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Contribution to the Theme Section 'Incorporating climate change into endangered species conservation'

REVIEW

Climate change and marine turtles

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ABSTRACT: Marine turtles occupy a wide range of terrestrial and marine habitats, and many aspects of their life history have been demonstrated to be closely tied to climatic variables such as ambient temperature and storminess. As a group, therefore, marine turtles may be good indicators of climate change effects on coastal and marine habitats. Despite the small number of species in the taxon and a growing body of research in the field, the evidence base to predict resultant impacts of climate change remains relatively poor. We review the data from peer-reviewed publications to assess the likely impacts of climate change on marine turtles and highlight the types of data that would be most useful for an accurate assessment of future effects. The cumulative indications from these previous studies indicate that future research should focus on: (1) climate change effects on key habitats upon which turtles depend; (2) factors that influence nest site selection; (3) the consequences of skewed primary sex ratios; and (4) the effect of climate change on turtles at sea, for example range shifts and dietary breadth. Although it is too early to give detailed management recommendations, careful protection of coastlines along which turtles nest should be considered, as should the protection of beaches that produce male hatchlings, which may be of increased importance in the future. More active management approaches, for example translocation of eggs to suitable yet vacant nesting beaches, may be necessary to consider under worst-case scenarios.

KEY WORDS: Global warming · Sea turtle · Temperature · Sex ratio · Phenology · Range · Conservation management · Sea level rise

INTRODUCTION

According to the latest meteorological data (IPCC 2007), air temperatures have increased to levels not seen since atmospheric records began in 1850. For example, 11 of the 12 yr between 1995 and 2006 were the warmest on record (Brohan et al. 2006), and global mean ocean temperatures are thought to be 0.7°C warmer than at any time in the last 420 000 yr (Hoegh-Guldberg et al. 2007). These warming trends are expected to increase at accelerated rates (in conjunction with the continued emission of high levels of CO_2). Approximately 80 % of the extra warmth is likely to be absorbed by the oceans (IPCC 2007) and will result in thermal expansion, which could produce an 18 to 60 cm rise in sea level by 2100 (Meehl et al. 2005, IPCC 2007). Extreme weather events (e.g. colder winters and warmer summers) are likely to occur with greater variability (IPCC 2007) and could combine with other physical climate factors to drive changes in ocean chemistry, such as pH decreases of 0.3 to 0.5, which would be unprecedented in the context of the last 200

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to 300 million yr and could have significant effects (Harley et al. 2006, Hoegh-Guldberg et al. 2007). Although the effect of climate change will be global, there will likely be much variation in impacts at regional levels. Downscaling of general circulation models (GCMs) to useful resolution poses a significant challenge for climate change risk assessments (e.g. Wilby et al. 2002, effects on biodiversity).

In biological systems, from polar terrestrial to tropical marine environments, data demonstrate a coherent pattern of change in accord with those of climate change (Hughes 2000, Sala et al. 2000, Davis & Shaw 2001, McCarty 2001, Walther et al. 2002, Visser & Both 2005, Hickling et al. 2006), with phenological and spatial shifts recorded and predicted for many species from invertebrates (Parmesan et al. 1999, Beaugrand et al. 2002, Davies et al. 2006) to birds (Brown et al. 1999, Winkler et al. 2002, Butler 2003, Mills 2005, Springer et al. 2007) and marine mammals (Learmonth et al. 2006, Robinson et al. 2009, MacLeod 2009, this Theme Section). All 7 species of marine turtles are of conservation concern and are affected by a range of natural and anthropogenic threats. However, although much effort has been expended over the last 2 decades to understand and mitigate the threats to marine turtles (Lutcavage et al. 1997, Watson et al. 2005), the threat of climate change on this taxon has, until recently, been given little attention (Fig. 1; although see seminal papers by Mrosovsky 1984a and Davenport 1989).

Marine turtles occupy a wide range of different habitat types throughout their life history (Fig. 2), including temperate and tropical sandy beaches, oceanic frontal systems and gyres, coastal mangrove forests, neritic reefs, seagrass beds and other shallow foraging areas (Musick & Limpus 1997). During their development, marine turtles may cross entire ocean basins, and adults and juveniles have been shown to interact with major oceanic surface currents (Hawkes et al. 2006, Polovina et al. 2006, Seminoff et al. 2007, Shillinger et al. 2008). Temperature is of profound importance as an environmental factor for marine turtles, affecting features of their life history from hatchling sex determination (Yntema & Mrosovsky 1980) to adult distribution (Spotila & Standora 1985, Seebacher & Franklin 2005). Other climatic aspects, such as extreme weather events, precipitation, ocean acidification and sea level rise also have potential to affect marine turtle populations. Given current climate change predictions (reviewed in the IPCC 2007 report), we comprehensively reviewed the literature published on marine turtles. Here, we report on the data published on (1) breeding sites, including availability of beach, selection of nest locations, timing of nesting and incubation conditions; (2) open ocean habitat used by turtles, including hatchlings, juveniles and adults; and (3) coastal habitats used by turtles, including herbivorous, spongivorous and omnivorous turtles. Finally, we highlight major gaps that remain in our knowledge of potential climate change impacts on marine turtles.

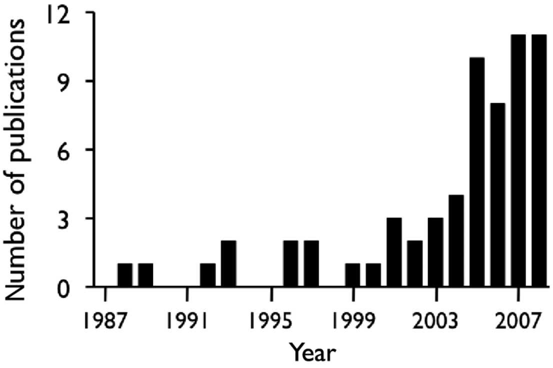

Fig. 1. Increase in interest in marine turtles and climate change. Number of published studies per year (resulting from ISI Web of Science search, 28 January 2009) containing the search terms 'marine turtles OR sea turtles' and 'climate change OR global warming' in the title, abstract or entire article. All papers are cited within the review

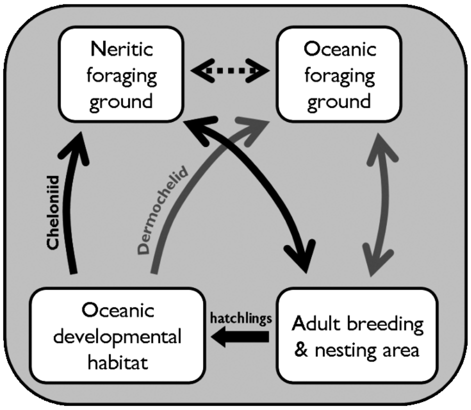

Fig. 2. Typical life cycle of a marine turtle, adapted from Musick & Limpus (1997). For schematic purposes the cycle has been greatly simplified; most adult Cheloniid turtles are now known to occupy neritic foraging habitats and Dermocheliid turtles oceanic foraging habitats. There may be greater plasticity in foraging strategies (for example in loggerhead, green and olive ridley turtles, see 'Marine turtles and the open ocean: adult turtles'). Dashed line indicates potential switching between the 2 foraging strategies

MARINE TURTLES AT BREEDING SITES

The beach

In all species of marine turtles, successful reproduction depends primarily on available terrestrial habitat (Fig. 3). Female turtles must emerge onto beaches to lay several clutches of eggs over the course of a nesting

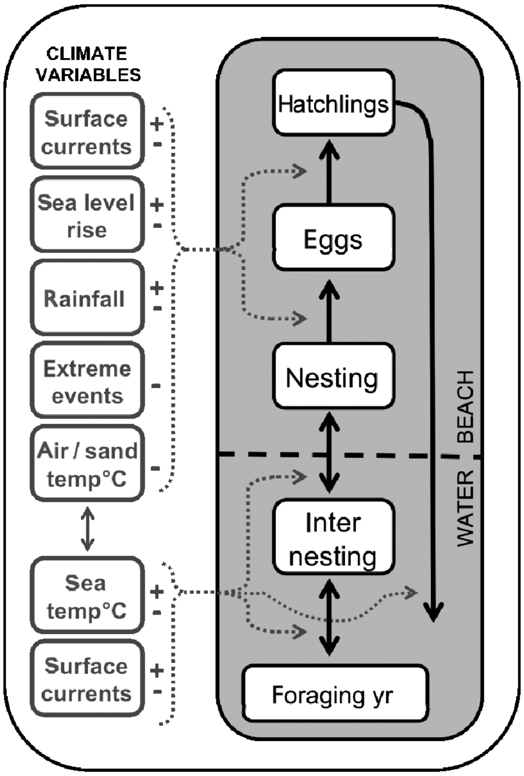

Fig. 3. Breeding and nesting phase of marine turtles. Dotted grey arrows represent the potential climate variables and their indirect effects, + or – indicate likely direction of effect

season (Miller 1997). Predicted increases in sea level (an average of 4.2 mm per year until 2080; Church et al. 2001, IPCC 2007) have the potential to compromise availability of nesting beaches, particularly on low-lying narrow coastal and island beaches (Nicholls 1998, Fish et al. 2005, Baker et al. 2006, Jones et al. 2007, Mazaris et al. 2009) and where coastal development prevents landward migration of beaches — also known as coastal squeeze (Fish et al. 2008). Only these 5 studies have so far examined the potential effect of sea level rise on marine turtle nesting beaches, of which 3 (Nicholls 1998, Baker et al. 2006, Jones et al. 2007) used high precision digital elevation models (DEMs) with simple inundation ('bathtub') flooding models, and a fourth used categorical scoring of the coincidence of turtle nesting beach with 'high risk' beaches (considered low relief, with high wave energy and more than 1.1 m of beach retreat annually; Daniels et al. 1993). The fifth study (Mazaris et al. 2009) used the 2-dimensional Bruun rule to model beach recession from sea level rise and, consequently, the maximum number of nests that could be supported ('carrying capacity') on the nesting beach (but see Cooper & Pilkey 2004). Although the 'bathtub' methodology is potentially overly simplistic, as it does not take into account the dynamics of the coast (e.g. wind, waves, tide), it readily produces estimates that are relatively easy to compute, using data that can be collected using a GPS unit. A study in the northwestern Hawaiian Islands (Baker et al. 2006) predicted that up to 40% of green turtle *Chelonia mydas* nesting beaches could be flooded with 0.9 m of sea level rise, while studies in Barbados (Fish et al. 2008) and Bonaire (Fish et al. 2005) suggested similar losses of hawksbill turtle *Eretmochelys imbricata* nesting habitat (means 50% and 51% decrease, respectively). In the absence of equipment or software, the simple overlay study by Daniels et al. (1993) provides a suitable alternative methodology, albeit with appropriate caveats.

Compounding the threat of sea level rise is the likelihood of an increase in fortification of coastal areas to protect human settlements (using e.g. sea walls, groynes and other hard sea defences). Such 'shoreline protection' is already in widespread use (for example in the Caribbean, Burke & Maidens 2004). It effectively reduces total sandy beach availability (Pilkey & Wright 1988, Kraus & McDougal 1996, Zheng et al. 2007, Schlacher et al. 2008) and leads to a disproportionate loss of dry upper inter-tidal beach area (Dugan et al. 2008), and, in some cases, entire beaches (Koike 1996, Lutcavage et al. 1997, Airoldi et al. 2005). Despite this, there are no studies to our knowledge that examine the impact of beach fortification on regional turtle nesting populations. In some coastal areas, attempts are made to mitigate beach loss using 'renourishment,' in which transplanted sand is pumped onto the beach to replace eroded material (Montague 2008); this technique is used in urbanised coastal areas. However, this issue is worthy of careful consideration, as the transplanted material may provide unsuitable incubation conditions (Crain et al. 1995, Milton et al. 1997, Rumbold et al. 2001, Peterson & Bishop 2005). Other beach-stabilizing technologies may negatively affect nesting females by blocking beach access, disorientating turtles, or by rendering sand inappropriate for nesting (Bouchard et al. 1998, Brock et al. 2009).

An increase in the proportion of extreme weather events in the most severe categories, such as hurricanes or typhoons, could also occur with changes in the global climate (Goldenberg et al. 2001, Webster et al. 2005, IPCC 2007), which may cause significant loss/erosion of or damage to shorelines. Leslie et al. (2007) reported that, although the total number of tropical cyclones over the southwest Pacific would stay the same, the proportion of Category 4 and 5 storms would increase by 15%, and that their tracks and genesis regions would move polewards by approximately 2° latitude over 50 yr (to 2050, but see also Nolan & Rappin 2008). Such storms often make landfall in warm temperate and tropical areas (Bengtsson 2001, Goldenberg et al. 2001), including those where marine turtles nest. Five studies have examined the spatio-temporal coincidence of marine turtle nesting with hurricanes, cyclones and storms (Martin 1996, Ross 2005, Pike & Stiner 2007, Prusty et al. 2007, Van Houton & Bass 2007), and they suggest that cyclical loss of nesting beach, decreased hatching success and hatchling emergence success could occur with greater frequency. However, susceptibility to storm-related threats may vary by species (Pike & Stiner 2007), such that species with lower nest-site fidelity (for example leatherback turtles *Dermochelys coriacea*, Witt et al. 2008) would be less vulnerable than those with higher site fidelity (for example hawksbill turtles, Kamel & Mrosovsky 2005). At some highly dynamic and inter-seasonally variable nesting beaches in the Guianas (Plaziat & Augustinius 2004), turtles are able to maintain successful nesting (Girondot & Fretey 1996, Rivalan et al. 2005, Kelle et al. 2007) despite the fact that some beaches disappear between nesting years. Such behavioural flexibility may offer one of the most promising avenues for adaptation in marine turtles. Marine turtles are certainly able to colonise new beaches, with nesting now occurring at recently formed sites such as volcanic islands (Mrosovsky 2006), at man-made beaches (Hoggard 1991), and at areas opened after glacial retreats (Encalada et al. 1998, Hamann et al. 2007).Whether turtles can colonise nesting areas made available, either thermally or geographically, by climate change remains to be seen.

Selecting nesting locations

Although the factors driving the selection of a nest site on a specific beach are not well understood for marine turtles (Limpus et al. 1983, Hays et al. 1995, Mortimer 1990, Wood & Bjorndal 2000, Miller et al. 2003, Kamel & Mrosovsky 2005), several factors may be influential in the choice of an optimal nesting site (e.g. low salinity, high humidity, infrequently inundated, well ventilated, with nearshore oceanography conducive to dispersal of hatchlings into oceanic currents; Miller 1997, Foley et al. 2006). There should be sufficient space above the high tide line for nesting to take place and, for some species and/or locations, there should be adequate beach vegetation for clutch shading (Naro-Maciel et al. 1999, van de Merwe et al. 2005, Kamel & Mrosovsky 2006). However, persistence of a nesting site depends on the successful production of hatchlings that re-nest later at the same site, so the success of a particular nesting beach is only revealed after a period of many years. Adding to the complexity are species-specific behavioural characteristics of nest site selection: some species are reported to lay clutches far above the high tide line, while others prefer to nest closer to the water line (Mrosovsky 1983, Whitmore & Dutton 1985, Hays et al. 1995, Kamel & Mrosovsky 2004, 2005). Additionally, as detailed in the previous section, there appears to be possible inter-specific variation in responses to rapid changes in beach availability, width or configuration (see also Mrosovsky 2006, Wetterer et al. 2007).

Although some beaches may be inundated and lost, one possible result of climate change is an increase in thermally suitable nesting habitat, both geographically and temporally. With an increase in mean air, and therefore beach sand temperatures, previously unsuitable habitat, for example beaches at higher latitudes than current nesting areas, may become suitable for successful egg incubation. This has apparently occurred in the past, when warmer temperatures in interglacial periods facilitated the expansion of loggerhead sea turtles *Caretta caretta* into higher latitudes (Bowen et al. 1993). It is of note that leatherback turtle nests are now being recorded at their most northerly in a decade of monitoring (Rabon et al. 2004). Temporally, warmer temperatures for a greater number of months of the year may either extend the nesting season for some marine turtles and/or facilitate year-round nesting (Pike et al. 2006, Yasuda et al. 2006). However, data are lacking on how quickly marine turtles would be able to take advantage of these changes. It has recently been suggested that although avian spatial distributions are shifting polewards with changing climate, their rate of adaptation is slower, and they therefore lag behind climate warming by approximately 182 km (Devictor et al. 2008).

Timing of reproduction

Marine turtles are capital breeders (Bonnet et al. 1998) and the different resource requirements for reproduction of females compared to males may explain a difference in observed remigration intervals (the period between reproductive years), which is thought to be lower for males (Godley et al. 2002a, Hamann et al. 2003, Schroeder et al. 2003). Environmental conditions in foraging areas may drive prey availability and resource acquisition and, therefore, the decision to breed in a given year as well as the timing of migration to the breeding grounds (Kwan 1994, Miller 1997, Broderick et al. 2001b, Solow et al. 2002, Price et al. 2004, Wallace et al. 2006, Saba et al. 2007, 2008, Chaloupka et al. 2008, Reina et al. 2009).

Future climate change could also alter the intra-annual timing of nesting, such that warmer water temperatures may contribute to an earlier onset of nesting (by 12 to 18 d $1°C^{-1}$ for loggerhead turtles, Hawkes

2007b, but see Pike in press for green turtles), a decrease in the inter nesting interval (Sato et al. 1998, Webster & Cook 2001, Hays et al. 2002, Hamel et al. 2008) and the earlier onset of peak (median) nesting date (5 to 6 d 1°C^{-1}, Weishampel et al. 2004, Pike et al. 2006). Ultimately, temperature may also affect the length of the nesting season (for loggerhead turtles: Pike et al. 2006, Hawkes et al. 2007b). However, the total clutch frequency per female per season will likely vary with resources stored from foraging areas (Chaloupka et al. 2008), which could further complicate interpretation of the patterns of adaptation. These relationships warrant further investigation and testing across species and nesting sites, particularly between populations that nest at equatorial versus temperate sites and in the warmest and cooler parts of the year.

Incubation conditions and sex ratios

Marine turtle clutches are sensitive to temperature changes and typically incubate successfully only between 25 and 35°C (Ackerman 1997, Carthy et al. 2003), with embryos incubating at high temperatures becoming females and those at lower temperatures becoming males, and 50% of either sex produced at the 'pivotal temperature,' between 28 to 31°C (Mrosovsky 1988; Fig. 4b). A mixture of sexes is produced within a 'transitional range of temperatures' (e.g. between approximately 27.5 and 30.5°C in loggerhead turtles, Mrosovsky 1988). However, in addition to diel variations in incubation temperature, egg placement within a nest may mean that eggs at the top

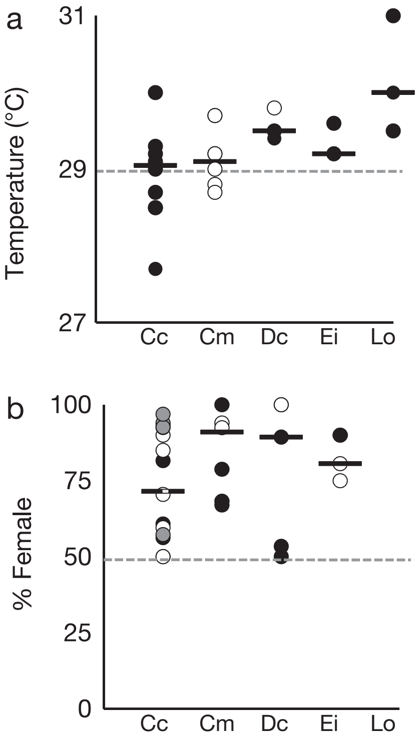

Fig. 4. (a) Lab (●) and field (○) estimates of pivotal temperatures for loggerhead (Cc), green (Cm), leatherback (Dc), hawksbill (Ei), olive ridley (Lo) turtles; horizontal bars show median values; dashed line indicates reference temperature of 29°C. (b) Primary sex ratios estimated using histology (●), incubation duration (●) and sand or nest temperature (○) as reported in peer reviewed literature. Horizontal bars show median values; dashed horizontal line indicates reference primary sex ratio of 50% female. Source data for (a) and (b) are in Table 1

Table 1. Literature sources of pivotal temperatures and primary sex ratios for loggerhead, green, leatherback, hawksbill, and olive ridley turtles

	Pivotal temperatures	Primary sex ratios
Loggerhead	Georges et al. (1994), Kaska et al. (1998), Limpus (1985), Marcovaldi et al. (1997), Mrosovsky (1988), Mrosovsky et al. (2002), Yntema & Mrosovsky (1982)	Baptistotte et al. (1999), Chu et al. (2008), Godley et al. (2001a,b), Hanson et al. (1998), Hawkes et al. (2007), Houghton & Hays (2001), Kaska et al. (1998, 2006), Marcovaldi et al. (1997), Mrosovsky & Provancha (1992), Mrosovsky et al. (1984b), Oz et al. (2004), Rees & Margaritoulis (2004), Schmid et al. (2008), Zbinden et al. (2007)
Green	Broderick et al. (2000), De Ocampo & Jaojoco (1998), Godfrey & Mrosovsky (2006), Godley et al. (2002c), Leh et al. (1985), Miller & Limpus (1981), Standora & Spotila (1985)	Booth & Freeman (2006), Broderick et al. (2000), Casale et al. (2000), De Ocampo & Jaojoco (1998), Godfrey et al. (1996), Kaska et al. (1998), Spotila et al. (1987)
Leatherback	Binckley et al. (1998), Chan & Liew (1995), Chevalier et al. (1999)	Binckley et al. (1998), Chan & Liew (1995), Godfrey et al. (1996), Houghton et al. (2007), Rimblot-Baly et al. (1985)
Hawksbill	Dobbs et al. (in press), Godfrey et al. (1999), Mrosovsky & Provancha (1992)	Glen & Mrosovsky (2004), Godfrey et al. (1999), Kamel & Mrosovsky (2006), Mrosovsky et al. (1992), Wibbels et al. (1999)
Olive ridley	McCoy et al. (1983), Mohanty-Hejmadi & Dimond (1986), Wibbels et al. (1998)	

of a nest experience temperatures a degree or more warmer than eggs at the bottom (e.g. 1.4°C for loggerhead turtles, Kaska et al. 1998) and thus possibly lead to mixed sex ratios. The thermal properties of the turtle nesting beach itself will also contribute to incubation temperatures and are determined by a variety of factors, including physical (sand grain size, composition, albedo; Hays et al. 2001, Reece et al. 2002), climatic (Godfrey et al. 1996, Matsuzawa et al. 2002, Houghton et al. 2007) temporal (rainy vs. dry season; Godfrey et al. 1996), and geographic (tropical vs. subtropical) features, which together can have a profound influence on the embryonic development of marine turtles (Naro-Maciel et al. 1999). Predicted increases in temperature in the future could affect primary sex ratios (Mrosovsky et al. 1984a, Janzen 1994, Davenport 1997, Glen & Mrosovsky 2004, Hatase & Sakamoto 2004, Hawkes et al. 2007c) as well as survivorship of clutches (Miller 1985, Broderick et al. 2001a, Godley et al. 2001a, Hamann et al. 2007, Hawkes et al. 2007b).

Despite studies on the sex ratio production of loggerhead, green, leatherback and hawksbill turtles, major gaps remain in our understanding of primary sex ratios of marine turtles (Fig. 4b). Sex ratio production can change within and across seasons (Mrosovsky et al. 1984a,b, Godfrey et al. 1996); however, not all existing long-term datasets on primary sex ratios have been published in the peer-reviewed literature. Most existing estimates of primary sex ratios for nesting beaches, for example in the Mediterranean (Broderick et al. 2000, 2001a, Godley et al. 2001a,b, Oz et al. 2004, Zbinden et al. 2007), North America (Mrosovsky & Provancha 1992, Hanson et al. 1998, Hawkes et al. 2007b) and South America (Marcovaldi et al. 1997, Baptistotte et al. 1999, Godfrey et al. 1999) rely at least in part on indirect indices of sex ratio. For example, Godley et al. (2001b) recorded nest incubation durations over a 5 yr period and used previously published data relating incubation duration to sex ratio to estimate the proportion of female hatchlings (see also Marcovaldi et al. 1997, Godfrey et al. 1999, Oz et al. 2004, Hawkes et al. 2007b, Zbinden et al. 2007). The advantage of this method, validated by Mrosovsky et al. (1999), is that incubation durations are normally readily available from most turtle nesting projects, and could therefore be used in future work to give a wider estimate of primary sex ratios. However, as noted in Mrosovsky et al. (1999), values can be inaccurate by as much as 10% and must therefore be used with appropriate caution. Other studies have used beach air (Hays et al. 2003, Hawkes et al. 2007b) or sand temperature (Mrosovsky et al. 1992, Baptistotte et al. 1999, Casale et al. 2000, Rees & Margaritoulis 2004, Kamel & Mrosovsky 2006) to reconstruct likely incubation temperatures with which to estimate sex ratios using published conversion curves (e.g. hawksbill turtles: Mrosovsky et al. 1992; green turtles: Kaska et al. 1998; loggerhead turtles: Mrosovsky et al. 2002). Since these studies require only a small amount of relatively inexpensive equipment (temperature recording loggers) and little specialist knowledge or software, this technique offers a viable approach for sex ratio estimation. However, it should be noted that these studies use correlative approaches to derive estimates and that, to our knowledge, no analyses of the potential error inherent in this approach exist. In addition, the majority of studies do not take into account the threshold range of temperatures (TRT; in which a mixture of sexes are produced), which may be an important metric in assessing resilience to climate warming (Hulin et al. 2009). Future work should address this to validate the method for estimation of sex ratios for greater numbers of nesting rookeries. Finally, other studies record the temperature of the nest itself and use validated conversion curves (detailed in Table 1) to estimate sex ratio (Mrosovsky & Provancha 1992, Hanson et al. 1998, Kaska et al. 1998, Broderick et al. 2000, Godley et al. 2001b, Houghton & Hays 2001, Glen & Mrosovsky 2004, Booth & Freeman 2006, Houghton et al. 2007, Schmid et al. 2008).

Relatively few studies have used direct estimation of sex ratio by histologically examining the gonads of a selection of hatchlings from each nest (Mrosovsky 1984a,b, Rimblot et al. 1985, Spotila et al. 1987, Mrosovsky & Provancha 1992, Chan & Liew 1995, Godfrey et al. 1996, Binckley et al. 1998, De Ocampo & Jaojoco 1998, Kaska et al. 1998, Mrosovsky et al. 1999, Kaska et al. 2006, Schmid et al. 2008). While direct approaches should be accurate, there are 2 major drawbacks: (1) lethal sampling of hatchlings must normally be carried out under special permit and requires careful ethical assessment and specialist skills, and (2) variation of sex ratio response to incubation temperature between individuals and populations is not yet fully understood (see Mrosovsky 1994 for more discussion). Therefore, although indirect approaches are known to have inherent inaccuracies and may leave room for improvement (Ewert et al. 2005, Delmas et al. 2008), they offer approaches that can be used by most nesting beach projects, regardless of budget or specialist knowledge. Regional validations of each method need to be carried out, as they are largely lacking from the published literature but will enormously facilitate a rapid assessment of sex ratios and, thereby, the risk of feminisation through the warming effects of climate change.

It is unclear whether marine turtles will (or can) adapt either behaviourally or physiologically to altered incubation conditions to counter potential feminization associated with warmer temperatures. At the individual level, the physiological mechanism by which temperature affects sexual differentiation could change, specifically with alterations to the pivotal and/or transitional range of temperatures (Hulin & Guillon 2007). However, evidence seems to suggest this is unlikely — reported pivotal temperatures across species and populations are relatively conserved (Fig. 4a). Individuals could also adapt behaviourally by choosing nest locations that are cooler (e.g. in the shade of vegetation, in rainy seasons, at higher latitudes) or by nesting earlier or later during cooler periods of the season. This could help to maintain production of mixed sex ratios, contributing to population viability (Doody et al. 2004, Zbinden et al. 2007, but see Schwanz & Janzen 2008). Since warmer water temperatures in near-shore nesting areas are known to affect the onset and periodicity of nesting (Sato et al. 1998, Weishampel et al. 2004), a mechanism may already exist for this strategy, at least for loggerhead turtles. At the population level, sex ratio skew may be ameliorated by smaller nesting populations at extremes of nesting ranges producing more balanced hatchling sex ratios (e.g. in North Carolina, USA, and Espirito Santo, Brazil, for loggerheads in the West Atlantic; Baptistotte et al. 1999, Hawkes et al. 2007b), such that ratios are in effect balanced across the population (Hulin & Guillon 2007). On the other hand, the capacity for marine turtles to quickly adapt is questionable; as a group, they are long-lived, late maturing (Avise et al. 1992, Zug et al. 2002) and have evolved with a climate changing at a much slower rate than projections suggest for the next 100 yr (Hamann et al. 2007). In addition, many populations of marine turtles have been documented at relictual levels compared to the historical past (McClenachan et al. 2006, Bell et al. 2007) and may therefore have limited capacity for selection on key traits. Available evidence suggests that the genetic capacity for marine turtle adaptation may be lower than for other vertebrates (Avise et al. 1992, FitzSimmons et al. 1999).

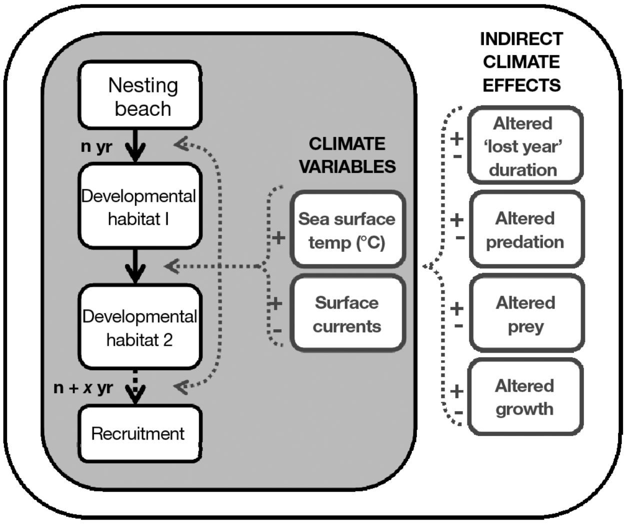

Fig. 5. Oceanic-developmental phase of marine turtles. Recruitment to adult foraging areas occurs at varying durations (*x* yr) after development. Dotted grey arrows represent the potential climate variables and their indirect effects, + or – indicates direction of effect

Temperature also drives incubation duration, such that incubation duration is inversely correlated with incubation temperature (Mrosovsky et al. 1999, Matsuzawa et al. 2002), so warmer nests incubate on the beach for a shorter period. Shifts in phenology and range of other species due to climate effects (Root et al. 2003) may alter the type, abundance and behaviour of predators and may therefore also affect the number of surviving hatchlings (Hamann et al. 2007). Finally, temperature has been shown to influence hatchling phenotype, where size and locomotor performance vary with incubation conditions (Booth & Astill 2001, Booth et al. 2004, Booth 2006, Hamann et al. 2007) so that hatchlings produced at warmer temperatures may be smaller and swim faster, and have faster growth rates (Du & Ji 2003, Glen et al. 2003, Deeming 2004). The fitness consequences of these traits are, however, untested.

MARINE TURTLES AND THE OPEN OCEAN

Hatchling and juvenile turtles

Hatchling and small juvenile marine turtles of all species likely suffer high levels of predation in the sea (Gyuris 1994). During the post emergence swim frenzy (Wyneken & Salmon 1992), hatchlings are subject to predation from a range of avian and fish predators. The swim frenzy generally lasts for 2 to 3 d, at which time hatchlings are thought to become associated with floating matter at frontal systems of major ocean currents (Witherington 2002), where they may derive some protection. However, there is evidence that the phenology and spatial distribution of many bird and fish species is changing with the climate (Carscadden et al. 1997, Root et al. 2003, Lehikoinen et al. 2004, Sims et al. 2004), which may include predators of hatchling or juvenile marine turtles. Although the direction and magnitude is difficult to estimate, the relative type or intensity of predation on hatchling turtles could change (Fig. 5). During the swim frenzy, hatchlings have been shown to swim in directions that should entrain them in local surface currents (Lohmann & Lohmann 2003, 2006), facilitating their movements across ocean basins, and currents may also be influential in the distribution of juvenile turtles (Bolten 2003, Witt et al. 2007b). Under future predicted scenarios of climate change, with changes in temperature and freshwater input at the poles, thermohaline circulation patterns are expected to change in intensity and direction (Rahmstorf 1997, Stocker & Schmittner 1997). The consequence of such changes for hatchling turtles are unknown and difficult to estimate, but may mean that developing turtles do not disperse as widely or to the same areas as at present (Hamann et al. 2007). This may have important energetic consequences for hatchlings no longer able to rely on passive transport in surface currents for migration.

The factors that determine the duration of the pelagic developmental phase for juvenile marine turtles are not known, but are likely affected by a combination of food availability, growth rates, ambient temperature and surface currents (Bolten & Balazs 1995). Changes to the pelagic community concurrent with patterns of climate change have been demonstrated (Greve et al. 2001, Beaugrand et al. 2002, Hays et al. 2005), and they may alter the available prey for juvenile turtles, leading to potential trophic mismatch (Edwards & Richardson 2004). Ultimately, if resources are more or less abundant than at present, the current mean period between hatching and recruitment to larger juvenile/adult foraging areas could change (Verity et al. 2002). The direction and magnitude of this change is hard to quantify with currently available data; the response of marine turtle growth rates and the productivity of oceanic areas with warmer temperatures could be markedly different and likely react at different time scales.

Adult turtles

Adult leatherback sea turtles (Eckert 2006, McMahon & Hays 2006, Witt et al. 2007a) and some populations of adult Cheloniid turtles (loggerhead turtles: Hatase et al. 2002a, 2007, Hawkes et al. 2006, McClellan & Read 2007; green turtles: Hatase et al. 2006, Seminoff et al. 2007; and olive ridley turtles *Lepidochelys olivacea*: Polovina et al. 2004, Whiting et al. 2007) forage in the open ocean off the continental shelf (Fig. 2). Generally, such turtles have broad ranges, from hundreds to thousands of km^2 (Hays et al. 2004, Hawkes et al. 2006). It is conceivable that such large ranges could mitigate negative climate effects on foraging area, but this remains untested.

Sea surface temperature (SST) is possibly the most important determinant of Cheloniid turtle distribution (Milton & Lutz 2003). The influence of sea surface currents on migratory movements of marine turtles (and hence their distribution) is not yet well understood, but may also be important (Luschi et al. 2003a,b, Gaspar et al. 2006, Hawkes et al. 2006, Bailey et al. 2008, Lambardi et al. 2008, Shillinger et al. 2008). Likewise, water temperature and current patterns will be important determinants of the availability of suitable prey for these turtle populations, particularly near major frontal zones where some of these turtle forage. Changes to major surface currents, such as the Gulf Stream, under future climate scenarios (Rahmstorf 1997, 1999, Stocker & Schmittner 1997) may therefore have profound effects.

Dermocheliid turtles

The main prey of leatherback turtles are soft-bodied jellyfish and medusae (Bjorndal 1997, Davenport 1998, James & Herman 2001), which are known to respond sensitively to changes in climate (Beaugrand et al. 2002, Edwards & Richardson 2004), peaking in abundance earlier in the year and possibly in larger numbers (Mills 2001, Hays et al. 2005). In addition, McMahon & Hays (2006) showed that the potential range of occupation by leatherback turtles, based on satellite telemetry and remotely sensed data, has moved 300 km north in the last 17 yr (see also James et al. 2006). Thus, it is possible that climate change could benefit this species in the Atlantic. Foraging conditions in the oceanic zone may affect how often females can return to breed (Saba et al. 2007, Reina et al. 2009) and, therefore, govern lifetime reproductive success. The Pacific Ocean currently exhibits a higher degree of climatic variability than the Atlantic or Indian Oceans (Saba et al. 2008, Chavez et al. 2003). Tropical Pacific circulation patterns have already been documented as being affected by climatic changes (Vecchi et al. 2006), with disruption of upwellings and likely reduced productivity in the region, which are vital for jellyfish occurrence. For the declining Pacific leatherback populations (Sarti-Martinez et al. 2007), this effect of climate change could be significant.

Cheloniid turtles

The diet of pelagic loggerhead turtles and green turtles nesting in the Japanese archipelago has been examined using stable isotope analysis and is hypothesised to consist of epipelagic prey items (Hatase et al. 2002b, 2006). Likewise, the diet of oceanic olive ridley turtles is known to consist largely of pyrosomes and salps (Polovina et al. 2004) and other surface-associated organisms. Consequently, due to the nature of their foraging strategy, these turtles are probably fairly opportunistic with a wider dietary range than is known for many neritic Cheloniid species (see next section), which could confer greater adaptive ability than that of populations with narrower dietary ranges.

Marine turtles in coastal in-water habitats

Most adult populations of Cheloniid marine turtles occupy coastal habitats along the continental shelf (Bjorndal 1997; Fig. 2) where temperatures, surface currents and foraging depths are suitable for energetically efficient foraging. Of these factors, temperature probably best explains marine turtle occurrence, since all Cheloniid species are ectothermic and temperatures below 10°C can induce 'cold stunning' (Milton & Lutz 2003), a condition that can be lethal. Some populations of loggerhead turtles make seasonal latitudinal migrations to forage in waters inhabitable only on a seasonal basis (Shoop & Kenney 1992, Plotkin & Spotila 2002, Dodd & Byles 2003, Schroeder et al. 2003, Ferraroli et al. 2004, Houghton & Hays 2006, Hawkes et al. 2007a), returning to warmer areas in winter to enter 'hibernation' (Godley et al. 2002b, Hochscheid et al. 2005, 2007, Broderick et al. 2007, Hawkes et al. 2007a). In Australia, green turtles have been observed to forage in water temperatures as low as 15°C (Read et al. 1996). As the climate changes, however, these seasonal habitats may become less predictable in time and space (Robinson et al. 2009), and migrations between the two may become mismatched with likely environmental cues (e.g. photoperiod). However, rising temperatures may actually increase the availability of suitable foraging habitat for many Cheloniid species and, therefore, their total range, although species differences in fidelity to 'home ranges' (Renaud & Carpenter 1994, Broderick et al. 2007) may make this pattern harder to recognise.

Herbivorous turtles

Green turtles are thought to be largely herbivorous (but see Seminoff et al. 2002) and are known to be important regulators of sea grass pasture productivity and biomass in coastal marine habitats (Thayer et al. 1984, Williams 1988, Moran & Bjorndal 2005, 2007, Kuiper-Linley et al. 2007). Changes in SST, along with sediment disturbance, altered penetration of ultra violet light, eutrophication and acidification of coastal waters (Sabine et al. 2004, Hall Spencer et al. 2008), which are all possible under climate change scenarios, have been shown to cause changes in the distribution and types of macroalgal species present in coastal habitats (Lapointe 1999, Bjork et al. 2008), leading to a regime shift towards seagrass-dominated communities (Harley et al. 2006, Hall Spencer et al. 2008). Such an effect could be beneficial for green turtles, populations of which have been documented to increase for several index sites (Chaloupka & Limpus 2001, Balazs & Chaloupka 2004, Broderick et al. 2006, Chaloupka et al. 2008). However, it should be noted that seagrasses themselves could ultimately be negatively affected by increased temperatures, salinities and other stress factors; this could alter growth rates, physiology and distribution (Short & Neckles 1999, Bjork et al. 2008, Ehlers et al. 2008). In addition, increased runoff due to increased precipitation and 'blow out' events, where seagrass pastures are effectively cleared by storm surges, may become more widespread with increasing severity of extreme weather events. Such events have been shown to alter habitat heterogeneity and grazing dynamics for parrot fish species (Macia & Robinson 2005) and could also influence grazing green turtles. The potential for ecosystem-wide effects of alteration of either this fundamental and valuable habitat type (seagrass pastures, Ehlers et al. 2008) or keystone predator pressure (green turtles) through climate change is evident (Hamann et al. 2007), but the direction and magnitude of change is, as yet, difficult to predict. Some populations of green turtles appear to specialize in the consumption of algae (Bjorndal 1997) and mangroves (Limpus & Limpus 2000). It is unknown how quickly green turtles may be able to adapt their foraging behaviour to changing availability of seagrasses or algae; previous research has suggested that microbial flora of intestinal tracts of green turtles are specialized for either seagrasses or algae (Bjorndal 1980, Fuentes et al. 2006).

Spongivorous turtles

The majority of the diet of hawksbill turtles at some sites is thought to consist of just a few species of sponges (Meylan 1988, Leon & Bjorndal 2002). Like herbivorous green turtles, hawksbill turtles may play a key role in maintaining habitat health by grazing on coral competitors (Hill 1998, Leon & Bjorndal 2002), thereby maintaining reef biodiversity. While this narrow dietary range in itself may confer some disadvantage in coping with a future changing climate, it is not known how sponges may react to climate change effects. Some larger hawksbill turtles may forage deep in the 'sponge belt' (at 80 to 120 m depth, Ghiold et al. 1994, Blumenthal et al. 2008), which may be buffered from climate fluctuations. Equally important may be the effect of coral bleaching (Hoegh-Guldberg 1999, Vincent 2004, Barton & Casey 2005, Gardner et al. 2005, Mora 2007), which can alter reef competition dynamics to a stable state dominated by macroalgae (Hughes 1994, Mumby et al. 2007). The relative abundance of sponges under these alternate stable states, however, is not well understood, but the possibility remains that an increase in sponge abundance could result, which may be beneficial for hawksbill turtles.

Increases in hawksbill nesting numbers in some areas (Garduno-Andrade et al. 1999, Richardson et al. 2006, Beggs et al. 2007, Marcovaldi et al. 2007) despite concerns related to reef health (Gardner et al. 2005) could, in part, be reflective of increased forage availability and warrants further investigation. In addition, alterations in the phenology of plankton abundance (Beaugrand et al. 2002) could potentially disrupt trophic relationships for filter feeding species, such as sponges. Further, ocean acidification (Hall Spencer et al. 2008) could reduce the ability of reefs to calcify and grow (Hoegh-Guldberg et al. 2007), which may further compromise the competitive ability of corals and have effects on reef dynamics. The dietary breadth of hawksbill turtles is as yet understudied.

Omnivorous turtles

For the majority of loggerhead, Kemp's ridley, olive ridley and flatback *Natator depressus* turtle populations that have been studied in coastal waters, known prey species consist of a variety of benthic dwelling invertebrates (Bjorndal 1997). These omnivorous turtles likely consume a wider variety of prey types than either green or hawksbill turtles (Bjorndal 1997). Although profound changes to benthic communities, including trophic uncoupling, are likely under warmer climate conditions (Sims et al. 2001, Schiel et al. 2004, Perry et al. 2005), omnivorous species are probably less likely to suffer prey shortage than species with narrow or specific diets. This may already be evident in the seasonality and numbers of turtles nesting annually at key sites; Broderick et al. (2001b) showed that inter-annual variability in nesting numbers was greater for herbivorous green turtles than omnivorous loggerheads. However, Chaloupka et al. (2008) showed that, for the northwestern Pacific, there were lower numbers of nesting loggerhead turtles when the mean annual sea surface temperatures in the core foraging ground in the preceding year were higher.

Research priorities and knowledge gaps

Overall, climate change could supersede current documented threats posed to marine turtle populations (e.g. bycatch in fisheries: Lewison et al. 2004; habitat destruction: Myers & Ottensmeyer 2005; pollution: Derraik 2002). Longitudinal data, describing nesting and foraging behaviour, exist for various species and should be integrated with climate change information to increase our understanding of the likely effects of climate change. In particular, we suggest 4 key research areas that should be addressed:

(1) How will climate change affect the ecology of key habitats on which turtles are thought to depend (e.g. sea grass pastures for green turtles, coral reef systems for hawksbill turtles)? How will these changes affect population dynamics of marine turtles?

(2) What is the potential for marine turtles to mitigate the effects of increasing air and sea temperatures and cope with loss of current nesting beaches by nesting at alternative, but suitable sites? What other behaviours could be adapted within the time scale of individual life spans?

(3) What is the current primary sex ratio of females to males from which to measure future, climate-induced changes, what are secondary sex ratios and how many males are necessary to maintain a fertile and productive population (and to what extent can manipulation of sex ratios produce successful results — Girondot et al. 1998)? What degree of plasticity for adaptation exists within the physiological mechanism of temperature-sensitive sex determination?

(4) How will climate change affect turtles at sea in terms of their distribution (range shifts), behaviour (phenology) and dietary breadth? How will this differ for turtle species and what levels of potential resilience might this confer?

An increased understanding of these ecological effects of climate change on marine turtles would inform conservation and management practices and may be key in supporting mitigation work (e.g. protection and preservation of key nesting or feeding sites; Brooke 2008, Robinson et al. 2009). Meanwhile, conservation strategies at turtle rookeries should focus on the managed retreat and preservation of coastlines used by marine turtles, as well as the particular protection of nesting beaches thought to produce male hatchlings. Increased impacts on marine turtles from climate change in the future may require more active management measures, such as creating cooler egg incubation temperatures (e.g. by sprinkling water on incubating nests, Naro-Maciel et al. 1999), actively relocating clutches to cooler beaches (Shaver 2005), and completely reducing all other anthropogenic threats (Lutcavage et al. 1997).

CONCLUSION

The 7 extant species of marine turtle have survived paleo-climatic regimes including dramatic temperature fluctuations (Hamann et al. 2007), but the mechanisms and speed with which they have coped in the past is not known. It is likely that many current nesting beaches, migratory routes and foraging grounds are radically different to even 10 000 yr ago (FitzSimmons et al. 1999, Hamann et al. 2007). However, future climate change is anticipated to occur at unprecedented rates and the resilience with which marine turtles may be able to cope with the predicted change is uncertain. Ultimately, if turtles cannot adapt to the effects of climate change through combination of physiological and behavioural mechanisms, they could face local to widespread extirpation without zealous management. Turtles migrate and forage over huge spatial scales, which may also confer greater resilience and adaptive capacity to the negative effects of climate change. Despite the small number of marine turtle species, their life history is challenging to study. Consequently, supporting data are few with which to predict the likely results of future changing climate with any confidence. Longitudinal data sets describing marine turtle distribution, nesting (including all reproductive parameters addressed in this review), and foraging should be integrated across populations with increasingly reliable empirical and modelled climate information to work towards assessments of adaptive capacity and resilience of marine turtles to climate change (Williams et al. 2008).

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