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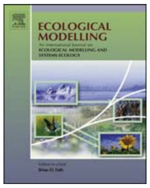

Using a microclimate model to evaluate impacts of climate change on sea turtles

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ABSTRACT

Sea turtles are thought to be particularly vulnerable to climate change as projected increases in temperature may skew the sex ratio of their hatchlings, decrease hatchling success and thus threaten population persistence. Given the seriousness of the threat from climate change it is critical to understand the rate at which soil temperatures at sea turtles' nesting grounds are likely to change. This has stimulated the development of correlative models to assess and project how projected increases in temperature may impact sea turtle's reproductive output. Correlative models correlate climatic variables to soil temperature and hatchling sex ratio. These models have been widely used due to their simplicity and the flexibility of their data requirement. However, outputs are restricted by the environmental conditions used for the model and thus does not allow exploration of daily variation in sand temperature. Further, the potential error inherent in this approach has not been determined.

Researchers working with other animals with temperature-dependent sex determination (TDS) have developed microclimate models to determine nest temperature and potential impacts from climate change. Microclimate models use the interaction between climate, soil, and topography with physiology and nesting behavior of animals to determine future production of hatchling sex ratios. Until now, microclimate models have never been applied to sea turtles and its correlation and consistency with correlative models has never been explored. To address this, we used the Niche Mapper$^{\mathrm{TM}}$ microclimate model to project soil temperature at key sea turtle nesting grounds under various scenarios of global warming. Results from the microclimate model are compared to published projections from correlative models. The two approaches accurately and congruently model current soil temperature and project a feminization of the northern Great Barrier Reef green turtle population as climate change progresses. To provide guidance of when to use each approach we also reviewed the applicability and effectiveness of each model. The microclimate model provided a more robust picture of the incubating environment as it has the potential for projecting soil temperature for every hour of the day at various locations and depths within a nesting ground. This allows exploration of whether animals with TDS can counteract the impacts of global warming by changing nest depth and nesting distribution. With time and the validation of the microclimate model with short-term projections, the microclimate model can also be used to refine short-term adaptive management strategies as they can provide explicit recommendations on site-specific scales for translocation of eggs and alteration of the nesting environment.

1. Introduction

Global climate change is a major issue in ecosystem and wildlife management throughout the world (Fuentes et al., 2012). It has already produced significant and measurable impacts on almost all ecosystems, taxa and ecological processes and its impacts are expected to increase rapidly (Hughes, 2000; Peterson et al., 2002; Walther et al., 2002; Parmesan and Yohe, 2003). To respond effectively to predicted climatic changes it is important to understand how changes will affect biodiversity (Margules and Pressey, 2000; Kearney and Porter, 2009; Mokany and Ferrier, 2011). This need has stimulated the development of various models to assess and project future impacts from climate change (Botkin et al., 2007; Trivedi et al., 2008). This is particularly true for animals that are thought to be especially vulnerable to climate change. An example is oviparous reptiles, such as sea turtles that have life history, physiology and behavioral traits that are extremely influenced by environmental temperature. Sea turtles have temperature-dependent sex determination (TDS) – wherein the sex of their hatchlings is determined by the incubation temperature during embryonic development (Janzen and Paukstis, 1991; Mrosovsky

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and Pieau, 1991). Therefore, projected increases in temperature may skew the sex ratio of sea turtle hatchlings and threaten population persistence (Nelson et al., 2004; Hulin et al., 2009; Fuentes et al., 2010).

Consequently, there is a clear need to understand the rate at which soil temperatures are likely to change at sea turtle nesting grounds and the extent to which associated changes in hatching success and sex ratio will vary spatially as climate change progresses (Hays et al., 2003; Fuentes et al., 2009). This need has stimulated the development of correlative models to assess and project how forecasted increases in temperature may impact sea turtle reproductive output. Correlative models correlate climatic variables to soil temperature and hatchling sex ratio (e.g. Janzen, 1994; Hays et al., 1999, 2003; Glen and Mrosovsky, 2004; Hawkes et al., 2007; Fuentes et al., 2010). These models have been widely used due to their simplicity, the flexibility of their data requirement and the need for non-specialized software skills and for relatively inexpensive equipment (e.g. temperature data loggers) (Mitchell et al., 2008; Hawkes et al., 2009). However, the potential error inherent in this approach has not been determined and it cannot be used when environmental conditions vary outside the range of the correlative model (Mitchell et al., 2008). Thus outputs are restricted by the input data and does not allow for exploration of daily fluctuation of soil temperatures.

Microclimate models can be used to determine soil temperature and to project future production of hatchling sex ratios by using the interaction between climate, soil, and topography with physiology and nesting behavior of animals. Until now, microclimate models have never been applied to sea turtles but it has been used to determine nest temperature and potential impacts of climate change to tuatara, which also have temperature-dependent sex determination (TDS) (see Mitchell et al., 2008). Given the concern over the potential impacts of climate change on sea turtles and the growing number of studies that are attempting to project soil temperature at sea turtle nesting grounds the objective of this study is to explore the applicability of a microclimate model: the Niche Mapper^{TM}, to project soil temperature at sea turtle nesting grounds and to compare the applicability and effectiveness of this microclimate model with the more commonly used correlative models. This will help guide future decisions on which model to use when assessing the impacts of climate change on animals with TDS, such as sea turtles.

2. Methods

2.1. Population and study site

The applicability and effectiveness of the microclimate submodel was explored with the northern Great Barrier Reef (nGBR) green turtle population. Recent concern over the impacts of climate change on the nGBR green turtle population has been expressed by stakeholders and researchers (e.g. Limpus et al., 2003; Fuentes et al., 2011). The nGBR green turtle population is the largest green turtle population in the world with 50,000 turtles nesting during a high nesting year (Limpus et al., 2003). This population has important ecological roles (e.g. maintenance of seagrass and algal ecosystems) (Moran and Bjorndal, 2007), social importance to indigenous people (Johannes and Macfarlane, 1991), and value to the tourism industry (Wilson and Tisdell, 2001). Nesting for this population occurs in the northern Great Barrier Reef and Torres Strait region (Fig. 1). Selected nesting grounds for this study (Bramble Cay, Raine Island and Sandbank 7) encompass almost the whole latitudinal range of the nesting grounds used by this population and include the biggest nesting ground in the northern Great Barrier Reef (Raine Island) and Torres Strait (Bramble Cay) (see gray dots at Fig. 1).

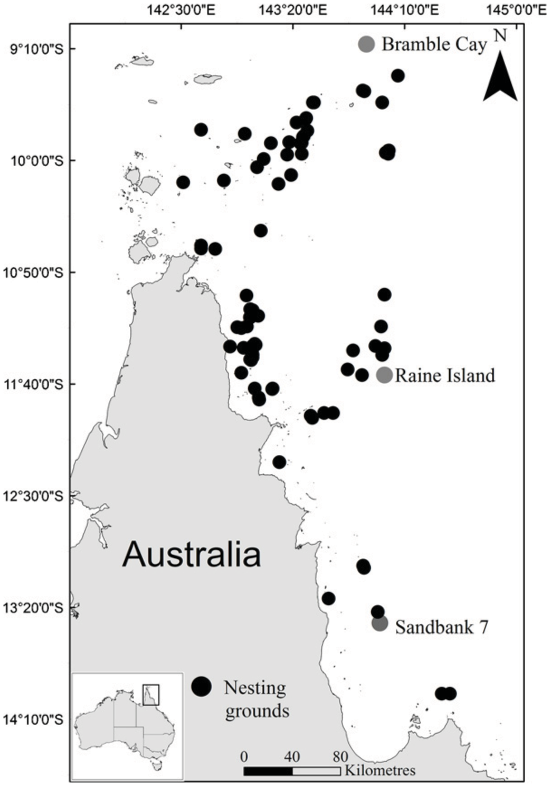

Fig. 1. Map of nesting grounds used by the northern Great Barrier Reef green turtle population. Dots represent nesting grounds, with gray dots indicating selected nesting grounds for this study.

2.2. Microclimate model

The microclimate submodel in Niche Mapper^{TM} (McCullough and Porter, 1971; Porter et al., 2002; Porter and Mitchell, 2006) was used to estimate soil temperature on the selected nesting grounds (see Section 2.1) under a current climate (November 2007–March 2008) and a 'conservative' (C) (B1 emissions scenario, IPCC, 2007) and 'extreme' (E) (A1T emissions scenario, IPCC, 2007) scenario of climate change for 2030 and 2070 (Table 1).

The Niche Mapper^{TM} microclimate submodel includes a subroutine for computing clear sky solar radiation given a specific time, latitude, longitude, elevation, slope and aspect (McCullough and Porter, 1971), and requires climate maximum and minimum data (e.g. air temperature, wind speed, humidity, percentage of cloud cover) for arbitrary time intervals, e.g. monthly, weekly or daily, and physical properties of the soil (e.g. thermal conductivity, density, specific heat and substrate reflectivity) as major input variables (Mitchell et al., 2008). The equations that define the microclimate model are in Porter et al. (1973) and a conceptual

Table 1
Projected regional increases in sea surface (SST), and air (AT), temperatures, under conservative (based on B1 emissions scenario, IPCC, 2007) and extreme (based on A1T emissions scenario, IPCC, 2007) scenarios (CSIRO, 2007).

Year	Scenario	Projected increase in SST (°C)	Projected increase in AT (°C)
2030	Conservative	0.3	0.7
	Extreme	0.6	1.2
2070	Conservative	1.2	1.8
	Extreme	1.5	3.4

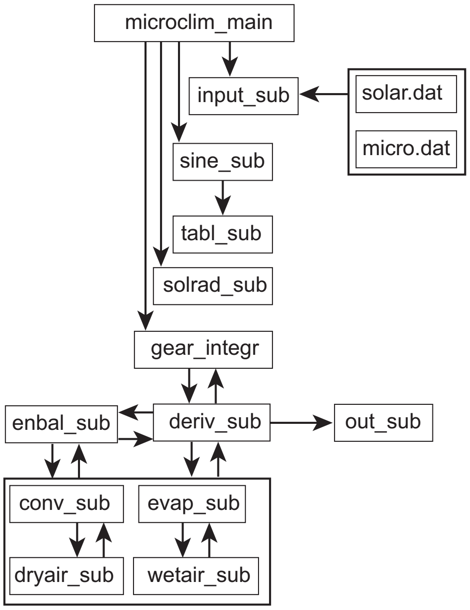

Fig. 2. Conceptual flowchart for the microclimate model Niche Mapper^{TM}. Adapted from Porter et al. (2010).

diagram of the model adapted from Porter et al. (2010) is represented in Fig. 2. Niche Mapper^{TM} uses a variety of subroutines that initially read two input data files (solar.dat and micro.dat) (Fig. 2). "Solar.dat" contains atmospheric properties used in calculating clear sky solar radiation available on the surface of the earth as a function of latitude, longitude and elevation. "Micro.dat" contains the time independent and time-dependent variables for the local pixel properties. The time independent data include soil properties like density, specific heat, thermal conductivity and reflectivity. The time-dependent properties include maximum and minimum values for each of the days to be simulated for air temperature, relative humidity, wind speed, percent shade and cloud cover. Once these data are loaded, the maximum/minimum time-dependent data for each day are processed (sine_sub) into sine wave functions that interpolate between maximum and minimum values for each day (Fig. 2). The timing of the maximum and minimum values is user defined relative to sunrise and solar noon. Default values for the maximums are assumed to occur one hour after solar noon and the minimums at sunrise. This is true for air temperature and wind speed. Default values for relative humidity and cloud cover are assumed to have maximums at sunrise and minimums one hour after solar noon. Once the interpolations are complete, the data are transferred to a subroutine, tabl_sub, that converts them into hourly values so that there are time/value data pairs for each hour of the day (Fig. 2). Once the data are arranged by hour, the main program calls the solar radiation subroutine which generates hourly output for each day simulated. The program then invokes the numerical integrator, gear_integr, which then calls a derivative subroutine that computes time-dependent temperature transients for the soil surface down to deep soil at node depths specified by the user (Fig. 2). The set of one-dimensional finite difference equations for the soil surface and deeper soil nodes are then solved by three successive repeats of each individual day to establish a steady periodic temperature oscillation at each node. The boundary conditions are the 2 m hourly air, humidity, wind and cloud cover data and the deep soil temperature data which is the average annual temperature. The derive_sub subroutine has the heat balance at the soil surface which includes solar and longwave infrared thermal radiation heat fluxes, convection and evaporation terms computed by subroutines conv_sub and evap_sub and conduction equations in the derivative subroutine (derive_sub) for the surface and deeper layers in the soil (Fig. 2). The properties of air needed for convection and evaporation computations are embedded in the subroutines dryair_sub and wetair_sub (Fig. 2). On the third replication of each day, the hourly output is transferred to out_sub, which creates the output files metout, soil, shadmet and shadsoil (Fig. 2). The first two files are for the warmest sunniest location above and below ground. The third and fourth files are for the coolest shadiest location on the pixel.

The microclimate model is available free for collaboration or for purchase (see details at http://www.zoology.wisc.edu/faculty/por/por.html#niche). For this study, a new highly compact format was created in the submodel to allow user specification of depths used in the computations and the ability to specify temporal and spatial variation of soil properties listed above. These modifications allow, for example, for variation in water level in the soil as it affects thermal conductivity, which is a common phenomenon in shore environments due to tidal cycles. These features also allow for snow deposition or other surface or subsurface modifications as they may occur in time due to natural events.

Climate maximum and minimum data for each month from November 2007 to March 2008 was calculated from hourly measurements from each nesting ground at unshaded locations. Daily air temperature (AT) and relative humidity (RH) for Bramble Cay was obtained from calibrated weather stations (Hasting Data Loggers, Port Macquarie, Australia) deployed according to requirements by the Australian Bureau of Meteorology (see Canteford, 1997). AT data for Raine Island was obtained from the International Comprehensive Ocean Atmosphere Data Sets (ICOADS) (http://www.cdc.noaa.gov/coads) (as per Hays et al., 2003; McMahon and Hays, 2006; Fuentes et al., 2009). Data from ICOADS was only used when more than 10 observations were recorded (as in Hays et al., 2003). RH for Raine Island was obtained from the Australian Bureau of Meteorology (BOM) weather station at Thursday Island (less than 100 km from Raine Island). Wind speed for Bramble Cay and Raine Island were also obtained from the Australian Bureau of Meteorology (BOM) weather station at Thursday Island. AT, RH and wind speed data for Sandbank 7 was obtained from the Commonwealth Scientific and Industrial Research Organization in Australia (CSIRO) and from the Australian Bureau of Meteorology (BOM) weather station at Coen airport (less than 100 km from Sandbank 7). Data on cloud cover was not available so we assumed clear sky conditions as an upper bound for all the nesting grounds during the study period (November 2007–March 2008).

Soil properties were obtained from samples collected in November 2007 from the dune of each nesting beach as this is the region where most of the turtles nest (Limpus et al., 1983; Kikukawa et al., 1999). Reflectivity properties of the soil were determined using an ASD spectrometer, which measures reflectance across the spectral range of 350–2500 nm with a bandwidth resolution of 3 nm at 700 nm and 10 nm at 1400/2100 nm. The sampling interval is 1.4 nm from 350 to 1050 nm and 2 nm at 1000–2500 nm. Scanning time is 100 ms. Other technical data may be found at http://www.asdi.com/products/fieldspec-3-portable-spectroradiometer. Sterilized sand samples were placed in 3 cm diameter Petri dishes with a sand depth of 0.7 cm. All measurements were performed in a photographic darkroom. A white light source within the measuring probe illuminated the sample and reflected light was transported by a fiber optics cable to the three resident spectrometers in the unit. After the spectral data were collected with electronic labels, each was processed first into reflectance/transmittance data formats and then averaged over the solar spectrum using ViewSpecPro, free software from ASD. Reflectance was measured from a set of samples from the dune at different orientation of the beach (e.g. east, south); averaged values were used as input data. To explore potential changes in soil temperature as a result of the range of reflectivity values we ran a sensitivity analysis with the range of reflectivity values found at each island. Sensitivity analysis was made for an extreme scenario of climate change in 2070. Sand density was taken from http://www.simetric.co.uk/si_materials.htm. Sand thermal conductivity ranges were determined from Smits et al. (2009). Sand specific heat values were from data at http://www.engineeringtoolbox.com/specific-heat-capacity-d_391.html. Soil thermal properties are presented in table S1. We assumed a uniform soil type on each island and set the microclimate model to project soil temperature at depths between 50 and 200 mm. For analysis, we selected output data in the middle of the day for unshaded sites. An example of a data input file used for current climate (2007–2008) simulations is shown in the electronic supplementary material, table S2.

2.2.1. *Using the microclimate model to project impacts on sea turtles*

To simulate projected increases in temperature we increased current (from November 2007 to March 2008) mean minimum and maximum air temperatures in the microclimate submodel by seasonal increments projected by the Commonwealth Scientific and Industrial Research Organization in Australia (CSIRO) and the Australian Bureau of Meteorology (as per Table 1). As per Mitchell et al. (2008) the other variables (wind, cloud cover and relative humidity) were kept constant as no reliable projections exists, for the studied region, for these variables in the future.

To investigate the implications from the projected soil temperature to sea turtles we assumed that sand temperatures at 29.3 °C produces 50% females and 50% males, that temperatures below 27.8 °C produces all males, temperatures above 30.8 °C produce all females and that the proportion of females increases linearly between 27.8 °C and 30.8 °C (as per Fuentes et al., 2010).

2.3. *Correlative model*

The best correlative model to describe the soil temperature at the selected nesting grounds correlates air and sea surface temperatures with soil temperature (see Fuentes et al., 2009). Fuentes et al. (2009, 2010) developed correlative models for Bramble Cay, Raine Island and Sandbank 7 by correlating mean monthly air and sea surface temperatures at each nesting ground from April 2007 to November 2008 (for an example of data used to develop the correlative model see supplementary table S3 and for correlative models see electronic supplementary table S4). Similarly to this study, Fuentes et al. (2009, 2010) used correlative models to project monthly soil temperature at 50 cm for 2030 and 2070 under an extreme and conservative scenario of climate change. The published results from these correlative models are compared with the results from the microclimate model used here (see Section 2.4).

2.4. *Model comparison and validation*

To investigate the efficiency of the microclimate and correlative models we ran the models for a current scenario (November 2007 to March 2008), determined the deviation between the measured and modelled temperatures and conducted a 2-tailed sample *t*-test between the results and the empirical observations of current soil temperature. Current soil temperature was obtained by recording soil temperature every hour at the study sites from November 2007 to March 2008 using Tinytag TK-4014 data loggers (Hasting Data Loggers, Port Macquarie, Australia) (for data summary see supplementary table S5). All data loggers were calibrated before and after deployment against a mercury thermometer and had an accuracy of ±0.1 °C. Dataloggers were located in representative nesting areas and deployed at a standard depth of 50 cm, which is close to green turtles' average nest depth (as per Spotila et al., 1987; Hewavisenthi and Parmenter, 2002; Matsuzawa et al., 2002). To provide further guidance of which model to use we compared the input variables necessary to run each approach, the outputs generated, and the drawbacks and advantages of using each model.

3. Results

3.1. *Sand properties*

The selected nesting sites presented an average reflectivity value of 0.54–0.64, with standard deviations within island ranging from 0.02 to 0.04. Our sensitivity analysis with the range of reflectivity values showed that temperatures at 50 cm varied in average by 0.09 °C, with a range of variation of 0.06–0.12 °C, which is negligible for the purpose of our study. Thus the results presented are only for the average reflectivity value for each nesting site (for values see supplementary table S1).

3.2. *Microclimate model*

The microclimate submodel in Niche Mapper^{TM} proved useful to reconstruct soil temperature at the selected sea turtle nesting grounds as no significant difference was found between the reconstructed soil temperature and the observed temperatures at the selected nesting grounds (paired *t*-test, $t = 0.703$, df = 14, $P = 0.494$). Modelled temperature tended to be higher than observed at Bramble Cay and Raine Island and lower than observed at Sandbank 7.

The submodel explained more than 58% ($r^2 > 0.58$) of the variability in sand temperature at each of the selected nesting grounds, with the mean deviation between the mean monthly observed and the modelled temperature ranging from 0.45 to 1.01 °C (Table 2). Thus, with caution the microclimate model can be used to provide insights into the potential outcomes if scenarios envisaged under climate change do occur.

Soil temperature projections by the microclimate model indicate that Bramble Cay is projected to be the warmest nesting ground as climate change progresses and Sandbank 7 the coolest (Fig. 3). In the long term (by 2070) under an extreme scenario of

Table 2
Average deviations (°C) (±SE) between measured and modelled temperatures at 50 cm from each nesting ground from November 2007 to March 2008.

Location	Model	Nov	Dec	Jan	Feb	Mar	Mean	R2 with empirical data
Bramble Cay–North Open beach	Microclimate	−0.94 ± 0.81	1.61 ± 0.91	−0.02 ± 1.5	−0.83 ± 0.54	0.66 ± 0.70	0.31 ± 0.52	0.79
Bramble Cay–North Open beach	Correlative	0.7 ± 0.08	−0.33 ± 0.27	−0.18 ± 0.03	−0.26 ± 0.12	−0.05 ± 0.18	−0.02 ± 0.04	0.79
Raine Island–South open beach	Microclimate	1.37 ± 0.74	−1.84 ± 0.68	−1.90 ± 1.03	−0.49 ± 0.25	0.57 ± 0.71	−0.45 ± 0.46	0.64
Raine Island–South open beach	Correlative	0.79 ± 0.36	−0.82 ± 0.24	−1.07 ± 0.41	0.94 ± 0.31	−0.06 ± 0.04	0.32 ± 0.26	0.84
Sandbank 7 north open beach	Microclimate	0.50 ± 0.62	0.29 ± 0.44	1.07 ± 0.23	1.71 ± 0.52	1.49 ± 0.38	1.04 ± 0.22	0.58
Sandbank 7 north open beach	Correlative	0.30 ± 0.20	0.60 ± 0.27	0.47 ± 0.29	1.05 ± 0.37	0.46 ± 0.30	0.48 ± 0.35	0.83

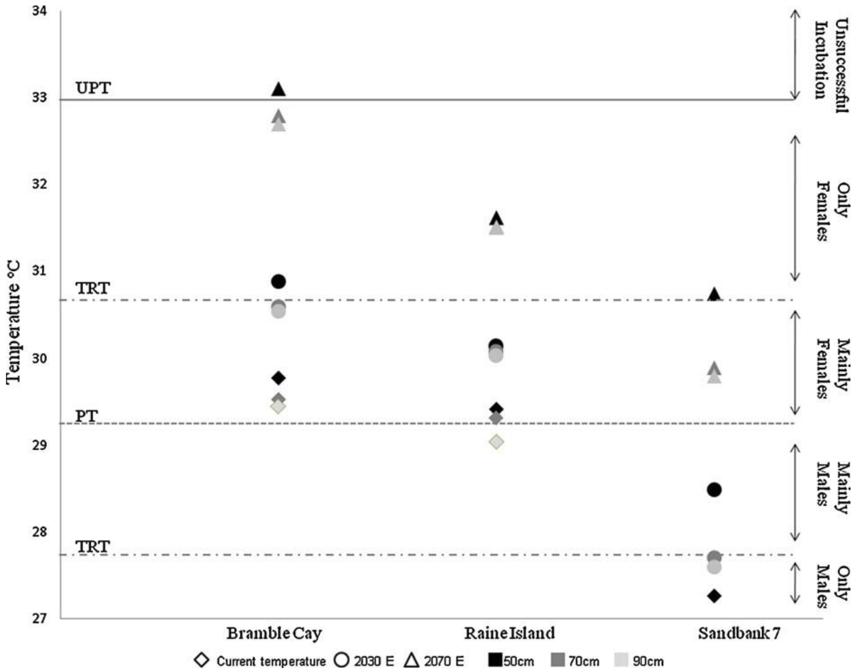

Fig. 3. Microclimate modelled current (November 2007–March 2008) and projected mean sand temperature (°C) during nesting season (November to March) for each nesting ground under an extreme climate change scenarios for 2030 and 2070. Pivotal temperature (PT) refers to the temperature where a 50:50 male to female sex ratio is produced, transitional range temperature (TRT) is the range of temperature where sex ratio shifts from all males to all females. Upper thermal threshold (UPT) is the upper threshold for sea turtle eggs to successfully incubate.

climate change mainly female hatchlings will be produced at the nesting grounds studied (Fig. 3). At Bramble Cay, temperatures will be near the upper thermal threshold (UPT) for incubation, while Raine Island and Sandbank 7 are projected to have mainly female producing temperatures. In the short term (by 2030), Bramble Cay will produce mainly female hatchlings and both male and female hatchlings will be produced at Raine Island and Sandbank 7 (Fig. 3).

3.3. Comparison between models

Both models explained well the variability in sand temperature at the selected nesting grounds (Table 2). The correlative model showed stronger correlations and usually smaller deviation between the mean monthly observed and the modelled temperature (Table 2). However, as the correlative model only constructs soil temperature averaged across the day for one set depth (in this case 50 cm) it does not create a clear picture of the thermal environment at each nesting ground and insights of how temperature fluctuates during the day. The microclimate submodel constructs soil temperature at multiple specified depths for every hour of the day and thus provides a better picture of the incubating environment at each nesting ground (Fig. 3). This helps account for the complexity of nesting behavior of animals with TDS. The simplicity in the outputs from the correlative models is translated from their data requirements (Table 3). Most correlative models only correlate air temperature with soil temperature, with more recent correlative models also using sea surface temperature data. In contrast, the microclimate model requires a more extensive dataset, which includes air temperature, wind speed, humidity, and percentage of cloud cover as well as information on soil properties (Table 3).

The microclimate and correlative models produced similar range projections (Table 2), with differences between the projections from each model varying from 0.04 to 1.32 °C (Table 4). Projected temperature by the microclimate model was lower than the projected temperatures by the correlative model at Bramble Cay and Sandbank 7 and higher at Raine Island (Table 4).

4. Discussion

The microclimate submodel in Niche Mapper^{TM} proved efficient in reconstructing and projecting soil temperature at sea turtle nesting grounds. Projections of soil temperature with the microclimate model where generally congruent with published results from correlative models. Despite a variation of up to 1.32 °C between projections with each model the projective implication of temperatures at 50 cm would be the same at Bramble Cay and Sandbank 7. With both approaches it is projected that sand temperature at 50 cm, by 2070 under an extreme scenario of climate change, at Bramble Cay will be near/above the maximum thermal threshold (33 °C) and at Sandbank 7 will produce only female hatchlings. At Raine Island the situation is different, according to the correlative model a small proportion of male hatchlings will still be produced by 2070 under an extreme scenario of climate change whereas the microclimate model projects that only females will be produced. Regardless, at first instance both modelling approaches project a bleak picture for the northern Great Barrier Reef green turtle population. It is important to keep in mind that these projections are only for one soil depth (50 cm) and for one region within each nesting ground.

However, when investigating the potential impacts of climate change on animals with temperature dependent sex determination it is necessary to take into account the relationship between temperature, embryonic and sexual development as well as their nesting behavior, operational sex-ratio and potential capacity to adapt (Fuentes et al., 2010; Mitchell et al., 2008). The effect of temperature on sea turtle development is nonlinear as the time spent at different temperatures nonlinearly affects sexual development and sex ratio; therefore average temperatures across the day, which is the usual output format of the correlative model, can misinterpret

Table 3
Comparison between the microclimate and correlative models.

	Microclimate model	Correlative model
Input variables necessary	Days of the year to simulate, geographic coordinates, elevation, slope, aspect, solar reflectivity, time-dependent maximum and minimum data for air temperature, wind speed, wind speed, relative humidity, and percentage of cloud cover. Soil properties at nesting area (thermal conductivity, density, specific heat, and substrate reflectivity). Baseline soil temperature to validate model.	Climatic variables (air and sea surface temperatures). Baseline soil temperature to validate model.
Output data	Hourly temperature at all specified depths including the surface for each day of simulation.	Soil temperature at a set depth and time of the day depending on input data.
Advantages	Accounts for the complexity of nesting behavior of animals with TSD (nesting at different depths and locations). Allows exploration of adaptive responses by animals (e.g. whether nesting at different depths will counteract impact from climate change) and efficiency of adaptive management (e.g. translocation of eggs).	Relative inexpensive equipment necessary (data loggers). Little specialist knowledge of software.
Drawbacks	More time needed for data collection and assembly from field, as there is the need to obtain soil samples and determine their properties. Knowledge of Niche Mapper TM data structure necessary.	The potential error inherent in this approach has not been determined. Cannot be used when environmental conditions vary outside the range to generate the correlative model. Only reconstructs soil temperature for one depth and for a specific time of the day.
Selected studies that have used this model	Christian et al. (1984), Jones et al. (1987), Dunham et al. (1989), Huey et al. (1989), Grant and Porter (1992), Adolph and Porter (1993, 1996), Porter et al. (2000, 2006, 2010), Natori and Porter (2007), Mitchell et al. (2008), Kearney et al. (2009a,b, 2010a,b), Fort et al. (2009), Bartelt et al. (2010), Levy et al. (2012)	Mrosovsky and Provancha (1992), Janzen (1994), Baptistotte et al. (1999), Hays et al. (1999, 2003), Casale et al. (2000), Glen and Mrosovsky (2004), Nelson et al. (2004), Kamel and Mrosovsky (2006), Hawkes et al. (2007), Fuentes et al. (2009, 2010), Patino-Martinez et al. (2012)

correct estimates of sex ratio. Further, sea turtles are known to lay their eggs at various depths and to nest at different locations in the beach (Hays and Speakman, 1993; Kamel and Mrosovsky, 2004) and may adapt to climate change by changing their nest-site choice and nest depth (Hays et al., 2001; Limpus, 2006). Thus, when exploring the potential impacts of climate change on sea turtles it is extremely important to project soil temperature at various locations and depths in the beach. Our results clearly demonstrate this. For example, if we only look at projections of soil temperature at Sandbank 7 at 50 cm for an extreme scenario of climate change in 2070 we may conclude that incubating eggs at this site will only experience temperatures that produce females, however if we look at temperatures at other depths (see Fig. 3) we can see that they will also experience temperatures that produce some males. This clearly demonstrates the need to explore temperature at various depths to obtain a more a realistic picture of what incubating environments will be available for turtles in the future and the impacts that they may experience.

The microclimate submodel in Niche Mapper^{TM} proved efficient in reconstructing and projecting soil temperature at various depths (up to ten depths a time). To project soil temperature at various depths with the correlative approach it is necessary to create several models one for each desired depth. It is also important to explore temperature at various locations within a beach (Fuentes et al., 2010). To project soil temperature at various locations the microclimate model requires slope, aspect and percent shade input variables for different locations within the beach. For the correlative model it is necessary to generate correlative models for various locations in the beach. Fuentes et al. (2010) addressed the “beach location” issue by creating different correlative models for beaches with northern, eastern, southern and western aspect and for open and shaded locations within a nesting island.

Table 4
Difference between model projection (correlative model – microclimate model) for 2030 and 2070 under a conservative (C) and extreme (E) scenario of climate. Models were run to predict soil temperature at 50 cm at midday during the nesting season (November to March). Results from the correlative models were obtained from Fuentes et al. (2009, 2010).

	Difference between models (°C)			
	2030 C	2030 E	2070 C	2070 E
Bramble Cay–North open beach	0.53	0.52	0.61	0.60
Raine Island–South open beach	−0.04	−0.24	0.19	−0.82
Sandbank 7–North open beach	1.32	1.21	1.00	0.26

The usefulness of constructing soil temperature for an array of depths and location is well demonstrated by Mitchell et al. (2008), where they used a microclimate model to investigate if tuatara could behaviorally compensate for sex bias by nesting at different depths and assessed the suitability of current reserves and future translocation sites for tuatara under various depths. Thus, in addition to constructing current and future soil temperature, microclimate models can also be used as a tool to investigate whether species with TDS can counteract the negative impacts of increase in temperature by altering their nesting behavior. With time and the validation of the microclimate model with short-term projections, the microclimate model can also be used to refine short-term adaptive management strategies as they can provide explicit recommendations on site-specific scales for translocation of eggs and alteration of the nesting environment (Mitchell et al., 2008).

The more extensive dataset required to run the microclimate model may limit its applicability, and some users may opt to utilize the correlative model instead. However, particular care should be taken when interpreting the results from the correlative models as they usually only represent one location and depth at a particular nesting ground. Thus, importantly all the assumptions related to the results should be clearly stated. As soil temperature is dependent on the interaction of many variables, such as rainfall, cloud cover, slope, aspect, reflectivity, wind speed and humidity, there is still room to improve the currently used correlative models by incorporating these variables into models. Regardless of the model, selected results should only be used to provide insights on potential outcomes if scenarios envisaged under climate change do occur.

Three things are necessary to increase the applicability of the models described here and our understanding of what results like the one from this study mean to the future sustainability of turtle populations. First, we need to understand the uncertainties associated with the models; from uncertainties related to the input data to the modelling process. Secondly, we need to increase our confidence of the representativeness and accuracy of the models. This could be achieved with continuous testing of the models, in the short-term, using data from the field. Lastly, we also need to improve our understanding on some of their biological parameters related to sea turtles. Major gaps still remain in our knowledge of the viable adult sex ratio for key sea turtle populations and of their capacity to adapt and counteract the impacts of climate change (Hawkes et al., 2009; Poloczanska et al., 2009; Fuentes et al., 2011; Patino-Martinez et al., 2012).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.12.020.

References

Adolph, S.C., Porter, W.P., 1993. Temperature, activity, and lizard life histories. The American Naturalist 142, 273–295.

Adolph, S.C., Porter, W.P., 1996. Growth, seasonality, and lizard life histories: age and size at maturity. Oikos 77, 267–278.

Baptistotte, C., Scalfoni, J.T., Mrosovsky, N., 1999. Male-producing thermal ecology of a southern loggerhead turtle nesting beach in Brazil: implications for conservation. Animal Conservation 2, 9–13.

Bartelt, P.E., Klaver, R.W., Porter, W.P., 2010. Modeling amphibian energetics, habitat suitability, and movements of western toads, Anaxyrus (=Bufo) boreas, across present and future landscapes. Ecological Modelling 221, 2675–2686.

Botkin, D., Saxe, H., Araujo, M., Betts, R., Bradshaw, R., Cedhagent, T., Chesson, P., Dawson, T., Etterson, J., Simon, D., Guisan, F., Hansen, A., Hilbert, D., Loehle, G., Margules, C., New, M., Sobel, M., Stockwell, D., 2007. Forecasting the effects of global warming on biodiversity. BioScience 57, 227–236.

Canteford, R., 1997. Guidelines for the Sitting and Exposure of Meteorological Instruments and Observing Facilities. Bureau of Meteorology, Department of the Environment, Sports and Territories Australia, Observational specification.

Casale, P., Gerosa, G., Yerli, S.V., 2000. Female biased primary sex ratio of the green turtle, Chelonia mydas, estimated through sand temperatures at Akyatan, Turkey. Zoology in the Middle East 20, 33–42.

Christian, K.A., Tracy, C.R., Porter, W.P., 1984. Physiological and ecological consequences of sleeping-site selection by the Galapagos land iguana (*Conolophus pallidus*). Ecology 65, 752–758.

CSIRO, 2007. Climate change in Australia. Technical Report. CSIRO, Australia.

Dunham, A.E., Overall, K.L., Porter, W.P., Forster, C.A., 1989. Implications of ecological energetics and biophysical and developmental constraints for life-history variation in inosaurs. In: Farlow, J.O. (Ed.), Paleobiology of the Dinosaurs. , Geological Society of America Special Paper 238.

Fort, J., Porter, W.P., Gremillet, D., 2009. Thermodynamic modelling predicts energetic bottleneck for seabirds wintering in the northwest Atlantic. The Journal of Experimental Biology 212, 2483–2490.

Fuentes, M.M.P.B., Fish, M., Maynard, J., 2012. Management strategies to mitigate the impacts of climate change on sea turtle's terrestrial reproductive phase. Mitigation and Adaptation Strategies for Global Change 17, 51–63.

Fuentes, M.M.P.B., Hamann, M., Limpus, C.J., 2010. Past, current and future thermal profiles of green turtle nesting grounds: implications from climate change. Journal of Experimental Marine Biology and Ecology 383, 56–64.

Fuentes, M.M.P.B., Limpus, C.J., Hamann, M., 2011. Vulnerability of sea turtle nesting grounds to climate change. Global Change Biology 17, 140–153.

Fuentes, M.M.P.B., Maynard, J.A., Guinea, M., Bell, I.P., Werdell, P.J., Hamann, M., 2009. Proxy indicators of sand temperature help project impacts of global warming on sea turtles in northern Australia. Endangered Species Research 9, 33–40.

Glen, F., Mrosovsky, N., 2004. Antigua revisited: the impact of climate change on sand and nest temperatures at a hawksbill turtle (*Eretmochelys imbricata*) nesting beach. Global Change Biology 10, 2036–2045.

Grant, B.W., Porter, W.P., 1992. Modelling global macroclimatic constraints on ectotherm energy budgets. American Zoologist 32, 154–178.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2007. Investigating the potential impacts of climate change on a marine turtle population. Global Change Biology 13, 923–932.

Hawkes, L.A., Broderick, A.C., Godfrey, M.H., Godley, B.J., 2009. Climate change and marine turtles. Endangered Species Research 7, 137–154.

Hays, G.C., Speakman, J.R., 1993. Nest placement by loggerhead turtles, Caretta-Caretta. Animal Behaviour 45, 47–53.

Hays, G.C., Godley, B.J., Broderick, A.C., 1999. Long-term thermal conditions on the nesting beaches of green turtles an Ascension Island. Marine Ecology Progress Series 185, 297–299.

Hays, G.C., Broderick, A.C., Glen, F., Godley, B.J., 2003. Climate change and sea turtles: a 150-year reconstruction of incubation temperatures at a major marine turtle rookery. Global Change Biology 9, 642–646.

Hays, G.C., Ashworth, J.S., Barnsley, M.J., Broderick, A.C., Emery, D.R., Godley, B.J., Henwood, A., Jones, E.L., 2001. The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. Oikos 93, 87–94.

Hewavisenthi, S., Parmenter, C.J., 2002. Incubation Environment and Nest Success of the Flatback Turtle (Natator depressus) from a Natural Nesting Beach. Copeia 2002, 302–312.

Huey, R.B., Peterson, C.R., Arnold, S.J., Porter, W.P., 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology 70, 931–944.

Hughes, L., 2000. Biological consequences of global warming: is the signal already apparent? Trends in Ecology & Evolution 15, 56–61.

Hulin, V., Delmas, V., Girondot, M., Godfrey, M., Guillon, J.-M., 2009. Temperature-dependent sex determination and global change: are some species at greater risk? Oecologia 160, 493–506.

IPCC, 2007. Climate change 2007: the physical basis. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change.

Janzen, F.J., 1994. Vegetational cover predicts the sex ratio of hatchling turtles in natural nests. Ecology 75, 1593–1599.

Janzen, F.J., Paukstis, G.L., 1991. Environmental sex determination in reptiles: ecology, evolution, and experimental design. The Quarterly Review of Biology 66, 149–179.

Johannes, R.E., Macfarlane, J.W., 1991. Traditional Fishing on the Torres Strait Islands. CSIRO Division of fisheries, Hobart.

Jones, S., Ballinger, R.E., Porter, W.P., 1987. Physiological and environmental sources of variation in reproduction: prairie lizards in a food rich environment. Oikos 48, 325–335.

Kamel, S.J., Mrosovsky, N., 2004. Nest site selection in leatherbacks, *Dermochelys coriacea*: individual patterns and their consequences. Animal Behaviour 68, 357–366.

Kamel, S.J., Mrosovsky, N., 2006. Deforestation: risk of sex ratio distortion in hawksbill sea turtles. Ecological Applications 16, 923–931.

Kearney, M., Porter, W.P., 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12, 334–350.

Kearney, M., Shine, R., Porter, W.P., 2009a. The potential for behavioural thermoregulation to buffer "cold-blooded" animals against climate warming. PNAS 106, 3835–3840.

Kearney, M.R., Wintle, B.A., Porter, W.P., 2010a. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. Conservation Letters 3, 203–213.

Kearney, M., Porter, W.P., Williams, C., Ritchie, S., Hoffmann, A.A., 2009b. Integrating biophysical models and evolutionary theory to predict climatic impacts on species' ranges: the dengue mosquito *Aedes aegypti* in Australia. Functional Ecology, http://dx.doi.org/10.1111/j. 1365-2435.2008.01538.x.

Kearney, M.R., Briscoe, N.J., O'Dwyer, C., Karoly, D.J., Porter, W.P., Norgate, M., Sunnucks, P., 2010b. Early emergence in a butterfly causally linked to anthropogenic warming. Biological Letters 6, 674–677.

Kikukawa, A., Kamezaki, N., Ota, H., 1999. Factors affecting nesting beach selection by loggerhead turtles (Caretta caretta): a multiple regression approach. Journal of Zoology 249, 447–454.

Levy, O., Dayan, T., Kronfeld-Schor, N., Porter, W.P., 2012. Biophysical modelling of the temporal niche: from first principles to the evolution of activity patterns. The American Naturalist http://www.jstor.org/stable/10.1086/665645

Limpus, C., 2006. Impacts of climate change on sea turtles: a case study. Roundtable on Migratory species and climate change. CMS COP, Nairobi, November 2005.

Limpus, C.J., Miller, J.D., Parmenter, C.J., Limpus, D.J., 2003. The green turtle, *Chelonia mydas*, population of Raine Island and the northern Great Barrier Reef: 1843–2001. Memoirs of the Queensland Museum 49, 349–440.

Limpus, C., Parmenter, C., Baker, V., Fleay, A., 1983. The Crab Island sea turtle rookery in the north-eastern Gulf of Carpentaria. Wildlife Research 10, 173–184.

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. Nature 405, 243–253.

Matsuzawa, Y., Sato, K., Sakamoto, W., 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. Marine Biology 140, 639–646.

McCullough, E.C., Porter, W., 1971. Computing clear day solar radiation spectra for the terrestrial ecological environment. Ecology 52, 1008–1015.

McMahon, C.R., Hays, G.C., 2006. Thermal niche, large-scale movements and implications of climate change for a critically endangered marine vertebrate. Global Change Biology 12, 1330–1338.

Mitchell, N.J., Kearney, M.R., Nelson, N.J., Porter, W.P., 2008. Predicting the fate of a living fossil: how will global warming affect sex determination and hatching phenology in tuatara? Proceedings of the Royal Society B: Biological Sciences 275, 2185–2193.

Mokany, K., Ferrier, S., 2011. Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level modelling. Diversity and Distributions 17, 374–380.

Moran, K., Bjorndal, K., 2007. Simulated green turtle grazing affects nutrient composition of the seagrass *Thalassia testudinum*. Marine Biology 150, 1083–1092.

Mrosovsky, N., Pieau, C., 1991. Transitional range of temperature, pivotal temperatures and thermosensitive stages for sex determination in reptiles. Amphibia-Reptilia 12, 169–179.

Mrosovsky, N., Provancha, J., 1992. Sex ratio of hatchling loggerhead sea turtles: data and estimates from a 5-year study. Canadian Journal of Zoology 70, 530–538.

Natori, Y., Porter, W.P., 2007. Model of Japanese Serow (*Capricornis crispus*) Energetics Predicts Distribution on Honshu, Japan. Ecological Applications 17, 1441–1459.

Nelson, N.J., Thompson, M.B., Pledger, S., Keall, S.N., Daugherty, C.H., 2004. Do TSD, sex ratios, and nest characteristics influence the vulnerability of tuatara to global warming? International Congress Series 1275, 250–257.

Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421, 37–42.

Patino-Martinez, J., Marco, A., Quiñones, L., Hawkes, L., 2012. A potential tool to mitigate the impacts of climate change to the caribbean leatherback sea turtle. Global Change Biology 18, 401–411.

Peterson, T., Taylor, M., Demeritte, R., Duncombe, D., Burton, S., Thompson, F., Porter, A., Mercedes, M., Villegas, E., Semexant, R., Tank, A., Martis, A., Warner, R., Joyette, A., Mills, W., Alexander, L., Gleason, B., 2002. Recent changes in climate extremes in the Caribbean region. Journal of Geophysical Research 107, 4601.

Poloczanska, E.S., Limpus, C.J., Hays, G.C., 2009. Vulnerability of marine turtles to climate change. In: David, W.S. (Ed.), Advances in Marine Biology, vol. 56. Academic Press, pp. 151–211.

Porter, W.P., Mitchell, J.W., 2006. System and method for calculating the spatial–temporal and other effects of climate and other environmental conditions on animals. U.S. Patent, pp. 155–377.

Porter, W.P., Mitchell, J.W., Beckman, W.A., DeWitt., C.B., 1973. Behavioral implications of mechanistic ecology: thermal and behavioral modeling of desert ectotherms and their micro-environment. Oecologia 13, 1–54.

Porter, W.P., Ostrowski, S., Williams, J.B., 2010. Modelling Animal Landscapes. Physiological and Biochemical Zoology 83, 705–712.

Porter, W.P., Budaraju, S., Stewart, W.E., Ramankutty, N., 2000. Calculating climate effects on birds and mammals: impacts on biodiversity, conservation, population parameters, and global community structure. American Zoologist 40, 597–630.

Porter, W.P., Vakharia, N.P., Klousie, W.D., Duffy, D., 2006. Po'ouli landscape bioinformatics models predict energetics, behavior, diets and distribution on Maui. International Society for Computational Biology 46, 1143–1158.

Porter, W.P., Sabo, J., Tracy, C.R., Reichman, J., Ramankutty, N., 2002. Physiology on a landscape scale: plant–animal interactions. Integrative and Comparative Biology 42, 431–453.

Smits, K.M., Sakaki, T., Limusuwat, A., Illangasekare, T.H., 2009. Determination of the thermal conductivity of sands under varying moisture, drainage/wetting, and porosity conditions- applications in near-surface soil moisture distribution analysis. Hydrology Days, 57–65.

Spotila, J.R., Standora, E.A., Morreale, S.J., Ruiz, G., 1987. Temperature-dependent sex determination in the green turtle (*Chelonia mydas*): effects on the sex ratio on a natural nesting beach. Herpetologica 43, 74–81.

Trivedi, M.R., Berry, P.M., Morecroft, M.D., Dawson, T.P., 2008. Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. Global Change Biology 14, 1089–1103.

Walther, G.R., Prost, E., Convey, P., Menzels, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O., Bairlein, F., 2002. Ecological responses to recent climate change. Nature 416, 389–395.

Wilson, C., Tisdell, C., 2001. Sea turtles as a non-consumptive tourism resource especially in Australia. Tourism Manage 22, 279–288.