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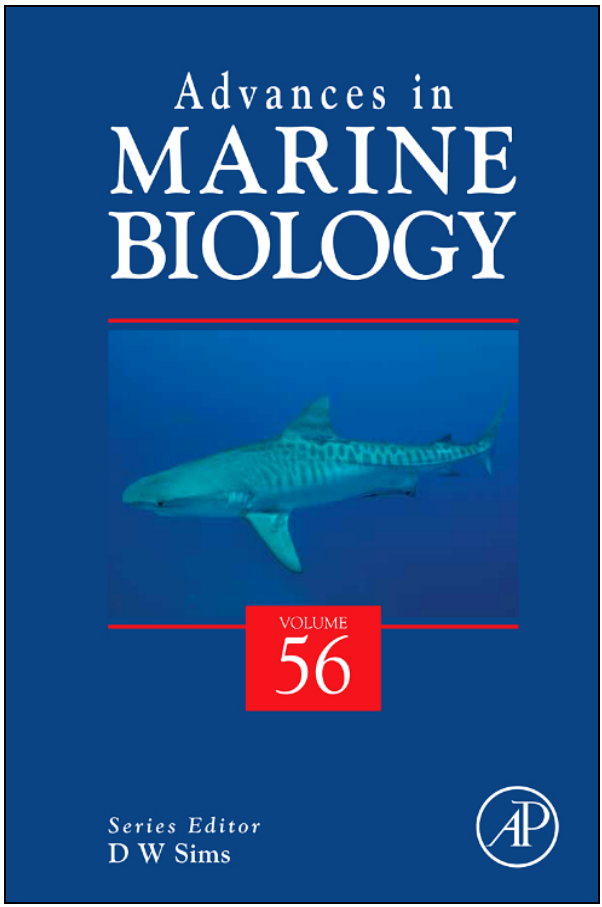

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CHAPTER TWO

Vulnerability of Marine Turtles to Climate Change

Elvira S. Poloczanska,* Colin J. Limpus,† *and* Graeme C. Hays‡

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Abstract

Marine turtles are generally viewed as vulnerable to climate change because of the role that temperature plays in the sex determination of embryos, their long life history, long age-to-maturity and their highly migratory nature. Extant species

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of marine turtles probably arose during the mid–late Jurassic period (180–150 Mya) so have survived past shifts in climate, including glacial periods and warm events and therefore have some capacity for adaptation. The present-day rates of increase of atmospheric greenhouse gas concentrations, and associated temperature changes, are very rapid; the capacity of marine turtles to adapt to this rapid change may be compromised by their relatively long generation times. We consider the evidence and likely consequences of present-day trends of climate change on marine turtles. Impacts are likely to be complex and may be positive as well as negative. For example, rising sea levels and increased storm intensity will negatively impact turtle nesting beaches; however, extreme storms can also lead to coastal accretion. Alteration of wind patterns and ocean currents will have implications for juveniles and adults in the open ocean. Warming temperatures are likely to impact directly all turtle life stages, such as the sex determination of embryos in the nest and growth rates. Warming of 2 °C could potentially result in a large shift in sex ratios towards females at many rookeries, although some populations may be resilient to warming if female biases remain within levels where population success is not impaired. Indirectly, climate change is likely to impact turtles through changes in food availability. The highly migratory nature of turtles and their ability to move considerable distances in short periods of time should increase their resilience to climate change. However, any such resilience of marine turtles to climate change is likely to be severely compromised by other anthropogenic influences. Development of coastlines may threaten nesting beaches and reproductive success, and pollution and eutrophication is threatening important coastal foraging habitats for turtles worldwide. Exploitation and bycatch in other fisheries has seriously reduced marine turtle populations. The synergistic effects of other human-induced stressors may seriously reduce the capacity of some turtle populations to adapt to the current rates of climate change.

Conservation recommendations to increase the capacity of marine turtle populations to adapt to climate change include increasing population resilience, for example by the use of turtle exclusion devices in fisheries, protection of nesting beaches from the viewpoints of both conservation and coastal management, and increased international conservation efforts to protect turtles in regions where there is high unregulated or illegal fisheries (including turtle harvesting). Increasing research efforts on the critical knowledge gaps of processes influencing population numbers, such as identifying ocean foraging hotspots or the processes that underlie the initiation of nesting migrations and selection of breeding areas, will inform adaptive management in a changing climate.

1. Introduction

Climate change is one of the major threats facing our world over the coming century and impacts on biodiversity are already being recorded (Parmesan, 2006; Rosenzweig *et al.*, 2007; Walther *et al.*, 2002). The IUCN

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(International Union for Conservation of Nature) Marine Turtle Specialist Group through its Burning Issues assessment (http://www.iucn-mtsg.org/hazards/) recently identified global warming as one of the top five major hazards to marine turtles globally; the other threats being fisheries impacts, direct harvesting of adults and eggs, coastal development, and pollution and pathogens. Life-history characteristics of marine turtles such as temperature-dependent sex determination, long age-to-maturity and a highly migratory nature may make marine turtles vulnerable to climate change. In this chapter, we consider the evidence and likely consequences of the potential impacts of climate change on marine turtles. Impacts are likely to be complex and there will be positive as well as negative impacts; however, adverse impacts are likely to be exacerbated by other anthropogenic-induced stressors such as capture by fisheries and coastal pollution.

A long history of capture of adult turtles and harvesting of turtle eggs has reduced many populations worldwide to precarious levels. Marine turtles are iconic animals, especially given increases in eco-tourism and overseas travel, which acts to raise conservation awareness. Recent conservation efforts have resulted in a trend of increasing nesting numbers for several populations (e.g. Broderick *et al.*, 2006; Chaloupka *et al.*, 2008a; Hays, 2004; Seminoff and Shanker, 2008), but there are still a number of pressing conservation matters including climate change. For example, increasing temperatures and rising sea levels linked to large-scale climate changes are of particular concern for future nesting success. Shifts towards greater proportion of female hatchlings have been recorded on warming beaches (Chu *et al.*, 2008; Glen and Mrosovsky, 2004; Hays *et al.*, 2003a). However, earlier nesting has also been recorded at loggerhead, *Caretta caretta*, colonies in Florida and the Mediterranean, which may alleviate the impact of rising temperatures, to some degree, on hatchling sex ratios (Mazaris *et al.*, 2008; Pike, 2009a; Weishampel *et al.*, 2004).

Extant turtle species probably arose during the middle–late Jurassic period (180–150 million years ago) when the world was warmer and more humid (Sellwood and Valdes, 2008). They have survived past shifts in climate, including glacial periods and warm events, by probably altering migratory routes, redistributing breeding and foraging sites and adjusting physiological parameters. Evidence of these can be found in contemporary populations. For example, in northern Australia, where temperatures are extremely high during the austral summer, flatback turtle *Natator depressus* populations breed during the winter. While on the Australian east and west coasts, at higher latitudes and hence cooler temperatures, *N. depressus* populations from adjacent genetic stocks nest during the summer months (Limpus, 1971). The timing of peak nesting at each location thus coincides with beach temperatures (25–32 °C) compatible with high incubation success and suitable male/female hatchling ratios. The time period over

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which reproductive phenology shifted is unknown, but is likely to have been over a time scale of thousands of years.

The question is can marine turtles adapt to future climate change given the rapid projected rates of global warming in the coming century? Rapid climate change coupled with high anthropogenic impacts on turtle populations, particularly pollution and high mortality through directed harvest and bycatch in fisheries, may seriously comprise the ability of turtle populations to adapt to our changing climate. On the other hand, climate change may benefit marine turtle populations through expansion of potential nesting and foraging areas and increased food supplies for various life stages. Impacts on trophic resources and key habitats such as open-ocean gelatinous zooplankton, seagrass beds and coral reefs may be critical for marine turtles.

In this chapter, we review climate variability and change impacts on the life stages of marine turtles in five different habitats: embryos and hatchlings on nesting beaches, reproductive turtles on inshore breeding grounds, juveniles and adults foraging in oceanic waters, juveniles and adults on inshore foraging grounds, and during oceanic migrations. We also discuss the responses of marine turtle populations to past climatic change and the potential for adaptation to projected climate change by marine turtle populations. Long-term climate-related trends in marine turtle populations are generally obscured by heavy exploitation historically, in addition to the effects of current conservation efforts which are leading to recent increases in targeted populations (Broderick *et al.*, 2006; Chaloupka *et al.*, 2008a; Seminoff and Shanker, 2008). We conclude our chapter by discussing the current status and trends of marine turtle stocks worldwide and with some recommendations for conservation and research.

2. Marine Turtle Biology and Life History

There are seven living species of marine turtle: flatback *Natator depressus*, green *Chelonia mydas*, loggerhead *Caretta caretta*, olive ridley *Lepidochelys olivacea*, Kemp's ridley *Lepidochelys kempii*, hawksbill *Eretmochelys imbricata* and leatherback *Dermochelys coriacea* (Fig. 2.1). They are classified into two taxonomic families: the Dermochelyidae, which contains only the leatherback turtle, and the Cheloniidae, which contains the other six species. All of these, with the exception of the flatback *N. depressus*, are classified as 'vulnerable', 'endangered' or 'critically endangered' in the International Union for the Conservation of Nature (IUCN) Red List (IUCN, 2009; Seminoff and Shanker, 2008). The flatback, *N. depressus*, which occurs only in Indo-Pacific waters, is currently 'data deficient' for IUCN Red List assessment purposes but is considered 'vulnerable' in Australian waters

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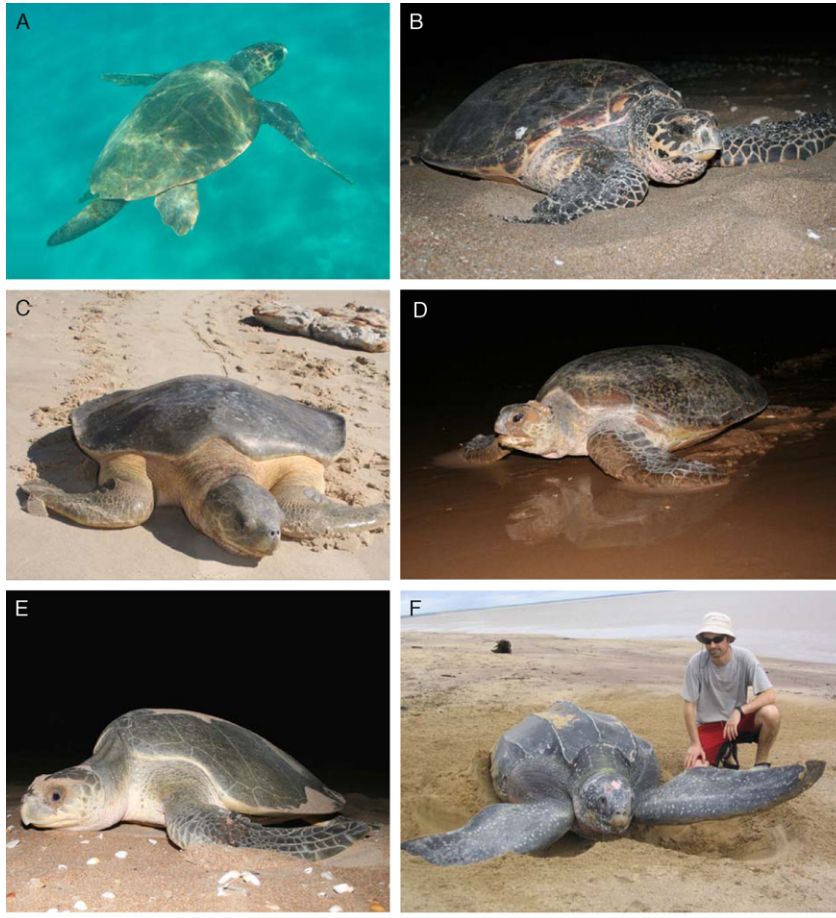

Figure 2.1 Marine turtles: (A) loggerhead (*Caretta caretta*), (B) hawksbill (*Eretmochelys imbricata*), (C) flatback (*Natator depressus*), (D) green (*Chelonia mydas*), (E) olive ridley (*Lepidochelys olivacea*), and (F) leatherback (*Dermochelys coriacea*).

(Environment Protection and Biodiversity Conservation Act, Australian Government 1999) where all known nesting occurs.

Cheloniid turtles are distributed throughout the world's tropical and sub-tropical waters, but may appear seasonally in cooler waters of the north-western Atlantic (Hawkes *et al.*, 2007a; Morreale and Standora, 2005) or sporadically year round in cool waters of the south-western Pacific (C.J. Limpus, unpublished data). Marine turtles are generally considered ectothermic with their thermoregulatory capacity varying among species and with body size (Hochscheid *et al.*, 2002; Spotila and Standora, 1985; Standora *et al.*, 1982; Still *et al.*, 2005). The largest turtles, adult leatherbacks,

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D. coriacea, display the greatest degree of endothermy (Bostrom and Jones, 2007; Eckert, 2002; Frair *et al.*, 1972; Goff and Lien, 1988; James *et al.*, 2005a, 2007; Mrosovsky and Pritchard, 1971; Southwood *et al.*, 2005; Spotila and Standora, 1985; Wallace and Jones, 2008; Witt *et al.*, 2007a). Mechanisms for heat retention such as counter-current heat exchangers in their flippers, thick body insulation and large body size enable adult leatherbacks (*D. coriacea*) to penetrate cold, high-latitude waters (Paladino *et al.*, 1990; Wallace and Jones, 2008).

Flatbacks, *N. depressus*, and Kemp's ridleys, *L. kempii*, have the most restricted distributions with *N. depressus* only found in the continental shelf waters of northern Australia, eastern Indonesia and southern Papua New Guinea, while Kemp's ridleys (*L. kempii*) occur mainly in the Gulf of Mexico and the eastern seaboard of the USA.

Marine turtle species display common life-history traits which include long-distance migrations, natal homing, no parental care of eggs and young, and temperature-dependent sex determination in the nest (Carr *et al.*, 1978; Meylan and Meylan, 1999). Marine turtles are long-lived and may not reach sexual maturity for many decades (e.g. Casale *et al.*, 2003; Chaloupka *et al.*, 2004; Limpus, 1992; Limpus and Chaloupka, 1997; Zug *et al.*, 1997). They show strong fidelity to natal and foraging areas and undertake long breeding migrations between these regions, generally at intervals greater than 1 year (Avens *et al.*, 2003; Bowen *et al.*, 2004; Limpus and Limpus, 2003; Limpus *et al.*, 1992; Luschi *et al.*, 2003).

During nesting, females come ashore and lay eggs in nests dug above the high water line on sandy beaches in the tropics and sub-tropics (Fig. 2.2). Typically, a female will make repeated visits to lay multiple clutches within one breeding season (Carr *et al.*, 1978; Hays *et al.*, 2002a; Limpus and Reed, 1985a; Limpus *et al.*, 1983a, 1984, 2001). Sex of the hatchlings is determined by the nest temperature during the middle third of the incubation period, with higher temperatures producing females (see Fig. 2.3; Hewavisenthi and Parmenter, 2002; Merchant Larios *et al.*, 1997; Miller and Limpus, 1981; Yntema and Mrosovsky, 1982). The 'pivotal' temperature, at which a 50:50 sex ratio is produced, is around 29 °C for most marine turtle populations (Binckley *et al.*, 1998; Broderick *et al.*, 2002; Godfrey and Mrosovsky, 2006; Hewavisenthi and Parmenter, 2000; Limpus *et al.*, 1985; Mrosovsky, 1988; Mrosovsky *et al.*, 1992, 2002; Yntema and Mrosovsky, 1982).

Hatchlings (Fig. 2.2) disperse to open-ocean foraging areas where as juveniles they may spend many years foraging in oceanic waters on gelatinous and other plankton, often at ocean fronts and eddies (Bolton *et al.*, 1998; Bowen *et al.*, 1995; Carr, 1987; Casale *et al.*, 2007; Parker *et al.*, 2005; Polovina *et al.*, 2001; Salmon *et al.*, 2004). The exception to this general pattern being the flatback (*N. depressus*), which remains in the continental shelf waters off northern Australia (Limpus, 2008; Walker and Parmenter, 1990). The juvenile

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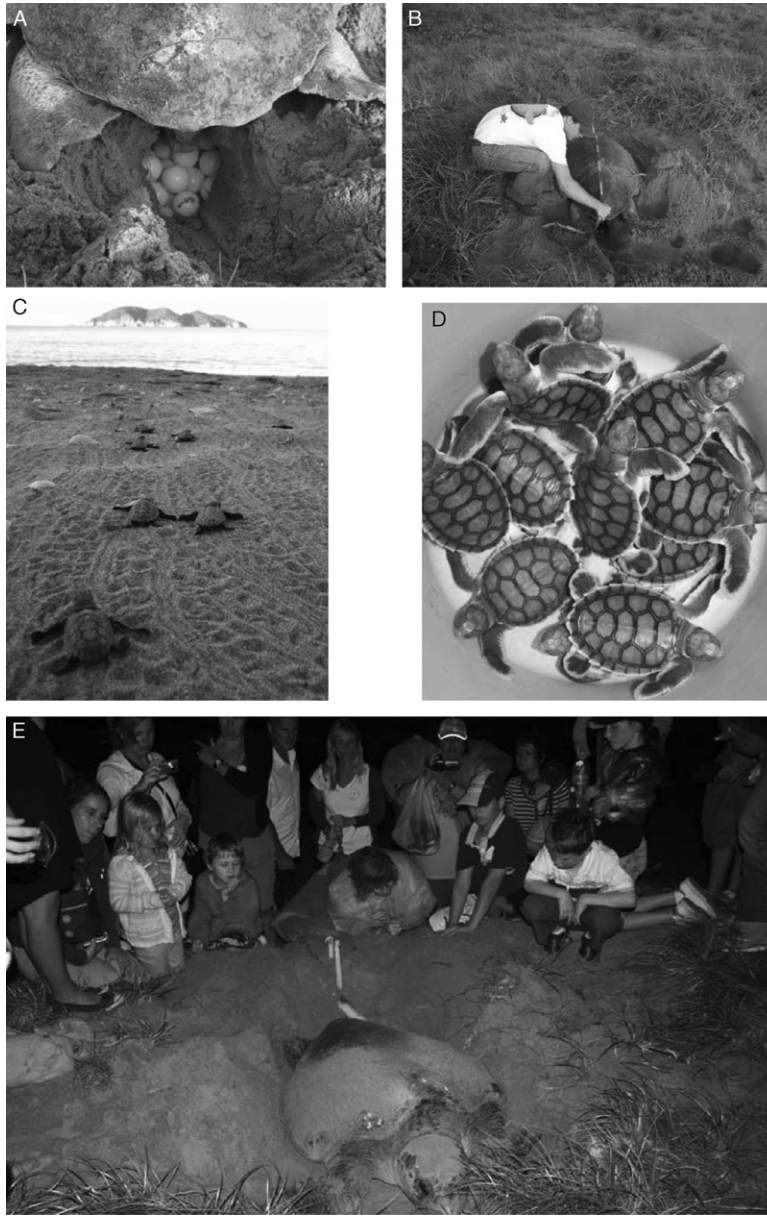

Figure 2.2 (A) Green turtle (*Chelonia mydas*) laying eggs, Mon Repos, Queensland, Australia. (B) Monitoring green turtle (*Chelonia mydas*) nesting, Mon Repos. (C) Loggerhead (*Caretta caretta*) hatchlings heading to the ocean. (D) Flatback (*Natator depressus*) hatchlings. (E) Tourists watch a nesting green (*Chelonia mydas*) turtle.

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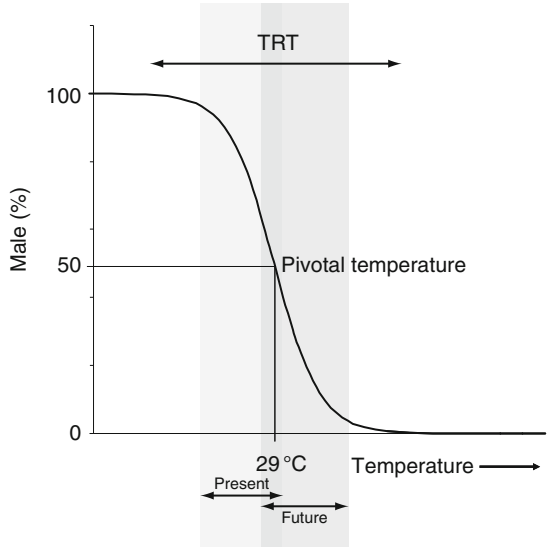

Figure 2.3 Generalised scheme of temperature-dependent sex determination in sea turtles and the effect of warming temperatures. A 1:1 sex ratio is produced at the pivotal temperature (around 29 °C); cooler temperatures produce a male bias and warmer temperatures produce a female bias. TRT is the transitional range of temperatures over which sex ratios shift from 100% male to 100% female. The blue shading marked PRESENT corresponds to the range of temperatures currently experienced by hypothetical turtle nests at a rookery over the breeding season; red shading marked FUTURE indicates nest temperatures following climate warming—the sex ratio has shifted from male biased to female biased.

pelagic period has been termed 'the lost years' (Carr *et al.*, 1978) as, until relatively recently, little was known of the distribution and ecology of the young turtles during these years. For some populations, particularly of leatherbacks (*D. coriacea*), olive ridleys (*L. olivacea*) and Kemp's ridleys (*L. kempii*), this is still the case.

Different species, populations and age classes display a wide range of foraging modes. Foraging grounds of adults and large juveniles of hawksbills *E. imbricata*, loggerheads (*C. caretta*), Kemp's ridleys (*L. kempii*), flatbacks (*N. depressus*) and green turtles (*C. mydas*) tend to be in coastal waters, and the larger immature and adult turtles spend most of their time in these foraging habitats. Hawksbills, *E. imbricata*, are omnivorous and forage around coral reefs and rocky outcrops, eating benthic invertebrates such as sponges and algae, and occasionally jellyfish (Blumenthal *et al.*, 2009; Houghton *et al.*, 2003; León and Bjorndal, 2002; Meylan, 1988). Loggerheads (*C. caretta*) and Kemp's ridleys (*L. kempii*) are generally carnivorous, taking invertebrates such as crustaceans and molluscs (Godley *et al.*, 1997; Limpus *et al.*, 2001; Plotkin *et al.*, 1993; Seney and Musick, 2007;

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Wallace *et al.*, 2009). Leatherbacks (*D. coriacea*) and eastern Pacific olive ridleys (*L. olivacea*) tend to forage in oceanic environments as sub-adults and adults, exploiting gelatinous plankton and planktonic crustaceans (Benson *et al.*, 2007; Houghton *et al.*, 2006; James and Herman, 2001; Salmon *et al.*, 2004; Wallace *et al.*, 2006). In the Australasian region, olive ridleys (*L. olivacea*) are benthic, foraging on crustaceans and molluscs (Whiting *et al.*, 2007). Flatbacks (*N. depressus*) also are carnivorous, feeding on soft bodied invertebrates (Limpus, 2008). In contrast, green turtles (*C. mydas*) are primarily herbivorous feeding on mostly seagrass and algae (Andre *et al.*, 2005; Brand-Gardner *et al.*, 1999; Fuentes *et al.*, 2006; Garnett *et al.*, 1985; Lopez-Mendilaharsu *et al.*, 2005; Mortimer, 1981). However, recent studies reveal *C. mydas* may continue to consume of gelatinous zooplankton even as adults during foraging periods along benthic coastal habitats (Arthur *et al.*, 2007).

3. Observed and Projected Changes in Oceans and Atmosphere

Climate varies over spatial and temporal scales from seasonal changes to decadal or even millennial variations. The geological record reveals a positive relationship between atmospheric CO_2 concentrations and global temperatures (Doney and Schimel, 2007). Present-day atmospheric CO_2 concentrations were last reached, at a minimum, 650,000 years ago (Denman *et al.*, 2007). The Earth may now be within approximately 1 °C of maximum temperatures of the past million years (Hansen *et al.*, 2006). While many patterns are evident in the global climate, what is now, unequivocal, is that global climate has warmed over the past century due to anthropogenic greenhouse gas emissions (IPCC, 2007). Owing to the inertia of the atmosphere–ocean system, temperatures will continue to rise over the next few decades, if not longer, regardless of any attempts at mitigation of greenhouse gas emissions (IPCC, 2007; Matthews and Caldeira, 2008).

Evidence for climate change manifests not only through observed warming temperatures but also through associated changes in the ocean–atmosphere system, such as alternation of rainfall and storm patterns, rising sea level and changes in ocean salinity, all of which will impact the various life stages of marine turtles.

3.1. Air and ocean temperature

Average global surface temperatures have risen by 0.74 °C over the hundred years since 1906, with warming in recent decades being the most rapid (Trenberth *et al.*, 2007). Eleven of the twelve warmest years since records

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began in 1850 (to 2006) occurred from 1995 onwards (Trenberth *et al.*, 2007). Warm days and nights have become more frequent over most land areas over the past few decades and are projected to continue to increase in frequency while the frequencies of cold extremes are declining (IPCC, 2007; Shiogama *et al.*, 2007). The Northern Hemisphere is warming much faster than the Southern Hemisphere and surface air temperatures are rising faster over land than over the ocean (Hansen *et al.*, 2006; IPCC, 2007). Warming air temperatures may impact the hatching success and hatchling sex ratios of marine turtles globally.

Ocean temperatures have also been rising, albeit at a slower rate than air temperatures given the large thermal capacity of the oceans. Over the last 50 years, ocean temperature has risen by 0.1 °C to depths of 700 m. Ocean warming is projected to evolve with the upper ocean warming first, then penetration of warming to the deep ocean by the end of the twenty-first century, and particularly so in mid-latitude regions (IPCC, 2007).

3.2. Rainfall, storms and cyclones

Rainfall is highly variable both temporally and spatially, but long-term observed trends during the past several decades are evident over many regions linked to rising atmospheric CO_2 levels (IPCC, 2007; Zhang *et al.*, 2007). The trends show a drying of Northern Hemisphere tropics and sub-tropics and a moistening of Southern Hemisphere tropics (Zhang *et al.*, 2007). Tropical wet seasons are projected to get wetter, particularly over the tropical Pacific, while dry seasons may get dryer or remain unchanged (Chou *et al.*, 2007). As the frequency of intense rainfall increases over many land areas, including tropical areas, so will the risk of flood events (Meehl *et al.*, 2007). There may also be a tendency for more intense mid-latitude storms over this century and an associated increase in wave height (Meehl *et al.*, 2007).

The intensity of cyclones has increased in some regions such as the tropical North Atlantic, the Indian Ocean and Southwest Pacific Oceans (IPCC, 2007; Saunders and Lea, 2008). A 0.5 °C rise in August–September sea surface temperature (SST) over the period 1965–2005 resulted in an approximately 40% increase in cyclone activity during the storm season (August–October) in the tropical Atlantic (Saunders and Lea, 2008). Climate model projections suggest that the strength of intense storms is likely to further increase over the coming century (Bengtsson *et al.*, 2007; Meehl *et al.*, 2007). For example, simulations of a regional climate model for the Cairns coastline, northeast Australia, showed that projected increases in cyclone intensity can result in a storm surge event with a return period of 100 years, becoming a 55-year event by 2050 and a 40-year event when sea-level rise is also considered (McInnes *et al.*, 2003).

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The global areas affected by tropical storms may widen polewards, particularly in the Southern Hemisphere (IPCC, 2007). There is evidence to indicate a polewards shift in storm tracks has already occurred over the second half of the twentieth century (IPCC, 2007; Seidel *et al.*, 2007). The destructive effects of cyclones, such as flooding, may, therefore, impact at higher latitudes as global temperatures warm (Isaac and Turton, 2009).

3.3. Sea level

Sea level has risen by an estimated 1.7 mm/year during the twentieth century due to thermal expansion of the oceans and widespread melting in glaciers and ice caps (IPCC, 2007). Sea-level rise is projected to continue but at a greater rate than over the last several decades. The rates of sea-level rise vary between regions with some areas rising much faster than the global mean rise, while in other areas sea level appears to be falling. Sea levels in the western Pacific and eastern Indian Oceans, where a myriad of tropical islands are found, and many of which contain turtle nesting beaches, are rising in accordance with the average global sea-level rise (Church *et al.*, 2006). The differences in sea-level rise among regions depend largely on regional hydrodynamics and geology. Low-lying, small islands, such as coral atolls, are considered 'especially vulnerable' to sea-level rise and extreme events, particularly in the Pacific, although studies have indicated some islands may be morphologically resistant (Mimura *et al.*, 2007). Generally, coral atoll islands are low-lying with the majority of land lying less than 2 m above mean sea level, and are thus vulnerable to storms which can redistribute large quantities of sand and rubble so eroding or building shorelines (Woodroffe, 2008). Islands which have lithified sediments and contain high vegetative cover may be more resilient than unconsolidated or unvegetated islands (Woodroffe, 2008).

Large storm surges and tidal surges can be extremely destructive to low-lying coastlines and magnify effects of sea-level rise (Zhang *et al.*, 2004). Sandy beaches are dynamic systems, undergoing continual processes of erosion and accretion (Short, 2006; Zhang *et al.*, 2004) as sea levels and ocean climate alter. As long as beaches can evolve naturally, there should be a continuum of nesting beaches of marine turtles on regional scales. However, beaches that are trapped in a 'coastal squeeze' between human developments and climate change will be least resilient, especially considering the present-day recessional nature of the majority sandy beaches globally (Fish *et al.*, 2005; Jones *et al.*, 2007; Schlacher *et al.*, 2007; Zhang *et al.*, 2004).

3.4. Winds and ocean currents

Rising temperatures will affect atmosphere and ocean circulation. No significant global trends in marine wind speeds have been identified but regional trends are apparent in the tropics and extratropics (regions between

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30° and 60° latitude from the equator) (IPCC, 2007). A polewards shift and strengthening of the westerly wind belts, driven by rising atmospheric CO_2 concentration, has resulted in a strengthening of the East Australian Current (EAC), which carries tropical water from the Coral Sea, and an enhancement of warming rates in the Tasman Sea, impacting marine fauna in this region (Cai, 2006; Cai *et al.*, 2005; Hill *et al.*, 2008; Poloczanska *et al.*, 2007). The Kuroshio Extension current in the western North Pacific, an important foraging hotspot for juvenile turtles (Polovina *et al.*, 2004b, 2006) has increased and moved southwards after 1976, this shift being linked to spin-up by the sub-tropical wind in the North Pacific influencing the wind-driven sub-tropical ocean gyre (IPCC, 2007; Sakamoto *et al.*, 2005). There is no evidence to date for a trend in the strength of the Gulf Stream in the North Atlantic, a subject of much public deliberation (IPCC, 2007).

3.5. Large-scale ocean–atmosphere patterns

The El Niño-Southern Oscillation (ENSO), a large-scale ocean–atmosphere phenomenon, has profound influence inter-annually on regional seas but with teleconnections to global climatology. Described simply, ENSO events fluctuate irregularly between two phases: El Niño and La Niña although each ENSO event evolves slightly differently. There are well-documented impacts of ENSO on atmospheric and ocean climates and ecosystems. For example, during El Niño years seasonal rainfall increases over the central and eastern-central Pacific Ocean, and decreases in the Western Pacific and Indian Ocean with a weakening of monsoons in Asia. The ENSO signal has been found in marine ecosystems at all trophic levels from phytoplankton and algae (Turk *et al.*, 2001); to tropical corals (Baker *et al.*, 2008; Grottoli and Eakin, 2007), marine turtles (Limpus and Nicholls, 1988; Saba *et al.*, 2007) and predatory fish (Lehodey *et al.*, 1997).

Historically, El Niño events occur every 3–7 years but El Niño events appear to have become dominant since the 1976–1977 'climate shift' when global temperatures started to rise rapidly due to anthropogenic forcing by greenhouse gas emissions (IPCC, 2007; Power and Smith, 2007). While climate models project a weak shift towards 'El-Niño-like' conditions in future climate there is no consistent indication of changes in amplitude and intensity (IPCC, 2007).

3.6. Ocean acidification

Ocean acidification is not a direct effect of climate change but is a consequence of fossil fuel CO_2 emissions, which are the main driver of recent climate change (see Denman *et al.*, 2007). The oceans are a major buffer of anthropogenic CO_2 emissions absorbing over 40–50% in the past 200 years (Raven *et al.*, 2005). Open-ocean surface waters are slightly alkaline with an

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average pH of around 8.2 (Raven *et al.*, 2005). The average pH of the oceans has lowered by about 0.1 units, representing a 30% increase in hydrogen ion concentration, since 1750 (around the advent of the Industrial Revolution) when anthropogenic emissions of CO_2 into the atmosphere started to increase substantially. The ocean surface is projected to acidify by up to 0.5 units over the twenty-first century (Caldeira and Wickett, 2003, 2005). The pH decrease over the coming centuries may be greater than any changes over the past 300 million years as inferred from the geological record (Caldeira and Wickett, 2003). Acidification leads to a decrease in the saturation state of calcium carbonate and a reduction in the depth below which calcium carbonate dissolves, thus impacting biological calcification rates (Orr *et al.*, 2005; Riebesell, 2004).

In waters under-saturated with respect to calcium carbonate, biological calcification rates decrease. For example, calcifying plankton shows dissolution, deformation and/or reduced calcification of shells and liths in under-saturated marine waters (Engel *et al.*, 2005; Moy *et al.*, 2009; Riebesell *et al.*, 2000). Reduced calcification with increased acidity has also been shown in molluscs (Gazeau *et al.*, 2007), coralline algae (Jokiel *et al.*, 2008; Martin and Gattuso, 2009), echinoderms (Clark *et al.*, 2009; Dupont *et al.*, 2008) and reef-building corals (Jokiel *et al.*, 2008; Silverman *et al.*, 2009). Much concern has been raised over the severity of the threat of ocean acidification to the survival of coral reefs; by the end of this century all coral reef systems globally may display net dissolution of carbonate with deleterious consequences for coral ecosystems and coastal protection (Hoegh-Guldberg *et al.*, 2007; Silverman *et al.*, 2009).

Ocean acidification may have far reaching impacts on ocean biodiversity beyond reduced biological calcification rates, depressing metabolisms and impacting physiologies of species ranging from invertebrates (Clark *et al.*, 2009; Ellis *et al.*, 2009; Kurihara, 2008) to fish (Munday *et al.*, 2009). Increased dissolution of CO_2 will increase physiological stress on organisms such as dissolved oxygen levels decrease and metabolic rates and physiological pathways are affected (Ishimatsu *et al.*, 2005; Pörtner *et al.*, 2005; Raven *et al.*, 2005; Wilson *et al.*, 2009). There is potential for the widespread disruption of marine food chains and ecosystems (Fabry *et al.*, 2008).

4. Climate Change Impacts on Marine Turtles

Climate change manifests in biological systems as changes in the distributions and abundance of species, alteration of phenology such as earlier occurrence of spring and other events, and the lengthening of vegetative growing seasons. Polewards distribution shifts consistent with recent warming have been recorded in many marine species ranging from

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plankton to fish (Beaugrand *et al.*, 2002; Edwards, 2004; Mieszkowska *et al.*, 2005; Perry *et al.*, 2005) and phenological shifts are also evident in marine systems (Chambers, 2004; Edwards and Richardson, 2004; Mackas *et al.*, 1998). Climate change will impact all life stages of marine turtles (Table 2.1).

4.1. Embryos and hatchlings on nesting beaches

4.1.1. Air temperature

A major concern for marine turtles with respect to the effects of global warming is the impact on hatchling sex ratios, size and quality, and therefore on population dynamics (e.g. Booth and Astill, 2001a; Burgess *et al.*, 2006; Glen *et al.*, 2003; Godley *et al.*, 2002a,b; Hewavisenthi and Parmenter, 2001; Mazaris *et al.*, 2008). The temperature range over which sex ratios shift from 100% male to 100% female varies between marine turtle species and populations, but in general the range lies between 1 and 4 °C (Wibbels, 2003). Small changes in temperature close to the pivotal temperature (~29 °C) can result in large changes in the sex ratio of hatchlings (see Fig. 2.3; Glen and Mrosovsky, 2004; Janzen, 1994; Limpus *et al.*, 1985; Yntema and Mrosovsky, 1982). This suggests that warming of a couple of degrees centigrade, well within the warming expected over the coming century, can potentially result in a large shift in sex ratios. Air temperatures at many turtle nesting beaches worldwide have already warmed to, or are close to, all female-producing temperatures (e.g. Antigua, Caribbean: Glen and Mrosovsky, 2004; Ascension Island, South Atlantic: Hays *et al.*, 2003a; Australasia, Western Pacific: Chu *et al.*, 2008). As global temperatures rise, the ambient surface air temperatures at many turtle nesting sites globally will warm (Fig. 2.4) thus reducing or eliminating the likelihood of males.

There is evidence to indicate, however, that turtles may not be as vulnerable to warming temperatures as first anticipated. Some nesting beaches have persisted with strong female biases over a few decades or even longer (Broderick *et al.*, 2000; Godfrey *et al.*, 1999; Hays *et al.*, 2003a; Marcovaldi *et al.*, 1997; Reed, 1980). There is no evidence to date that a low production of male hatchlings has resulted in a low reproductive success within populations (e.g. Broderick *et al.*, 2000; Glen and Mrosovsky, 2004), although it is possible that the long-term population declines due to exploitation and other factors may mask such effects. Population units may also span many rookeries, so although individual nesting beaches may be female-producing, other beaches within the region may produce the necessary males and conservation of these beaches may become increasingly important as temperatures warm (Hawkes *et al.*, 2007b; Hays *et al.*, 2003a). Furthermore, temperatures will fluctuate during the nesting seasons so may be below pivotal temperatures for at least some of the season (Godfrey *et al.*, 1996; Mrosovsky and Provancha, 1992; Reed, 1980).

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Table 2.1 Summary of marine turtle life stages, habitat and potential major climate change impacts on the different life stages

Turtle life stage	Habitat (and distribution)	Warming air and ocean temperatures	Alteration of rainfall, storms and cyclones	Rising sea level	Alteration of winds and ocean currents	Alteration of large-scale ocean–atmosphere patterns	Ocean acidification
Incubation and hatching	Sandy beaches in the tropics and sub-tropics	√Air	√	√		√	
Breeding and nesting	Coastal waters and sandy beaches in the tropics and sub-tropics	√Ocean	√	√		√	
Oceanic juvenile and adults	Open ocean, tropics to cool-temperate latitudes	√Ocean			√	√	√
Neritic juveniles and adults	Coastal and shelf waters, tropics to temperate latitudes	√Ocean	√	√		√	√
Migrations	Shelf seas and open ocean, hundreds of kilometres to across ocean basins	√Ocean			√	√	

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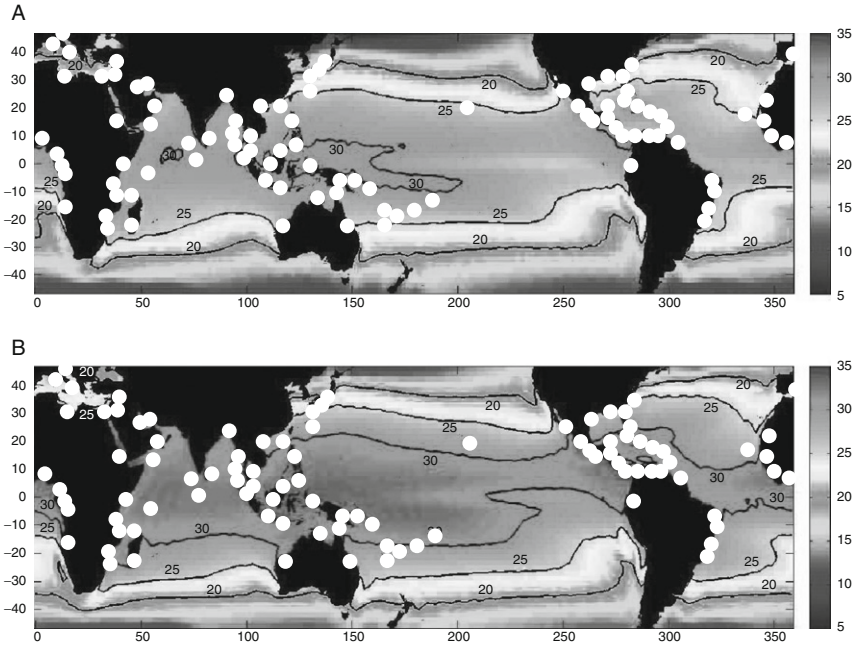

Figure 2.4 Mean annual surface air temperature projections for (A) 2001–2010 and (B) 2091–2100 from CSIRO Mk 3.5 General Circulation Model (GCM) under greenhouse gas emission scenario SRES A2. The 20°, 25° and 30° contours drawn. GCM projections downloaded from the IPCC data hosted by PCMDI and processed at CSIRO marine research. Locations of major nesting sites for loggerheads (*Caretta caretta*), hawksbills (*Eretmochelys imbricata*) and leatherbacks (*Dermochelys coriacea*) (white dots) taken from maps printed by SWoT (2005, 2006, 2007). Full citations for each data point are given in SWoT (2005, 2006, 2007).

The propensity for female biases and likelihood of declining male production for some populations raises theoretical questions about the evolutionary significance of temperature-dependent sex determination (Godfrey *et al.*, 1999; Hulin and Guillon, 2007; Hulin *et al.*, 2009; Mrosovsky and Provancha, 1992; Reece *et al.*, 2002; Wibbels, 2003), and as well as the importance for population dynamics of polyandry (multiple paternity) observed in some species to date (Lee and Hays, 2004; Theissinger *et al.*, 2009; Zbinden *et al.*, 2007). However, data series for hatchling production tend to be short or patchy and sample sizes small. Some of the longest data are for marine turtles nesting in the south-western Pacific over the last quarter century. These reveal long-term, highly skewed sex ratios towards females [hawksbill turtles (*E. imbricata*): Limpus and Miller, 2008; green turtles (*C. mydas*): Limpus, 2009] or towards males [loggerhead turtles (*C. caretta*): Limpus and Limpus, 2003]. Resolving such theoretical challenges may become increasingly important as global

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temperatures warm. We suggest concerns should be raised if sex ratios for regional stocks, that is, the sex ratio across all nesting beaches for a particular stock, approach 1:4 (male to female). Urgent work is also needed to establish the breeding periodicity of male and female turtles. There has been the suggestion that males may return to breed (the remigration interval) more frequently than females which generally only breed every 2–5 years depending on the population. Shorter remigration rates by males might help balance the sex ratios on the breeding grounds compared to hatchling sex ratios. To date, there has been little targeted work on males.

The likelihood of males being produced is also determined by variations in localised factors such as sand albedo, sand grain size and vegetative cover which produce small-scale differences in thermal properties of nesting areas (Booth and Astill, 2001b; Hays *et al.*, 2001a, 2003a; Hewavisenthi and Parmenter, 2002; Loop *et al.*, 1995; Speakman *et al.*, 1998), in addition to environmental factors such as rainfall (see below). For example, Mon Repos beach on the mainland in south Queensland has brown sand produces predominantly female loggerhead (*C. caretta*) hatchlings while the white sands of nearby (~150 km) coral cay islands, such as Heron Island, produce mostly male hatchlings (see Fig. 2.5A and B; Limpus *et al.*, 1983b). On Heron Island itself, the northern beach is warmer at nest depth than the more shaded southern beach and hence green turtle (*C. mydas*) hatchlings have a female bias from the northern beach and a male bias from the southern beach (Booth and Freeman, 2006; Limpus *et al.*, 1983b). It will take temperature shifts of several degrees to change these male-producing beaches into beaches producing 100% female hatchlings. Beaches of contrasting sand colour within a population nesting regions are also found in other areas such as on Ascension Island (see Fig. 2.5C; Hays *et al.*, 2001a).

4.1.2. Rainfall, storms and cyclones

Turtles tend to nest just above the high water mark but cyclones, storm surges and heavy rainfall can inundate nests or erode sand dunes resulting in significant nest and egg loss (Edminston *et al.*, 2008; Foley *et al.*, 2006; Pike and Stiner, 2007a; Ragotzkie, 1959; Whiting *et al.*, 2007; Xavier *et al.*, 2006). Populations of marine turtles with nesting seasons that overlap with storm seasons will be most vulnerable to projected increases in storm intensity (Pike and Stiner, 2007a,b). The expected polewards expansion of tropical storm regions (Seidel *et al.*, 2007) will increase impacts on populations nesting at higher latitudes. Rising sea levels, increases in wave heights, coastal erosion and increased storm intensities may all act to increase the risk of tidal inundation of nests at higher beach levels.

Heavy rainfalls, such as those caused by storms and cyclones, may act to re-dress the balance in sex ratios through a cooling effect on sand temperature (Reed, 1980). Rainfall is accompanied by a drop in sand temperatures

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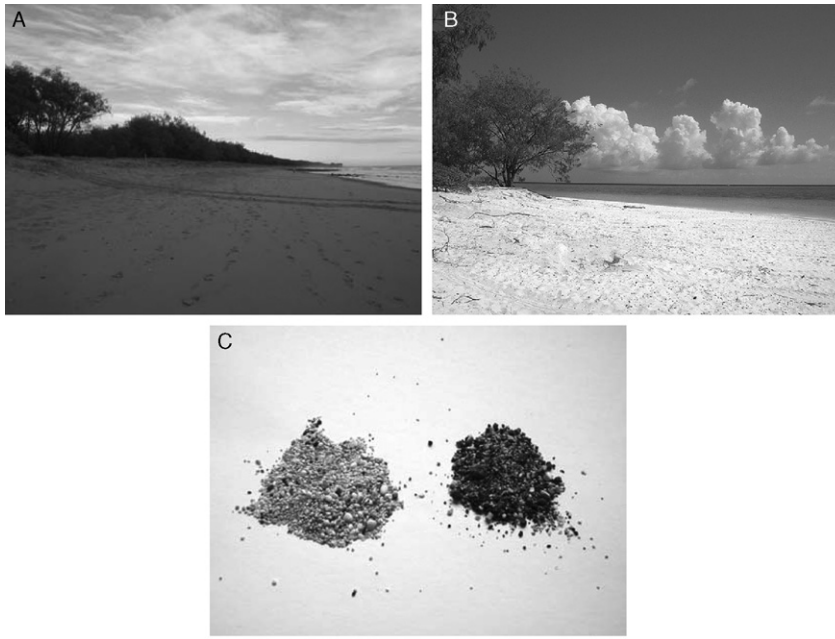

Figure 2.5 Contrasting sand colours of beaches within nesting regions of marine turtles in (A, B) the southern Great Barrier Reef and (C) Ascension Island. (A) Mon Repos beach, mainland southern Queensland, Australia. (B) Heron Island, southern Queensland, Australia. (C) Sand from Long Beach, Ascension Island (left) and North East Bay beach, Ascension Island (right).

and it has been shown that protracted rainfall can have a marked, although short-term, cooling effect on nests (Booth and Freeman, 2006; Gyuris, 1993; Houghton *et al.*, 2007; Loop *et al.*, 1995), skewing sex ratios towards males if coinciding with critical periods for sex differentiation (Godfrey *et al.*, 1996; Houghton *et al.*, 2007; Reed, 1980). For example, a significant negative relationship between monthly rainfall and sex ratios has been shown for leatherbacks, *D. coriacea*, and green turtles, *C. mydas*, nesting in Suriname (Godfrey *et al.*, 1996). In general, a reduction in tropical rainfall globally is projected over the coming century which coupled with rising temperatures may exacerbate female biases in hatchling sex ratios. Regional increases, such as that projected for summer rainfall in north-western Australia (Nicholls, 2006), or short-term extreme increases in rainfall during storm events, may act to cool nests, if nesting coincides with rainfall and hence increase male production from otherwise female-producing beaches (Reed, 1980).

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4.1.3. Sea level

Coupled with increases in storm intensity, rising sea levels may results in increased risk of tidal inundation or destruction of turtle nests on low-profile beaches, thereby reducing population reproductive success (see above). Nesting beaches backed by coastal developments or salt marshes and lagoons that hindered beach evolution may be at most risk from rising sea levels (Fish *et al.*, 2005, 2008). Where the area of beach available for nesting is substantially reduced, turtles may be forced to dig nests in beach zones that are sub-optimal for hatching success, for example in low regions with high salt-water inundation risk. Nesting area reduction may also result on subsequent increases in nesting density, thus increasing the risk of nest destruction during digging of neighbouring nests and the risk of predation (Mazaris *et al.*, 2009). If nest density increases the likelihood of a disturbance impacting a larger proportion of nests on the beach may increase.

4.1.4. Large-scale ocean–atmosphere patterns

The large-scale atmospheric patterns such as El Niño influence local and regional climatology, such as the tropical monsoon season in the northern Indian Ocean. Any alteration in the pattern and intensity of El Niño events will impact turtle nests through changes in rainfall, temperature and storm regimes.

4.2. Reproductive turtles on inshore breeding grounds

4.2.1. Air and ocean temperature

Air temperatures directly affect nest incubation temperatures and therefore hatchling sex ratios (see above) and hatchling production. Nest temperatures are modified by factors such as the presence of vegetation and nest depth, so the nesting choices of females will influence hatchling sex ratios (e.g. Booth and Astill, 2001b; Foley *et al.*, 2006; Hays *et al.*, 2001a; Kamel and Mrosovsky, 2006; Speakman *et al.*, 1998).

Within a breeding year, successive nests may be clustered on the beach, but there is little evidence this represents fidelity to a specific beach area (Hays *et al.*, 1995; Kamel and Mrosovsky, 2004; Limpus *et al.*, 1984; Nordmoe *et al.*, 2004; Xavier *et al.*, 2006). Fidelity to beach zones such as dune areas or forest edges rather than specific beach regions has been shown for some populations but not for others, and it is unknown if such choices are genetically determined (Garmestani *et al.*, 2000; Kamel and Mrosovsky, 2006; Nordmoe *et al.*, 2004; Pfaller *et al.*, 2009). Hawksbills, *E. imbricata*, have been shown to consistently select the same beach area for each successive nesting (Mrosovsky, 2006) but there is a lack of evidence to suggest some individuals in the population are genetically programmed to consistently nest in 'poor' areas (Pike, 2008a). Turtles are likely to use

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multiple environmental cues during the multiple phases of the nesting process which includes emergence, beach crawls and nest site selection (Mazaris *et al.*, 2006). There is little evidence that females will shift nesting locations on beaches in response to the local environment; for example selecting heavily vegetated sites in warmer years (Hays *et al.*, 1995; Loop *et al.*, 1995; Mazaris *et al.*, 2006; Tiwari *et al.*, 2005; Weishampel *et al.*, 2006) although loggerhead (*C. caretta*) females with nesting experience have been shown to select a higher proportion of successful nest sites on a beach than unexperienced females (Pfaller *et al.*, 2009).

Alteration of nesting dates may mitigate effects of warming temperatures on embryos (Kamel and Mrosovsky, 2004; Mazaris *et al.*, 2008; Morjan, 2003). Shifts in nesting dates and other spring/early summer events have been extensively recorded in Northern Hemisphere birds, butterflies, amphibians and fish (Parmesan, 2007; Root *et al.*, 2003; Rosenzweig *et al.*, 2007). Correlations between peak nesting date and spring (April and May) SSTs were found in populations of loggerheads, *C. caretta*, nesting at two beaches in Florida, USA (Pike *et al.*, 2006; Weishampel *et al.*, 2004) and at a beach in North Carolina (Hawkes *et al.*, 2007a). Median nesting date on the beaches in Florida has advanced by around 8–10 days over 15 years and appears correlated with warming May SSTs, although these warming trends were apparently not significant (Pike *et al.*, 2006; Weishampel *et al.*, 2004). Earlier nesting with significant increasing SST has been shown in loggerheads, *C. caretta*, in the Mediterranean, with first nesting emergence advancing by 17 days over 19 years (Mazaris *et al.*, 2008). Egg production may be resource limited in *C. caretta* (Broderick *et al.*, 2003) which may account for the shorter nesting seasons recorded for this species in warmer years when first laying commences earlier (Pike *et al.*, 2006).

Turtles aggregate on breeding grounds before nesting commences for a number of weeks or longer (Fossette *et al.*, 2007; Hays *et al.*, 2002b; Myers and Hays, 2006). Feeding while in these breeding aggregations and during the subsequent inter-nesting phase is at least minimal and may even be absent (Limpus *et al.*, 2001; Tucker and Read, 2001). Nevertheless, temperatures on breeding grounds can directly affect female physiology, for example by increasing metabolic rates (Hamann *et al.*, 2003; Kwan, 1994; Sato *et al.*, 1998). The shorter inter-nesting intervals observed during warmer years are suggestive of increased metabolic rates and may result in shorter nesting seasons for some populations with highly seasonal nesting (Hays *et al.*, 2002a; Mrosovsky *et al.*, 1984; Pike *et al.*, 2006; Sato *et al.*, 1998).

However, nesting phenologies are most probably influenced by the geographic position of nesting beaches. At present, turtle nesting sites appear to be constrained by an annual mean surface air temperature of around 25 °C in the Southern Hemisphere and around 20 °C in the Northern Hemisphere (Fig. 2.4). Nesting in the cooler Northern Hemisphere regions, such as the Mediterranean and Japan, is highly seasonal

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taking place during the summer when seasonal mean surface air temperatures are greater than 25 °C and air temperatures are likely to be above the pivotal temperature for balanced sex ratios (~29 °C) for at least some of this period. For example, in Sarawak, Malaysia (latitude ~ 3 °N) where monthly average maximum air temperatures are above 29 °C all year, green turtles, *C. mydas*, nest year round with a peak in July–September. In Cyprus (latitude ~ 35 °N) *C. mydas* nesting is concentrated largely within 4 months (May–August) when monthly average maximum air temperatures reach 24–34 °C so even at these cooler, higher latitudes, sex ratios can be female-biased. Data loggers deployed in turtle nests on Cypriot beaches have recorded temperatures that range from 25 to 33 °C depending on sand albedo and date of egg-laying with a prevalence at higher temperatures (Godley *et al.*, 2001; Hays *et al.*, 2001a). Populations of turtles breeding at northern hemisphere, higher latitude regions have thus adapted to the strong seasonality in temperatures.

Adaptation to strongly seasonal temperature regimes is evident on other life-history stages (discussed further below) of turtles in northern hemisphere waters, with feeding migrations to higher latitudes during warmer months and dormancy as a response to low temperatures recorded for turtles in the Atlantic and Mediterranean.

Warming temperatures may lengthen nesting seasons, even if nesting seasons of individuals are shortened due to increased metabolic rates, provided other environmental conditions, such as rainfall intensity, remain favourable. Warming temperatures may also expand availability of favourable breeding habitat for marine turtles (see Fig. 2.4), as beaches outside present-day high-latitude nesting boundaries warm (provided suitable nesting habitat is available). Although turtles show natal fidelity this tends to be to wider regions rather individual beaches within the region. Once a female selects an area during first breeding, she will show strong fidelity to that area, though not necessarily to individual beaches within the area. Turtles nesting on highly dynamic coastlines where beaches and sandbars accrete and erode over short time times (years to decades), such as Suriname, French Guiana and deltas in Myanmar, may regularly shift nesting following natural beach modification or colonise newly formed nesting habitat (Fossette *et al.*, 2008; Kelle *et al.*, 2009; Thorbjarnarson *et al.*, 2000). Further, turtle nesting is sporadically reported, in very low numbers, from beaches where nesting has previously been unrecorded (e.g. Alava *et al.*, 2007; Lima *et al.*, 2003; Tomas *et al.*, 2008) although in some cases this may be due to poor reporting rather than colonisations (Petro *et al.*, 2007). Loggerheads (*C. caretta*), green turtles (*C. mydas*) and leatherbacks (*D. coriacea*), in particular, nest sporadically on beaches at higher latitudes outside major rookeries (e.g. Soto *et al.*, 1997). For example, loggerheads (*C. caretta*) are recorded nesting regularly in low densities on beaches in southern Queensland and northern New South

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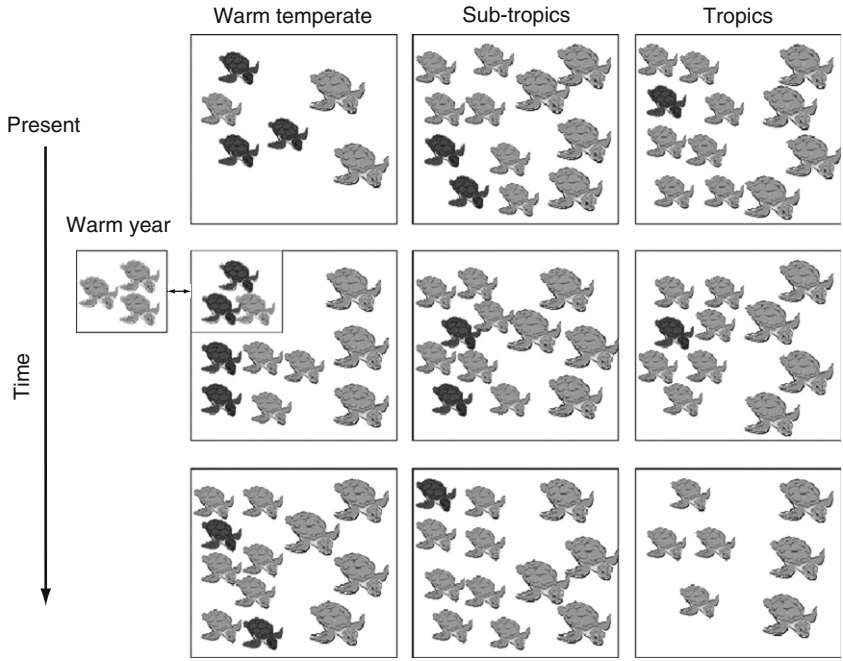

Figure 2.6 Potential changes in turtle nesting populations with warming temperatures over generational time at three latitudes: tropics, sub-tropics and warm temperate, showing trends in nesting females (large turtles) and hatchlings (small turtles). The proportion of male hatchlings (blue) declines as temperatures warm. At the lower latitude (warm-temperate) rookeries, pulses of females (in box) are produced during extreme warm years (shown) while cool years will produce pulses of males (not shown).

Wales, Australia that have been too cool to have produced females within the last 100 years (C.J. Limpus, unpublished data).

So how will turtle nesting populations shift with warming temperatures? Two mechanisms may come into play (Fig. 2.6): First, a gradual warming of temperatures may result in the warmest areas becoming all female producing (if not already), with an increased probability of females on previously cool beaches. High temperatures could also increase hatchling mortality (so a slow population decline may occur at the warmest beaches). However, given many turtle populations already operate with female-biased sex ratios, populations may persist in these regions and a gradual expansion of breeding success may occur at cooler distributional edges of the nesting range. Secondly, inter-annual variability in warming temperatures may also produce 'pulses' of females on cooler beaches during 'hot' years or *vice versa*.

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4.2.2. Rainfall, storms and cyclones

Marine turtles nest on tropical beaches where intense rainfall can occur during summer months, particularly in monsoonal regions, and nesting at many colonies overlaps with tropical storm and cyclone seasons. Timing of nesting is probably determined by climatic pattern of the nesting location, for example whether rainfall is seasonal and predictable or seasonal but unpredictable and heavy (monsoonal rainfall in the wet–dry tropics; see Shine and Brown, 2008) coupled with temperature regimes and other environmental cues. Prolonged rainfall can lower nest temperatures (Houghton *et al.*, 2007) but may also submerge or destroy nests (Foley *et al.*, 2006) and can affect sand stability. At Ascension Island, where the sand tends to be very dry and unstable, therefore unsuitable for digging, nesting occurs during the wettest months (Mortimer and Carr, 1987). In addition, turtle eggs require certain levels of moisture in the sand, depending on species, to avoid desiccation (Bustard and Greenham, 1968; Limpus *et al.*, 2001; Mortimer, 1990). Interestingly, the hydric environment appears to have little influence on the hatching success of flatback, *N. depressus*, eggs which nests on the generally arid, tropical Australian coastline (Hewavisenthi and Parmenter, 2000, 2001).

At immediate timescales, rainfall may directly influence female nesting behaviour. Heavy rainfall may render nest sites unsuitable for digging or egg incubation or may mask cues that trigger female emergence. During intense rainfall events, coastal waters are often turbid and salinity is reduced. Some populations of olive ridley turtles, *L. olivacea*, display mass nesting events known as 'arribadas' when females emerge synchronously to lay eggs. *L. olivacea* arribadas in Costa Rica have been found to postpone mass nesting during periods of heavy rainfall (Plotkin *et al.*, 1997). In contrast, loggerhead turtles (*C. caretta*) nesting in Florida, USA, were shown to increase nesting activity during periods of heavy rainfall (Pike, 2008b). The actual benefits occurred by nesting during rainfall periods are unclear and it is likely that there are a number of environmental cues that drive nesting emergence.

The destructive effects of storms, cyclones and heavy rainfall are mostly likely to be directly on the nests and eggs (see above) and on beach nesting habitat. Storms and cyclones can be highly destructive causing rapid erosion of beaches and dune systems behind the foreshore and loss of aquatic vegetation or coral reef destruction (Edminston *et al.*, 2008; Thom and Hall, 1991; Woodroffe, 2008). New beach can also be formed during these events (Woodroffe, 2008). Projected increases in severe storms and cyclones and increases in significant wave height are expected to impact sandy beaches globally, particularly when coupled with other anthropogenic influences (Nicholls *et al.*, 2007). For example, coastal development, such as sea walls and dune destruction, can reduce the natural resilience of beach systems to disturbance events (Brown and McLachlan, 2002; Jones *et al.*, 2007;

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Nicholls *et al.*, 2007; Schlacher *et al.*, 2007). Turtle nests on beaches with high coastal development and burgeoning human populations (e.g. Central America: Tomillo *et al.*, 2008; India: Mohanty *et al.*, 2008; Indo-Asia: Hamann *et al.*, 2006) are likely to be most at risk. Remote nesting beaches, such as many of the mainland nesting sites throughout Northern Australia or on south Pacific islands, are likely to be more resilient assuming the integrity of associated ecosystems such as coral reefs and seagrass beds are not impaired.

4.2.3. Sea level

Sea-level rise may also be a major threat for turtle breeding beaches, particularly on beaches where coastal development acts as a barrier constraining landward movement of beaches or hindering natural accretion of beach material and the evolution of beach morphology (Fish *et al.*, 2005, 2008; Jones *et al.*, 2007; Nicholls *et al.*, 2007). It is suggested that the dynamics of shoreline systems means the horizontal recession of sandy beaches can be much more rapid (50–100 times) than vertical sea-level rise, although evidence is generally lacking in this area (see Jones *et al.*, 2007; Nicholls *et al.*, 2007). However, there may be little change to beaches, especially those with an extensive dune system, other than a landward migration (Jones *et al.*, 2007).

Sandy beaches are highly dynamic systems undergoing periods of accretion and erosion; however, the majority of the world's beaches have retreated over the past century (Nicholls *et al.*, 2007). Sea-level rise may not be the primary driver of these retreats as alteration of wind patterns, river inflow and offshore bathymetric changes can cause beach erosion (Nicholls *et al.*, 2007). Turtle nesting beaches in regions with high costal development, whether for industry, coastal defence, habitation or tourism, may be most strongly impacted. For example, a 0.5-m rise in sea level could lead to the loss of 32% of total beach area in the Netherlands Antilles, Caribbean, and 26% of beach area in Barbados with the most vulnerable beaches being those that back onto salt lakes and coastal developments (Fish *et al.*, 2005, 2008). Prohibiting construction within 30–50 m of beaches in Barbados could substantially reduce loss of Hawksbill (*E. imbricata*) nesting beach area although losses on some beaches may still be severe (Fish *et al.*, 2008).

Sea-level rise may result in a reduction or loss of small islands, particularly in the Pacific (Mimura *et al.*, 2007). Interactions with adjoining ecosystems may be particularly important in maintaining resilience of these islands to rising sea levels. For example, the integrity of the surrounding coral reefs is important for the shoreline protection of low-lying islands on coral atolls as the reefs dissipate wave energy, thus helping reduce coastal erosion (Sheppard *et al.*, 2005). Declines in reef health through pollution, eutrophication, over-exploitation and fishing, warming temperatures (coral bleaching) and increasing cyclone intensity, may accelerate coastal erosion

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of small tropical islands (Mimura *et al.*, 2007), thereby impacting turtle breeding beaches.

4.2.4. Large-scale ocean–atmosphere patterns

The number of nesting turtles can vary considerably year to year with the largest inter-annual variations generally found in the herbivorous green turtle (*C. mydas*) populations (Broderick *et al.*, 2001; Limpus *et al.*, 2001). There is evidence of large-scale environmental forcing on numbers of nesting turtles at widely separated rookeries. These may be a reflection of wide-scale ocean–atmosphere forcing such as the ENSO, although the exact mechanisms remain to be determined (Balazs and Chaloupka, 2004; Chaloupka, 2001; Chaloupka and Limpus, 2001; Limpus and Nicholls, 1988; Saba *et al.*, 2007; Solow *et al.*, 2002). An example illustrating this idea is that the numbers of nesting green turtles, *C. mydas*, at rookeries in the western Pacific have been correlated with ENSO with an 18–24 month lag, with the highest numbers following El Niño events (Chaloupka, 2001; Limpus and Nicholls, 1988).

The numbers of turtles breeding each year are likely to be driven by environmental conditions on foraging grounds. Turtles are capital breeders—they deposit fat reserves that can be mobilised later for reproduction (Hamann *et al.*, 2003; Kwan, 1994). Vitellogenesis, the process by which egg yolks are formed, commences at least 8–10 months before the breeding season and can partly explain the lag between environmental signals and breeding numbers (Hamann *et al.*, 2003). The cues to initiate vitellogenesis are unknown but could be environmental such as threshold temperatures or genetic factors such as an energy 'threshold' where breeding is initiated only when the turtle has acquired a large enough energy store to sustain itself over the breeding period and breeding migration (Hamann *et al.*, 2003; Hatase and Tsukamoto, 2008). ENSO affects temperature, rainfall and storm patterns over wide Pacific regions but there can be considerable variation in these environmental signals within a region. Further, other large-scale climate modes, such as Indian Ocean Dipole, may dominate signals in some regions. These low frequency climate signals can synchronise breeding of turtles across widely distributed foraging grounds.

Females in a nesting area may have migrated from widely spaced foraging areas, which raises questions as to which cues are operating to trigger breeding and how are females responding to these cues (Hamann *et al.*, 2003). Certainly, there is some evidence of differing initiation dates for migration for females from different foraging areas that utilise the same nesting region (Miller and Limpus, 1981).

Peak nesting of leatherback, *D. coriacea*, turtles in Costa Rica has been shown to have a strong ENSO signal suggesting oceanographic conditions on offshore foraging grounds are influencing female nesting (Saba *et al.*, 2007, 2008). Peak nestings were associated with the high surface

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productivity of oceanic, foraging regions that develops during La Niña events and following termination of El Niño events. It has been suggested that recent increases in green turtle, *C. mydas*, nesting populations in the southern Great Barrier Reef may be attributable to concurrent increases in the frequency of ENSO anomalies (Chaloupka and Limpus, 2001). The breeding season of austral summer 1998/1999 was one of the largest on record (Dethmers *et al.*, 2006; Limpus *et al.*, 2003). This record breeding followed the 1997–1998 'super El Niño', which led to 1998 being the warmest year (between 1856 and 2005) for SSTs (Trenberth *et al.*, 2007). Other biological impacts of this super El Niño included the most severe global episode of mass coral bleaching that has occurred to date (Hoegh-Guldberg, 1999).

4.3. Juveniles and adults foraging in oceanic waters

4.3.1. Ocean temperature

Adult turtle distribution throughout the global ocean is generally limited by minimum temperatures around 15–20 °C (Coles and Musick, 2000; Davenport, 1997; McMahon and Hays, 2006). Optimal temperature ranges can vary between species, age classes and seasonally. For example, juvenile loggerheads, *C. caretta*, generally occupy waters ranging from 15 to 25 °C while juvenile olive ridleys, *L. olivacea*, are found in much warmer temperatures of 23–28 °C (Polovina *et al.*, 2004b). Large leatherbacks, *D. coriacea*, show the greatest adaptations for metabolic heat production and retention (Davenport *et al.*, 1990; Frair *et al.*, 1972; Paladino *et al.*, 1990; Wallace and Jones, 2008), and can make seasonal transitory forays into waters below 10 °C (Eckert, 2002; James *et al.*, 2006; McMahon and Hays, 2006).

Warming ocean temperatures are likely to extend the potential global pelagic habitat of marine turtles further polewards (McMahon and Hays, 2006). For example, satellite tracking of leatherback turtles, *D. coriacea*, in the North Atlantic suggests that the 15 °C SST isotherm may encapsulate the northern boundary of distributions, although they are routinely reported from colder waters (McMahon and Hays, 2006). The mean monthly 15 °C SST isotherm has moved 330 km north in the last 17 years (McMahon and Hays, 2006). However, this warming is within variability over the past 150 years, and as such may not be due to global warming *per se*, but such events are occurring with increasing frequency (Hobson *et al.*, 2008). Warming projected over the coming century is expected to move this contour further northwards thus increasing leatherback, *D. coriacea*, foraging areas, particularly in the northeast Pacific and northeast Atlantic (Fig. 2.7). It is likely that these isotherms integrate oceanographic and trophic processes, such as the availability of gelatinous zooplankton, that influence movements of *D. coriacea* (Houghton *et al.*, 2006; Witt *et al.*, 2007b).

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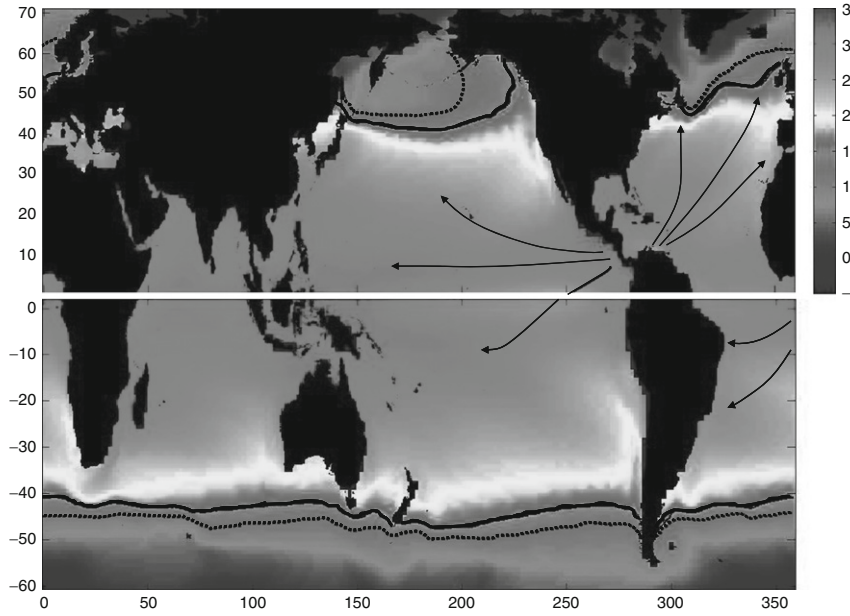

Figure 2.7 Mean sea surface temperature projections for 2001–2010 summers in the Northern hemisphere (June–August) and in the Southern hemisphere (December–February) from CSIRO Mk 3.5 General Circulation Model (GCM). The position of the 15 °C isotherm (black solid line) is indicated, which may effectively encompass the distribution of foraging leatherback, *Dermochelys coriacea*, turtles. The position of the mean 15 °C isotherm (black dotted line) for boreal and austral summers, projected for 2091–2100 under greenhouse gas emission scenario SRES A2, is also shown. Black arrows indicate the general pattern of dispersal away from nesting beaches measured with satellite tags in the North Atlantic, Pacific and Southern Africa and inferred from recaptures of flipper tagged for *D. coriacea* (indicated by black dots) nesting in West Africa. The movement of *D. coriacea* nesting in the Andaman Islands (Indian Ocean) is not known. GCM projections downloaded from the IPCC data hosted by PCMDI and processed at CSIRO marine research.

Dense jellyfish aggregations are a natural feature in oceanic ecosystems, but severe blooms are being reported with increasing frequency in recent decades (Richardson *et al.*, 2009). Will climate change therefore be good news for foraging turtles in oceanic waters? The factors driving long-term changes in prey fields, such as gelatinous zooplankton, remain too poorly resolved to address this question. Overfishing (fish are major competitors and predators of jellyfish), eutrophication, habitat modification and climate change may all be regulating jellyfish density (Purcell, 2005; Richardson *et al.*, 2009). For example, there have been reported increases in the abundance of jellyfish in the Benguela upwelling system (Lynam *et al.*, 2006)

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that have been attributed to eutrophication and overfishing although the details of mechanisms remain enigmatic. However, in the North Sea, long-term changes in the abundance of various species of jellyfish have been linked to climatic signals (Lynam *et al.*, 2004).

Overall, we are left with the impression that prey abundance is closely linked to the fitness of sea turtles inhabiting oceanic waters and the prey abundance is likely to be heavily shaped by climate change although the specific causes remain obscure (Hays *et al.*, 2004). Strong associations between ocean productivity and associated plankton landscapes and turtle distributions have been suggested (Houghton *et al.*, 2006; Polovina *et al.*, 2001; Witt *et al.*, 2007b). Future alterations of open-ocean prey abundance may be a critical issue for marine turtles, but one that has as yet received very little attention.

Warming of the sea surface can enhance stratification of the water column, leading to nutrient-poor waters (potentially favouring jellyfish) and a reduction in productivity (Polovina *et al.*, 2008; Richardson *et al.*, 2009). Over the last half century in the western Pacific, a negative correlation between the slowly increasing mean annual SSTs in the core, foraging areas for loggerhead turtles, *C. caretta*, and the trend in the size of annual nesting populations during the following respective summers in Japan and eastern Australia has been identified (Chaloupka *et al.*, 2008b). The authors suggested a relationship between warming ocean temperatures and reduced ocean productivity, with the resultant reduction in food supply potentially influencing the annual breeding numbers of Pacific loggerheads, *C. caretta*, unless they adapted by shifting their foraging habitat to cooler regions. The gradual warming of the Pacific Ocean appears to be a major risk factor for these populations.

In the western Atlantic, reported sightings of leatherbacks, *D. coriacea*, in Canadian waters were found to increase by 12.5% for each degree rise in mean weekly SST, although it was acknowledged that turtles may be responding to seasonal availability of gelatinous zooplankton in these waters rather than directly to temperature (James *et al.*, 2006). Temperature and declines in prey abundance may also play a role in triggering departures from these grounds, but it is also possible that other factors such as a reduction in feeding efficiency or a threshold for body fat deposition may interact to trigger migrations (Sherrill-Mix *et al.*, 2008).

In the North Atlantic, water temperatures play a role in the seasonal movements of turtles to high-latitude foraging grounds (Hawkes *et al.*, 2007a; James *et al.*, 2006; Morreale and Standora, 2005; Morreale *et al.*, 1992; Renaud and Williams, 2005). Warming temperatures may therefore result in increased frequency of leatherbacks, *D. coriacea*, reported from high-latitude North Atlantic waters and a longer seasonal residence in these waters. For example, most sightings of marine turtles in UK waters, taken from records over the past century, have been recorded in the past

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40 years and sightings are increasing, which is suggestive of a possible shift or expansion in distributions (Robinson *et al.*, 2005). A competing explanation is the hypothesis that increases in turtle populations globally have resulted in a proportional increase in the number of young 'strays' (Carr, 1987) and summer migrants carried to British waters by the North Atlantic drift (Witt *et al.*, 2007a). However, increased contemporary sightings of turtles in UK waters may also be an artefact of better reporting and improved public education in recent decades (Robinson *et al.*, 2005; Witt *et al.*, 2007a).

4.3.2. Wind and currents

Currents play a number of roles in the distribution of juvenile turtles at sea. They may influence turtle movements through advection, offer a thermal refuge from colder waters and will influence to a large degree the availability of planktonic prey. Ocean circulation patterns may thus help define turtle distributions and deflect turtle movements, particularly those of juvenile turtles (Bowen *et al.*, 2007; Polovina *et al.*, 2006; Revelles *et al.*, 2007a). For example, circulation patterns into and within the Mediterranean Sea are thought to retain immature loggerheads, *C. caretta*, hatched on Mediterranean beaches until they attain sufficient size and strength to swim against currents and are able to exit into the Atlantic (Revelles *et al.*, 2007a,b). A proportion of green turtles, *C. mydas*, on foraging grounds in the eastern Caribbean have been shown to originate from Ascension Island rookeries and are probably transported there by the North Atlantic gyre (Luke *et al.*, 2004).

Evidence for the influence of ocean circulation patterns on juvenile dispersal and possible fidelity to particular water masses has been shown through genetic and tagging studies (Bass *et al.*, 2006; Carreras *et al.*, 2006; Casale *et al.*, 2007; Luke *et al.*, 2004; Naro-Maciel *et al.*, 2007). Clearly then, straying outside ocean gyre and currents systems can be fatal for young turtles if the temperature difference is large (Carr, 1986, 1987; Lohmann and Lohmann, 1996). Loggerheads (*C. caretta*) in the North Atlantic have been shown to use the warm waters at the edge of the Gulf Stream as a thermal refuge (Hawkes *et al.*, 2007a). At temperate latitudes, the temperature difference within such currents, which originate in tropical latitudes, and surrounding waters may be large. For example, in southeast Australian waters, the temperature difference between the warm-water East Australian Current (EAC) and surrounding waters may be over 5 °C (see Zann, 2000). Juvenile and adult marine turtles seasonally appear in New Zealand waters (34–38 °S) and off southeast Australia, either carried or assisted by the poleward extension of the EAC (Gill, 1997; Limpus and McLachlan, 1979; Scott and Mollison, 1956). The numbers of records of turtle mortality in this region have increased in recent decades, with high influx years coinciding with a recent strengthening of the EAC as well as rising ocean temperatures (Cai, 2006; Gill, 1997). The EAC has strengthened driven by

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changes in the circumpolar westerly wind belt due to warming temperatures; the EAC is projected to strengthen by 20% by the 2070s (Cai *et al.*, 2005). This has resulted in a warming of waters off Tasmania, southeast Australia, of 2.28 °C in 60 years (Hill *et al.*, 2008). With the strengthening of the EAC, observations of juveniles in New Zealand waters are expected to increase.

4.3.3. Large-scale ocean–atmosphere patterns

The large-scale atmospheric patterns such as El Niño influence regional oceanography and productivity. Fluctuations in the abundance of gelatinous zooplankton in regions of the world's oceans are related to large-scale climate indices such as El Niño and the North Pacific Decadal Oscillation (Anderson and Piatt, 1999; Attrill *et al.*, 2007; Dawson *et al.*, 2001; Purcell, 2005; Raskoff, 2001). How these evolve, as global climate changes, will have repercussions for marine turtle populations globally.

4.3.4. Ocean acidification

Ocean acidification will affect the acid–base cellular regulation of marine organisms but as air breathers, marine turtle physiology will be less susceptible to changes in ocean chemistry. The indirect effects of ocean acidification on primary and secondary production may have consequences for marine turtles, particularly if coral reefs decline (see above) or ocean productivity decreases.

4.4. Juveniles and adults on inshore foraging grounds

4.4.1. Ocean temperature

Water temperatures in coastal waters tend to be more variable than in open-ocean waters and strongly seasonal. Foraging turtles are frequently reported from high-latitude, coastal and shelf waters during the summer months (Goff and Lien, 1988; James *et al.*, 2006). Cold stunning of turtles at higher latitudes is a frequent occurrence and, if exposures to low temperatures are prolonged, morbidity and death may occur (Morreale *et al.*, 1992; Still *et al.*, 2005). In partially enclosed seas, such as the Mediterranean (~40 °N), green turtles, *C. mydas*, can show periods of 'dormancy' rather than migration to tropical waters. During dormancy individuals rest in mid-water or on the bottom (although some level of activity is retained) during periods of low water temperatures (Godley *et al.*, 2002c; Hochscheid *et al.*, 2007). This behaviour appears to be an adaptation of the Mediterranean populations since green turtles, *C. mydas*, in southeast Australia (~30–35 °S) do not show dormancy at temperatures similar to the low Mediterranean temperatures. The observed trend to warmer temperatures in the Mediterranean (Bindoff *et al.*, 2007) should reduce the occurrence of dormancy in resident

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turtle populations, thus potentially increasing foraging times and improving resultant body condition.

Increased temperatures may also expand the availability of potential turtle coastal foraging habitat polewards and influence food resources. However, turtles show some fidelity to foraging areas, depending on species and population, which may constrain invasion of higher latitude areas as temperatures warm although if foraging regions can no longer support turtle populations then turtles will be driven to locate alternative grounds.

4.4.2. Rainfall, storms and cyclones

The increase in tropical, cyclone intensities projected with global warming will impact most heavily on turtles that nest during the storm season or on turtles that forage in shallow coastal habitats such as green turtles. Turtles can survive severe storms and cyclones by reducing time spent at the surface and moving to deeper water (Storch *et al.*, 2006). However, cyclones and large storm surges will cause damage, stress, starvation and death of turtles if foraging grounds are in very shallow areas (Carr, 1987; Limpus and Reed, 1985b). For example, Cyclone *Kathy* which crossed the Gulf of Carpentaria, Northern Australia in 1984, led to large-scale stranding of 500–1000 adult green turtles, *C. mydas*, on one section of coastline with a large proportion of these subsequently dying (Limpus and Reed, 1985b).

Large storm events can have long-lasting impacts on turtle populations. A 1200 km^2 of seagrass beds were destroyed off southern Queensland, Australia in 1992 following two cyclones in quick succession and a major river flood event (Preen *et al.*, 1995). The seagrass die-off was followed some 5 months later with a record number of strandings of dead dugongs, *Dugong dugon* (large marine herbivores) on the adjacent coastal areas (Preen and Marsh, 1995). During the same period there was an increased number of strandings of dead green turtles, *C. mydas*, on the adjacent Hervey Bay coast (EPA Marine Wildlife Stranding and Mortality Database, Brisbane, Australia). In western Shoalwater Bay, Australia, following Cyclone *Joy* in early 1990 which caused similar regional loss of seagrass, it was found the proportion of foraging green turtle (*C. mydas*) adults that prepared for breeding migrations for the 1991 breeding season was severely depleted and remained below average until 1996 (Limpus *et al.*, 2005). Growth rates of immature *C. mydas* foraging in the same area were depressed during the same period (Chaloupka *et al.*, 2004).

Understanding the impact of climate change in marine turtles in coastal areas will require a more detailed examination of storm and rainfall patterns together with local bathymetry and topography. However, the degree of destruction of coastal marine systems by a cyclone will depend on many factors including cyclone track, topography and coastal hydrodynamics. A severe cyclone may not necessarily be a destructive one for coastal marine systems, particularly for submerged fauna and flora. Seagrass beds appear

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remarkably resilient to storm disturbance as long as the plants are not uprooted or heavily smothered (Carruthers *et al.*, 2002; Cruz-Palacios and van Tussenbroek, 2005; Tilman *et al.*, 1994). For example, Hurricanes Ivan (in 2004) and Katrina (in 2005) were found to have resulted in little loss of seagrass beds in Alabama despite extensive damage on land (Byron and Heck, 2006). However, if damage or destruction does occur, then re-vegetation can take 10 years or more and will have implications for marine herbivores.

Storms, cyclones and heavy rainfall events can increase turbidity in coastal waters and can cause rapid drops in salinity affecting the stability of coastal waters. They also wash nutrients from the land which can often lead to harmful algal blooms in coastal waters, particularly in waters which are oligotrophic. For example, higher than average rainfall, coupled with warmer temperatures, may have contributed to a toxic cyanobacterium bloom on an important green turtle, *C. mydas*, foraging ground in Queensland, Australia (Arthur *et al.*, 2007). The turtles were found to be ingesting the cyanobacterium with potential long-term detrimental effects to their health. Red tides, which are also toxic algal blooms, can develop in coastal and shelf waters following heavy intense rainfall (Lee, 2006; Vargo, 2009). Mass mortalities of marine flora and fauna, including turtles, are often reported from the red tides (e.g. Florida, USA: Gannon *et al.*, 2009; Landsberg *et al.*, 2009; Simon and Dauer, 1972; South Africa: Stephen and Hockey, 2007; Korea: Lee *et al.*, 2007a; Japan: Koizumi *et al.*, 1996). The potential consequences of climate change for harmful algal bloom production and severity are unknown, but it must be assumed the rising CO_2 levels and temperatures coupled with alteration of rainfall patterns and expanding human populations (hence increasing likelihood of coastal eutrophication) may lead to more frequent or severe outbreaks of toxic algae.

4.4.3. Sea level

Nearshore foraging habitats of marine turtles, such as seagrass beds and coral reefs, may be vulnerable to rising sea levels (Duarte, 2002; Short and Neckles, 1999). Although sea levels are presently rising at 1–2 mm a year, the rise is slow compared to the rates of coral growth (20 cm/year; Done, 2003) and hence is not a major challenge to healthy coral populations. However, additional stressors such as warming temperatures, ocean acidification and pollution may slow coral growth considerably (Hoegh-Guldberg *et al.*, 2007). Benthic marine plants and algae may be more at risk. It is estimated a 50-cm rise in sea level will result in a 30–40% reduction in the growth of the widespread Northern Hemisphere seagrass *Zostera marina* (Short and Neckles, 1999), which is likely to reduce the area of green turtle, *C. mydas*, foraging grounds.

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4.4.4. Large-scale ocean–atmosphere patterns

Evidence of ENSO influences on green turtle, *C. mydas*, populations on foraging grounds can be seen in the numbers nesting every year (see above). Increase in 'El Niño-like' conditions may enhance seagrass and algal growth in the tropics and sub-tropics with positive consequences for feeding *C. mydas*.

4.4.5. Ocean acidification

Ocean acidification is like to impact two key, coastal, turtle-foraging habitats: coral reefs and seagrasses. The threat of ocean acidification is a major concern for coral reefs globally (Hoegh-Guldberg, 2007; Kleypas *et al.*, 2001). Coral reefs are restricted to high-latitude warm waters which have relatively high aragonite saturation states compared to colder lower latitude waters (Hoegh-Guldberg, 2007; Kleypas *et al.*, 2001). Not only may climate change lead to a net dissolution of coral reefs, but also the potential for poleward expansion of coral reefs with rising temperatures may be restricted to a few hundred kilometres at the most by the lower carbonate saturation levels of seawater at higher latitudes (Kleypas *et al.*, 2001). Furthermore, recent warming of the oceans has led to repeated coral bleaching events, not seen anywhere globally before 1979 (Hoegh-Guldberg, 1999). In Australia, for example, temperature thresholds for coral reef bleaching may be exceeded every year by the middle of this century (Hoegh-Guldberg, 1999). The additional stressor of ocean acidification coupled with warming temperatures may lead to a decline in coral density and diversity globally, associated losses of coral-associated fish and invertebrates and an increase in macroalgal cover (Hoegh-Guldberg *et al.*, 2007).

Coral reefs form major coastal foraging grounds for turtles, in particular hawksbills, *E. imbricata*, and these would be vulnerable if reef systems deteriorated, even though the abundance of hawksbill, *E. imbricata*, turtles foraging on the rocky reefs of sub-tropical Queensland and northern New South Wales suggests that they are not necessarily limited by coral reef distribution (Speirs, 2002). However, a long-term decline in coral reef habitat will have severe repercussions for many tropical marine ecosystems (Hoegh-Guldberg *et al.*, 2007) including the long-term persistence of hawksbill (*E. imbricata*) populations.

Seagrasses primarily rely on dissolved CO_2 and so are photosynthetically inefficient in seawater (Invers *et al.*, 1997; Short and Neckles, 1999). Increased CO_2 levels could potentially increase seagrass biomass, providing that optimal temperature regimes exist (Invers *et al.*, 2002; Zimmerman *et al.*, 1997); this response may therefore benefit the herbivorous green turtles, *C. mydas*. However, seagrass beds are declining globally as a result of other anthropogenic stressors, such as reductions in water quality, which may cancel the climate change benefits to seagrasses (Ferwerda *et al.*, 2007; Waycott *et al.*, 2009).

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4.5. Oceanic migrations

Turtles can make long migrations between breeding and foraging areas, depending on species and population (Hays *et al.*, 2002c; James *et al.*, 2005b; Limpus *et al.*, 1983c). The actual strategies used by turtles to navigate during these journeys have been subject of much research and debate. While there is some evidence turtles may use the Earth's magnetic field to orientate and possibly to navigate (Lohmann, 2007; Lohmann and Lohmann, 1996), and may use currents opportunistically (Luschi *et al.*, 2003), it is still largely unknown how they home precisely to natal and foraging regions (Lohmann *et al.*, 2008). While the mechanisms used during migration remain enigmatic, the return migratory abilities of sea turtles are now fairly well established. For example, both tagging and genetic studies have revealed the ability of turtles to return to breed within natal areas (e.g. Lee *et al.*, 2007b). Furthermore, tracking studies have shown that turtles may undertake long-distance movements during the breeding season, sometimes of several hundred kilometres, and yet return directly to nesting regions (e.g. Georges *et al.*, 2007; Fig. 2.8). These tracking results imply turtles have some geospatial knowledge of their environment. Yet turtles artificially displaced tens or hundreds of kilometres from nesting sites often show searching behaviour and are unable to return directly to their starting point (Luschi *et al.*, 2001). This finding illustrates that active searching may be an integral component of turtle migrations, especially across finer spatial scales, and suggests that even with some climate-induced alterations of homing clues, an active search strategy may still help turtles to find nesting sites (Sims *et al.*, 2008). Set against this backdrop it is particularly difficult to make specific predictions about how climate change might impact migrations.

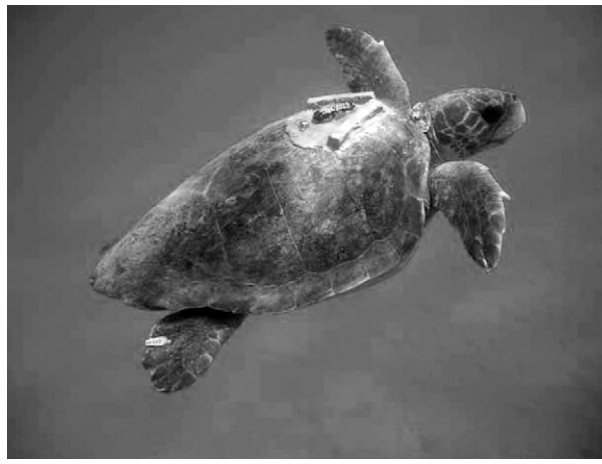

Figure 2.8 Loggerhead (*Caretta caretta*) turtle with GPS tag.

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4.5.1. Wind and currents

There has been considerable debate on the role that the major ocean currents play in turtle migrations: do turtles use currents opportunistically, do currents represent migration corridors for marine turtles, or are currents a challenge to be overcome by swimming turtles if migrating in a different direction to current flow? The answer may be all of these, depending on species and population. Certainly, the major current systems play a role in linking foraging and nesting areas in turtle populations (Bass *et al.*, 2006).

Juveniles and adults may use current flows to facilitate transport, for example, juvenile loggerheads, *C. caretta*, originating from Japanese populations have been identified from feeding grounds off Baja California, representing a journey that crosses the entire Pacific Ocean, most likely aided by the North Pacific Current (Bowen *et al.*, 1995). Adult loggerheads, *C. caretta*, have also been tracked using satellite tagging, crossing the Indian Ocean (Luschi *et al.*, 2003) and the Pacific Ocean (Nicols *et al.*, 2000) in the direction of prevailing ocean currents. The increasing use of satellite tagging has revealed turtles do make use ocean currents during their long-distance migrations (Bentivegna *et al.*, 2007; Hays *et al.*, 1999, 2001b, 2002c; Luschi *et al.*, 2003).

Long-distance migrations may not rely solely on the directions of these currents. Turtles have also been tracked swimming against prevailing currents suggesting the use of currents may be opportunistic or, at least, not obligate (Bentivegna *et al.*, 2007; Cardona *et al.*, 2005; Luschi *et al.*, 2003; Miller *et al.*, 1998; Polovina *et al.*, 2004a, 2006). Migrations across large expanses of oceans are often direct until coastal waters are reached (Hays *et al.*, 2002c; James *et al.*, 2005b), although currents have been found to deflect turtle migratory paths (Gaspar *et al.*, 2006; Girard *et al.*, 2006). There is evidence of persistent migration corridors for adult turtles that do not necessarily coincide with current flow or other oceanographic features (Hays *et al.*, 2001b; Morreale *et al.*, 1995; Shillinger *et al.*, 2008; Troëng *et al.*, 2005). Disruption or displacement of major ocean current systems could therefore have repercussions for turtle stocks by influencing turtle movements and the impacts may be greatest on juveniles. It is more likely that impacts will manifest through associated changes in ocean productivity.

5. Responses to Past Climate Change

The first turtles appear in the fossil record at least 200 million years ago and the turtle lineage (Testudines) probably diverged around this time (Hedges and Poling, 1999; Rieppel and Reisz, 1999). Extant turtles may have arisen some 50–100 million years ago. The most recent period with a

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climate warmer than the present-day climate (2–3 °C above pre-industrial temperatures), particularly at mid- and high latitudes, was the middle Pliocene (~3 million years ago). Tropical sea surface temperatures and air temperatures were probably little different to present day or slightly warmer (1–4 °C) and wetter, whereas high latitudes were significantly warmer (Haywood *et al.*, 2000; Jansen *et al.*, 2007). Sea levels were around 15–25 m higher than present day. Since then, climate has cooled, undergoing a cycle of glacial and interglacial periods with the last glacial maxima (LGM) being ~21,000 years ago and a mid-Holocene warm period 6000 years ago. During the last glacial maximum, global temperatures were cooler (~5 °C) particularly at higher latitudes with extensive ice cover and sea levels were up to 120 m lower. Genetic analysis has revealed that over the past 100 million years the tropics acted as a refuge during glacial cycles for many nesting turtles with sub-division and isolation of populations as sea levels and temperatures altered (Formia *et al.*, 2006; Reece *et al.*, 2005). Nesting turtles were likely to have been continually displaced by cooling periods and changes in sea level, particularly loggerheads, *C. caretta*, which generally nest at higher latitudes on the sub-tropical and warm-temperate beaches (Bowen and Karl, 2007).

Sea levels have been rising since the Last Glacial Maximum (LGM), substantially altering coastal areas and displacing turtle nesting sites. A case study for northern Australia green turtles, *C. mydas*, provides evidence of past adaptation to climate change by marine turtles (Dethmers *et al.*, 2006). Much of the shelf area off northern Australia would have been exposed 21,000 years ago. Most of the present-day nesting beaches were inaccessible, being far inland (Dethmers *et al.*, 2006; Limpus, 2008), The Gulf of Carpentaria would have been an inland lake until it was flooded when sea levels began to rise 6000–10,000 years ago. A land bridge between Australia and Papua New Guinea would have existed until around 10,000 years ago (~450 turtle generations) effectively separating turtle stocks breeding in eastern Australia from those breeding in northern and western Australia, as shown by genetic analysis of green turtles *C. mydas* (Dethmers *et al.*, 2006). Green turtles, *C. mydas*, nesting in the Gulf of Carpentaria appear to have invaded from western populations, but have since altered the timing of breeding (from austral summer to the austral winter) to adapt to local temperature regimes. Migration routes have also changed as some green turtle populations in the Gulf of Carpentaria, Northern Australia, migrate between nesting and foraging areas contained entirely within the Gulf representing migratory routes in the order of hundreds of kilometres rather than the thousands of kilometres found in other green turtle (*C. mydas*) populations (Kennett *et al.*, 2004).

Evidence of similar phenological shifts and/or colonisation events are also found in other turtle populations. For example, genetic analysis of green, *C. mydas*, turtles nesting in the Indian Ocean suggests the turtle

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population nesting at rookeries in the South Mozambique Channel (south-west Indian Ocean) have recently colonised from the Atlantic Ocean around the tip of South Africa (Bourjea *et al.*, 2007). Suitable green turtle-foraging habitat occurs close to the tip of South Africa due to warm water flows in this region but no analogous habitat is found along cold-upwelling system that dominates the west coast. The cold South African waters are considered a major geographical barrier for *C. mydas* dispersal and, prior to the discovery of Atlantic haplotypes in the southern Mozambique Channel populations, no evidence has been found of gene flow between the Indian and Atlantic Oceans over the last 1.5 million years. Further, it is unlikely this colonisation is an ongoing process and the genetic differentiation of the southern Mozambique Channel populations is maintained by the oceanographic currents in this region (Bourjea *et al.*, 2007).

6. Adaptation and Resilience

Marine turtles are considered vulnerable to climate change given the strong role temperature plays in all life stages (Davenport, 1997). Much discussion with regard to marine turtles and climate change is centred on the temperature-dependent sex determination of embryos in the nest. Warming expected over the coming century may result in shifts to neat to 100% female-producing beaches for some populations. However, the differences in breeding seasons observed at rookeries within the same genetic stock and recent evidence of some relationships between peak nesting and temperature (Pike *et al.*, 2006; Weishampel *et al.*, 2004) suggests some capacity for adaptation to altered climate by breeding marine turtles. Such responses may not occur at a fast enough rate to keep pace with projected rapid warming over the next 100 years.

Loss of suitable nesting sites may be countered by colonisation of new sites as has happened over past, much greater, shifts in sea level and climatic alteration. Fidelity to breeding beaches by turtles may not be as strong as generally supposed. A study of 2891 nesting green turtles, *C. mydas*, along the Australian east coast, all of which have nested in previous years, revealed 6% changed rookeries (nesting beaches) between nesting seasons, with 1.6% having changed rookeries within a nesting season (Dethmers *et al.*, 2006). Turtles may track changing coastal environments by moving to nearby beaches, as may have happened when the Gulf of Carpentaria flooded (Dethmers *et al.*, 2006). Or events may be long-distance, as in a recent (on an evolutionary scale) colonisation of green turtles, *C. mydas*, from the Atlantic Ocean into the Indian Ocean via the Cape of Good Hope (Bourjea *et al.*, 2007).

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Many turtle populations have operated with a strong female bias over many decades, if not longer. Thus, some populations may be resilient to warming if female biases remain within or at levels where population success is not impaired. At present, there is little information about the biases that populations can sustain (Hamann *et al.*, 2007). Given the projected warming at turtle rookeries globally, it must be assumed that some populations will be under threat.

Resilience of marine turtles to climate change is likely to be compromised by other anthropogenic influences. Development of coastlines may threaten nesting beaches and reproductive success and reduce the availability of alternative breeding areas if current regions become unsuitable. Pollution and eutrophication, in addition to coastal development, is threatening important coastal foraging habitats for turtles worldwide. Around 29% of seagrass beds have disappeared in the last 130 years and rates of decline have accelerated since 1990 (Waycott *et al.*, 2009). Losses are attributed to a loss of water quality from changes in land use and eutrophication, coastal development, invasive species and climate change (Abal and Dennison, 1996; Kirkman, 1997; Ruiz and Romero, 2003; Walker *et al.*, 1999; Waycott *et al.*, 2009). The world has also lost 19% of the original area of coral reefs with a further 20% under serious threat over the next 20–40 years from anthropogenic-induced degradation including climate change (Wilkinson, 2008). Major losses of coral reefs are reported from the occurred in the Caribbean and in the heavily populated regions of Asia.

Exploitation and bycatch in other fisheries has seriously reduced marine turtle populations; marine turtles may once have been extremely common in coastal ecosystems until hunting associated with the rise of seafaring reduced numbers relatively rapidly (Jackson, 1997). Turtles themselves have been the target of major fisheries in the past which have drastically reduced turtle numbers; many populations are still reduced from exploitation over a century ago (Aitken *et al.*, 2001; Daley *et al.*, 2008; Jackson, 1997; Tripathy and Choudbury, 2007) and in some areas, particularly Indo-China, are still exploited. Turtles are also exploited, often illegally, for their eggs and their shells (e.g. Barnett *et al.*, 2004; Hope, 2002; Lagueux and Campbell, 2005). Large numbers of turtles die as the result of being caught as bycatch in pelagic longline and trawl fisheries every year (Ferraroli *et al.*, 2004; Hays *et al.*, 2003b; James *et al.*, 2005a; Kaplan, 2005; Kotas *et al.*, 2004; Lewison and Crowder, 2007).

The cumulative effects of other human-induced stressors may seriously reduce the capacity of some turtle populations to cope with the additional stressor of climate change. The widespread and global nature of many of the anthropogenic-induced stressors means that many turtle populations may be threatened at every life stage. Conservation efforts targeting critical life stages or highly threaten populations should increase resilience.

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7. Global Trends

The IUCN Red List in 2009 included marine turtles as vulnerable, endangered or critically endangered, with the exception of the flatback, *N. depressus*, which is data deficient (IUCN, 2009; Seminoff and Shanker, 2008). Many marine turtle populations globally are increasing (although still severely depleted) as the result of conservation efforts resulting in the IUCN listings being contested as misleading (Broderick *et al.*, 2006; Hays, 2004; Seminoff and Shanker, 2008). For example, green turtles, *C. mydas*, nesting at Ascension Island have increased by an estimated 285% since the 1970s (Broderick *et al.*, 2006). Increases are also reported for *C. mydas* populations elsewhere (Australia: Chaloupka and Limpus, 2001; Hawaii: Balazs and Chaloupka, 2004; Costa Rica: Bjorndal *et al.*, 1999; Troëng and Rankin, 2005). Similar increases have been recorded for other species. For example, a 10-fold increase in 11 years in nesting activity of olive ridley turtles, *L. olivacea*, in Brazil has been reported (da Silva *et al.*, 2007). Observations from the US Virgin Islands suggest leatherback populations, *D. coriacea*, nesting there have been increasing at a rate of around 13% per annum since the 1990s (Dutton *et al.*, 2005), while an recent upward trend has been found in hawksbill, *E. imbricata*, nesting numbers in Antigua (Richardson *et al.*, 2006).

8. Recommendations

Management of marine turtle populations in the face of a rapidly changing climate will require a concerted effort globally, both to reduce the direct impacts of climate change and to increase resilience of turtle populations. Clearly, a beneficial approach to many animal species including turtles would be an international effort to mitigate greenhouse gas emissions. However, while that is being achieved, reducing other stressors should be seen as *a priority* for helping to increase the resilience of turtle populations.

Conservation efforts to date have tended to focus on nesting beaches as these are the most accessible of the turtle habitats and therefore the most cost effective to manage. On a local scale, strategies such as increasing shading to cool nest temperatures, for example, by increasing shoreline vegetative or relocation of eggs, has been used as a management tool, although the costs of large-scale programmes may be prohibitive (Dutton *et al.*, 2005; Hamann *et al.*, 2007; Pfaller *et al.*, 2009; Pike, 2008a). It has been argued that survival to reproductive age of individual hatchlings is extremely low so the likelihood of hatchlings from 'saved' nests contributing to the future populations are minimal (Pike, 2008c). This also raises questions about whether such

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strategies interfere with the natural ability of populations to respond to climate variability (Mrosovsky, 2006). Concerns have been raised that egg relocation will distort gene pools by imposing artificial selection on 'poor' nesters, if individual females consistently select unfavourable sites and if such traits are heritable (Mrosovsky, 2006; Pike, 2008c). Egg relocation would be a viable conservation strategy for populations with low repeatability in individual selection of nest sites (Pfaller *et al.*, 2009). In this case the 'doomed nests' may result from a large percentage of the population so would not distort gene pools.

Other strategies have involved 'head-starting' turtles where juveniles are raised in hatcheries and released in the wild; however, generally such approaches have not been successful. Options for beach re-nourishment and restoration of low-lying beaches to counteract sand loss due to rising sea levels or storm erosion could also be explored. The success of beach nourishment is currently under discussion with both increases and declines in reproductive output reported (Brock *et al.*, 2009; Fuentes and Hamann, 2009; Pike, 2008c, 2009b). Protection of nesting beaches and protection of nests from land-based predators will increase reproductive successes, while protection of cooler (hence male-producing) beaches, may become critical as temperatures warm. In this context, minor, high-latitude rookeries may become increasingly important.

In the open ocean, longline fisheries have received attention as a high source of turtle mortality (Ferraroli *et al.*, 2004; Hays *et al.*, 2003b; James *et al.*, 2005a; Kaplan, 2005; Kotas *et al.*, 2004; Lewison and Crowder, 2007) and efforts to reduce turtle catch in these fisheries should improve the health of turtles stocks globally. The introduction of turtle exclusion devices in trawl fisheries, such as the Northern Prawn Fishery in the Gulf of Carpentaria, Australia or prawn fisheries in the Gulf of Mexico, has greatly reduced turtle bycatch (Brewer *et al.*, 2006; Lewison *et al.*, 2003).

Many turtle nesting beaches and foraging grounds are in regions of the world where regulated and unregulated fishing and harvesting are high, both of turtles and of turtle eggs. Conservation programmes within these regions will play an important role in conserving turtle stocks. Strong recoveries of seriously depleted green turtle, *C. mydas*, populations were found in only a few decades following increases in protection of nesting populations (Chaloupka *et al.*, 2008a).

There are many knowledge gaps to be filled before a deeper understanding of turtle population dynamics and life histories will be possible. Advances in genetic approaches are revealing phylogeography of turtle populations worldwide and informing on responses to past climate change which, in turn, will inform us about some of the potential responses of marine turtles to future climate change. Advances in satellite tagging are supplying much needed information on key turtle-foraging regions in the open ocean and turtle migrations, but there is still much to be learnt (Hays,

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2008). Long-term monitoring studies, both at major rookeries and at peripheral nesting beaches, as well as modelling studies, are required to understand how sex ratios respond to a fluctuating environment and how these affect long-term turtle population dynamics.

Reproductive studies have tended, for obvious reasons, to concentrate on turtle nesting beaches, but channelling efforts solely on the present-day rookeries ignores the processes driving variability in turtle nesting behaviour and distributions. As research on marine turtles expands, so does our insight into the processes that underlie the initiation of nesting migrations and selection of breeding areas. The paradigm that turtles return to their natal beach to nest has been replaced by a view that turtles return to a natal region as evidence arises of variability in beach selection between years and between individuals in the same breeding stock. This view may alter further as our marine turtle data sets lengthen to encompass multi-generational observations. We recommend that investigation of knowledge gaps of the processes driving breeding site selection is critical for adaptive management decisions in the face of a changing climate.

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