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The impacts of climate change on marine turtle reproductive success

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WHY MARINE TURTLES?

Ectothermic species are fundamentally affected by environmental temperatures, which largely dictate their metabolic rate. In marine turtles, foraging behavior, migratory patterns, and ultimately breeding success may be modulated by the environment and influenced by climate change. This has the potential to have both positive and negative effects. The seven species of marine turtles broadly occupy three foraging niches (planktivory, herbivory, and omnivory) and occur in almost every non-polar ocean basin in the world, from shallow coastal seas to open ocean habitats. The effects of climate change to marine turtles likely will be wide ranging and of direct relevance to other marine animals in these varied habitats. Marine turtles are a fascinating "canary in the coal mine" with which to study the effects of climate change in marine habitats, and there has been an exponential increase in interest in the effects of climate change on them in the last decade (Poloczanska *et al.*, 2009; Hamann *et al.*, 2010; Hawkes *et al.*, 2010). Marine turtles are also generally considered charismatic, making them ideal subjects with which to raise awareness of climate change effects to biodiversity and to increase support for effective management and conservation of marine environments.

In addition, marine turtles have survived dramatic climate change in the past. Marine turtles are among the most ancient of the marine vertebrates, with fossil evidence of leatherback turtles (*Dermochelys coriacea*) suggesting that they have existed in their extant form for at least 900 000 years (Dutton *et al.*, 1999). Over this period the climate has undergone dramatic fluctuations, and marine turtles have evidently adapted and persisted, surviving to the present day. However, many marine turtle populations are now

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dramatically depleted, having been harvested for their meat, eggs, and attractive shells in huge numbers up until the end of the nineteenth century (reviewed in McClenachan *et al.*, 2006). Consequently, six of the seven species of marine turtles were added to the IUCN red list of threatened species in 1986 (www.iucnredlist.org; the seventh species, the flatback turtle (*Natator depressus*), was added in 1994), with many modern populations at relictual levels compared to historic past. For example, Caribbean green turtles (*Chelonia mydas*) are thought to be at only 0.3% of historic population numbers (McClenachan *et al.*, 2006; Bell *et al.*, 2007, 2009). Massive-scale population reduction of this sort can inhibit the ability of a population to recover through depensation, affecting fitness and reproduction, although evidence for this phenomenon is, as yet, lacking in marine turtles (Bell *et al.*, 2009). Although hunting pressure is now largely absent and some populations of marine turtles are thought to be increasing (Allen *et al.*, 2010), the modern threat of climate change will be set against a very different biological background than marine turtles would have experienced in the past.

Since its inception, the study of marine turtle biology has been biased toward studies on beaches, where marine turtles are more accessible for research than in the open ocean. Projects observe and record female turtles arriving on shore to lay nests of approximately 100 eggs at two-week intervals (although this varies by species) and often follow the clutches of eggs for up to two months until they hatch. The precocial hatchling turtles typically enter the water at night *en masse* and disperse to largely unknown developmental grounds. This window of opportunity for study has been used for some six decades, and much of the breeding biology of marine turtles, particularly a few key species and regions, is now well understood. The effects of climate change on it, however, are not.

In this chapter, we will describe the effects that climate change may have on the reproductive cycle of marine turtles (Figure 10.1), from adult turtles as they arrive in breeding areas to mate, to females ascending their natal beach to lay successive clutches of eggs, how the embryos themselves develop underground, effects of the incubation environment on hatchling morphology, sex, and survivorship, and finally as hatchlings emerge from the beach and depart to the ocean.

TIMING OF BREEDING

Marine turtles congregate to mate in the vicinity of their natal beaches, the region where they hatched some decades earlier (Limpus, 1993;

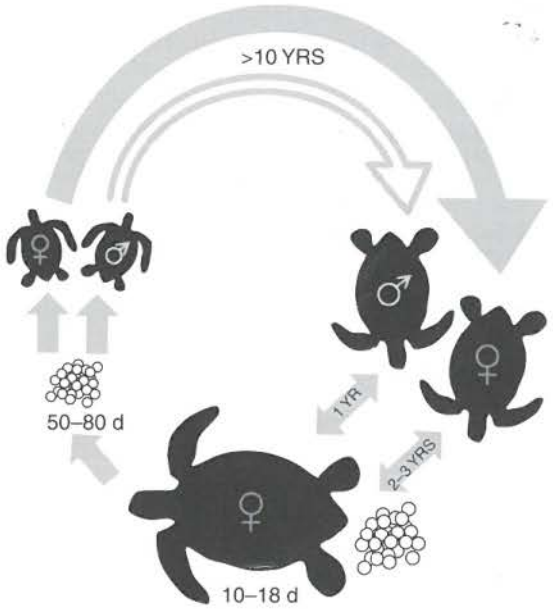

Figure 10.1 Schematic showing the generalized life cycle of marine turtles. Adult female turtles visit the nesting beach every 2–3 years, laying up to eight clutches of eggs at 10- to 18-day intervals. Adult male turtles are thought to visit the nesting beach annually. Nests (with 80–140 eggs) incubate for between 50 and 80 days, with incubation temperature determining hatchling sex. Hatchling and juvenile sea turtles develop in cryptic and poorly understood nursery areas before recruiting back to the adult foraging areas some decades later. (See color plate section.)

Fitzsimmons *et al.*, 1997; Lee *et al.*, 2012. Adult female turtles are known to breed every two to three years (Miller, 1997; Beggs *et al.*, 2007), while adult male turtles are thought to visit breeding areas annually (FitzSimmons *et al.*, 1997; James *et al.*, 2005a, 2005b; Hays *et al.*, 2010, but see Wright *et al.* 2012, which suggests that male green turtles in Cyprus may not breed annually). This tendency may reflect the differential overall investment of the sexes in reproduction, with females probably investing considerably more than males (Pearse & Avise, 2001). The resources for this investment will have been derived from foraging areas, the quality of which is linked to environmental conditions; therefore, a turtle's decision to breed or not in a given year may be affected by the changing climate (Kwan, 1994; Broderick *et al.*, 2001; Solow *et al.*, 2002; Wallace *et al.*, 2006; Saba *et al.*, 2007, 2008; Chaloupka *et al.*, 2008; Reina *et al.*, 2009). Given that seas are already warming and are expected to continue to do so in the future, we

Table 10.1 *Studies assessing changes in marine turtle nesting season onset and duration (nesting phenology) in response to increased sea surface temperatures recorded nearby the nesting beach.*

Species	Location	Nesting season onset	Nesting season length	Key reference(s)
Loggerhead	Archie Carr Wildlife Refuge, FL USA	Earlier	Shorter	Weishampel *et al.*, 2004, 2010
Loggerhead	Cape Canaveral, FL USA	Earlier	Shorter	Pike *et al.*, 2006
Loggerhead	Bald Head Island, NC USA	Earlier	Longer	Hawkes *et al.*, 2007
Loggerhead	Zakynthos, Greece	Earlier	No change	Mazaris *et al.*, 2009
Loggerhead	USA and Mediterranean	Earlier	Longer	Mazaris *et al.*, 2013
Loggerhead	FL, USA	Earlier	Longer	Lamont & Fujisaki, 2013
Green	Archie Carr Wildlife Refuge, FL USA	Earlier	Longer	Weishampel *et al.*, 2010
Green	Cape Canaveral, FL USA	No change	No change	Pike, 2009
Hawksbill	Long Island, Antigua	Earlier	No change	Ditmer & Stapleton, 2012

might expect phenological changes, that is, changes in the onset and the duration of the reproductive cycle, to be occurring (Witt *et al.*, 2010); indeed, there is evidence that this is happening (Table 10.1). Warmer spring sea-surface temperatures appear to elicit earlier onset of nesting, although the effect of temperature on the duration of the nesting season is uncertain (Mazaris *et al.*, 2013; Table 10.1). Additionally, there is no method at present to document the long-term arrival dates of male and female turtles to the breeding grounds (except to satellite track individuals at considerable expense per turtle). The effects of climate change to turtle mating phenology appear to vary in strength with latitude of nesting beaches (Mazaris *et al.*, 2013). Additionally, phenological changes in reproduction may be challenging to document for some nesting populations because the reproductive population may consist of cohorts of turtles that migrate from different foraging areas and are subject to varying environmental cues early in the reproductive cycle (Hamann *et al.*, 2007). Moreover, monitoring of nesting beaches may not occur early or late enough in the nesting season to document subtle changes in the timing of nesting. Nevertheless, phenological changes in reproductive seasonality may be one of the most tractable ways for marine turtles to adapt to climate change.

NESTING BEACH AVAILABILITY

Gravid female turtles are known to lay their clutches of eggs on or near their natal beaches. This mechanism promotes evolutionary selection for beaches that deliver successful incubation and hatching and selects against poor quality beaches from which fewer hatchlings successfully emerge (Freedberg & Wade, 2001).

Climate change may reduce the availability of nesting beaches by a combination of: (1) sea level rise; (2) coastal squeeze, where natural beaches cannot recede due to human coastal developments in the way (Fish *et al.*, 2005, 2008); and (3) coastal erosion due to increased frequency and severity of storms (Fuentes *et al.*, 2010, 2011). Marine turtles are poor locomotors on land, and consequently almost all marine turtle nesting beaches tend to be low-lying with short tidal ranges (Mortimer, 1990; Miller, 1997). In the simplest case scenario, sea level rise would mean a typical nesting beach would be inundated higher up the shoreline, reducing the net area available for egg-laying and successful incubation. In modeled case studies in Barbados, Bonaire, Greece, and Hawaii, up to half the beach was lost (Fish *et al.*, 2005, 2008; Baker *et al.*, 2006; Mazaris *et al.*, 2009). However, in most natural shoreline systems, beaches may not only be eroded but also accreted, and highly dynamic dune systems behind them simply retract and expand accordingly, with environmental forces governing their zonation (Thom & Hall, 1991). Such beach retreat has probably made suitable nesting beach available for marine turtles for millennia. Beach retreat, however, cannot occur where coastal development (e.g. buildings, sea walls, and coastal fortifications) exists close to the tide line (Nicholls, 1998; Fish *et al.*, 2005, 2008; Baker *et al.*, 2006; Jones *et al.*, 2007; Mazaris *et al.*, 2009; Witherington *et al.*, 2011a, 2011b). Coastal erosion takes place instead, often with loss of high value coastal property (as well as turtle nesting beach; Figure 10.2). As a consequence, shoreline protection (fortification of human coastal settlements using sea walls, jetties, and other hard-engineered structures) has been erected in many key turtle nesting areas, leading to partial or total loss of nesting beaches (Pilkey & Wright, 1988; Koike, 1996; Kraus & McDougal, 1996; Lutcavage *et al.*, 1997; Bouchard *et al.*, 1998; Burke & Maidens, 2004; Airoldi *et al.*, 2005; Zheng *et al.*, 2007; Dugan *et al.*, 2008; Schlacher *et al.*, 2008; Rizkalla & Savage, 2011).

Other projects seek to maintain the beach *in situ*, for example, using beach renourishment, but such approaches are yet far from ideal. This offshore-sourced material is not always suitable for nesting and incubation, having a high mud and silt content, which causes it to be compact and

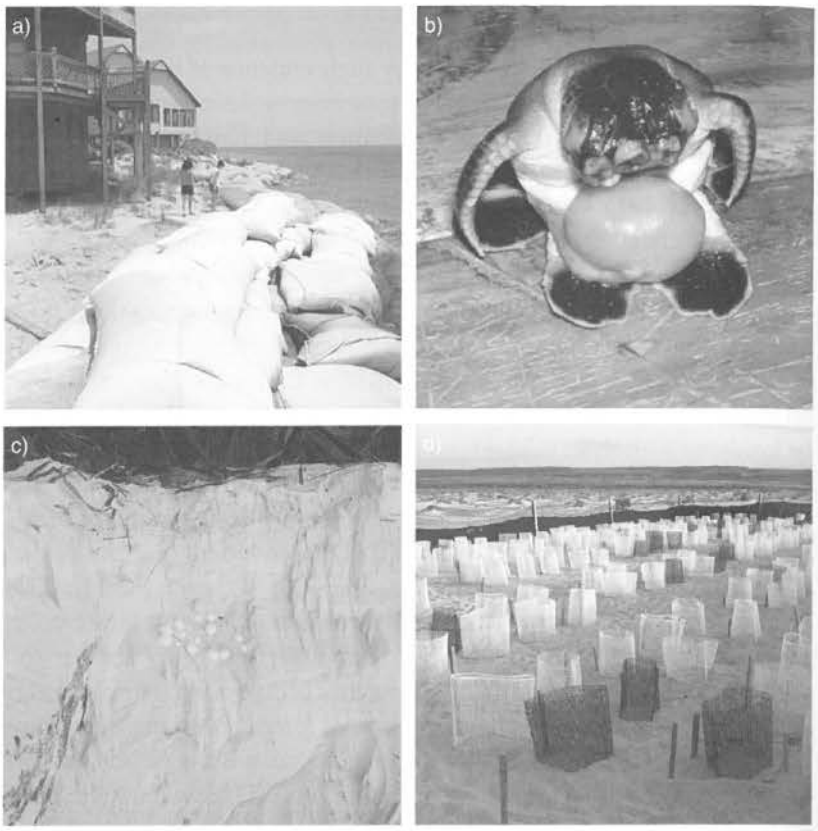

Figure 10.2 **(a)** Nesting beach may be lost through coastal squeeze, where beach is eroded but coastal development prevents its retreat (here valuable coastal property in North Carolina, USA is defended by sand bags); **(b)** hatchling deformities, such as this two-headed green turtle (*Chelonia mydas*) from a nest in Cyprus, may result from altered nest incubation temperatures; **(c)** nests can be washed out by storms and unusually high tides. This nest has been exposed in the bank of an escarpment; **(d)** eggs that may fail to develop due to unusually high incubation temperatures or non-viable incubation conditions may be moved to hatcheries. (Photo credits: (a) Matthew Godfrey, (c) David Wright, (b, d) Lucy Hawkes.) (See color plate section.)

difficult for turtles to dig nests in. Dredged material may also be darker in color than the original sand it replaces, and may have a higher content of environmental contaminants, particularly if dredged from shipping channels where fuel and fouling chemicals may be concentrated (Crain *et al.*, 1995; Milton *et al.*, 1997; Rumbold *et al.*, 2001; Peterson & Bishop, 2005; Montague, 2008; Brock *et al.*, 2009). There has even been a suggestion to use ground glass cullet as a fill material (Makowski *et al.*, 2008), although to

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date, egg incubation has not been tested in this material. Ideally, beaches should be renourished with sand matched to the original grain size, material content, and albedo of the target beach, but ultimately renourishment projects provide only short-term (and high-cost) solutions to beach erosion and sea level rise, with subsequent nourishment usually required after only a few years (Montague, 2008). More long-term studies are needed to assess cumulative impacts of repeated beach nourishment projects on marine turtles.

The loss of nesting beaches may be compounded by an increase in the proportion of extreme weather events (Goldenberg *et al.*, 2001; Webster *et al.*, 2005, Cowell *et al.*, 2006; Leslie *et al.*, 2007), many of which may make landfall at turtle nesting beaches in temperate and tropical areas (Martins, 1996; Bengtsson, 2001; Ross, 2005; Pike & Stiner, 2007; Prusty *et al.*, 2007; Van Houtan & Bass, 2007; Fuentes & Abbs, 2010). Extreme weather events may cause significant nesting beach loss, as well as washing out and terminating nests already incubating on beaches (Milton *et al.*, 1994), which will not be replaced, unlike many other taxa such as birds that exhibit parental care and can re-lay after nest loss. How marine turtles respond to total beach loss remains to be seen, although some insight may be gleaned from Suriname and French Guiana. There, green, leatherback, and olive ridley (*Lepidochelys olivacea*) turtle nesting beaches are so dynamic that they may be completely eroded from one season to the next (Schulz, 1975; Girondot & Fretey, 1996; Rivalan *et al.*, 2006; Kelle *et al.*, 2007), yet high-magnitude, successful nesting persists in the region. This observation suggests a high degree of plasticity in nesting beach fidelity, at least in this region, and may belie more flexibility in nest site selection by marine turtles than is commonly accorded. Species with lower site fidelity (nests spread over a greater area) might be expected to be more resilient to the effects of beach loss than species with highly precise repeat nest placement (Pike & Stiner, 2007).

Evidence exists that marine turtles are able to colonize new beaches, with nesting having been recorded at both newly formed natural and artificial beaches (Hoggard, 1991; Bowen *et al.*, 1993; Encalada *et al.*, 1998; Bell *et al.*, 2005; Mrosovsky, 2006; Hamann *et al.*, 2007), and it therefore seems likely that beaches that were previously too cool for successful incubation may be opened to nesting by climate change. Leatherback and loggerhead (*Caretta caretta*) turtles are now nesting at their furthest north since records began (Rabon *et al.*, 2004; Sénégas *et al.*, 2008; Bentivegna *et al.*, 2010), suggesting that this phenomenon might already be occurring. In addition, evidence exists that populations of turtles can be translocated – the critically endangered

Kemp's ridley turtle (*Lepidochelys kempii*) was subject to high levels of harvest at what was effectively its only nesting site in Mexico (Plotkin, 2007). In response, a conservation project moved entire clutches of eggs immediately after laying to beaches in Texas, USA, where they were afforded complete protection from harvest (Manzella *et al.*, 1988). Nesting by adult females from those clutches at these new natal beaches takes place today (Shaver & Caillouet, 1998).

NEST PLACEMENT

Marine turtles generally lay their eggs between the high-tide and vegetated line on temperate, subtropical, and tropical beaches, ensuring that eggs have a warm, dry incubation environment, safe from excessive tidal overwash that can reduce hatching success (Caut *et al.*, 2010). Different species of marine turtles appear to have different selection criteria for nesting beaches (Mrosovsky, 1983; Whitmore & Dutton, 1985; Hays *et al.*, 1995; Kamel & Mrosovsky, 2004, 2005). For example, the huge leatherback sea turtle selects short, steep nesting beaches to minimize the distance over which it must crawl to reach dry sand, while hawksbill turtles (*Eretmochelys imbricate*), a smaller marine turtle species, nest on much less dynamic, flatter beaches, and may travel far into dunes to lay their clutches. Varying beach types will be differentially affected by sea level rise (e.g. flatter beaches might be more quickly inundated and lose a greater total area than steeper beaches) (Slott *et al.*, 2006), leading to greater impacts for some turtle species or populations. However, factors influencing nest site selection are not understood, making it difficult to predict how marine turtles might respond to changing shorelines. Comparative studies involving different species will facilitate better prediction of how turtles may respond to changing beach profiles (Mrosovsky, 2006; Wetterer *et al.*, 2009; Cuevas *et al.*, 2010; Garcon *et al.*, 2010).

SEX RATIOS

For marine turtles (as well as many reptilian species), sex is determined by the temperature of the incubation environment. Marine turtles have temperature-dependent sex determination (TSD; Ewert *et al.*, 2004), where females are produced at warmer temperatures and males at cooler temperatures, with 50% of each sex at the pivotal temperature (Mrosovsky, 1988; Figure 10.3). The shape of the relationship between temperature and sex is sigmoidal, such that there is a narrow range of

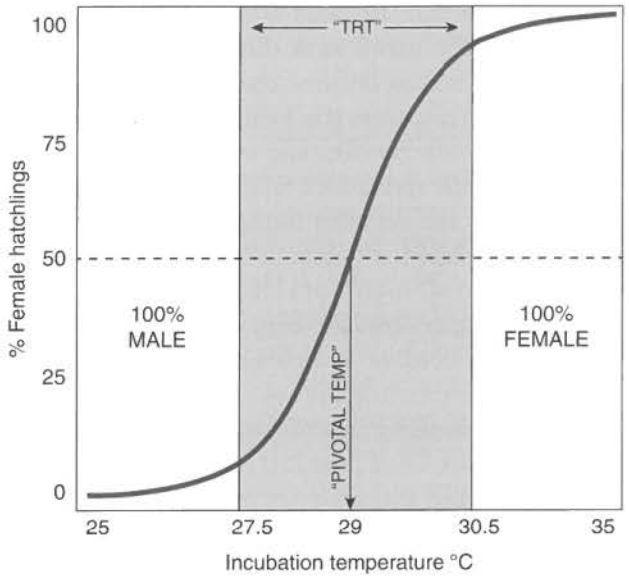

Figure 10.3 Schematic figure showing temperature-dependent sex determination (TSD) in a generic marine turtle species, where on a sigmoidal curve females are produced at warmer temperatures and males at lower temperatures. Production of equal numbers of males and females occurs at the pivotal temperature. A mixture of sexes can be produced in the Transitional Range of Temperatures (TRT), and eggs generally fail to successfully hatch outside of a ~10°C range of temperatures (26–36°C).

temperatures (the Transitional Range of Temperatures, TRT) over which both male and female offspring are produced (Yntema & Mrosovsky, 1980, 1982; Figure 10.3). Within each incubating clutch of eggs, temperature can vary; eggs at the periphery of the clutch are often cooler than eggs in the center, as are eggs at the bottom of the nest furthest from the penetrating warmth of the sun (Kaska *et al.*, 1998). A developing clutch of eggs produces enough metabolic heat to increase the overall incubation temperature by approximately 1°C; therefore, smaller clutches tend to be cooler than larger ones (Godfrey *et al.*, 1997; Broderick *et al.*, 2001; Zbinden *et al.*, 2006; Sandoval *et al.*, 2011). In addition, the extent to which the clutch is warmed by solar radiation will differ with sand albedo, as darker sands absorb and retain more heat (Standora & Spotila, 1985; Hays *et al.*, 1995; Reece *et al.*, 2002). Nests may also be subject to punctuated temperature changes. For example, rainfall events may reduce the clutch temperature by several degrees for a few hours (Godfrey *et al.*, 1996; Houghton *et al.*, 2007; Steckenreuter *et al.*, 2010). Daily thermal variance can have an impact on

sex ratios of turtles with TSD (Neuwald & Valenzuela, 2011), although this effect is likely minimal for marine turtle clutches placed deep within beach sand. Finally, on some nesting beaches, conservationists sometimes translocate and rebury eggs in hatcheries (Figure 10.2d), where eggs are thought to be safer from predation (by humans and other animals) or poor weather conditions (i.e. storms and spring high tides). In general, hatcheries host a higher density of nests and are often further up the shore, making them warmer than natural incubation conditions (Morreale *et al.*, 1982; Chan & Liew, 1995; Baptistotte *et al.*, 1999; Naro-Maciel *et al.*, 1999).

Temperature-logging devices have been used in the field to record nest temperatures on many beaches, and published equations describing the relationship between temperature and sex are used to estimate with increasingly sophisticated modeling approaches the proportion of male and female hatchlings that are being produced (Fuentes & Porter, 2013). Many studies have demonstrated that nests are normally female-biased, and in some cases produce no male hatchlings at all (Hawkes *et al.*, 2010). Given that females are produced at higher temperatures and that the climate is expected to warm, these data suggest that an even higher proportion of female hatchlings may result (Hawkes *et al.*, 2007; Fuentes *et al.*, 2009; Mitchell & Janzen, 2010; Fuentes & Porter, 2013), potentially leading to a shortage or extirpation of males. If this were to happen, marine turtles would have to adapt or modify one or more of four traits to persist in this new climate: (1) pivotal temperature; (2) TRT; (3) nest site fidelity; and (4) nesting phenology (Mitchell & Janzen, 2010). Changing the pivotal temperature (for example, to be higher) could mean that more males would be produced for the same incubation temperature. Changing the TRT (for example, making it wider) would mean that mixed-sex clutches could be produced over a wider range of temperatures (and it would be less likely that one sex would be in short supply). This adaptation has been recorded in freshwater turtles (Hulin *et al.*, 2009), where a wider TRT is linked to more mixed-sex clutches, and, interestingly, appears to be correlated to latitude, with wider TRT at higher latitudes (Ewert *et al.*, 2005). Alternatively, reducing nest site fidelity could increase the chances of nests being laid in cooler parts of the same beaches (in more shaded areas, or in paler sands) or on different beaches, and therefore could produce more males overall. Finally, changing nest phenology would mean that nests might be laid earlier or later in the year when temperatures are cooler, which would also produce more males. For example, Tucker and colleagues (2008) showed that, for red-eared sliders, an overall male-biased sex ratio can occur even with increased climatic warming due to changes in the length of the nesting season.

Some recent studies have suggested that marine turtles might already be adapting to the changing climate; some populations are apparently nesting earlier in the season (Table 10.1) or at higher latitudes (Rabon *et al.*, 2004; Weishampel *et al.*, 2004; Doody *et al.*, 2006; Hawkes *et al.*, 2007). Even failing to adapt might not be detrimental; along with overall increasing temperatures, the future climate is expected to become more interannually variable (IPCC, 2007), so clutch incubation temperatures from one year to the next are expected to be very different. This will potentially maintain more variable sex ratios (Neuwald & Valenzuela, 2011), which may support population growth and new nesting site colonization (Kallimanis, 2010).

Despite some concern that few male hatchlings are produced (Hawkes *et al.*, 2007; Fuentes *et al.*, 2009; Mitchell & Janzen, 2010; Valverde *et al.*, 2010), it is important to assess if this is likely to be a problem in the future (e.g. Bell *et al.*, 2009; Schwanz *et al.*, 2010). Because adult male sea turtles rarely leave the ocean, it is more difficult to count them than it is adult female turtles that are tagged on nesting beaches and followed through many reproductive seasons. Because sea turtles are promiscuous and do not form long-term pair bonds, one way to try to gain an understanding of how many reproductively active male turtles are at large relative to reproductively active females (the operational sex ratio) is to measure the number of fathers siring each clutch of eggs (multiple paternity). This measure should reflect the relative numbers of males at the breeding area prior to the nesting season (Hays *et al.*, 2010; Stewart & Dutton, 2011). For example, if males were in short supply, one should expect to see few fathers per clutch, or even unfertilized eggs laid on nesting beaches. Multiple paternity has been shown to occur in all seven sea turtle species (Table 10.2), although it does not occur in all populations or in all clutches laid within a single population (Phillips *et al.*, 2013). Generally, at least some clutches will be fathered by multiple males (polyandry), but those same males may have mated with other females (polygyny). A recent study by Wright and colleagues (2012) has shown that in a population of green turtles with 30% of clutches exhibiting multiple paternity, the estimated adult breeding sex ratio was 1.4 males : 1 female. Further work by Wright and colleagues (2012) demonstrated similar sex ratios in subsequent years. Multiple paternity may be complex; its drivers may vary with population size and mating strategy (Jensen *et al.*, 2006), and its fitness consequences may be questionable (Lee & Hays, 2004). Nevertheless, its presence may at least suggest that the operational sex ratio may not yet be dramatically skewed. No data yet exist to describe if multiple paternity changes over time, but these data should be collected as a priority.

Table 10.2 *Studies recording multiple paternity in egg clutches of marine turtles (see also summary tables in Pearse & Avise, 2001; Jensen* et al., *2006; Bowen & Karl, 2007; Uller & Olsson, 2008).*

Species	Proportion nests with MP (%)	Max. fathers	Country	Key reference(s)
Loggerhead	31.4	3	Florida, USA	Moore & Ball, 2002
Loggerhead	38.1	3	Mon Repos, Australia	Harry & Briscoe, 1988
Loggerhead	33.0	2	Florida, USA	Bollmer *et al.*, 1999
Loggerhead	94.7	5	Greece	Zbinden *et al.*, 2007
Loggerhead	50	2	Tunisia	Chaieb *et al.*, 2010
Loggerhead	75	7	Georgia, USA	Lasala *et al.*, in press
Loggerhead	43	3	Japan	Sakaoka *et al.*, 2011*[3]
Loggerhead	46	3	Japan	Sakaoka *et al.*, 2012*[3]
Green	30	4	Cyprus	Wright *et al.*, 2012**
Green	55.6	5	Ascension Island	Lee & Hays, 2004
Green	9.01	2	GBR, Australia	Fitzsimmons, 1998
Green	100	>2	Ascension Island	Ireland *et al.*, 2003
Green	100	3	Michoacán, Mexico	Lara-De La Cruz *et al.*, 2013
Green	54	3	Sri Lanka	Ekanayake *et al.*, 2013
Leatherback	39.5	2	US Virgin Islands	Stewart & Dutton, 2011
Leatherback	10.0	2	Pacific Costa Rica	Crim *et al.*, 2002*
Kemp's ridley	57.7	2	Mexico	Kichler *et al.*, 1999
Olive ridley	92.3	4	Costa Rica	Jensen *et al.*, 2006[1]
Olive ridley	30.7	4	Costa Rica	Jensen *et al.*, 2006[2]
Olive ridley	20.0	>2	Suriname	Hoekert *et al.*, 2002
Hawksbill	10.0	2	Sabah, Malaysia	Joseph & Shaw, 2011
Hawksbill	9.3	2	Seychelles	Phillips *et al.*, 2013
Flatback	69.0	3	Australia	Theissinger *et al.*, 2009

** Wright and colleagues' study used parentage analysis and found no males sired offspring with more than one female.

* Denotes studies that documented polyandry – the same male mating with multiple females.

[1] Sampled for a population exhibiting "arribada" behavior (mass nesting).

[2] Sampled for a population that does not nest *en masse*.

[3] Turtles in captivity.

HATCHLING DEVELOPMENT

Hatchling success is tied to incubation temperatures, with low hatching success at temperatures that are too cool or too warm (below approximately 25°C and above 35°C, respectively) (Miller, 1997; Matsuzawa *et al.*, 2002). Increasing sand temperatures associated with climate change may therefore negatively impact hatching success, even making some areas completely unsuitable for hatchling production at least during parts of the year (Hawkes *et al.*, 2007). Changes in phenology of nesting seasons may mitigate some of the predicted negative impacts of higher incubation temperatures associated with climate change (Ditmer & Stapleton, 2012). Incubation temperature also has an impact on hatchling size and behavior (Reece *et al.*, 2002; Mickelson & Downie, 2010). For instance, recent work has suggested that turtle hatchlings emerging from warmer nests are smaller and are slower swimmers than hatchlings from cooler nests (Mickelson & Downie, 2010; Booth & Evans, 2011; Micheli-Campbell *et al.*, 2011), although the mechanisms for this are unknown. The implication is that hatchlings produced from warmer nests might be more susceptible to predation while swimming away from the nesting beach (Gyuris, 1994). However, there is little information on long-term impacts of incubation temperatures on the traits or fitness of marine turtles; studies of non-marine turtles suggest that at least some differential fitness impacts of the incubation environment are transient (e.g. O'Steen, 1998). More long-term studies of individual turtles are needed to fully understand the potential impacts of climate change on fitness associated with incubation temperatures. Finally, growth and maturation of hatchling turtles at sea, referred to as the lost years (Reich *et al.*, 2007), is the least understood of the marine turtle life stages, but may be affected by climate-driven alterations to ocean currents and wind patterns and represents a major knowledge gap for marine turtle ecology.

SUMMARY

While a complete understanding of the effects of climate change on marine turtle breeding ecology is still lacking, it is apparent that breeding ecology may be fundamentally affected (Van Houtan & Bass, 2007; Baez *et al.*, 2011). Climate-correlated changes in the timing of reproduction and colonization of new beaches have been recorded, and alterations to the availability of nesting sites, primary sex ratios, and hatching success may be expected. Current net habitat available for reproduction may be lost due to sea level rise, although increases in temperature could open up new areas of

beach (either spatially at higher latitudes or temporally earlier/later in the year). The extent to which this is possible depends on the availability and accessibility of suitable beaches at higher latitudes and the adaptability of turtles to use new beaches. Further, a coherent understanding of fine-scale variability among females in nest site selection and subsequent consequences for their clutches/hatchlings is required, particularly as there is early evidence of thermal adaptation of eggs of some turtles on hotter nesting beaches (Weber *et al.*, 2011). The effects of altered thermal regimes may have the most dramatic and insidious effects if they undermine the fundamental ecology of marine turtle reproduction. In addition to changes to sex ratios, it is clear that the thermal conditions of the incubation environment affect the phenotype, survivorship, and growth rate of hatchling turtles and feed directly into demography. Such effects are likely to be difficult to monitor; therefore, pre-emptive management strategies could be investigated as a cautious approach going forward. Although there is much still to be understood about the potential effect of climate change on marine turtles, recent work has indicated that marine turtles and some other reptile species may be beginning to adapt (Iverson, 1991; Weishampel *et al.*, 2004; Doody *et al.*, 2006; Telemeco *et al.*, 2009; Weber *et al.*, 2011), which yields an exciting new field of study.

MANAGING FOR CLIMATE CHANGE

Managing for the effects of climate change should be an obligate part of any coastal biodiversity management plan and will be essential for successful conservation of habitats and species (Hansen *et al.*, 2010). Growing evidence of marine turtles already adapting to altered climate is noteworthy and suggests that interventionist management should proceed cautiously. For example, the current state of knowledge cannot dictate what the most appropriate primary or operational sex ratio or threshold of hatching success should be. Recommending management interventions is complex; for many aspects of marine turtle breeding ecology it is not yet possible to predict the direction, let alone the magnitude, of some of the expected changes. So far, protection of climate refugia, areas that might become important for marine turtle nesting as warmer climes move pole-ward, has been promoted (Baptistotte *et al.*, 1999; Hansen *et al.*, 2010; Hawkes *et al.*, 2010). This approach is essentially a no-risk strategy, as it does not try to manipulate the natural behavior of the population of concern. Higher risk, more invasive strategies have also been considered. Patino-Martinez and colleagues (2012) investigated the effect on hatching success and hatchling

fitness of shading nests (cooling them and producing more males), while other studies have investigated the effect of moving clutches of hatchlings to safer incubation environments (Pintus *et al.*, 2009) or manipulating the thermal environment of incubating eggs (Naro-Maciel *et al.*, 1999). These novel approaches are worth investigation should they be needed in the future (Fuentes *et al.*, 2012), but it would seem prudent not to roll them out widely until greater certainty about the direction and magnitude of climate change effects have been established.

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