Contribution of climate change to degradation and loss of critical fish habitats in Australian marine and freshwater environments

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Abstract.   Australia's aquatic ecosystems are unique, supporting a high diversity of species and high levels of endemism; however, they are also extremely vulnerable to climate change. The present review assesses climate-induced changes to structural habitats that have occurred in different aquatic ecosystems. Climatic impacts are often difficult to discern against the background of habitat degradation caused by more direct anthropogenic impacts. However, climate impacts will become more pronounced with ongoing changes in temperature, water chemistry, sea level, rainfall patterns and ocean currents. Each of these factors is likely to have specific effects on ecosystems, communities or species, and their relative importance varies across different marine and freshwater habitats. In the Murray–Darling Basin, the greatest concern relates to declines in surface water availability and riverine flow, owing to declining rainfall and increased evaporative loss. On the Great Barrier Reef, increasing temperatures and ocean acidification contribute to sustained and ongoing loss of habitat-forming corals. Despite the marked differences in major drivers and consequences of climate change, the solution is always the same. Greenhouse-gas emissions need to be reduced as a matter of urgency, while also minimising non-climatic disturbances. Together, these actions will maximise opportunities for adaptation by species and increase ecosystem resilience.

Additional keywords: biodiversity, disturbance, fishes, Great Barrier Reef, Murray–Darling Basin.

Introduction

In aquatic habitats, as on land, anthropogenic climate change is having significant and appreciable effects on ecosystems, communities and species (Walther *et al.* 2002; Parmesan and Yohe 2003; Hoegh-Guldberg and Bruno 2010). Major effects include declines in biodiversity and productivity (O'Reilly *et al.* 2003), changes in taxonomic composition and community dynamics (Hughes *et al.* 2003; Xenopoulos *et al.* 2005; Ficke *et al.* 2007), and shifts in the geographic ranges, distribution and abundance of species (Perry *et al.* 2005; Balston 2009; Pitt *et al.* 2010) mediated by increases in climate-related temperature and changes in many other physical characteristics. Aquatic habitats may be even more vulnerable, and changing more rapidly as a consequence of recent climate change, than are terrestrial ecosystems (Richardson and Poloczanska 2008). However, research on the effects of climate change in aquatic ecosystems lags behind that of terrestrial ecosystems. The number of marine and freshwater studies included in the Fourth Assessment Report of the IPCC (Rosenzweig *et al.* 2007) was <0.3% of land-based studies, reflecting a general imbalance in levels of scientific research undertaken in aquatic versus terrestrial systems (Richardson and Poloczanska 2008). Understanding of the effects of climate change in aquatic ecosystems is also difficult because of (1) their size or complexity, (2) inherent variability in environmental conditions and (3) limited long-term records of environmental variables (Richardson and Poloczanska 2008).

Although there is a strong terrestrial bias in documented effects of climate change on natural ecosystems and organisms (Parmesan 2007; Richardson and Poloczanska 2008), climate change has already had significant, and often spectacular, impacts in marine and freshwater ecosystems. In 1998, for example, warm ocean waters caused extensive bleaching and
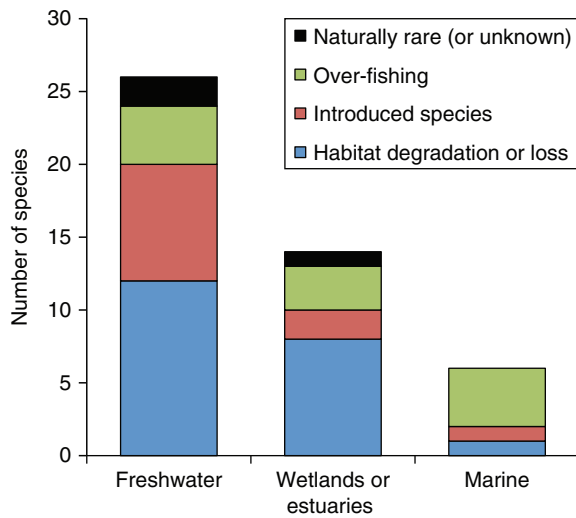
Fig. 1. Primary causes of declines in abundance and/ or geographic ranges of fishes listed under the *Environment Protection and Biodiversity Conservation Act 1999* (www.environment.gov.au/biodiversity/threatened/index. html; July 2010). Of the 46 fish species listed as extinct in the wild, critically endangered, endangered or vulnerable in Australia, most (56%) are from freshwater habitats.

widespread mortality of scleractinian corals throughout the world (Goreau *et al*. 2000; Wilkinson 2000). Links between increasing ocean temperatures and regional-scale bleaching of scleractinian corals are incontrovertible (Hughes *et al*. 2003; Hoegh-Guldberg *et al*. 2007), and climate-induced coral bleaching has greatly exacerbated ongoing declines in the abundance of habitat-forming scleractinian corals at many locations (Hoegh-Guldberg 1999; Wilkinson 2004). In freshwater ecosystems, climate change poses a direct threat to the existence of many habitats, thereby exacerbating already very high rates of species extinction and contraction of species ranges. Habitat degradation and loss is the major threat for threatened fish species in freshwater ecosystems, wetlands and estuaries (Fig. 1) and this will be exacerbated by changes in the quality and quantity of habitat as a result of increasing temperatures, altered rainfall and sea-level rise. In coastal freshwater habitats, for example, sea-level rise and reduced river flow will lead to increased saline intrusion (Bayliss *et al*. 1997; Mulrennan and Woodroffe 1998). Extinction rates of freshwater fishes are equal or higher than those of many terrestrial taxa (Heino *et al*. 2009), and are expected to increase in coming decades because of projected effects of global climate change (Xenopoulos *et al*. 2005).

The vulnerability of aquatic ecosystems to global climate change is due to the profound influence of environmental conditions (especially temperature, water flow or nutrient availability) on biological and ecological processes, and the sensitivities of species, within these systems. Coral reefs are considered to be among the most vulnerable ecosystems to climate change (Walther *et al*. 2002), owing to the temperature sensitivities of corals, which may bleach and die when sea temperatures exceed normal local limits by as little as 1.0°C (Jokiel and Coles 1990). There are few other ecosystems in which the major habitat-forming organisms function so close to their upper thermal limit.

Vulnerability of aquatic habitats to climate change is further heightened by the degraded state of many aquatic habitats (e.g. Schindler 2001; Valiela *et al*. 2001; Hughes *et al*. 2003; Worm *et al*. 2006). For the most part, effects of climate change compound on habitat degradation and losses that have occurred as a result of more localised anthropogenic disturbances, such as overfishing, pollution and habitat modification (e.g. Schindler 2001; Hughes *et al*. 2003). The cumulative effects of exploitation, pollution, and habitat modification and fragmentation on individual species may also make them much more vulnerable to climate change (e.g. Schindler 2001; Wooldridge 2009; Davies 2010). This is particularly so for freshwater and estuarine ecosystems, which are disproportionately affected by increasing development, land and water use.

Climate change may have an impact on any number of the ecological processes (e.g. nutrient cycling, energy transfer, sediment transport, recruitment, or dispersal of animals), and structural or biological components (e.g. communities or individual species) of aquatic habitats. For fishes living in marine and freshwater ecosystems, climate change will have both direct and indirect effects (Roessig *et al*. 2004; Munday *et al*. 2008; Pratchett *et al*. 2009b). Being ectotherms, changes in temperature will have direct effects on fish physiological condition, oxygen consumption, developmental rate, growth, swimming ability, reproductive performance and behaviour (e.g. Van der Kraak and Pankhurst 1997). Changes to water chemistry (especially reductions in pH), which are expected to occur by 2100 with current levels of greenhouse-gas emissions, have also been shown to interfere with sensory abilities of some marine fishes (e.g. Munday *et al*. 2009), which may have important ramifications for settlement and survivorship (Dixson *et al*. 2010). However, the most immediate effects of climate change on fishes are likely to be indirect, caused by changes in availability, structure and connections of critical marine and freshwater habitats. Climate-induced changes to habitat structure have already been recorded in many aquatic ecosystems, where they have had significant effects on both abundance and diversity of fishes (Swales *et al*. 1999; Wilson *et al*. 2006; Pratchett *et al*. 2008).

The purpose of the present review is to consider effects of climate change on critical fish habitats in Australia, comparing the major drivers of climatic impacts across freshwater ecosystems, tidal wetlands, seagrass beds, tropical coral reefs and temperate rocky reefs (Table 1). Australia's aquatic ecosystems are unique, supporting a high diversity of species and high levels of endemism (Unmack 2001; Poloczanska *et al*. 2007), and are extremely vulnerable to the major environmental changes expected to occur in some locations (Poloczanska *et al*. 2007). In general, there are very limited data available with which to assess the effects of climate change on aquatic ecosystems in Australia, especially compared with Europe and North America (Hughes 2003; Poloczanska *et al*. 2007). Two notable exceptions are the Great Barrier Reef (GBR) and the Murray–Darling Basin (MDB), for which anthropogenic threats and changes in ecosystem state have been documented for >100 years (e.g. Murray–Darling Basin Commission 2004a, 2004b; Daley and Griggs 2006, 2008; Davies *et al*. 2010). Within each of these distinct and iconic systems, the recent and observable effects of climate change will be compared with degradation and loss of

Table 1.   Differential effects of climate change on Australian aquatic habitats

Major changes are expected to occur across aquatic habitats as a result of degradation or loss of key structural species, but the major climatic effects and associated drivers vary greatly

Habitat	Critical habitat	Current threat	Major climatic effect	Key driver
Freshwater systems	Snags and fallen logs	Water extraction (irrigation), habitat modification, and reduced connectivity	Reduced runoff and river flow	Reduced rainfall
Tidal wetlands	Mangroves and saltmarshes	Deforestation and habitat modification	Increasing tidal inundation	Sea level rise
Seagrass beds	Seagrasses	Increasing sedimentation and nutrient discharge	Increasing physical disturbance	Increasingly severe storms and cyclones
Coral reefs	Scleractinian corals	Cyclonic disturbances and outbreaks of coral-eating starfishes	Coral bleaching and loss of physical habitat structure	Ocean warming and acidification
Temperate reefs	Giant kelp and macroalgae	Marine pollution and pest species	Shifts in geographical ranges for habitat-forming species	Ocean warming and strengthening of the EAC

critical fish habitats caused by other more direct anthropogenic disturbances. The projected effects of climate change will also be considered to assess their likely impacts in coming decades.

Major drivers of climatic impacts in different aquatic ecosystems

The fundamental cause of anthropogenic climate change is increases in atmospheric concentrations of greenhouse gases (mainly CO_2), which leads to increases in average atmospheric temperatures. In aquatic ecosystems, increasing atmospheric temperatures will warm surface waters of oceans, lakes and rivers (Levitus *et al*. 2000). However, because water has a higher heat capacity than air, this means that increases in water temperatures will lag behind those of atmospheric temperatures (Lough 2007). A significant component of anthropogenically produced CO_2 (approximately one-third, thus far) is also dissolved in the world's oceans, lakes and rivers (Roessig *et al*. 2004). Additional CO_2 dissolved in the ocean reacts with seawater to form weak carbonic acid, causing pH to decline and reducing the availability of dissolved carbonate ions required by many marine calcifying organisms (e.g. corals, other invertebrates and coralline algae) to build their shells or skeletons (Orr *et al*. 2005).

Other environmental changes linked to global climate change that will affect aquatic habitats include reduced rainfall, more extreme rainfall events, or altered rainfall patterns and especially long dry spells (CSIRO 2008), increased severity of tropical cyclones (Madin and Connolly 2006), sea-level rise (Short and Neckles 1999) and changes to ocean circulation and current patterns (Munday *et al*. 2008, 2009). Tropical cyclones may become more intense in a warmer world (Webster *et al*. 2005), which would cause greater damage to key habitat-forming species, such as corals and seagrasses (Madin and Connolly 2006). Sea-level rise will lead to a redistribution (where possible) of intertidal and shallow coastal habitats, as well as increased seawater intrusion into estuaries and the lower reaches of rivers (Short and Neckles 1999). Changes to ocean circulation and current patterns will alter dispersal of marine larvae (Munday *et al*. 2008, 2009) and, combined with

reductions in vertical water mixing, will limit the supply of nutrients and subsequent productivity. Changes to temperatures and flows in freshwater ecosystems are also likely to alter processes such as productivity and the downstream drift of larvae (Lake 2003). A complete loss of freshwater may occur for some habitats such as wetlands. Each of these factors is likely to have specific effects on ecosystems, communities or species; however, their relative importance will vary greatly among habitats (Table 1).

Freshwater ecosystems

For many freshwater systems (especially lotic systems), the most critical factor affecting habitat structure, as well as nutrient loading, transport of materials and organisms, is the amount of flow (Walker *et al*. 1995). Variation in river flow over time scales from days to decades is very important in setting the dynamic equilibrium among habitat patches (Thorp *et al*. 2006). Changes in flow dynamics resulting from climate change will therefore have profound effects on riverine habitats and the fishes that depend on them (Walker *et al*. 1995; Meyer *et al*. 1999). Declines in inflows, combined with increasing evaporation will also reduce lake levels (Carpenter *et al*. 1992; Hughes 2003). Xenopoulos *et al*. (2005) suggested that 75% of freshwater fish throughout the world will become extinct through part of their range by 2070 because of reduced river discharges. Australia has large areas of dryland rivers and highly variable flow regimes that are prone to periods of low or zero flow (Walker *et al*. 1995). Hence, reductions in river flows under a drier climate regime (CSIRO 2008) are likely to exacerbate the existing declines in fish species richness attributable to reduced flows.

Reductions to river flows because of water extraction have already been shown to affect native fishes in lowland reaches of the Murray–Darling river system (Gehrke and Harris 2000). Despite predictions of reduced total rainfall, increased intensity of rainfall may also result in increased turbidity from suspended sediments transported from surrounding catchments. The resultant reduced light penetration for photosynthesis by macrophytes, phytoplankton and benthic algae may potentially lead

to shifts in primary production in aquatic food webs (Bunn et al. 2003). Decreased rainfall and higher temperatures will increase the risk of fires within the catchment and subsequent erosion of sediments can lead to fish kills and the smothering of habitats (Lyon and O'Connor 2008).

Increased river temperatures are likely to affect the distribution of freshwater species, leading to increased elevation of cold-water species, accompanied by an potential upstream range extension of warm-water species (Buisson *et al.* 2008). Negative effects of increasing temperature are also likely to be exacerbated by loss of riparian vegetation, which reduces shading and increases evaporative water loss (McKergow *et al.* 2006; Rayne *et al.* 2008; Davies 2010). Warmer temperatures and increased evaporation rates, combined with a drier climate across much of Australia, will result in increased drying of wetlands and water-holes in ephemeral rivers, and may result in some permanent habitats becoming intermittent (Kennard *et al.* 2010). Some intermittent freshwater habitats may also cease to exist, have extended dry periods or will become much rarer leading to smaller geographic ranges of certain species or reduced connectivity among populations. Whereas increases in temperatures may allow southerly extensions to the range of some marine species (Booth *et al.* 2011), the discontinuous nature of freshwater catchments can prevent similar range changes and, indeed, may lead to range contractions for many freshwater species (Bond *et al.* 2011). For the most part, these effects will compound on to pre-existing threats associated with water extraction and aquifer draw-down, especially in dry inland areas (e.g. central Queensland).

Of the 46 fish species listed under the A*ustralian Environment Protection and Biodiversity Conservation (EPBC) Act 1999* (www.environment.gov.au/biodiversity/threatened/index. html; July 2010), most (56%) are from freshwater habitats (Fig. 1). The primary cause of declines in the geographic range or overall abundance of these freshwater fishes is habitat degradation or loss (Fig. 1; Pollard *et al.* 1990). The other major contributor to increased extinction risk of freshwater fishes in Australia is the introduction of exotic species or translocation of Australian native species, which prey on or compete with native species (e.g. Ingram *et al.* 1990). In 1990, an independent analysis of threatened species (Pollard *et al.* 1990) suggested that 34% (65 of 192 species) of Australia's freshwater fishes were already threatened by habitat loss, invasive species or overfishing.

Coastal wetlands

Coastal wetlands are critical intertidal habitats dominated by plant species (e.g. salt marshes and mangroves) and occupy very specific and often narrow zones, structured by the interactions between sea level, land elevation and sediment accretion (Morris *et al.* 2002). Coastal wetlands are therefore very sensitive to climate-related changes in atmospheric temperature, CO_2 concentrations, rainfall and freshwater input (Michener *et al.* 1997; Morris *et al.* 2002; Lovelock and Ellison 2007). However, the greatest effect of climate change on coastal wetlands (including mangroves and salt marshes) is expected to arise as a result of sea-level rise (Michener *et al.* 1997; Morris *et al.* 2002; Gilman *et al.* 2008).

Mangrove trees are well adapted to being inundated with saltwater; however, growth of trees declines or forests retreat landward with increasing frequency and duration of inundation. Previous episodes of sea-level rise have led to proliferation of mangroves in northern Australia (e.g. Woodroffe 1990), and increasing atmospheric CO_2 may actually lead to increased growth and productivity of mangroves (Lovelock and Ellison 2007). However, development and modification of coastal habitats have resulted in loss of wetlands, disruption to connectivity, enhanced nutrients, and generated physical barriers that reduce the potential for landward migration of wetlands along much of Australia's coastline (Lovelock and Ellison 2007), referred to as 'coastal squeeze' (Doody 2004). In Australia, current rates of sea-level rise are estimated to be 0.3–0.5 mm per year, which are much lower than most global estimates. However, mangroves are already progressing landward and encroaching on salt-marsh environments at many locations along Australia's south-eastern coast (e.g. Saintilan and Williams 1999), which may be partly due to sea-level rise. Since 1983, 14% of Australia's mangrove habitat has been lost (Valiela *et al.* 2001), and a further 231 km^2 is destroyed each year (Valiela *et al.* 2009), mostly as a result of land reclamation and deforestation. Declines in the areal extent of mangrove forests directly affect the diversity of mangrove species as well as ecosystem function (Duke *et al.* 2007). Globally, Nicholls *et al.* (1999) calculated that 13–31% of coastal wetlands have already been lost; however, only 0–2% of this habitat loss was attributable to sea-level rise. With current rates of deforestation, Valiela *et al.* (2009) suggested that mangroves will be lost before major impacts from projected sea-level rise become fully apparent.

Coastal wetlands are an important component of coastal ecosystems in providing a buffer zone between freshwater and marine environments. Mangroves and salt marshes are capable of high rates of denitrification and intercept land-based nitrates, thereby protecting coastal seagrass meadows and coral reefs from excessive eutrophication (Valiela *et al.* 2009). Salt-marsh and mangrove sediments also retain many industrial contaminants (e.g. heavy metals), which would otherwise affect in marine ecosystems (Twilley 1995). There is also a strong positive relationship between the spatial extent of wetlands and the productivity of adjacent seagrass meadows (Valiela *et al.* 2009). Coastal wetlands (including associated estuarine areas) are also important habitats in their own right, supporting up to 300 species of fishes (mainly in tropical environments) and up to 290 kg of fish biomass per hectare (Blaber 2002). The nutrient-rich water within, and flowing from, coastal wetlands supports many commercially important fish species. Along the Queensland coast, Manson *et al.* (2005) demonstrated that fishery catches of barramundi (*Lates calcarifer*) were positively correlated with the local extent of mangroves. Coastal wetlands provide significant subsidies (both in terms of nutrients and larval production) to other coastal habitats, whereby strong connectivity between mangroves and seagrasses, or mangroves and coral reefs leads to increases in fishery productivity (Mumby *et al.* 2004; Meynecke *et al.* 2008).

Increasing loss of coastal wetlands has significant ecological and geophysical impacts, including destabilisation of coastal shorelines and sediments, increased contamination and

eutrophication of coastal ecosystems leading to lower productivity, and loss of habitat for fishes, as well as for many other important species, such as migratory shorebirds (Valiela *et al.* 2009). There are currently 14 fish species from Australian coastal wetlands that are considered threatened, and the major threats to these species are habitat loss and overfishing (Fig. 1). Increasing coastal modification and fragmentation also poses a major threat to species within these vulnerable ecosystems by limiting potential for autonomous adaptation to climate change, whereby natural landward migration of key habitat types might otherwise keep pace with the projected sea-level rise. Changes in the elevation of mangroves are also constrained by several processes (e.g. groundwater inputs, local productivity, decomposition and compression of organic material) that control mangrove sediment surface elevation (Gilman *et al.* 2008). Consequently, there are some locations (e.g. sediment-deficit locations) where landward migration of mangroves will be unable to keep pace with sea-level rise, irrespective of anthropogenic modification of coastal habitats (Gilman *et al.* 2008).

Seagrass beds

Seagrass beds are a unique and important coastal habitat, formed by the growth of flowering plants (as distinct from algae or seaweed) in shallow sandy habitats throughout tropical and temperate biomes (Dennison 2009). Seagrasses as a whole are particularly sensitive to a wide range of environmental changes resulting from climate change, including changes in temperature, salinity, water clarity and nutrient loads, elevated CO_2 concentrations and ocean acidification, sea-level rise, as well as the frequency or severity of cyclones (e.g. Short and Neckles 1999; Waycott *et al.* 2007). In part, increases in CO_2 concentrations may actually increase growth and productivity of seagrasses. The major effect of climate change is expected to be a shift in the relative abundance of seagrass species, with increased abundance of more ephemeral species (e.g. Waycott *et al.* 2007). Complete loss of seagrasses is expected to be localised (e.g. at the mouths of rivers) and may be offset by increases in the extent of seagrasses in areas where seagrass growth is currently limited by nutrient availability (Waycott *et al.* 2007). However, the global extent of seagrass beds is declining at 1.5% (or $110\,km^2$ per year) as a result of direct disturbances (Waycott *et al.* 2009), mostly excessive eutrophication, sedimentation and disease (Orth *et al.* 2006; Waycott *et al.* 2009).

Australia has some of the most extensive and diverse seagrass beds in the world. On the Great Barrier Reef, the total area of seagrass beds is twice that of coral-dominated habitat (Dennison 2009). Moreover, extensive seagrass beds in southeastern Australia support one-third of all seagrass species (Carruthers *et al.* 2007). However, Kirkman (1997) estimated that the total area of seagrass beds in Australia declined by $1450\,km^2$ (or >20%) between 1986 and 1996, mostly in the tropics and mostly as a result of cyclonic disturbances. Recovery of tropical seagrasses subject to anthropogenic disturbances or cyclones is generally very rapid, although recovery has been hampered in some areas by habitat degradation (increasing sedimentation) and declining water quality. In temperate waters (e.g. Western Port in Victoria), where direct anthropogenic disturbances have killed off large areas of seagrass, there is limited prospect of recovery (Dennison 2009).

Seagrass habitats are an important component of coastal ecosystems, contributing greatly to their productivity. Although very sensitive to excessive nutrient loads, seagrasses also trap considerable amounts of nutrients arising from terrestrial and estuarine habitats (Orth *et al.* 2006). Seagrasses represent an important source of food for several threatened species, including dugongs and some sea turtles (Waycott *et al.* 2009). They may also serve as nursery grounds for economically or functionally important fishes that otherwise reside on coral reefs or other inter-connected habitats (Mumby *et al.* 2004). Localised declines in some fishes have been observed following the reduction in seagrass areas (e.g. Butler and Jernakoff 1999). It remains to be tested, however, what proportion of coastal fishes are specifically reliant on non-reef habitats such as seagrass beds, and whether these fishes could utilise alternative habitat types if seagrass beds were unavailable (e.g. Mumby *et al.* 2004).

Coral reefs

Climate change is widely recognised as the most important emerging threat to coral reef ecosystems and there are many ways that climate change will affect coral-reef species, communities and ecosystems (Hughes *et al.* 2003; West and Salm 2003; Hoegh-Guldberg *et al.* 2007; Wachenfeld *et al.* 2007). The most devastating effects of climate change, so far, have been large-scale and severe episodes of coral bleaching, resulting from increasing sea-surface temperatures (Goreau *et al.* 2000). In 1998, coral bleaching occurred in >50 countries throughout the world, killing up to 90% of corals, which then lead to marked changes in the taxonomic composition of coral assemblages (e.g. Reigl and Purkis 2009). In Australia, the effects of coral bleaching have so far been moderate or very localised (Wilkinson 2004). This is particularly true on the Great Barrier Reef, as will be discussed later; however, the most devastating effects of coral bleaching on Australian coral reefs were recorded at Scott Reef, on the north-western shelf (Smith *et al.* 2008). In 1998, very hot and calm conditions led to extensive bleaching of corals to a depth of 30 m, and many of these corals (up to 90%) subsequently died (Smith *et al.* 2008). Extensive coral loss was further implicated in localised declines in the abundance of coral reef fishes, especially butterfly fishes and damselfishes (Halford and Caley 2009). Although there was significant recovery in the aftermath of the bleaching, neither coral nor fish assemblages had returned to their pre-bleaching composition 6 years after the bleaching event (Smith *et al.* 2008; Halford and Caley 2009).

Coral loss, and associated changes in the biological and physical structure of coral-reef habitats, has an important influence on the abundance and diversity of coral-reef fishes (Wilson *et al.* 2006; Pratchett *et al.* 2008). Declines in coral cover have direct effects on the abundance of reef fishes, especially among coral-dependent species (e.g. Kokita and Nakazono 2001; Munday 2004; Pratchett *et al.* 2004). Extensive coral loss may also result in declines in habitat and topographical complexity (Sheppard *et al.* 2002; Graham *et al.* 2007), which are critical for sustaining high diversity of reef fishes and other reef-associated

organisms (Wilson *et al*. 2006; Pratchett *et al*. 2009*b*). When coral loss is combined with structural collapse of reef habitats, up to 65% of reef fishes may experience declines in abundance (e.g. Jones *et al*. 2004). Increasing frequency and severity of mass-bleaching events are clearly linked to climate change (Walther *et al*. 2002; Hughes *et al*. 2003) and the longer-term future is potentially catastrophic, not just for corals, but for coral-reef fishes as well.

Globally, coral reefs are facing significant and accelerating coral loss. Wilkinson (2004) estimated that 20% of the world's coral reefs have already been destroyed, whereby coral cover has declined by >90% and there is limited prospect of recovery. Coral cover has declined by 20–90% on a further 50% of the world's coral reefs, and these reefs may be destroyed by 2050 (Wilkinson 2004). The 1998 global mass-bleaching event contributed greatly to coral-reef degradation, especially in the Indian Ocean (e.g. Graham *et al*. 2008). However, coral-reef degradation is mostly concentrated in eastern Africa, South-east Asia, and the central and southern Caribbean (Wilkinson 1999). All these areas have relatively large human populations living adjacent to coral-reef habitats, and have also had a long history and high levels of exploitation (e.g. Pandolfi *et al*. 2003), indicating that coral loss is caused, or at least precipitated, by direct anthropogenic disturbances.

Whereas effects of climate change are already apparent on corals, it is also likely that the contribution of climate change to overall degradation of reef ecosystems will increase in the coming decades (Hoegh-Guldberg 1999; Wilkinson 1999). Given projected increases in sea-surface temperatures, and limited capacity for corals to acclimatise or adapt, coral-bleaching events will become more frequent and more severe through time (Hoegh-Guldberg 1999; Donner *et al*. 2005). By 2050, most coral reefs are expected to be subject to annual thermal anomalies equivalent to those experienced in 1998 (Hoegh-Guldberg 1999), suggesting that mass bleaching will occur at intervals much less than the time required for corals (populations and communities) to recover from successive major bleaching events (Donner *et al*. 2005). Effects of increasing temperature will also be further exacerbated by ocean acidification (Hoegh-Guldberg *et al*. 2007), which reduces coral growth and increases susceptibility to coral bleaching. Furthermore, the long history of anthropogenic degradation and the increased fragmentation of coral-reef habitats have partly eroded reef resilience, making coral-reef habitats much more susceptible to future climate change (Hughes *et al*. 2003).

Temperate rocky reefs

Australia has high biodiversity and endemicity of temperate marine flora (e.g. Kerswell 2006), which is considered to be very vulnerable to increasing ocean warming. Marine algae with latitudinal ranges centred in temperate Australia are generally cold-water specialists and cannot survive in warmer waters. Accordingly, the geographic ranges of some of these habitat-forming algae have contracted southwards over the past few decades (Wernberg *et al*. 2009), exhibiting an adaptation strategy for temperate species to avoid increasing temperatures. However, given the lack of landmasses and associated shallow coastal habitats to the south of Australia, most species will have

limited opportunity for further pole-ward shifts in their latitudinal ranges to accommodate further increases in ocean temperatures. Increasing ocean temperatures may also lead to southern range extensions for potentially devastating marine invasive species, such as the black sea urchin, *Centrostephanus rodgersii* (Thresher *et al*. 2003; Ling *et al*. 2009), which may be further enhanced by strengthening of the East Australian Current (EAC). Invasive species are one of the greatest contemporary threats to global biodiversity and climate change is expected to facilitate establishment and expansion of many new species on temperate reefs (Wernberg *et al*. 2009).

Climate change (specifically, increasing temperatures and strengthening of the EAC) has been directly linked to changes in distribution and abundance of herbivorous species along the south-eastern coast, which have contributed to declines in the abundance of giant kelps (Edgar 1999; Ling *et al*. 2009). The abundance of giant kelp (*Macrocysitis pyrifera*) has declined dramatically over the past 30 years, especially in south-eastern Tasmania (Edgar 1997). In the 1950s, the total area of kelp forests in Australia was estimated to be 120 km^2; however, more recent estimates of 8 km^2 in 1986, and 0.5 km^2 in 1988–1989, point to a major loss of giant kelp (Edgar 1997). Several factors may account for these dramatic losses, including increased southward penetration and influence of the EAC along the eastern coast of Tasmania, which has increased the water temperature by 1.5°C since 1940 (Edgar 1999). The currents and increased temperatures facilitated local increases of *Centrostephanus rodgersii*, which feeds on giant kelp (Edgar 1999). Further contributors to declines in abundance of giant kelp are marine pollution and the introduction of the Japanese kelp (*Undaria pinnatifida*), which has colonised many areas formerly occupied by *M. pyrifera* (Wernberg *et al*. 2009).

Globally, loss of kelp and macroalgal environments has resulted from increased disease, herbivory, physiological stress, and/or interactions among these processes (Steneck *et al*. 2002). At lower latitudes, periodic deforestations result from anomalies in temperature, salinity or nutrients that either kill kelps directly or trigger diseases that may kill physiologically stressed plants. At higher latitudes (40–60°), herbivory by sea urchins is the most common and most important agent of kelp deforestation. Both of these effects may be linked to sustained and ongoing climate change, although loss of kelp forests and changes in habitat conditions of temperate rocky reefs have been most pronounced in areas adjacent to urban centres, caused by coastal development, oil spills, fishery depletion of apex predators and invasions of introduced species. In heavily urbanised areas of Japan, for example, terrestrial deforestation and damming of rivers reduced availability of iron and humic substances necessary for kelp development (e.g. Suzuki *et al*. 1995). Loss of habitat-forming algae has important consequences for local biodiversity and ecological function (Steneck *et al*. 2002). Most notably, kelp forests concentrate and magnify secondary production, thereby supporting complex food webs in coastal zones. Kelp forests also provide habitat to high diversity and abundance of marine organisms, including mammals, fishes, crabs, sea urchins and molluscs (Mann 1973). Losses of kelp forests and temperate macroalgal habitats are expected to continue, if not accelerate, as a result of climate change and human population growth

(Steneck *et al.* 2002), contributing to widespread degradation of coastal habitats.

Observed *v.* predicted climate impacts

Global climate change is being caused by anthropogenic forcing of the climate system (Houghton *et al.* 2001), and not only are atmospheric concentrations of greenhouse gases rising, but the rate of increase is accelerating (e.g. Canadell *et al.* 2007). Similarly, increases in atmospheric temperatures are expected to continue throughout the next century and are likely to accelerate over the next two decades because of continued increases in greenhouse-gas emissions (Houghton *et al.* 2001). As a consequence, even if climatic impacts are not yet apparent (or have had minor influence compared with other, more direct anthropogenic disturbances), the effects of global climate change on ecosystems, communities and species will become greater over time. Accordingly, this section explores both current (observed) and projected effects of climate change in two specific aquatic systems, namely the Murray–Darling Basin and the Great Barrier Reef. These are both large, relatively well studied systems, of considerable ecological and economic importance to Australia.

The Murray–Darling Basin

The Murray–Darling Basin (MDB) is one of the world's largest catchments, covering more than 1 million km^2 and one-seventh of the area of mainland Australia (Crabb 1997). Ranging over 13 degrees of latitude (from 24°S to 37°S) and up to 2000 m in altitude, the MDB experiences a wide range of climatic conditions. The MDB consists of 24 major river catchments grouped into the northern Darling and southern Murray regions. The rivers are fed mainly by rainfall on the western slopes of the Great Dividing Range. The average annual river flow of the MDB (10 000–22 000 GL) is low by world standards (Maheshwari *et al.* 1995), although inter-annual variability in flow is extremely high, especially within the drier and temperate regions of the basin (Walker *et al.* 1995). Major riverbeds increasingly become completely dry, which causes extensive mortality of resident fishes (Fig. 2). Drought is a recurrent, natural event in the Murray–Darling Basin, and the native fish have evolved to cope with periodic reductions in habitat and river flow (Lintermans and Cottingham 2007; Bond *et al.* 2008). However, water extraction and flow regulation, for the purposes of agriculture, have greatly intensified the effects of droughts (e.g. Bond *et al.* 2008).

The MDB catchment yields AU$10 billion of agricultural produce annually, accounting for 40% of the agricultural production of Australia. Approximately 80% of the MDB has been cleared for agriculture, mostly for dryland grazing, although there are also small areas of intensive horticulture, cotton and cereal crops, which are heavily reliant on irrigation (CSIRO 2008). Current water use accounts for 48% of surface water availability across the entire MDB, representing an increase of >500% since 1925 (CSIRO 2008). Groundwater extraction has also increased (doubling in just the past 10–20 years), although records of groundwater use are very limited (CSIRO 2008). River flows are also highly regulated and there is intense and increasing competition between water-resource development

Fig. 2. Dry river bed of the Condamine River in April 2008. As water receded, many fishes (both native and introduced species) were stranded in isolated waterholes, and eventually died when even these remanent habitats dried out.

and environmental needs (Walker 1985, 1992; Gehrke and Harris 2000).

The MDB is inhabited by 46 species of native fish (Lintermans 2007), most of which have declined in abundance or become highly restricted in their spatial distribution throughout the past century (Murray–Darling Basin Commission 2004*a*, 2004*b*; Lintermans and Cottingham 2007). In total, 57% of these species are now listed as threatened under either Federal or State legislation (Lintermans 2007). In 2005–2007, fishes of the MDB were comprehensively sampled as part of the Sustainable Rivers Audit (Davies *et al.* 2010). Native fishes were not caught in many (43%) of the sample sites and zones where they were predicted to occur, and the biomass of exotic species often exceeded that of native species (Davies *et al.* 2010). The overall abundance of native fishes in the MDB is suggested to have declined to ~10% of pre-European levels (Murray–Darling Basin Commission 2004*b*). These declines are linked to a range of threats, including declining river flows, an overall scarcity of surface water habitats and limited flows during severe droughts. During droughts, the habitats available for fish are reduced and
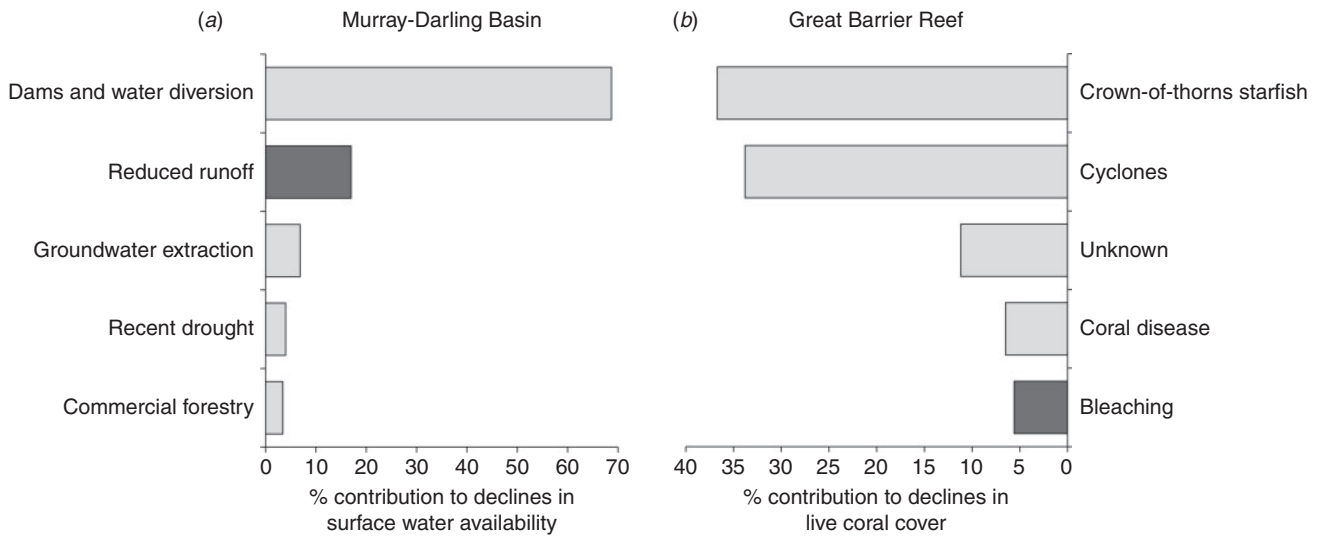
Fig. 3. Relative contribution of climatic (dark grey) *v.* non-climatic (light grey) drivers to recent habitat loss and degradation for (*a*) the Murray–Darling Basin (MDB) and (*b*) the Great Barrier Reef (GBR). Habitat loss and degradation for the MDB was assessed on the basis of documented declines in surface water availability (CSIRO 2008). For the GBR, habitat degradation was assessed on the basis of recent declines in coral cover at select reefs surveyed by Osborne *et al*. (2011).

isolated, and their quality (including water quality) deteriorates through time (Lintermans and Cottingham 2007; Fig. 2). Moreover, crowding of fish in refugia may increase exposure to alien species, and increases competition, predation and diseases (Lintermans and Cottingham 2007). It is during these periods when agricultural demands for water are at their peak that environmental flows are critical to reduce damage to important aquatic ecosystems, communities and species (Bond *et al*. 2008).

Observed climate impacts

Surface water availability is a major limiting factor for freshwater habitats in the MDB, and is influenced by several different climatic drivers, including atmospheric temperatures and seasonal patterns of rainfall. Average annual rainfall in the MDB in the 10 years to 2006 (440 mm) was 4% lower than the annual average for the period 1985–2006 (CSIRO 2008). These data are consistent with projected declines in average annual rainfall throughout Australia as a result of global climate change. However, there is high inter-annual and inter-decadal variability in rainfall for the MDB, and similar periods of low rainfall occurred in the 1890s, 1940s, 1960s and 1980s. Recent declines in average rainfall during the 'millenium' drought may or may not reflect global climate change, whereas average annual runoff recorded from 1997 to 2006 is 21% below the long-term average, and unprecedented in the historical (>100 years) record (CSIRO 2008). As a dryland river system, average evaporation is very high (94% of precipitation) and runoff averages only 4% of precipitation (Davies *et al*. 2010). CSIRO (2008) attributed this reduction in runoff to disproportionate declines in autumn and early winter rainfall in the southern MDB. As a consequence, the soils are less saturated, and together with moderate declines in winter rainfall, this greatly reduces runoff. Increasing atmospheric temperatures also exacerbate evaporative loss.

Non-climatic threats

Declines in runoff attributable to recent climate change (and specifically, temporal shifts in major rainfall periods) contribute significantly (up to 17%) to observed declines in surface water availability (Fig. 3; Van Dijk *et al*. 2006). However, recent and readily detectable changes in surface water availability are mostly attributable to the large number of dams and extensive diversion of flows (Fig. 3), especially in the upper Darling where 178% of average annual runoff can be stored and diverted (Kingsford 2000). Reduced runoff and surface water availability directly affect riverine flow throughout the MDB (Van Dijk *et al*. 2006), such that many rivers no longer flood and significant areas of floodplains are now permanent water storages (Kingsford 2000). Across the entire MDB, water retention in public and private dams, as well as direct extraction, reduces surface water availability by as much as 68% (CSIRO 2008). By comparison, the recent drought (1996–2006) contributed <5% to recent declines in surface water availability (Fig. 3). In all likelihood, recent reductions in river flow attributable to climate change (specifically, the reduced runoff as a result of increased evaporative loss) would have had negligible impacts on freshwater habitats were it not for pre-existing levels of water extraction, retention and diversion across the MDB (CSIRO 2008).

Major threats to the freshwater habitats and fishes in the MDB, and the 57 species of freshwater fishes that utilise these habitats, have been well documented (e.g. Cadwallader 1978; Koehn and O'Connor 1990; Murray–Darling Basin Commission 2004a; Davies *et al*. 2010). Foremost among these threats are (1) changes to flow regimes, including reduced flow as a result of water retention and diversion, and reduced seasonal variability in flow rates, (2) habitat degradation, including removal of riparian vegetation, removal of structural woody habitat (snags) and increasing sedimentation, (3) declines in water quality, resulting from addition of cold water (from dam

releases), land clearing, pesticides, nutrients, sediment and other contaminants, (4) barriers to flow and fish migration (dams, weirs and culverts), (5) historical over-fishing, and (6) high densities of non-native species. The relative importance of these different threats varies among locations and among different species of native fish; however, it is regulation of water flows that is considered to be the most critical change, with significant effects across a wide range of species and major impacts on the functioning and resilience of freshwater habitats (Gehrke and Harris 2000; Kingsford 2011). Gehrke and Harris (2000), for example, showed that regulated rivers contained a higher proportion of non-native fishes than did unregulated rivers, and also had lower than expected diversity of fishes in lower reaches. The effects of regulated flows are further compounded by overall reductions in riverine flow because of increasing retention and diversion of surface water (Kingsford 2011).

Degradation and loss of freshwater habitats in the MDB has been occurring for more than a century, and must be substantially reversed to re-establish viable populations for most native fishes (Murray–Darling Basin Commission 2004*b*). The MDB Ministerial Council *Native Fish Strategy* (Murray–Darling Basin Commission 2004*b*) aims to rehabilitate native-fish communities to 60% of their pre-European abundance and distribution. The major interventions required to achieve this aim are restoration of riverine and floodplain habitats (e.g. Davies 2010), as well as restoration of environmental flows. These two actions are expected to increase the abundance of native fishes in MDB by at least 45%. It is clear, however, that restoration and maintenance of historical flow rates will be increasingly challenged by ongoing climate change and competition with other water users (Van Dijk *et al*. 2006). To account for the declines in surface water availability attributed to recent climate change, current water storage and diversion would need to be reduced by 20–35% across the MDB. Moreover, water storage and diversion would need to be further reduced with ongoing climate change, whereas water-storage capacity is actually increasing at ∼6% per year (CSIRO 2008) and there are existing plans for many new dams across the MDB (Kingsford 2000).

Future climatic impacts

Recent declines in rainfall in the MDB cannot be unambiguously linked to climate change (e.g. Lough *et al*. 2011), although it is expected that large parts of Australia will become progressively drier in the coming decades. On the basis of projected declines in total rainfall over the next 20–50 years (especially in the south-eastern section of the Basin), river flows in the MDB are expected to further decline by 5–15% (Van Dijk *et al*. 2006). However, even if rainfall is unchanged, increasing atmospheric temperatures will reduce inflows to freshwater environments because of increasing evaporative water loss (Cai and Cowan 2008). The impact of climate change on water use is also likely to be significant (Van Dijk *et al*. 2006). Reduced rainfall and increased temperatures will increase the demand for irrigation water and reduce the amount of water in storage. Coupled with increasing water demands by human societies, climate change will put increasing pressure on environmental flows critical for sustaining freshwater habitats in the MDB. Other potential effects include decreases in the frequency and magnitude of

floodplain inundation, leading to increased salinity, altered sediment and nutrient delivery, anoxic episodes, and increased incidence of algal blooms (Van Dijk *et al*. 2006). Poor water quality can lead to an increased incidence of fish kills (Koehn 2005).

The overall effects of climate change on the MDB will largely depend on other activities being undertaken to reduce water use. Ironically, strategies to mitigate the effects of climate change may exacerbate some impacts on freshwater systems. Tree plantations established to sequester CO_2 emissions will reduce runoff from forested catchments and have the potential to further reduce stream flows (Hafi *et al*. 2010).

The Great Barrier Reef

Australia's Great Barrier Reef (GBR) is the largest coral reef system in the world, consisting of ∼2900 individual reefs spanning 14 degrees of latitude and stretching 2100 km from north to south. The GBR Marine Park was established in 1975 under the *GBR Marine Park Act*, and was declared the world's largest World Heritage Area in 1981 (Wachenfeld *et al*. 2007). On July 1st 2004, 33% of the area encompassed within the GBR Marine Park was closed to fishing (up from 4.5% previously), including at least 20% protection for each of 70 distinct bioregions (Fernandes *et al*. 2005). This increased level of protection was partly motivated by increased recognition of threats posed to the GBR from declining water quality, commercial and recreational fishing, and global climate change (Olsson *et al*. 2008). The new network of no-take areas was a key step towards increasing the resilience of the GBR, while maintaining important goods and services that are provided by this system (Fernandes *et al*. 2005). In contrast to the MDB, the GBR contains a total of at least 2000 species of fish.

The GBR provides significant social and economic benefits to Australia. Tourism activities in the GBR and its catchment contribute AU$6.1 billion per year directly to the Australian economy, and employ an estimated 63 000 people (Wachenfeld *et al*. 2007). Commercial fishing in the GBR generates a further AU$119 million per year, and employs 3600 people (Wachenfeld *et al*. 2007). There is also a significant value associated with intangible benefits (i.e. non-use values) associated with maintaining the 'near-pristine' status of the GBR (Oxford Economics 2009). However, increasing use of the GBR places considerable pressure on the overriding conservation objective of the GBR Marine Park Authority to ensure its ecological sustainability. The ecological status, as well as the economic value, of the GBR is also likely to be undermined by sustained and ongoing global climate change. However, climate change also provides additional incentive to improve current management of the GBR, whereby local actions (e.g. improving the water quality and reducing threats to reef habitats) could greatly increase coral-reef resilience (Marshall and Schuttenberg 2006). For example, Wooldridge (2009) estimated that significant improvements in water quality on the inshore GBR would enable local corals to withstand a further 2.0–2.5°C of temperature rise.

Observed climate impacts

As for coral reefs globally, the most obvious sign of climatic impacts on the GBR are recent increases in the incidence and

Table 2.   Recorded instances of mass coral bleaching on the Great Barrier Reef, since 1979

Seasonal 'paling' of some coral colonies occurs in nearly all years, and specific instances of mass-bleaching, whereby multiple colonies and species are simultaneously affected, has occurred nine times (at intervals of 1–6 years). Data presented show the percentage of reef considered to have had conspicuous evidence of bleaching, as well as the percentage of reefs with severe (>60%) bleaching

Year	n	Bleaching recorded (%)	Severely bleached (%)	Key reference
1980	5	100	0	Oliver 1985
1982	14	100	7	Oliver 1985
1983	14	100	0	Oliver 1985
1987	21	81	0	Oliver *et al.* 2009
1992	24	30	0	Oliver *et al.* 2009
1994	40	10	0	Oliver *et al.* 2009
1998	654	42	18	Berkelmans and Oliver 1999
2002	641	54	18	Berkelmans *et al.* 2004
2006	35	56	9	Weeks *et al.* 2008

severity of coral bleaching (Table 2). While coral-reef habitats account for <7% of the area encompassed within the GBR Marine Park, they are an ecologically and economically important component of this system (e.g. Pratchett *et al.* 2008). Moreover, coral-reef habitats are extremely vulnerable to increasing changes in temperature and ocean acidification (Walther *et al.* 2002; Hoegh-Guldberg *et al.* 2007). Major instances of coral bleaching have been recorded at fairly regular intervals on the GBR, extending back to 1980, when conspicuous bleaching of common corals (mostly *Acropora* and *Montipora*) was first noted at several isolated reefs between Townsville and Cairns (Oliver 1985). Since then, successive bleaching episodes have tended to occur over increasing geographic scales, affecting greater number of reefs, and greater numbers of coral species and colonies, with increased severity (Table 2; Oliver *et al.* 2009). Australia was largely spared during the 1998 global mass-bleaching, which caused extensive bleaching in virtually every region of the world, and killed up to 90% of corals, especially in the Indian Ocean (Wilkinson 2004). On the GBR, bleaching was conspicuous and widespread in 1998; however, bleached corals mostly recovered well (Wilkinson 2004) and overall mortality rates were generally low (Maynard *et al.* 2008; Anthony and Marshall 2009).

The most extensive and most severe bleaching episode to affect the GBR occurred in 2002 (Berkelmans *et al.* 2004; Maynard *et al.* 2008), corresponding with the highest sea-surface temperatures (often >33°C) recorded on the GBR. During this event, bleaching was recorded at 54% of reefs surveyed across the length and breadth of the GBR (Berkelmans *et al.* 2004). As with previous bleaching events, bleaching was more extensive and more severe on inshore reefs compared with offshore reefs (Berkelmans *et al.* 2004), but there is little data on mortality *v.* recovery of bleached corals (Baird and Marshall 2002; Maynard *et al.* 2008). The most recent bleaching event, in 2006, was mostly restricted to the southern GBR (south of 20°S), and effects were highly localised (Weeks *et al.* 2008). At the Keppel Islands, >90% of corals bleached in 2006 and 40% of corals subsequently died (Diaz-Pulido *et al.* 2009). Elsewhere (e.g. Heron Island), coral bleaching was relatively minor, owing to the frequent intrusions of cooler oceanic waters (Weeks *et al.* 2008). Effects of coral bleaching are typically very patchy within and among reefs of the GBR, which may promote

persistence of species and also enhances recovery and resilience of coral communities (Oliver *et al.* 2009).

Non-climatic threats

The GBR has been subject to a long history of exploitation and anthropogenic degradation, especially on near-shore reefs. Coastal populations of Indigenous Australians have harvested food from the GBR for millennia; however, exploitation of many species (e.g. turtles, dugongs, sea cucumbers) and degradation of reef habitats increased significantly following European settlement (Daley *et al.* 2008). Importantly, introduction of sheep and cattle in many major catchments adjacent to the GBR was initiated in the 1860s, after which, there was a doubling of sediment loads introduced to the GBR lagoon during major flood events (McCulloch *et al.* 2003). Although no longer pristine, the GBR has much lower levels of depletion for carnivores, herbivores and architectural species than do other major reef ecosystems (Pandolfi *et al.* 2003).

Inshore reefs of the GBR are considered to be much more degraded (Pandolfi *et al.* 2003), having less coral and more macroalgae than do offshore reefs (e.g. Wismer *et al.* 2009). To some extent, these cross-shelf differences are to be expected given natural gradients in terrestrial *v.* ocean influences, as well as differences in the composition of fish assemblages, especially reduced abundance of major herbivores on inshore reefs (Hoey and Bellwood 2008). However, inshore reefs are highly variable, and coral cover is extremely high (>80%) on some inshore reefs (Sweatman *et al.* 2007). However, inshore reefs are frequently exposed to flood plumes and to sediment that is resuspended from the shallow bottom by wave action (Larcombe and Woolfe 1999), and the lack of corals on some inshore reefs may have been exacerbated by anthropogenic activities (agriculture and development) in adjacent catchments. Photographic records of inshore reefs spanning >100 years reveal long-term changes in habitat structure at some sites (Wachenfeld 1997). At Stone Island, for example, photographs taken by Saville-Kent in 1890 reveal extensive cover of branching corals on the exposed reef flat. Comparable photographs of the same reef flat taken in 1994 do not show any corals, but patches of macroalgae interspersed across a mud flat (Fig. 4*a*). These long-term changes in habitat structure are
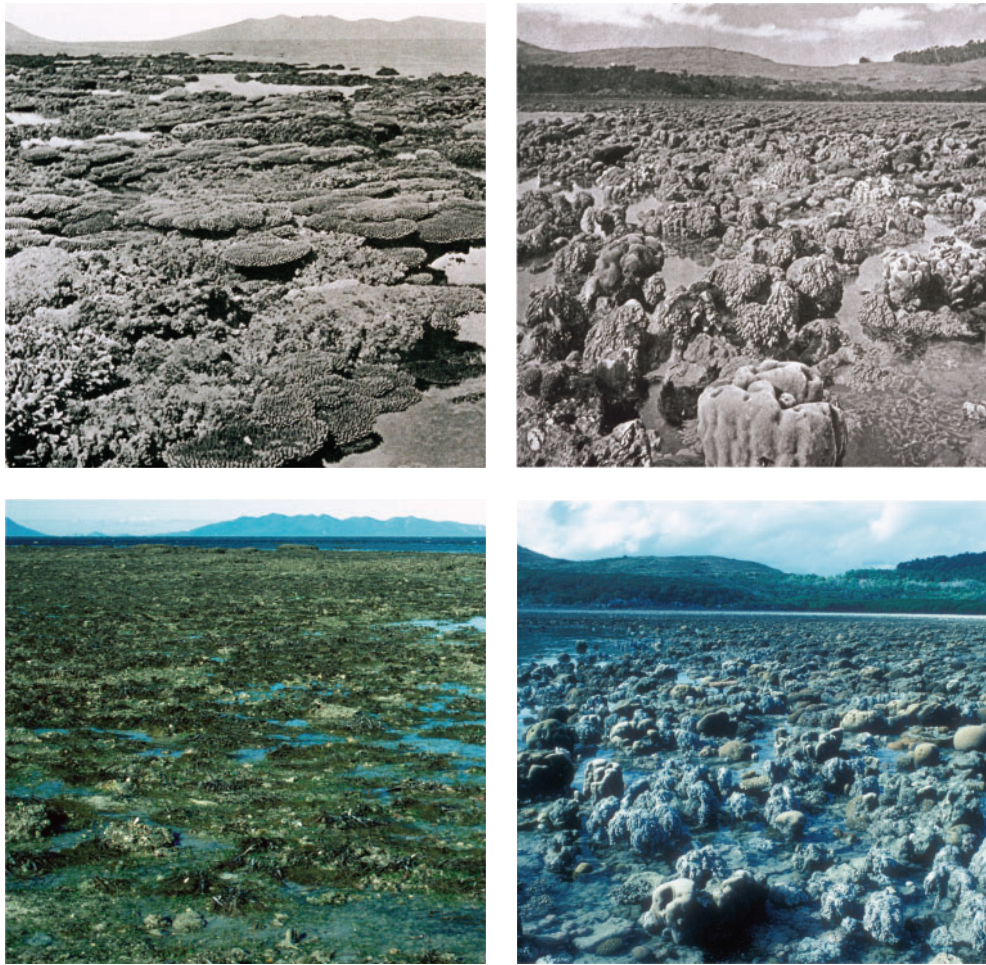
Fig. 4.   Historical *v.* contemporary reef-flat assemblages at Stone Island (left) and Orpheus Island (right). Historical photographs (top) were taken in 1890 by W. Saville-Kent. Contemporary photographs (bottom) were taken in the mid-1990s, revealing marked changes in reef-flat assemblages at Stone Island, and relatively little change at Orpheus Island.

largely attributed to chronic stresses associated with declining water quality (Hughes *et al*. 2010). However, detailed analyses of historical photographs by Wachenfeld (1997) revealed that these changes were not consistent across all locations, and many inshore reefs retain a habitat structure similar to that recorded pre-1950s (Fig. 4*b*).

More recently (mostly since 1960), coral reefs in the GBR have been subject to increasing large-scale disturbances. Bellwood *et al*. (2004) suggested that average coral cover declined >40% from 1960 to 2000, and attributed these losses to cumulative effects of increasing outbreaks of the corallivorous crown-of-thorns starfish (*Acanthaster planci*) and coral bleaching. Broad-scale and ongoing monitoring by the Australian Institute of Marine Science (e.g. Sweatman *et al*. 2008) shows that coral cover on the GBR is highly dynamic, caused by inter-reef variation in the effects of (and recovery from) several different types of disturbance, including cyclones, outbreaks of *A. planci*, bleaching and coral disease. Reef-wide coral cover declined very little between 1995 and 2009, and declines that were observed were mainly attributable to the effects of cyclones and outbreaks of *A. planci* rather than to those

of climate-related disturbances (Fig. 3; Osborne *et al*. 2011). Similarly, Bruno and Selig (2007) showed that climate change played a minimal part in protracted coral declines apparent across much of the Pacific. It is incontrovertible that regional-scale incidences of mass-bleaching are caused by climate-related increases in sea-surface temperatures (Hughes *et al*. 2003); however, bleaching currently accounts for <6% of coral loss recorded on the GBR between 1995 and 2009 (Fig. 3).

Climate change may have also exacerbated coral loss attributable to coral disease (Bruno *et al*. 2007) or cyclones (Webster *et al*. 2005); however, it is difficult to establish the contribution of climate change to these effects, although both have contributed greatly to recent coral loss (Fig. 3). Bruno *et al*. (2007) found a significant relationship between the occurrence of positive temperature anomalies and incidence of white syndrome, but only on reefs with high (>50%) coral cover. Moreover, white syndrome is only one of several different coral diseases that occurs on the GBR, and the links between global warming and these diseases (e.g. black-band and brown-band disease) is unclear. In terms of cyclones, the intensity (if not

occurrence) of severe tropical storms is influenced by sea-surface temperatures, and is expected to increase with ocean warming (Landsea *et al.* 2006). However, Klotzbach (2006) found no change in the frequency or intensity of tropical cyclones from 1986 until 2005, despite a 0.25°C increase in sea-surface temperature. Further, apparent long-term increases in cyclone intensity (e.g. Webster *et al.* 2005) are attributed to improved methods for quantifying cyclone intensity after 1984 (Landsea *et al.* 2006).

Future climatic impacts

So far, climate impacts on Australia's coral reefs have been relatively minor compared with the extent of coral loss caused by non-climatic disturbances (Fig. 3). Climate change-related increases in sea-surface temperatures and declines in ocean pH are, however, expected to increasingly affect coral reefs in the future (Hoegh-Guldberg 1999; Hoegh-Guldberg *et al.* 2007). Climate projections suggest that mass bleaching will become a biannual phenomenon by 2030 if corals do not acclimatise or adapt (Donner *et al.* 2005). Increased thermal tolerance by 0.5–1.0°C by 2050 could delay projected bleaching events by 5 years, possibly allowing affected reefs some recovery between major disturbances. The future cover and species composition of scleractinian corals and the ecosystems they support will depend on their ability to adjust to current rates of ocean warming and acidification. Despite this, very few data exist on which to evaluate the adaptive capacity of coral communities, species or populations to these trends.

Communities can adapt to climate change through shifts in community composition towards more tolerant species (Hughes *et al.* 2003). Shifts in community species composition following bleaching have been widely documented (e.g. Edwards *et al.* 2001; Loya *et al.* 2001). Recovery of reefs may occur through the growth of more resilient survivors (Loya *et al.* 2001)) or through recruitment and recovery of fast-growing but often more sensitive species (Edwards *et al.* 2001; Pratchett *et al.* 2009*a*). Therefore, although climate change is expected to change the community composition of reef corals, it is not yet clear whether a shift towards more tolerant species will occur.

Coral populations can acclimatise or adapt by increasing the frequency of more tolerant individuals (genotypes) within populations. Although increases in the thermal tolerance of some coral populations have been observed following major bleaching events (e.g. Maynard *et al.* 2008), no study has directly linked differences in allelic frequencies to thermal tolerance in coral (Maynard *et al.* 2008). D'Croz and Mate (2004) found genetic divergence between Caribbean populations of *Pocillopora damicornis* in cooler and warmer reef areas with corresponding thermal tolerances. Edmunds (1994) found that rates of natural bleaching differed among genotypes in *Montastrea anularis*; however, this author did not associate tolerance with specific alleles. Corals may also gain increased thermal tolerance by changing their dominant symbionts towards types with greater thermal tolerances, a process termed 'symbiont shuffling' (e.g. Berkelmans and van Oppen 2006). Although there are limits to thermal acclimatisation through symbiont shuffling (i.e. 1.5°C when dominated by GBR D type instead of C2 type), field evidence suggests that reef-wide

changes in dominant *Symbiodinium* type can offer corals some short-term protection against predicted temperature increases (Jones *et al.* 2008). However, increases in the proportion of thermally tolerant *Symbiodinium* can lead to reduced growth of the host coral (Jones and Berkelmans 2010), an effect which may exacerbate reduced calcification rates caused by ocean acidification.

The potential for adaptation of corals, and the time scales over which this can occur, can be modelled if quantitative genetic estimates of heritability are known. Heritability describes the amount of genetic variation in a population which natural selection can act on (i.e. additive genetic variation results in offspring with intermediate appearance to parents). At present, only two studies have estimated heritability in any coral trait (Meyer *et al.* 2009; Császár *et al.* 2010). Both studies found significant heritability in molecular and physiological traits of both host and symbionts, suggesting the potential for genetic adaptation in these traits. Estimates of heritability of more coral traits, as well as links between these traits and fitness (e.g. growth and survival) in a variety of temperature and pH scenarios, are required before effective modelling of coral's responses to climate-change effects can occur.

Managing effects of climate change

Clearly, urgent action is required to minimise global greenhouse-gas emissions and thereby reduce longer-term climatic impacts on Australia's aquatic ecosystems. However, drastic reductions in emissions, even if they are implemented immediately, will not guarantee the persistence of ecosystems, communities and species that are already being affected by global climate change and will be affected for some time into the future. It is predicted, for example, that global atmospheric temperatures will increase by >1°C by the end of the century, regardless of future emission scenarios, and Australia's climate is currently warming faster than the global average (Lough *et al.* 2011). Reductions in global greenhouse-gas emissions may limit extreme changes in environmental conditions and reduce rates of change to which species must adapt. In the short-term, however, management must attempt to facilitate the adaptation of species and ecosystems to inevitable climate change, however extreme that turns out to be.

Management will need to be both non-spatial and spatial (Fig. 5), although this section focuses principally on spatial management interventions. Non-spatial management approaches are often (although not always) applied without being area-specific. Some examples for aquatic ecosystems include regulation for sustainable harvest of species, reduced by-catch, quarantine arrangements to prevent the arrival of invasive species, environmental water allocations, and strategies to reduce water extraction from streams and wetlands for agricultural and urban uses. As a last resort, *ex situ* conservation might be necessary to avoid extinction of some species (e.g. translocations) for which spatial management options have been exhausted (L. Shoo, A. Hoffman, S. Williams, R. Pressey, and Y. Williams, unpubl. data).

Four kinds of spatial management are distinguished here that can help promote adaptation of aquatic ecosystems and species to climate change (Fig. 5). In practice, these would be applied in
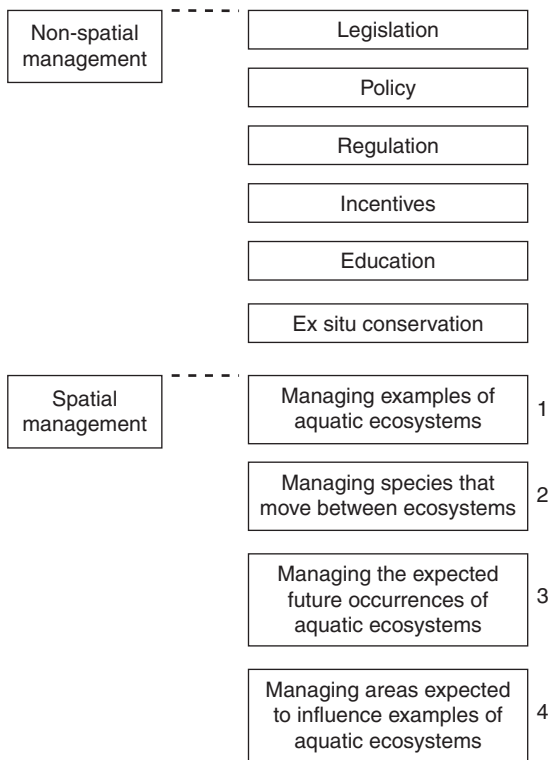
Fig. 5. A classification of management interventions for aquatic ecosystems under climate change. Numbered boxes are referenced in the text. Spatial management refers to any management action directed to a particular place. Protected areas are a widespread example. Non-spatial management refers to approaches that do not discriminate between particular areas. The main purpose of the classification is to illustrate a variety of options for management, rather than to produce mutually exclusive categories. Some management approaches, for example, blur the boundaries between spatial and non-spatial, as when policies are applied to particular places. An example is State Environmental Planning Policy No. 14 in New South Wales which required consent for developments affecting specific mapped coastal wetlands (Rogers and Saintilan 2002), albeit many of those along the eastern fringes of the State. Another example is the role of legislation in underpinning the rezoning of the Great Barrier Reef Marine Park in 2004 (Osmond et al. 2010).

various combinations, and often with the support of policy, regulation and other non-spatial approaches. The conventional, and still important, approach to conservation has been to establish protected areas to represent examples of ecosystems (Fig. 5: Box 1), given that few ecosystems can be managed for conservation in their entirety (Margules *et al.* 2002). Protected areas are not particularly applicable to habitats such as rivers, which are long and linear and subjected to upstream and downstream influences (Koehn 2003). More recently, however, conservation planning has begun to address a variety of spatially explicit management actions in addition to protected areas (Joseph *et al.* 2009). The protection of specific areas remains an important tool in a changing climate, to ensure that refugia, or areas that might be buffered from the effects of climate change, are effectively managed. Examples of this may be occurrences of mangroves that might undergo relatively mild effects of climate change (McLeod and Salm 2006) and coral reefs that

are buffered from rising sea-surface temperatures by cool upwellings and other physical factors (Marshall and Johnson 2007). An additional reason is to enhance the resilience of ecosystems to the effects of climate change. For coral reefs, spatial management can promote recovery of corals after bleaching events by maintaining healthy populations of herbivorous fish to reduce algal growth and by grouping protected reefs, so that bleached reefs are well supplied with coral propagules from unaffected reefs (Obura 2005). The protection of refuge pools in rivers or wetlands can allow opportunities for recolonisation under higher flows.

Resilience to climate change is likely to be an important goal of spatial management for aquatic ecosystems generally. Among the factors determining resilience are the attributes of the species (Crook *et al.* 2010) and the functional integrity of ecosystems. This can be expected to minimise the impacts of climate change on ecosystems or confer the ability to recover from those impacts. Stressors that can be directly managed, such as water extraction, sedimentation and eutrophication, should therefore be limited or reduced (Hughes *et al.* 2003) and fishing mortalities should be minimised (Bellwood *et al.* 2004; Marshall and Schuttenberg 2006). A related trend towards managing for resilience is the increasing attention given to spatial planning for the persistence of processes (Pressey *et al.* 2007). Recent work, for example, has begun to address time-series data and quantitative conservation objectives related to the spatio-temporal dynamics of the anomalies of sea-surface temperature and the risk of coral bleaching (Game *et al.* 2008; N. Ban, R. Pressey, and S. Weeks, unpubl. data).

Direct spatial management of aquatic ecosystems (Fig. 5: Box 1) also involves restoration. Spatial priorities can be identified, for example, to replant mangroves (McLeod and Salm 2006), to reverse the impacts of engineering works such as drainage and floodgates in coastal wetlands (Pressey and Middleton 1982) or enhance structural woody habitats (Nicol *et al.* 2004). In deciding whether restoration is warranted, managers must consider the historical condition of these ecosystems, the feasibility of returning areas to their pre-disturbance states, the cost of the interventions, and proximity to spatial management actions for other ecosystems. The success of some recovery actions such as revegetation could be compromised under climate-change scenarios.

Given that ecosystems are not self-contained units, a complementary management approach is to consider the requirements of species with life histories that involve moving among ecosystems (Fig. 5: Box 2). This is important for freshwater systems (Dudgeon *et al.* 2006) where diadromous fishes undertake extensive longitudinal migrations between headwaters and the estuaries or the open ocean (Beger *et al.* 2010). Functional riverine connectivity is essential to ensure that movements can continue. It is also important for the marine realm, where proximity of different ecosystems can determine the composition and abundance of species in each (Skilleter *et al.* 2005; Mumby 2006). Fully integrated management of aquatic ecosystems would also recognise the dependence of many terrestrial species on freshwater and marine systems (Dudgeon *et al.* 2006; Beger *et al.* 2010). Essentially, this approach to management requires knowledge of the complementary nature of particular ecosystems and appropriate conservation actions in each. Under

climate change, it will also require some understanding of how each of the ecosystems, and the biological connections between them, might change.

Climate change implies changes in the distribution of species and ecosystems; so, management for climate change must anticipate these changes and consider the areas to which aquatic ecosystems and species might move (Fig. 5: Box 3). One application of this approach would be to identify intertidal wetlands with the potential to move landward because of lack of adjacent development or seawalls, and to protect both of these wetlands and the inland areas that they will occupy with higher sea levels (McLeod and Salm 2006). A related application is the translocation of species. As problematic as this might appear, this may be the only prospect for the survival of species that are unable to disperse unassisted in responding to future suitable climates. Some progress has been made towards rigorous assessment of options and risks for translocation (Hoegh-Guldberg *et al*. 2008).

Even more so than in the terrestrial realm, aquatic ecosystems can be adversely affected by distant anthropogenic threats that may be compounded by climate change. The impacts of distant threats are particularly obvious in large catchments from which sediment, nutrients and toxins can affect freshwater, estuarine and marine ecosystems downstream (Brodie *et al*. 2009). Management approaches are therefore needed for areas expected to influence aquatic ecosystems, often from afar (Stoms *et al*. 2005), and these will be more effective with understanding of the influence of climate change on land use and runoff (Fig. 5: Box 4). In some regions, climate change will increase human needs for water and perhaps exacerbate the effects of reduced rainfall and runoff on freshwater ecosystems (Abell 2002). In other regions, the distributions and types of land uses will be adjusted to altered climates, with implications for surrounding ecosystems (Dudgeon *et al*. 2006). In this context, management of activities in catchments could reduce nutrient runoff to inshore marine waters and lessen the effects of high sea temperatures on coral bleaching (Marshall and Johnson 2007; Wooldridge and Done 2009). Ideally, management actions in catchments would integrate diverse objectives, including conservation of terrestrial ecosystems, reduced disturbance of freshwater ecosystems, and appropriate water quality of near-shore marine ecosystems. This would allow managers to more cost-effectively address multiple objectives by identifying areas that contributed to all of them.

Conclusions

The present review has revealed conspicuous evidence of recent climatic impacts across Australian aquatic habitats. In coastal wetlands, for example, mangroves are already progressing landward and encroaching on salt-marsh environments at many locations along Australia's south-eastern coast (e.g. Saintilan and Williams 1999). These changes will have significant effects on fishes that live within these habitats (e.g. Gillanders *et al*. 2011), and are expected to worsen with ongoing changes in temperature, water chemistry, sea level, rainfall patterns and ocean currents (Hobday and Lough 2011). Thus far, the effects of climate change have been relatively minor compared with the extended history and often-extensive habitat degradation caused

by more direct anthropogenic impacts (e.g. Fig. 3). However, effects of climate change compound on habitat degradation and losses that have already occurred as a result of more localised anthropogenic disturbances (e.g. Schindler 2001; Hughes *et al*. 2003). Moreover, the cumulative effects of exploitation, pollution, and habitat modification and fragmentation make aquatic populations and communities much more vulnerable to climate change (e.g. Schindler 2001; Wooldridge 2009; Davies 2010). Despite marked differences in the major drivers of climatic impacts in different aquatic ecosystems (Table 1), there are strong similarities in the management actions required to address effects of climate change. Minimising global greenhouse-gas emissions is important to reduce longer-term and more extreme impacts of climatic change in Australia's aquatic ecosystems, and immediate action is also required to reverse the effects of direct anthropogenic disturbances and restore ecosystem function and resilience to these ecosystems.

Acknowledgements

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