FUTURE CLIMATE IMPACTS TO MARINE TURTLE POPULATIONS, WITH A FOCUS ON THE NORTH PACIFIC OCEAN

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15 July 2010
I. Introduction
This review examines climate change impacts on marine turtle populations by focusing on the established population impacts from climate. First, I summarize published empirical studies that relate climate variables to turtle population indices. Marine turtles have various life stages existing in geographically distinct regions and each life stage may have unique influences. Second, I briefly cover the trends of the salient climate variables and their best forecasts over the next century. Third, I discuss how scientific uncertainty factors in marine turtle population dynamics and climate research. Lastly, I integrate the sections on population, climate, and uncertainty and summarize the scientific outlook. Throughout I pay particular attention to the North Pacific Ocean and the major marine turtle species therein: loggerhead (Caretta caretta), green (Chelonia mydas), and leatherback turtles (Dermochelys coriacea).

II. Known climate impacts
Empirical research shows climate affects turtle populations primarily through nesting. This happens in a number of ways involving various life stages and a number of climate variables. The dominant processes include: (i) breeding cues, (ii) hatching rates, (iii) offspring sex determination, and (iv) beach habitat loss. Fig. 1 diagrams the entire marine turtle life cycle and where climate is a well-established factor.

A particularly robust link between climate and marine turtle nesting involves remigration cues. Marine turtles exhibit great annual variability in nesting surveys\(^1\), presumably due to oceanographic productivity which fluctuates, promoting supra-annual breeding schedules. Females do not breed every year, but theoretically when conditions are most favorable for vitellogenesis, or yolk formation (Fig. 1). Nesting seasons following productive winters have higher recorded nests for loggerhead\(^2,3\), green\(^4\), and leatherback\(^5\) populations. But results vary by ocean basin. Nesting increases after cooler winter ocean surface temperatures (SST) in Pacific populations\(^2,3,5\). Atlantic populations, however, show increased nesting when winter SST is warmer\(^3,4\). These established empirical dynamics capture the influence from El Niño/La Niña events.

Tropical cyclones generate many conditions that harm marine turtle nests. Winds, currents, waves, and storm surge decrease hatching rates by inundating nests, eroding beaches, and exposing eggs\(^6\). Species are not equally affected, however, as nesting phenology varies. In Florida, green turtle nesting seasons overlap most with tropical cyclone activity and as a result their nests can be heavily impacted by such
storms. Loggerheads and leatherbacks, conversely, begin nesting up to months earlier, and though they can still be significantly influenced by tropical cyclones, their nests tend to interact with such storms less often than green turtle nests\textsuperscript{6,7}. Fig. 2 plots annual cyclone intensity against egg hatching rates. Cyclone intensity here revises a previous index\textsuperscript{6} by including an exponent variable similar to power dissipation index\textsuperscript{8,9} (PDI). Though cyclones are a documented threat to loggerhead nests in Japan\textsuperscript{10}, no systematic or long-term studies exist.

Sand temperatures determine the sex and survivorship of marine turtle eggs. Multiple laboratory and field studies show egg survival does not occur outside 25-35 °C, and temperatures above 30 °C produce mostly females\textsuperscript{11}. Nest temperatures vary according to latitude, nest location, egg position within a nest, time of day, day of year, substrate type, and precipitation\textsuperscript{11}, therefore a constant air temperature produces a multitude of nest temperatures. Considerable variability occurs therefore from the scale of the population to individual nests, indicating that a range of temperatures will produce a mixture of sexes\textsuperscript{12}, especially in populations distributed across latitudinal gradients. The complexity of these interactions, and lack of long-term (> 10 yrs) sand temperature records, limits understanding its influence on population dynamics over evolutionary time. This said, monitoring studies of Japan loggerhead nests since 2000 indicate nest temperatures are well within critical survival temperatures\textsuperscript{10,13,14}. Furthermore, the most recent loggerhead federal status review\textsuperscript{15} under the US Endangered Species Act estimated the North Pacific population to have a 1:1 male to female ratio throughout the population’s life stages.

Though sea-level rise is listed as a concern for marine turtle populations, there is no demonstrated link between sea-level rise and marine turtle population indices of any kind during the modern record. This is largely because observed sea-levels have only increased 10 cm since 1950 and just 6 cm since 1990,\textsuperscript{16} the period overlapping with most sea turtle datasets. A 6 cm increase compared to 20 years of population data is insufficient to detect robust population changes at any spatial scale. This does not mean that sea-level is not potentially important; it only means the observed and available data will not demonstrate meaningful correlations. As a result, sea-level changes are not considered a significant influence on marine turtle population or distribution dynamics in the last century.

Climate certainly influences additional population events besides nesting, but these relationships are poorly documented and their effect on population indices unknown. One potential area for increased understanding is how pelagic productivity influences juvenile survivorship\textsuperscript{3}. Juvenile loggerhead turtles – like most pelagic organisms – are not uniformly distributed across the North Pacific Ocean, but concentrated along temperature fronts\textsuperscript{17,18}. Though these fronts represent productive foraging habitat, their variability has not been linked to population dynamics. Another important topic for research is the impact from ocean acidification. Current studies suggest coral reefs and plankton may be seriously limited within 50 years\textsuperscript{19}, but sea grass communities may in turn benefit\textsuperscript{20}. Few studies have explored these relationships empirically or modeled their future impacts to turtle populations.
III. Climate trends and projections

Early climate change research focused on descriptions of trends in the earth’s temperature with more recent studies relating those increases to human forcing\textsuperscript{21}. Today there is considerable scientific agreement that surface temperatures have increased significantly in the instrumental record\textsuperscript{22} (0.6 °C century\textsuperscript{−1} since 1850) and that anthropogenic greenhouse gas emissions are the cause\textsuperscript{21,23-26}. A new report identifies the past decade, for example, as the warmest on record\textsuperscript{27}. The fourth assessment report\textsuperscript{25} (AR4) of the Intergovernmental Panel on Climate Change (IPCC) projects surface temperatures to increase 2.8 °C globally by 2100 under the A1B\textsuperscript{1} emissions scenario. (The trend over the Pacific Ocean including Japan is slightly higher.) AR4 forecasts\textsuperscript{25} further suggest summer precipitation will increase 5-20% during the next century across the North Pacific.

It is unclear how climatic change will affect tropical cyclones. Theory alone indicates warm oceans enhance surface evaporation and convective conditions favorable to cyclone formation\textsuperscript{28}. It therefore follows that warmer oceans could theoretically increase cyclone intensity\textsuperscript{29}. Models\textsuperscript{8,30} using data since 1970 indicate that annual cyclone intensity has increased during this period in concert with SST, even though the total number of cyclones has declined. These studies are balanced by research suggesting future cyclones will be more influenced by local/regional measures of SST\textsuperscript{9,31} and wind shear\textsuperscript{32} which forecast cyclone intensity to increase only marginally or decline, respectively. As a result, tropical cyclone forecasts over the next century face a great deal of uncertainty\textsuperscript{33}. In the Pacific Ocean, wind shear is modeled\textsuperscript{32} to increase in the eastern tropics and near Japan which would decrease cyclones, both in frequency and intensity.

Sea-level rise is among the more potentially catastrophic outcomes of changing climate. Studies from paleoclimatic\textsuperscript{34} and modern\textsuperscript{35} records suggest sea-levels will increase between 0.5-1.4m over the next century as a result of thermal expansion and glacier melting. Simple elevation models argue that the IPCC median scenario sea-level rise (0.5 m century\textsuperscript{−1}) will cause ~30% loss of current beach habitat in three island regions important for turtle nesting\textsuperscript{36-38}. These studies, however, do not account for dynamic geomorphology which can mitigate habitat loss from rising seas. A recent empirical study of 27 atoll islands in the central Pacific, for example, demonstrated that only 14% of islands decreased their area over a 19-60 year time span\textsuperscript{39}. This occurred in a region considered most vulnerable to sea-level rise\textsuperscript{16}, during a period in which sea-levels rose 2mm yr\textsuperscript{−1}. While most islands maintained (43%) or increased in area (43%) all islands demonstrated significant morphological shifts, thus explaining the otherwise counterintuitive results. Though low-lying tropical islands are considered the most exposed to sea-level rise\textsuperscript{16,38}, these historical data indicate that beach losses do not necessarily accompany sea-level increases. Moreover, the most recent comprehensive study on sea-level rise does not consider the Japanese archipelago a high risk area for coastal flooding\textsuperscript{16}.

\textsuperscript{1} Frequently interpreted as the most likely emissions scenario, assuming rapid economic growth under a balanced resource portfolio (both fossil-intensive and non-fossil fuels). There are more optimistic and pessimistic scenarios, A1B functions as a plausible median result, given current trends.
In addition to global forecasts, regional SST changes measured in the North Pacific may also be informative. Fig. 3 plots observed SST in two key ocean regions known to effect breeding turtle remigration and tropical cyclones approaching Japan. The series are built from region monthly averages obtained from ERSSTv2 (1950-1991) and ERSSTv3 (1981-2009) series and averaged when the series overlap. Since 1950, the area correlated to breeding remigration (Fig 3. “foraging zone”) increased 1 °C century \(^{-1}\) and the region influencing tropical cyclone impacts to Japan (Fig 3. “cyclone zone”) increased 0.75 °C century \(^{-1}\). Both series show little discernable trending from 1950-1990, then increase sharply in the 1990s, and decline after 2000.

IV. Scientific uncertainty
A great deal of uncertainty influences the scientific understanding of how climate may influence future marine turtle populations. This uncertainty comes in several forms and merits discussion. The uncertainty of the relationship between two variables arises when either: data are lacking, studies are few or geographically limited, multiple studies conflict, or the relationship between variables is noisy. Uncertainty in the first example can be remedied by gathering data and initiating its study. In the second and third example, uncertainty can be improved by expanding existing databases and replicating previous research. Unlike these examples, the fourth type of uncertainty – often known as stochasticity – is not simply improved with additional data and increasing sample sizes. Put simply, stochasticity is the unknown, but it can help identify flaws in the structure of scientific models themselves. Often this requires new research programs, new hypotheses, and new data streams altogether. Stochasticity can be difficult to resolve when variables have effects that are indirect, nonlinear, or involve time lags, among other things.

All types of uncertainty described here are involved in understanding the role of climate to future turtle populations. The relationship between juvenile survivorship and oceanographic productivity, for example, has largely been unexplored. Therefore any climatic predictions about pelagic upwelling and currents are not easily applied to existing turtle population knowledge. The effect of climatic change here is therefore “uncertain,” but it is perhaps a tractable uncertainty that could be mitigated through research and study.

V. Conclusions
The accelerating pace of global greenhouse gas emissions suggests surface temperatures will very likely increase nearly 3 °C this century with extended extreme heat becoming more frequent. The clearest and most significant threat from these changes appears to be the direct impact of higher sand temperatures to eggs. Though empirical incubation studies are very limited across spatial and temporal scales, absolute temperature thresholds for egg survival and sex-determination appear likely with multi-year extreme heat events on the increase. Simple projections of the effects to populations, however, are unclear because of the complex influences upon nest temperatures across geographic space. This relationship will be made clearer through empirical incubation analyses at population scales. A particular focus should be made on
the long-term, local sand temperatures and their variability with respect to regional surface temperatures.

The projected precipitation increases in the North Pacific\textsuperscript{25} would reduce the impact of higher sand temperatures. However, this precipitation forecast is based in part on the presumed more poleward tracking of tropical cyclones in concert with warmer SST. The AR4 precipitation forecast does not account for wind shear projections\textsuperscript{32}, which will likely increase in the North Pacific above 25°N, and therefore partially offset proposed precipitation increases. Wind shear and relative SST models\textsuperscript{9,33} disagree with cyclone predictions based on absolute SST\textsuperscript{8,30}. To cloud the outlook even further, recent studies document Florida turtles have begun nesting earlier in the calendar year in concert with warming ocean temperatures\textsuperscript{43,44}. If this pattern holds, the earlier onset of nesting might move more nests out of contact with tropical cyclones and therefore lessen the population-scale impacts of these storms (unless cyclones also shift temporally). As a result of both wind shear and nesting phenology, it is therefore possible that the future impacts of cyclones on nesting will decline.

Much research is required before the impacts of warming SST to remigration cues comes into focus. Data from the past 30 years strongly indicate that females cluster breeding attempts according to winter SST anomalies. In the Atlantic Ocean this seems to follow warmer winters and in the Pacific the opposite is observed. The mechanisms for these patterns are not clear, but are presumably due to oceanographic productivity. Because these correlations are based on relative SST (i.e. anomalies), absolute SST trends would impact remigration cues only if it affects ecosystem-level productivity, or annual SST variability. Bearing this in mind, future forecasts\textsuperscript{45} of the extent of oceanic biomes in the Pacific suggest temperate and subtropical biomes trend oppositely. Since loggerheads forage in both biomes, and on their marginal fronts, definitive conclusions about population impacts from these projections are not possible.

The majority of global circulation models have a high sensitivity to sea-level rise scenarios, meaning that climate forecasts hinge upon sea-level prediction accuracy. Since the AR4 just three years ago, median projected rates of sea-level rise have almost doubled from 0.6 to 1 m by 2100.\textsuperscript{16} Much of the uncertainty in these forecasts revolves around the fate of the Greenland and West Antarctica ice sheets, causing single models predictions to range nearly 1.3 m.\textsuperscript{46} Though island systems have dynamic geomorphology\textsuperscript{39}, they have a potentially greater risk of beach loss as a result of sea-level changes.\textsuperscript{16,36-38} Marine turtle nesting beaches in low-lying island areas should be monitored closely with specific attention to the available habitat area over time.

Climate is one of the least studied yet may have the largest influence on marine turtle populations. This gap limits understanding future climate impacts and underscores the need for more analyses that relate climate to turtle ecology. This review focuses on established relations between climate variables and turtle population indices. The potential also exists for climate change to have nonlinear interactions with other known population influences. Factors such as disease, trophic changes, and invasive species are major causes of biodiversity declines worldwide.\textsuperscript{47} Climatic changes may interact synergistically with these factors to further exacerbate population threats. These interactions as well as direct relationships deserve careful research attention.
VI. Figures

Figure 1. The life stages of marine turtles and their climatic influences. The primary documented effects of climate to marine turtles are with nesting; both in cueing females to breed and related to egg fates. Climate may potentially impact other life stages, but this must be demonstrated through empirical studies. Life stages with known climate impacts are yellow with environmental stochasticity noted in orange. Adapted from Chaloupka et al. 2004,18 used with permission.
Figure 2. Tropical cyclones cause extreme rain, wind, wave energy, and tide events that impact hatching rates. In Dry Tortugas National Park, Florida, nesting seasons with increased storm activity had more nests inundated and lower hatching rates over a ten year period. Tropical cyclone trends oscillate over decadal-scale periods and the trends presented here are a measure of local impacts during this period. These data represent the most comprehensive analysis of tropical cyclone impacts to hatchings rates. No such analyses exist for the Pacific. Trend line is fitted exponential decay model.
Figure 3. Observed sea surface temperatures (SST) near Japan known to impact female breeding and considered relevant to tropical cyclone intensities. Foraging zone SST plotted as the five year running mean of the region annual average (10-30°N, 120-140°E) shows an increase of 0.98 °C century\(^{-1}\). Cyclone zone SST plotted as the five year running mean of the region season average (20-40°N, 125-150°E, May-Sept) shows an increase of 0.75 °C century\(^{-1}\). Neither series shows a strong trend from 1950-1990. Both series display a sharp increase in the 1990s, but decline after 2000. Text describes methods and data sources\(^{40}\).
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