reefs and the cold-water corals found on the edge of the continental slope and on seamounts and to some plankton that are important for ecosystem functioning (Orr et al. 2005, Guinotte et al. 2006).

A schematic of many of the expected impacts of future climate change on Australian marine systems is shown in Figure 9. In coastal waters, tropical species of seagrasses, mangroves and fish have shifted further south. Dugongs have also moved further south following the expansion of tropical seagrasses. However, cold-water kelp species have disappeared from higher latitudes with



**Figure 9** (See also Colour Figure 9 in the insert.) Hypothetical Southern Hemisphere marine coastline and coastal waters ranging from low latitudes in the north to high latitudes in the south under present climate (top) and in the future under global warming scenario (bottom). As temperatures rise, species' distributions shift further south. The range of tropical and subtropical species extends to temperate latitudes while temperate species in the south decline. Rising temperatures and ocean acidification stress coral reefs leading to frequent coral bleaching and an increase in mortality while rapid sea level rise inundates the coral reefs. Ocean acidification also leads to the decline of calcifying plankton such as pteropods and coccolithophores. Rising sea-level encroaches on the mainland and on offshore islands. The sex ratio of marine turtle hatchlings, which is determined by ambient nest temperatures, is skewed in the future as warming produces more females.

a warming climate and the occurrence and distribution of venomous jellyfish has increased. Further offshore corals have bleached and declined in response to warmer temperatures and ocean acidification. Tropical pteropods and coccolithophores have also declined as the oceans acidify. The sex ratio of turtle hatchlings is heavily skewed toward females as nesting beaches heat up. Finally, rapid sea-level rise has drowned the coastline, islands and barrier reefs. Monitoring and strategic planning is sorely needed for Australia because numerous other climate change effects might be already occurring in Australia's marine realm.

### *Tropical and subtropical Australia*

Rising temperatures and ocean acidification are considered the major climate change threats to tropical coral reefs. Bleaching of coral reefs has occurred regularly over the last couple of decades and is projected to occur with increasing frequency over this century. Australian coral reefs are relatively healthy compared to many elsewhere in the world (Pandolfi et al. 2005). However, they are facing considerable pressures from changes to coastal water quality and overexploitation of key ecological functional groups, particularly in areas close to urban and agricultural developments. The role of coral reefs in underpinning coastal economies in Australia is becoming increasingly recognised. The pristine nature of Australian coral reefs attracts large numbers of tourists; the reef-associated tourist economy currently exceeds \$A4 billion per annum. Hoegh-Guldberg & Hoegh-Guldberg (2004) analysed the potential effect of losing the competitive edge for tourism if the coral reefs on the Great Barrier Reef deteriorated as a result of climate change. The effects vary, depending on domestic and international trends in aspects such as markets and politics. However, if one uses the reef-associated component of these economies as a guide to how things might change if reefs continue to degrade, degradation would reduce international tourist income by as much as \$A8 billion over 19 yr (Hoegh-Guldberg & Hoegh-Guldberg 2004).

Seagrass beds and mangroves commonly co-occur with tropical coral reefs and there are strong interactions between them (Harborne et al. 2006). Coral reef crests dissipate wave energy thus ensuring the calm conditions required by seagrass beds and mangroves further inshore, while mangrove and seagrasses filter riverine sediments and nutrients that would otherwise impact coral reefs. Many fish are found in mangroves and seagrasses as juveniles before undertaking ontogenetic shifts in habitat use onto coral reefs (Mumby et al. 2004, Dorenbosch et al. 2005, Mumby 2006). Deterioration in one or more of these systems due to climate change or other impacts may have deleterious consequences for the entire coastal ecosystem with associated economic losses. A reduction in seagrass beds and mangroves will have an immediate impact on the economic value of associated fisheries (Loneragan et al. 2005, Manson et al. 2005, McArthur & Boland 2006). Mangroves and seagrasses provide a range of ecosystem services such as recycling of carbon and nutrients, shoreline protection and enriched coastal productivity (Costanza et al. 1997, Ewel et al. 1998, Kathiresan & Bingham 2001, Duarte et al. 2005, Bloomfield & Gillanders 2005). Coastal fringing mangroves are important for shoreline protection from storms and erosion (Ewel et al. 1998, Badola & Hussain 2005, Kathiresan & Rajendran 2005).

### *Temperate Australia*

Over 46% of Australian's population live in the southeast (Zann 2000). Around Sydney, central New South Wales, the coastline is largely metropolitan with extensive industrial development (Zann 2000). The southeast is considered the most stressed from anthropogenic pressures, other than climate change, such as metal and sewage pollution (Hobday et al. 2006). Large demersal trawl fisheries operate in southeastern Australian waters. This region is also considered the most stressed

by fishing pressure, with a highest proportion of overexploited stocks (Caton & McLoughlin 2004, Hobday et al. 2006).

Marine ecosystems of southern Australia are strongly influenced by the Leeuwin Current and EAC (Maxwell & Cresswell 1981, Phillips 2001). The temperature difference between the EAC and surrounding waters can be more than 5°C (Zann 2000). The projected strengthening of the EAC and warming of the Tasman Sea as global climate warms will have detrimental effects for cold-temperate species in the southeast, particularly in Tasmanian waters. The shelf does not extend far south of Australia and the lack of alternative land mass until Antarctica means these species have no suitable habitat to occupy as global climate warms. The cold-water giant kelp is already in decline in this region and presumably other marine organisms in this region are also at high risk from climate change.

All marine groups investigated are expected to show some southward movement of members. The coccolithophore *Gephyrocapsa oceanica* is a good example; a tropical strain of it has already expanded into temperate waters in eastern Australia. The relatively productive temperate pelagic zone may shrink considerably in area and potentially become restricted to west of Tasmania by the 2070s, while the food web in formerly productive regions may shift toward a much less productive subtropical regime. The recent expansion of *G. oceanica* and decreasing stock sizes of jack mackerel in southeastern shelf waters and southern bluefin tuna returning to the east coast in winter indicate that the pelagic ecosystem may have started to change (Welsford & Lyle 2003, Blackburn 2005, Polacheck et al. 2006).

Venomous jellyfish and harmful algal blooms are a major threat to human health, but are largely phenomena associated with tropical waters or relatively warm and stratified waters, respectively. As a consequence of enhanced southward flow of warm currents such as the EAC and ocean warming these phenomena will likely extend into more southerly regions currently unaffected (jellyfish) or occur more frequently (in case of harmful algal blooms).

### Critical knowledge gaps and a way forward

In this review we have detailed the expected considerable and observed consequences of climate change for marine groups, some of which, such as bleaching of tropical corals, are already being observed in Australian waters. At present, it is impossible to determine if climate change is impacting many less-charismatic marine groups and habitats in Australia, despite compelling evidence from elsewhere in the world.

Long-term datasets are key to documenting and understanding the response of species to climate change. Australian marine scientists have long claimed that the lack of observable climate signals is a consequence of the paucity of ecological time series in the region. This claim is not unique to Australia. Despite an exponential increase in the initiation of long-term monitoring programmes in the world's oceans since World War II, 40% of these time series were discontinued during the 1980s because monitoring was viewed as poor science by administrators (Duarte et al. 1992). This negative perception began shifting during the late 1990s when the knowledge of consequences of climate change began emerging in scientific and political realms, and this has markedly improved the support for many monitoring programmes (Hays et al. 2005).

The case of zooplankton sampling in Australia highlights gaps in the present monitoring system. Zooplankton may be the most abundant multicellular organisms on the planet, are the major source of food of many marine organisms, and are considered sentinels of climate change (Hays et al. 2005). Globally there are zooplankton time series spanning more than 15 yr in no fewer than 30 countries, including relatively small or developing nations such as Bulgaria, Chile, Estonia, Greece, Kazakhstan, Latvia, Faroe Islands, Namibia, Peru, Turkey and the Ukraine. However, the longest



ongoing zooplankton time series in Australia is 2 yr and consists of a single cross-shelf transect off Perth. Given the diversity of marine habitats in Australia and the economic and social importance of fishing, Australia is clearly impoverished in long-term zooplankton and other datasets urgently required to assess climate change impacts (see Hobday et al. 2006). Without such datasets, Australia will be unaware of how its marine systems are altered by future climate change, continuing to rely on information gathered from systems elsewhere. This will make adaptation and mitigation strategies uncertain.

This review indicates that we have a general understanding of some of the likely mechanisms of climate effects on a few particular species, but we have limited knowledge about how Australian marine ecosystems will respond to climate change. It is only when Australia focuses on the entirety of its marine resources will we be able to tackle rigorously the impacts of climate change. There are a number of critical questions that need to be addressed to allow managers tasked with conserving biodiversity, locating marine protected areas, managing eco-tourism associated with cetaceans and turtles, and implementing management plans for the sustainable use of marine resources and indigenous harvesting:

- How will the distribution, abundance and phenology of marine species alter with climate change and how will these impact communities?
- Which species are candidate indicators to monitor climate change in Australian waters?
- Which areas are particularly sensitive to changing climate or are 'hot spots' of change?
- How will regional ocean productivity alter with climate change?
- How can ecosystem resilience to climate change be increased?
- How will climate change affect the socioeconomic productivity of marine ecosystems?

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## APPENDIX: THE CSIRO Mk3 CLIMATE SYSTEM MODEL

The CSIRO Mk3 Climate System Model (CSIRO Mk3) is a state-of-the-art climate model that represents all the major components of the Earth's climate system: atmosphere, land surface, sea ice and oceans. A detailed description of the CSIRO Mk3 is given in Gordon et al. (2002) and summarised below. The CSIRO Mk3 is ranked with the top international models.

CSIRO Mk3 model simulations are included in the Intergovernmental Panel on Climate Change (IPCC) Fourth Assessment Report (IPCC 2007). The Fourth Assessment Report assesses scientific, technical and socioeconomic information relevant for the understanding of climate change, its potential impacts, and the options for adaptation and mitigation. An essential component of this report is climate change projections of the impact of various scenarios of future levels of greenhouse gases on the earth's climate system. The CSIRO Mk3 simulations are an important contributor to these climate projections. For climate projection present in this study we use the IPCC SRES A2 greenhouse gas emission scenario, which projects atmospheric CO<sub>2</sub> levels of 536 ppm by 2050.

The CSIRO Mk3 atmospheric module has a spectral T63 horizontal grid ( $\sim 1.875^\circ$  latitude by  $1.875^\circ$  longitude) with 18 vertical levels (hybrid sigma-pressure vertical co-ordinate). The atmospheric model includes a comprehensive cloud microphysical parameterisation and convection parameterisation, which are linked via the detrainment of liquid and frozen water at the cloud top. Atmospheric moisture advection (vapour, liquid and frozen) is carried out by the semi-Lagrangian method. This module includes the direct radiative forcing of sulphate on atmospheric albedo.

The CSIRO Mk3 land surface scheme uses six layers of moisture and temperature with a vegetation canopy. The scheme uses multiple soil (9) and vegetation (12) types and includes a three-layer snow model.

The sea-ice module incorporates a dynamical-thermodynamic polar ice model that includes a variable fraction of leads. The CSIRO Mk3 ocean model is based upon the Modular Ocean Model version 2.2 (MOM2.2) of the Geophysical Fluid Dynamics Laboratory (GFDL) model. The oceanic component has horizontal resolution of  $\sim 0.9375^\circ$  latitude by  $1.875^\circ$  longitude. For every atmospheric grid point there are two ocean points in the meridional direction, which allows for the atmospheric model and ocean model subcomponents to have matching land-sea masks. There are 31 levels in the vertical, with the spacing of the levels gradually increasing with depth, from 10 m at the surface to 400 m at depth. The ocean model includes a parameterisation of mixing of tracers based on the formulation of Griffies et al. (1998) and improved vertical mixing in the tropical Pacific.

For the climate change projection in this manuscript we use the Mk 3.5 version of the climate system model which has a greatly improved simulation of the Southern Ocean from the original Mk 3 climate system model.