

Predicting the impacts of climate change on a globally distributed species: the case of the loggerhead turtle

M. J. Witt¹, L. A. Hawkes², M. H. Godfrey³, B. J. Godley¹ and A. C. Broderick^{1,*}

¹University of Exeter, Centre for Ecology and Conservation, School of Biosciences, Tremough Campus, Penryn, Cornwall TR10 9EZ, UK, ²Bangor University, School of Biological Sciences, Brambell Laboratories E30, Deiniol Road, Bangor, Gwynedd LL57 2UW, UK and ³North Carolina Wildlife Resources Commission, 1507 Ann Street, Beaufort, NC, USA

*Author for correspondence (a.c.broderick@ex.ac.uk)

Accepted 27 November 2009

Summary

Marine turtles utilise terrestrial and marine habitats and several aspects of their life history are tied to environmental features that are altering due to rapid climate change. We overview the likely impacts of climate change on the biology of these species, which are likely centred upon the thermal ecology of this taxonomic group. Then, focusing in detail on three decades of research on the loggerhead turtle (*Caretta caretta* L.), we describe how much progress has been made to date and how future experimental and ecological focus should be directed. Key questions include: what are the current hatchling sex ratios from which to measure future climate-induced changes? What are wild adult sex ratios and how many males are necessary to maintain a fertile and productive population? How will climate change affect turtles in terms of their distribution?

Key words: climate change, marine turtles, predictive modelling.

Introduction A changing world

The Earth's climate is warming: increases in average air and ocean temperatures, melting of land and sea ice, as well as rising sea levels have been observed and are likely caused by increases in anthropogenic atmospheric emissions (Hansen et al., 2006; IPCC, 2007). The observed changes in the climate since 1996 have actually been greater than anticipated (Rahmstorf et al., 2007), leading to concern regarding the future environment. Global average surface temperatures have increased by 0.8°C over the last 100 years (Hansen et al., 2006), with greater increases in temperature over the land than the sea surface (IPCC, 2007). Future surface temperature increases of 2–3°C are expected by 2100 (Hansen et al., 2006). Concurrent increases in sea level have been recorded at 1.8 mm per year over the last 42 years (IPCC, 2007) or at 3.4 mm per year per degree Celsius of warming observed (Rahmstorf, 2007). The majority of sea level rise is contributed by thermal expansion (57%), with another significant contribution (28%) by surface ice melting (IPCC, 2007), and may also be increasing faster than previously predicted (Rahmstorf, 2007). In addition, although an overall decrease in average rainfall is predicted (IPCC, 2007), an increase in heavy rainfall is expected (Milly et al., 2002). Both genesis and tracks of storms are predicted to move poleward, and may increase in intensity in some regions (Bengtsson et al., 2006). Finally, the uptake of atmospheric CO₂ by the ocean since the industrial era has meant that ocean pH has decreased by 0.1 pH units (IPCC, 2007). A further decrease of 0.35 pH units could occur over the next 100 years.

It is recognised that climate change must be incorporated into species conservation planning (Araújo et al., 2004; Hannah et al., 2002), with spatial and temporal alterations to species ranges, in accordance with climate change patterns, observed in 84% of species investigated (Parmesan and Yohe, 2003). Indeed, species extinctions as a result of climate change have been already documented

(Pounds et al., 1999), and some authors have suggested that as much as one fifth to a third of terrestrial species could be at risk of extinction (Thomas et al., 2004). It has also become apparent that marine species are likely to be impacted (Croxall et al., 2005; MacLeod, 2009; Newson et al., 2009; Gremillet and Bioulinier, 2009) (Fuentes et al., in press), although far fewer studies have been conducted in comparison with terrestrial species.

Climate change in sea turtles

Although climate change was identified as a potential problem to sea turtles in seminal papers by Mrosovsky (Mrosovsky, 1984) and Davenport (Davenport, 1989), it is only recently that significant research effort has been expended on the field (for reviews, see Hamann et al., 2007; Hawkes et al., 2009). Although sea turtles are exposed to climate change threats both at sea and at the nesting beach, it is at the beach where the majority of research effort has been focused as it provides opportunity for more logistically feasible work. One of the primary effects of climate change to nesting beaches is sea level rise, where higher water levels will directly decrease the availability of suitable nesting sites. Recent work suggests that up to half of the current available nesting areas could be lost with predicted sea level rise (Fish et al., 2005; Fish et al., 2008; Mazaris et al., 2009), particularly at islands where no retreat options exist (Baker et al., 2006) or where anthropogenic coastal fortification causes 'coastal squeeze' (Fish et al., 2008). This coastal squeeze may indeed be exacerbated in the forthcoming decades by a growing population whose densities at the margins of the global land mass are considerably greater than the global land average (Small and Nicolls, 2003), potentially carrying fitness consequences for nesting female turtles (Pike, 2008). Even on available areas of nesting beach, incubating clutches could be at risk from sea level rise if water tables rise, effectively flooding the nest from below. Some species could be at greater risk than others, for example, green turtles (*Chelonia mydas* L.) lay deeper nests than

loggerhead turtles (*Caretta caretta*) (Hannan et al., 2007), and leatherback turtles (*Dermochelys coriacea* Vandelli) tend to nest closer to the high tide line than green turtles or loggerhead turtles nesting on the same beach (Wetterer et al., 2009; Whitmore and Dutton, 1985).

Turtles on the nesting beach are profoundly affected by temperature, such that temperature can influence nesting phenology (Hawkes et al., 2007b; Hays et al., 2002; Pike et al., 2006; Sato et al., 1998; Webster and Cook, 2001; Weishampel et al., 2004), incubation success (Ackerman, 1997; Carthy et al., 2003), incubation duration (Matsuzawa et al., 2002; Mrosovsky et al., 1999; Pike et al., 2006) and, as sex determination is by temperature, sex of offspring (Yntema and Mrosovsky, 1980). Increasing temperatures, therefore, have the potential to change current nest incubation regimes as well as skew sex ratios (Hawkes et al., 2007b) (but see Bowden et al., 2000), potentially with wider implications for the

whole population. Alternatively, increasing temperatures may open up areas that were previously inaccessible to nesting. Incubating sea turtle clutches can also be damaged or lost due to storm activity (Van Houtan and Bass, 2007), including surges, wave action and sand wash out events. The effects to the incubating nest can range from reducing hatching success to total loss of clutches on a particular beach (Snow and Snow, 2009).

The effects of climate change on turtles at large in the ocean are more challenging to study, because turtles range across entire ocean basins and are late maturing and long lived (Avisé et al., 1992; Zug et al., 2002). There is compelling evidence from multiple species to suggest that the distribution and behaviour of Chelonid sea turtles are influenced by temperature (Hawkes et al., 2007a; Sato et al., 1998). Leatherback sea turtles are probably affected to a lesser extent by thermal conditions due to gigantothermy (Frair et al., 1972; Paladino et al., 1990) and anatomical adaptations (Davenport et al.,

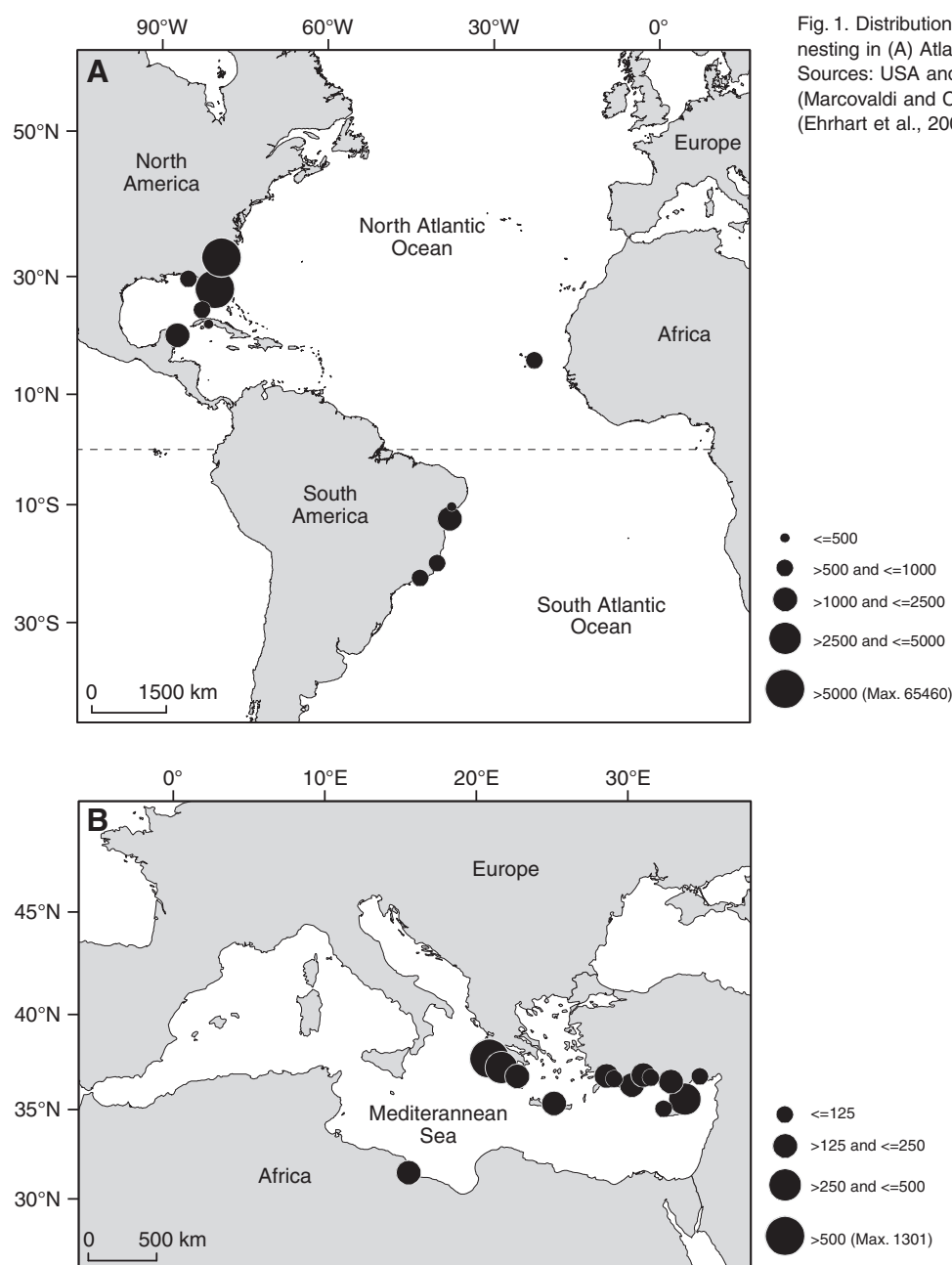


Fig. 1. Distribution and abundance of loggerhead sea turtle nesting in (A) Atlantic Ocean and (B) Mediterranean Sea. Sources: USA and Bahamas (Conant et al., 2009); Brazil (Marcovaldi and Chaloupka, 2007); other Atlantic locations (Ehrhart et al., 2003); Mediterranean (Margaritoulis et al., 2003).

2009), and range further from the equator, such as into Canadian waters (James et al., 2005) and those of the northeast Atlantic Ocean (Doyle et al., 2008; McMahon and Hays, 2006; Witt et al., 2007a). We know that ocean currents play an important role in dispersing hatchling turtles (Bolten, 2003; Lohmann and Lohmann, 2003; Witherington, 2002; Witt et al., 2007b), and that these currents may change in magnitude or direction (Rahmstorf, 1997; Stocker and Schmittner, 1997), which may influence future juvenile developmental phase durations (Hamann et al., 2003). In addition, changes to the pelagic community as a result of climate change could alter trophic dynamics (Edwards and Richardson, 2004) and juvenile growth rates and therefore further alter developmental duration (Bjorndal et al., 2000; Verity et al., 2002). For adults, changes to thermal regimes and sea surface currents could alter current adult foraging habitat as well as the location and size of home ranges and diet (Bjorndal, 1997; Davenport, 1998; Meylan, 1988; Polovina et al., 2004), which has ramifications for population breeding phenology and success.

The loggerhead sea turtle

The most intensively studied sea turtle species is the loggerhead turtle, and in this review we focus on the populations of this species within the Atlantic Ocean and the Mediterranean Sea. The loggerhead turtle nests in tropical and sub-tropical regions. The largest known rookeries are in the southeast United States of America and Republic of Cape Verde (Fig. 1A), with nesting also occurring along the Brazilian coast within the South Atlantic basin. In the Mediterranean Sea (Fig. 1B), nesting is almost exclusively restricted to the Eastern basin, with notable aggregations occurring in Cyprus, Greece and Turkey (Broderick et al., 2002; Margaritoulis et al., 2003).

All species of sea turtle demonstrate natal philopatry, returning as an adult to their natal beach regions to breed. Females typically breed every 2–3 years (Miller, 1997), with the seasonal magnitude of nesting in any one year dependent upon trophic conditions encountered by female turtles in the years preceding breeding and nesting (Broderick et al., 2001b; Chaloupka et al., 2008). Following reproductive activity, while some female loggerhead turtles move to oceanic areas (Hawkes et al., 2006), most will undertake migrations of varying distances to neritic foraging grounds (Girard et al., 2009; Godley et al., 2003; Plotkin and Spotila, 2002; Zbinden et al., 2008), demonstrating considerable levels of site fidelity (Broderick et al., 2007). During winter periods, their range appears to be thermally constrained (Hawkes et al., 2007a), and individuals apparently hibernate during the coolest months (Broderick et al., 2007; Hawkes et al., 2007a; Hochscheid et al., 2005).

Here we consider the thermal biology of loggerhead sea turtles in relation to projected climate change, highlighting the progress

that has been made and identifying the next key steps to understanding likely impacts.

Hatchling sex ratios

Temperature-dependent sex determination in sea turtles was first documented in loggerhead turtles by Yntema and Mrosovsky (Yntema and Mrosovsky, 1980), with warmer incubation temperatures producing more females and cooler temperatures producing more males. Although early work was conducted in laboratory conditions, attention moved to field studies to assess whether hatchling sex ratios were different from 1:1 as predicted by Fisher (Fisher, 1930). Initial assessments of loggerhead turtle sex ratios suggested that sex ratios vary from beach to beach and also from month to month within a nesting season (Mrosovsky et al., 1984). Further work using laboratory incubation suggested that the response of loggerhead turtle eggs to temperature was fairly conserved, at least in terms of pivotal temperature – the temperature that produces a 1:1 sex ratio (Mrosovsky and Pieau, 1991), across different populations from different latitudes in the northwest Atlantic (Mrosovsky, 1988). Subsequent studies of laboratory incubation of loggerhead turtle eggs from Brazil and Greece have also found pivotal temperatures that are relatively similar – close to 29°C (Marcovaldi et al., 1997; Mrosovsky et al., 2002). Thus, variation in sex ratios observed in the wild is thought to be driven largely by local environmental conditions, specifically egg temperatures during incubation (Godfrey and Mrosovsky, 2001).

A major constraint in the study of loggerhead turtle sex ratios has been the challenge of assigning sex. Sea turtles do not have sexually dimorphic sex chromosomes nor do they express visible external phenotypic differences between the sexes prior to adulthood. The only fully reliable method of assigning sex to hatchling loggerhead turtles has been through histological examination of the gonads (Yntema and Mrosovsky, 1980), which is labour intensive and destructive. Attempts to use dead-in-nest hatchlings for sexing are hampered by low sample sizes and a possible influence of sex-biased mortality. There have been attempts to develop other non-destructive markers of phenotypic sex, with varying degrees of success, including assessing ratios of hormone titres in the chorioallantoic fluid remaining in eggs after hatching (Gross et al., 1995) and laparoscopy of hatchlings raised in captivity for several months (Wyneken et al., 2007). Regardless of their reliability, these alternative methods of directly assigning sex present logistical challenges that would hamper studies of sex ratios on a large scale in the field.

Other researchers have pursued methods that indirectly estimate sex ratios of hatchlings, most commonly by using environmental parameters such as sand and air temperature (Hawkes et al., 2007b; Matsuzawa et al., 2002; Mrosovsky and Provancha, 1992). Some researchers have also used the incubation duration of loggerhead

Table 1. Pivotal temperatures for loggerhead sea turtles in the Atlantic Ocean and Mediterranean Sea

Location	Pivotal temperature	Latitude	Longitude	Source
Cumberland Island, GA, USA	28.5	30.86	–81.42	Mrosovsky, 1988*
Northern Cyprus	28.5	35.55	33.78	Fuller, 2008†,‡
Turkey/Cyprus	29.0	35.93	32.35	Kaska et al., 1998‡,§
Jupiter Island, FL, USA	29.2	27.07	–80.12	Mrosovsky, 1988*
Bald Head Island, NC, USA	29.2	33.84	–77.97	Mrosovsky, 1988*
Bahia, Brazil	29.2	–10.38	–37.67	Marcovaldi et al., 1997*
Kyparissia, Greece	29.3	37.25	21.66	Mrosovsky et al., 2002*

*Study used two clutches; †study used dead offspring and live offspring from Kaska et al. (Kaska et al., 1998) for Cyprus beaches only; ‡field-based; §two study clutches from one beach in Cyprus and six from four different beaches in Turkey combined to calculate pivotal temperature.

nests as an indirect measure of sex ratio, because the rate of embryonic development is linked to temperature (Godfrey and Mrosovsky, 1997; Godley et al., 2001; Marcovaldi et al., 1997). While these methods of indirectly estimating sex ratios have helped generate larger datasets (Hawkes et al., 2007a), few have been validated (but see Mrosovsky et al., 1999; Mrosovsky et al., 2009). This is especially important as most of these studies use pivotal temperature or pivotal incubation data from laboratory studies that are also based on few clutches using constant incubation temperatures. To date, there have been published pivotal temperature studies for only six different loggerhead nesting beaches in the Atlantic and Mediterranean Sea, with each pivotal value based on just two clutches. While reported pivotal temperature values from loggerhead turtles (Table 1) appear to be remarkably conserved around 29°C to date, more studies are needed to increase reliability of these values and illuminate the individual variation and capacity

for adaptation in this trait. Indeed, pivotal temperature studies of freshwater turtles using many clutches suggest that pivotal temperatures are much more variable within a particular species, due either to intrinsic differences between and/or variability of maternal contributions, e.g. hormones, in the eggs (Bowden et al., 2000; Dodd et al., 2006). The development of a non-destructive but accurate marker of phenotypic sex of hatchlings would also greatly facilitate the generation of hatchling sex ratio datasets, both directly and indirectly, although to date there has been little success in this endeavour (Wibbels, 2003).

Despite the logistical challenges of accurately assigning sex to hatchling sea turtles, loggerhead turtles have been the focus of a number of sex ratio studies, based on either direct or indirect assessments of offspring sex. Within the Atlantic Ocean there is a general trend, although statistically insignificant, of more female-biased hatchling sex ratios for rookeries located closer to the equator

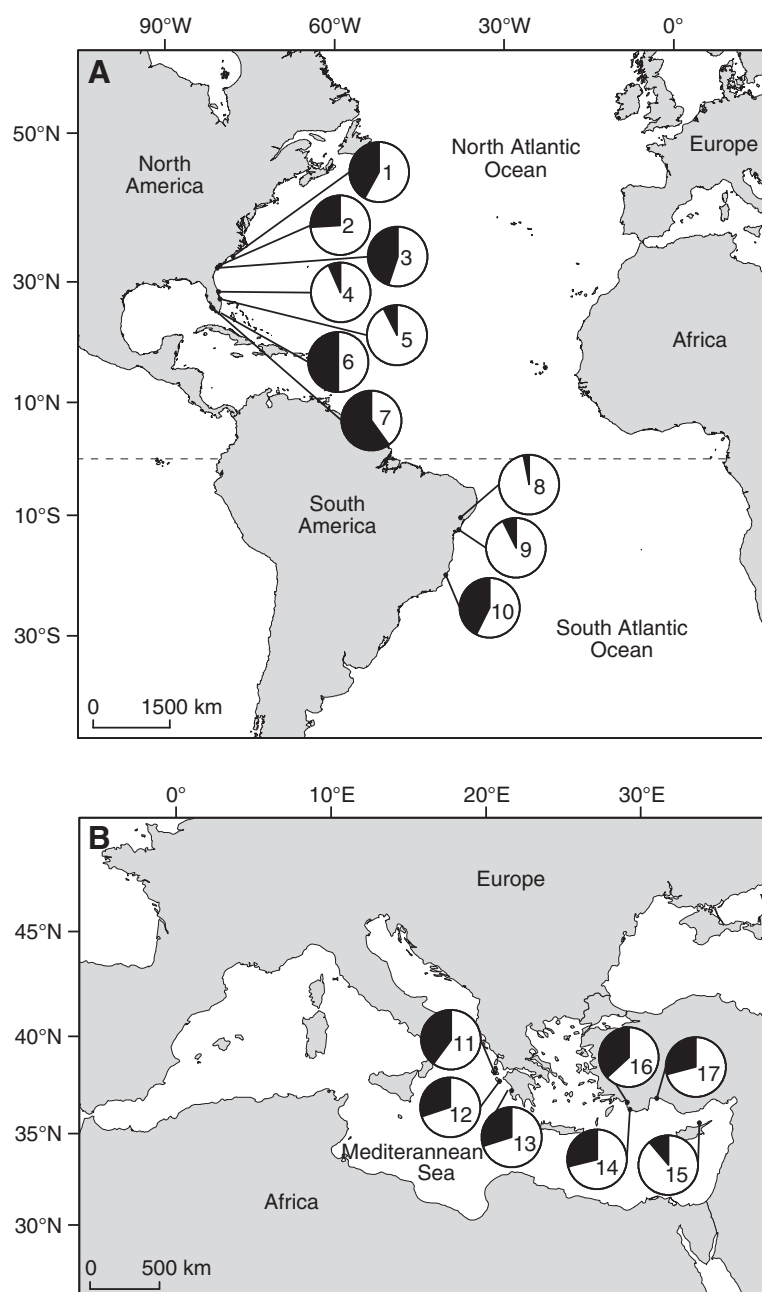


Fig. 2. Estimated proportion of male (black) and females (white) hatchling production at selected loggerhead sea turtle nesting rookeries in (A) Atlantic Ocean and (B) Mediterranean sea. Sources: ¹(Hawkes et al., 2007b); ²(Bell, 2003); ³(Mrosovsky et al., 1984); ⁴(Mrosovsky and Provancha, 1992); ⁵(Hanson et al., 1998); ⁶(Schmid et al., 2008); ⁷(Foley et al., 2000); ⁸⁻¹⁰(Marcovaldi et al., 1997); ¹¹(Houghton and Hays, 2001); ¹²(Zbinden et al., 2006); ¹³(Rees and Margaritoulis, 2004); ¹⁴(Oz et al., 2004); ¹⁵(Fuller, 2008); ¹⁶(Kaska et al., 1998) and ¹⁷(Oz et al., 2004).

and more balanced sex ratios, i.e. closer to 1:1, at rookeries that are further away from the equator (Fig. 3A, Spearman rank-order correlation using absolute latitude *versus* arcsine-transformed percentage of females produced at each rookery, $\rho = -0.22$, $P = 0.54$). In the case of the southeast United States of America, the more southerly rookeries in eastern Florida are estimated to produce nearly 90% female hatchlings (Hanson et al., 1998; Mrosovsky and Provancha, 1992), while more northerly rookeries in Georgia, South Carolina and North Carolina are thought to produce closer to 55–60% female hatchlings (Hawkes et al., 2007b; Mrosovsky et al., 1984). There are exceptions to this trend, including reported 1:1 hatchling sex ratios on some smaller, vegetated beaches in western Florida (Foley et al., 2000). A similar latitudinal trend exists south of the equator in Brazil, where the more northerly populations of Sergipe and Bahia produce nearly all female hatchlings (Marcovaldi et al., 1997; Naro-Maciel et al., 1999), while the more southerly rookery in Espirito Santo produce closer to 1:1 hatchling sex ratios (Baptistotte et al., 1999; Marcovaldi et al., 1997). Note that hatchling sex ratios studies have not been randomly designed, and there remain many nesting beaches both north and south of the equator, some of them major rookeries, that have not been adequately studied for hatchling sex ratio production, e.g. Yucatan Peninsula in Mexico and Rio de Janeiro in Brazil. Therefore, caution is needed in interpreting large spatial scale trends based on limited available information.

In the Mediterranean Sea most loggerhead nesting occurs in the Eastern basin (Fig. 1B), and loggerhead hatchling sex ratios (Fig. 2B) are estimated to be female biased on most beaches (Godley et al., 2001; Oz et al., 2004; Zbinden et al., 2006), with beaches of southerly latitude showing a general trend towards a greater female bias (Fig. 3B, Spearman rank-order correlation, $N = 7$, $\rho = -0.75$, $P = 0.06$). Exceptional loggerhead nests laid on beaches of the central and western Mediterranean Sea (Sénégas et al., 2008; Tomas et al., 2008) may experience cooler incubation environments, and thus may produce male-biased hatchling sex ratios, although relative numbers of these nests are quite small.

There are several issues that hamper our understanding of this important population parameter, including (a) the lack of long-term datasets, which are needed to discern overall trends instead of short-term studies that may reflect temporary variations only; (b) the lack of systematic sampling for sex ratios across nesting populations that encompass the entire nesting season, making it difficult to interpret available data; and (c) a reliable, simple and non-destructive marker of phenotypic sex of hatchlings. More concentrated effort on issue c would contribute towards resolving issues a and b. In the meantime, more work should be focused on better refining currently employed techniques of indirectly estimating the sex of hatchlings, including temperature and duration of incubation. For instance, more pivotal temperature experiments, to capture (or rule out) spatio-temporal variability both within and among nesting beaches, e.g. variation with latitude, are needed, and should include information on the transitional range of temperature that produces both sexes (Hulin et al., 2009). Additionally, validation of indirect estimates against direct estimates (histological examination of the gonads) within the same study will help define rates of error associated with indirect estimates (Mrosovsky et al., 2009). Finally, long-term monitoring of index sites should be set up as soon as possible, to establish baselines against which to measure possible future changes to hatchling sex ratio induced by climate change.

Predicting future hatchling sex ratios and nest death

It is commonly acknowledged that global air and sea surface temperatures will rise, and with them so will sand temperatures at

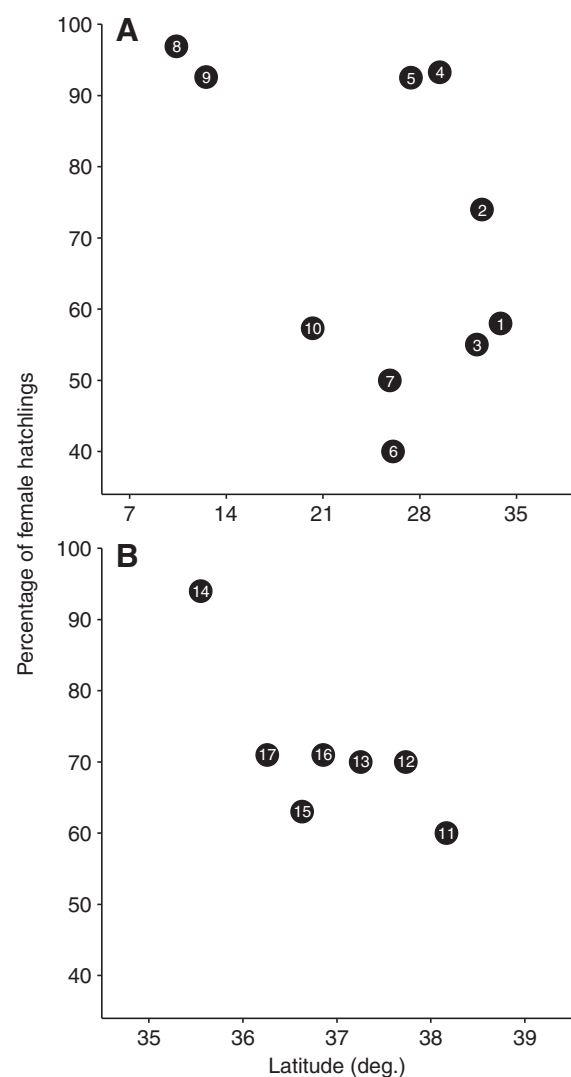


Fig. 3. Relationship between latitude and percentage of female hatchlings produced at nesting rookeries in (A) Atlantic Ocean and (B) Mediterranean Sea. The latitude of nesting rookeries with sex ratio data were expressed as absolute values. Numbers indicate source literature as described in Fig. 2.

nest depth on loggerhead nesting beaches. More effort is urgently needed to predict how such changes may impact future hatchling sex ratios of populations (Fuentes et al., 2009). If sea turtles do not adapt by shifting their geographical ranges, phenology of breeding or pivotal temperatures, sex ratios, many of which are already highly female biased, will become further skewed. Some studies have recorded an earlier onset of nesting (e.g. Pike et al., 2006; Weishampel et al., 2004), others have not (e.g. Hawkes et al., 2007b; Pike, 2009). Given that females may select cooler sites (e.g. shaded) to lay their clutch at existing or new locations, the recording of clutch temperatures will be the main indicator for monitoring adaptation (or lack of) to rising temperatures.

Although some have inferred past sex ratios from historic air temperature (Hawkes et al., 2007b; Hays et al., 2003), there have been surprisingly few studies that have attempted to predict how future climate change may impact hatchling production of sea turtles, and those that have addressed this issue have predicted sex ratios and hatching success at set elevated temperatures (Hawkes et al., 2007b) as opposed to estimating future sex ratios under modelled

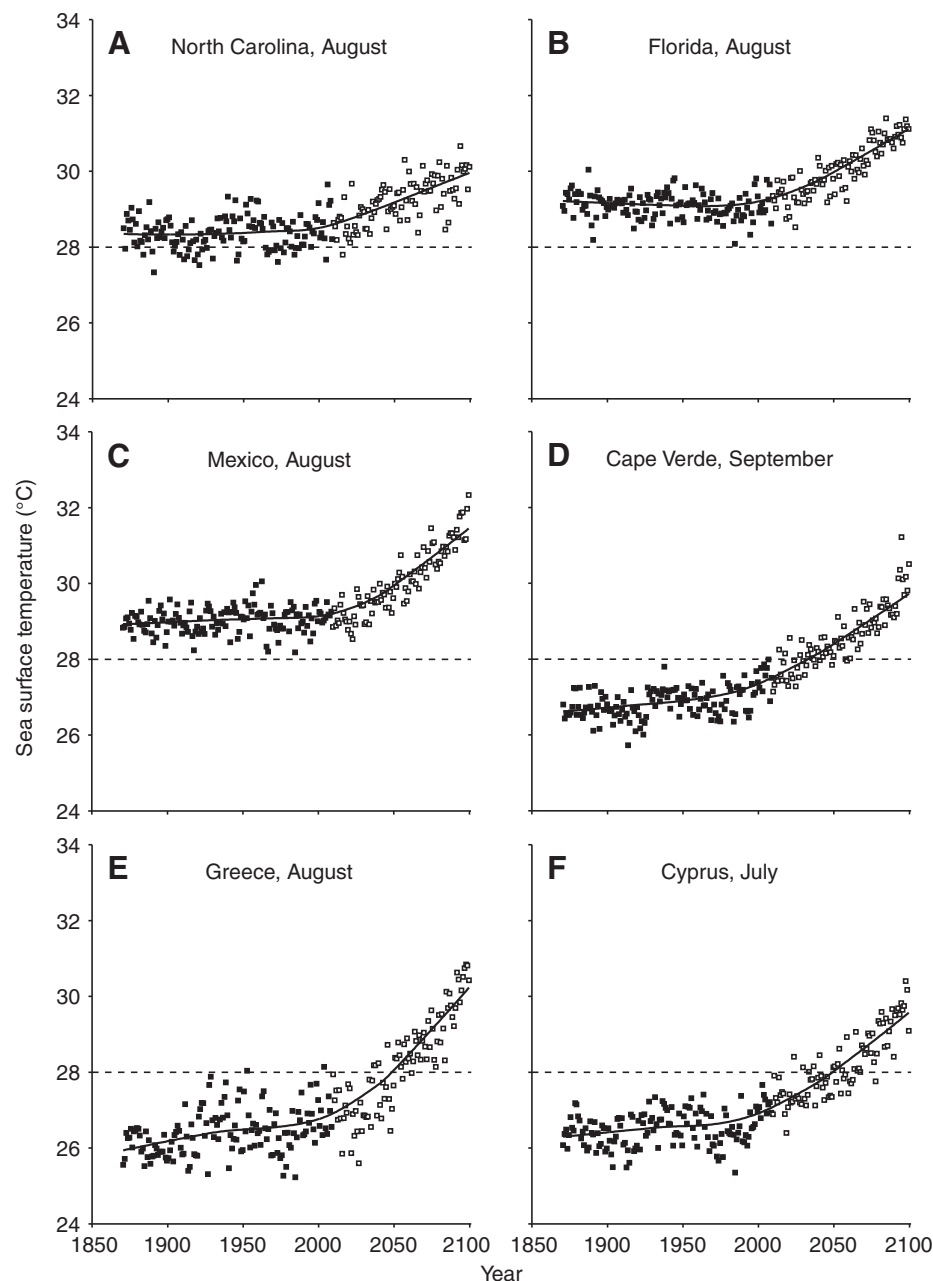


Fig. 4. Historic and forecast near-shore sea surface temperature for loggerhead sea turtle nesting (A–F) rookeries for the predominant month of incubation. Historic sea surface temperature [filled squares, January 1870 to May 2009; Hadley Ice and Sea Surface Temperature (HadISST) dataset (Rayner et al., 2003)]. Forecast sea surface temperature (open squares, June 2009 to November 2089; Hadley Global Earth Model 1 (HadGEM1) using IPCC SRES A2 scenario (IPCC, 2000; Johns et al., 2006) available from the World Climate Research Programme's (WCRP's) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model dataset (Meehl et al., 2007). Monthly gridded HadGEM1 data were spatially resampled and variance and trend adjusted (Sheppard, 2003) according to the temporal and spatial structure of HadISST data using Matlab (version 7.8.0, MathWorks Inc., Natick, MA, USA). Robust locally weighted scatter plot smooth (Cleveland, 1979) (solid line, $R=0.5$). Reference line to aid visual interpretation (28°C , broken line). In Cyprus, nest temperatures are typically 4°C greater than sea surface temperatures (see text for details).

climate change scenarios (IPCC, 2000). For those clutches that normally produce at least some males, a rise in temperature within a clutch will most likely increase the proportion of females produced. If temperatures rise above the threshold for successful development for extended periods ($\sim 33^{\circ}\text{C}$) embryonic death will increase (Miller, 1997).

To illustrate how variable predictions of hatchling sex ratios might be, we examined temporal trends in historic and global circulation model forecasts of sea surface temperature for the month of peak incubation at six loggerhead turtle nesting colonies (Fig. 4). From this information alone one might predict that regions that are currently experiencing higher incubation temperatures might be most at risk from further increases, potentially leading to complete feminisation in hatchling production. From our detailed studies in Cyprus in the Mediterranean Sea, however, we know that mean clutch temperatures from 1996 to 1999 (Godley et al., 2001) for

example were $\sim 4^{\circ}\text{C}$ warmer than sea surface temperature, probably as a result of sand albedo (Hays et al., 2001). In addition, other variables such as depth of clutch and clutch size have been shown to influence clutch temperature (Broderick et al., 2001a) but have been the focus of few sex ratio studies to date. Understanding how these variables influence clutch temperature is crucial for predicting nest fate for future climate scenarios. For sites at risk, i.e. those that are currently experiencing extreme bias in sex ratios and near-lethal temperatures, accurate predictions are needed and monitoring strategies with intervention plans put into place in case limited or no adaptation to climate change occurs.

Sex ratios in advanced demographic groups

Less well understood are sex ratios of pelagic stage neonate turtles, older juveniles and adults (Blanvillain et al., 2008; Hawkes et al., 2009). Sex ratios of older size classes are an important component

Table 2. Reported juvenile and adult sex ratios for loggerhead turtles

Location	Life stage	% ♀	Method	Source
Atlantic, USA	Juvenile	67.7	LAP	Braun-McNeill et al., 2007
Atlantic, USA	Juvenile	74.5	RIA	Braun-McNeill et al., 2007
Atlantic, USA	Juvenile	66.0	OBS	Stabenau et al., 1996
Atlantic, USA	Juvenile	65.3	OBS	Shoop et al., 1998
Mediterranean	Adult	76.5	OBS	Casale et al., 2005
Mediterranean	Juvenile	54.2	OBS	Casale et al., 2006

Method of sexing: observation of gross anatomical features (OBS), laparoscopy (LAP), radioimmunoassay (RIA).

of population dynamics (Frankham, 1995), affecting both genetic variation within the population and mating systems. Given that effective population size (N_e) will seldom be twice that of the rarer sex (Milner-Gulland et al., 2003), populations with highly skewed sex ratios are likely to suffer negative impacts through random drift and loss of genetic variation, compromising their ability to respond to selection pressures and impeding population recovery. In order to understand juvenile and adult sex ratios, at-sea surveys to catch and sex wild turtles, either laparoscopically, by hormonal assay (Blanvillain et al., 2008; Braun-McNeill et al., 2007), or by secondary sexual features in mature individuals, have to be undertaken. Notwithstanding cost, such studies require careful permission and should be undertaken over a long period (>10 years). It is not surprising, therefore, that there exist few data in the peer-reviewed literature (Casale et al., 2006) to elucidate whether skewed hatchling sex ratios are reflected in larger size classes.

Work that has been published for loggerhead turtles, however, suggests that a female bias remains in the juvenile and adult populations (approximately three females to two males; Table 2).

A lag between hatchling sex ratio and older life stage turtles (large juveniles and adults), however, would be approximately 30 years [based on age to maturity estimates in Casale et al. (2009) and Heppell et al. (Heppell et al., 2003)], such that future juvenile and adult sex ratios could be more female biased than at present. Although marine turtle fertility levels remain quite robust even at very low rookery size (Bell et al., 2009) it is conceivable that there will be a critical adult sex ratio after which fertility will become reduced.

Distribution

As satellite tracking data have become more widely integrated with oceanographic data (Godley et al., 2008), the parameters describing the preferable habitat for loggerhead sea turtles, e.g. seabed depth preference, surface current strength, upper and lower thermal preference, have become clearer. Habitat suitability models, utilising some of these parameters (Hawkes et al., 2007a; McMahon and Hays, 2006), are now being developed and these will provide the foundation to which global circulation models, used to build climate

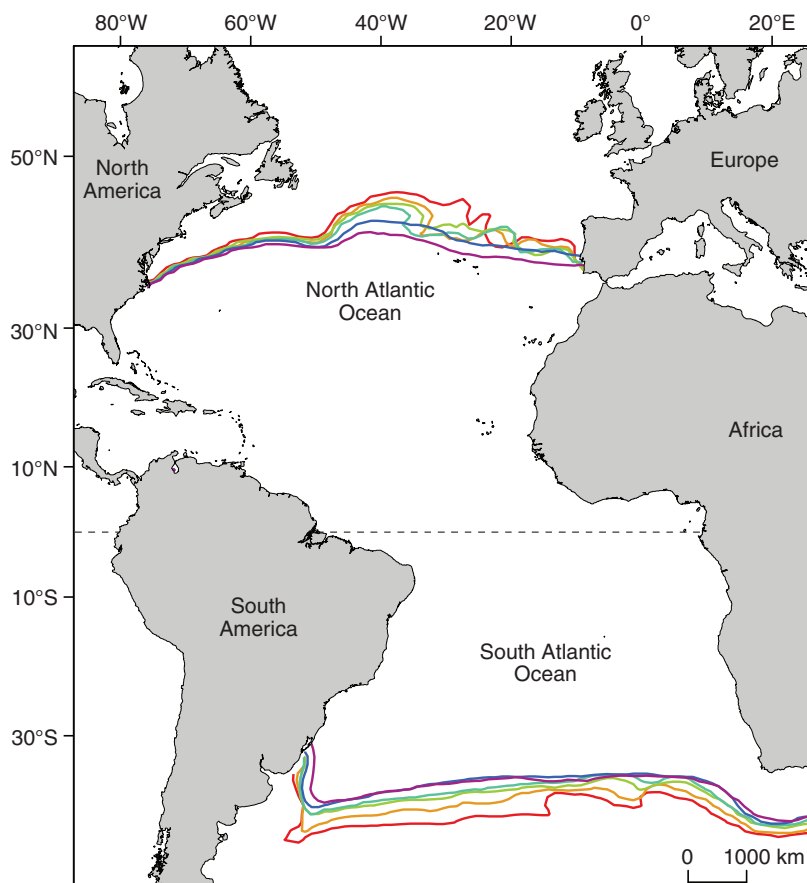


Fig. 5. Historic and forecast loggerhead turtle habitat suitability for the Atlantic Ocean. Forecast sea surface temperature data (HadGEM1) were variance and trend adjusted and merged with historic (HadISST) data. Six 20-year duration sea surface temperature datasets were constructed. Each 20-year dataset comprised of 240 months of spatially gridded mean monthly sea surface temperature data. Each pixel of each 20-year gridded sea surface temperature dataset was scored as 0 or 1 according to thermal suitability, i.e. $<15^{\circ}\text{C}=0$ and $15^{\circ}\text{C}=1$, following the method of Hawkes et al. (Hawkes et al., 2007a). The temporal availability of habitat was calculated by dividing the number of months that each cell was suitable against the total number of months analysed. The proportion of time that each cell (pixel) was thermally accessible was subsequently expressed as percentage. Isolines of 90% habitat suitability were derived using cubic interpolation using Matlab (MathWorks, Inc.).

change predictions, might be applied. With further characterisation of habitat preference, for example mapping prey distribution (Witt et al., 2007a), models might predict available habitat with greater specificity than temperature alone, which is the predominant variable used in bioclimatic envelope modelling.

In order to investigate how climate change may alter current thermal ranges for loggerhead sea turtles, we integrated oceanographic habitat preferences for adult loggerhead turtles [temperatures warmer than 15°C; derived from Hawkes et al., (Hawkes et al., 2007a)] with historic and forecast monthly mean sea surface temperatures. For the Atlantic Ocean these data were used to model the past, present and future thermally accessible range (1970–2089, Fig. 5). For the Mediterranean Sea we took an alternative approach, displaying the mean March 15°C isotherm over successive 20-year periods (Fig. 6). Within the annual cycle of sea surface temperature in the Mediterranean Sea, March represents the coldest month when Chelonid sea turtles are most likely to be spatially constrained by temperature. Broadly, these simple thermal envelope (niche) models describe an increase in available habitat through time. For the Atlantic Ocean we see the 90% habitat suitability contour migrating poleward with greatest range extension in the mid north Atlantic and some 75–100 km poleward extension along the US Atlantic coast. This model represents habitat suitability using a year-round approach; however, during warmer summer months loggerhead turtle distribution regularly extends further north than the annualised 90% habitat suitability contours. In the Mediterranean Sea, we see the Western basin becoming increasing favourable to occupation during winter months, by 2089 only a small area of the Mediterranean Sea, south of France, will remain inaccessible to year round occupation.

Despite the obvious utility of models such as ours in predicting and managing for future range changes, it should be noted that insufficient data describing the oceanographic parameters of habitat occupation have been published for the seven species of sea turtles. In particular, the habitat preferences of juvenile turtles and adult males are largely unknown, and future tracking efforts need to address this shortcoming (Godley et al., 2008). These data are fundamental to both the development and accuracy of future models and at present it has not been possible to develop robust models for many major rookeries.

As ectotherms, sea turtles are likely to have range distributions largely defined by temperature (Hawkes et al., 2007a; Milton and Lutz, 2003; Sato et al., 1998). However, distribution is also likely to be defined by other factors especially food availability (Witt et al., 2007a). Ecosystems are likely to suffer significant shifts due to climate change, which may impact trophic relationships and, given inter-specific differences in foraging ecology, these will vary between species (Bjorndal, 1997). For loggerhead turtles, which have been shown to have such a broad generalist diet (Bjorndal, 1997; Godley et al., 1997; Tomas et al., 2001), limitation of specific food items is less likely to impact distribution unless there is a low overall abundance of potential dietary items. This compares with species that are more specialist such as hawksbill turtles (*Eretmochelys imbricata* L.), which often prey upon sponges (Leon and Bjorndal, 2002; Meylan, 1988), or green turtles (*Chelonia mydas*), which typically forage on seagrasses and algae (Bjorndal, 1997). For these latter species, approaches will need to encompass modelling of the likely distribution of key habitats as well as the thermal envelope approach suggested here.

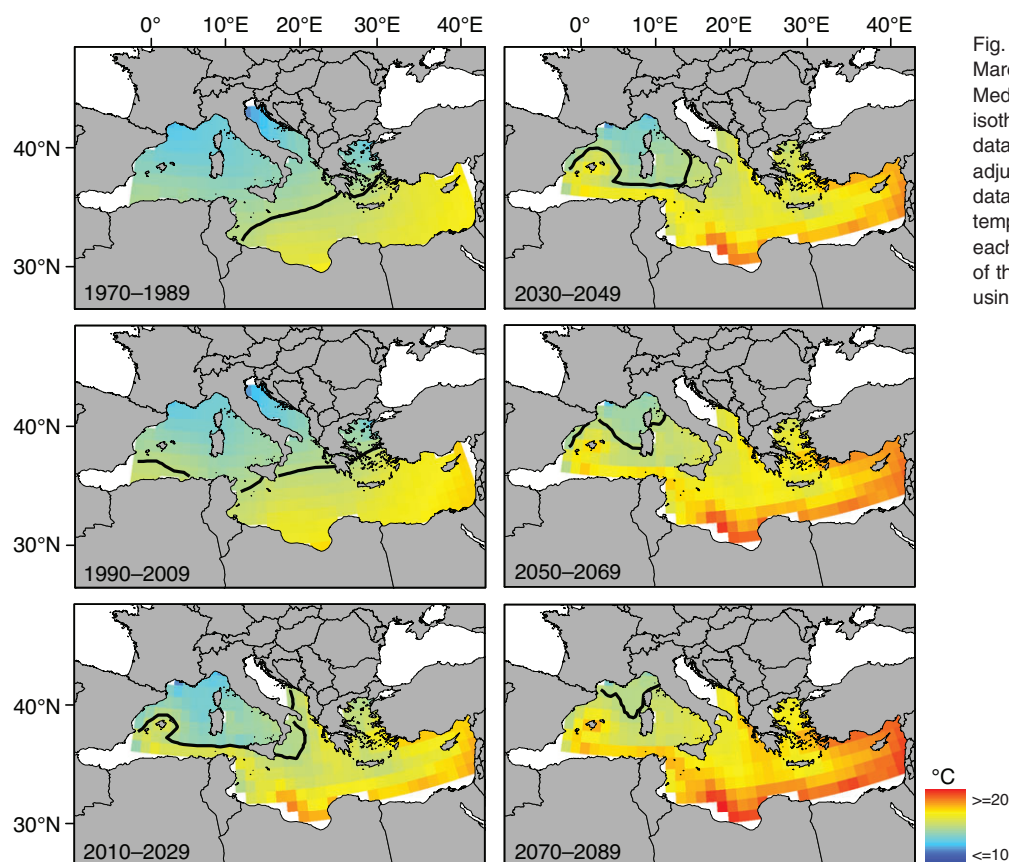


Fig. 6. Historic and forecast 20-year mean March sea surface temperature for the Mediterranean Sea with 20-year mean 15°C isotherm. Forecast sea surface temperature data (HadGEM1) were variance and trend adjusted and merged with historic (HadISST) data. Six 20-year duration sea surface temperature datasets were constructed. For each 20-year dataset the mean March position of the 15°C isotherm was identified (solid line) using cubic interpolation.

Conclusion

In this review we have highlighted some of the primary threats from climate change faced by these species, the current knowledge of sex ratios, temperature-dependent sex determination and species distribution, and recommend future studies that will provide critical information for the prediction of the potential effects of climate change, which will inform possible adaptive management practices. These practices might include artificial nest shading or watering of nests to reduce incubation temperatures (e.g. Naro-Maciel et al., 1999), translocation of clutches to cooler sites on current nesting beaches or reseeded populations to new locations (Hoegh-Guldberg et al., 2008). We do, however, urge that robust experiments be conducted to test the effectiveness of such practices (Pintus et al., 2009). In addition further empirical studies, in particular the development of a marker to sex offspring, are urgently needed to aid accurate prediction of sex ratios and hence identify populations that may require mitigation activities. Finally, the threats from climate change experienced by these species of conservation concern, as with many migratory taxa (Robinson et al., 2009), are only part of a suite of other threats such as direct exploitation, fisheries by catch and habitat loss that potentially hinder marine turtle population recovery. Targeting these latter threats will better engender resilience in marine turtle stocks while they adjust to changes in conditions as they have done in the past.

Acknowledgements

This work was prepared for an invited presentation at The Company of Biologists *Journal of Experimental Biology* symposium: Survival in a Changing World, held in Japan in August 2009. M.J.W. is supported by the Peninsula Research Institute for Marine Renewable Energy (PRIMARE) through the South West of England Regional Development Agency. L.A.H. is supported by the Biotechnology and Biosciences Research Council at Bangor University. Synthesis of climate change work by L.A.H. was carried out with support from the MacArthur Foundation and the Kaplan Foundation to the World Wildlife Fund Canada. A.C.B. and B.J.G. are supported by the Darwin Initiative, European Union and the Natural Environment Research Council (UK). The AVHRR Oceans Pathfinder SST data were obtained from the Physical Oceanography Distributed Active Archive Center (PO.DAAC) at the NASA Jet Propulsion Laboratory, Pasadena, CA. The European Centre for Medium-Range Weather Forecasts (ECMWF) ERA-Interim data used in this work have been provided by ECMWF and have been obtained from the ECMWF Data Server. We acknowledge the modelling groups, the Program for Climate Model Diagnosis and Intercomparison (PCMDI) and the World Climate Change Research Programmes (WCRP) Working Group on Coupled Modelling (WGCM) for their roles in making available the WCRP CMIP3 multi-model dataset. Support of this dataset is provided by the Office of Science, US Department of Energy.

References

- Ackerman, R. A. (1997). The nest environment and the embryonic development of sea turtles. In *The Biology of Sea Turtles*, vol. 1 (eds P. L. Lutz and J. A. Musick), pp. 83-106. Boca Raton: CRC Press.
- Araújo, M. B., Cabeza, M., Thuiller, W., Hannah, L. and Williams, P. H. (2004). Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Chang. Biol.* **10**, 1618-1626.
- Avise, J. C., Bowen, B. W., Lamb, T., Meylan, A. B. and Bermingham, E. (1992). Mitochondrial DNA evolution at a turtles pace-evidence for low genetic variability and reduced microevolutionary rate in the testudines. *Mol. Biol. Evol.* **9**, 457-473.
- Baker, J., Littnan, C. and Johnston, D. (2006). Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the Northwestern Hawaiian Islands. *Endanger. Species Res.* **2**, 21-30.
- Baptistotte, C., Scalfoni, J. T. and Mrosovsky, N. (1999). Male-producing thermal ecology of a southern loggerhead turtle nesting beach in Brazil: implications for conservation. *Anim. Conserv.* **2**, 9-13.
- Bell, C. D., Blumenthal, J. M., Broderick, A. C. and Godley, B. J. (2009). Investigating potential for depensation in marine turtles: how low can you go? *Conserv. Biol.* **24**, 226-235.
- Bengtsson, L., Hodges, K. I. and Roegner, E. (2006). Storm tracks and climate change. *J. Climate* **19**, 3518-3543.
- Bjorndal, K. A. (1997). Foraging ecology and nutrition of sea turtles. In *The Biology of Sea Turtles*, vol. II (eds P. L. Lutz, J. A. Musick and J. Wyneken), pp. 199-231. Boca Raton: CRC Press.
- Bjorndal, K. A., Bolton, A. B. and Martins, H. R. (2000). Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Mar. Ecol. Prog. Ser.* **202**, 265-272.
- Blanvillain, G., Pease, A., Segars, A., Rostal, D., Richards, A. and Owens, D. (2008). Comparing methods for the assessment of reproductive activity in adult male loggerhead sea turtles *Caretta caretta* at Cape Canaveral, Florida. *Endanger. Species Res.* **6**, 75-85.
- Bolten, A. B. (2003). Active swimmers-passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In *Loggerhead Sea Turtles* (eds A. B. Bolten and B. E. Witherington), pp. 63-78. Washington: Smithsonian Books.
- Bowden, R. M., Ewert, M. A. and Nelson, C. E. (2000). Environmental sex determination in a reptile varies seasonally and with yolk hormones. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **267**, 1745-1749.
- Braun-McNeill, J., Epperly, S. P., Owens, D. W., Avens, L., Williams, E. and Harms, C. A. (2007). Seasonal reliability of testosterone radioimmunoassay (RIA) for predicting sex ratios of juvenile loggerhead (*Caretta caretta*) turtles. *Herpetologica* **63**, 275-284.
- Broderick, A. C., Godley, B. J. and Hays, G. C. (2001a). Metabolic heating and the prediction of sex ratios for green turtles (*Chelonia mydas*). *Physiol. Biochem. Zool.* **74**, 161-170.
- Broderick, A. C., Godley, B. J. and Hays, G. C. (2001b). Trophic status drives interannual variability in nesting numbers of marine turtles. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **268**, 1481-1487.
- Broderick, A. C., Glen, F., Godley, B. J. and Hays, G. C. (2002). Estimating the number of green and loggerhead turtles nesting annually in the Mediterranean. *Oryx* **36**, 227-235.
- Broderick, A. C., Coyne, M. S., Fuller, W. J., Glen, F. and Godley, B. J. (2007). Fidelity and over-wintering of sea turtles. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **274**, 1533-1538.
- Carthy, R. R., Foley, A. M. and Matsuzawa, Y. (2003). Incubation environment of loggerhead turtle nests: effects on hatching success and hatchling characteristics. In *Loggerhead Sea Turtles* (eds A. B. Bolten and B. E. Witherington), pp. 144-153. Washington: Smithsonian Books.
- Casale, P., Freggi, D., Basso, R. and Argano, R. (2005). Size at male maturity, sexing methods and adult sex ratio in loggerhead turtles (*Caretta caretta*) from Italian waters investigated through tail measurements. *Herpetol. J.* **15**, 145-148.
- Casale, P., Lazar, B., Pont, S., Tomas, J., Zizzo, N., Alegre, F., Badillo, J., Di Summa, A., Freggi, D., Lackovic, G. et al. (2006). Sex ratios of juvenile loggerhead sea turtles *Caretta caretta* in the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* **324**, 281-285.
- Casale, P., Mazaris, A. D., Freggi, D., Vallini, C. and Argano, R. (2009). Growth rates and age at adult size of loggerhead sea turtles (*Caretta caretta*) in the Mediterranean Sea, estimated through capture-mark-recapture records. *Sci. Mar.* **73**, 589-595.
- Chaloupka, M., Kamezaki, N. and Limpus, C. (2008). Is climate change affecting the population dynamics of the endangered Pacific loggerhead sea turtle? *J. Exp. Mar. Biol. Ecol.* **356**, 136-143.
- Cleveland, W. S. (1979). Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* **74**, 829-836.
- Conant, T. A., Dutton, P. H., Eguchi, T., Epperly, S. P., Fahy, C. C., Godfrey, M. H., MacPherson, S. L., Possardt, E. E., Schroeder, B. A., Seminoff, J. A. et al. (2009). *Loggerhead Sea Turtle (Caretta caretta) 2009 Status Review Under the U.S. Endangered Species Act. Report of the Loggerhead Biological Review Team to the National Marine Fisheries Service*, 222pp. <http://www.nmfs.noaa.gov/pr/species/statusreviews.htm>
- Croxall, J. P., Silk, J. R. D., Phillips, R. A., Afanasyev, V. and Briggs, D. R. (2005). Global circumnavigations: tracking year-round ranges of nonbreeding albatrosses. *Science* **307**, 249-250.
- Davenport, J. (1989). Sea turtles and the greenhouse effect. *Brit. Herpetol. Soc. Bull.* **29**, 11-15.
- Davenport, J. (1998). Sustaining endothermy on a diet of cold jelly: energetics of the leatherback turtles *Dermochelys coriacea*. *Brit. Herpetol. Soc. Bull.* **62**, 4-8.
- Davenport, J., Fraher, J., Fitzgerald, E., McLaughlin, P., Doyle, T., Harman, L. and Cuffe, T. (2009). Fat head: an analysis of head and neck insulation in the leatherback turtle (*Dermochelys coriacea*). *J. Exp. Biol.* **212**, 2753-2759.
- Dodd, K. L., Murdoch, C. and Wibbels, T. (2006). Interclutch variation in sex ratios produced at pivotal temperature in the Red-Eared Slider, a turtle with temperature-dependent sex determination. *J. Herpetol.* **40**, 544-549.
- Doyle, T. K., Houghton, J. D. R., O'Suilleabhain, P. F., Hobson, V. J., Marnell, F., Davenport, J. and Hays, G. C. (2008). Leatherback turtles satellite-tagged in European waters. *Endanger. Species Res.* **4**, 23-31.
- Edwards, M. and Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881-882.
- Ehrhart, L. M., Bagley, D. A. and Redfoot, W. E. (2003). Loggerhead turtles in the Atlantic ocean: geographic distribution, abundance, and population status. In *Loggerhead Sea Turtles* (eds A. B. Bolten and B. E. Witherington), pp. 157-174. Washington: Smithsonian Books.
- Fish, M. R., Cote, I. M., Gill, J. A., Jones, A. P., Renshoff, S. and Watkinson, A. R. (2005). Predicting the impact of sea-level rise on Caribbean sea turtle nesting habitat. *Conserv. Biol.* **19**, 482-491.
- Fish, M. R., Cote, I. M., Horrocks, J. A., Mulligan, B., Watkinson, A. R. and Jones, A. P. (2008). Construction setback regulations and sea-level rise: Mitigating sea turtle nesting beach loss. *Ocean Coast. Manag.* **51**, 330-341.
- Fisher, R. A. (1930). *The Genetical Theory Of Natural Selection*. Oxford: Oxford University Press.
- Foley, A. M., Peck, S. A., Harman, G. R. and Richardson, L. W. (2000). Loggerhead turtle (*Caretta caretta*) nesting habitat on low-relief mangrove islands in southwest Florida and consequences to hatchling sex ratios. *Herpetologica* **56**, 433-445.
- Frair, W., Ackman, R. G. and Mrosovsky, N. (1972). Body temperatures of *Dermochelys coriacea*: warm turtle from cold water. *Science* **177**, 791-793.
- Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: a review. *Genet. Res.* **66**, 95-107.
- Fuentes, M., Maynard, J., Guinea, M., Bell, I., Werdell, P. and Hamann, M. (2009). Proxy indicators of sand temperature hep project impacts of global warming on sea turtles in northern Australia. *Endanger. Spec. Res.* **9**, 33-40.

- Fuentes, M. M. P. B., Limpus, C. J. and Hamann, M. (In press). Vulnerability of sea turtle nesting grounds to climate change. *Glob. Change Biol.* doi: 10.1111/j.1365-2486.2010.02192.x
- Fuller, W. J. (2008). *The Ecology and Conservation of Mediterranean Marine Turtles*. PhD Thesis. Exeter: University of Exeter.
- Girard, C., Tucker, A. D. and Calmettes, B. (2009). Post-nesting migrations of loggerhead sea turtles in the Gulf of Mexico: dispersal in highly dynamic conditions. *Mar. Biol.* **156**, 1827-1839.
- Godfrey, M. H. and Mrosovsky, N. (1997). Estimating the time between hatching of sea turtles and their emergence from the nest. *Chelonian Conserv. Biol.* **2**, 581-585.
- Godfrey, M. H. and Mrosovsky, N. (2001). Relative importance of thermal and nonthermal factors on the incubation period of sea turtle eggs. *Chelonian Conserv. Biol.* **4**, 217-218.
- Godley, B. J., Smith, S. M., Clark, P. F. and Taylor, J. D. (1997). Molluscan and crustacean items in the diet of the loggerhead turtle, *Caretta caretta* (Linnaeus, 1758) (Testudines: Cheloniidae) in the eastern Mediterranean. *J. Mol. Stud.* **63**, 474-476.
- Godley, B. J., Broderick, A. C., Downie, J. R., Glen, F., Houghton, J. D. R., Kirkwood, I., Reece, S. and Hays, G. C. (2001). Thermal conditions in nests of loggerhead turtles: further evidence suggesting female skewed sex ratios of hatching production in the Mediterranean. *J. Exp. Mar. Biol. Ecol.* **263**, 45-63.
- Godley, B. J., Broderick, A. C., Glen, F. and Hays, G. C. (2003). Post-nesting movements and submergence patterns of loggerhead marine turtles in the Mediterranean assessed by satellite tracking. *J. Exp. Mar. Biol. Ecol.* **287**, 119-134.
- Godley, B. J., Blumenthal, J., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Hawkes, L. A. and Witt, M. J. (2008). Satellite tracking of sea turtles: where have we been and where do we go next? *Endanger. Spec. Res.* **3**, 3-22.
- Gremillet, D. and Boulinier, T. (2009). Spatial ecology and conservation of seabirds facing climate change: a review. *Mar. Ecol. Prog. Ser.* **391**, 121-137.
- Gross, T. S., Crain, D. A., Bjorndal, K. A., Bolten, A. B. and Carthy, R. R. (1995). Identification of sex in hatchling loggerhead turtles (*Caretta caretta*) by analysis of steroid concentrations in chorioallantoic/amniotic fluid. *Gen. Comp. Endocrinol.* **99**, 204-210.
- Hamann, M., Limpus, C. J. and Owens, D. W. (2003). Reproductive cycles of males and females. In *The Biology of Sea Turtles*, vol. 2 (eds P. L. Lutz, J. A. Musick and J. Wyneken), pp. 135-162. Boca Raton: CRC Press.
- Hamann, M., Limpus, C. and Read, M. (2007). Chapter 15, Vulnerability of marine reptiles in the Great Barrier Reef to climate change. In *Climate Change and the Great Barrier Reef: A Vulnerability Assessment* (eds J. Johnson and P. Marshall), pp. 465-496. Hobart: Great Barrier Reef Marine Park Authority and Australia Greenhouse Office.
- Hannah, L., Midgley, G. F. and Millar, D. (2002). Climate change-integrated conservation strategies. *Glob. Ecol. Biogeog.* **11**, 485-495.
- Hannan, L. B., Roth, J. D., Ehrhart, L. M. and Weishampel, J. F. (2007). Dune vegetation fertilization by nesting sea turtles. *Ecology* **88**, 1053-1058.
- Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W. and Medina-Elizade, M. (2006). Global temperature change. *Proc. Natl. Acad. Sci. USA* **103**, 14288-14293.
- Hanson, J., Wibbels, T. and Martin, R. E. (1998). Predicted female bias in sex ratios of hatching loggerhead sea turtles from a Florida nesting beach. *Can. J. Zool. Rev.* **76**, 1850-1861.
- Hawkes, L. A., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Lopez-Jurado, L. F., Lopez-Suarez, P., Merino, S. E., Varo-Cruz, N. and Godley, B. J. (2006). Phenotypically linked dichotomy in sea turtle foraging requires multiple conservation approaches. *Curr. Biol.* **16**, 990-995.
- Hawkes, L. A., Broderick, A. C., Coyne, M. S., Godfrey, M. H. and Godley, B. J. (2007a). Only some like it hot-quantifying the environmental niche of the loggerhead sea turtle. *Div. Dist.* **13**, 447-457.
- Hawkes, L. A., Broderick, A. C., Godfrey, M. H. and Godley, B. J. (2007b). Investigating the potential impacts of climate change on a marine turtle population. *Glob. Chang. Biol.* **13**, 923-932.
- Hawkes, L. A., Broderick, A. C., Godfrey, M. H. and Godley, B. J. (2009). Climate change and marine turtles. *Endang. Spec. Res.* **7**, 137-154.
- Hays, G. C., Ashworth, J. S., Barnsley, M. J., Broderick, A. C., Emery, D. R., Godley, B. J., Henwood, A. and Jones, E. L. (2001). The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. *Oikos* **93**, 87-94.
- Hays, G. C., Broderick, A. C., Glen, F., Godley, B. J., Houghton, J. D. R. and Metcalfe, J. D. (2002). Water temperature and interesting intervals for loggerhead (*Caretta caretta*) and green (*Chelonia mydas*) sea turtles. *J. Therm. Biol.* **27**, 429-432.
- Hays, G. C., Broderick, A. C., Glen, F. and Godley, B. J. (2003). Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. *Glob. Chang. Biol.* **9**, 642-646.
- Heppell, S., Snover, M. and Crowder, L. (2003). Sea turtle population ecology. In *The Biology of Sea Turtles*, vol. 2 (eds P. L. Lutz, J. A. Musick and J. Wyneken), pp. 275-306. Boca Raton: CRC Press.
- Hochscheid, S., Bentivegna, F. and Hays, G. C. (2005). First records of dive durations for a hibernating sea turtle. *Biol. Lett.* **1**, 82-86.
- Hoegh-Guldberg, O., Hughes, L., McIntyre, S., Lindenmayer, D. B., Parmesan, C., Possingham, H. P. and Thomas, C. D. (2008). Assisted colonization and rapid climate change. *Science* **321**, 345-346.
- Houghton, J. D. R. and Hays, G. C. (2001). Asynchronous emergence by loggerhead turtle (*Caretta caretta*) hatchlings. *Naturwissenschaften* **88**, 133-136.
- Hulin, V., Delmas, V., Girondot, M., Godfrey, M. H. and Guillon, J. M. (2009). Temperature-dependent sex determination and global change: are some species at greater risk? *Oecologia* **160**, 493-506.
- IPCC (2000). *Emissions Scenarios*. Cambridge, UK: Cambridge University Press.
- IPCC (2007). *Climate Change 2007, Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Geneva, Switzerland: IPCC.
- James, M. C., Myers, R. A. and Ottensmeyer, C. A. (2005). Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **272**, 1547-1555.
- Johns, T. C., Durman, C. F., Banks, H. T., Roberts, M. J., McLaren, A. J., Ridley, J. K., Senior, C. A., Williams, K. D., Jones, A., Rickard, G. J. et al. (2006). The new Hadley Centre Climate Model (HadGEM1): Evaluation of coupled simulations. *J. Clim.* **19**, 1327-1353.
- Kaska, Y., Downie, R., Tippet, R. and Furness, R. W. (1998). Natural temperature regimes for loggerhead and green turtle nests in the eastern Mediterranean. *Can. J. Zool. Rev. Can. Zool.* **76**, 723-729.
- Leon, Y. M. and Bjorndal, K. A. (2002). Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Mar. Ecol. Prog. Ser.* **245**, 249-258.
- Lohmann, K. J. and Lohmann, C. M. F. (2003). Orientation mechanisms of hatchling loggerheads. In *Loggerhead Sea Turtles* (eds A. B. Bolten and B. E. Witherington), pp. 44-62. Washington: Smithsonian Books.
- MacLeod, C. D. (2009). Global climate change, range changes and potential implications for the conservation of marine cetaceans: a review and synthesis. *Endang. Species Res.* **7**, 125-136.
- Marcovaldi, M. A. and Chaloupka, M. (2007). Conservation status of the loggerhead sea turtle in Brazil: an encouraging outlook. *Endang. Species Res.* **3**, 133-143.
- Marcovaldi, M. A., Godfrey, M. H. and Mrosovsky, N. (1997). Estimating sex ratios of loggerhead turtles in Brazil from pivotal incubation durations. *Can. J. Zool. Rev. Can. Zool.* **75**, 755-770.
- Margaritoulis, D., Argano, R., Baran, I., Bentivegna, F., Bradai, M. N., Camiñas, J. A., Casale, P., De Metrio, G., Demetropoulos, A., Gerosa, G. et al. (2003). Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In *Loggerhead Sea Turtles* (eds A. B. Bolten and B. E. Witherington), pp. 175-198. Washington: Smithsonian Books.
- Matsuzawa, Y., Sato, K., Sakamoto, W. and Bjorndal, K. A. (2002). Seasonal fluctuations in sand temperature: effects on the incubation period and mortality of loggerhead sea turtle (*Caretta caretta*) pre-emergent hatchlings in Minabe, Japan. *Mar. Biol.* **140**, 639-646.
- Mazaris, A. D., Kramer-Schadt, S., Tzanopoulos, J., Johst, K., Matsinos, G. and Pantis, J. D. (2009). Assessing the relative importance of conservation measures applied on sea turtles: comparison of measures focusing on nesting success and hatching recruitment success. *Amphibia-Reptilia* **30**, 221-231.
- McMahon, C. R. and Hays, G. C. (2006). Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. *Glob. Chang. Biol.* **12**, 1-9.
- Meehl, G. A., Covey, C., Delworth, T., Latif, M., McAvaney, B., Mitchell, J. F. B., Stouffer, R. J. and Taylor, K. E. (2007). The WCRP CMIP3 multi-model dataset: a new era in climate change research. *Bull. Am. Meteorol. Soc.* **88**, 1383-1394.
- Meylan, A. (1988). Spongivory in Hawksbill turtles: a diet of glass. *Science* **239**, 393-395.
- Miller, J. D. (1997). Reproduction in sea turtles. In *The Biology of Sea Turtles*, vol. 1 (eds P. L. Lutz and J. A. Musick), pp. 51-82. Boca Raton: CRC Press.
- Milly, P. C. D., Wetherald, R. T., Dunne, K. A. and Delworth, T. L. (2002). Increasing risk of great floods in a changing climate. *Nature* **415**, 514-517.
- Milner-Gulland, E. J., Bukreeva, O. M., Coulson, T., Lushchekina, A. A., Kholodova, M. V., Bekenov, A. B. and Grachev, I. A. (2003). Conservation-reproductive collapse in saiga antelope harems. *Nature* **422**, 135-135.
- Milton, S. L. and Lutz, P. L. (2003). Physiology and genetic responses to environmental stress. In *The Biology of Sea Turtles*, vol. 2 (eds P. L. Lutz, J. A. Musick and J. Wyneken), pp. 163-197. Boca Raton: CRC Press.
- Mrosovsky, N. (1984). Editorial. *Mar. Turtle News* **28**, 1-2.
- Mrosovsky, N. (1988). Pivotal temperatures for loggerhead turtles (*Caretta caretta*) from northern and southern nesting beaches. *Can. J. Zool.* **66**, 661-669.
- Mrosovsky, N. and Pieau, C. (1991). Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. *Amphibia-Reptilia* **12**, 169-179.
- Mrosovsky, N. and Provancha, J. (1992). Sex ratio of hatchling loggerhead sea turtles-data and estimates from a 5-year study. *Can. J. Zool. Rev. Can. Zool.* **70**, 530-538.
- Mrosovsky, N., Hopkinsmurray, S. R. and Richardson, J. I. (1984). Sex ratio of sea turtles-seasonal changes. *Science* **225**, 739-741.
- Mrosovsky, N., Baptiste, C. and Godfrey, M. H. (1999). Validation of incubation duration as an index of the sex ratio of hatchling sea turtles. *Can. J. Zool. Rev. Can. Zool.* **77**, 831-835.
- Mrosovsky, N., Kamel, S., Rees, A. F. and Margaritoulis, D. (2002). Pivotal temperature for loggerhead turtles (*Caretta caretta*) from Kyparissia Bay, Greece. *Can. J. Zool. Rev. Can. Zool.* **80**, 2118-2124.
- Mrosovsky, N., Kamel, S. J., Diez, C. E. and Robert, P. V. D. (2009). Methods of estimating natural sex ratios of sea turtles from incubation temperatures and laboratory data. *Endang. Species Res.* **8**, 147-155.
- Naro-Maciel, E., Mrosovsky, N. and Marcovaldi, M. A. (1999). Thermal profiles of sea turtle hatcheries and nesting areas at Praia do Forte, Brazil. *Chelonian Conserv. Biol.* **3**, 407-413.
- Newson, S. E., Mendes, S., Crick, H. Q., Dulvy, N. K., Houghton, J. D., Hays, G. C., Hutson, A. M., MacLeod, C. D., Pierce, G. J. and Robinson, R. A. (2009). Indicators of the impact of climate change on migratory species. *Endang. Species Res.* **7**, 101-113.
- Oz, M., Erdogan, A., Kaska, Y., Dusen, S., Aslan, A., Sert, H., Yavuz, M. and Tunc, M. R. (2004). Nest temperatures and sex-ratio estimates of loggerhead turtles at Patara beach on the southwestern coast of Turkey. *Can. J. Zool. Rev. Can. Zool.* **82**, 94-101.
- Paladino, F. V., O'Connor, M. P. and Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* **344**, 858-860.
- Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37-42.

- Pike, D. A. (2008). Natural beaches confer fitness benefits to nesting marine turtles. *Biol. Lett.* **4**, 704-706.
- Pike, D. A. (2009). Do green turtles modify their nesting seasons in response to environmental temperatures? *Chelonian Conserv. Biol.* **8**, 43-47.
- Pike, D. A., Antworth, R. L. and Stiner, J. C. (2006). Earlier nesting contributes to shorter nesting seasons for the loggerhead sea turtle, *Caretta caretta*. *J. Herpetol.* **40**, 91-94.
- Pintus, K., Godley, B. J., McGowan, A. and Broderick, A. C. (2009). Impact of clutch relocation on green turtle offspring. *J. Wildl. Manage.* **73**, 1151-1157.
- Plotkin, P. T. and Spotila, J. R. (2002). Post-nesting migrations of loggerhead turtles *Caretta caretta* from Georgia, USA: conservation implications for a genetically distinct subpopulation. *Oryx* **36**, 396-399.
- Polovina, J. J., Balazs, G. H., Howell, E. A., Parker, D. M., Seki, M. P. and Dutton, P. H. (2004). Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish. Oceanogr.* **13**, 36-51.
- Pounds, J. A., Fogden, M. P. L. and Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature* **398**, 611-615.
- Rahmstorf, S. (1997). Risk of sea-change in the Atlantic. *Nature* **388**, 825-826.
- Rahmstorf, S. (2007). A semi-empirical approach to projecting future sea-level rise. *Science* **315**, 368-370.
- Rahmstorf, S., Cazenave, A., Church, J. A., Hansen, J. E., Keeling, R. F., Parker, D. E. and Somerville, R. C. J. (2007). Recent climate observations compared to projections. *Science* **316**, 709-709.
- Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., Kent, E. C. and Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res. Atmos.* **108**, doi:10.1029/2002JD002670.
- Rees, A. F. and Margaritoulis, D. (2004). Beach temperatures, incubation durations and estimated hatchling sex ratios for loggerhead sea turtles in southern Kyparissia Bay, Greece. *Testudo* **6**, 23-36.
- Robinson, R. A., Crick, H. Q., Learmonth, J. A., Maclean, I. M., Thomas, C. D., Bairlein, F., Forchhammer, M. C., Francis, C. M., Gill, J. A., Godley, B. J. et al. (2009). Travelling through a warming world: climate change and migratory species. *Endang. Species Res.* **7**, 87-99.
- Sato, K., Matsuzawa, Y., Tanaka, H., Bando, T., Minamikawa, S., Sakamoto, W. and Naito, Y. (1998). Internesting intervals for loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, are affected by temperature. *Can. J. Zool. Rev. Can. Zool.* **76**, 1651-1662.
- Schmid, J. L., Addison, D. S., Donnelly, M. A., Shirley, M. A. and Wibbels, T. (2008). The effect of Australian Pine (*Casuarina equisetifolia*) removal on Loggerhead sea turtle (*Caretta caretta*) incubation temperatures on Keewaydin Island, Florida. *J. Coast. Res.* **55**, 214-220.
- Sénégal, J.-B., Hochscheid, S., Groul, J.-M., Lagarrigue, B. and Bentivegna, F. (2008). Discovery of the northernmost loggerhead sea turtle (*Caretta caretta*) nest. *Mar. Biodiv. Rec.* **2**, e81.
- Sheppard, C. R. C. (2003). Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature* **425**, 294-297.
- Shoop, C. R., Ruckdeschel, C. A. and Kenney, R. D. (1998). Female-biased sex ratio of juvenile loggerhead sea turtles in Georgia. *Chelonian Conserv. Biol.* **3**, 93-96.
- Small, C. and Nicolls, R. J. (2003). A global analysis of human settlement in coastal zones. *J. Coast. Res.* **19**, 584-599.
- Snow, M. M. and Snow, R. K. (2009). Modeling, monitoring and mitigating sea level rise. *Man. Environ. Qual.: Int. J.* **20**, 422-433.
- Stabenau, E. K., Stanley, K. S. and Landry, A. M. (1996). Sex ratios from stranded sea turtles on the upper Texas Coast. *J. Herpetol.* **30**, 427-430.
- Stocker, T. F. and Schmittner, A. (1997). Influence of CO₂ emission rates on the stability of the thermohaline circulation. *Nature* **388**, 862-865.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., de Siqueira, M. F., Grainger, A., Hannah, L. et al. (2004). Extinction risk from climate change. *Nature* **427**, 145-148.
- Tomas, J., Aznar, F. J. and Raga, J. A. (2001). Feeding ecology of the loggerhead turtle *Caretta caretta* in the western Mediterranean. *J. Zool.* **255**, 525-532.
- Tomas, J., Gazo, M., Alvarez, C., Gozalbes, P., Perdiguero, D., Raga, J. A. and Alegre, F. (2008). Is the Spanish coast within the regular nesting range of the Mediterranean loggerhead sea turtle (*Caretta caretta*)? *J. Mar. Biol. Assoc. UK* **88**, 1509-1512.
- Van Houtan, K. S. and Bass, O. L. (2007). Stormy oceans are associated with declines in sea turtle hatching. *Curr. Biol.* **17**, R590-R591.
- Verity, P. G., Smetacek, V. and Smayda, T. J. (2002). Status, trends and the future of the marine pelagic ecosystem. *Environ. Conserv.* **29**, 207-237.
- Webster, W. D. and Cook, K. A. (2001). Intraseasonal nesting activity of loggerhead sea turtles (*Caretta caretta*) in southeastern North Carolina. *Am. Mid. Nat.* **145**, 66-73.
- Weishampel, J. F., Bagley, D. A. and Ehrhart, L. M. (2004). Earlier nesting by loggerhead sea turtles following sea surface warming. *Glob. Chang. Biol.* **10**, 1424-1427.
- Wetterer, J. K., Wood, L. D., Johnson, C., Krahe, H. and Fitchett, S. (2009). Predaceous ants, beach replenishment, and nest placement by sea turtles. *Environ. Entomol.* **36**, 1084-1091.
- Whitmore, C. P. and Dutton, P. H. (1985). Infertility, embryonic mortality and nest-site selection in leatherback and green sea turtles in Suriname. *Biol. Conserv.* **34**, 251-272.
- Wibbels, T. (2003). Critical approaches to sex determination in sea turtles. In *The Biology of Sea Turtles*, vol. 2 (eds P. L.utz, J. A. Musick and J. Wyneken), pp. 103-134. Boca Raton: CRC Press.
- Witherington, B. E. (2002). Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. *Mar. Biol.* **140**, 843-853.
- Witt, M. J., Broderick, A. C., Johns, D. J., Martin, C., Penrose, R., Hoogmoed, M. S. and Godley, B. J. (2007a). Prey landscapes help identify potential foraging habitats for leatherback turtles in the northeast Atlantic. *Mar. Ecol. Prog. Ser.* **337**, 231-244.
- Witt, M. J., Penrose, R. and Godley, B. J. (2007b). Spatio-temporal patterns of juvenile marine turtle occurrence in waters of the European continental shelf. *Mar. Biol.* **151**, 873-885.
- Wyneken, J., Epperly, S. P., Crowder, L. B., Vaughan, J. and Esper, K. B. (2007). Determining sex in posthatchling loggerhead sea turtles using multiple gonadal and accessory duct characteristics. *Herpetologica* **63**, 19-30.
- Yntema, C. and Mrosovsky, N. (1980). Sexual differentiation in hatchling loggerheads (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* **36**, 33-36.
- Zbinden, J. A., Margaritoulis, D. and Arlettaz, R. (2006). Metabolic heating in Mediterranean loggerhead sea turtle clutches. *J. Exp. Mar. Biol. Ecol.* **334**, 151-157.
- Zbinden, J. A., Aebischer, A., Margaritoulis, D. and Arlettaz, R. (2008). Important areas at sea for adult loggerhead sea turtles in the Mediterranean Sea: satellite tracking corroborates findings from potentially biased sources. *Mar. Biol.* **153**, 899-906.
- Zug, G. R., Balazs, G. H., Wetherall, J. A., Parker, D. M. and Murakawa, S. K. K. (2002). Age and growth of Hawaiian green sea turtles (*Chelonia mydas*): an analysis based on skeletochronology. *Fish. Bull.* **100**, 117-127.