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

Short title: Marine turtles and climate change

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Abstract

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 ultimately centre upon the thermal ecology of this taxonomic group. Then, focussing in detail on three decades of research on the loggerhead turtle (*Caretta caretta*), 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?
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 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%) from 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 and ‘great flood’ events 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 CO$_2$ 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 recognized 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; Gremillet and Bioulénier, In press; Hawkes et al., 2007b; MacLeod, 2009; Newson et al., 2009); 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 (1984) and Davenport (1989), it is only recently that significant research effort has been expended on the field (reviewed by Hamann et al., 2007; Hawkes et al., 2009). Although sea
turtles are exposed to climate change threats both at sea and on 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 on 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 current available nesting area 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 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). On available areas of nesting beach, incubating clutches could be
at risk from an increasing sea level 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) lay
deeper nests than loggerhead turtles (Caretta caretta) (Hannan et al., 2007), and leatherback turtles
(Dermochelys coriacea) 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;
Cathy 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). Alternatively, increasing temperatures may open up
areas that were previously inaccessible to nesting. Indeed, nests are now being discovered
increasingly further north (see Bentivegna et al. (2005); Sénégas et al.(2008); Tomas et al. (2008)).
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 (Avise 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 is 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.,
2009), and range further from the equator, such as into Canadian (James et al., 2005) waters 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 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**

Likely as a result of extensive presence within the waters of affluent nations such as USA, Japan, Australia and those of the Mediterranean, the loggerhead turtle (*Caretta caretta*) is one of the most studied sea turtle species, and we therefore select it for the focus of this review. For the purposes of this work we have taken an Atlantic and Mediterranean wide view of this species due to the wealth of published data describing reproductive biology, feeding ecology and population trends from long term studies available for populations from these two ocean basins. We consider several aspects of the thermal biology of loggerhead sea turtles in relation to projected climate change, highlighting the progress that has been made and the steps towards predicting and understanding impacts.

The loggerhead turtle nests in tropical and sub-tropical regions. The largest known rookeries are in the southeast United States of America and Cape Verde (Figure 1a); with nesting also occurring along the Brazilian coast within the South Atlantic basin. In the Mediterranean Sea (Figure 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 are thought to demonstrate some degree of natal philopatry (Bowen and Karl (2007), although with some variations, see Lee (2008)) returning as adults to their natal beach regions to breed. Females typically reproduce 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 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 (1980), with warmer incubation temperatures producing more females, and cooler temperatures producing more males. Although early work was conducted under laboratory conditions, attention moved to field studies to assess whether hatchling sex ratios were different from 1:1 as predicted by 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 has been conducted by incubating eggs, from a variety of different populations from different latitudes, in controlled laboratory conditions, and has suggested that there is little variation in the pivotal temperature (Mrosovsky 1988, Mrosovsky and Pieau, 1991). Subsequent studies of laboratory incubation of loggerhead turtle eggs from Brazil and Greece have found similar pivotal temperatures - close to 29 °C, as have field-based estimates of pivotal temperature from the Mediterranean (Table 1). Thus variation in sex ratios observed in the wild (Figure 2) are 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 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 period of loggerhead 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., 2001b; 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 (Mrosovsky et al., 1999). Validation is especially important as most of these studies use pivotal temperature or pivotal incubation data from laboratory studies that also are 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 most pivotal values based on just two clutches (Table 1). 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 and more balanced sex ratios (i.e. closer to 1:1) at rookeries that are further away from the equator (Figure 3a, Spearman rank-order correlation using absolute latitude versus arc-sine transformed percentage of females produced at each rookery, n = 10, rho = -0.22, p = 0.54). In the case of the south-east USA, 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, Rio de Janeiro state 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 (Figure 1b), and loggerhead hatchling sex ratios (Figure 3b) are estimated to be female biased on most beaches (Godley et al., 2001b; Oz et al., 2004; Zbinden et al., 2006), with beaches of southerly latitude showing a general trend towards a greater female bias (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 average global air and sea surface temperatures will rise, and with them so will sand temperatures at 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., In press). If sea turtles do not adapt by shifting their geographic 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 loggerhead turtle 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 thereof) 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 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 (~33°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 (Figure 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 detailed studies in Cyprus we know, for example, that mean clutch temperatures during 1996 to 1999 (Godley et al., 2001a) were ~4 °C warmer than sea surface temperature, likely, at least in part, 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 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: Blanvillain et al. (2008), by hormonal assay (possible in individuals >2-3 years age): Braun-McNeill et al., (2007), or by secondary sexual features in mature individuals, have to be undertaken. Notwithstanding cost, such studies require expertise and need to be undertaken over a long period (>10 years). It is not surprising therefore that there exist few data in the peer-reviewed literature to elucidate whether skewed hatchling sex ratios are reflected in the wider population.

Work that has been published for loggerhead turtles however, suggests that a female bias remains in the juvenile and adult population (approximately 2 females to 1 male; Table 2). A lag between hatching 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., (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., In press) it is conceivable that there will be a critical adult sex ratio beyond 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 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 change predictions, might be applied. The predominant variable used in bioclimatic envelope modelling is temperature, and as ectotherms it is likely a good descriptor of the fundamental niche of sea turtles. However, the realised niche may be somewhat smaller, as augmented by prey and predator distribution and inter and intra-specific competition. Therefore with further characterisation of these variables (Witt et al., 2007a), models might predict
available habitat under future climate change scenarios with greater specificity. In the absence of such data for loggerhead turtles, we limit our discussion to modelling the fundamental (thermal) niche.

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) 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 to 2089, Figure 5). For the Mediterranean Sea we took an alternative approach, displaying the mean March 15°C isotherm over successive 20-y periods (Figure 6). Within the annual cycle of sea surface temperature in the Mediterranean Sea, March represents the coldest month when cheloniid 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 to 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. These models do not, as yet, factor in potential habitat losses, if any, to exceptionally warm waters. Furthermore, they can not reasonably factor in predicted changes in prey distribution, given the generalist diet of the loggerhead turtle. Truly holistic predictive modelling for these species is far from trivial. However, when available, future habitat suitability models could be integrated with climate change predictions, using methodologies such as ours, to make and test predictions about range alterations.
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 reseeding 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 non-destructive marker to identify hatchling sex, 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 are only part of a suite of other threats such as direct exploitation, fisheries bycatch 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.
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References


Caretta caretta, testing areas at Praia do Forte, Brazil. Hatchling loggerhead sea turtles at Patara beach on the southwestern coast of Turkey.


Legends

Figure 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).


Figure 3. Relationship between latitude and percentage of female hatchlings produced at nesting rookeries in (a) Atlantic Ocean and (b) Mediterranean Sea. The latitudes of nesting rookeries with sex ratio data were expressed as absolute values. Arabic numbers indicate source literature as described in Figure 2.

Figure 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, Jan. 1870 to May 2009; Hadley Ice and Sea Surface Temperature (HadISST) dataset; Rayner et al., (2003)). Forecast sea surface temperature (open squares, Jun. 2009 to Nov. 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 Intercomparision 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, Massachusetts, US). 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).

Figure 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-y duration sea surface temperature datasets were constructed. Each 20-y dataset comprised of 240 months of spatially gridded mean monthly SST data. Each pixel of each 20-y gridded SST dataset was scored as 0 or 1 according to thermal suitability (i.e. < 15°C = 0 & ≥ 15°C =1), following the method of 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.

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

Table 1. Pivotal temperatures for loggerhead sea turtles in the Atlantic Ocean and Mediterranean Sea. 1Study used 2 clutches; 2Field-based; 3Two study clutches from one beach in Cyprus and six from four different beaches in Turkey combined to calculate pivotal.

<table>
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<th>Location</th>
<th>Pivotal °C</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Source</th>
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<tr>
<td>Cumberland Is., GA, USA</td>
<td>28.5</td>
<td>30.86</td>
<td>-81.42</td>
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</tr>
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<td>35.93</td>
<td>32.35</td>
<td>Kaska et al., (1998)(^2,3)</td>
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<tr>
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<td>27.07</td>
<td>-80.12</td>
<td>Mrosovsky (1988)(^1)</td>
</tr>
<tr>
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<td>33.84</td>
<td>-77.97</td>
<td>Mrosovsky (1988)(^1)</td>
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<tr>
<td>Bahia Brazil</td>
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<td>-10.38</td>
<td>-37.67</td>
<td>Marcovaldi et al., (1997)(^1)</td>
</tr>
<tr>
<td>Kyparissia, Greece</td>
<td>29.3</td>
<td>37.25</td>
<td>21.66</td>
<td>Mrosovsky et al., (2002)(^1)</td>
</tr>
</tbody>
</table>

Table 2: Reported juvenile and adult sex ratios for loggerhead turtles. Method of sexing: laparoscopy (LAP), radioimmunoassay (RIA) or observation of gross anatomical features (OBS).

<table>
<thead>
<tr>
<th>Location</th>
<th>Life stage</th>
<th>% ♀</th>
<th>Method</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Atlantic, USA</td>
<td>Juvenile</td>
<td>67.7</td>
<td>LAP</td>
<td>Braun-McNeill et al., (2007)</td>
</tr>
<tr>
<td>Atlantic, USA</td>
<td>Juvenile</td>
<td>74.5</td>
<td>RIA</td>
<td>Braun-McNeill et al., (2007)</td>
</tr>
<tr>
<td>Atlantic, USA</td>
<td>Juvenile</td>
<td>66.0</td>
<td>OBS</td>
<td>Stabenau et al., (1996)</td>
</tr>
<tr>
<td>Atlantic, USA</td>
<td>Juvenile</td>
<td>65.3</td>
<td>OBS</td>
<td>Shoop et al., (1998)</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>Adult</td>
<td>76.5</td>
<td>OBS</td>
<td>Casale et al., (2005)</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>Juvenile</td>
<td>54.2</td>
<td>OBS</td>
<td>Casale et al., (2006)</td>
</tr>
</tbody>
</table>
Figure 1
Figure 2
Figure 3