Investigating the potential impacts of climate change on a marine turtle population

L. A. HAWKES*†, A. C. BRODERICK*, M. H. GODFREY‡ and B. J. GODLEY*

*Marine Turtle Research Group, Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn TR10 9EZ, UK, †Bald Head Island Conservancy, PO Box 3109, 7000 Federal Road, Bald Head Island, NC 28461-7000, USA, ‡North Carolina Wildlife Resources Commission, 1507 Ann Street, Beaufort, NC 28516, USA

Abstract

Recent increases in global temperatures have affected the phenology and survival of many species of plants and animals. We investigated a case study of the effects of potential climate change on a thermally sensitive species, the loggerhead sea turtle, at a breeding location at the northerly extent of the range of regular nesting in the United States. In addition to the physical limits imposed by temperature on this ectothermic species, sea turtle primary sex ratio is determined by the temperature experienced by eggs during the middle third of incubation. We recorded sand temperatures and used historical air temperatures (ATs) at Bald Head Island, NC, to examine past and predict future sex ratios under scenarios of warming. There were no significant temporal trends in primary sex ratio evident in recent years and estimated mean annual sex ratio was 58% female. Similarly, there were no temporal trends in phenology but earlier nesting and longer nesting seasons were correlated with warmer sea surface temperature. We modelled the effects of incremental increases in mean AT of up to 7.5 °C, the maximum predicted increase under modelled scenarios, which would lead to 100% female hatchling production and lethally high incubation temperatures, causing reduction in hatchling production. Populations of turtles in more southern parts of the United States are currently highly female biased and are likely to become ultra-biased with as little as 1 °C of warming and experience extreme levels of mortality if warming exceeds 3 °C. The lack of a demonstrable increase in AT in North Carolina in recent decades coupled with primary sex ratios that are not highly biased means that the male offspring from North Carolina could play an increasingly important role in the future viability of the loggerhead turtle in the Western Atlantic.

Keywords: Caretta caretta, climate change, loggerhead turtle, temperature dependant sex determination, warming

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Introduction

Global temperatures have warmed by approximately 0.6 °C in the last century at a rate that has been unprecedented in the last 1000 years [mean air and sea surface; Intergovernmental Panel on Climate Change (IPCC), 2001; Levitus *et al.*, 2001; Brohan *et al.*, 2006]. Modelled projections for climate change in the next 100 years predict further accelerated levels of warming between 0.3 and 7.5 °C for North America (IPCC, 2001; Zwiers, 2002; low and high emissions scenarios).

Correspondence: Dr Brendan J. Godley, tel. +44 (1326) 371861, fax +44 (1326) 371859, e-mail: bgodley@seaturtle.org

However, this future climate change is expected to be heterogeneous, and not all areas will experience warming or similar rates of change in temperature. Therefore, biodiversity conservation strategies must increasingly look to the future and plan for potential outcomes over a range of possible changes in global, regional and local climate.

There is now a sizeable body of literature documenting advances in the annual phenology (timing of seasonal activities) of many animal and plant species in concert with observed climate change (see review in Walther *et al.*, 2002). Most commonly, spring events occur earlier (e.g. arrival at breeding grounds), reproductive seasons end earlier (Pike *et al.*, 2006) but there

have also been records of later onset of autumnal events (e.g. delayed migration). Eighty-seven percent of species (from plants to vertebrates) reviewed by Parmesan & Yohe (2003) that exhibited shifts in phenology did so highly significantly in accord with climate change. For example, first plant flowering, tree budburst, arrival of migrant butterflies and birds, and timing of bird nesting have all occurred earlier with increasing spring air temperatures (ATs) (see review in Parmesan & Yohe, 2003). Arrival and departure dates of bird species in breeding grounds are often well recorded due to their visible nature and public appeal, and such dates have advanced for many short and medium distance migrants (Butler, 2003; Lehikoinen *et al.*, 2004; Mills, 2005). Additionally, larger clutch sizes and faster offspring development have been documented in some European and North American bird species (Järvinen, 1989; McCleery & Perrins, 1998; Visser *et al.*, 1998; Bergman, 1999; Brown *et al.*, 1999; Winkler *et al.*, 2002). In the marine environment, variations in temperatures directly drive abundance and distribution of many organisms. Seasonal peaks in copepod and zooplankton abundance have occurred up to 11 weeks earlier in response to increasing sea surface temperatures (SSTs; Greve *et al.*, 2001), while migratory fish species have been moving to spring spawning grounds earlier (Carscadden *et al.*, 1997; Sims *et al.*, 2004).

In temperate zones, where cold winter temperatures often exceed physiological tolerance thresholds, many animals adapt by moving seasonally to more tolerable habitats to avoid stress or death. However, if temperatures were to increase with climate change, isotherms could shift poleward (Hughes, 2000), moving tolerable habitats, and therefore species distributions, towards higher latitudes (Shine *et al.*, 2002). Such range expansions have been recorded for many plant and animal species (see reviews in Walther *et al.*, 2002; Hickling *et al.*, 2006), with butterfly species, for example, exhibiting particularly significant range shifts to the order of several hundred kilometres north (Parmesan *et al.*, 1999; Davies *et al.*, 2006).

In addition to effects on phenology and distribution, climate change may have more direct impacts on thermally sensitive organisms (Walther *et al.*, 2002). In particular, ectotherms are sensitive to thermally available conditions that directly affect their performance, survival and reproduction. Many reptile species exhibit temperature-dependant sexual determination (TSD) where primary sex ratio is influenced by the temperature experienced by eggs during incubation. Even slight changes (∼1 °C) to incubation temperatures during this period may radically alter offspring sex ratios of TSD species (Janzen, 1994). For populations of species with TSD that have already been shown to produce highly skewed primary sex ratios, climate change could further skew production of only one sex, for example, if no males are produced, females could lay unfertilized clutches, annual cohorts of hatchlings would be lost and could lead towards local extinctions.

In marine turtles, sex is determined by temperature in the middle third of incubation with female offspring produced at higher temperatures and males at lower temperatures within a thermal tolerance range of 25–35 °C (Ackerman, 1997). A mixture of sexes is produced within the threshold range of temperatures (TRT, approximately 4 °C wide for the loggerhead sea turtle, *Caretta caretta*; Yntema & Mrosovsky, 1979) and 50% of either sex at the 'pivotal temperature' (around 29.0 °C, Mrosovsky, 1988). The loggerhead sea turtle is a species with TSD, mostly nesting on oceanic beaches outside the tropics, producing predominantly female hatchlings at most sites studied (Mrosovsky & Provancha, 1989, 1992; Mrosovsky, 1994; Marcovaldi *et al.*, 1997; Hanson *et al.*, 1998; Godley *et al.*, 2001a, b; Öz *et al.*, 2004) and is the most studied marine turtle species for TSD. In North America, loggerhead turtles are found nesting from southern Florida to southern Virginia. At the northern limit of the nesting range, where sand temperatures are cooler, a greater proportion of male offspring are thought to be produced in comparison with the highly female-biased sex ratios recorded in Florida (Mrosovsky *et al.*, 1984; Mrosovsky & Provancha, 1992; Heppell *et al.*, 2003).

Under future scenarios of climate warming, and given the conservation concern regarding this species, it is important to widen our understanding of the potential effects of temperature increases on sea turtle populations and their potential to cope with such changes. Here, we review 26 years (1980–2005) of detailed data from a northerly nesting site for loggerhead turtles. In concert with six decades of local climate data we predict primary sex ratios, describe climate change patterns and investigate whether any shifts in phenology have occurred or are possible at this site. In addition, we estimate recent historical patterns in primary sex ratio and model possible future outcomes in the face of warming expected for turtles nesting at the northern portion, as well as further south, of the range.

Methods

Nesting data between May and October were recorded from 1980 to 2005 by a nightly sea turtle monitoring programme at Bald Head Island, NC, USA (33°50′N, 77°57′W, Fig. 1; see Hawkes *et al.*, 2005). Incubation duration was recorded as the number of days between egg laying and hatchling emergence at the sand surface. The duration of the nesting season (the number of days
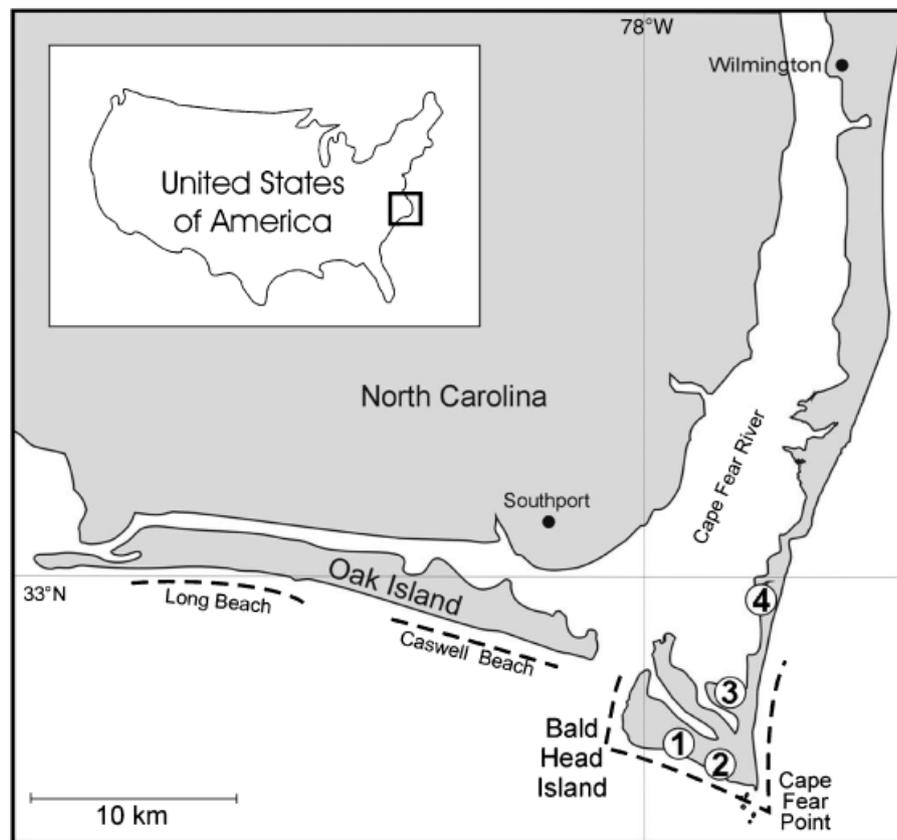
Fig. 1 Map of Bald Head Island, NC, USA, showing the location of the Southport weather station and location of control sites for temperature data loggers (numbered circles 1–4).

between the first and last egg laying events) was calculated for each year as were the median and inter-quartile dates of nesting for each season.

Local AT data were obtained from the State Climate Office of North Carolina (http://www.nc-climate.ncsu.edu/services/request.html) for Southport, North Carolina (6.4 km northwest of study site, Fig. 1), from January 1940 to December 2005. Station instruments are maintained by the US National Weather Service and quality controlled by the US National Climatic Data Centre. Mean weekly SST data were sampled from the Met Office Hadley Centre's sea ice temperature and SST data sets (HadISST1) for 34.057°N and −77.189°W between 1980 and 2005. HadISST1 replaces the global sea ice and SST (GISST) data sets and contains *in situ* monthly sea surface observations and satellite derived estimates at the sea surface on a 1° latitude–longitude grid.

As pivotal temperature is a relatively conservative characteristic in sea turtles (Freedberg & Wade, 2001), typically varying <1.8 °C around 29.2 °C for the logger-head sea turtle (Ackerman, 1997), we used published models for loggerhead turtles from this population

relating incubation temperature to proportion of female hatchlings produced (Mrosovsky, 1988) to estimate past and present hatchling sex ratios. As we were not able to record individual nest temperatures for the study period we modelled, nest temperatures as follows: sand temperatures were recorded during the 2003 nesting season using four calibrated temperature data loggers (Gemini data loggers, Chichester, UK) buried at 45 cm depth (mean nest depth for Bald Head Island, L. A. Hawkes, unpublished data) at four control locations on the beach (Fig. 1) and hourly temperatures were collected from 5 July until 14 November 2003. We examined the relationship between mean daily sand temperature and mean daily AT collected at Southport for 2003 (highly significantly related: sand temperature $= 0.72$ AT $+ 9.60$, $R^2 = 0.80$; regression $F_{1,131} = 513.37$, $P < 0.001$) and used this to model sand temperatures for the study period (1980–2005). Metabolic heating of the clutch during incubation must be considered (Broderick *et al.*, 2001) and therefore we added an estimate of metabolic heating of loggerhead turtle eggs from Florida, USA in the middle third period of incubation (Hanson *et al.*, 1998; 1.1 °C) to predict nest

temperatures in the middle third of incubation for the study period (1980–2005).

Further, in order to heuristically model the possible effects of climate change on primary sex ratios, we added the resulting increases in sand temperature from predicted increases in AT of 1–7.5 °C (the predicted range of maximum rise in global temperature by 2100; Houghton, 2001) to the estimated nest temperatures 1980–2005 and modelled the resulting primary sex ratios. We repeated the same process for half-month average sand temperature recorded for a Florida nesting beach (1986–1990, Cape Canaveral Air Force Station; Mrosovsky & Provancha, 1992), using the deepest sand temperature data recorded (60 cm) on the low shore, to parsimoniously generate the minimum plausible temperatures and least female biased estimates.

Results

Long-term mean ATs at Southport, NC (1940–2005), have decreased significantly over the 64 years (by approximately 1.7 °C, regression: $F_{1,62} = 13.88$, $P < 0.01$, $R^2 = 0.18$, Fig. 2a). The same significant decrease is evident if temperatures during the nesting season of each year are sampled (approximately 1.9 °C decrease, 4 May to 15 November 1940–2005, regression: $F_{1,63} = 14.79$, $P < 0.01$, $R^2 = 0.19$, Fig. 2b). During the study period (1980–2005) annual SST was significantly related to annual AT (Pearsons $r = 0.452$, $n = 26$, AT = 1.3 SST °C −13.5, $P < 0.05$). Although SST warmed significantly (regression: annual $F_{1,25} = 12.31$, $P < 0.01$, $R^2 = 0.34$, seasonal $F_{1,25} = 22.89$, $P < 0.01$, $R^2 = 0.49$, Fig.

2c and d), AT did not (regression: annual $F_{1,25} = 1.47$, $P > 0.05$, $R^2 = 0.06$, seasonal $F_{1,25} = 2.05$, $P > 0.05$, $R^2 = 0.08$) and we highlight this as a caveat of this type of study. There were also no trends in ATs in the month preceding the nesting season (April regression: $F_{1,24} = 0.56$, $P > 0.05$, $R^2 = 0.02$).

Given the predicted climate change by the IPCC (2001), we investigated metrics of phenology in relation to inter annual variability in environmental conditions to see whether changes in nesting patterns were driven by climate. Because sea turtles experience ambient temperature through the water rather than air, we investigated relationships with SSTs. In years with warmer spring (April and May) SSTs, nesting started significantly earlier (mean April SST vs. first nest regression: $F_{1,22} = 4.72$, $P < 0.05$, first nest = −3.9 SST °C + 223.5, $R^2 = 0.18$, 12 days earlier per 1 °C and mean May SST vs. first nest regression: $F_{1,22} = 8.20$, $P < 0.01$, first nest = −5.2 SST °C + 265.2, $R^2 = 0.28$, 18.3 days earlier per 1 °C, Fig. 3). This increased the duration of the nesting season significantly in warmer years (April regression $F_{1,22} = 7.15$ $P < 0.05$, duration = 4.8 SST °C–14.5, $R^2 = 0.25$, 18.3 days longer per 1 °C, May regression $F_{1,22} = 3.47$, $P < 0.05$, duration = 5.1 SST °C–34.8, $R^2 = 0.14$, 36 days longer per 1 °C) but the date of last nest laid was not significantly related to any metric of SST. Although we have demonstrated the link among environment and phenology and a significant increase in SSTs over the study period, there was no significant temporal trend in the date of first nest laid or duration of the nesting season (first nest regression $F_{1,22} = 2.26$, $P > 0.05$, $R^2 = 0.1$; duration regression $F_{1,22} = 0.36$,
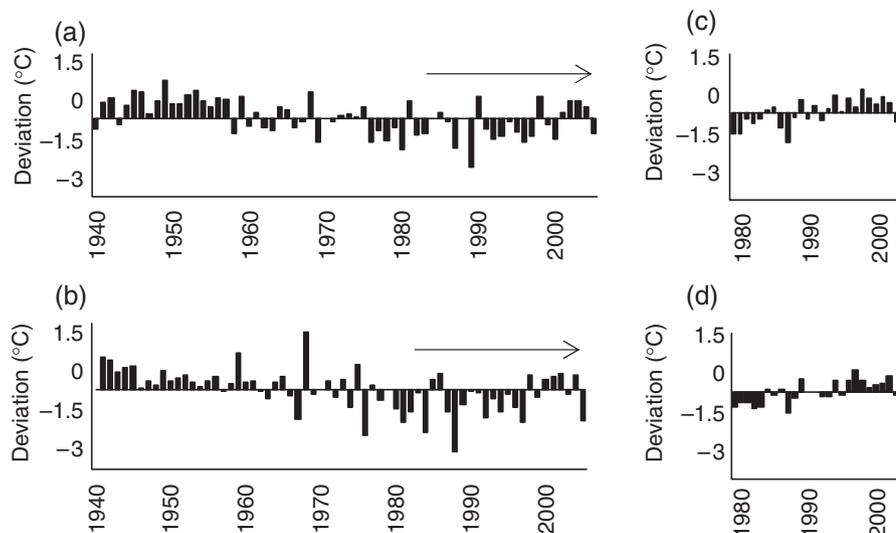

Fig. 2 Long-term trends in temperature: Annual deviation from (a) long-term mean annual air temperature (17.28 °C) and (b) long-term mean seasonal air temperature (May–November each year; 22.70 °C) recorded at Southport, NC, USA, between 1940 and 2005 and (c) long-term mean annual sea surface temperature (SST; 23.23 °C) and (d) long-term mean seasonal SST (25.93 °C) recorded at Cape Fear, NC between 1980 and 2005. The study period (1980–2005) is indicated in parts (a) and (b) by the horizontal arrow.
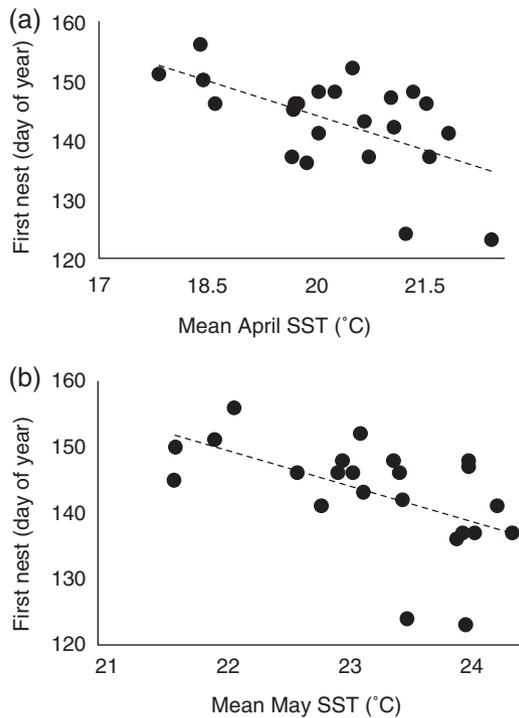
Fig. 3 Relationship between first nest laid each year and mean a) April sea surface temperature (SST) and (b) May SST at Bald Head Island 1983–2005. Data for 1980–1982 have been excluded due to incomplete records in nesting metrics.

$P > 0.05$, $R^2 = 0.04$). None of the other phenological attributes (date of latest hatchling emergence, lower and upper quartiles and median egg-laying date) were significantly related to air or SST over the temporal period studied.

The estimated mean sex ratio for the study period (calculated from modelled nest temperatures) (Fig. 4) was 58% female hatchlings. There was no significant temporal change in annual sex ratio production estimated using modelled incubation temperature (1980–2005, regression: $F_{1,23} = 1.12$, $P > 0.05$, $R^2 = 0.05$). With the predicted rise in future AT, nests will begin to incubate at sand temperatures above the pivotal temperature (29.2 °C; Mrosovsky, 1988) for loggerheads, producing more female offspring. Simple heuristic simulation of likely hatchling sex ratios under these conditions (Fig. 5a and b) show that over 80% female hatchling production is predicted to occur in this part of North Carolina with 2 °C increase in AT. Further south, at Cape Canaveral, Florida, total feminization would occur with 2 °C of warming in AT and after 3 °C clutches would begin to incubate at temperatures above the lethal limit (35 °C; Ackerman, 1997). However, such clutch death is not likely to begin until 5 °C of warming in AT has occurred in North Carolina. With the maximum 7.5 °C of predicted warming in AT, more than
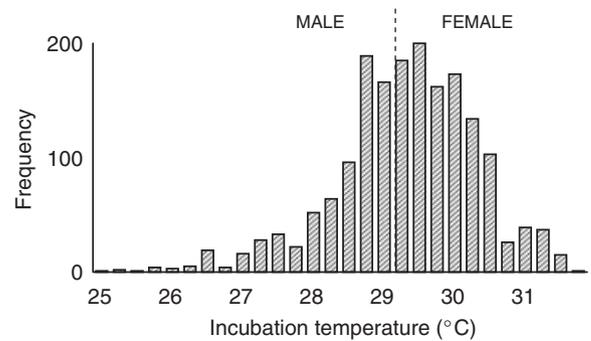

Fig. 4 Frequency histogram of modelled mean temperatures experienced by nests at Bald Head Island (1980–2005) during the middle third of incubation, including an estimate of metabolic heating. Pivotal incubation temperature (29.2 °C) is shown as vertical dashed line and with male biased and female biased incubation temperatures indicated.
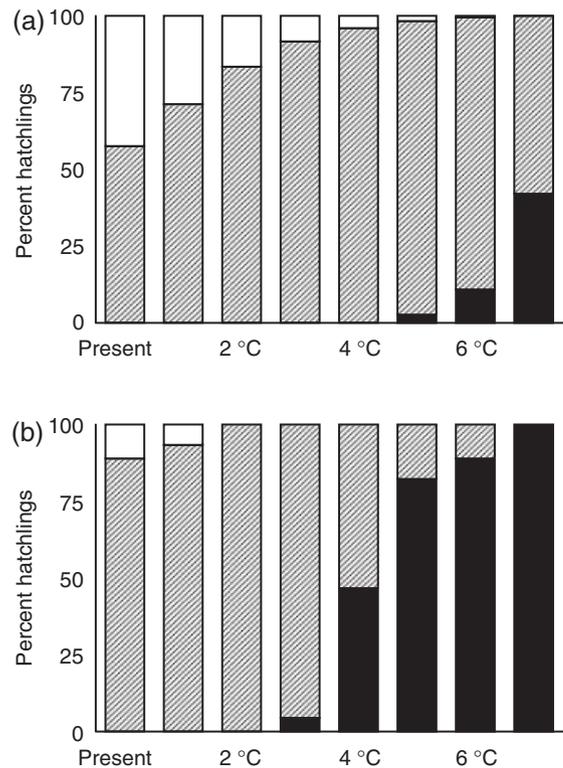

Fig. 5 Ratios of resultant sex of hatchlings at present and under varying predictions of future climate change for (a) Bald Head Island, NC and (b) Cape Canaveral, Florida, 1986–1990 showing proportion female (grey) and proportion male (white). Black signifies the expected mortality resulting from incubation over the upper tolerance limit (35 °C) in response to increases in air temperature between 1 and 7.5 °C, where the final bar shows 7.5 °C of warming.

40% of clutches at our study site and 100% of clutches at Cape Canaveral, will incubate at temperatures above the lethal limit, suggesting that nest incubation would
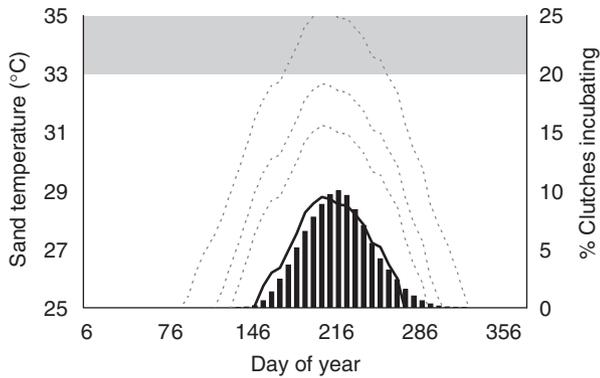
Fig. 6 Thermal niche available for incubation, showing current (solid line) and modelled (broken lines) sand temperatures (primary *y*-axis) resulting from increases of 2, 4 and 7.5 °C in air temperature (sand temperature = 0.7154 air temperature +9.6023). Black bars show proportion of clutches incubating in each week of the season (1980–2005, secondary *y*-axis). Shaded area represents the upper thermal limit (UTL) for incubation (33–35 °C; Ackerman, 1997).

no longer be viable at some Florida beaches during the current seasonal window of nesting. However, with climate warming, the actual thermal niche available to turtles for nesting will become wider (as a very simplistic example, with a mean increase of 7.5 °C AT, the worst case scenario of warming, the suitable thermal conditions for incubation almost doubles, Fig. 6), providing sea turtles the opportunity to alter temporal nesting distribution to earlier and/or later months to mitigate increased incubation temperatures.

Discussion

The climate system of North Carolina is one of the most complex in North America (Boyles & Raman, 2003). The proximity of the Gulf Stream to coastal North Carolina acts as an ameliorating influence to climatic variations and combines with local topography to produce a highly variable regional climate that can differ substantially to climate patterns observed elsewhere on the south eastern coast of the United States, although 10 of the last 12 years have been above the long-term average. North Carolina has not yet experienced pronounced warming and it may be that the study area is less likely to experience the significant warming expected elsewhere in the Northern Hemisphere by the IPCC. Boyles & Raman (2003) found that average ATs were warmest during a period between 1949 and 1958 and decreased slightly after. This is consistent with the gradual cooling trend we observed in AT at Southport since 1940.

Our results, based on 26 years of data, suggest that loggerhead nests in North Carolina currently produce

proportionally more males (42% males) than nests laid in Florida (typically <10% males; Mrosovsky & Provancha, 1989). These results are in accord with previous studies of sex ratios from the northern nesting sites in the United States (Mrosovsky *et al.*, 1984; Webster & Gouveia, 1989). This is one of only a few studied loggerhead rookeries that are not predominantly female producing, others located in Espirito Santo, Brazil (Marcovaldi *et al.*, 1997; Baptistotte *et al.*, 1999) and Heron Island, Australia (Limpus *et al.*, 1983). Taken in concert with the environmental data sampled in this study, it appears that the primary sex ratio in North Carolina is not likely to become radically female biased in future years unless warming is severe.

However, given that Florida could likely experience warming (IPCC, 2001) and is not buffered by oceanic features as in North Carolina (Boyles & Raman, 2003), there is a real possibility of further skewing or even complete feminization of the primary sex ratios in Florida, which holds the vast majority of nesting in the United States (Shoop & Kenney, 1992). The results of our simple modelling show that 2 °C increase in ATs (within the minimum expected warming scenario of the IPCC, 2001) is sufficient to result in total feminization and with 3 °C of warming, many nests in southern Florida would begin to experience incubation temperatures above lethal limits. Therefore, in addition to extreme primary sex ratios, decreased or zero hatch success is worthy of consideration for all nesting populations with current highly skewed sex ratios (e.g. Mediterranean: Broderick *et al.*, 2000; Godley *et al.*, 2001a, b; Öz *et al.*, 2004; Florida: Mrosovsky & Provancha, 1992; Mrosovsky, 1994; Hanson *et al.*, 1998; Brazil: Marcovaldi *et al.*, 1997). However, it should be noted that primary sex ratios may not reflect those of the adult population, although in-water studies suggest that female biases are maintained in juvenile and sub-adult loggerhead turtles (Wibbels *et al.*, 1987, 1991; Owens, 1997).

If warming occurs, turtles from northern and southern beaches could prevent extremely skewed sex ratios by (a) adapting *in situ* by adjusting their pivotal temperature, (b) altering nesting spatially (e.g. latitude, height on the beach, depth or substrate type, Hays *et al.*, 2001) or (c) altering nesting temporally (e.g. nesting in cooler periods at the beginning and end of the season in order to exploit incubation environments likely to produce more males; Mrosovsky *et al.*, 1984; Naro-Maciel *et al.*, 1999; Hays *et al.*, 2003; Pike *et al.*, 2006). Pivotal temperature is a relatively conservative TSD character in sea turtles (Mrosovsky, 1988; Freedberg & Wade, 2001; Godfrey & Mrosovsky, 2006) with little variation observed across the wide-ranging geographic locations and latitudes over which it has been

studied (e.g. Wibbels, 2003; Godfrey & Mrosovsky, 2006; but see studies in fresh water turtles e.g. Ewert et al., 2005). We, therefore, consider it unlikely that turtles would be able to adapt pivotal temperature in the short-term (less than several hundred years; cf. Morjan, 2003; Glen & Mrosovsky, 2004; Nelson et al., 2004), although plasticity in the transitional range of temperatures surrounding the pivotal temperature could potentially be adaptive (Girondot, 1999).

The ability to adapt spatially in response to thermally variable habitat occurs in some reptile species where females have been shown to consistently select nest microenvironments with similar thermal conditions, even in different locations (e.g. the painted turtle, Chrysemys picta, Janzen & Morjan, 2001; and the hawksbill turtle, Eretmochelys imbricata, Kamel & Mrosovsky, 2005). For example, at warmer sites, female painted turtles seek more shaded nest locations, and can thus manipulate the thermal habitat, and potentially the sex ratio, of their offspring (but see Morjan, 2003). However, as loggerhead turtles usually maintain a degree of nest site fidelity, returning to nest within 0–5 km of previous nests both within and between nesting seasons (Miller et al., 2003) and climate warming would be expected to occur over a large (regional) scale, the different scales over which change could occur could prevent adaptation by turtles shifting nesting location en masse. Loggerhead turtles could, however, alter the specific nest environment by nesting, as Hawksbill turtles do, in cooler microclimates, such as in areas shaded by vegetation (Kamel & Mrosovsky, 2006) or closer to the sea, (Foley et al., 2006), and natal homing of newly recruiting nesting turtles could contain a margin of geographical error that could mitigate philopatry that cannot be ruled out at this point. In addition, as more females are produced in the larger southern subpopulation, the frequency of nesting should be expected to increase in the south relative to the north due to philopatry (Morjan, 2003).

Loggerhead turtles at Bald Head Island currently nest throughout the available temporal window that provides a tolerable environment for nests (Fig. 6) but the actual niche available for turtle nesting under future climate scenarios could be very different. Phenological correlations in this study and others (Mrosovsky et al., 1984; Weishampel et al., 2004; Pike et al., 2006) suggest that either changing temperatures in the future could drive adaptive phenological change to maintain current thermal conditions in nests or that turtles may adapt the temporal spread of nesting to suit the available thermal niche. However, it should be noted that Pike et al. (2006) demonstrated that earlier seasons can also end earlier, probably because sea turtles are capital breeders (Bonnet et al., 1998), meaning that the fundamental and realised thermal niches for nesting may not necessarily be the same. Because the distribution of nesting has a low variance (Fig. 6), our model shows that turtles would have to alter the temporal distribution of nesting very little (by only a few days) to adapt to 1 °C of warming, and by up to a week for 3 °C of warming (worst expected under lower case emissions scenario; IPCC, 2001). This strategy could, therefore, offer the most likely adaptive mechanism available to marine turtles in response to climate change.

However, relying on accumulated energy reserves for breeding, they typically make long migratory journeys to get from foraging to breeding areas. Turtles, therefore, must not only have stored energy from the foraging grounds (which may be some 800 km away, L. A. Hawkes et al., in press) for reproduction before the nesting season, but environmental conditions at the foraging grounds likely influence vitellogenesis and may therefore constrain the timing of migration and breeding, thus complicating phenological adaptation. Although we have described earlier nesting in years with warmer SST, this may reflect more rapid egg production following mating as oogenesis is likely driven by prevailing environmental temperature (Hays et al., 2002; Hamann et al., 2003), and females are thought to migrate to the nesting beach ca. 1 month before beginning laying (Godley et al., 2002). Because capital breeding constrains reproductive output (loggerhead turtles normally lay two to four clutches per nesting season, maximum seven clutches; Schroeder et al., 2003), even if turtles started to nest earlier in the season, later clutches would still incubate in the period of very high temperatures (above thermal tolerance with maximum levels of warming) and turtles are unlikely to still be nesting in the later, cooler part of the season (Pike et al., 2006).

Irrespective, the fact that many loggerhead sea turtle populations that already exhibit heavily female-biased primary sex ratios may be negatively impacted by climate warming merits further investigation. The potentially disproportionate importance of male producing beaches (e.g. Mrosovsky et al., 1984; Baptistotte et al., 1999) that can interbreed with female producing rookeries (Bowen et al., 2005) needs to be carefully examined, particularly nesting beaches such as Bald Head Island that not only exhibit more balanced sex ratios but appear less likely to be affected by climate change. Emphasis should be placed on maintaining suitable nesting habitat for sea turtles in North Carolina and other regions that are important for male production. Anthropogenic activities likely to alter the thermal properties of naturally available nesting habitat should be given careful consideration. In particular, beach

'nourishment' programs (which are increasingly widespread) that deposit sand on eroded beaches along the oceanic coastline of the United States to protect beachfront property (Crain *et al.*, 1995; Milton *et al.*, 1997; Rumbold *et al.*, 2001; Peterson & Bishop, 2005) often use sand that differs radically from natural sands and are often darker in colour. Nests in darker sand incubate at higher temperatures producing more females (Hays *et al.*, 2001). Moreover, although turtles have evolved with continuously eroding and accreting oceanic beaches, the combination of renourishment programs, along with other anthropogenic threats such as beachfront development, and predicted sea level rise (from 0.11 to 0.43 mm yr^{-1}; IPCC, 2001) could cause a 'coastal squeeze', where landward movement of beaches is prevented by physical (anthropogenic) barriers such as beachfront development (Fish *et al.*, 2005). In addition, increased storm surges and coastal land loss will threaten beaches backed by salt marshes, such as those making up the majority of the outer banks of North Carolina.

The sex ratios generated in this model should be tempered with elements of caution; actual primary sex ratios from sea turtle nesting beaches can be influenced by numerous factors including (but not limited to) humidity, rainfall, tidal inundation, the total number of eggs incubating, egg position in nest (Carthy *et al.*, 2003), nest relocation, nest substrate, hatching success, egg loss and intra-seasonal variation in temperatures and were not controlled for in the model. Rather, the results of this study shed light on potential outcomes if scenarios envisaged under climate warming do occur. Note that climate change (and sea level rise) is not expected to be geographically uniform (IPCC, 2001) and it is likely that some areas may not experience the profound warming predicted.

Even though climate change models are subject to controversy and the sex ratios generated in this study are based on a simplistic model, there are some important take home messages from this study. That there are nesting beaches that are both male producing and somewhat shielded from future climate change is noteworthy and the thermal conditions of these beaches should be protected from anthropogenic activities likely to alter the natural state of the incubation environment. The highly female-skewed southern Florida population may, under worst case scenarios, reach a 100% female asymptote, at which point males from further north in the population may be essential for the continued production of hatchlings from southern beaches. Finally, with a few degrees of warming, large proportions of the clutches of the largest loggerhead nesting population in the world may begin to experience high levels of thermal mortality.

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