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TITLE: Climate change impacts on nesting and internesting leatherback sea turtles using 3D animated computational fluid dynamics and finite volume heat transfer

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ABSTRACT

Shifting suitable range limits under global warming will threaten many species. Modeling and mapping these potential range shifts is important for conservation. As global warming will introduce new sets of abiotic conditions, predictive empirical niche models may not perform well and the best method to model a specie's projected range shifts may be to model their fundamental niche with a biophysical mechanistic niche model. However, this class of model requires many physiological parameters that are difficult to measure for species not easily kept in captivity. It is also difficult to estimate these parameters for marine species given the interactions among their in-water motion, metabolism, and heat transfer. To surmount these difficulties, we use our previously verified novel technique combining 3D digital design, computational fluid dynamics, and finite volume heat transfer modeling to find animal core temperatures. We then use this method to build a fundamental niche map for interesting and nesting leatherback sea turtles (*Dermochelys coriacea*). With these niche maps we analyze three main nesting areas. We show that global warming poses a large overheating risk to leatherbacks in Southeast Asia, a slight risk to leatherbacks in the West Atlantic and a low risk to leatherbacks in the East Atlantic. We also show that the impact may be less on leatherbacks that shift their nesting location or who are smaller. Methods such these are important to produce efficiently and economically accurate maps of regions that will become inhospitable to species under global warming conditions.

KEY WORDS: Biophysical ecology, Climate change, Global warming, Leatherback, Niche model, Sea turtle

1 INTRODUCTION

Global warming poses a large extinction risk for many species (Thomas et al., 2004). A species' inability to shift its current range to match the future suitable range accounts for much of the extinction risk (Parmesan and Yohe, 2003). Therefore, managers and conservationists will likely need accurate range shift predictions to successfully address the global warming threat to their focal species. For leatherback sea turtles (*Dermochelys coriacea*) estimating new suitable ranges is quite complex. The first difficulty is that leatherbacks are gigantotherms, endothermic poikilotherms, whose large body size traps waste heat thus elevating their core temperature (Paladino et al., 1990). This effect means that leatherbacks are neither thermal conformers nor regulators and thus makes predicting their core body temperature difficult. The second difficulty is their complex life history. They have the largest range of any reptile (Saba, 2013) and are biphasic (nesting on land and living in the water). Thus, global warming will affect leatherbacks over a wide geographic range as well as in two distinct environments. Hence, there is not only a need to determine the leatherback's marine distribution (National Marine Fisheries Service and U.S. Fish and Wildlife Service, 1992) but also potential future nesting locations (Fuentes et al., 2012).

Despite the logistic difficulties of tracking leatherbacks given their pelagic life history, scientists have tracked this species for over three decades and are now producing studies with hundreds of tracks (Fossette et al., 2014). While these studies can provide information on the lower thermal limits of leatherbacks, they cannot analyze the potential future threat of increased water temperatures in the leatherback's equatorial ranges because water temperatures as high as those under climate change do not yet occur. In addition to higher temperatures, global warming may introduce new combinations of abiotic conditions, thus the best method to model

leatherbacks' response to climate change may be to model their fundamental niche using a biophysical mechanistic niche model (Kearney and Porter, 2009; Porter et al., 2002). However, this class of model requires many physiological parameters that are difficult to measure for leatherbacks as they are not easily kept in captivity (Jones et al., 2011). Since leatherbacks are marine species, it is also difficult to estimate these parameters given the interaction between their in-water motion, metabolism, and heat transfer (Boisclair and Tang, 1993).

In our earlier work we avoided these difficulties by simply making reasonable assumptions about missing physiological parameters and simplifying assumptions about the leatherbacks physiology in general (Dudley and Porter, 2014). In this current work, we attempt to address and overcome these difficulties by using an animated, 3D computational fluid dynamics (CFD) simulation and a numerical internal heat transfer model. Our previous work showed how CFD simulations can match the forces on and heat transfer from complex animal shapes in wind tunnel experiments (Dudley et al., 2013). In later work we then demonstrated that, using only stroke frequency, ambient water temperature and an allometric relation for resting metabolic rate (RMR), this method is able to accurately predict leatherback core temperatures in a laboratory environment. (Dudley et al., 2014). Thus, by combining the data from our CDF model (power, heat transfer coefficients, infrared (IR) absorption and radiation, and internal temperature profiles) with global climate models (GCMs) we can predict regions within the leatherback's current marine and terrestrial range that may become inaccessible under global warming conditions. We examine potential shifts in nesting and internesting time and, range, as well as body geometry and size. To our knowledge, this is the first projection of the fundamental niche of an organism using this high level of detail, which can only come from CFD and numerical heat transfer models (Dudley et al., 2013).

2 METHODS

2.1 Outline

The modeling process has three steps and each of these steps is done for the leatherback while it is in the marine environment (“internesting phase”) and while it is on land laying eggs (“nesting phase”). The first step (“CFD simulation step”) uses CFD to calculate heat transfer coefficients from the leatherback, and, for the internesting phase, power required to maintain a set swimming speed. The second step (“heat transfer simulation step”) takes the results of the first step and uses them in a heat transfer model to calculate the leatherback’s core temperature given varying environmental conditions. The third step (“niche model step”) takes the relations between environmental conditions and leatherback core temperature and combines those with climate models to produce maps of leatherback core temperatures under two climate change scenarios. Figure 1 is a diagram of the modeling approach.

Figure 1 A diagram of the modeling procedure. The procedure is divided into three steps (CFD, heat transfer, and niche model) each done on two different phases (interesting and nesting). The computational fluid dynamic (CFD) step produces heat transfer coefficients and work (in the interesting phase). The heat transfer step produces a function of environmental conditions (water temperature (T_w), air temperature (T_a), land temperature (T_l), radiant temperature (T_r), and air velocity (v_a)) which predicts the turtle's core temperature, or change in core temperature during the nesting phase (in water (T_{cw}) and on land (ΔT_{cl})). The niche model phase uses the previously established relations to map the turtle's core temperature under climate change.

2.2 Internesting Phase

2.2.1 CFD Simulation Step

We drew five different anatomically realistic adult leatherbacks in a non-uniform rational basis splines (NURBS) format using commercial 3D design software (MoI). NURBS are 2D irregular surfaces that can produce realistic 3D models of biological forms. The five different models are: one with the largest curved carapace length (CCL) to curved carapace width (CCW) ratio (1.5) and the longest CCL (171 cm) (called long narrow (LN)); one with the smallest ratio (1.2) and the longest CCL (called long wide (LW)); one with the largest ratio and the smallest CCL (128) (called short narrow (SN)); one with the smallest ratio and the smallest CCL (called short wide (SW)); and one which had an average ratio (1.4) and an average CCL (150 cm) (called average (Av)) (see Figure A.1 and Table A.1 in Appendix S1 in Supporting Information). These leatherbacks would weigh approximately 477 kg, 633 kg, 201 kg, 266 kg, and 337 kg respectively. The ratios and lengths are based on data from three sources (James et al., 2007; “Jupiter Island sea turtle tagging project (JISTTP),” 2012; Médicci et al., 2011). This size range more than covers the typical standard deviation observed in CCLs of sampled leatherbacks (typically less than 10 cm). The flipper length scaled with CCL and not with CCW (Walker, 2010). We placed one side of the model in a virtual half cylinder with buffer distances of approximately 4 m between the turtle’s flipper tip and the cylinder’s wall, which is adequate space to not affect the stroke mechanics. The plane dividing the cylinder in half also divides the turtle along the midsagittal plane. Using half the turtle and a symmetry boundary condition on the plane bisecting the turtle increases computational efficiency by only solving the fluid dynamics around one half of the turtle. This setup resulted in volumes ranging from 440 to 1450 m³ depending on the size of the turtle. We meshed all the fluid domains with tetragons (a

standard choice for an unstructured computational grid in CFD). All domains contained approximately 150,000 elements which is adequate to produce accurate results (Dudley et al., 2014).

We use a commercial CFD program, ANSYS Fluent (ANSYS, Inc., Cecil Township, Pennsylvania, USA). We wrote a supplemental program using Fluent's "DEFINE_GRID_MOTION" macro, which describes the leatherbacks' swimming motion (additional details Dudley et al., 2014). To mimic a turtle's flipper motion, we used ImageJ software (National Institutes of Health, Bethesda, Maryland, USA) to analyze frames from publicly available video of leatherbacks freely swimming. The flipper had four zones. The 14% of the flipper closest to the shoulder was the transition zone from no motion to steady roll (flipper moving dorsally to ventrally) and yaw (flipper moving posteriorly to anteriorly). The next 22% of the flipper was the transition zone from steady roll and yaw to steady roll, yaw, and pitch (flipper twisting). The next 21% of the flipper was a zone of constant roll, yaw, and pitch. The last 43% of the flipper was the transition zone from steady roll, yaw, and pitch to roll, yaw, pitch, and bend (flexing of the flipper in the roll plane). The stroke had four phases. There was a down stroke (32.3% of stroke period, -0.95 radians of roll, 0.00 radians of pitch, -0.15 radians of yaw, and 0.00 radians of bend), a turn at the bottom and at the top of the stroke (17.0% of stroke period for each, 0.00 radians of total roll, ± 2.40 radians of pitch, 0.00 radians of total yaw, and ± 0.80 radians of bend), and an up stroke (33.7% of stroke period, 0.95 radians of roll, 0.00 radians of pitch, 0.15 radians of yaw, and 0.00 radians of bend). To prevent discontinuities in the motion, we programmed smooth transitions into the top and bottom phases. To correctly position the flipper, there was also a 0.5 s setup time.

To set the interesting swimming velocity we averaged 64 records of leatherbacks swimming during their interesting phase (Byrne et al., 2009; Eckert, 2002; Hughes et al., 1998; Lambardi et al., 2008; Luschi et al., 2003; Shillinger et al., 2008). Most of these studies measured the turtles' speed by satellite tracking, however, one study used ultramarine velocity recorders (UVRs) on five turtles to measure actual swim speed (Eckert, 2002). Given the small difference between the two measurement methods (less than 14%), the small sample size using UVRs and that average current effects should be small since leatherbacks orient randomly with respect to current (Galli et al., 2012), we used the average of all 64 as the interesting swim speed (0.53 m/s). The stroke periods for the leatherbacks to produce this speed were 2.01 s, 2.19 s, 1.63 s, 1.72 s, and 1.81 s for LN, LW, SN, SW, and Av respectively.

The simulation used the $k-\omega$ shear stress transport (SST) model in Fluent, with a constant velocity inlet (0.53 m/s) and a zero pressure outlet. The $k-\omega$ SST model provides accurate near "wall" performance (i.e. flow around the turtle's body) as well as accurate free stream performance (i.e. flow away from the turtle's body). The virtual fluid the turtle swam in had the properties of seawater (density: 1015 kg/m^3 , specific heat: 4053 J/kg K , thermal conductivity: 0.6 W/m K and viscosity: $9.68 \times 10^{-3} \text{ kg/m s}$). We set the time step to 0.001 s and ran the simulation for one full stroke cycle. We know from our previous work that this time step is short enough to produce accurate results. In all analyses, we removed the initial 500 setup steps. We calculated average thrust, work, and flipper and body heat transfer coefficients. To translate the work done on the fluid into expended energy, we used the aerobic efficiency of tortoise muscle (35% (Woledge, 1968)).

2.2.2 Heat Transfer Simulation Step

The internal model is the same model we used in our previous work except scaled to each leatherback's size (Dudley et al., 2014). Details of the model are in our previous work but, in brief, we divided the inertial region into insulating blubber, muscle/internal viscera, and counter current heat exchanger regions. We found necessary thermal properties for all of these regions in the literature (Table A.2). The internal thermal conductivity varied with temperature to simulate vasoconstriction and vasodilation given cold or hot temperatures. We set a resting metabolic rate from an allometric relation (Wallace and Jones, 2008) and scaled that with temperature according to a Boltzmann factor. The external heat transfer coefficients came from our swimming simulations described above. We calculate the core temperature by taking the average temperature of the body region inside the insulating blubber region

The resting metabolic rate (RMR) scales with core temperature and we are attempting to determine actual core temperature, therefore assigning a metabolic rate to the internal simulation is problematic. Therefore, we ran several simulations for a single ambient water temperature. Each of these simulations had a different metabolic rate corresponding to a different thermal gradient (ranging from 2°C to 18°C). For each set of simulations, we then have two relations. One relation is the guessed thermal gradient between the turtle's core and the environment vs. metabolic rate and the other is the simulated thermal gradient vs. metabolic rate. The actual thermal gradient for a given ambient temperature is when the guessed thermal gradient equals the simulated thermal gradient.

2.2.3 Niche Model Step

Using the relations between ambient water temperature and core leatherback temperature from the internal swimming simulation, we developed a marine niche model program for leatherback turtles. The niche-modeling program uses the relations we found in the CFD

simulations to determine the core temperature based on the ambient water temperature. Consistent with observations, our leatherbacks spend 90 percent of their time stroking and 10 percent gliding (Southwood et al., 2005a). As a leatherback can decrease its ambient temperature by diving deeper, longer and more frequently, if a leatherback in a certain area would have a core temperature above a goal temperature of 29°C it could access colder water by diving deeper, longer, or more often up to a limit. Based on literature on interesting leatherback dive profiles, we set the depth and time limit to be two standard deviations above the average dive depth and time (115 m and 17 minutes respectively). We removed from the calculation for depth limit any study where the author suggested that shallow water capped the dive profiles. We set the surface recovery time to be the average of the minimums observed (30 s) (Eckert et al., 1996, 1989, 1986; Eguchi et al., 2006; Fossette et al., 2010, 2008, 2007; Reina et al., 2005; Southwood et al., 2005b, 1999; Wallace et al., 2005). While leatherbacks are capable of diving longer/deeper than this, we are attempting to set a limit on their average behavior not any individual behavior.

Based on Knutti et al., we selected four global climate models (GCMs) from the CMIP5 multi-model ensemble to use as the climate inputs for our niche model (2010). We selected high performing models that had the outputs we needed. As ocean temperature is the most influential environment variable in our model the highest performing models are those with the least sea surface temperature bias in hindcasts (Wang et al., 2014). The four models are the Met Office Hadley Centre's Hadley Centre Global Environment Model, version 2 (Earth System) (HadGEM2-ES), the Institute Pierre-Simon Laplace's Earth System Model for the 5th IPCC report (mid-resolution) (IPSL-CM5A-MR), The University of Tokyo's Atmosphere and Ocean Research Institute, National Institute for Environmental Studies, and Japan Agency for Marine-

Earth Science and Technology's Model for Interdisciplinary Research on Climate (MIROC5), and the low resolution Max Planck Institute for Meteorology's Earth System Model (MPI-ESM-LR). We selected the monthly average data sets from January 2006 to December 2095 for relative concentration pathway (RCP) 4.5 (a stabilizing scenario) (Clarke et al., 2007; Smith and Wigley, 2006; Wise et al., 2009) and 8.5 ('business as usual') (Riahi et al., 2007). We set the interesting region to be areas within ~200 km of shore which should encompass the regions leatherbacks occupy during interesting behavior (Almeida et al., 2011; Eckert et al., 2006). We calculated the leatherbacks core temperature by running our niche model with each GCM individually before analyzing the results. This method allows us to average the results from the four GCMs to find the average core temperature in regions as well as look at the range of core temperatures different CGMs produce. We then graphed a 10 year moving average of the core temperatures to remove annual fluctuations and display long term trends.

2.3 Nesting Phase

2.3.1 CFD Simulation Step

We setup the land model's fluid dynamics component to calculate the heat transfer coefficients of the leatherback's body and flipper at different wind speeds. For this model, we added a plane below the plastron of the leatherback to simulate the ground. The ground covered 24% of the leatherback's surface area. We enclosed this geometry in a virtual half pipe with 5 m buffers around the leatherback. We meshed the leatherback virtual pipe environment with 1.2 million elements using a combination of tetrahedrons, pyramids and wedges. The simulation used the $k-\omega$ SST model with a variable velocity inlet (0.1 to 20.0 m/s) and a zero pressure outlet.

2.3.2 Heat Transfer Simulation Step

The internal land model geometry was similar to the swimming geometry with the exception that we divided the surface area into three areas. The bottom area exchanged heat with the ground by conduction. This portion of the plastron and the bottom of the flipper accounted for 33% of the leatherback's surface area. The middle area exchanged heat by convection with the air and infrared (IR) radiation with the ground and accounted for 22% of the surface area. The top portion exchanged heat through convection with the air and IR radiation with the sky and accounted for the remaining 55% of the surface area. We set the IR temperature of the ground to that of the ambient temperature multiplied by sand's emissivity. We set the IR temperature of the sky using the Swinbank relation (Swinbank, 1963). Our previous, more simplified model had demonstrated that evaporative cooling has little effect, thus we neglected it (Dudley and Porter, 2014). The internal heat generation used metabolic rates of nesting leatherbacks (1.05 W/kg when crawling (Paladino et al., 1996, 1990), 1.38 W/kg when digging and covering (Paladino et al., 1990), and 0.15 when laying (Lutcavage et al., 1990; Paladino et al., 1996)). The nesting timetable was 3 minutes to crawl up, 22 minutes to dig, 15 minutes to lay, 45 minutes to cover, and 8 minutes to return (Carr and Ogren, 1959). We set the initial temperature of all leatherbacks to 29.85 °C and set air and land temperatures relative to this initial temperature. Preliminary runs showed that core temperature on an absolute scale made little difference in temperature increase and that difference between the initial core temperature and ambient was the important factor. We ran the Av internal model for five different air temperatures, five different wind speeds, and nine different land temperatures for a total of 225 combinations. This number of points proved to give excessive resolution and so we ran the remaining four leatherbacks with three different air temperatures, three different wind speeds, and three different land temperatures for a total of 27 combinations.

2.3.3 Niche Model Step

The land niche model used the 255 or 27 element matrix to interpolate the temperature increase a leatherback would experience in a given region. We used the same four models as the marine niche model taking monthly averages for soil temperature, daily minimum temperature, and wind velocity. We took the nearest marine core temperatures to each of the land cells. We only examined land areas that directly bordered water. We again graph a 10 year moving average.

3 RESULTS

3.1 Marine Simulation

From the marine CFD simulation we calculated power and heat transfer coefficients. The power profile was similar for all five morphologies. There was a rise in power output during the down phase, a spike in power in the middle of the bottom phase, a spike followed by a plateau during the up phase, and a spike in power in the middle of the top phase (Fig. A.2). For the average power during the stroke, the LN had the largest while the SW had the smallest (Fig. A.3). Note that LN and SN used more power to swim at the same speed than LW and SW respectively. This difference is because the narrowing of the carapace moves the flippers closer together and reduces their propeller efficiency (useful power/ available power). Also note that attempting to calculate power by using the force necessary to overcome static drag would have underestimated power output by 50% even given a low 15% propeller efficiency. Our calculated propeller efficiency in the simulation (work that moves the turtle forward divided by the work turtle does on the fluid) is 16.7% which is similar to other studies (Feldkamp, 1987; Webb,

1971). Examining the Av leatherback's pressure profile during the stroke, it is evident that most of the power comes from the flipper's distal region (Fig. 2).

Figure 2 The pressure contours on the Av leatherback as it moves through one stroke period. Black arrows indicate the direction of the image sequence. The other 4 sizes of turtle show similar patterns.

For the heat transfer coefficient, there is a relatively stable coefficient for the body and a changing coefficient on the flipper. The flipper heat transfer coefficient is highest during the down stroke and lowest during the bottom portion of the stroke. The Av leatherback had the

highest coefficients while the SN had the lowest (Fig. A.3). The heat flux through the skin as the Av leatherback moves through its stroke shows higher heat fluxes in the flipper's distal region and in the lateral portion of the carapace posterior to the flipper. Since these simulations only get the heat transfer coefficient, the leatherback skin is set at a constant temperature and the actual leatherback's heat flux (below) will differ.

The internal simulation produced a relation for each of the five leatherbacks between ambient temperature and leatherback core temperature (Fig. 3). SN and SW had the lowest core temperature for a given ambient temperature, Av was slightly above them, and LW and LN were warmer still and close together. The shallow slope of the graphs around 20 °C is due to the leatherback controlling its core conduction through vasoconstriction and dilation. In these simulations, the highest heat flux through the skin is around the soft tissue of the shoulder regions.

Figure 3 The core body temperature of a swimming leatherback given the ambient water temperature and morphology (long wide (LW), long narrow (LN), short wide (SW), short narrow (SN), and average (Av)). The bold, horizontal, black line demarks the critical thermal maximum (CTM) while the dotted lines demark the standard deviation in the CTM measurement.

The Marine niche model produces 1080 maps (one for each month from January 2006 to December 2005) for a given set of conditions. As an example we show a map of the Av leatherback's core temperature using the HadGEM2-ES RCP8.5 inputs for August 2005 (Fig. 4), (All niche maps in NetCDF format will be archived with Dryad upon acceptance). The orange to red areas on the map indicate regions where the leatherbacks are within one standard deviation of their critical thermal maximum (CTM) (40.2 ± 1.3 °C) (Drake and Spotila, 2002) and the black

areas are where they are above one standard deviation of their CTM.

Nesting

Internesting

Core Temperature (°C)

Figure 4 The core temperature of an Av interesting leatherback using the HadGEM2-ES RCP8.5 inputs during August 2095. Areas in orange to red are areas where the leatherback's core temperature is within one standard deviation of the CTM. The calculation only extends from 40°N thru 40°S.

Looking at the condition of the Av leatherback during local nesting seasons at some specific areas (Fig 5.) with large leatherback nesting populations (French Guiana and Suriname (FG&S) (nesting March-July), Gabon and Congo (G&C) (nesting November-February), and West Papua, Indonesia (WP) (nesting May-September)), we see that leatherback interesting core temperatures will increase. Only WP under RCP8.5 shows overlap between the leatherback's CTM and the range of the ten year moving average of the niche models calculated core temperature. None of the scenarios show the average from all four models reaching the CTM zone by the 2095 mark (which is the average of 2085-2095) (Fig. 6).

Figure 5 The three regions specifically analyzed in this study. In the plate containing Papua the west most polygon is the site initially considered while the east most site is used to examine the effects of shifting nesting grounds on leatherback core temperatures.

Figure 6 The Av interesting leatherback's core temperature in a given region from 2006 to 2095 for two climate change scenarios. The graphs are the 10 year moving averages for the relevant nesting months at each location (French Guiana and Suriname (FG&S) (nesting March-July), Gabon and Congo (G&C) (nesting November-February), and West Papua (WP) (nesting May-September)). The "Avg." line is the average core temperature across the four climate models. The "Max/Min"

dashed lines represent the maximum and minimum core temperatures found among the four models. The Size dotted lines represents the maximum temperature found among the four models for the LW turtle and the minimum temperature found among the four models for the SN turtle. The gray band represents the leatherbacks CTM range (39.8 to 41.5 °C). °

3.2 Terrestrial Simulation

The terrestrial niche model produces another 1080 maps (one for each month) for a given set of conditions. (All niche maps in NetCDF format will be archived with Dryad upon acceptance). A leatherback heats up while nesting except during the laying portion where the low metabolic rate allows it to cool. Again, like the swimming turtle, the highest heat flux was around the shoulder area. Our terrestrial data in our three regions of interest yield similar results to the marine niche map (Fig. 7). As might be expected each nesting core temperature graph matches its corresponding internesting graph in shape but is a few degrees higher. Two strategies leatherback populations in WP could use as refuges are changing location and changing nesting time. We analyzed those two options. Changing the nesting time (shifting the nesting season later or earlier by two months) offers no substantial relief; location change (nesting north of Papua New Guinea) provides some relief (Fig. 8). Figures 6 and 7 also show that leatherbacks of smaller size are better equipped to deal with the increasing ambient temperatures.

The LW leatherback is in distress in places outside of WP. For example, the range of the nesting niche model outputs for the LW leatherback overlaps the CTM in FG&S under both RCP4.5 and 8.5 (Fig. 9).

Figure 7 The Av nesting leatherback's core temperature in a given region from 2006 to 2095 for two climate change scenarios. The graphs are the 10 year moving averages for the relevant nesting months at each location (French Guiana and Suriname (FG&S) (nesting March-July), Gabon and Congo (G&C) (nesting November-February), and West Papua (WP) (nesting May-September)). The "Avg." line is the average core temperature across the four climate models. The "Max/Min" dashed lines represent the maximum and minimum core temperatures found among the four models. The Size dotted lines represents the maximum temperature found among the four models for the LW turtle and the minimum temperature found among the four models for the SN turtle. The gray band represents the leatherbacks CTM range (39.8 to 41.5 °C).

Figure 8 A comparison between the nesting core temperatures of leatherback using current nesting timing and location in WP and alternative timing and the alternative location. Figure 5 shows the alternative location.

Figure 9 The LW nesting leatherback’s core temperature in French Guiana and Suriname (FG&S) from 2006 to 2095 for two climate change scenarios. The graphs are the 10 year moving averages for the relevant nesting months in FG&S (nesting March-July). The “Avg.” line is the average core temperature across the four climate models. The “Max/Min” dashed lines represent the maximum

and minimum core temperatures found among the four models. The gray band represents the leatherbacks CTM range (39.8 to 41.5 °C).

4 DISCUSSION

This study shows that using 3D CFD in conjunction with a biophysical niche model is a useful method to model future ranges under projected global climate change scenarios. For animals with complex and difficult-to-measure physiologic characteristics, or for animals whose physiological data are expensive to collect, this method proved a useful alternative for gathering accurate physiological data. In comparison to an empirical niche model this method is superior especially considering global warming because forming an empirical niche map for novel conditions requires complex statistical methods and may still be inappropriate or inaccurate (Dormann, 2007; Kearney et al., 2008). Using the leatherback sea turtle, we showed how these physiological data can be used to predict an animal's future fundamental niche and projected range shift under global warming conditions.

Our results show that global warming, especially if mitigation efforts are not successful, will be damaging for leatherbacks particularly in Southeast Asia. While all leatherback internesting core temperatures will increase, in the three regions we examined, only those in Southeast Asia will likely approach their CTM. For larger leatherbacks, FG&S nesting populations will also experience some thermal distress especially under RCP 8.5. We also see from our results that leatherbacks in WP could shift their nesting location and find refuge from increased temperatures. Also smaller leatherbacks have much lower body temperatures in general which may be an advantage to them in the future. While the body size of the population could decrease in response to increased temperatures, observed cases of rapid decreases in body size are in species with shorter generation times (Grant and Grant, 2002; Heimsath et al., 2003; Jackson et al., 2001; Shackell et al., 2010).

These predictions are conservative in some respects but leatherbacks may also be able to compensate for higher temperatures in ways not considered in the model. The results are conservative particularly in the terrestrial phase. Our model used the average monthly minimum temperature, and an efficient nesting schedule. If leatherbacks nest slower or on a warmer day or time of day, especially if the sun is up (rare daytime nesting), they are facing more thermal risk than our model considers. Leatherbacks may be able to compensate for the increased temperature in other ways such as reducing their swim speed or spending more time resting, however, both these behavioral changes may impact leatherback fitness in unknown ways.

Several other works address the question of modeling sea turtle ranges, habitats, or niches. Pike uses a model that mapped a suitability index onto current nesting sites for all sea turtle species (2013). While the work is limited to current conditions, this approach could perhaps be expanded to make future projections. Hawkes et al. used loggerhead tracking data off the U.S. east coast to make a suitability index considering preferred temperature (2011, 2007), and Pikesley et al. have done similar work with olive ridley sea turtles off the coast of west Africa (2013). Our paper is the first to use a biophysical model to map on a global scale and consider global warmings effects.

Comparing this to our earlier work (Dudley and Porter, 2014), we see that that research underestimated the threat global warming poses to leatherbacks, particularly in Southeast Asia. Most likely this underestimate is due to the lower field metabolic rate we used which came from a doubly labeled water (DLW) study (Wallace et al., 2005). Our metabolic rate is higher and their results may suffer from the difficulties of conducting DLW experiments on a marine vertebrate (Jones et al., 2009).

The data from this research will help managers and conservationists, particularly in Southeast Asia, predict when leatherbacks may stop nesting at local beaches to seek more hospitable waters.

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DATA ACCESIBILITY

All niche maps in NetCDF format will be archived with Dryad upon acceptance.

Appendix

Table A.1 The curved carapace length, volume, mass, and surface area for the long wide (LW), long narrow (LN), short wide (SW), short narrow (SN), and average (Av) leatherbacks

Morphology	CCL (m)	Volume (m ³)	Mass (kg)	Surface Area (m ²)
Av	1.5	0.332	338	3.90
LW	1.71	0.624	636	5.72
LN	1.71	0.472	482	5.00
SN	1.28	0.262	268	3.20
SW	1.28	0.198	202	2.80

Table A.2 Physical properties and respective citations for the internal regions of the leatherback simulation.

Variable	Value	Units	Citation
Insulating region density	980	kg/m ³	(Parry 1949)
Muscle/internal viscera density	1035	kg/m ³	calculated
Thermal conductivity of insulating region	0.28	W/m/kg	(Kvadsheim <i>et al.</i> 1996)
Counter current heat exchanger thermal conductivity	0.531	W/m/kg	(Cheng & Plewes 2002)
Insulating regions heart capacity	2.94x10 ³	J/kg/K	(Cedeno <i>et al.</i> 2000; Davenport <i>et al.</i> 2009; Bagge <i>et al.</i> 2012)
Muscle/internal viscera heat capacity	4.18x10 ³	J/kg K	(Cheng & Plewes 2002)
Activation energy in Boltzmann factor	0.76	eV	(Gillooly <i>et al.</i> 2001)

Figure A.1 The five different leatherback morphologies we modeled are long narrow (LN), long wide (LW), average (Av), short narrow (SN), and short wide (SW). These turtles would weigh approximately 477 kg, 633 kg, 337 kg, 201 kg, and 266 kg respectively.

Figure A.2 The power the leatherback's flippers put into the water as a function of fraction of stroke complete. The vertical lines separate each portion of the stroke (down stroke, bottom, up stroke, top). We fine tuned the leatherback's stroke period so that forces in the swimming direction summed to zero over one stroke period.

Figure A.3 The average data from the five leatherback morphologies. The graph shows power, flipper heat transfer coefficient (F HTC), and body heat transfer coefficient (B HTC). A smaller propeller efficiency makes the LN and SN require more power than the LW and SW respectively.