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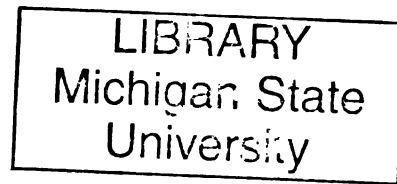
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**MULTIPHASE TRANSPORT PROCESSES IN SEA TURTLE NESTING
BEACHES**

By

Nathan Andrew Miller

A DISSERTATION

**Submitted to
Michigan State University
in partial fulfillment of the requirements
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ABSTRACT

MULTIPHASE TRANSPORT PROCESSES IN SEA TURTLE NESTING BEACHES

By

Nathan Andrew Miller

Sea turtle embryos develop in nest environment determined by the interaction between their own development and the ability of the nest substrate to transport the important commodities of heat, water, and respiratory gases. Relatively little is known of the nest microclimates or how physical characteristics of the nest site determine the nest environment. This study reports on the nest microclimate in natural loggerhead turtle nests and presents a computational model which predicts which nest and nest site characteristics most influence the nest microclimate.

The nest pO_2 in loggerhead turtle nests on Sapelo Island, GA was measured during the summer of 2006 using fiber-optic O_2 sensors. The rate that nest pO_2 declined and the minimum nest pO_2 varied considerably between nests with some nests exhibiting rates of decline and minimum pO_2 s 2.3 and 1.4 times greater, respectively, than others. While the mean minimum nest pO_2 (13.8 ± 0.21 kPa)

differed little from previous work, the pO_2 declined much more rapidly suggesting that the nest pO_2 may be low for much longer than previously thought.

To account for this variability in nest microclimate a three-dimensional, computational model (Beach-MPT) was developed to predict the multiphase transport of heat, gas, and water in and around turtle nests. The model was solved using the finite element method to take full account of the highly heterogeneous, multilayered beach substrate and variable clutch characteristics. Model evaluations using physical nest models demonstrated that the model accurately predicts heat and gas transfer in dry sand. The model less successfully predicted transport in damp sand.

Subsequent sensitivity analyses demonstrated that nest pO_2 and temperature were as sensitive, if not more sensitive, to the abiotic parameters of the nest substrate compared to the more typically measured biotic characteristics. Additional simulations demonstrated that nest temperature and nest pO_2 respond differentially to changes in the abiotic parameters. My results suggest that sea turtle nest management and conservation must focus more that it has on abiotic nest characteristics because processes that alter nesting substrate can dramatically alter nest environments. This suggests that directed habitat alterations could lead to increases in nest success while alternatively, haphazard management of nesting substrate can easily decrease nest success.

This dissertation is dedicated to my parents, Robert and Karen Miller for their unwavering love and belief in me during what has been a long and sometimes tumultuous process. This dissertation is your support manifested in print.

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Images in this dissertation are presented in color

INTRODUCTION

The sandy beaches of the Eastern and Gulf coasts of the United States serve as nesting habitat for the loggerhead turtle (*Caretta caretta*), the green turtle (*Chelonia mydas*), the leatherback turtle (*Dermochelys coriacea*), the hawksbill turtle (*Eretmochyles imbricate*), and the Kemp's ridley turtle (*Lepidochelys kempî*). All marine turtles are listed as endangered or critically endangered by the World Conservation Union (IUCN), and therefore questions of habitat use and suitability are of the utmost importance (IUCN 2004). Little is known of their lifespans, although it is speculated that some species may require 25-35 years to reach reproductive maturity and they may live for 50-60 years. Once reproductively mature, female turtles migrate to terrestrial nesting sites and deposit their eggs on sandy beaches within flask-shaped nests. A loggerhead female typically lays two to three clutches of 110-120 eggs each, every two to three years (Ackerman 1997).

Postovipositional care is absent in turtles, and as the eggs develop over the course of 50-70 days, the nest site is an important determinant of the developmental environment for each embryo. Laboratory work has shown that the nest environment can have dramatic effects on the survival and phenotype of turtle embryos. Physical characteristics of the nest environment such as temperature, moisture, and respiratory gas pressure influence incubation length (Mrosovsky and Yntema 1980, Ackerman 1981, Drake and Spotila 2002), sex determination (Matsuzawa et al. 2002), and embryonic survival (Mrosovsky and Yntema 1980, Kraemer and Bell 1980, Mortimer 1990). These physical characteristics may also alter other important phenotypic traits including body size (Tracy et al 1978, Hewavisenthi and Parmenter 2001), growth

rate (Kam 1993, Rhen and Lang 1995), and running speed (Miller et al. 1987).

Therefore, nest site characteristics have far reaching consequences for turtle ecology, evolution, and conservation.

Despite considerable laboratory-derived knowledge concerning the effects of temperature, moisture, and respiratory gases on turtle embryos, and despite broad recognition that successful marine turtle conservation is dependent on an understanding of the clutch environment (Ackerman 1980), remarkably little is known about the microclimates within natural turtle nests (Maloney et al. 1990). Even less is known about how the physical characteristics of the nest site influence the nest microclimate. As a result, an understanding of the physical processes that determine nest environment rarely drives terrestrial management decisions (e.g., decisions about beach nourishment, nest movement, and hatchery construction). As dune modification, coastal development, erosion, and rising sea levels continue to alter sandy beaches (Titus 1998, IPCC 2001, Titus and Richman 2001), there is a growing need to ensure that the integrity of marine turtle nesting habitat is maintained.

Achieving balance between economically viable beaches and nesting habitat requires a *predictive* understanding of the physical processes that determine the nest environment. In the past this has been accomplished through retrospective analyses, which attempted to correlate nest site characteristics with a measure of nest success. In the future what is needed are prospective analyses which use first principles to develop predictions of the nest microclimate. Additionally, because sea turtles are endangered and attempts to measure the relevant parameters *in situ* necessarily alter the nest environment, strictly empirical studies must be supplemented by alternative

techniques. In the past, to circumvent these challenges, researchers have used analytical models to examine how the physical characteristics of the nesting beach influence the nest microenvironment (Ackerman 1977). The drawback of analytical models is that transport phenomena of interest must be represented by rudimentary, uncoupled equations, and the habitat must be represented by simple geometry. As a result, much of the physical and biological complexity these models are built to explore must be ignored.

The inherent limitations of analytical models will not allow us to generate the accurate, quantitative predictions we need. In this study I have combined disciplines (a biological problem explored with engineering technology), models (computational and physical models), and techniques (using computational, laboratory, and field studies) in an effort to improve our understanding of how the physical characteristics of the nest site influence the nest microclimate. To this end, I have used a numerical modeling technique, the finite element method (Kaliakin 2002, Logan 2002), which differs in several ways from the analytical models that biologists have traditionally used (e.g., Ackerman 1977, Seymour and Roberts 1991, Seymour and Seely 1996). This method is widely used in engineering fields to model complex systems, but is currently underutilized in biological fields. The method allows model parameters (such as thermal or hydraulic conductivity or porosity) to vary realistically in both space and time. It also permits inclusion of realistic geometries and can couple nonlinear transport phenomena so their simultaneous operation can be understood. I have combined this solution method with physical models of turtle nests and field studies of actual conditions within sea turtle nests under natural conditions. Through

this multifaceted approach I have assessed quantitatively the impact of conditions such as nesting substrate heterogeneity, clutch metabolism, and microbial respiration dynamics on nest microclimates and nest survival.

The environment within a sea turtle nest is determined by complex interactions between biotic clutch characteristics and abiotic characteristics of the nest and nest site, with important consequences for embryonic development. Several authors have reported empirical data on the gaseous environment (Ackerman 1977, Mortimer 1991, Wallace *et al.*, 2004, Ralph *et al.*, 2005) within artificial or hatchery nests. All of these studies, however, used methods which required the removal of nest air to measure the nest pO_2 . Such methods raise serious concerns because the removal of gases from the nest will induce the bulk flow of gases into the nest, thereby altering the current measurement and all subsequent measurements as well. Wallace *et al.* (2004) and Ralph *et al.* (2005) both recognize that their methods could induce significant bulk flow and attempted to quantify and discount the effect. They also used methods that tended to minimize the potential for generating dramatic bulk flow. Despite these important steps concern remains over whether the previously reported nest pO_2 's represent actual nest pO_2 's or include methodologically-induced artifacts. In addition, all previous studies primarily examined nests that were relocated to hatcheries and thus may not have represented the conditions found in nests at natural nest sites. To quantify accurately the nest pO_2 in natural nests, measurements must be made in nests at natural nest sites and be made in a manner which does not alter the gaseous environment in the nest.

With this in mind, I describe in Chapter 1 the results of a field study demonstrating the robust nature of a relatively new O₂ sensing technology, use of fiber-optic oxygen sensors, which does not alter pO₂'s or induce bulk gas transport, and then I document for the first time unaltered nest pO₂'s in loggerhead turtle nests at natural nesting sites. The data from this study identify the undisturbed pO₂ levels within sea turtle nests in natural nest locations and demonstrate the variability that exists among nests.

Although the results presented in Chapter 1 show the considerable variability that exists between nests in terms of pO₂, the reasons for this variability are unclear. Clarifying the factors that drive this variability requires an understanding of how heat, water, and gases move in and around a turtle nest. To describe the mechanisms that contribute to the nest pO₂, nest temperature, and moisture levels I developed a dynamic computer model using the finite element method. In Chapter 2, I begin by briefly describing the finite element method and then provide a detailed discussion of the structure of the computational model (Beach-MultiPhase Transport, Beach-MPT), including parameter values and governing equations. I conclude Chapter 2 by describing the results of a series of rigorous laboratory experiments which confirm the Beach-MPT model's ability to predict temperature, water content, and pO₂ under controlled laboratory conditions. I carried out these laboratory tests because of my recognition that whereas models are inherently simplifications of the real world (Oreskes et al. 1994), there is a need to demonstrate that a model exhibits internal consistency and is capable of generating accurate and useful predictions.

After demonstrating the ability of Beach-MPT to predict transport accurately within sandy beaches (in Chapter 2), I use the model in a heuristic manner in Chapter 3 to explore how variation in nesting substrate (both natural and human-induced), microbial respiration, nest depth, and other environmental and clutch-specific characteristics influence nest microclimates. A series of sensitivity analyses elucidate which model parameters most influence the nest temperature and pO_2 . I then use the model to explore the potential consequences of beach nourishment and nest crowding on nest microclimates.

This dissertation broadens our understanding of the microclimate in sea turtle nests and the biotic and abiotic factors that influence it. Combining empirical field studies with physical and computation models has provided new insights into how nest microclimates are determined, what physical and biological characteristics are most important in this determination, and how these characteristics may interact. This type of understanding provides insights into the developmental environment in natural turtle nests, suggests the consequences of human-induced changes to these characteristics, and provides a basis for informed sea turtle conservation.

CHAPTER 1

pO₂ in Loggerhead sea turtle (*Caretta caretta*) nests measured using novel fiber-optic oxygen sensors

1.1 INTRODUCTION

All sea turtles are listed as endangered or critically endangered by the World Conservation Union (IUCN 2001), and therefore questions of habitat use and suitability are of the utmost importance. During the nesting season loggerhead sea turtles migrate to terrestrial nesting sites and deposit their eggs on sandy beaches within flask-shaped nests. A loggerhead female typically lays two to three clutches of 110-120 eggs each, every two to three years. Postovipositional care is absent in turtles, and as the eggs develop over the course of 50-70 days, the features of the nest site are important determinants of the developmental environment for each embryo. Laboratory work has shown that the nest environment can have dramatic effects on the survival and phenotype of turtle embryos. Physical characteristics of the nest environment such as temperature, moisture, and respiratory gas pressure influence incubation length (Ackerman 1981; Drake and Spotila 2002; Matsuzawa et al. 2002), sex determination (Mrosovsky and Yntema 1980; Yntema and Mrosovsky 1980), and embryonic survival (Kraemer and Bell 1980; Ackerman 1981; Mortimer 1990). These physical characteristics may also alter other important phenotypic traits including body size (Tracy et al. 1978; Hewavisenanthi and Parmenter 2001), growth rate (Kam

1993; Rhen and Lang 1995), and running speed (Miller et al. 1987). Therefore, nest site characteristics have far reaching consequences for turtle ecology, evolution, and conservation.

Despite considerable laboratory-derived knowledge concerning the effects of temperature, moisture, and respiratory gases on turtle embryos, and broad recognition that successful marine turtle conservation is dependent on an understanding of the clutch environment (Ackerman 1980), remarkably little is known about the microclimates within natural turtle nests. Even less is known about how the physical characteristics of the nest site influence the nest microclimate. There is every reason to think that sand type, for instance, could affect respiratory gas pressure or other attributes of the nest microclimate. Because of a lack of information on such effects, however, management decisions about beach nourishment, nest relocation, and hatchery construction are rarely driven by knowledge of the ways in which the physical setting of nests will influence the nest environment. As dune modification, coastal development, erosion, and rising sea levels continue to alter sandy beaches (Titus 1998; IPCC 2001; Titus and Richman 2001), there is an increasing need for an understanding of the physical determinants of the environments in which turtle nestlings develop. This is additionally important because nests which may be threatened by waves, vehicles, or foot-traffic are often relocated by managers to “superior” locations. Without a better understanding of how the physical environment determines the nest environment, the superiority of the new nest site is simply speculative.

Nest temperature has been the most measured component of the sea turtle nest microclimate, in part because of the dramatic effects of temperature on sex determination. Nest temperature has also been the most reliably measured component. Miniature temperature dataloggers buried within nests, for example, can record temperature with little concern that the methods are affecting the results.

In contrast the nest oxygen partial pressure (pO_2) has been measured comparatively few times. Moreover, the methods heretofore available for measuring nest pO_2 have potentially altered the pO_2 to at least a small extent because all such methods have required that gas flow be induced in the nests. In several cases gas samples for analysis were withdrawn from the nest through plastic tubing by syringe (Ackerman 1977; Maloney et al. 1990; Clusella-Trullas 2000). More recently, pO_2 measurements were made by pumping gases from the nest, through a portable gas analyzer, and back to the nest (Wallace et al. 2004; Ralph et al. 2005). Both methods raise concerns because the removal of gases from the nest will invariably induce bulk flow of interstitial gases into the nest, thereby possibly altering not only the current measurement, but all subsequent measurements as well. Wallace et al. (2004) and Ralph et al. (2005) recognized this concern and minimized the potential for generating bulk flow during their measurements, while at the same time quantifying the errors such flow would generate.

The recent development of fiber optic pO_2 sensors has created the opportunity for noninvasive measurement of pO_2 . Fiber optic sensors, which do not consume O_2 and require no gas movement to carry out accurate measurements, capitalize on the ability of O_2 to dynamically quench the fluorescence of an O_2 sensitive dye. A small

amount of the fluorescent dye is immobilized on the tip of a fiber optic cable. When blue light is transmitted down the cable, the dye is excited and fluoresces. The fluorescent signal travels up the fiber optic cable, and the fluorescence lifetime (the length of time the dye fluoresces) is measured. In the presence of O_2 , molecular collisions between the excited dye and the O_2 result in an energy transfer from the dye to the O_2 molecules. This energy transfer decreases the fluorescence lifetime of the dye, and the decreased fluorescence lifetime is proportional to the O_2 concentration (Klimant 1995; Glud et al. 2000). Physically, a fiber optic O_2 sensor consists of an arbitrarily long piece of small-gauge fiber optic cable with the dye immobilized on one end and the other end connected to an excitation/read-out device. In application to sea turtle nests, the dye-treated tip is placed within a nest and the connecting cable is threaded to the sand surface. Measurements, as earlier noted, do not themselves alter the pO_2 , nor do they require or induce gas movements. Installing a cable requires manipulation of the sand, but after a cable is in position, it requires no maintenance and can be left in place, undisturbed, indefinitely.

Fiber optic O_2 sensors provide the opportunity to assess directly whether pO_2 measured by traditional flow-based methods are realistic. In the past, the potential errors that gas flow might induce could be assessed through modeling but not by direct comparison of the data obtained with data from a non-flow-based method.

Fiber optic O_2 sensors also provide the opportunity to sort out paradoxes in the literature because the potential for flow-based artifacts can be eliminated from consideration. To illustrate, Wallace et al. (2004) found no significant relationship between minimum nest pO_2 and hatching success, attributing the lack of significance

to the large variability in interclutch hatching success. Ralph et al. (2005) also reported no relationship between nest pO_2 and developmental success and suggested that other environmental variables such as substrate moisture might control hatching success. These results from field studies of natural nests are paradoxical because laboratory experiments have shown that under low pO_2 , hatching success and embryonic growth rate decrease (Ackerman 1981). Does the lack of a relationship between minimum nest pO_2 and hatching success in the field data indicate that field biology is different from lab biology, or is it possibly a reflection that the nest pO_2 has not been accurately or thoroughly quantified with the field methods? Fiber optic methods promise to address this question because they are intrinsically less likely to induce pO_2 artifacts than flow-based methods, and they permit especially thorough studies because individual measurements require little labor.

The objective of this research was to develop a noninvasive means of accurately measuring the nest pO_2 in loggerhead turtle nests in natural nest locations, evaluate the extent of the change in pO_2 during incubation in multiple nests, and examine the relationship between nest pO_2 and hatching success, incubation length, and certain management-motivated nest relocation protocols. Given the apparent importance of pO_2 for metabolism, growth rate, and hatching success in laboratory studies (Ackerman 1981; Kam 1993), I suspect that a relationship between nest pO_2 and hatching success has not been detected in the field because of the methods used to measure nest pO_2 . I further suspect that by accurately measuring nest pO_2 using a relatively non-invasive O_2 sensing technology, fiber-optic oxygen sensors, I would find that the minimum nest pO_2 alters hatching success and incubation length. Finally,

I suspect those nests that have been moved by managers to “superior” locations will have higher pO_2 s than those nests left in their initial location.

1.2~ METHODS

This study was conducted during the summer of 2006 on the undeveloped beaches of Sapelo Island, a barrier island along the coast of Georgia, USA (Figure 1). The nesting season on Sapelo Island runs from late May through early August, with all nests hatching by the middle of October. Freshly laid nests were located each morning and randomly assigned to an *in situ* or relocated treatment as part of a Georgia Department of Natural Resources (DNR) study. At *in situ* nests, which were left at the sites where mothers constructed them, the sand immediately above each nest was removed until the upper surface of the nest was located. Twelve to fifteen eggs were removed to create an opening into the center of the nest. Then an oxygen sensor was placed in the middle of the nest, the eggs that had been removed were replaced, and the nest was recovered with sand. Relocated nests were moved to new locations that appeared, based on the judgment of expert managers, to be of equivalent or better quality than the original nest site. For example, nests laid low on the beach were moved into the primary dunes, and nests laid in the primary dunes were relocated to equivalent sites in the dunes. Each new nest was constructed by hand, ensuring that it was the same depth and width as the original nest. After half of the eggs had been placed in the new nest, an oxygen sensor was placed in the middle of the nest before the remaining eggs were added and the nest covered with sand. The aboveground portion of fiber optic cable was protected in a small, plastic container, when not being employed for data collection. At four randomly chosen locations, O₂ sensors were buried at a depth of 40 cm in sand where there were no nests, to serve as controls. Within several days, both wind and rain had thoroughly packed the

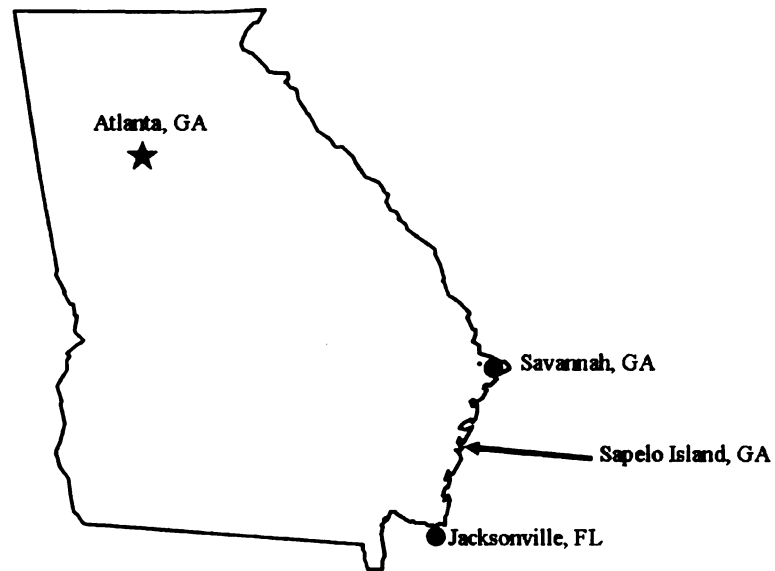


Figure 1. A map of Georgia, USA, with the location Sapelo Island, GA illustrated.

sand, and all measurements were made on naturally weathered nests. All O₂ sensors were left in place for the duration of the study.

1.2.1~ Fiber-optic Oxygen Sensors

Five meter multimode simplex optical fiber patchcords (Anixter, Grand Rapids, MI, USA, 100/140, ST,ST) and the fluorescent dye, Pt(II) meso-tetra(pentafluorophenyl) porphine (Frontier Scientific, Utah, USA) were employed to construct the sensors, following the method of Klimant et al. (1995). Sensors were then mounted inside golf-ball-sized Wiffle [™] balls (Figure 2). The pO₂ measurements were made using a Microx-TX3 excitation/measurement unit manufactured by Presens Precision Sensing GmbH, Germany and the corresponding software (OxyView, version. TX3_v531). Each sensor could be connected to the Microx-TX3 by use of a ST-type fitting. A thermocouple was arranged in tandem with each sensor, providing a measure of nest temperature and of the temperature of the fluorescent dye, necessary for calculating pO₂.

1.2.2 Sensor Calibration

Each sensor was individually calibrated using a two-point calibration protocol. The first calibration point was the pO₂ of humid atmospheric air and was performed in a flask containing a moist towel. The pO₂ of an oxygen-free 1% sodium sulfite solution served as the second calibration point. Rechecks of the calibration of numerous sensors demonstrated that the calibration did not change over time [as also reported by Klimant et al. 1995 and Gatti et al. (2002)].

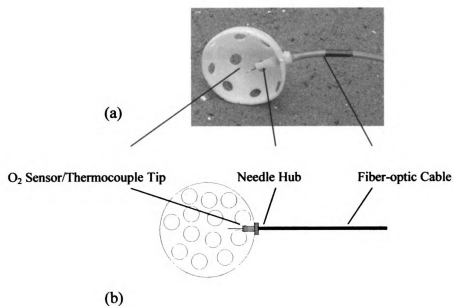


Figure 2. Diagram of O₂ sensor placed in turtle nest. (a) Wiffle golf ball cut in half to show the O₂ sensor and thermocouple inside. (b) Diagram illustrating components of the sensor.

1.2.3~ Schedule of pO₂ Measurement

pO₂ measurements were made every 3 days at the same time of day throughout incubation. After day 47 of incubation, the pO₂ was measured daily so as to better quantify the nest pO₂ just before and just after hatching. When possible, the nest pO₂ was measured for 10 days following hatchling emergence from the nest.

1.2.4~ Nest characteristics

At each nest, the depth to the top of the nest, the width of the nest cavity, the depth of the sensor, and the number of eggs in the clutch were recorded (Table 1). The elevation of all nests above mean sea level was measured by a Georgia DNR survey crew.

Ten days post-emergence, the number of successful hatchlings from a nest was calculated by excavating the nest and counting the number of whole eggs, hatchlings, and broken and torn shells in the nest cavity. The procedure was carried out by the Georgia DNR, which used a 50% rule, whereby a shell fragment that represented more than 50% of the total egg shell was counted as representing a complete hatched egg. All smaller fragments were not considered to represent hatched eggs. It has been shown that this practice results in a small, 6% error in the estimation of the number of hatched eggs (Mark Dodd, GA DNR, *personal communication*). The number of unhatched eggs, and the number of live and dead hatchlings in each nest was recorded at the same time.

1.2.5~ Statistical Procedures

Differences between *in situ* and relocated nests were assessed using one-way ANOVA, and all linear correlations were calculated using SPSS (ver. 14).

1.3~ RESULTS

Fifty-nine nests had oxygen sensors placed in them, but three sensors either failed or broke during the measurement period. Time constraints limited the number of nests in which pO_2 could be recorded for the full duration of egg development, from egg deposition to hatchling emergence. Of the 59 nests containing sensors, 27 were followed until hatchling emergence. An additional 8 nests were followed to within 5 days of hatchling emergence. Two nests, numbered 30 and 47, studied throughout development, were washed over by high spring tides several times, and while these nests were of considerable interest, they were not included in any summary statistics or statistical analyses involving nest pO_2 . As a result, of the 56 nests containing working O_2 sensors, 33 were used in analyses involving nest pO_2 and 35 were used in all other analyses, unless otherwise noted (Table 1).

The minimum nest pO_2 did not differ between *in situ* and relocated nests (one-way ANOVA, $F_{3,29} = 1.829$, $P = 0.164$) though *a priori*, independent contrasts demonstrated that the minimum nest pO_2 of the nests was significantly different from that of the control locations (Contrast test, $df = 4.9$, $t = -7.56$, $p = 0.001$). For all subsequent analyses the nests were combined.

In the nests followed up to the date of hatching (or to within 5 days of that date), the nest pO_2 declined throughout development, the rate of decline being greater during the second half of incubation in all nests (Figure 3). The pO_2 also declined in all nests that were not followed for the full duration of incubation. Control sites (those without nests) showed much slower declines in pO_2 , though the pO_2 at control sites was 2-3 kPa below atmospheric levels by the end of the measurement period (Figure 4). There

was a significant relationship between the rate at which the nest pO₂ declined and the minimum nest pO₂ (Pearson correlation = -0.837, $p < 0.0001$). A strong negative relationship was observed between the date that a nest was laid and the length of incubation (Pearson correlation = -0.73, $p < 0.0001$, Figure 5), with nests laid later in the season exhibiting incubation periods that were approximately 6 days shorter than the earliest nests. There was no evidence of a significant linear relationship between minimum nest pO₂ and incubation length (Pearson correlation = -0.316, $p = 0.084$) or clutch size and minimum nest pO₂ (Pearson correlation = 0.016, $p = 0.931$). However, a significant quadratic or hump-shaped relationship was observed between minimum nest pO₂ and the arcsin of hatching success (one-way ANOVA, $F_{2,30} = 4.2$, $p = 0.025$, Figure 8)

The two nests (30 and 47) washed over by high tides during the course of incubation showed dramatic declines in nest pO₂ following the washover events, but pO₂ levels began to rise within 2 days (Figure 9). Both nests suffered high mortality with hatching success of 13.6% (16/117) and 0.0% (0/82), in nest 30 and 47, respectively.

Table 1. Summary statistics of nest which were followed to within 5 days of hatching. Sample size, range and mean values of several important nest parameters measured during the study. The minimum nest pO₂ of the controls was 18.5 ± 0.24 kPa.

	N	Range	Mean ± SE
Depth to Top of Nest (cm)	35	17.0 – 44.0	28.8 ± 1.15
Depth of Sensor (cm)	34	27.0 – 57.0	42.8 ± 1.43
Width of Nest Chamber (cm)	32	17.5 – 30.0	23.0 ± 0.63
Hatching Success (%)	34	0.0 - 97.7	75.6 ± 4.19
Minimum Nest pO ₂	33	11.4 – 16.4	13.8 ± 0.21
Clutch Size	35	71 - 165	116 ± 3.3

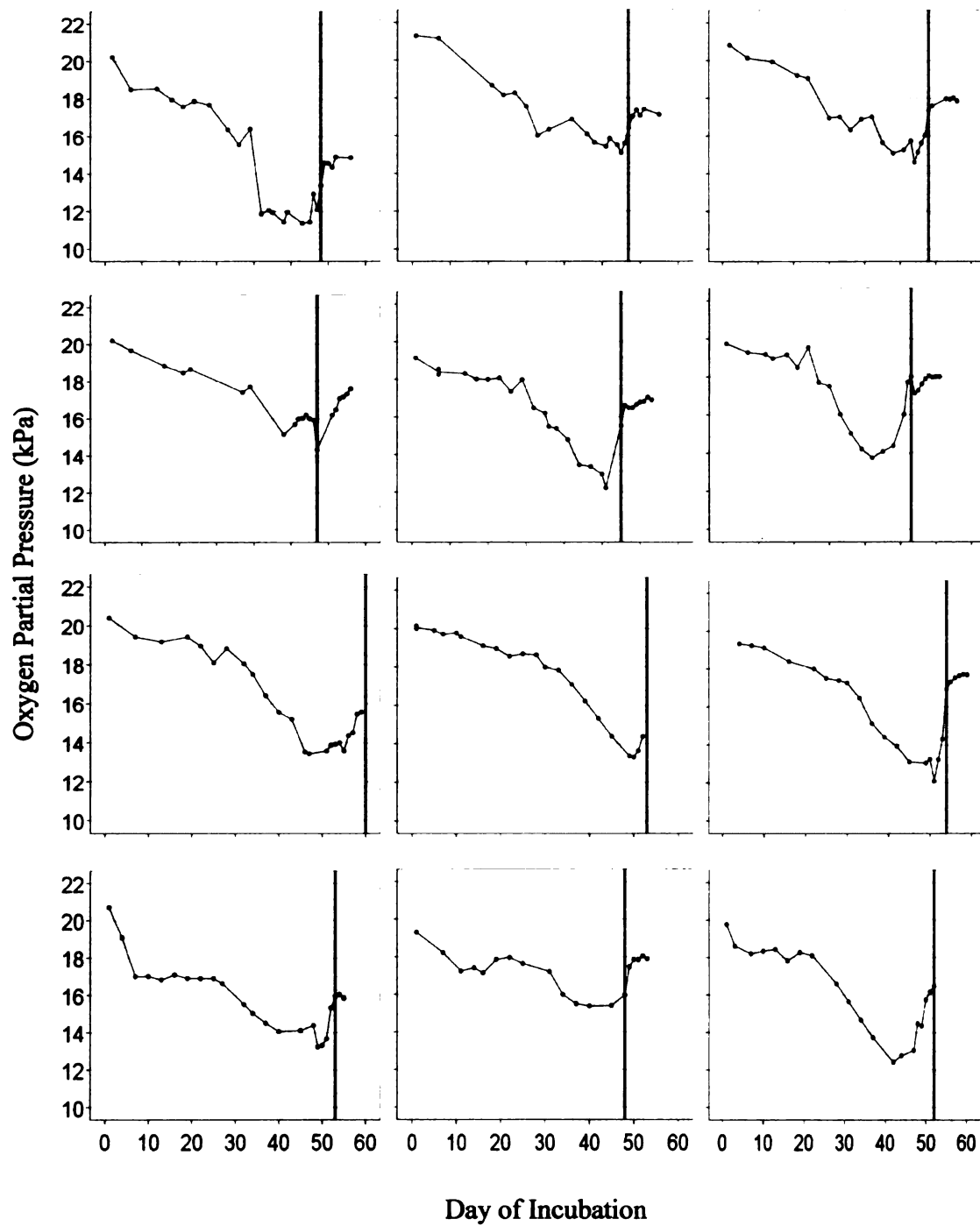


Figure 3. Loggerhead turtle nest pO₂s measured over the full course of incubation in 20 randomly selected nests. The bold line indicates the day of hatchling emergence.

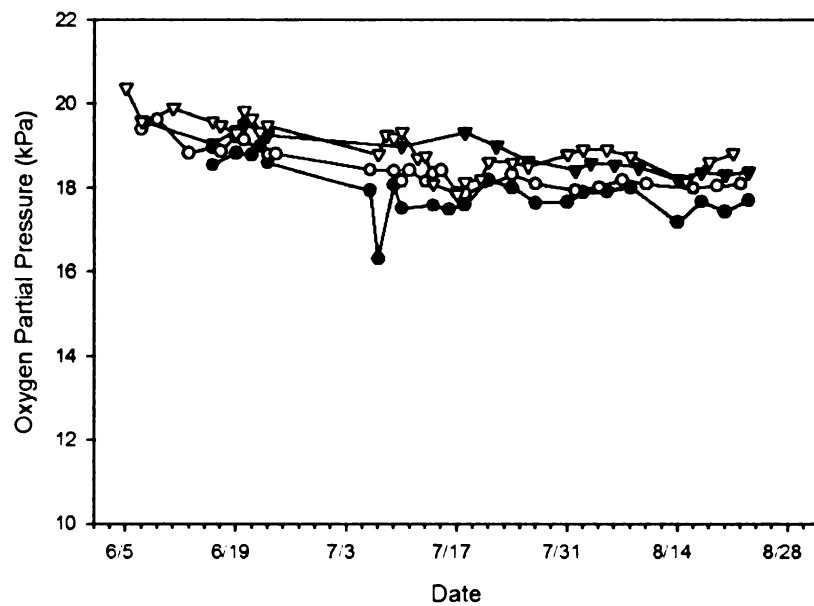


Figure 4. pO_2 measured at four control (nest-free) locations at a depth of 40 cm during the course of the study.

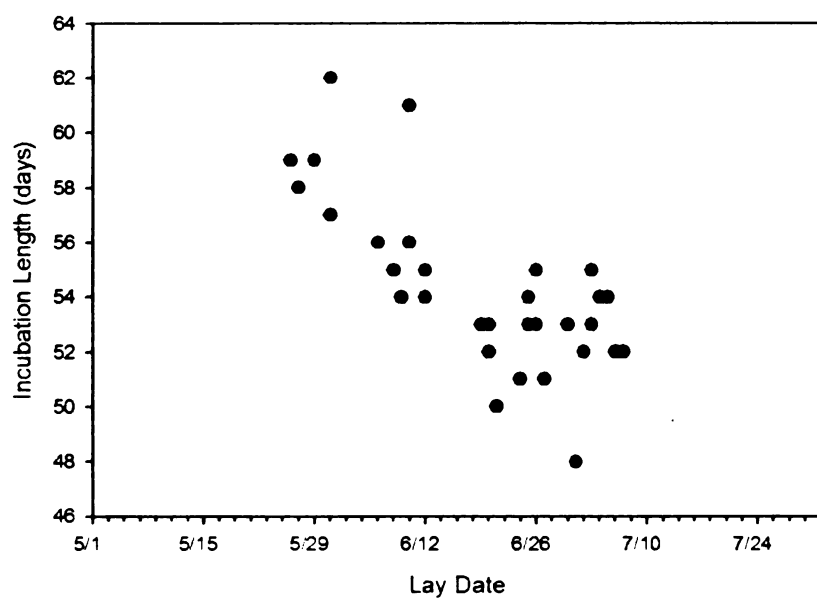


Figure 5: Relationship between the date a nest was laid and the length of incubation (Pearson correlation = -0.73, $p < 0.0001$).

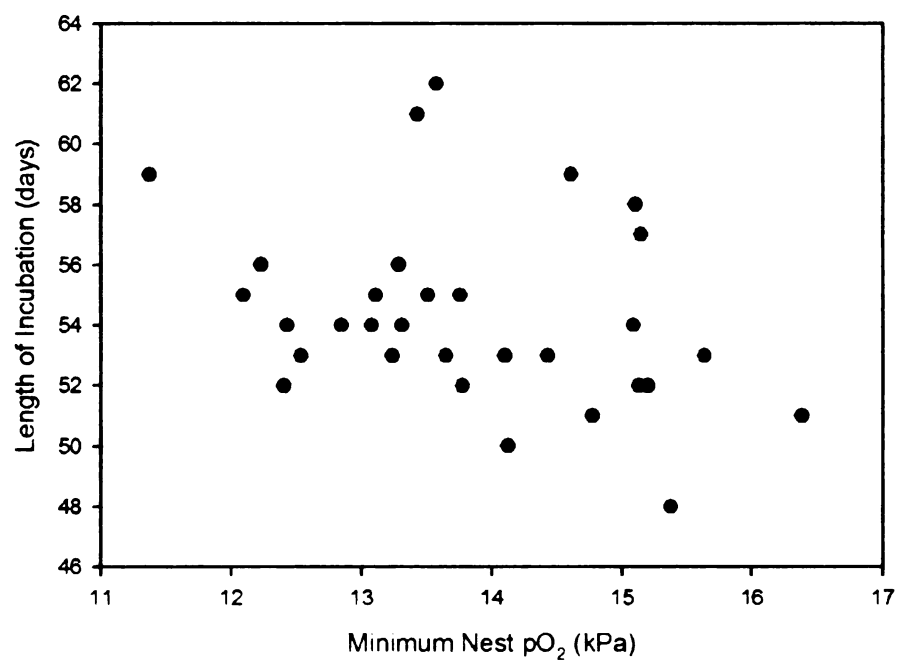


Figure 6. Relationship between the minimum nest pO₂ and the length of incubation (Pearson correlation = -0.316, p = 0.084).

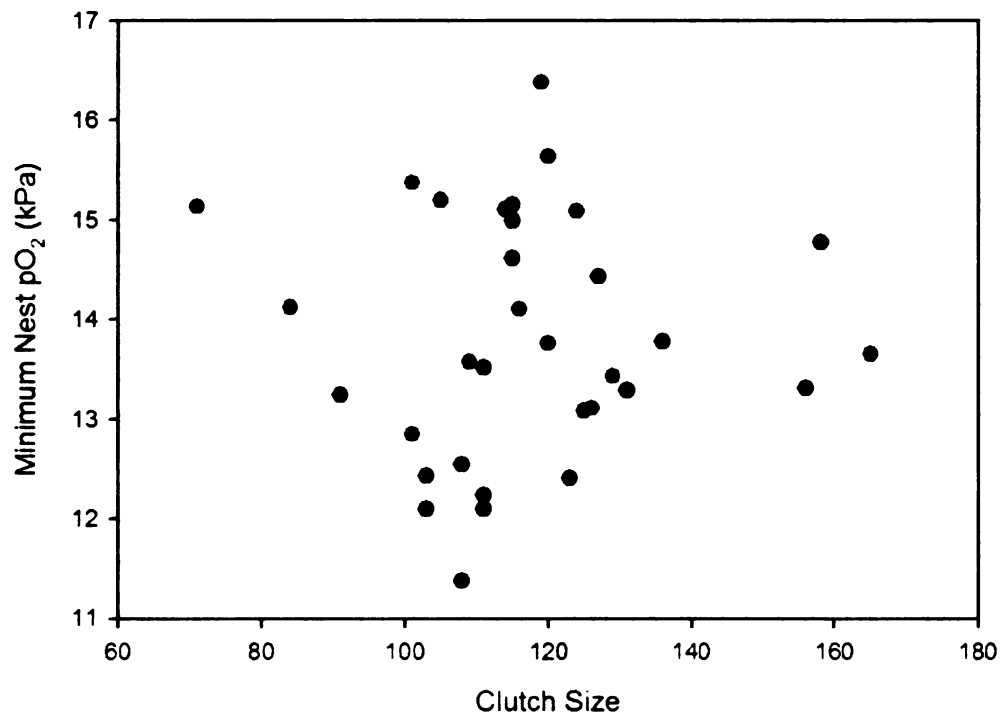


Figure 7. Relationship between clutch size and the minimum nest pO₂ (Pearson correlation = 0.016, p = 0.931).

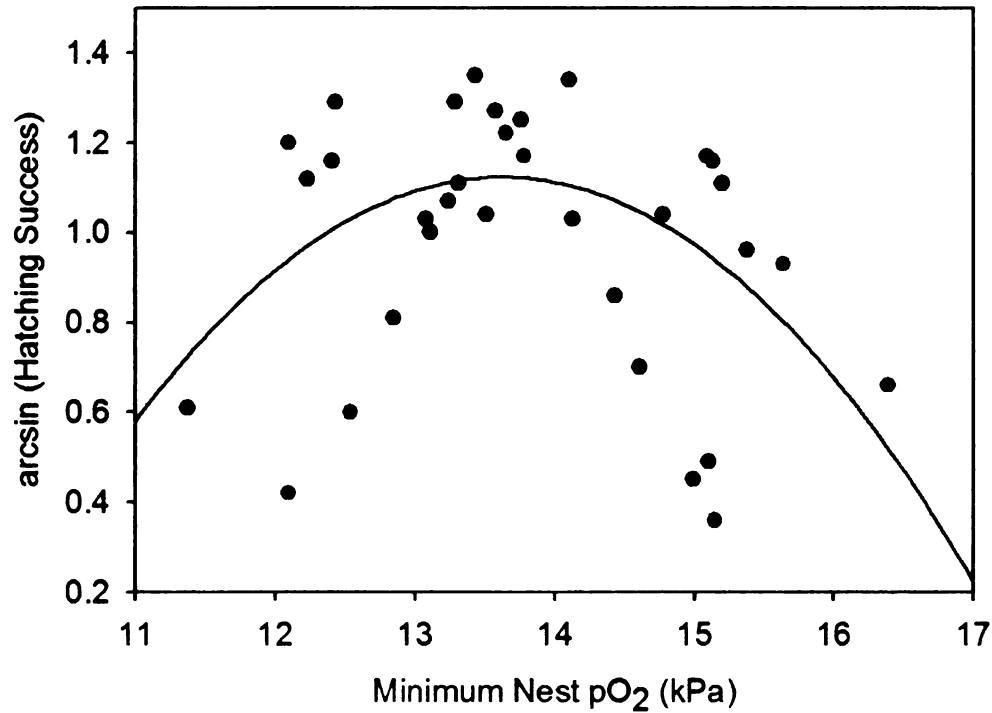


Figure 8. Relationship between the minimum nest pO₂ in each nest and the arcsin of hatching success of in that nest. A significant quadratic relationship was found suggesting intermediate, minimum nest pO₂s are indicative of nests that will be more successful (one-way ANOVA testing the significance of the regression, $F_{2,30} = 4.2$, $p = 0.025$).

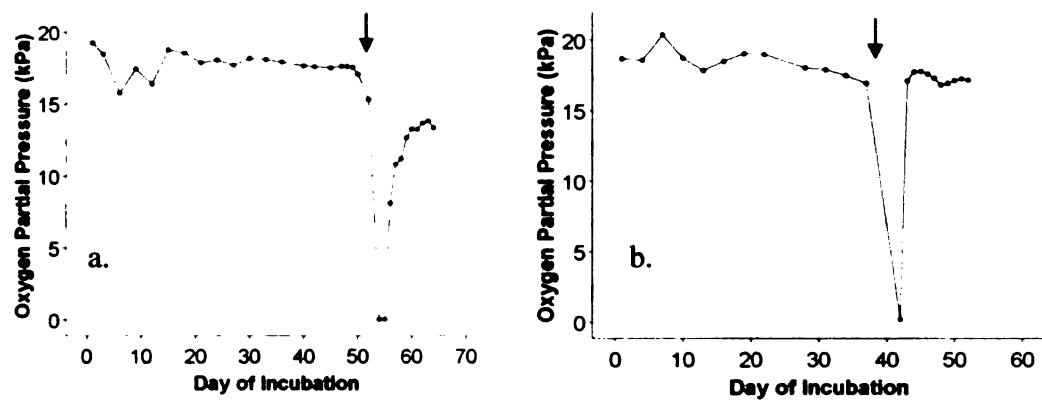


Figure 9: Nest pO₂ following washover by a high tide. a) nest 30, b) nest 47. The arrows approximate the time of initial tidal washover.

1.4~ DISCUSSION

The nest microclimate within sea turtle nests may have dramatic effects upon embryonic survival and hatchling phenotype, and prudent conservation requires careful documentation of the variability in nest conditions. I report here, for the first time, the use of fiber-optic O₂ sensors in measuring O₂ partial pressures in sea turtle nests. Because these sensors do not consume O₂ or induce bulk flow they represent a more certain means of measuring nest O₂ levels compared to previous methods. Fiber-optic O₂ sensors have been used to measure pO₂ in sediment boundary layers, microbial mats, and benthic respiration in deep sea sediments (Glud et al. 1999; Gatti *et al.* 2002). These sensors have also been used to quantify the pO₂ in amphibian eggs (Warkentin et al. 2005) and decapod crustacean egg masses (Fernández et al. 2002). The present research, however, represents one of the first uses of these sensors in a terrestrial system and one of the longest sensor deployments (~60 days). It also represents the first time that undisturbed nest pO₂'s have been recorded for sea turtles.

I recognize that the initial placement of these sensors may significantly alter the nest pO₂. However, all sensors were placed in the nests the morning after each nest was laid and while the nesting substrate was still disturbed from the nesting female. Therefore, the additional disturbance at this time should have little affect on subsequent nest pO₂ values. Relocated nests clearly experience additional disturbance, but the minimum nest pO₂ in relocated nests did not differ from those measured in *in situ* nests, suggesting that the additional disturbance does not have long term consequences for nest pO₂.

Not unexpectedly, the pO_2 in all nests was found to decline throughout the incubation period. The rate and extent of the decline varied considerably between nests, however. The rate of decline was 2.3 times as great in certain nests than others, and the minimum pO_2 was 1.4 times as great in certain ones than others. Whereas previous authors found that the nest pO_2 did not begin to decline until the second half of incubation (Ackerman 1977, Wallace et al. 2004), I found that the nest pO_2 began declining within a few days of the nest having been laid. It is quite possible that using techniques that withdraw nest gases during the early stages of development masked early declines in nest pO_2 (possibly less sensitive techniques are able to detect reduced nest pO_2 only after nest metabolism has risen to a threshold value). It is also of interest that whereas the control (nest-free) sites used by other authors closely approximated atmospheric pO_2 's (Ackerman 1977, Wallace et al. 2004, Ralph et al. 2005), I found that the pO_2 at my control sites declined to a level 2-3 kPa below atmospheric levels (Figure 4). Microbial or root respiration may account for the lower O_2 levels at the control locations, though further studies are needed. It may be that the control sites of other authors simply lacked microbial populations, or it may be that the fiber optic method is more suited to detecting small differences than other methods.

Despite the different measurement methods, the mean minimum nest pO_2 recorded in this study (13.8 ± 0.21 kPa) is in general agreement with the results of Ackerman (1977) who measured minimum nest pO_2 's of 9.3-14.6 kPa in loggerhead and green turtle nests and Maloney *et al.* (1990) who measured nest pO_2 's of 16.8-17.5 kPa in several loggerhead turtle nests. These values are significantly lower than

minimum pO_2 s measured in the nests of leatherback (Wallace et al. 2004; Ralph et al. 2005) and olive ridley turtles (Clusella-Trullas 2000) (Table 2). The differences in minimum nest pO_2 s between species cannot be explained as a consequence of nest depth because the leatherback nests were 0.75 m deep, whereas the average depth of the loggerhead turtle nests was 0.40 m in Ackerman's study and 0.29 m in this study. Wallace et al. (2004) suggest that tidal pumping could account for the high pO_2 s in leatherback nests at Playa Grande, Costa Rica, but comparative studies of the importance of tidal pumping in nests on divergent beaches have not been performed.

Wallace et al. (2004) and Ackerman (1977) both found a significant relationship between clutch size and minimum nest pO_2 , but I failed to detect this relationship. I did find a significant quadratic relationship between minimum nest pO_2 and hatching success (Figure 8), a result which was not observed by Wallace et al. (2004) or Ralph et al. (2005). It may be that Wallace et al. (2004) and Ralph et al. (2005) did not consider the possibility of a quadratic relationship between minimum nest pO_2 and hatching success or it may be that given their smaller sample sizes such a relationship was not discernable. It is not possible to assess either of these possibilities from either reference. This hump-shaped relationship is not entirely unexpected. Those nests that exhibited dramatically low pO_2 s would be expected to have low hatching success. Alternatively, those nests that had much higher minimum nest pO_2 s might simply be those nests in which the embryos died early in development so the nest pO_2 was never drawn down. Those nests with intermediate pO_2 s represent nests which contain respiring embryos as well as sufficient gas exchange.

Table 2. Reported values of minimum pO₂s in sea turtle nests. Summary of the data available on the minimum pO₂ measured in the nests of sea turtles. Means are included when they were given or could be calculated from the data provided in each reference. In some cases, the minimum nest pO₂s were obtained from figures and as a result were approximate.

Species	Nest Number	Minimum nest pO₂ (± SE if available)	Reference
Leatherback Turtle (<i>Dermochelys coriacea</i>)	16	Mean: 18.9 ± 0.28 kPa	Ralph et al. (2005)
Leatherback Turtle (<i>Dermochelys coriacea</i>)	21	Mean: 18.9 ± 0.16 kPa	Wallace et al. (2004)
Olive Ridley Turtle (<i>Lepidochelys olivacea</i>)	1	15.2 kPa	Clusella-Trullas (2000)
Loggerhead Turtle (<i>Caretta caretta</i>)	2	16.4 kPa	Maloney (1990)
Loggerhead Turtle (<i>Caretta caretta</i>)	10	~14.5 kPa	Ackerman (1977)
Loggerhead Turtle (<i>Caretta caretta</i>)	34	Mean: 13.8 ± 0.21 kPa	This study
Green Turtle (<i>Chelonia mydas</i>)	10	~9.5 kPa	Ackerman (1977)

The lack of a relationship between minimum nest pO_2 and incubation length was also unexpected given the critical pO_2 (pO_{2c} : the pO_2 below which metabolism is reduced) of loggerhead embryos. Kam (1993) found that at day 22 of incubation the pO_{2c} of loggerhead turtle embryos was 16.5 kPa and the pO_{2c} increased over the course of development to a maximum of 18.1 kPa on day 45. Embryos exposed to pO_2 's lower than the pO_{2c} should exhibit depressed metabolic rates, which may slow development, increase the length of incubation, and require the greater consumption of yolk stores in the egg. On average I found that the nest pO_2 dropped below 16.5 kPa by day 34. With an average incubation length of 53 days, the developing embryos appear to spend a third of incubation below their pO_{2c} , presumably experiencing depressed metabolic rates. If this is in fact the case, the metabolic depression did not manifest itself in an increased incubation length. Further laboratory studies of embryonic metabolism in sea turtles, and the consequences of temperature and pO_2 on embryonic metabolism, are clearly needed. In particular, measurements of Q_{10s} during development would be very useful.

While there was no clear relationship between low nest pO_2 and incubation length, I did find that nests washed over by high tides suffered dramatic mortality. The two nests subjected to tidal washover exhibited dramatic declines in nest pO_2 immediately following the washover event (Figure 9). Within a few days the nest pO_2 began to rise. Both nests had very low hatching success, suggesting the impact of relatively short periods of reduced nest pO_2 . The small sample size makes generalizations difficult, but it is interesting to note that the nest with more developed embryos (nest 30) had higher hatching success than the nest containing less

developed embryos. This is counter to what one might expect given the increased oxygen demand of older embryos. Additional studies in which nests are exposed to simulated washover at different stages of development, with differing degrees of inundation, while ethically troubling, would provide great insights into the interaction between developmental stage and the tolerance of low pO_2 's induced by tidal washovers. At this point, however, given the high mortality in inundated nests and the fact that relocated and *in situ* nests did not differ in pO_2 , it seems prudent to relocate any nest constructed below the spring high tide line.

This study demonstrates that fiber optic oxygen sensors can be deployed for long periods on open beaches to measure the pO_2 in sea turtle nests and that such sensors provide exceptionally detailed and dependable information on incubation environment. It also suggests that previous measurements of nest pO_2 using methods that may induce bulk flow may be reasonably accurate in predicting the minimum nest pO_2 . This study, however, indicates that a reassessment is needed of the rate and timing of the decline in nest pO_2 that occurs during development. Even in relatively dry sands of the sort on Sapelo Island, developing embryos may experience low nest pO_2 s, with the associated depressed metabolism, for a significant portion of their development. In this study there was a hump shaped relationship between the nest pO_2 on hatching success, though the reason for this relationship remains unclear. While the pO_2 in most nests may depress metabolism, it appears unlikely to be lethal for the majority of the embryos. This is not to say that the low pO_2 is inconsequential, because it may have consequences on hatchling size or dispersal success. However, these variables have yet to be considered in relation to nest pO_2 s in the field, and as a

result it remains difficult to predict the consequences of the low nest pO_2 . Now that we have a robust measurement of the nest pO_2 , there is a clear need for additional studies delineating how tolerant sea turtle embryos are to decreased pO_2 and the consequences of low pO_2 in terms of survival and measures of fitness (e.g., body size or swimming speed). It is also important to recognize the considerable variability that exists among nests, making it difficult to specify the environment within a typical loggerhead turtle nest.

CHAPTER 2

The Structure and Evaluation of a Finite Element Model Predicting Transport Processes In and Around Sea Turtle Nests

2.1~ INTRODUCTION

The finite element method (FEM) is a numerical technique for obtaining approximate solutions to complex problems. In both engineering and biological contexts there is a need to examine such problems as the stresses imposed on an irregular shape, the transport of gases in a non-uniform background, or fluid flow in a system of branching tubes. For such systems it is quite simple to write out the governing equations and even the boundary conditions, but it quickly becomes apparent that a simple analytical solution is unavailable. When faced with this situation there are two solutions. The first is to make a series of simplifying assumptions and reduce the problem to one that can be solved analytically. Several useful texts (Carslaw and Jaeger 1986; Crank 1980) provide analytical equations for solving heat transfer and diffusion problems involving common geometries. Analytical solutions have been widely used in engineering and mathematics, and they have been the almost exclusive solutions used in biology. Yet, the use of analytical solutions often ignores much of the complexity that made the research question initially interesting. With increasing computer processor speed, approximate numerical solutions to complex problems are becoming a more reasonable alternative.

A typical finite element problem begins with a problem domain. The problem domain might be roof joist, a brake pad, a carnivore skull, or a section of beach sand. Within this domain there is a variable of interest, referred to as the field variable. When considering heat transfer the field variable is temperature; in structural mechanics the field variable could be displacement. The distribution of the field variable in the problem domain is typically described by a set of partial differential equations. In many cases such equations are very difficult or impossible to solve analytically. The finite element method is able to solve these problems because it proceeds by breaking the partial differential equation into a set of more manageable ordinary differential equations. As a result, this method produces a piecewise approximation of the partial differential equation.

To illustrate the finite element method, consider the problem of gas transport in insects. The internal tissues of insects are supplied with O_2 through small air-filled tubes (tracheal and tracheolar tubes) that extend from the exoskeletal surface to the tissues. O_2 then diffuses out of the tubes into the surrounding tissues. One objective might be to predict the oxygen partial pressure (P_{O_2}) in the muscle tissue given a specified P_{O_2} in the tracheoles. Figure 8a provides a diagram of a small section of insect muscle tissue with three tracheal tubes running through it representing the problem domain. In this example, the tissue P_{O_2} is referred to as the field variable and its distribution is described by a governing equation of the form

$$\frac{\partial P_{O_2}}{\partial t} = \frac{\partial}{\partial x} \left(D_g \frac{\partial P_{O_2}}{\partial x} \right), \text{ where } D_g \text{ is the diffusion coefficient, } t \text{ is time, and } x \text{ is the}$$

one dimensional coordinate system. At the boundaries of the tissue (outer edges of

the block and the tube surfaces) the field variable (P_{O_2}) is assumed known and specified. The complex geometry of this system makes it difficult to find an analytical solution, but a numerical solution through FEM is possible. In a finite element analysis, the tissue block is first broken into a large, but finite, number of parts or elements (Figure 8b). All elements are interconnected at specific points on each element called nodes, and each element is assigned an interpolation function, which describes how the value of the field variable varies in each element. The interpolation functions can vary from simple linear functions to complex quadratics depending on the complexity of the transport properties of the substance. Each element is also assigned a set of physical characteristics (porosity, diffusion coefficients). Each node is assigned a simple form of the governing equation, which generates a set of

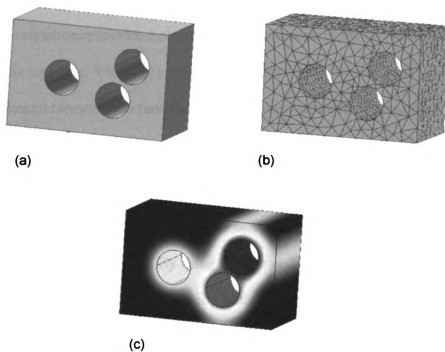


Figure 10. a) Diagram of a section of insect muscle tissue with tracheolar tubes, b) tissue section broken into many small elements as part of the finite element method (FEM), c) FEM solution of oxygen diffusion from tracheoles into muscle tissue. Light areas have high pO_2 , and dark areas are lower pO_2 .

simultaneous equations calculating the field variable, one for each node. Solving these equations provides a piecewise approximation of the field variable across the whole structure. Values at positions not defined by nodes are calculated using the elemental interpolation functions. In the current example, solving the system of simultaneous equations provides an approximate solution to the P_{O_2} distribution within the entire tissue (Figure 8c). The precision of the solution can be enhanced by dividing the tissue into more elements or by assigning more precise interpolation functions to each element. By using smaller and smaller elements it is also possible to approximate highly irregular objects without adopting a simplified approximation of the geometry. In addition, solving the problem in parts (at the element level) allows each element to have a different set of physical properties from the others, and allows the model to accommodate systems that vary both spatially and temporally in their physical properties.

Here I describe a computational model (Beach MultiPhase Transport, Beach-MPT) for predicting transport processes in and around sea turtle nests, its governing equations, and parameters. I then describe a series of four laboratory experiments which used physical models of turtle nests to evaluate the model's predictions of heat and gas transfer.

2.2~ Beach-MPT Model:

Beach-MPT is a three-dimensional model of variably-saturated water flow, heat transfer, and gas transfer constructed using COMSOL Multiphysics (Comsol, Inc., Burlington MA) finite element modeling software. All transport phenomena are coupled to one another. This means, for example, that the movement of water influences the movement of heat and vice versa. The model solves the Richard's equation (Jury et al. 1991) for variably saturated water flow and convection/ diffusion equations for both heat and gas transport. The heat transport portion accounts for heat transfer by conduction, convective heat transfer by flowing water, and latent heat transfer by water vapor. The governing gas transport equations account for mass transfer by convection in flowing water, as well as diffusion in the gas phase. The model also takes full account of a highly heterogeneous, multilayered beach substrate.

2.2.1~ Model Geometry:

Within Beach-MPT the geometry describing the beach and one or more turtle nests within the beach is flexible. In the current working version, the geometry consists of $\frac{1}{4}$ of a 0.2 m diameter turtle nest centered at a depth of 0.45 m and the surrounding sand (Figure 9). This geometry represents an average loggerhead sea turtle nest with its immediate surroundings. By assuming that the sand characteristics do not depend upon which side of the nest one examines I can simply examine $\frac{1}{4}$ of the nest and surroundings, reducing the computational cost associated with each simulation. This geometry provides a baseline with which to compare alternative geometries, including models in which the nest depth is either increased or decreased, or models in which nest size or the number of nests within close proximity is varied.

The model's predictions for these alternative geometries will be discussed in Chapter

3.

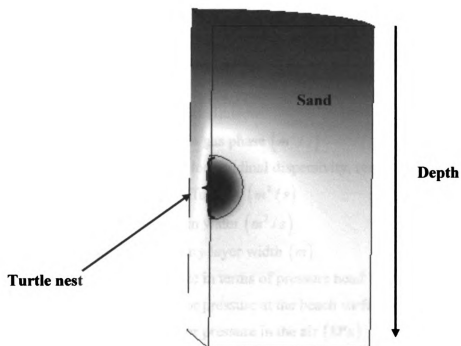


Figure 11: In the base-version of the Beach-MPT model, $\frac{1}{4}$ of the nest and surrounding sand is analyzed to reduce the computational cost. Other geometries, including those considering the interaction among several nests are possible.

Table 2. Symbols used in the Beach-MPT model with associated units.

Arabic

A_1, A_2, A_3	constants used in calculating oxygen solubility.
$C(h)$	specific water capacity (-)
C_n	volumetric heat capacity of the turtle nest ($J / m^3 K$)
C_T	total volumetric heat capacity of the sand ($J / m^3 K$)
C^g, C^w, C^m	volumetric heat capacity of gas, water, and quartz, respectively ($J / m^3 K$)
$D_{i,j}, D_{i,j}, D_{i,k}$	O ₂ dispersion coefficients
D_g	O ₂ diffusivity in gas phase (m^2 / s)
D_T, D_L	transverse and longitudinal dispersivity, respectively
D_v	water vapor diffusivity (m^2 / s)
D_w	O ₂ diffusivity in water (m^2 / s)
d	surface boundary layer width (m)
E	evaporation rate in terms of pressure head (m / s)
e_{sT}	saturation vapor pressure at the beach surface (kPa)
e_a	saturation vapor pressure in the air (kPa)
F	O ₂ source or sink (kPa)
f_w	latent heat correction factor
g_a, g_c	thermal conductivity shape factors
g_v	vapor conductance at sand surface (m / s)
h	hydraulic pressure head (m)
h_r	relative humidity
K	sand-system hydraulic conductivity (m / s)
K_s	saturated hydraulic conductivity (m / s)
K_H	total sand-system thermal conductivity ($W / m K$)
k_a	thermal conductivity of air ($W / m K$)
k_g, k_w, k_m	thermal conductivity of sand gas phase, pore water, and sand particles, respectively ($W / m K$)
k_f	fluid conductivity of the sand ($W / m K$)
p	O ₂ partial pressure (kPa)

p_a	atmospheric pressure (kPa)
q	Darcian water flux (m/s)
$ q $	magnitude of the velocity vector (m/s)
q_{sT}	specific humidity at sand surface (kg/kg)
q_a	specific humidity in the air (kg/kg)
R	universal gas constant ($m^3 kPa / mol K$)
S	heat source or sink
t	time(s)
T	sand temperature (K)
T_a	air temperature (K)
u	constant in latent heat correction
x, y, z	Cartesian coordinates (m)

Greek

β_w	O ₂ solubility in water ($mol / m^3 kPa$)
β_g	factor converting gas pressures to gas concentrations ($mol / m^3 kPa$)
θ_T	total sand porosity ($m^3 pore space / m^3 soil$)
θ_w	volume fraction of water-filled pore space ($m^3 H_2O / m^3$)
θ_r	residual water filled pore space after sand has air-dried ($m^3 H_2O / m^3$)
θ_m	volume fraction of sand solids (m^3 / m^3)
θ_g	volume fraction of air-filled pore space (m^3 / m^3)
θ_0	volumetric water content at which flow ceases ($m^3 H_2O / m^3$)
Se	effective saturation
α, N, M, L	van Genuchten constants for calculating K , θ_w , and $C(h)$
λ	latent heat of vaporization of water (J / mol)
Δ	slope of the saturation vapor pressure function
τ_w	gas transport tortuosity in water filled pores
τ_g	gas transport tortuosity in air-filled pores
τ_n	gas transport tortuosity in turtle nest
$\hat{\rho}$	molar density of air (mol / m^3)
ξ_g, ξ_w, ξ_m	weighting fraction for calculating thermal conductivity

Table 3: Constants used in the base model with values and units.

Term	Value (units)	Reference
K_s	7.44e^{-5} (m/s)	Schaap and Leij (1999)
θ_r	0.0 (m^3/m^3)	
θ_T	0.49 (m^3/m^3)	
α	2.57	Schaap and Leij (1999)
N	1.68	Schaap and Leij (1999)
L	0.5	Van Genuchten (1980)
R	8.314e^{-3} ($\text{m}^3 \text{ kPa} / \text{mol K}$)	
d	0.005 (m)	Campbell (1999)
C^m	7.44e^{-2} ($\text{J} / \text{m}^3 \text{ K}$)	Campbell (1999)
C^w	4.19e^9 ($\text{J} / \text{m}^3 \text{ K}$)	Campbell (1999)
C^g	1.256e^6 ($\text{J} / \text{m}^3 \text{ K}$)	Campbell (1999)
k_a	0.025 ($\text{W} / \text{m K}$)	Campbell (1999)
D_T	0.0001	Bear (1979)
D_L	0.005	Bear (1979)
p_a	101.325 (kPa)	
k_m	8.8 ($\text{W} / \text{m K}$)	Incropera and DeWitt (2002)
k_w	0.6 ($\text{W} / \text{m K}$)	Incropera and Dewitt (2002)
θ_0	0.05 (m^3/m^3)	Campbell et al. (1994)
u	2.0	Campbell et al. (1994)
g_a	0.1	Campbell (1994)
σ	5.6697e^{-8} ($\text{W} / \text{m}^2 \text{ K}^4$)	Krieth and Bohn (1993)

2.2.2~ Governing Equations:

2.2.3~ Variably-saturated water flow:

The governing equation for variably saturated water flow in a porous medium where the air phase does not influence water flow is the Richard's equation (Jury et al. 1991).

$$C(h) \frac{\partial h}{\partial t} = -(\nabla \cdot K) \cdot \nabla (h + z)^* \quad C(h) = \frac{\partial h}{\partial \theta_w} \quad (2.1)$$

where h is the pressure head (m), K is the hydraulic conductivity (m/s), $C(h)$ is the specific water capacity, θ_w is the water content (m^3/m^3), t is time (s), and z is the vertical Cartesian coordinate (m). The unsaturated soil hydraulic properties (water content, hydraulic conductivity, and specific water capacity) are based upon the closed-form expressions of van Genuchten (1980) shown in equations 2.2, 2.3, and 2.4. The van Genuchten function for water content is given by

$$\theta_w = \begin{cases} ((\theta_T - \theta_r)^* Se + \theta_r) & (h < 0) \\ \theta_T & (h \geq 0) \end{cases} \quad (2.2)$$

where θ_T is the saturated water content (m^3/m^3), θ_r is the residual water content (m^3/m^3), Se is the effective saturation given by

$$Se = \left(1 - (\alpha^* |h|)^N\right)^{-M}$$

where α , N , and M are constants specific to a porous medium type.

* The symbol ∇ is a gradient operator. (e.g. $(\nabla \cdot K)$ is shorthand for $\left(\frac{\partial K}{\partial x} + \frac{\partial K}{\partial y} + \frac{\partial K}{\partial z}\right)$)

The expression for hydraulic conductivity is given by van Genuchten (1980)

$$K = \begin{cases} K_s * Se^L * \left(1 - \left(1 - Se^{1/M}\right)^M\right)^2 & (h < 0) \\ K_s & (h \geq 0) \end{cases} \quad (2.3)$$

where, K_s is the saturated hydraulic conductivity (m/s) and L is a fitting parameter, typically taken to be 0.5. The expression for specific water capacity is given by

$$C(h) = \begin{cases} \alpha * M * \frac{(\theta_r - \theta_r)}{(1 - M) * Se^{1/M} * \left(1 - Se^{1/M}\right)^M} & (h < 0) \\ 1 & (h \geq 0) \end{cases} \quad (2.4)$$

2.2.4~ Boundary conditions:

The surface boundary setting can take three forms: evaporation, rainfall (followed by rainfall infiltration), and flooding.

Evaporation boundary condition:

The evaporative boundary is in part dependent upon the surface temperature predicted from the heat transport portion of the model using a variation of Campbell (1999)

$$E = -[g_v * (h_r * q_s T - q_a)] \quad (2.5)$$

where the evaporation rate (E , in m/s) is dependent upon the vapor diffusion rate through the surface boundary layer (g_v in m/s), the relative humidity of the sand at the beach surface (h_r), the saturated specific humidity of the sand at the beach surface at the surface temperature ($q_s T$ in kg/kg), and the specific humidity of the air (q_a in kg/kg). The variables in equation 2.5 are defined in equations 2.6, 2.7, 2.8, 2.9, and 2.11.

The relative humidity is a function of the hydraulic pressure head at the beach surface (h in m), the molecular weight of water (M_w , $0.018 kg/mol$), the beach surface temperature (T in K), and the ideal gas constant (R , $8.314e^{-3}, m^3 * kPa/mol * K$) (Warrick 2002).

$$h_r = \exp\left(\frac{9.8 * MW * h}{R * T}\right) \quad (2.6)$$

The vapor diffusion through the surface boundary layer (g_v in m/s) is a function of the vapor diffusion coefficient (D_v in m^2/s) and the thickness of the boundary layer (d in m) (Campbell 1999).

$$g_v = \frac{D_v}{d} \quad (2.7)$$

The vapor diffusion coefficient (D_v) is dependent upon the beach surface temperature (Campbell 1999).

$$D_v = 2.4 \times 10^{-5} * \left(\frac{T}{293.15}\right)^{1.75} \quad (2.8)$$

The specific humidity at the beach surface (q_{sT} in kg / kg), is an empirical function of the saturated vapor pressure (e_{sT} in kPa) at the beach surface (Campbell 1999).

$$q_{sT} = 0.622 * \left(\frac{e_{sT}}{101.325 - 0.378 * e_{sT}} \right) \quad (2.9)$$

The saturated vapor pressure (e_{sT} in kPa) in Eq. (2.9) in turn a function of the beach surface temperature (T in K) (Campbell 1999).

$$e_{sT} = 0.611 * \exp \left(\frac{17.27 * (273 - T)}{36 - T} \right) \quad (2.10)$$

The specific humidity of the air (q_a in kg / kg) is calculated in much the same way as the specific humidity of the sand q_{sT} (Campbell 1999).

$$q_a = 0.622 * \left(\frac{e_a}{101.325 - 0.378 * e_a} \right) \quad (2.11)$$

where the saturated vapor pressure in the air (e_a in kPa) in Eq (2.11) is a function of air temperature (T_a , K) (Campbell 1999).

$$e_a = 0.611 * \exp \left(\frac{17.27 * (273 - T_a)}{36 - T_a} \right) \quad (2.12)$$

Rainfall boundary:

The rainfall boundary condition takes the form of a Neumann boundary condition,

$$-K \frac{\partial h}{\partial z} = Rf$$

where Rf is the rainfall rate (m/s) and K is the hydraulic conductivity (m/s).

Flooding boundary:

The flooding boundary condition is simply a Dirichlet boundary with a specified pressure head at the sand surface, corresponding to the depth (h_f in m) of the ponded water, $h = h_f$.

A single simulation can have one or all of these boundaries expressed at different times throughout the simulation so that the simulation may begin with an evaporative surface, switch to a rainfall boundary, and then return to an evaporative boundary following the rainfall event.

The bottom boundary is variable and can be specified depending upon specific modeling goals. The bottom boundary can be specified as a flux boundary, $q = \frac{\partial h}{\partial z}$ (m/s), with water draining from the beach profile. The boundary can also be specified as a permanent unmoving water table ($h = 0$) or a specified distance above an unmoving water table ($h < 0$). A final possible boundary specification is one that features a beach water table that fluctuates on a sinusoidal tidal cycle of 12 hr 50 min.

$$h = 0.3 * \sin\left(\frac{\pi}{46200 * t}\right)$$

All other boundaries are specified as no-flux or symmetry boundaries

$$\left.\frac{\partial h}{\partial x}\right|_{x=0} = \left.\frac{\partial h}{\partial x}\right|_{x=1} = \left.\frac{\partial h}{\partial y}\right|_{y=0} = \left.\frac{\partial h}{\partial y}\right|_{y=1} = 0$$

Liquid water transport is assumed to not occur within the turtle nest.

2.2.5~ Heat Transport:

Heat transport is described by a convection/conduction equation (Bird et al. 2002)

$$C_T \frac{\partial T}{\partial t} = -(\nabla \cdot K_H) \cdot \nabla T - (\nabla \cdot q) \cdot C^w \nabla T + S \quad (2.13)$$

where C_T is the total volumetric heat capacity of the sand ($J / m^3 K$), K_H is the thermal conductivity of the soil ($W / m K$), C^w is the heat capacity of water ($J / m^3 K$), q is the Darcian water flux (m / s , coupled with the water transport portion of the model), T is temperature (K), and S is a heat source term (W / m^3).

Volumetric Heat Capacity

The volumetric heat capacity of the porous medium (C_T) is a function of the volumetric heat capacity of the constituents of the medium and the volume fraction of each constituent (DeVries 1963).

$$C_T = C^m \theta_m + C^w \theta_w + C^g \theta_g \quad (2.14)$$

In equation 2.13, the C^m , C^w , and C^g are the volumetric heat capacities ($kJ / m^3 K$) of quartz, water, and air, respectively, while θ_m , θ_w , and θ_g are the volume fractions (m^3 / m^3) of sand, water, and air, respectively.

Thermal conductivity:

Within porous media, heat flows through a complicated system of mineral, water, and air paths, and the conductivity and quantity of each constituent strongly influences the behavior of the composite mixture. In addition, a substantial quantity

of heat is carried by evaporation and condensation in soil pores, and these processes are influenced by both water content and temperature. To account for this the Beach-MPT model computes thermal conductivity as weighted sum of the conductivity of the constituents as proposed by DeVries (1963).

$$K_H = \frac{\theta_w \xi_w k_w + \theta_g \xi_g k_g + \theta_m \xi_m k_m}{\theta_w \xi_w + \theta_g \xi_g + \theta_m \xi_m} \quad (2.15)$$

Here θ is the volume fraction (m^3 / m^3), ξ is the weighting fraction, and k is the thermal conductivity ($W / m K$) of the constituent, and the subscripts, w , g , and m indicate the water, gas, and mineral fractions.

The thermal conductivity of the gas phase (k_g) is the sum of the thermal conductivity of air and the apparent conductivity resulting from latent heat transport. The complete expression is (DeVries 1963)

$$k_g = k_a + \frac{\lambda \Delta h_r f_w \hat{\rho} D_v}{p_a - e_a} \quad (2.16)$$

Here k_a is the thermal conductivity of air ($W / m K$), λ is the latent heat of vaporization of water (J / mol), h_r is the relative humidity, $\hat{\rho}$ is the molar density of air (mol / m^3), D_v is the vapor diffusivity of soil (m^2 / s), p_a is total atmospheric pressure (kPa), and e_a is the vapor pressure (kPa). Δ is the slope of the saturation vapor pressure function.

$$\Delta = \frac{bc e_{sT}}{(c + (T - 273.15))^2} \quad (2.17)$$

e_{sT} is the saturation vapor pressure, the constants are $b = 17.502$, $c = 240.97$, and T is temperature (K) (Campbell 1999).

The correction factor f_w in equation 2.15 accounts for water vapor movement. Under saturated conditions when opposite sides of soil pore differ in initial temperature water may evaporate from the warmer side, diffuse across the pore in the air space and condense on the cooler side of the pore. The latent heat of vaporization in this case is carried with the water across the pore. After the water condenses it can undergo mass flow back to the warmer side of the pore and evaporate again. As the soil water content declines the return liquid flow declines, as does the contribution of latent heat to the entire heat transfer process. Campbell *et al.* (1994) suggest that the f_w term, if defined as now written, corrects for this declining latent heat contribution.

$$f_w = \frac{1}{1 + \left(\frac{\theta_w}{\theta_0} \right)^{-u}} \quad (2.18)$$

Here θ is the volumetric water content, θ_0 represents the water content at which the return flow declines, and u determines how rapidly it declines. The θ_0 term ranges from 0.05 for course sand to 0.25 for heavy clay. The constant u ranges from 2-6 with course materials having lower values.

The weighting factors for calculating soil conductivity depend upon the shapes, conductivities, and volume fractions of the constituents.

$$\begin{aligned}
\xi_g &= \frac{2}{3[1 + g_a(k_g/k_f - 1)]} + \frac{1}{3[1 + g_c(k_g/k_f - 1)]} \\
\xi_w &= \frac{2}{3[1 + g_a(k_w/k_f - 1)]} + \frac{1}{3[1 + g_c(k_w/k_f - 1)]} \\
\xi_m &= \frac{2}{3[1 + g_a(k_m/k_f - 1)]} + \frac{1}{3[1 + g_c(k_m/k_f - 1)]}
\end{aligned} \tag{2.19}$$

k_f is the fluid conductivity for the soil and according to Campbell (1994) is calculated as $k_f = k_g + f_w(k_w - k_g)$. It can be seen that in dry soil (as $f_w \rightarrow 0$) the fluid conductivity is that of the gas phase and for a saturated soil it is the value for water. The g_a and g_c terms are shape factors and depend on the shape of the soil particles.

$$g_a \begin{cases} 0.1 \text{ for mineral soils} \\ 0.33 \text{ for organic soils} \end{cases}$$

$$g_c = 1 - 2g_a$$

Thermal characteristics of the nest:

The thermal conductivity of the nest is a composite conductivity including both the conductivity of the air filled spaces around individual eggs and the conductivity of the eggs themselves, $k_{nest} = k_{air-space} + k_{eggs}$. The fractions of the nest volume that are air-filled pore space and occupied by eggs are calculated by assuming the eggs are packed in the nest in a face-centered array. By this standard, eggs constitute 74.05% of the nest volume and 25.95% of the nest volume is air space. Given these values and assuming the thermal conductivity of each egg is the average

conductivity of a chicken egg ($k_{egg} = 0.45 \text{ W / m K}$, Polley et al. 1980) it is possible to calculate a nest thermal conductivity.

The heat capacity of the nest is treated similarly. Assuming a turtle egg has the specific heat of a chicken egg (3.3 kJ/kg K, Romanoff and Romanoff 1949) and given that an average loggerhead turtle egg has a mass of 32.7 grams and a volume of 36.2 mL (density = 903.31 kg/m³, Ackerman 1997) the volumetric heat capacity of an egg is $2.9809 \times 10^6 \text{ kJ/m}^3 \text{ K}$. The volumetric heat capacity of air is $1.256 \times 10^3 \text{ kJ/m}^3 \text{ K}$. For a nest in which the eggs are packed in a face-center fashion the volumetric heat capacity is

$$C_{H_n} = \left(0.7405 * 2.9809 \times 10^6 \frac{\text{kJ}}{\text{m}^3 \text{K}} \right) + \left(0.2595 * 1.256 \times 10^3 \frac{\text{kJ}}{\text{m}^3 \text{K}} \right)$$

The first term accounts for the portion of the nest volume composed of eggs, while the second term accounts for the air filled spaces.

Heat produced through the metabolism of the developing embryos is modeled using metabolism data from the Ackerman (1981) assuming a respiratory exchange ratio (REE) of 0.7. For example, a loggerhead turtle nest approaching the end of incubation containing 100 eggs, has an oxygen consumption rate of $\sim 6.661 \times 10^{-4}$ moles O₂/m³ s. Assuming an REE of 0.7, a calorific coefficient of 443,520 J/mole O₂, and an egg density of the heat production of the nest is $\sim 295 \text{ J/m}^3 \text{ s}$.

2.2.6~ Boundary conditions:

The surface boundary temperature is calculated using a sin function, which specifies the hottest portion of the day at 15:00.

$$T_a = 310.5 + 12 * \sin\left(\frac{\pi}{43200 * t} - \frac{7}{12} \pi\right) \quad (2.20)$$

Here t is the time (s) and the average surface temperature is 310.5 K with amplitude of 12 degrees.

Convective heat transport at the bottom boundary takes the form of a Neumann boundary condition and is dependent upon the results of the water flow portion of the model $\frac{\partial T}{\partial t} = -K_H \cdot \nabla T - (q * T)$. All other boundaries are specified as no-

flow or symmetry boundaries, $\frac{\partial T}{\partial x}\bigg|_{x=0} = \frac{\partial T}{\partial x}\bigg|_{x=1} = \frac{\partial T}{\partial y}\bigg|_{y=0} = \frac{\partial T}{\partial y}\bigg|_{y=1} = 0$

2.2.6~ Respiratory Gas Transport:

Gas transport in both the gas and liquid phase is described by

$$\left(\beta_w + \beta_g\right) \frac{\partial p}{\partial t} = -\left(D_{i,i}\beta_w + D_{i,j}\beta_w + D_{i,k}\beta_w + D_g\tau_g\beta_g\right) \cdot \nabla p - \nabla q(p\beta_w) + F \quad (2.21)$$

Where β_w is the gas solubility in water; β_g converts gas pressure to gas concentration; $D_{i,i}$, $D_{i,j}$, and $D_{i,k}$ are hydrodynamic dispersion coefficients; D_g is the gas phase diffusivity; τ_g is the gas phase tortuosity; q is the Darcian water flux (coupled from the water flow portion of the model); p is the gas partial pressure, and F is a gas source term (Freeze and Cherry 1979).

The solubility of oxygen in water (β_w , $mol / m^3 kPa$) is temperature dependent and expressed as:

$$\beta_w = \left(\exp \left[A_1 + A_2 \left(\frac{100}{T} \right) + A_3 \ln \left(\frac{T}{100} \right) \right] \right) / (101.325 * 0.0224)$$

Here A_1 , A_2 , and A_3 are constants fitted by Weiss (1970). The solubility values calculated using this equation are nearly identical to those calculated using the equation found in Battino (1980).

The gas conversion factor (β_g , $mol / m^3 kPa$) assumes ideal gas behavior and is temperature dependent:

$$\beta_g = \frac{1}{RT}$$

where R is the universal gas constant ($8.314 \times 10^{-3} m^3 kPa / mol K$) and T is the temperature (K).

The hydrodynamic dispersion coefficients describe the spreading of gas in solution by mechanical mixing and molecular diffusion (Bear 1979).

$$(D_{xx}) = D_L \frac{q_x^2}{|q|} + D_T \frac{q_y^2 + q_z^2}{|q|} + D_w \tau_w \quad (D_{xy}) = (D_{yx}) = (D_L - D_T) \frac{q_x q_y}{|q|}$$

$$(D_{yy}) = D_L \frac{q_y^2}{|q|} + D_T \frac{q_x^2 + q_z^2}{|q|} + D_w \tau_w \quad (D_{yz}) = (D_{zy}) = (D_L - D_T) \frac{q_y q_z}{|q|}$$

$$(D_{zz}) = D_L \frac{q_z^2}{|q|} + D_T \frac{q_x^2 + q_y^2}{|q|} + D_w \tau_w \quad (D_{zx}) = (D_{xz}) = (D_L - D_T) \frac{q_z q_x}{|q|}$$

Here those functions in the form of D_{ii} represent the principal components of the dispersion tensor and those in the form of D_{ij} represent the cross terms of the dispersion tensor. D_L is the longitudinal dispersivity, D_T is the transverse dispersivity, $|q|$ is the magnitude of the velocity vector, q_i is the Darcian water flux in the i^{th} direction, D_w is the oxygen diffusion coefficient in water, and τ_w is the tortuosity factor in the liquid phase.

The magnitude of the velocity vector is calculated as (Bear 1979):

$$|q| = \sqrt{(q_x^2 + q_y^2 + q_z^2)}$$

The diffusion coefficients both in the liquid D_w and gas phases D_g are temperature dependent and expressed as (Campbell 1999):

$$D_w = 2.67e-9 * \left(\frac{T}{293.15} \right)^{1.75}$$

$$D_g = 2.15e-5 * \left(\frac{T}{293.15} \right)^{1.75}$$

The tortuosity factors for the liquid τ_w and gas phase τ_g are expressed as (Millington and Quirk 1961):

$$\tau_w = \frac{\theta_w^{10/3}}{\theta_T^2} \qquad \tau_g = \frac{\theta_g^{10/3}}{\theta_T^2}$$

2.2.7~ *Boundary Conditions:*

The upper surface boundary is a Dirichlet boundary with a specified oxygen partial pressure of 21.23 kPa (approximate average atmospheric value). At the bottom boundary, a Neumann boundary yields convective transport of dissolved gas and is dependent upon the results of the water flow portion of the model.

Gas Characteristics of the Nest:

The nest oxygen consumption rate is included as a diffuse sink term, parameterized by use of the same metabolism curves used to calculate nest heat production (Ackerman 1981). Within the nest, gas transport occurs solely by diffusion through the air-filled pore spaces between individual eggs. The pore space is again calculated using a face-centered arrangement yielding a fractional air-filled pore-space of 0.2495. Individual eggs are not modeled, but instead total nest metabolism is modeled as a diffuse consumption throughout the egg-filled nest volume. Nest gas transport is calculated as

$$(\beta_g) \frac{\partial p}{\partial t} = -(D_g * \tau_n * \beta_g) \cdot \nabla p$$

The variables are defined in the same manner as equation 2.21 except that τ_n is the

nest tortuosity $\left(\tau_n = \frac{0.2495^{(10/3)}}{0.2495^2} \right).$

2.3~ Beach-MPT Evaluation Experiments:

Models in the biological sciences can be broken into two classes: those that describe and those that explain (Ginzberg and Jensen 2004). Models in the first class are typically statistical in nature, and data are used to fit the parameters in the model through maximum likelihood or least squares procedures. These models are used to predict or resolve basic relationships between specific variables and often exhibit good predictive ability. These models, however, do not describe causal relationships, but rather, describe the statistical relationships among components of a biological system (Peck 2004).

Models in the second class attempt to explain biological phenomena. These models represent a theory about how the components of a biological system work causally to produce a given outcome. Additionally, this second class of model allows researchers to run simulations and therefore, provides an *in silico* experimental system (Peck 2004, McCulloch and Huber 2002). Experiments can be designed and carried out in much the same way as in a real system, but with complete control. Simulation experiments allow for experimentation that would otherwise be impossible, too costly, too time consuming, or unethical in a real system (Peck 2004). Simulation models are powerful, therefore, because they provide insight into “what the world would look like if it worked the way we think it does” (Peck 2004).

In order for a simulation model to serve as an experimental system in which the experimental results are accepted by the scientific community, some measure of the model’s validity is required. To evaluate the usefulness of the Beach-MPT model in predicting temperature, moisture, and oxygen gradients around sea turtle nests, I

have developed a set of four model evaluation experiments. Each experiment uses a sand mesocosm containing an artificial turtle nest. Measurements of sand temperature, water content, or oxygen partial pressure are measured around the nest in the mesocosm. Comparing the actual measurements to those predicted by the Beach-MPT model provides a valuable measure of the model's usefulness and provides a springboard for subsequent explorations using the model.

2.4~ METHODS:

2.4.1~ *Mesocosm:*

The predictions from the Beach-MPT model were evaluated in a laboratory setting using a sand mesocosm to replicate a segment of sandy beach. The mesocosm consisted of a 0.23 m³ (0.61 x 0.61 x 0.61 m) plywood box, with a bottom of fine, stainless steel mesh (320 mesh), and was filled with quartz sand. In all trials the thermal conductivity of the sand solids was assumed to be that of quartz.

The bulk density of the sand was calculated from the mass of a known volume of sand from the mesocosm. The porosity of the sand was calculated from the sand bulk density as, $\text{Porosity} = \left(1 - \frac{\text{bulk density}}{\text{mineral density}} \right)$. The mineral density was assumed to be the particle density of quartz (2.65 g/cm³, Skopp 2002).

2.4.2~ *Temperature Evaluation:*

Experiment 1:

The Beach-MPT model predicts the temperature gradients in the sand around a nest based upon a set of sand and nest characteristics. These include the nest heat output, the thermal conductivity of the sand, the porosity of the sand, the water content of the sand, the temperature of all boundaries, and the initial sand temperature. To evaluate the computer model, a mesocosm experiment in which all these parameters were known was run. To replicate a developing turtle nest, a 20-cm-diameter artificial nest was constructed from a wire mesh sphere covered in a thin membrane. The membrane minimally impeded heat transfer while keeping the sand from filling the nest. Within the nest heat was generated by a series of resistors (total resistance = 12 Ohms). The heat output of the resistors was calculated using Ohm's

law, and a range of heat outputs were realized by manipulating the applied DC voltage. A 1.5-watt computer fan in the nest ensured even heat distribution. The heat output of the fan and the resistors together represented the heat output of the nest.

The temperatures of the inner surfaces of the mesocosm and the sand surface were measured periodically during each experiment using surface thermistors, and the sand temperature at predetermined coordinates around the artificial nest was measured with multiple thermocouples (30-gauge, Type-T) and logged using a datalogging program written in LabVIEW (ver. 6.0, National Instruments, Austin, TX). Each thermocouple recorded the temperature every 10 s during an experiment (which ran 4-6 h), and 10-min averages were calculated.

Experiment 2:

Using the same set-up as just described, a second experiment was conducted with a layer of wet sand ($0.1 \text{ m}^3 \text{ H}_2\text{O}/\text{m}^3$) placed between a depth of 20 and 40 cm in the mesocosm.

2.4.3~ $p\text{O}_2$ Evaluation:

Experiment 1:

Figure 10 provides a diagram of the experimental set-up for the $p\text{O}_2$ experiments using a second 20-cm-diameter artificial nest covered by fine, stainless steel cloth (320 mesh) that excluded sand from the nest. The sand in these experiments was dry. To realize a known and specific $p\text{O}_2$ within the nest, N_2 and O_2 were passed at regulated flow rates through a large mixing chamber and into the hollow nest. A small fan in the nest ensured the gases remained mixed. An outlet was provided by a length of tubing (1.5 m, 1.27 cm I.D.) of sufficient diameter and length

that it ensured atmospheric pressure within the nest and inhibited ingress of atmospheric gas. A water manometer connected to the nest verified the pressure equality during all experiments.

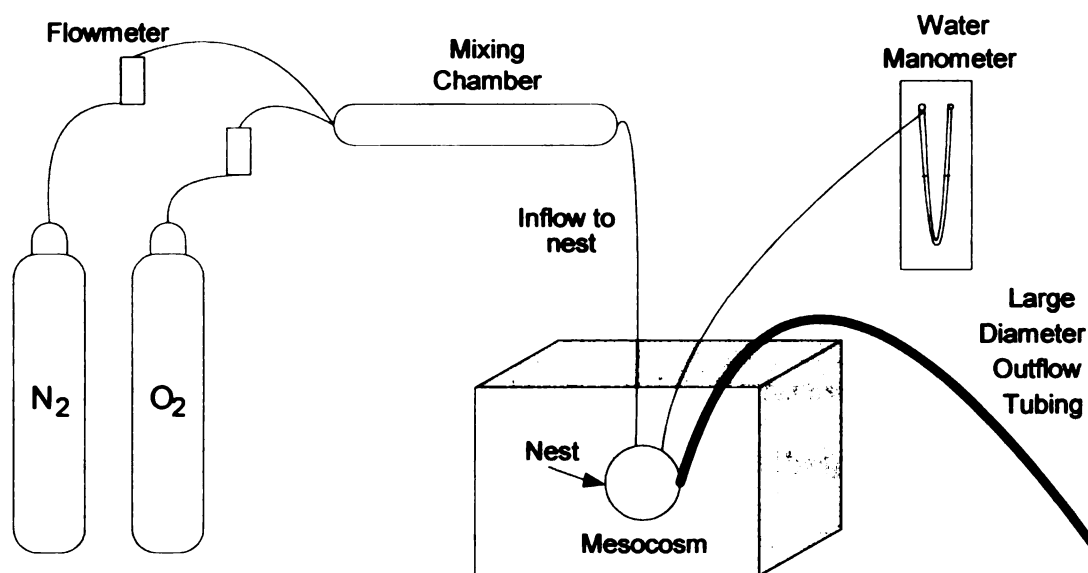


Figure 12. Diagram of experimental setup for O₂ evaluation.

Fiber-optic Oxygen Sensors:

For monitoring pO₂ in the pO₂ evaluation experiments, fiber optic O₂ sensors were used. These have the advantage that they do not alter the pO₂ measured (Klimant et al. 1995). The fiber-optic sensors were made of 5-meter lengths of multimode simplex optical fiber patchcord (Anixter, Grand Rapids, MI, USA, 100/140, ST.ST) coated at the active end with the fluorescent dye Pt(II)meso-tetra(pentafluorophenyl) porphine (Frontier Scientific, Utah, USA) following the method of Klimant et al. (1995). The active ends of the sensors were mounted inside syringes so that they

would be protected during insertion in the sand yet extended during measurements by using the syringe plunger (Figure 11). The pO_2 measurements were made using a Microx-TX3 excitation/measurement unit manufactured by Presens Precision Sensing GmbH, Germany and the corresponding software (OxyView, version TX3_v531). A thermocouple was arranged in tandem with each sensor to provide data on the temperature of the fluorescent dye, necessary for calculating pO_2 .

Sensor Calibration:

Each fiber-optic O_2 sensor was individually calibrated using a two-point calibration protocol. The first calibration point was the pO_2 of humid atmospheric air and was performed in a flask containing a moist towel. The pO_2 of an oxygen-free, 1% sodium sulfite solution served as the second calibration point. Rechecks of the calibration of numerous sensors demonstrated that the calibration did not change over time [as also reported by Klimant et al. (1995) and Gatti et al. (2002)].

Sensor locations:

Each experiment employed six oxygen sensors placed at defined coordinates within the sand mesocosm. One sensor was also placed in the center of the artificial nest to measure the nest pO_2 . At the beginning of each experiment, an initial pO_2 was recorded from each sensor. Flow from the O_2 and N_2 tanks was then initiated (and the fan activated) to produce an altered pO_2 within the model nest. Thereafter, pO_2 measurements were made at the six locations in the sand every min for the first hour and every 10 min thereafter (for ~4 hours).

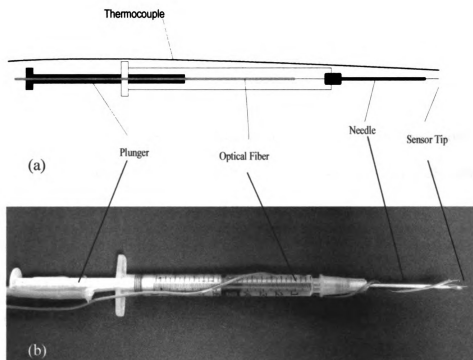


Figure 13: Diagram (a) and photograph (b) of a fiberoptic O_2 sensor mounted in syringe.

Experiment 2:

Using the identical experimental set-up a second set of experiments were conducted with a layer of wet sand ($0.1 \text{ m}^3 \text{ H}_2\text{O}/\text{m}^3$) placed at a depth of 20 to 40 cm in the mesocosm.

2.4.4~ Comparison to Beach-MPT predictions:

Temperature:

In all experiments the model's usefulness in predicting temperatures was evaluated by using characteristics of the sand mesocosm as inputs for a set of Beach-MPT simulations. Visual comparison between model predictions and mesocosm measurements provides the first measure of the model's accuracy. Secondly, when possible 95% confidence intervals around the mesocosm measurements and the model's predictions were calculated to determine if the intervals overlapped. In cases when the intervals did not overlap I determined the distance between the confidence intervals (example shown in Figure 12) and if this distance was less than 0.5°C the model accuracy was considered acceptable.

To further characterize the fit of the model I calculated the difference between the time-specific model predictions and the corresponding time-specific mesocosm measurements (mesocosm – model) and plotted the difference against time (diff/time plots). The slope of this relationship provides an index of how well the model predictions fit the mesocosm measurements over time. A positive slope demonstrates that over time the model increasingly underpredicted the mesocosm temperature, while a negative slope demonstrates that over time the model increasingly overpredicted the mesocosm temperature, and a slope of zero demonstrates no tendency for the model's accuracy to change over time. Only diff/time plots

reasonably fit by linear regression were used in this analysis, so situations in which the model initially overpredicted, then underpredicted, and then overpredicted near the end of the experiment were not considered. Plotting the slope against the distance between the sensor and the nest also explored whether the model's accuracy varied with nest proximity.

Oxygen Partial Pressure:

Around natural nests changes in pO_2 occur much more gradually than the rapid changes in pO_2 generated in the mesocosm trials. To assess the model under the conditions where it will be used, the model's predictions were compared to the mesocosm measurements after a steady-state condition was achieved. I considered *a priori* an average difference of 0.5 kPa between the model prediction and the mesocosm measurements to be excellent and a difference of 0.5 – 0.75 was considered acceptable. Any greater difference was deemed unacceptable.

2.5~ RESULTS

2.5.1~ *Temperature Experiments:*

Dry Sand Temperature Experiment:

Comparisons of the temperatures predicted by the model and those measured in the mesocosm measurements at each sensor location are shown in Figure 11. The temperature evaluation experiments using the dry sand mesocosm demonstrated reasonable agreement between the mesocosm measurements and the Beach-MPT predictions (Figure 12). The 95% confidence intervals for 5 of the 20 sensor locations showed consistent overlap. In only three cases when the 95% confidence intervals did not overlap was the difference between the intervals greater than 0.5° C (Table 4). There was a significant relationship between the mean slope of the diff/time plots and the distance between a sensor and the nest (Pearson correlation = - 0.931, $p = 7.8 \times 10^{-9}$). The mean slope was consistently negative, but the variation in the mean slope decreased considerably with increasing distance from the nest (Figure 13). This suggests that near the nest the model is more consistent at points further from the nest, but because the total temperature change also declined with distance it may be that the model is simply more accurate when temperature changes are small.

Damp Sand Temperature Experiment:

Experiments conducted using a 20-cm thick damp sand layer in the mesocosm between a depth of 20 and 40 cm showed considerable agreement between Beach-MPT model temperature predictions and mesocosm temperature measurements (Figure 14). The temperature predicted by the model, however, always exceeded the temperature measured in the mesocosm. The 95% confidence intervals for 10 of the 13 sensor locations showed consistent overlap. At an additional location the

difference between the confidence intervals was considered acceptable at $\Delta < 0.5^{\circ} \text{C}$. The confidence intervals at the last two sensor locations did not overlap and the difference between the confidence intervals was greater than 0.5°C (Table 5). There was no significant relationship between the mean slope of the diff/time plots and the distance between the sensor and the nest though the slope was consistently positive (Figure 15). The variation in the slope appeared to decline with distance from the nest, again suggesting that the model may be more accurate as one moves away from the nest (Figure 15). As one moves away from the nest the maximum change in sand temperature declines as well, which might suggest that it is not that the model is necessarily more accurate due to increasing distance from the nest, but is simply more accurate when predicting smaller temperature changes.

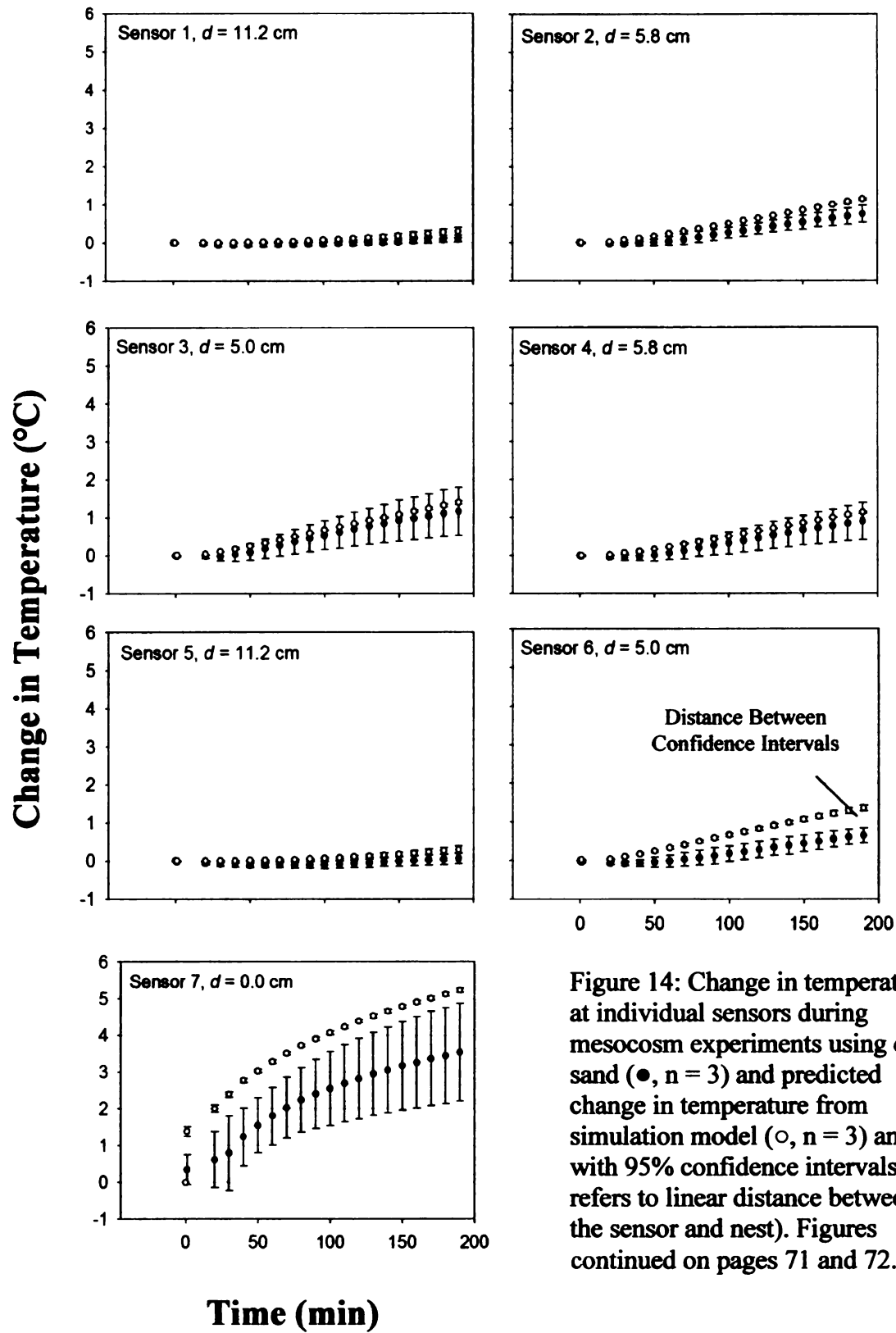


Figure 14: Change in temperature at individual sensors during mesocosm experiments using dry sand ($\bullet$, $n = 3$) and predicted change in temperature from simulation model ($\circ$, $n = 3$) and with 95% confidence intervals (d refers to linear distance between the sensor and nest). Figures continued on pages 71 and 72.

Figure 14, continued

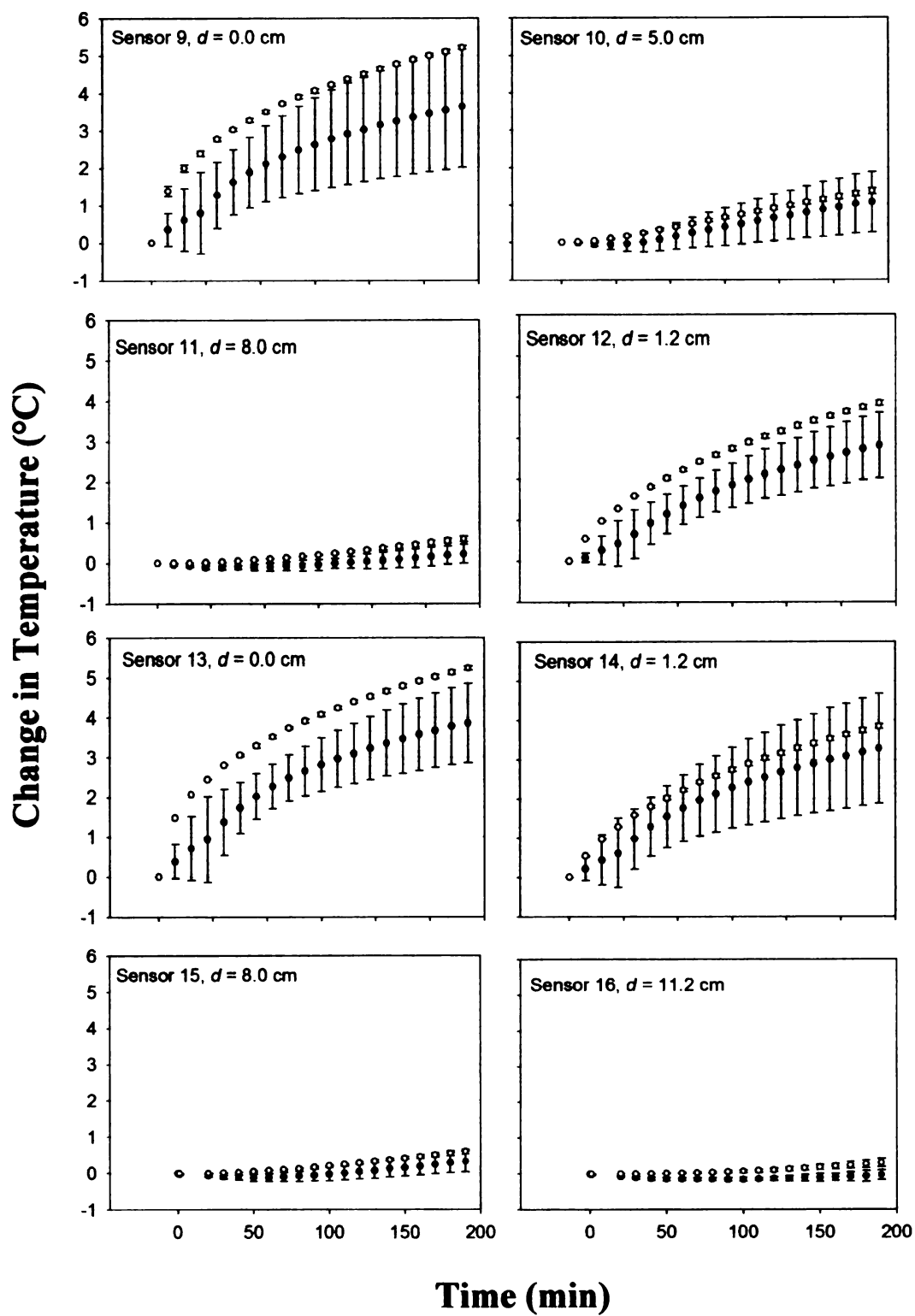


Figure 14, continued

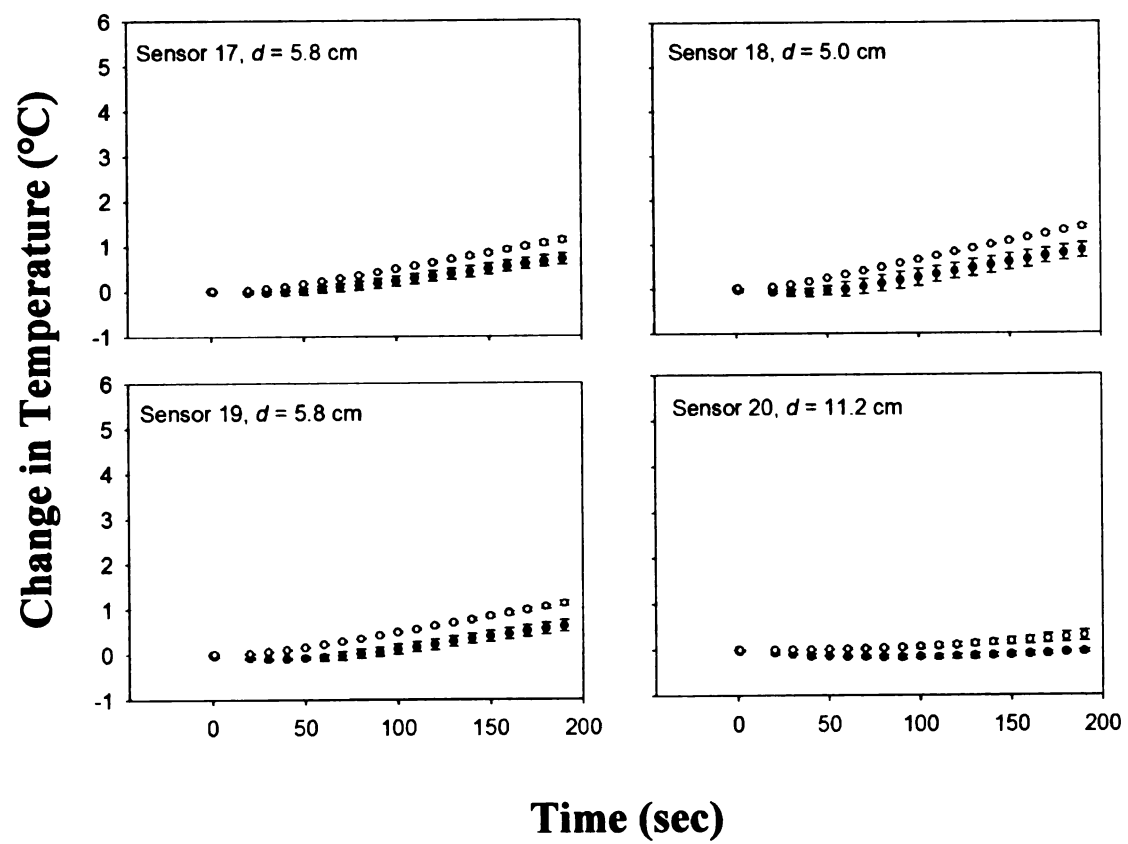


Table 4: Dry Sand Temperature Experiment. The coordinate location of each sensor, the linear distance from each sensor to the nest, and the maximum difference between the 95% confidence intervals for the model predictions and the dry sand mesocosm at each location. The coordinates for each sensor location are measured in centimeters. The x and y coordinates are measured from a single corner of the mesocosm and the z coordinate increases from the bottom of the mesocosm to the top. The max difference calculated as described on page 70. If the 95% confidence intervals overlap the difference is reported as zero.

Sensor	Coordinates (x, y, z)	Max Difference (°C)
1	0.15, 0.30, 0.15	0.07
2	0.25, 0.30, 0.15	0.13
3	0.30, 0.30, 0.15	0.00
4	0.35, 0.30, 0.15	0.00
5	0.45, 0.30, 0.15	0.07
6	0.15, 0.30, 0.30	0.43
7	0.20, 0.30, 0.30	0.69
9	0.40, 0.30, 0.30	0.57
10	0.45, 0.30, 0.30	0.00
11	0.15, 0.30, 0.40	0.11
12	0.25, 0.30, 0.45	0.36
13	0.30, 0.30, 0.40	0.65
14	0.35, 0.30, 0.40	0.00
15	0.45, 0.30, 0.40	0.09
16	0.15, 0.30, 0.45	0.16
17	0.25, 0.30, 0.45	0.00
18	0.30, 0.30, 0.45	0.33
19	0.35, 0.30, 0.45	0.32
20	0.45, 0.30, 0.45	0.21

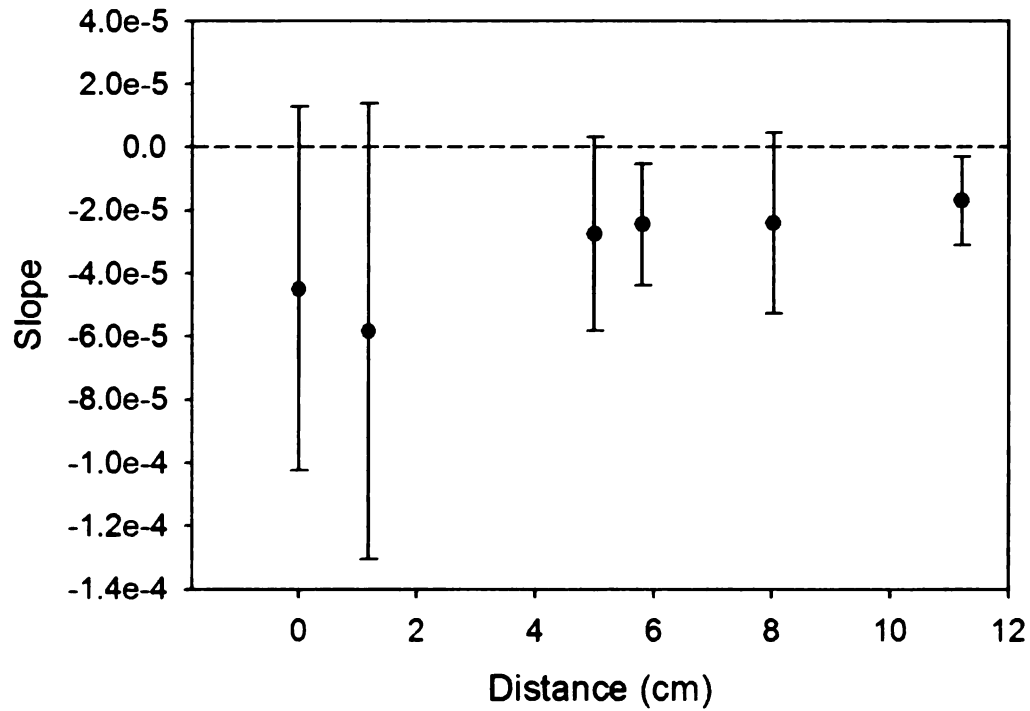


Figure 15: Relationship between a sensor's distance from the nest and the mean slope of the difference between model predictions and the dry sand mesocosm measurements plotted as a function of time (with 95% CI). Negative slopes show the model increasingly overpredicts the mesocosm temperatures. A slope of zero shows that the difference between the model predictions and the mesocosm temperatures remains constant over time.

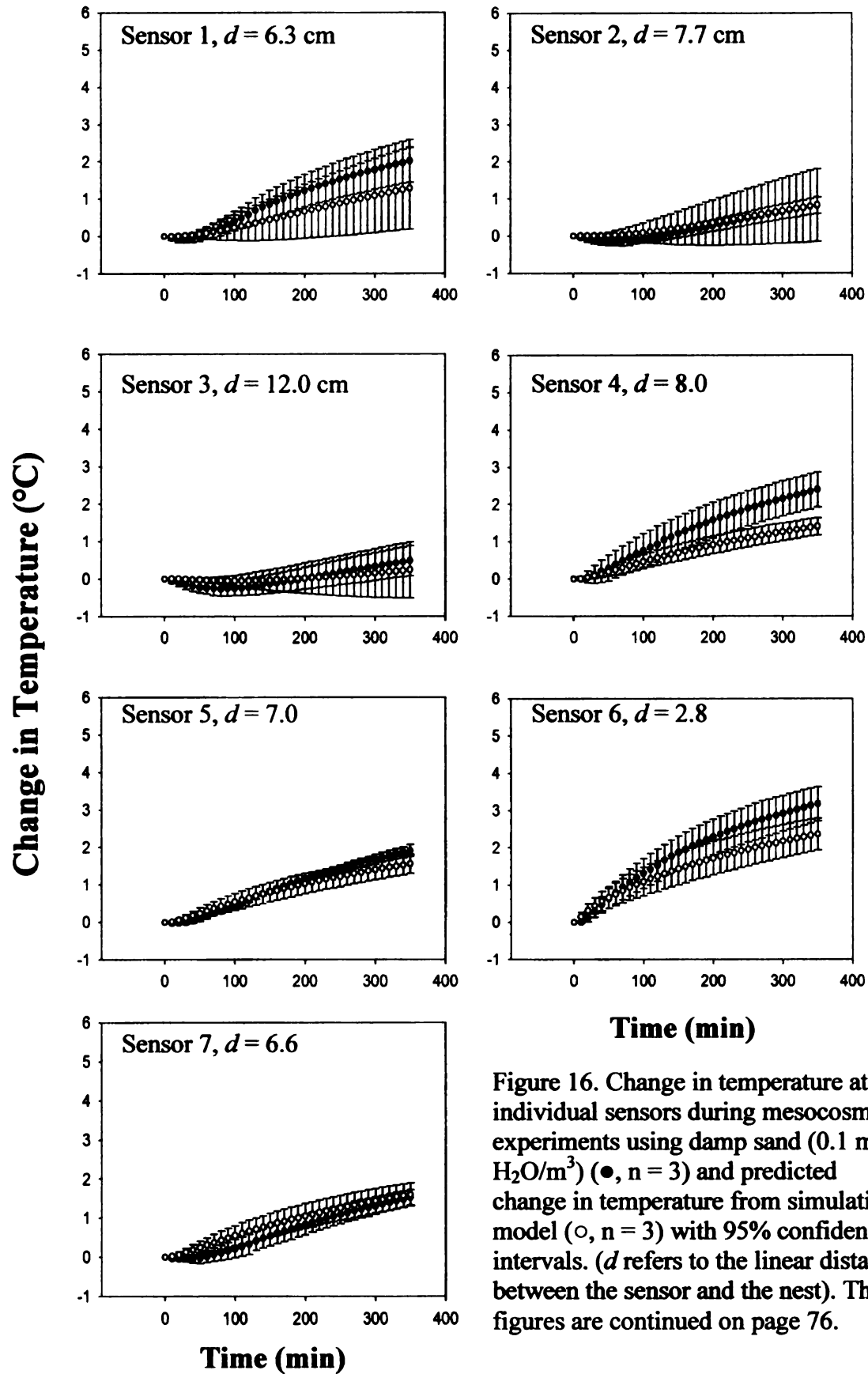


Figure 16. Change in temperature at individual sensors during mesocosm experiments using damp sand ($0.1 \text{ m}^3 \text{ H}_2\text{O}/\text{m}^3$) ($\bullet$, $n = 3$) and predicted change in temperature from simulation model ($\circ$, $n = 3$) with 95% confidence intervals. (d refers to the linear distance between the sensor and the nest). These figures are continued on page 76.

Figure 16, continued.

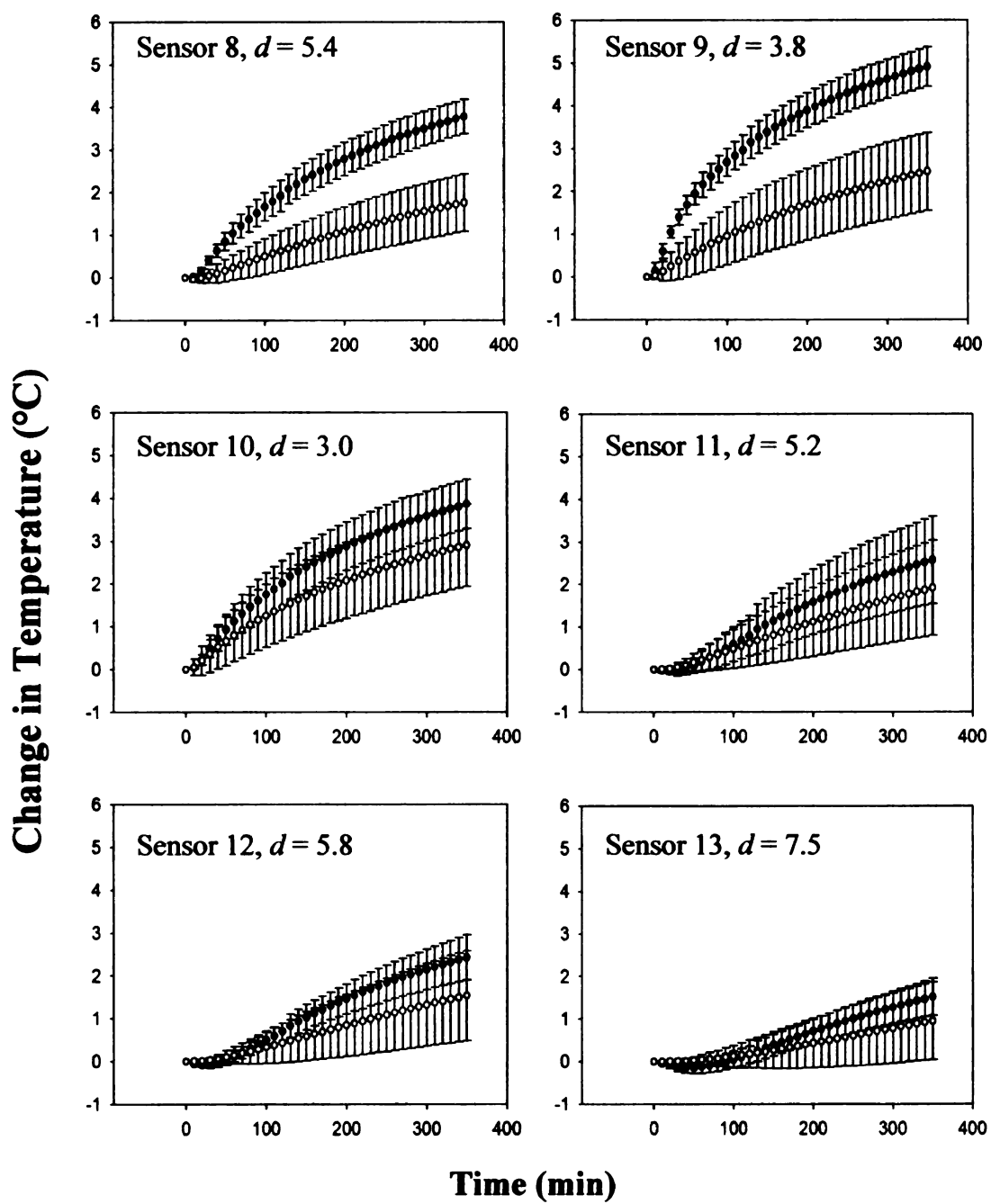


Table 5. Damp Sand Temperature Experiment. The coordinate location of each sensor, the linear distance from each sensor to the nest, and the maximum difference between the 95% confidence intervals for the model predictions and the damp sand mesocosm are shown at each location. The coordinates for each sensor location are measured in centimeters. The x and y coordinates are measured from a single corner of the mesocosm and the z coordinate increases from the bottom of the mesocosm to the top. The max difference is calculated as described on page 65. If the 95% confidence intervals overlap the difference is reported as zero.

Sensor	Coordinates (x, y, z)	Linear Distance to Nest (cm)	Max Difference (°C)
1	0.24, 0.28, 0.15	6.3	0.0
2	0.35, 0.38, 0.15	7.7	0.0
3	0.14, 0.32, 0.15	12.0	0.0
4	0.12, 0.31, 0.30	8.0	0.29
5	0.29, 0.47, 0.30	7.0	0.0
6	0.40, 0.22, 0.30	2.8	0.0
7	0.44, 0.39, 0.30	6.6	0.0
8	0.20, 0.24, 0.40	5.4	0.95
9	0.25, 0.22, 0.40	3.8	1.1
10	0.38, 0.28, 0.40	3.0	0.0
11	0.28, 0.29, 0.45	5.2	0.0
12	0.35, 0.31, 0.45	5.8	0.0
13	0.30, 0.39, 0.45	7.5	0.0

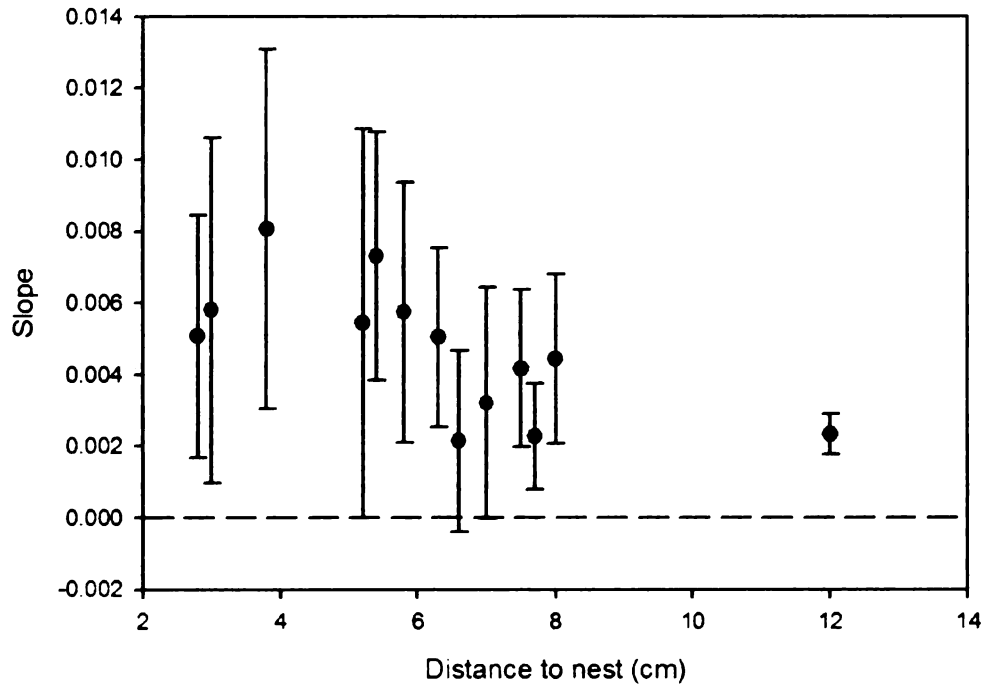


Figure 17: Relationship between a sensor's distance from the nest and the mean slope of the difference between model temperature predictions and the damp sand mesocosm measurements potted as a function of time (with 95% CI). Positive slopes show that over time the model increasingly underpredicts the mesocosm temperature. A slope of zero shows that the difference between the model predictions and the mesocosm temperatures remains constant over time.

2.5.2~ Oxygen Partial Pressure Experiments:

Dry Sand pO₂ Experiments:

The two experiments testing the Beach-MPT model's predictions of O₂ transport in dry sand showed close agreement between actual and predicted pO₂s (Figure 16 and Figure 17). There was reasonably good agreement during the period of rapid pO₂ decline, but more importantly there was good agreement after the pO₂ began to stabilize (time > 75 min). During the first experiment, four of the six sensor locations showed excellent agreement in the average difference between the model predictions and the mesocosm measurements, values being less than 0.5 kPa. The other two locations had a larger average difference, but were both acceptable ($\Delta < 0.75$ kPa). The pO₂ predicted by the Beach-MPT model was always lower than the pO₂ measured in the mesocosm. There was no significant relationship between a sensor's distance from the nest and the accuracy of the model's predictions (Pearson correlation = 0.18, $p = 0.73$). There was no relationship between sensor location (in terms of being below, beside, or above the nest) and the accuracy of the model's predictions either (Table 5).

In the second experiment, the agreement between the model and the mesocosm was excellent at two sensor locations with the difference between the model and the mesocosm values < 0.5 kPa (Figure 17). At the other four locations the differences were greater than 0.5 kPa. Of these, three locations were considered acceptable, and one was clearly unacceptable (Table 6). Again there was no significant relationship between sensor's distance from the nest and the agreement between the model predictions and the mesocosm measurements (Pearson correlation = -0.65, $p = 0.16$).

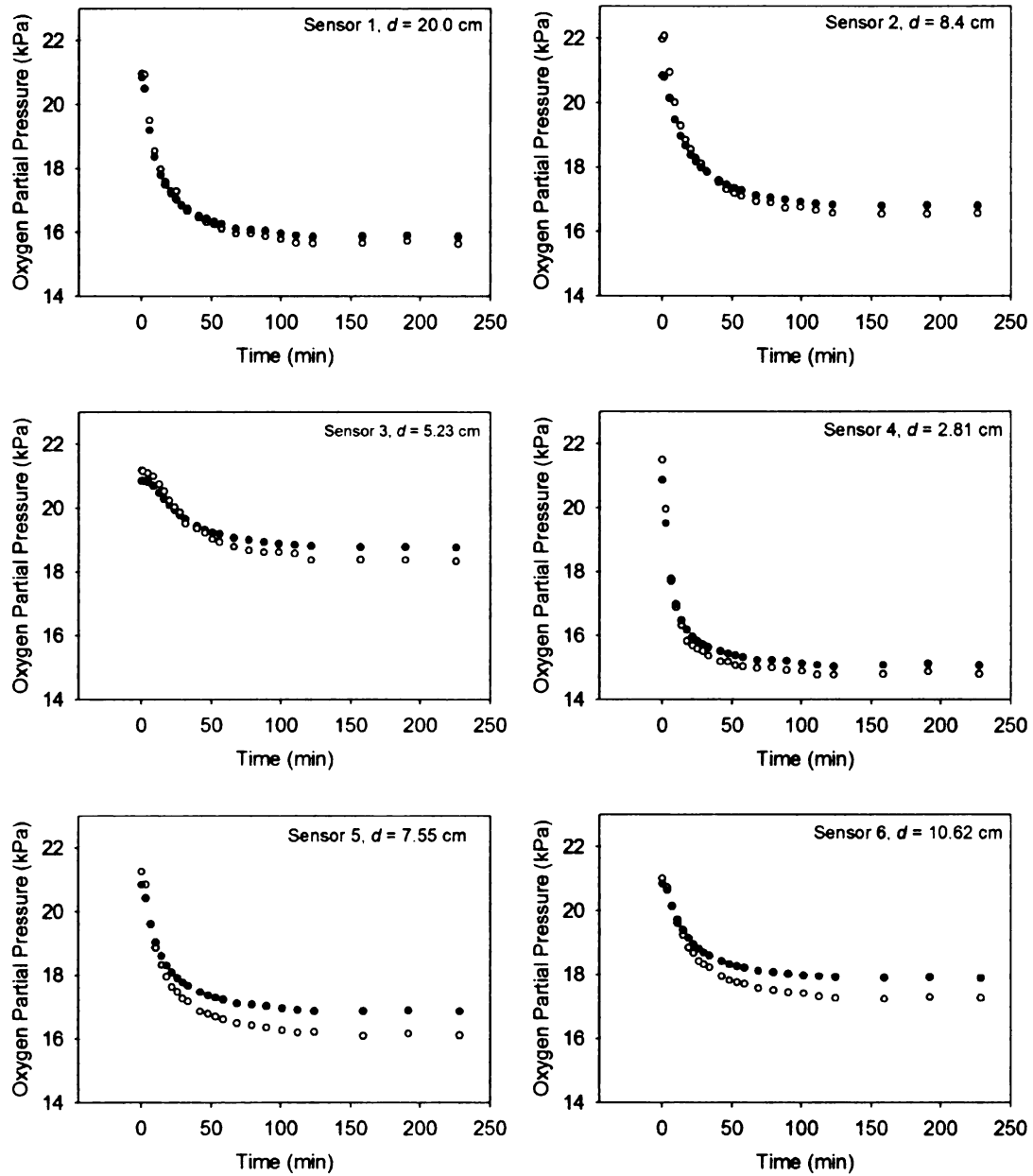


Figure 18. Dry Sand pO_2 Experiment 1. Comparison of pO_2 predictions from the Beach-MPT model (●) and measurements made in the dry sand mesocosm (○). Artificial nest internal $pO_2 \sim 13$ kPa. (d refers to linear distance between the sensor and nest).

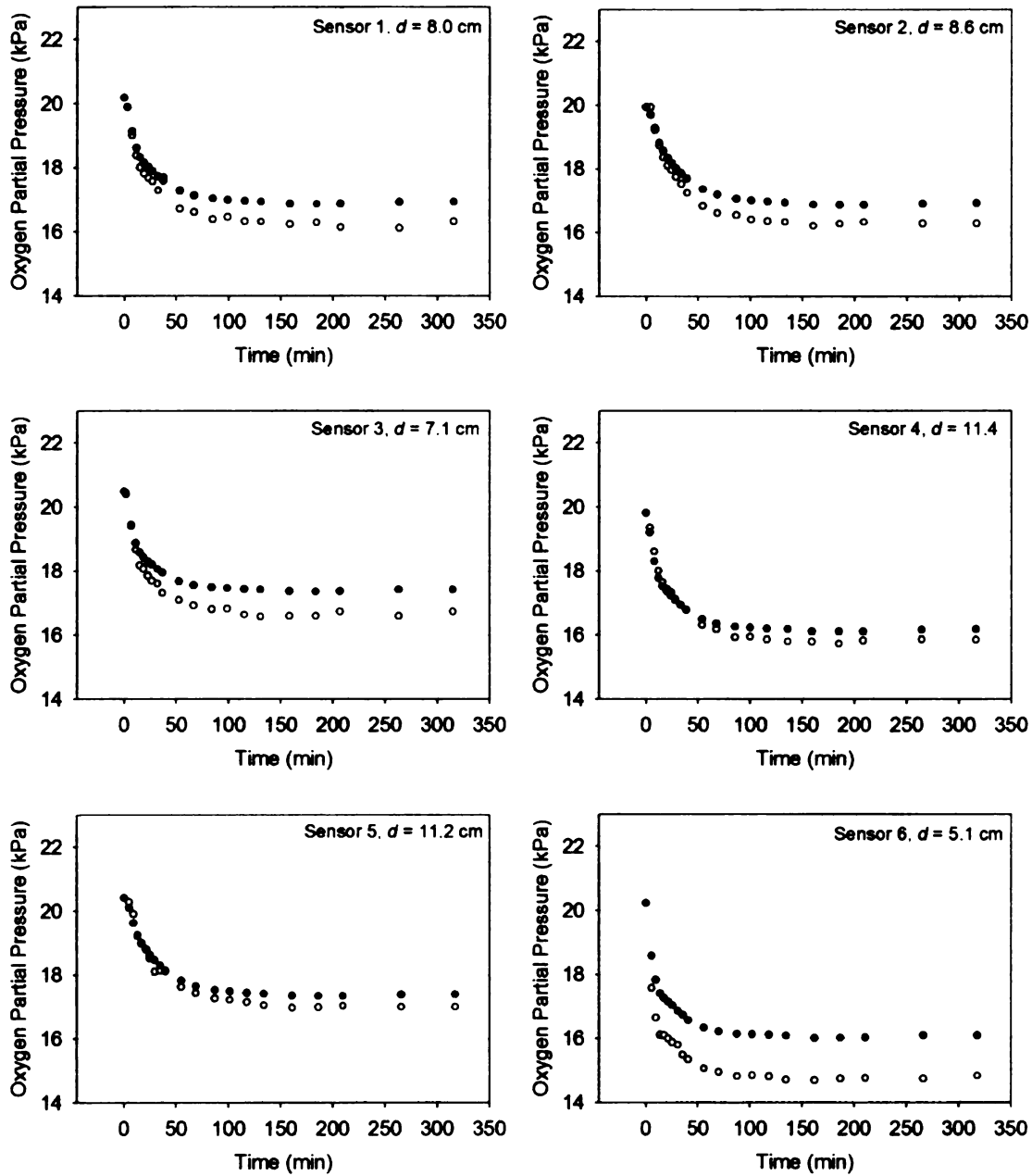


Figure 19: Dry Sand pO_2 Experiment 2. Comparison of pO_2 predictions generated by the Beach-MPT model (●) and pO_2 measurements made in the dry sand mesocosm (○). Artificial nest internal $pO_2 \sim 13.5$ kPa. (d refers to linear distance between the sensor and nest).

Table 6. Dry Sand pO₂ Experiments. Assessing the accuracy of the Beach-MPT model in (a) Dry Sand pO₂ Experiment 1 and (b) Dry Sand pO₂ Experiment 2. Provided are the linear distance (in cm) between each sensor and the nest and the mean difference in pO₂. The mean difference in pO₂ for each sensor was calculated as the mean difference between the pO₂ predicted by the Beach-MPT model and the actual mesocosm pO₂ measurement during the final 8 or 9 measurements in each experiment (time > 75 min).

(a)

Sensor	Linear distance to nest (cm)	Mean difference in pO ₂ (kPa, 8 measurements)
1	20.0	0.36
2	8.4	0.23
3	5.23	0.19
4	2.81	0.27
5	7.55	0.70
6	10.62	0.61

(b)

Sensor	Linear distance to nest (cm)	Mean difference in pO ₂ (kPa, 9 measurements)
1	8.0	0.74
2	8.6	0.64
3	7.1	0.33
4	11.4	0.60
5	11.2	0.33
6	5.1	1.31

Damp Sand pO_2 Experiments

In the three experimental trials testing the accuracy of the Beach-MPT model's predictions of O_2 transport in a mesocosm containing a 20-cm thick layer of damp sand, there was considerable difference between the predicted and actual pO_2 values (Figure 18). All six sensors showed roughly the same error at the end of the experimental period (2.0 – 3.0 kPa, Table 7). There was no relationship between a sensor's distance from the nest and the degree to which it differed from the model predictions (Pearson correlation = 0.12, $p = 0.82$).

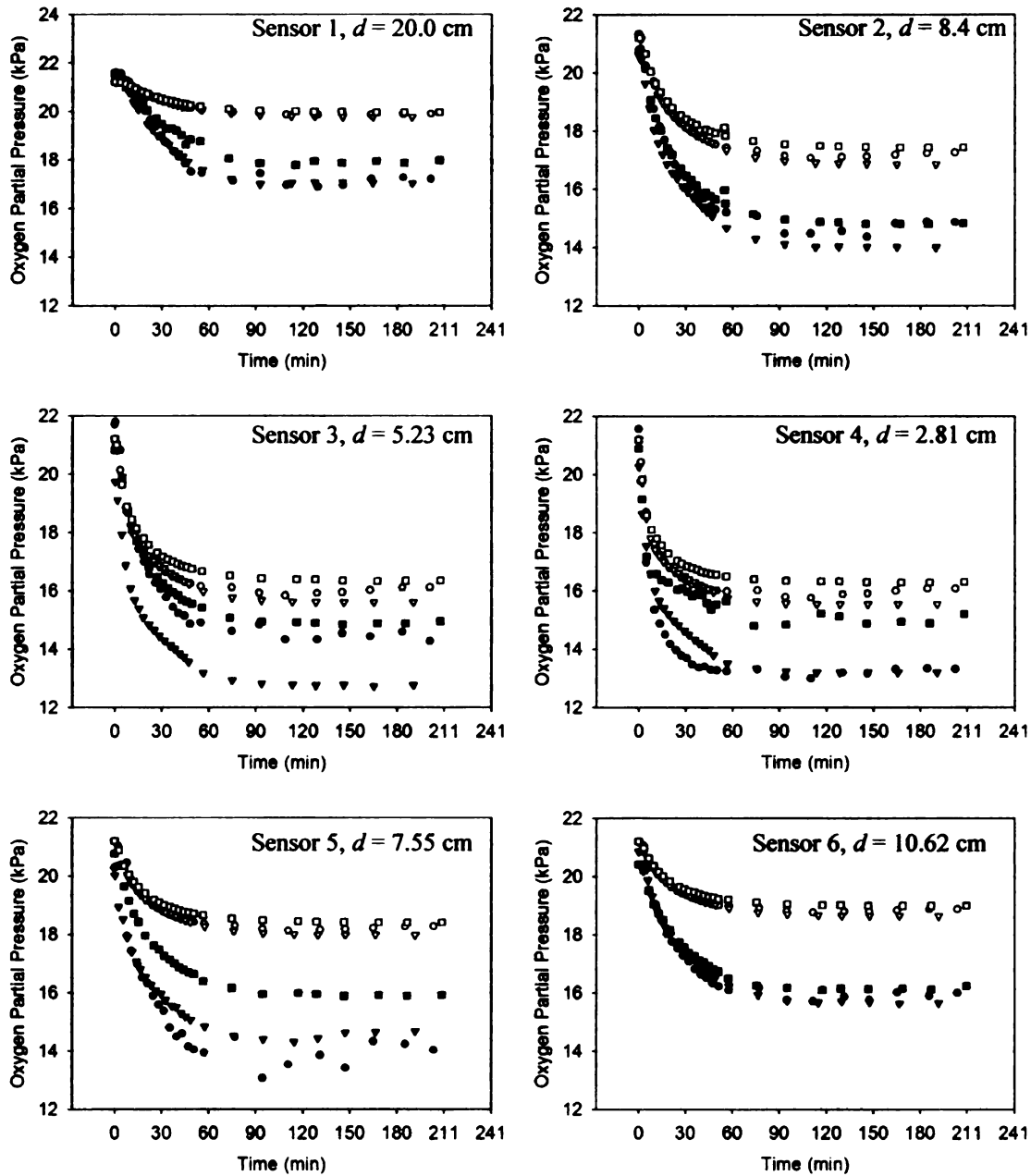


Figure 20. Comparison of pO_2 predictions generated by the Beach-MPT model ($\circ, \Delta, \square$) and pO_2 measurements made in the damp sand mesocosm ($\bullet, \blacktriangledown, \blacksquare$). Sensor coordinates are also shown. Mean pO_2 in nest was 11.4 kPa. The values in parentheses are the sensor coordinates. The x and y coordinates are measured from a single corner of the mesocosm and the z coordinate increases from the bottom of the mesocosm to the top.

Table 7: Damp Sand pO₂ Experiments. Provided are the coordinates of each sensor (in cm), the linear distance from each sensor to the nest (in cm), and the mean difference in pO₂. The mean difference in pO₂ was calculated for each sensor as the mean difference between the pO₂ predicted by the Beach-MPT model and the actual mesocosm pO₂ measurement after the pO₂ levels were roughly constant (the 8 measurements made after each experiment was run ~75 min). The x and y coordinates are measured from a single corner of the mesocosm and the z coordinate increases from the bottom of the mesocosm to the top.

Sensor	Coordinates (x, y, z)	Linear distance to nest (cm)	Mean pO ₂ difference (kPa, n = 8)
1	0.30, 0.04, 0.15 (below nest, in dry sand)	20.0	2.52
2	0.44, 0.18, 0.30 (beside nest, in damp sand)	8.4	2.67
3	0.36, 0.44, 0.30 (beside nest, in damp sand)	5.23	1.9
4	0.38, 0.30, 0.40 (above nest, dry/damp transition)	2.81	2.55
5	0.38, 0.18, 0.40 (above nest, dry/damp transition)	7.55	3.44
6	0.20, 0.40, 0.45 (above nest, in dry sand)	10.62	2.91

2.6~ DISCUSSION

Simulation models offer the opportunity to explore and test ideas by creating an artificial, but realistic environment in which to experiment. The results generated by simulation models must be validated under controlled conditions. In this study I demonstrated that the Beach-MPT model is able to accurately predict temperature and pO₂ gradients that develop around artificial nests.

2.6.1~ Temperature Evaluation Experiments:

Dry Sand

The dry sand temperature evaluation experiments demonstrated that the model accurately predicted the temperatures at most thermocouple locations. The correspondence was quite good, with 17 of the 20 locations exhibiting overlapping confidence intervals or confidence intervals that differed by less than 0.5° C (Table 3). Only three locations (7, 9, and 13) had confidence intervals that differed by more than 0.5° C. At these three locations the thermocouples were placed in direct contact with the nest surface and I suspect the lack of agreement at these locations is a consequence of this. When sensors are further from the nest and their temperature more dependent upon heat transfer processes in the sand, the model appears to be accurate. It is under these conditions that the model will be used, and therefore I argue that the lack of agreement at locations 7, 9, and 13 detracts little from the model's overall usefulness.

Damp Sand

The damp sand evaluation experiments also showed a close correspondence between the predicted and actual sand temperatures. Eleven of the 13 thermocouple

locations exhibited overlapping confidence intervals or confidence intervals that differed by less than 0.5° C. The errors at locations 8 and 9 may be due in part to the relatively large temperature changes at these sensor locations, with a mean change in temperature at sensors 8 and 9 of 3.8° C and 4.9° C in six hours, respectively. Nest temperature changes will not occur at such high rates in natural nests so these results may illustrate the model's limitations, but should not discount the model entirely. The consistent overlap of the model predictions and mesocosm measurements suggests that the model captures the important aspects of heat transfer and as a result is very capable of predicting heat transfer in damp sand.

2.6.2~ Oxygen Partial Pressure Evaluation Experiments:

Dry Sand

The pO₂ evaluation experiments using dry sand demonstrate that the Beach-MPT model can accurately predict gas transport as well. Both experiments demonstrate that the difference between the model and the mesocosm measurements was typically acceptable and often excellent (Table 5 and Table 6). Only once was the difference between the mesocosm measurements and the model predictions unacceptable by the standards specified. The unacceptable result is not explained by the sensor's location relative to the nest, though inaccurate sensor placement is possible. While the model is sufficiently accurate, it is important to note that in all cases it overpredicted the pO₂ values. The consistent overprediction suggests that there is a systematic error in some aspect of the model. This could be something as simple as an inaccurate specification of the sand porosity or a more fundamental error in the structure of the governing equation for gas transport. Whatever the error, its

consequence appears quite small and the model is consistently accurate in predicting gas transport in dry sand.

Damp Sand

The pO_2 evaluation experiments using damp sand showed much less agreement between the model and mesocosm measurements than the other evaluation experiments. The model consistently overpredicted the pO_2 in the mesocosm by 2 to 3 times. The degree to which the model and the mesocosm data differed was not a consequence of the distance between the sensor and the nest, the fact that a sensor was above or below the nest, or the water content of the sand layer in which the sensor was located. It seems that the damp sand layer simply did not impede gas transfer as much as the model predicted.

The lack of agreement suggests that there are inaccuracies in the mesocosm experiments or the model's gas transport equations. Alternatively the model might not include all the parameters which are important for predicting gas transfer in damp sand. The fact that the model accurately predicts transport processes under other conditions suggests that the mesocosm experiments are adequately controlled and accurate. In addition, the accurate prediction of gas transport in dry sand suggests that the basic gas transport equations are well constructed. Given that the model accurately predicts heat transfer in damp sand and accurately predicts gas transport in dry sand suggests that inaccuracy stems not from inaccuracies in the water flow or gas transport portions of the model, but from the interaction of the two. The mostly likely culprit is the tortuosity function. This function relates the amount of water-filled pore-space to the tortuousness of the diffusion path for a given gas molecule.

Tortuosity is not directly measured, but there are several methods of predicting tortuosity from measurements of other parameters including the sand water content and the total porosity. In the original simulations, I adopted the widely used theoretical method of calculating tortuosity from Millington and Quirk (1961), but beyond its widespread use and general acceptance there are no additional reasons to assume this method will accurately predict the tortuosity in the sand mesocosm. To explore whether an alternative method of calculating tortuosity might improve the model's predictions, I ran the model using an alternative tortuosity function from Penman (1940),

$$\tau = 0.66\theta \quad (2.22)$$

where θ is the sand water content (m^3/m^3). This method is also widely used and mathematically much simpler than the Millington and Quirk (1961) function.

The results suggest that using the Penman tortuosity function narrows the gap between the model's predictions and the mesocosm measurements, but the model remains relatively inaccurate at predicting gas transfer involving a damp sand layer (Table 8). The damp sand evaluation experiments consistently overpredicted the pO_2 values, in the same manner as the dry sand experiments, but to a much greater degree. While the errors associated with the damp sand experiments may be a direct consequence of the model's ability to predict transport in damp sand it is also possible that they errors do not represent a poor ability to predict transport in damp sand, but a reduced ability to predict transport through layered sands. The model might exhibit

Table 8: Consequences of the tortuosity function on pO_2 . Provided is the mean difference in the pO_2 at each sensor location during the damp sand experiment when two different methods of calculating the sand tortuosity (Millington and Quick (1961) or Penman (1940)) were used. The mean difference in pO_2 was calculated for each sensor as the mean difference between the pO_2 predicted by the Beach-MPT model and the actual mesocosm pO_2 measurement after the pO_2 levels were roughly constant (the 8 measurements made after each experiment was run ~75 min).

Sensor	Mean Difference in pO_2 (kPa) Millington and Quick (1961)	Mean Difference in pO_2 (kPa) Penman (1940)
1	2.52	1.35
2	2.67	1.8
3	1.9	1.11
4	2.55	0.45
5	3.44	1.66
6	2.91	1.75

equally poor predictions if instead of including a damp sand layer, a layer of coarse sand was added to the mesocosm. To tease apart the affects of damp sand from those of sand layering it would be necessary to run several experiments in which the entire mesocosm was filled with damp sand. If the model accuracy increased under such conditions one would concluded that the model accurately predicts gas transport in damp sand, but poorly predicts gas transport in layered sands. To date, such experiments have not been conducted.

The errors observed in the damp sand/ pO_2 experiments may also demonstrate that an important real-world parameter has not been included in the model. Because

of the highly controlled nature of the mesocosm, it is difficult to speculate what the neglected parameters might be.

The four evaluation experiments described in this chapter suggest that the Beach-MPT model is quite capable of predicting heat and gas transport in dry sands and heat transport in sand profiles containing a damp sand layer. This is quite impressive given that the model is based strictly upon transport principles and was not fitted or calibrated to the mesocosm. The results of the damp sand pO_2 experiments are less reassuring. While the model captures the general trend in sand pO_2 under such conditions, it is quantitatively inaccurate in predicting gas transport in sand profiles containing a damp sand layer. This suggests that in its current form the Beach-MPT model can be used to generate quantitative predictions with regards to heat and gas transfer under dry conditions and heat transfer under damp conditions. However, the model should be used cautiously when attempting to predict gas transfer in damp sands and under such conditions the model's pO_2 predictions should be viewed as capturing general trends rather than precise pO_2 values. Despite the current limitations, the Beach-MPT model is clearly a new and powerful tool for assessing the potential and very practical repercussions of habitat change on sea turtle nests. In addition, by manipulating various nest parameters will allow researchers to explore more theoretical consequences of clutch size, nest depth, or even nest crowding on nest microclimates.

CHAPTER 3

The Consequences of Nest Site Characteristics for the Microclimates within Sea Turtle Nests: A Simulation Study

3.1~ INTRODUCTION

The conditions within the nests of sea turtles are the expression of a complex set of interactions among the physical characteristics of the nest site and the biotic characteristics of the developing clutch (Maloney et al. 1990, Wallace et al. 2004). The biotic half of this story has been reasonably well told through laboratory and field studies examining the effects of temperature, moisture, and respiratory gases on turtle embryos (Tracy et al. 1978, Ackerman 1981, Kam 1993), but comparatively little is known about the physical characteristics that influence the transport of heat, water, and respiratory gases to the embryos (Mortimer 1990). As a consequence, our understanding of the interaction between the physical and the biotic, and our understanding of the nest microclimate remains incomplete.

In a recent study (Chapter 1) I found that the minimum nest pO_2 in loggerhead turtle nests varies considerably among nests and is unrelated to clutch size. The lack of relation to clutch size suggests that the variability in pO_2 cannot be explained by variability in nest metabolism, but rather represents variability in the rate of O_2 transport to nests at different sites. This variability could be the consequence of differences in nest morphology (e.g., depth to the top and bottom of nest, nest width),

in nest temperature, sand porosity, sand water content, biotic characteristics of the sand such as microbial populations or root densities, or tidal pumping due to nest location.

Exploring all these possibilities empirically, while important for successful sea turtle conservation, is unreasonable given constraints on time and money. This is especially true given the likelihood that many of these possibilities will actually have limited impacts on the nest pO_2 . Simulation modeling provides the opportunity to narrow this list of possibilities by quickly simulating, for example, the consequences of different nest morphologies or sand porosities. Subsequent, empirical work can then focus on the most promising areas of study.

To this end, I developed a computational model (Beach-MPT) which simulates heat, water, and gas transport in and around turtle nests, and I report here on a set of simulations which make use of this model. I begin by describing two sensitivity analyses which investigated the relative importance of biotic and abiotic parameters to the variability in predictions of nest pO_2 and nest temperature. Such analyses suggest which parameters must be measured accurately during empirical studies, as well as parameters that might be most sensitive to human intervention, both positive (e.g., conservation) and negative (e.g., habitat alteration).

In my second set of simulations, I used the model to consider two scenarios that are of significant concern in the area of sea turtle conservation: beach nourishment and nest crowding. Beach nourishment has arisen as a potential threat to sea turtles in the United States because of pervasive erosion along the Atlantic and Gulf coasts. Beach nourishment involves either pumping sand from offshore sand

deposits or trucking sand from upland areas, and then using heavy machinery to rebuild a beach. Over the past 15 years, considerable evidence has accumulated that nourished beaches are far different from the original beaches they replace (Meylan et al. 1995). Water-holding capacity, porosity, thermal conductivity, and albedo have all been shown to differ following nourishment (Steinitz et al. 1998). Empirical studies of the implications for sea turtle nesting and nest survival have yielded mixed results. Some studies have found that nourished beaches negatively impact nest construction and embryonic survival (Crain et al. 1995, Trindell et al. 1998), whereas others have found little change in nest success (Davis et al. 1999). By clarifying how the physical characteristics of a nest site influence the nest microclimate, the Beach-MPT model can help us develop a systematic understanding of the effects of beach nourishment on sea turtle development.

The consequences of nest crowding, the second scenario, have long been a concern in the construction of hatcheries. Often managers have assumed that spacing nests at least 0.5 meter apart is sufficient to eliminate nest interactions based on the simple, single-nest model of Ackerman (1977). Whether this spacing actually eliminates the interactions between two or more nests is unknown. The consequence of nest crowding during arribadas (the coordinated, mass-nesting events exhibited by olive-ridley sea turtles) or on densely nested beaches is unclear. Recent empirical work suggests that nest crowding may influence nest microclimates (Honarvar et al. 2007). However, while the empirical work is still in its early stages, the Beach-MPT model can be used to suggest the potential consequences of nest crowding. As

empirical data becomes available, comparisons with the model's predictions will help to clarify our understanding of the system.

I conclude with a third set of simulations which consider how well the model might predict nest pO_2 changes that occur during development. The simulation experiments I have already described focus exclusively on a few days at the end of incubation when the embryonic metabolism is at its highest and nest conditions may therefore be at their most extreme (highest embryonic metabolism and lowest nest pO_2). Beach-MPT was originally evaluated (see Chapter 2) with a focus on those days at the end of incubation and the model therefore would be considered most accurate during those days. However, to explore how well the model could predict nest pO_2 s over the entire developmental period, I simulated ~50 days of development and compared the results to actual nest pO_2 s.

3.2~ METHODS

3.2.1~ Sensitivity Analysis:

To explore the relative influence that clutch metabolism, sand porosity, sand water content, nest depth, rainfall, and sand microbial respiration have on late-incubation nest pO₂ and nest temperature, two sensitivity analyses were conducted using the Beach-MPT model. Parameters in the Beach-MPT model were individually varied using the values shown in Table 9, and the resultant change in nest pO₂ or nest temperature was recorded. For each parameter value a sensitivity index of late-incubation nest pO₂ or nest temperature was calculated using the following equation,

$$S = \left| \frac{\frac{R_A - R_o}{R_o}}{\frac{P_A - P_o}{P_o}} \right| \quad (3.1)$$

in which R_o is the pO₂ or temperature predicted by the model using the original parameter value, while R_A is the pO₂ or temperature predicted when the original parameter value is increased or decreased. In the denominator, P_o represents the original parameter value and P_A represents the new parameter value. S is the sensitivity index. For simplicity of interpretation, parameters such as sand microbial respiration, sand porosity, and sand water content, were applied uniformly throughout the sand profile and not as a function of depth. The sensitivity index provides a means of comparing how much changes in individual parameters alter nest pO₂ and temperature, when the absolute value of each parameter differs.

3.2.2~ Consequences of Beach Renourishment and Nest Crowding

To explore the consequences of beach nourishment using the Beach-MPT model, two sets of simulations were conducted. The first set considered the

consequences of the water holding capacity; nourished beaches tend to have increased water holding capacity (Steinitz et al. 1998), and the effect of this increased capacity on the pO_2 and temperature gradients in and around a turtle nest was explored. The parameter values for these simulations are shown in Table 10. Beach nourishment may also reduce sand porosity and this effect was explored in a second set of simulations in which the sand porosity was reduced ~10% (Table 11). Because the temperature results were highly sensitive to the initial temperature conditions, I conducted the simulations with two different initial conditions. The cooler simulations had an initial temperature gradient which ranged from 25° C at the bottom of the profile to 27° C at the surface. The warmer simulations had an initial temperature gradient which ranged from 27° C at the bottom of the profile to 37° C at the surface. All results were presented as vertical transects through the nest and represented conditions near the end of development.

The consequence of nest crowding on nest pO_2 was first explored by including two nests in the Beach-MPT model. In separate simulations the distance between the nests was varied from 0.3 meters to 0.5 meters, and then 1 meter. The nest pO_2 s resulting from each arrangement were compared to identify the potential consequences of nest crowding. To further characterize the impacts of nest crowding, the nest pO_2 values resulting from nest densities of 4 and 9 nests per square meter were also simulated. The physical parameters used in all nest crowding simulations are shown in Table 11.

3.2.3~ Simulation of Development

To simulate developmental changes, the Beach-MPT model was independently parameterized using the physical measurements from four nests at Sapelo Island, GA shown in Table 12. Fifty days of development were simulated for each nest. In these simulations the nest metabolic rate was assumed to increase during development according to the logistic equation from Ackerman (1981),

$$V_{O_2} = \frac{125}{1 + e^{-0.16(t-37.0)}}$$

where V_{O_2} is the oxygen consumption rate ($\text{cm}^3 \text{O}_2/\text{day}$) and t is the day of incubation.

Table 9. Parameter values used in the Beach-MPT sensitivity analyses.

Parameter	Values	Comments
Sand Porosity (m^3/m^3)	0.35, 0.40, 0.45	Typical porosity values of beach sand are in this range (personal obs.)
Sand Water Content ($\text{m}^3 \text{H}_2\text{O}/\text{m}^3$)	0.03, 0.09, 0.15	Typical beach sand water content (personal obs.)
Rainfall Rate ($\text{cm H}_2\text{O}/\text{hr}$ for 1 hour)	0.0, 2.5	Typical rainfall duration and rate along Georgia coast (GCE-LTER Data Portal, 2006)
Depth to Top of Nest (m)	0.2, 0.4, 0.6	Typical depths to the top of turtle nests (Chapter 1)
Sand Microbial Respiration ($\text{cm}^3 \text{O}_2/\text{m}^3\text{s}$)	0.0, 0.16, 1.2	Microbial respiration rates in beach sands have been measured in this range (Urban-Malinga and Opalinski 1999)
Sand Thermal Conductivity ($\text{W}/\text{m K}$)	6.8, 8.8, 10.8	The thermal conductivity of quartz is $8.8 \text{ W}/\text{m K}$ (Krieth and Bohn 1993) 6.8 and 10.8 are $\pm \sim 25\%$ the quartz value.
Clutch Size (eggs)	50, 100, 150	Typical clutch size values are in this range. (Miller 1997 and this study Chapter 1)

Table 10. Parameter values used in Beach-MPT simulations exploring the consequences of beach renourishment. Because beach nourishment may lead to increased sand water content or decreased sand porosity both situations were simulated using the parameters listed here.

Parameter	Increased Sand Water Content Simulation	Decreased Porosity Simulation	Comments
Sand Porosity (m^3/m^3)	0.4	0.35	Reasonable reduction in beach sand porosity following nourishment (Crain 1995).
Sand Water Content ($\text{m}^3 \text{H}_2\text{O}/\text{m}^3$)	0.1	0.03	Sand water contents in natural and nourished beaches are in this range. Rimkus and Ackerman (1995)
Nest Metabolism ($\text{cm}^3 \text{O}_2/\text{hour}$)	390	390	Standard value for nests containing 100 eggs. (Ackerman 1977)
Depth to Top of Nest (m)	0.4	0.4	This study, Chapter 1
Nest Radius (m)	0.1	0.1	Represents an average nest radius. (Ackerman 1977, and this study, Chapter 1)

Table 11. Parameter values used in Beach-MPT simulations exploring the consequences of nest crowding.

Parameter	Value	Comments
Sand Porosity (m^3/m^3)	0.4	A reasonable sandy beach porosity (This study, Chapter 1)
Sand Water Content ($\text{m}^3 \text{H}_2\text{O}/\text{m}^3$)	Linear increase from 0.05 at upper surface to 0.11 at bottom of the profile	Realistic water content gradient in a sandy beach (Ackerman 1997)
Nest Metabolism ($\text{cm}^3 \text{O}_2/\text{hour}$)	390	Reasonable estimate of the metabolic rate for a nest containing 100 eggs. (Ackerman 1977)
Depth to Top of Nest (m)	0.4	Average depth of loggerhead turtle nest (This study, Chapter 1)
Nest Radius (m)	0.1	Represents an average nest radius. (Ackerman 1977, and this study, Chapter 1)

Table 12. Data on four nests studied at Sapelo Island (Chapter 1), used to parameterize Beach-MPT simulations testing the model's ability to predict pO_2 changes through the entire incubation period. During the summer of 2006 measurements of the depth to the top and bottom of the loggerhead nests along with measurements of nest width, sand water content, sand porosity, and nest pO_2 were made on Sapelo Island, GA. Detailed methods are described in Chapter 1. The nest depth refers to the distance from the sand surface to the top of the nest, while nest height refers to the distance between the top and the bottom of the nest. The nest width was measured horizontally at the widest portion of the nest.

Nest	Clutch Size (eggs)	Mean Sand Porosity ($\pm$ S.E.) (m^3/m^3)	Mean Sand Water Content ($\pm$ S.E.) ($m^3 H_2O/m^3$)	Nest Width (m)	Nest Depth (m)	Nest Height (m)
10	115	0.47 (± 0.004) n = 9	0.07 (± 0.01) n = 9	0.2	0.3	0.24
11	109	0.49 (± 0.007) n = 9	0.04 (± 0.005) n = 9	0.28	0.17	0.33
19	101	0.47 (± 0.01) n = 9	0.08 (± 0.018) n = 9	0.23	0.26	0.38
23	103	0.48 (± 0.007) n = 9	0.07 (± 0.005) n = 9	0.26	0.3	0.33

3.3~ RESULTS

3.3.1~ Sensitivity Analysis

Late-Incubation Nest pO₂:

The sensitivity analysis demonstrates that both increases and decreases in nest metabolism had equivalent, but opposite effects on the nest pO₂ (Table 13). This is not the case with alterations in sand water content where the nest pO₂ is more sensitive to increases in sand water content. The same general pattern is observed when the porosity was varied, with the nest pO₂ more sensitive to decreases in porosity. The nest pO₂ was relatively insensitive to rainfall or differences in rainfall rate over the rates and duration (1 hour) simulated. Relative to the other parameters examined, the nest pO₂ appeared moderately sensitive to sand microbial respiration and nest depth, but the sensitivity did not depend on whether either parameter was increased or decreased. Ranking the sensitivity of the nest pO₂ to each parameter gave the following order from most influential to least: sand water content, nest metabolism, sand porosity, sand microbial respiration, and rainfall.

Late-Incubation Nest Temperature:

The second sensitivity analysis showed that the nest temperature was not nearly as sensitive to parameter variation as the nest pO₂ (Table 14). Increasing or decreasing nest metabolism had equivalent, but minor effects on the nest temperature. The nest temperature was also quite insensitive to changes in sand water content, the rate of sand microbial respiration, and the thermal conductivity of the sand solids. Changes in nest depth had minor effects on nest temperature, but the nest temperature was most sensitive to variation in sand porosity. Ranking the parameters in terms of

their relative influence upon nest temperature from most to least influential results in the following list: sand porosity, nest depth, nest metabolism, sand water content, thermal conductivity of the sand solids, microbial respiration, and rainfall.

3.3.2~ Consequences of Beach Nourishment and Nest Crowding

Beach Nourishment Simulations

The Beach-MPT model predicts that nests laid in nourished beaches may have pO_2 values that are lower than those laid in natural beaches. In the beach nourishment simulations which assumed that nourishment simply increased the water content of the sand, the nest core pO_2 decreased from 17.1 kPa to 14.7 kPa, even when the nest depth and sand porosity were held constant (Figure 19a). Alternatively, when beach nourishment was assumed to decrease sand porosity, the nest core pO_2 decreased 0.5 kPa (Figure 19b). When beach nourishment was assumed to both decrease porosity and increase sand water content (Figure 20), the nest pO_2 was reduced to 13.8 kPa. Altering initial sand temperatures had no significant effect on the response of nest pO_2 to simulated beach nourishment.

Beach nourishment appears to have weaker effects on nest temperature, though the effect of beach nourishment in part depends upon the initial sand temperature used in the model. With cooler initial conditions the model suggests that nests laid in nourished beaches which hold more water may be 4°C warmer in the middle and 3° C warmer at the top of the nest compared to nests laid in natural beaches (compare Figure 21-a to 21-c). The difference in nest temperatures between natural and nourished beaches is largely lost if the initial sand temperature is warmer (compare Figure 21-b to 21-d), and in fact, the upper portion of the nest is predicted

to be slightly (0.5°C) warmer in the natural beach. When beach nourishment is assumed to reduce sand porosity, beach nourishment has no effect on nest temperatures and changes in initial sand temperature simply shift the temperature transects to warmer values (Figure 22).

Nest Crowding Simulations

In the nest crowding simulations involving two nests, the pO_2 changed very little as the distance between the nests was reduced. The nest core pO_2 decreased from 17.6 kPa, to 17.3, to 17.2 kPa as the distance between the nests was reduced from 1 meter, to 0.5 meters, to 0.3 meters, respectively (Figure 23). When four nests were simulated in a 1-m^2 area of beach each nest had a core pO_2 of 17.1 kPa, while the pO_2 between the nests was ~ 18.8 kPa (Figures 24 and 25). When nine nests were packed into 1-m^2 (nest edges 0.05 meters apart) the pO_2 in each nest differed significantly from that found in the other nest arrangements. The nests on the corners had core pO_2 s of 14.6 kPa, whereas those in the middles of the sides had core pO_2 s of 14.0 kPa, and the nest in the middle had a core pO_2 of 13.2 kPa (Figures 26 and 27).

3.3.3~ Simulation of Development

Based on simulations of the four selected nests, the Beach-MPT model is qualitatively accurate in capturing the trends in actual nest pO_2 throughout incubation. Quantitatively, however, the model is routinely in error by 1-2 kPa (Table 15) and tends to overestimate the nest pO_2 . Nest 10 appears to be the exception with the model underestimate the nest pO_2 . Despite the errors the rate of pO_2 decline is captured relatively well during the first half of incubation.

Table 13: Response of end-incubation nest pO₂ to changes in parameter values. As part of the sensitivity analysis the model parameters were individual assigned the values shown here. The resulting nest pO₂ was recorded and used to calculate a sensitivity index (S) using equation 3.1. Parameters with larger sensitivity indices have larger affects on the nest pO₂ than parameters with smaller indices.

Description	Parameter Shift	Parameter Δ	Response of nest pO ₂	S
50% Increase in Nest Metabolism	100 eggs → 150 eggs	50	-1.843	0.215
50% Decrease in Nest Metabolism	100 eggs → 50 eggs	-50	1.844	0.215
↑ Sand Water Content	0.09 m ³ H ₂ O/m ³ → 0.15 m ³ H ₂ O/m ³	0.06	-3.369	0.294
↓ Sand Water Content	0.09 m ³ H ₂ O/m ³ → 0.03 m ³ H ₂ O/m ³	-0.06	2.387	0.209
↑ Porosity	0.40 m ³ /m ³ → 0.45 m ³ /m ³	0.05	0.351	0.160
↓ Porosity	0.40 m ³ /m ³ → 0.35 m ³ /m ³	-0.05	-0.472	0.224
Moderate Rainfall (1 hour)	0.0 cm/hr → 2.5 cm/hr	2.5	-0.032	0.0019
↓ Microbial Respiration	0.16 cm ³ O ₂ /m ³ s → 0.0 cm ³ O ₂ /m ³ s	-0.16	1.249	0.068
↑ Microbial Respiration	0.16 cm ³ O ₂ /m ³ s → 1.2 cm ³ O ₂ /m ³ s	1.04	-8.939	0.080
↓ Depth	40 cm → 20 cm	-20	0.58	0.068
↑ Depth	40 cm → 60 cm	20	-0.6	0.07

Table 14: Response of end-incubation nest temperature to changes in parameter values. As part of the sensitivity analysis the model parameters were individual assigned the values shown here. The resulting nest temperature was recorded and used to calculate a sensitivity index (S) using equation 3.1. Parameters with larger sensitivity indices have larger affects on the nest temperature than parameters with smaller indices.

Description	Parameter Shift	Parameter Δ	Response of nest T	S
50% Increase in Nest Metabolism	100 eggs $\rightarrow$ 150 eggs	50	0.75	0.005
50% Decrease in Nest Metabolism	100 eggs $\rightarrow$ 50 eggs	-50	-0.74	0.005
$\uparrow$ Sand Water Content	0.09 m ³ H ₂ O/m ³ $\rightarrow$ 0.15 m ³ H ₂ O/m ³	0.06	0.04	2.0 x 10 ⁻⁴
$\downarrow$ Sand Water Content	0.09 m ³ H ₂ O/m ³ $\rightarrow$ 0.03 m ³ H ₂ O/m ³	-0.06	-1.24	0.006
$\uparrow$ Porosity	0.4 m ³ /m ³ $\rightarrow$ 0.45 m ³ /m ³	0.05	-0.03	0.24
$\downarrow$ Porosity	0.40 m ³ /m ³ $\rightarrow$ 0.35 m ³ /m ³	-0.05	-0.03	0.24
$\downarrow$ Microbial Respiration	0.16 cm ³ O ₂ /m ³ s $\rightarrow$ 0.0 cm ³ O ₂ /m ³ s	-0.16	-0.09	3.0 x 10 ⁻⁴
$\uparrow$ Microbial Respiration	0.16 cm ³ O ₂ /m ³ s $\rightarrow$ 1.2 cm ³ O ₂ /m ³ s	1.04	-0.18	9.2 x 10 ⁻⁵
$\downarrow$ Depth	40 cm $\rightarrow$ 20 cm	-20	2.59	0.017
$\uparrow$ Depth	40 cm $\rightarrow$ 60 cm	20	-2.29	0.015
$\downarrow$ Thermal Conductivity	8.8 W/m K $\rightarrow$ 6.8 W/m K	-2	-0.02	2.9 x 10 ⁻⁴
$\uparrow$ Thermal Conductivity	8.8 W/m K $\rightarrow$ 10.8 W/m K	2	0.13	0.002

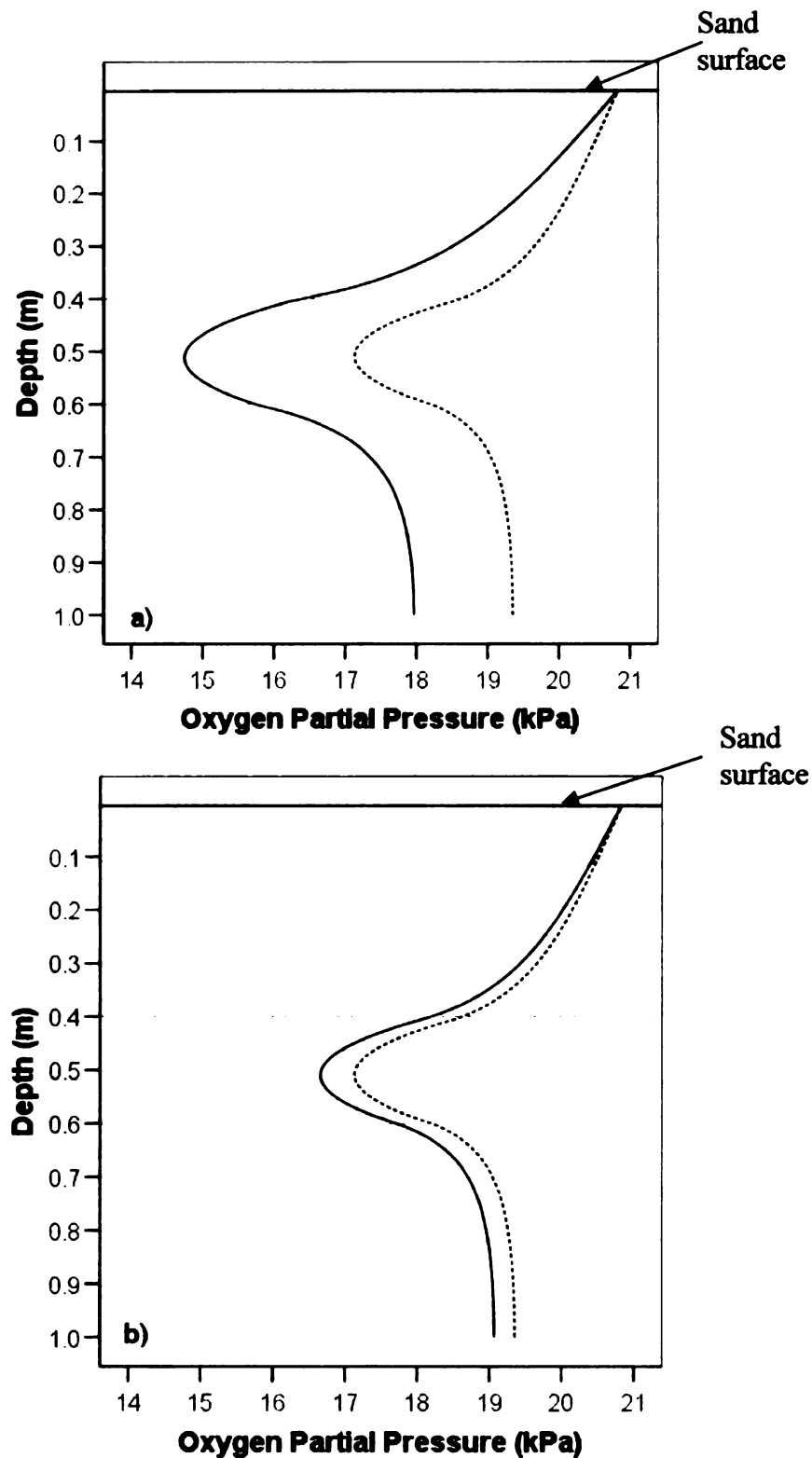


Figure 21. Vertical transect through a beach in which a 0.1 meter radius turtle nest is positioned at 0.4-0.6 m depth. a) simulated pO_2 values around a nest in a natural beach (---) and a nourished beach (—) which holds ~3 times the water, b) simulated pO_2 values around a nest in a natural beach (---) and a nourished beach (—) in which the porosity is decreased by $0.05 \text{ m}^3/\text{m}^3$ or ~10%. Horizontal dashed lines delineate the nest boundaries.

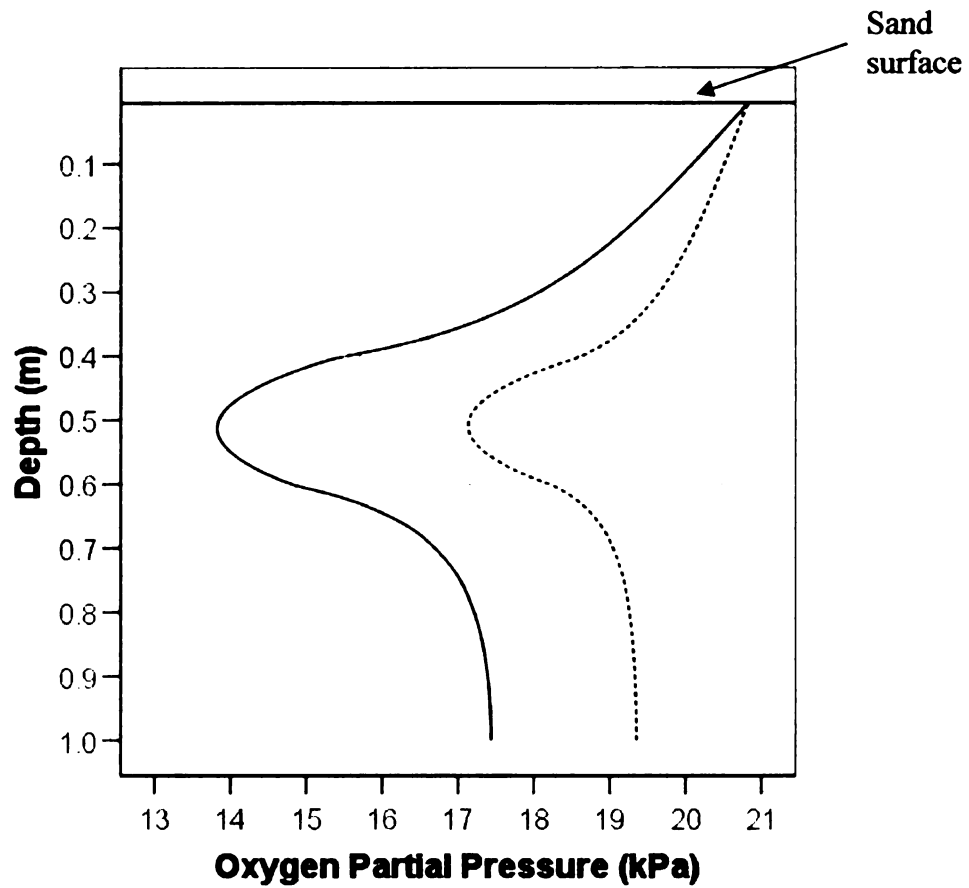


Figure 22. Vertical transect through a beach in which a 0.1 meter radius turtle nest is positioned at 0.4-0.6 m depth. Simulated pO_2 values around nest in a natural beach (- -) and a nourished beach (—) in which the water holding capacity was increased ~3 times the water and the porosity was decreased by $0.05 \text{ m}^3/\text{m}^3$ or ~10%. Horizontal dashed lines delineate the nest boundaries.

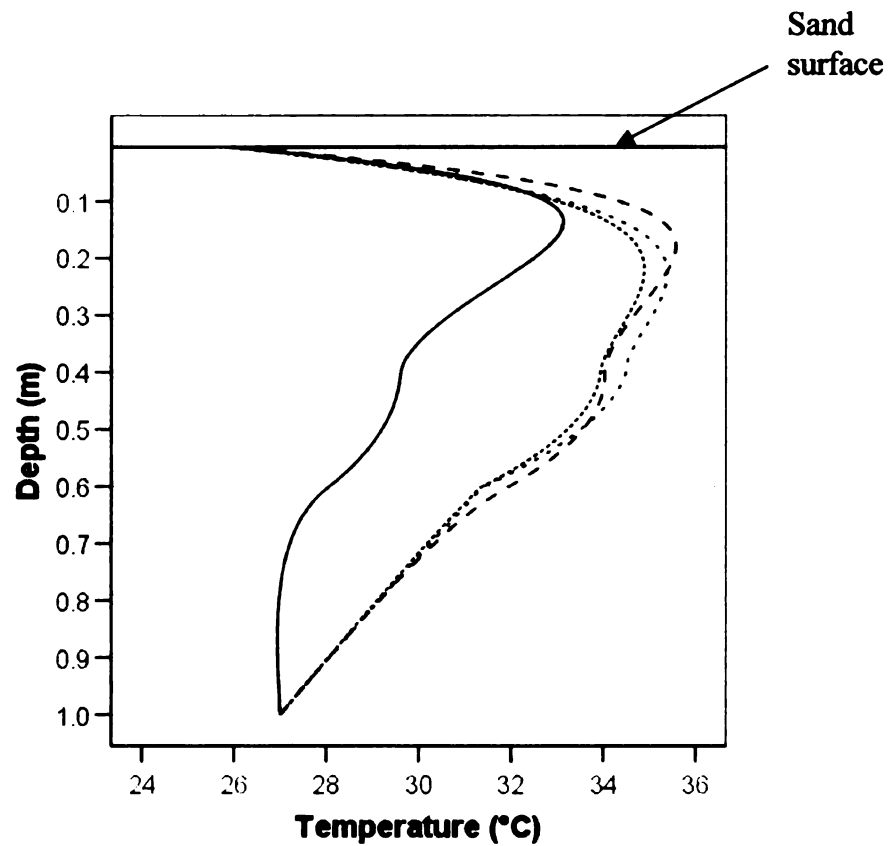


Figure 23. Vertical transect through both a natural and a nourished beach in which a 0.1 m radius turtle nest is positioned at 0.4-0.6 m depth. The nourished beach holds ~3 times more water than the natural beach. Horizontal dashed lines delineate the nest boundaries.

- a) (—) temperature gradient in a natural beach with initially cooler temperature
- b) (- - -) temperature gradient in natural beach with initially warmer temperature
- c) (····) temperature gradient in nourished beach with initially cooler temperature
- d) (- -) temperature gradient in nourished beach with initially warmer temperature

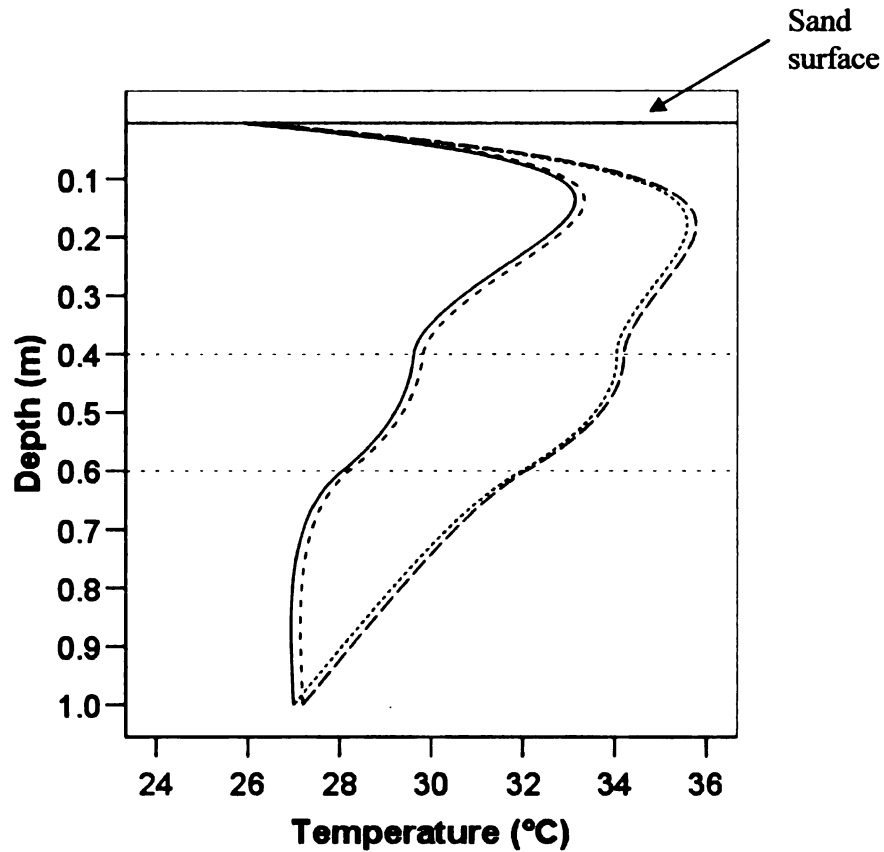


Figure 24. Vertical transect through both a natural and a nourished beach in which a 0.1 m radius turtle nest is positioned at 0.4-0.6 m depth. The porosity of the nourished beach is reduced by $0.05 \text{ m}^3/\text{m}^3$ (~10% lower than the porosity of the natural beach). Horizontal dashed lines delineate the nest boundaries. To prevent overlap and aid in visualization, a 0.2°C displacement was added to the lines representing the nourished beaches.

- a) (—) temperature gradient in a natural beach with initially cooler temperature
- b) (····) temperature gradient in natural beach with initially warmer temperature
- c) (---) temperature gradient in nourished beach with initially cooler temperature
- d) (- -) temperature gradient in nourished beach with initially warmer temperature

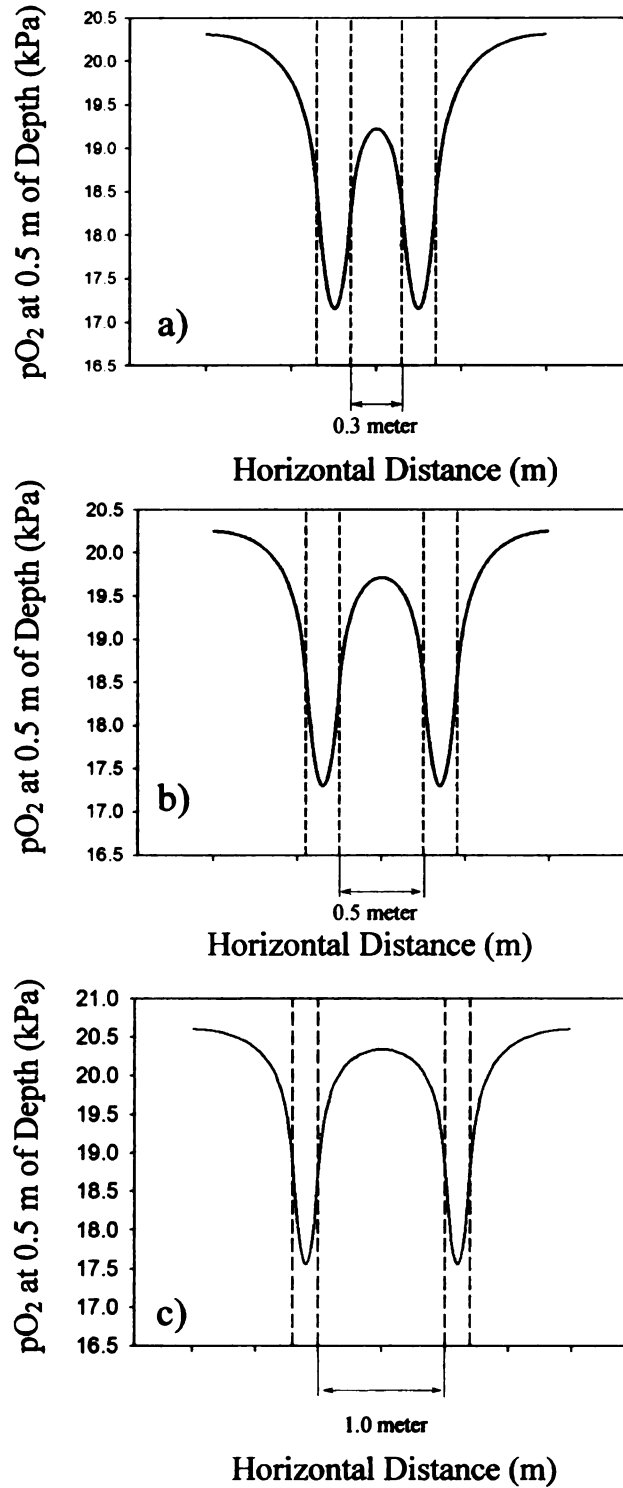


Figure 25. Results of Beach-MPT simulation showing the pO_2 gradients within and around two nearby nests. Both nests had a radius of 0.1 meter and were centered at a depth of 0.5 meters. The solid lines represent horizontal transects drawn through the centers of each nest at a depth of 0.5 meters. A) nests 0.3 meters apart, b) nests 0.5 meters apart, c) nests 1 meter apart. Parameters used in simulations are provided in table 3.

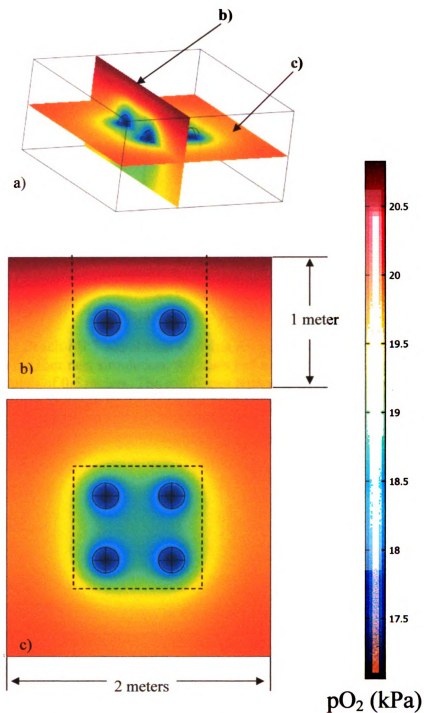


Figure 26. Simulation of pO_2 gradients in and around a set of four, 0.1 meter diameter nests, centered at a depth of 0.5 meters. a) Three-dimensional reference for the images shown in Figure 24b and Figure 24c. b) pO_2 gradients as seen from the side. The sand surface is the upper boundary. c) the pO_2 gradients around the four nests as viewed from above. The black dashed lines in Figure 3b are one meter apart and in Figure 3c the dashed square is one square meter. The minimum pO_2 in all four nests was 17.1 kPa.

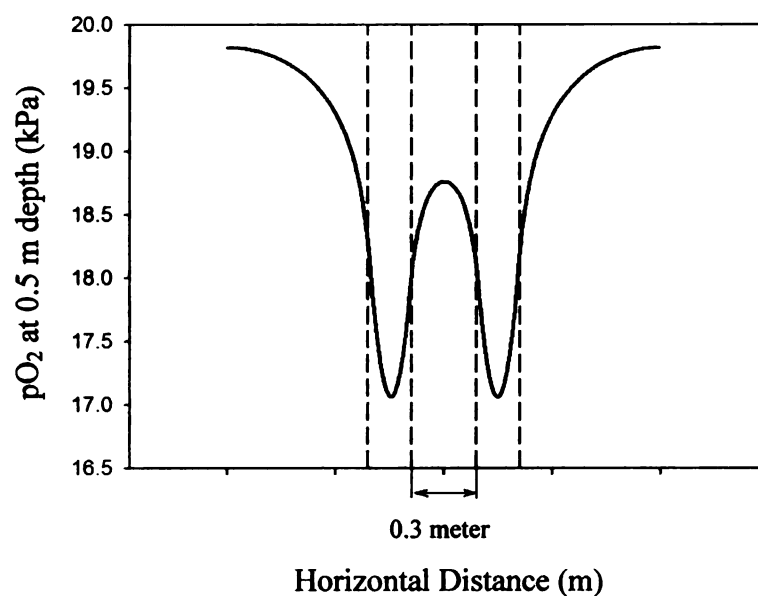


Figure 27. Results of Beach-MPT simulation showing the pO_2 gradients within and around two nests in the four nest simulation. All nests had a radius of 0.1 meter and were centered at a depth of 0.5 meters. The solid lines represent a horizontal transect drawn through the centers of each nest at a depth of 0.5 meters.

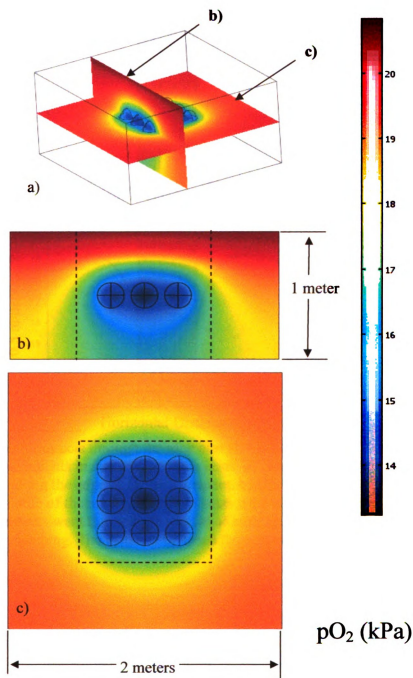


Figure 28. Simulated of pO_2 gradients in and around a set of nine, 0.1 meter diameter nests, centered at a depth of 0.5 meters. a) Three-dimensional reference for the images shown in Figure 26b and Figure 26c. b) pO_2 gradients as seen from the side. The sand surface is the upper boundary. c) the pO_2 gradients around the nine nests as viewed from above. The black dashed lines in figure 3a are one meter apart and in figure 3b the dashed square is one square meter. The minimum pO_2 was 13.2 kPa in the central nest.

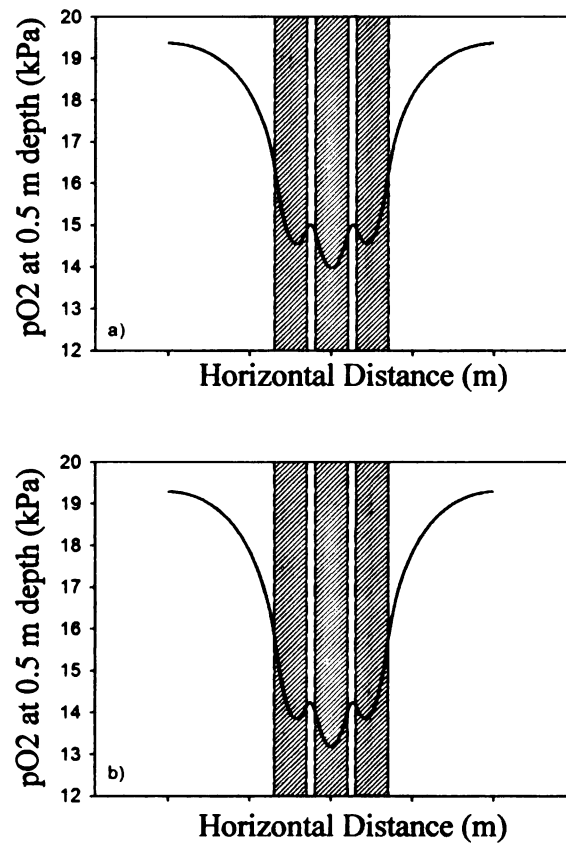


Figure 29. Horizontal transects through the nine nest simulation shown in figure 8 illustrating the pO_2 gradients in and around three nests. a) Horizontal pO_2 transect through three nests along the edge of the arrangement. b) Horizontal transect through three nests in the middle of the arrangement. All nests were centered at a depth of 0.5 meters and both transects went through the middle of each nest. Nest locations are shown by the cross-hatching. The distance between the nest edges was 0.05 meters.

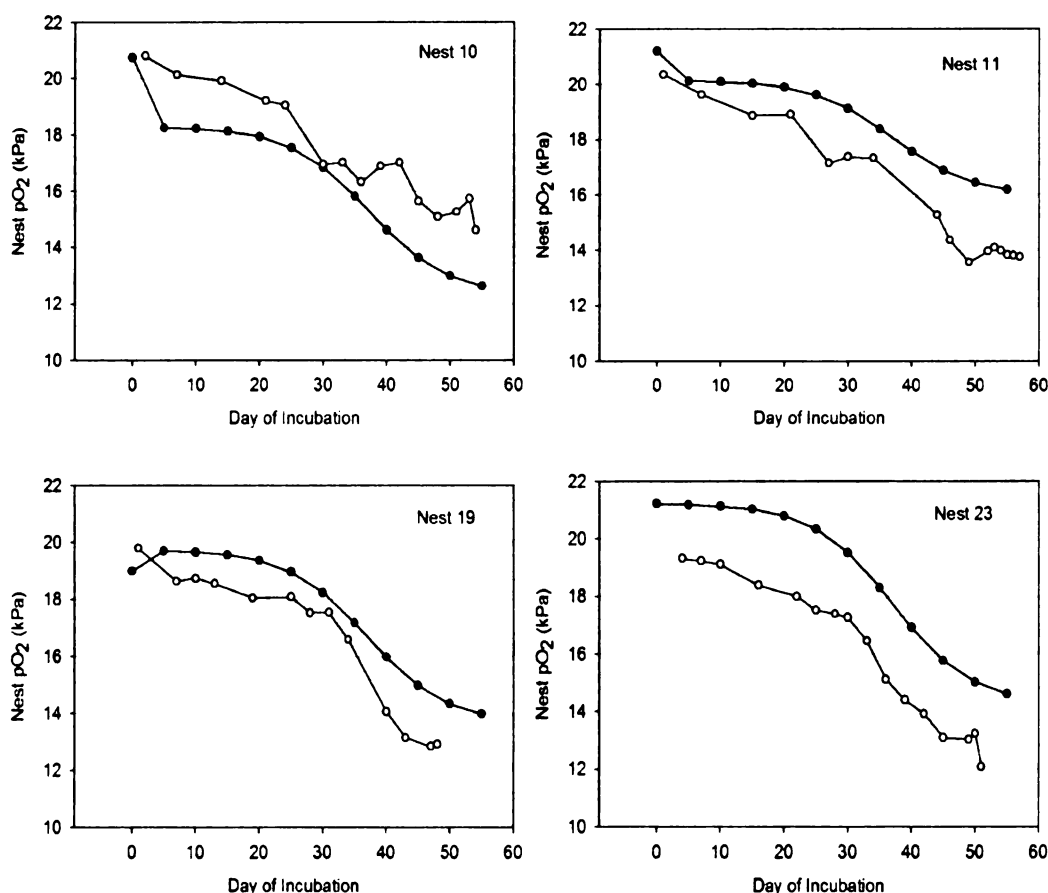


Figure 30. Comparisons of predicted (●) and actual (○) nest pO₂s throughout the course of nest incubation in the four nests selected for study. In each case the model was parameterized with the field data shown in Table 12. The actual nest pO₂s were measured during the 2006 nesting season on Sapelo Island, GA.

Table 15. Mean difference, throughout the incubation period, between the actual nest pO₂s and the nest pO₂s predicted by the Beach-MPT model (shown in Figure 28).

Nest	Mean (kPa)	Range (kPa)
10	1.4 ± 0.25	0.1 – 2.3
11	1.6 ± 0.27	0.5 – 2.9
19	1.1 ± 0.13	0.6 – 1.9
23	2.5 ± 0.15	1.8 – 3.2

3.4~ DISCUSSION

Physical characteristics of the nest environment such as temperature, moisture level, and respiratory gas pressures have been shown to influence incubation length, sex determination, and embryonic survival (Mrosovsky and Yntema 1980, Matsuzawa et al. 2002). These physical characteristics may also alter other important phenotypic traits, including body size, growth rate, and running speed with the potential for long-term consequences (Ackerman 1981, Miller et al. 1987). I recently demonstrated that one of these characteristics, nest pO_2 , varies considerably among loggerhead turtle nests and that this variability was not driven by clutch size (Chapter 1). This suggests that nest site characteristics and their variation may have profound consequences on developing turtles. Despite modest knowledge concerning the effects of temperature, moisture, and respiratory gases upon turtle embryos, we know remarkably little about the microclimates within natural turtle nests. Less is known about how the physical characteristics of the nest site influence the nest microclimate.

The sensitivity analyses reported here were designed to address this area of limited knowledge by clarifying the influence of nest and nest-site characteristics on the nest temperature and nest pO_2 . These analyses suggest that while nest pO_2 is sensitive to changes in clutch metabolism it is equally sensitive to changes in sand porosity and sand water content (Table 13). The fact that the model is similarly sensitive to sand porosity and sand water content is not unexpected given that both of these parameters affect the amount of air-filled pore space available for gas diffusion. This finding suggests that when considering nest pO_2 it is important to recognize that

the characteristics of the substrate around the nest may be just as important as the characteristics of the developing clutch.

There were some additional surprises in the pO_2 sensitivity analysis. Nest depth, which is often considered very important in determining nest microclimate, had a moderate affect on nest pO_2 , but nest pO_2 is less sensitive to nest depth than both porosity and water content (Table 13). Short-term rainfall events (1 hour, 2.5 cm/hr) were also found to have relatively little effect upon the nest pO_2 . Presumably, the low impact of the rainfall is because the O_2 in the sand serves as a reserve supply during the relatively short period of time that the surface sand pores approach saturation during rain. Relatively large fluctuations in respiration by sand microbial populations were also found to have little affect on the nest pO_2 , suggesting that empirical quantification of microbial populations is unnecessary to understand variation in nest microclimates (Table 13). Taken together my sensitivity analysis suggests that the large variability in nest pO_2 is mostly like due to variation in sand porosity or sand water content, and developing more accurate means of measuring these variables in the field is an important goal. It also suggests that any processes, natural or otherwise, that alter the nesting substrate will have important consequences on nest pO_2 .

Nest temperature was less sensitive than pO_2 to changes in all of the parameters that were included in the sensitivity analysis. The nest temperature, however, was relatively sensitive to changes in sand porosity. The sensitivity to porosity may be a consequence of the fact that as the porosity changes, so too does the thermal conductivity of the sand system because of the low thermal conductivity

of air. Relatively porous sands contain more air and therefore exhibit a lower thermal conductivity than more densely packed sands. Changes in water content might be expected to have a considerable affect on the nest temperature, because high water content results in less air, and the thermal conductivity of water is far higher than air. The potential effect of water content is not realized in practice, however. The nest temperature was relatively insensitive to changes in water content, presumably a consequence of the high specific heat of water which would tend to buffer temperature changes. Changes in nest metabolism had a relatively small affect on nest temperature, once again demonstrating that the nest microenvironment is often less a function of the biotic processes in the nest and more a consequence of the abiotic characteristics of the nest site.

Given that the nest environment may often be a consequence of the physical characteristics of the nest site, one would expect that activities such as beach nourishment, which alter nest site characteristics, can dramatically alter the nest environment. The Beach-MPT model predicts that nests laid in nourished beaches may have pO_2 levels that are significantly lower than those found in nests laid in natural beaches (Figure 19 and 20). The actual reduction in nest pO_2 depends on whether beach nourishment increases the sand water content, decreases the porosity, or both. There has been some disagreement over whether beach nourishment actually alters porosity (Ackerman 1997). My analysis, however, suggests that effects of changes in porosity are dwarfed by the effects of changes in water holding capacity, which is much less in doubt (Crain et al. 1995). Given that the critical pO_2 (pO_{2c} : the pO_2 below which metabolism is reduced) of loggerhead embryos has been found to

be 18.1 kPa during late incubation (Kam 1993) the Beach-MPT model predicts that embryos developing in nests laid in nourished beaches may experience significantly depressed metabolic rates, which may slow development, and increase the length of incubation.

Beach nourishment appears to have weaker effects on nest temperature, though the thermal effect of beach nourishment depends upon the initial sand temperature used in the model. When the initial sand temperature is low and beach nourishment increases the water holding capacity of the sand, the nest temperatures increase dramatically (Figure 21). This effect is lost if the initial sand temperature is higher, which suggests that the consequences of beach nourishment could vary seasonally. Nests laid earlier in the nesting season are exposed to lower sand temperatures, and the model suggests that these nests may be more sensitive to beach nourishment than nests laid later in the season and exposed to warmer sand temperatures. Such a possibility deserves attention. Both nest temperature and pO_2 are most affected when beach nourishment increases the water holding capacity of the sand rather than when beach nourishment lowers porosity (Figure 19 and 22). This suggests that care should be taken when nourishing beaches to maintain natural levels of water holding capacity. The water holding capacity is largely the result of particle size and packing or bulk density (Horn and Baumgartl 2002). Therefore, it is important to ensure that the sand being used for nourishment is of a similar particle size as that naturally found on the beach.

Nest crowding may negatively impact the nest environment for nests placed in hatcheries, those laid naturally in heavily nested beaches, or those laid during the

simultaneous, mass-nesting arribadas of the olive ridley sea turtle. The Beach-MPT model suggests that when only 2 nests are nearby, the pO_2 in both nests changes very little (~ 0.5 kPa) as the distance between nests is reduced. The pO_2 gradient in the sand between the nests changes much more however (~ 2.5 kPa). This suggests that measuring the pO_2 between two nests may not provide a good measure of the conditions within the nests. More importantly, measuring the pO_2 between two nests may not provide a good measure of how much the two nests interact. In fact, it appears that despite the fact that the pO_2 values in the sand between two nests declines considerably as they are moved closer to one another, the nests themselves interact minimally.

Even at a density of four nests per 1 m^2 (0.3 meters between nest edges), the pO_2 within each nest did not differ significantly from the two-nest simulations in which the nests edges were 0.3 meters apart (compare Figure 23a to Figure 25). It was only when the nests were packed nine per square meter that the nest pO_2 clearly declined. These results suggest that considerable crowding is required before the nest pO_2 is negatively impacted. Therefore, while nest crowding may be a concern under special conditions, under most conditions nests are predicted to not interact significantly. As more empirical work becomes available, it will be interesting to test the validity of these predictions.

While an understanding of the developmental environment to which sea turtle eggs are exposed clearly requires consideration of the biotic parameters within the nest, I have demonstrated using the Beach-MPT model that often the abiotic characteristics of the nest site may be of equal importance. Currently, most managers

measure nest parameters such as clutch size, nest depth, hatching success, or the distance to mean high water line when assessing nest success and suitable nest locations. My results suggest that supplementing these measurements with accurate measurements of nest site characteristics such as sand porosity and sand water content will improve our ability to predict which nest sites may be successful. These results also suggest that practices that alter nesting substrate can dramatically alter nest environments. Therefore, increasing nest success may be achieved through directed habitat alterations. Alternatively, haphazard management of nesting substrate, could easily decrease nest success.

APPENDIX I

Mesh and solver parameters used in individual Beach-MPT simulations.

Dry Sand pO2 simulations

Element Number: 1168
Degrees of Freedom: 32636
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Damp Sand pO2 Simulations

Element Number: 6586
Degrees of Freedom: 30990
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Dry Sand Temperature Simulations

Element Number: 1496
Degrees of Freedom: 30990
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Damp Sand Temperature Simulations

Element Number: 18072
Degrees of Freedom: 79617
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Two Nests, 1 meter apart

Element Number: 4066
Degrees of Freedom: 18983
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Two Nests, 0.5 meter apart

Element Number: 3899
Degrees of Freedom: 19063
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Two Nests, 0.3 meter apart

Element Number: 3985
Degrees of Freedom: 19008
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Four Nests

Element Number: 15345
Degrees of Freedom: 64969
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

Nine Nests

Element Number: 20248
Degrees of Freedom: 83484
Element Type: Tetrahedral
Element Interpolation: Lagrange-Quadratic
Time Stepping: Free
Time-dependent Solver: GMRES
Preconditioner: Geometric multigrid

APPENDIX II

A model report describing all parameters, equations, and functions were included in the Beach-MPT model.

Model Properties

Property	Value
Model name	
Author	
Company	
Department	
Reference	
URL	
Saved date	Jan 22, 2007 3:39:43 PM
Creation date	Feb 4, 2006 4:03:51 PM
COMSOL version	COMSOL 3.3.0.511

File name: C:\Documents and Settings\NATHAN MILLER\My Documents\Nest Simulations\2Nest\2Nests 1meterapart.mph

Application modes and modules used in this model:

- Geom1 (3D)
 - PDE, General Form
 - Convection and Conduction
 - PDE, General Form
- Geom2 (2D)

Constants

Name	Expression	Value	Description
Cs		2.13e6	
Cw		4.19e6	
Ca		1.256e3	
MW		0.018	
THETAr		0.0	
N		1.68	
M		1-1/N	
L		.5	
ALPHA		2.57	
R		8.314e-3	
Ks		7.44e-5	
DL		0.005	
DT		0.0001	
d		0.005	
sigma		5.6697e-8	
patm		99.41	
A1		-58.3877	
A2		85.8079	
A3		23.8439	
a		.611	
b		17.502	
c		240.97	
theta0		0.05	
q		2	
rhoair		41.4	
ka		0.025	
kw		.6	
kquartz		8.8	
ga		.1	
gc		1-2*ga	
beta		.2	
Cegg		2.980923e6	

5. Geom1

Space dimensions: 3D

Independent variables: x, y, z

5.1. Expressions

5.1.1. Subdomain Expressions

Subdo	1	2-3
main		
tauw	$\text{theta}^{(10/3)} * (\text{hp} < 0) / \text{THETAs}^2$	
av	$\text{THETAs} - \text{theta} * (\text{hp} < 0)$	
theta	$((\text{THETAs} - \text{THETAr}) * \text{Se} + \text{THETAr}) * (\text{hp} < 0) + \text{THETAs} * (\text{hp} \geq 0)$	
K	$\text{Ks} * \text{Se}^L * (1 - (1 - \text{Se}^{(1/M)})^M)^2 * (\text{hp} < 0) + \text{Ks} * (\text{hp} \geq 0)$	
qx	$1e-010 * (t == 0) - K * \text{hpx}$	
qy	$-K * \text{hpy}$	
qz	$-K * (1 + \text{hpsz})$	
absq	$\text{sqrt}(\text{qx}^2 + \text{qy}^2 + \text{qz}^2)$	
C	$\text{ALPHA} * M * (\text{THETAs} - \text{THETAr}) * \text{Se}^{(1/M)} * (1 - \text{Se}^{(1/M)})^M * (\text{hp} < 0) / (1 - M)$	
CH	$2 * \text{Cs} * \text{VolS} + \text{Cw} * \text{theta} + \text{Ca} * \text{av} * (\text{hp} < 0) + \text{Cw} * \text{THETAs} * (\text{hp} \geq 0)$	$0.7405000000000001 * \text{Cegg} + 0.2595 * \text{Ca}$
Se	$(1 + (\text{ALPHA} * \text{abs}(\text{hp}))^N)^{-M}$	
hr	$\text{exp}(9.800000000000001 * \text{MW} * \text{hp} / (\text{R} * \text{T})) * (\text{hp} < 0)$	
hra	0.7	
VolS	$1 - \text{THETAs}$	
Dwl	2.67e-009	
Dgl	$0.0021784875 * (0.00341 * \text{T})^{1.75 / \text{patm}}$	$0.00218 * (0.00341 * \text{T})^{1.75 / \text{patm}}$
bw	$0.4405907440999996 * \text{exp}(\text{A1} + 100 * \text{A2} / \text{T} + \text{A3} * \log(0.01 * \text{T}))$	

bg	$1/(R*T)$	$1/(R*T)$
taug	$av^{(10/3)}*(hp<0)/THETAs^2$	0.1655
MO2	0.0006661	
thetaD xx	$DL*qx^2/absq+DT*(qy^2+qz^2)/absq+Dw1*tauw$	
thetaD yy	$DL*qy^2/absq+DT*(qx^2+qz^2)/absq+Dw1*tauw$	
thetaD zz	$DL*qz^2/absq+DT*(qx^2+qy^2)/absq+Dw1*tauw$	
thetaD xy	$(DL-DT)*qx*qy/absq$	
thetaD xz	$(DL-DT)*qx*qz/absq$	
thetaD yz	$(DL-DT)*qy*qz/absq$	
Dv	$2.4e-005*(0.00341*T)^{1.75}$	
Dh	$2.15e-005*(0.00341*T)^{1.75}$	
lamda	$2.501-0.002361*T$	
esT	$a*exp(b*(273-T)/(273-T-c))$	
delta	$b*c*esT/(-273+T+c)^2$	
ea	$esT*hr$	
fw	$1/(1+(theta/theta0)^{(-q)})$	
fg	$ka+lamda*delta*hr*fw*rhoair*Dv/(patm-ea)$	
kf	$kg+fw*(kw-ka)$	
epa	$2/(3*(1-ga*(1-ka/kf)))+1/(3*(1-gc*(1-ka/kf)))$	
epw	$2/(3*(1-ga*(1-kw/kf)))+1/(3*(1-gc*(1-kw/kf)))$	
epm	$2/(3*(1-ga*(1-kquartz/kf)))+1/(3*(1-gc*(1-kquartz/kf)))$	
Ksoil	$(theta*epw*kw+av*epa*ka+VolS*epm*kquartz)/(theta*epw+av*epa+VolS*epm)$	
kg	$ka+lamda*delta*hr*fw*rhoair*Dv/(patm-ea)$	
Kn		$0.7405*Kwater+0.2595*Kair$
Kair		$0.024+6.999e-005*T$
Kwate		$0.56+0.0018*T$
r		
Ta	$310.5+12*sin(2.3148e-005*pi*t-0.583*pi)$	

Initial -21.119-587.21*z^4+954.09*z^3-
H2O 430.48*z^2+57.807*z
THET 0.46
As

5.2. Mesh

5.2.1. Mesh Statistics

Number of degrees of freedom	18983
Number of mesh points	943
Number of elements	4066
Tetrahedral	4066
Prism	0
Hexahedral	0
Number of boundary elements	1128
Triangular	1128
Quadrilateral	0
Number of edge elements	142
Number of vertex elements	18
Minimum element quality	0.335
Element volume ratio	0.003

5.3. Application Mode: PDE, General Form (Water)

Application mode type: PDE, General Form

Application mode name: Water

5.3.1. Application Mode Properties

Property	Value
Default element type	Lagrange - Quadratic
Wave extension	Off
Frame	Frame (xyz)
Weak constraints	Off

5.3.2. Variables

Dependent variables: hp, hp_t

Shape functions: shlag(2,'hp')

Interior boundaries not active

5.3.3. Point Settings

Point	1-18
style	{0,{0,0,255}}

5.3.4. Edge Settings

Edge	1-30
style	{0,{0,0,255},'solid'}

5.3.5. Boundary Settings

Boundary	1-2, 4-14	3
Type	Neumann boundary condition	Neumann boundary condition
(g)	0	qz

5.3.6. Subdomain Settings

Subdomain	1
Damping/Mass coefficient (da)	$(C+Se*(THETAs-THETAr))*(hp<0)+(THETAs-THETAr)*(hp>=0)$
Source term (f)	0
Conservative flux source term (ga)	$\{-K*hp_x;-K*hp_y;-K*(hp_z+1)\}$
Subdomain initial value	1
hp	InitialH2O

5.4. Application Mode: Convection and Conduction (Energy)

Application mode type: Convection and Conduction

Application mode name: Energy

5.4.1. Application Mode Properties

Property	Value
Default element type	Lagrange - Quadratic
Analysis type	Stationary
Equation form	Non-conservative
Frame	Frame (xyz)
Weak constraints	Off

5.4.2. Variables

Dependent variables: T
 Shape functions: shlag(2,'T')
 Interior boundaries active

5.4.3. Boundary Settings

Boundary	1-2, 5, 14-18	6-13
Type	Thermal insulation	Continuity
Temperature (T0) K	0	0
Boundary	3	4
Type	Temperature	Temperature
Temperature (T0)	300	Ta

5.4.4. Subdomain Settings

Subdomain	1	2-3
Thermal conductivity (k)	W/(m·K) Ksoil	Kn
Density (rho)	kg/m ³ 1	1
Heat capacity (C)	J/(kg·K) CH	CH
Heat source (Q)	W/m ³ 0	800.4529
x-velocity (u)	m/s qx	0
y-velocity (v)	m/s qy	0
z-velocity (w)	m/s qz	0
Subdomain initial value	1	2-3
Temperature (T)	K 300-2*z	305

5.5. Application Mode: PDE, General Form (Gas)

Application mode type: PDE, General Form

Application mode name: Gas

5.5.1. Application Mode Properties

Property	Value
Default element type	Lagrange - Quadratic
Wave extension	Off
Frame	Frame (xyz)
Weak constraints	Off

5.5.2. Variables

Dependent variables: pO2, pO2_t

Shape functions: shlag(2,'pO2')

Interior boundaries not active

5.5.3. Point Settings

Point	1-18
style	{0,{0,0,255}}

5.5.4. Edge Settings

Edge	1-30
style	{0,{0,0,255},'solid'}

5.5.5. Boundary Settings

Boundary	1-2, 5, 14-18	3
Type	Neumann boundary condition	Neumann boundary condition
(g)	0	$qz \cdot pO2$
(r)	-pO2	-pO2
Boundary	4	
Type	Dirichlet boundary condition	
(g)	0	
(r)	$-pO2 + (.2095 \cdot patm)$	

5.5.6. Subdomain Settings

Subdomain	1	2-3
Damping/ Mass coefficient (da)	$(\theta * bw + av * bg) * (hp < 0) + (THETA_s * bw) * (hp \geq 0)$	$0.2595 * bg$
Source term (f)	0	$-1.154e-3$
Conservative flux source term (ga)	$\{ \{ -$ $(bw * \theta_{Dxx} + bw * \theta_{Dxy} + bw * \theta_{Dxz} + \tau_{aug} * Dg1 * bg) * pO2x - q_x * (bw * pO2); -$ $(bw * \theta_{Dyy} + bw * \theta_{Dxy} + bw * \theta_{Dyz} + \tau_{aug} * Dg1 * bg) * pO2y - q_y * (bw * pO2); -$ $(bw * \theta_{Dzz} + bw * \theta_{Dxz} + bw * \theta_{Dyz} + \tau_{aug} * Dg1 * bg) * pO2z - q_z * (bw * pO2) \} \}$	$\{ \{ -$ $(\tau_{aug} * Dg1 * bg) * pO2x; -$ $(\tau_{aug} * Dg1 * bg) * pO2y; -$ $(\tau_{aug} * Dg1 * bg) * pO2z \} \}$
Subdomain initial value	1	2-3
pO2	19	19

7. Interpolation Functions

7.1. Interpolation Function: NestVO2

Interpolation method: Piecewise Cubic

Data source type: Table

x	f(x)
86400	$5.812e-6$
432000	$1.099e-5$
864000	$2.4285e-5$
1296000	$5.31932e-5$
1728000	$1.14355e-4$
2160000	$2.36582e-4$
2592000	$4.55193e-4$
3024000	$7.78374e-4$
3456000	$1.143016e-3$
3888000	$1.447763e-3$

4320000	1.644808e-3
4752000	1.751949e-3
5184000	1.804773e-3

7.2. Interpolation Function: NestHeat

Interpolation method: Piecewise Cubic

Data source type: Table

x	f(x)
86400	2.5778
432000	4.875
864000	10.771
1296000	23.5922
1728000	50.7186
2160000	104.929
2592000	201.887
3024000	345.224
3456000	506.95
3888000	642.111
4320000	729.505
4752000	777.025
5184000	800.4529

8. Solver Settings

Solve using a script: off

Auto select solver On

Solver	Time dependent
Solution form	Automatic
Symmetric	Off
Adaption	Off

8.1. GMRES

Solver type: Linear system solver

Parameter	Value
Relative tolerance	1.0E-6
Factor in error estimate	400.0
Maximum number of iterations	10000
Number of iterations before restart	50
Preconditioning	Left

8.1.1. Geometric multigrid

Solver type: Preconditioner

Parameter	Value
Number of iterations	2
Multigrid cycle	V-cycle

8.1.1.1. SOR

Solver type: Presmoothing

Parameter	Value
Number of iterations	2
Relaxation factor (omega)	1.0

8.1.1.2. SORU

Solver type: Postsmoothing

Parameter	Value
Number of iterations	2
Relaxation factor (omega)	1.0

8.1.1.3. UMFPACK

Solver type: Coarse solver

Parameter	Value
Drop tolerance	0.0
Pivot threshold	0.1
Memory allocation factor	0.7

8.2. Time Stepping

Parameter	Value
Times	0:86400:172800
Relative tolerance	0.01
Absolute tolerance	0.0010
Times to store in output	Specified times
Time steps taken by solver	Free
Manual tuning of step size	Off
Initial time step	0.0010
Maximum time step	1.0
Maximum BDF order	5
Singular mass matrix	Maybe
Consistent initialization of DAE systems	Backward Euler
Error estimation strategy	Include algebraic
Allow complex numbers	Off

8.3. Advanced

Parameter	Value
Constraint handling method	Elimination
Null-space function	Automatic
Assembly block size	5000
Use Hermitian transpose of constraint matrix and in symmetry detection	Off
Use complex functions with real input	Off
Stop if error due to undefined operation	On
Type of scaling	Automatic
Manual scaling	
Row equilibration	On
Manual control of reassembly	Off
Load constant	On
Constraint constant	On
Mass constant	On
Damping (mass) constant	On
Jacobian constant	On
Constraint Jacobian constant	On

10. Variables

10.1. Boundary

Name	Description	Expression
ndflux_T_Energy	Normal conductive heat flux, T	$nx_Energy * dflux_T_x_Energy + ny_Energy * dflux_T_y_Energy + nz_Energy * dflux_T_z_Energy$
ncflux_T_Energy	Normal convective heat flux, T	$nx_Energy * cflux_T_x_Energy + ny_Energy * cflux_T_y_Energy + nz_Energy * cflux_T_z_Energy$
ntflux_T_Energy	Normal total heat flux, T	$nx_Energy * tflux_T_x_Energy + ny_Energy * tflux_T_y_Energy + nz_Energy * tflux_T_z_Energy$

10.2. Subdomain

10.2.1. Subdomain 1

Name	Description	Expression
abshpx_Water	$ \text{grad}(hp) $	$\text{sqrt}(hpx^2 + hpy^2 + hpz^2)$
absgalx_Water	$ galx $	$\text{sqrt}(galx^2 + galy^2 + galz^2)$
grad_T_x_Energy	Temperature gradient, T, x component	T_x
dflux_T_x_Energy	Conductive heat flux, T, x component	$-kxx_T_Energy * T_x - kxy_T_Energy * T_y - kxz_T_Energy * T_z$
cflux_T_x_Energy	Convective heat flux, T, x component	$\rho_T_Energy * C_T_Energy * T * u_T_Energy$
tflux_T_x_Energy	Total heat flux, T, x component	$dflux_T_x_Energy + cflux_T_x_Energy$
grad_T_y_Energy	Temperature gradient, T, y component	T_y
dflux_T_y_Energy	Conductive heat flux, T, y component	$-kyx_T_Energy * T_x - kyy_T_Energy * T_y - kyz_T_Energy * T_z$

	y component	
cflux_T_y_Energy	Convective heat flux, T, y component	$\rho_T \text{Energy} * C_T \text{Energy} * T * v_T \text{Energy}$
tflux_T_y_Energy	Total heat flux, T, y component	$dflux_T_y_Energy + cflux_T_y_Energy$
grad_T_z_Energy	Temperature gradient, T, z component	T_z
dflux_T_z_Energy	Conductive heat flux, T, z component	$-k_{zx}_T \text{Energy} * T_x - k_{zy}_T \text{Energy} * T_y - k_{zz}_T \text{Energy} * T_z$
cflux_T_z_Energy	Convective heat flux, T, z component	$\rho_T \text{Energy} * C_T \text{Energy} * T * w_T \text{Energy}$
tflux_T_z_Energy	Total heat flux, T, z component	$dflux_T_z_Energy + cflux_T_z_Energy$
beta_T_x_Energy	Convective field, T, x component	$\rho_T \text{Energy} * C_T \text{Energy} * u_T \text{Energy}$
beta_T_y_Energy	Convective field, T, y component	$\rho_T \text{Energy} * C_T \text{Energy} * v_T \text{Energy}$
beta_T_z_Energy	Convective field, T, z component	$\rho_T \text{Energy} * C_T \text{Energy} * w_T \text{Energy}$
grad_T_Energy	Temperature gradient, T	$\sqrt{grad_T_x_Energy^2 + grad_T_y_Energy^2 + grad_T_z_Energy^2}$
dflux_T_Energy	Conductive heat flux, T	$\sqrt{dflux_T_x_Energy^2 + dflux_T_y_Energy^2 + dflux_T_z_Energy^2}$
cflux_T_Energy	Convective heat flux, T	$\sqrt{cflux_T_x_Energy^2 + cflux_T_y_Energy^2 + cflux_T_z_Energy^2}$
tflux_T_Energy	Total heat flux, T	$\sqrt{tflux_T_x_Energy^2 + tflux_T_y_Energy^2 + tflux_T_z_Energy^2}$
cellPe_T_Energy	Cell Peclet number, T	$h * \sqrt{beta_T_x_Energy^2 + beta_T_y_Energy^2 + beta_T_z_Energy^2} / Dm_T \text{Energy}$
Dm_T_Energy	Mean diffusion	$(k_{xx}_T \text{Energy} * \rho_T \text{Energy}^2 * C_T \text{Energy}^2 * u_T \text{Energy}^2 + k_{xy}_T \text{Energy} * u_T \text{Energy} * v_T \text{Energy} + k_{yx}_T \text{Energy} * v_T \text{Energy} * u_T \text{Energy} + k_{yy}_T \text{Energy} * v_T \text{Energy}^2 + k_{yz}_T \text{Energy} * v_T \text{Energy} * w_T \text{Energy} + k_{zy}_T \text{Energy} * w_T \text{Energy} * v_T \text{Energy} + k_{zz}_T \text{Energy} * w_T \text{Energy}^2) / 3$

coefficient, T		$\begin{aligned} & \rho_T_Energy^2 * C_T_Energy^2 * \\ & v_T_Energy + kxz_T_Energy * u_T_Energy * \\ & \rho_T_Energy^2 * C_T_Energy^2 * \\ & w_T_Energy + kyx_T_Energy * v_T_Energy * \\ & \rho_T_Energy^2 * C_T_Energy^2 * \\ & u_T_Energy + kyy_T_Energy * \rho_T_Energy^2 * \\ & C_T_Energy^2 * v_T_Energy^2 + kyz_T_Energy * \\ & v_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * \\ & w_T_Energy + kzx_T_Energy * w_T_Energy * \\ & \rho_T_Energy^2 * C_T_Energy^2 * \\ & u_T_Energy + kzy_T_Energy * w_T_Energy * \\ & \rho_T_Energy^2 * C_T_Energy^2 * \\ & v_T_Energy + kzz_T_Energy * \rho_T_Energy^2 * \\ & C_T_Energy^2 * w_T_Energy^2) / ((\rho_T_Energy * \\ & C_T_Energy * u_T_Energy)^2 + (\rho_T_Energy * \\ & C_T_Energy * v_T_Energy)^2 + (\rho_T_Energy * \\ & C_T_Energy * w_T_Energy)^2 + eps) \end{aligned}$
res_T_Energy y	Equation residual for T	$\begin{aligned} & -kxx_T_Energy * Txx - kxy_T_Energy * Txy - \\ & kxz_T_Energy * Txz + Tx * \rho_T_Energy * \\ & C_T_Energy * u_T_Energy - kyx_T_Energy * Tyx - \\ & kyy_T_Energy * Tyy - kyz_T_Energy * Tyz + Ty * \\ & \rho_T_Energy * C_T_Energy * v_T_Energy - \\ & kzx_T_Energy * Tzx - kzy_T_Energy * Tzy - \\ & kzz_T_Energy * Tzz + Tz * \rho_T_Energy * \\ & C_T_Energy * w_T_Energy - Q_T_Energy \end{aligned}$
res_sc_T_Energy	Shock capturing residual for T	$\begin{aligned} & Tx * \rho_T_Energy * C_T_Energy * u_T_Energy + Ty * \\ & \rho_T_Energy * C_T_Energy * v_T_Energy + Tz * \\ & \rho_T_Energy * C_T_Energy * w_T_Energy - \\ & Q_T_Energy \end{aligned}$
da_T_Energy	Total time scale factor, T	$Dts_T_Energy * \rho_T_Energy * C_T_Energy$
abspO2x_Gas	grad(pO2)	$\sqrt{pO2x^2 + pO2y^2 + pO2z^2}$
absga3x_Gas	ga3x	$\sqrt{ga3x^2 + ga3y^2 + ga3z^2}$

10.2.2. Subdomain 2-3

Name	Description	Expression
abshpx_Water	$ \text{grad}(\text{hp}) $	
absgalx_Water	$ \text{galx} $	
grad_T_x_Energy	Temperature gradient, T, x component	T_x
dflux_T_x_Energy	Conductive heat flux, T, x component	$-k_{xx} T_{\text{Energy}} * T_x - k_{xy} T_{\text{Energy}} * T_y - k_{xz} T_{\text{Energy}} * T_z$
cflux_T_x_Energy	Convective heat flux, T, x component	$\rho T_{\text{Energy}} * C_T * T * u_T_{\text{Energy}}$
tflux_T_x_Energy	Total heat flux, T, x component	$dflux_T_x_Energy + cflux_T_x_Energy$
grad_T_y_Energy	Temperature gradient, T, y component	T_y
dflux_T_y_Energy	Conductive heat flux, T, y component	$-k_{yx} T_{\text{Energy}} * T_x - k_{yy} T_{\text{Energy}} * T_y - k_{yz} T_{\text{Energy}} * T_z$
cflux_T_y_Energy	Convective heat flux, T, y component	$\rho T_{\text{Energy}} * C_T * T * v_T_{\text{Energy}}$
tflux_T_y_Energy	Total heat flux, T, y component	$dflux_T_y_Energy + cflux_T_y_Energy$
grad_T_z_Energy	Temperature gradient, T, z component	T_z
dflux_T_z_Energy	Conductive heat flux, T, z component	$-k_{zx} T_{\text{Energy}} * T_x - k_{zy} T_{\text{Energy}} * T_y - k_{zz} T_{\text{Energy}} * T_z$
cflux_T_z_Energy	Convective heat flux, T, z component	$\rho T_{\text{Energy}} * C_T * T * w_T_{\text{Energy}}$
tflux_T_z_Energy	Total heat	$dflux_T_z_Energy + cflux_T_z_Energy$

energy	flux, T, z component	
beta_T_x_Energy	Convective field, T, x component	$\rho_T_Energy * C_T_Energy * u_T_Energy$
beta_T_y_Energy	Convective field, T, y component	$\rho_T_Energy * C_T_Energy * v_T_Energy$
beta_T_z_Energy	Convective field, T, z component	$\rho_T_Energy * C_T_Energy * w_T_Energy$
grad_T_Energy	Temperature gradient, T	$\sqrt{grad_T_x_Energy^2 + grad_T_y_Energy^2 + grad_T_z_Energy^2}$
dflux_T_Energy	Conductive heat flux, T	$\sqrt{dflux_T_x_Energy^2 + dflux_T_y_Energy^2 + dflux_T_z_Energy^2}$
cflux_T_Energy	Convective heat flux, T	$\sqrt{cflux_T_x_Energy^2 + cflux_T_y_Energy^2 + cflux_T_z_Energy^2}$
tflux_T_Energy	Total heat flux, T	$\sqrt{tflux_T_x_Energy^2 + tflux_T_y_Energy^2 + tflux_T_z_Energy^2}$
cellPe_T_Energy	Cell Peclet number, T	$h * \sqrt{beta_T_x_Energy^2 + beta_T_y_Energy^2 + beta_T_z_Energy^2} / Dm_T_Energy$
Dm_T_Energy	Mean diffusion coefficient, T	$(kxx_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * u_T_Energy^2 + kxy_T_Energy * u_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * v_T_Energy + kxz_T_Energy * u_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * w_T_Energy + kyx_T_Energy * v_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * u_T_Energy + kyy_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * v_T_Energy^2 + kyz_T_Energy * v_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * w_T_Energy + kzx_T_Energy * w_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * u_T_Energy + kzy_T_Energy * w_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * v_T_Energy + kzz_T_Energy * \rho_T_Energy^2 * C_T_Energy^2 * w_T_Energy^2) / ((\rho_T_Energy * C_T_Energy * u_T_Energy)^2 + (\rho_T_Energy * C_T_Energy * v_T_Energy)^2 + (\rho_T_Energy * C_T_Energy * w_T_Energy)^2 + eps)$
res_T_Energy	Equation residual for T	$-kxx_T_Energy * T_{xx} - kxy_T_Energy * T_{xy} - kxz_T_Energy * T_{xz} + T_x * \rho_T_Energy *$

		$ \begin{aligned} &C_T_Energy * u_T_Energy - k_{yx_T_Energy} * T_{yx} - \\ &k_{yy_T_Energy} * T_{yy} - k_{yz_T_Energy} * T_{yz} + T_y * \\ &\rho_T_Energy * C_T_Energy * v_T_Energy - \\ &k_{zx_T_Energy} * T_{zx} - k_{zy_T_Energy} * T_{zy} - \\ &k_{zz_T_Energy} * T_{zz} + T_z * \rho_T_Energy * \\ &C_T_Energy * w_T_Energy - Q_T_Energy \end{aligned} $
res_sc_T_Energy	Shock capturing residual for T	$ \begin{aligned} &T_x * \rho_T_Energy * C_T_Energy * u_T_Energy + T_y * \\ &\rho_T_Energy * C_T_Energy * v_T_Energy + T_z * \\ &\rho_T_Energy * C_T_Energy * w_T_Energy - \\ &Q_T_Energy \end{aligned} $
da_T_Energy	Total time scale factor, T	$Dts_T_Energy * \rho_T_Energy * C_T_Energy$
abspO2x_Gas	grad(pO2)	$\sqrt{pO2x^2 + pO2y^2 + pO2z^2}$
absga3x_Gas	ga3x	$\sqrt{ga3x^2 + ga3y^2 + ga3z^2}$

APPENDIX III

To test the basic coding of the water flow equation in the Beach-MPT model, the model calculations were compared to two simple, analytical solutions shown here.

Water Flow in a Saturated, Uniform Sand Column

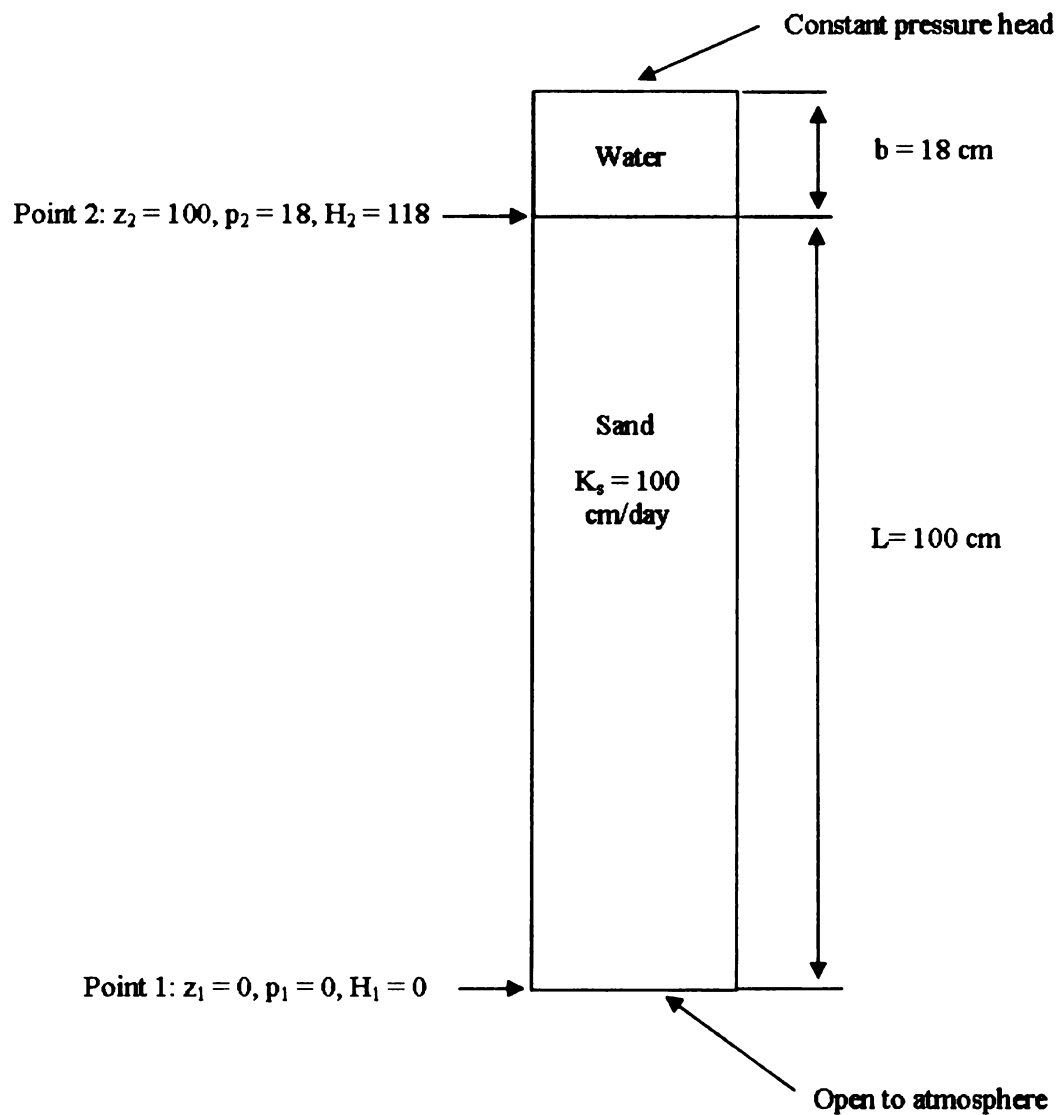


Figure A.1. Uniform, saturated soil column used in the first test demonstrating the proper coding of the water flow equation in the Beach-MPT model.

The first test uses the sand column shown in Figure A1. The saturated conductivity (K_s) is assumed constant everywhere in the 100 cm long soil column and a constant pressure head of 18 cm is applied to the upper surface. Below I detail how Darcy's law is used to calculate the hydrostatic pressure (p) at any location in the soil column and these values are compared to the hydrostatic pressure predicted by the Beach-MPT model.

To calculate the hydrostatic pressure at a location (z) in the sand column Darcy's law (Eq. A.1) is applied between the arbitrary point (z) where p is unknown and the bottom of the column where $z = 0$ and $p = 0$. This gives Eq A.2.

$$J_w = -K_s \frac{(H_2 - H_1)}{(z_2 - z_1)} \quad (\text{A.1})$$

$$J_w = -K_s \frac{(p + z)}{z} \quad (\text{A.2})$$

We can also apply Darcy's law across the entire column because we know the flux (J_w) in terms of the pressure at $z = L$ ($p = b$), giving equation A.3.

$$J_w = -K_s \frac{(b + L)}{L} \quad (\text{A.3})$$

Setting A.2 equal to A.3 and solving for p we find that

$$p = \frac{b * z}{L} \quad (\text{A.4})$$

Using equation A.4 we can calculate the hydrostatic pressure at any point (z) and compare this to the Beach-MPT prediction.

At $z = 40$ cm, using equation A.4, the hydrostatic pressure p is 7.2 cm.

At $z = 75$ cm, $p = 13.5$ cm.

At $z = 23$ cm, $p = 4.14$ cm

Figure A.2 shows the Beach-MPT model predictions, which match those calculated analytically.

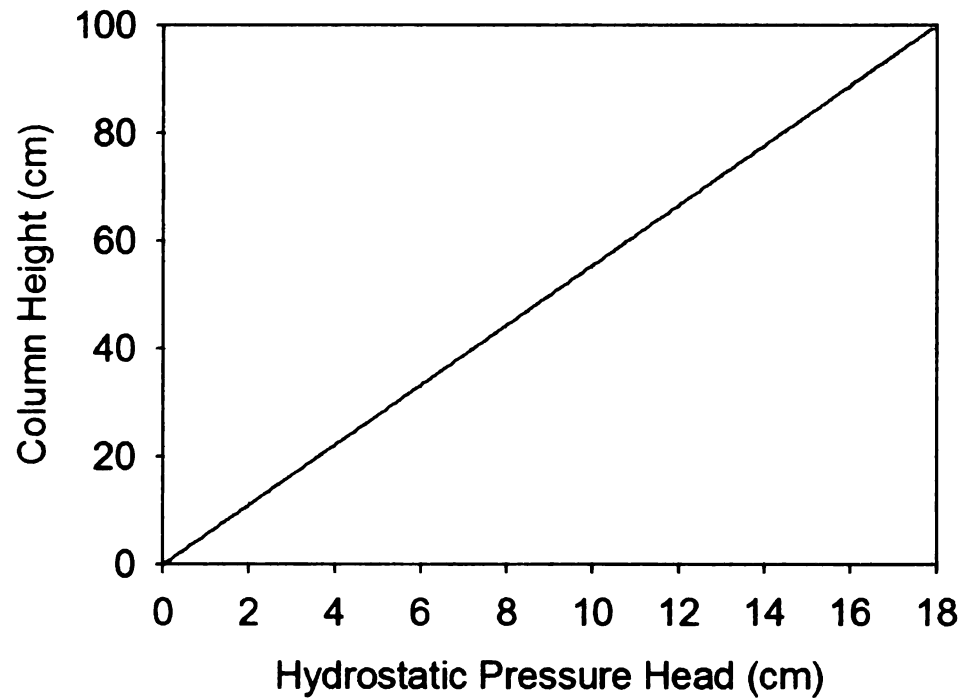


Figure A.2. The hydrostatic pressure head distribution within the sand column shown in Figure A.1 as calculated by the Beach-MPT model. The distribution matches exactly the hydrostatic pressure head calculated analytically using Darcy's law and equation A.4.

Water Flow in Saturated Layered Soil

A second test of the coding of water flow in Beach-MPT was performed using the saturated, layered soil column shown in Figure A.4.

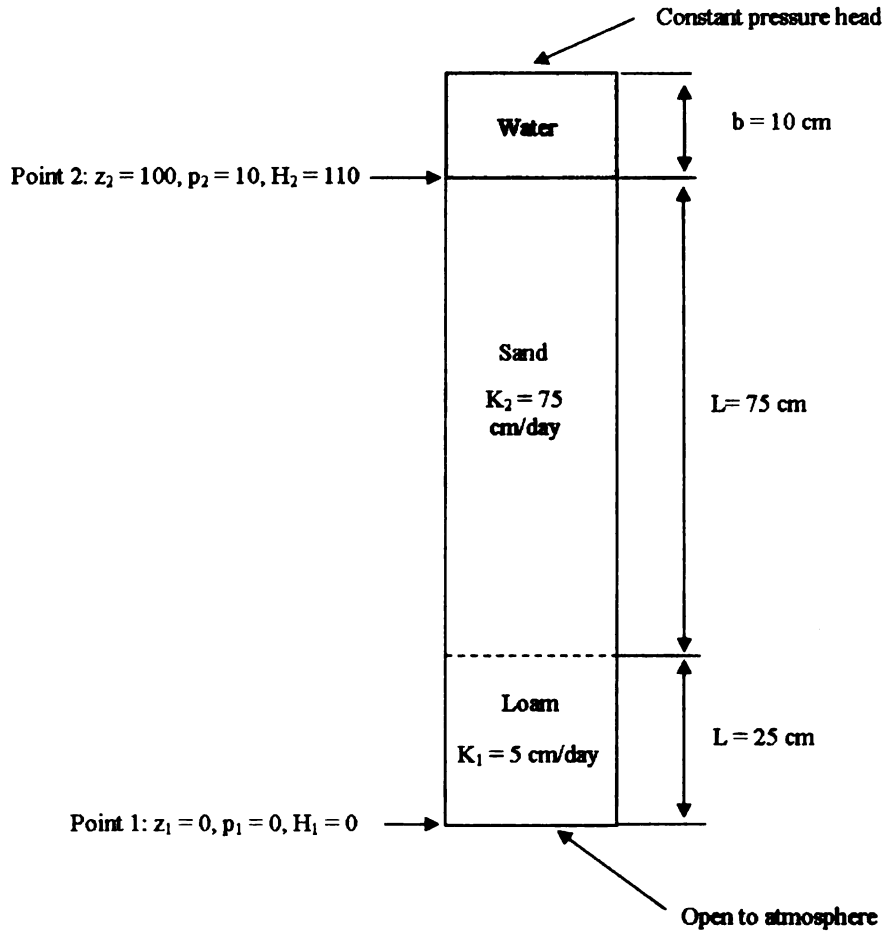


Figure A.3. Saturated, layered soil column used in the second test demonstrating the proper coding of the water flow equation in the Beach-MPT model.

A layered vertical soil column consists of 25 cm of a loam soil with a saturated hydraulic conductivity of $K_1 = 5 \text{ cm/day}$ overlain by 75 cm of a sandy soil with a saturated hydraulic conductivity of $K_2 = 25 \text{ cm/day}$. The top of the column has water ponded to a constant height of 10 cm above the column, and the bottom is open to the atmosphere. To test the coding of the water flow portion of the Beach-MPT model I calculated the hydrostatic pressure distribution in the column using Darcy's law and compared the results to the Beach-MPT predictions.

To solve this problem by hand it is first necessary to calculate an effective saturated hydraulic conductivity for the entire column, using equation A5.

$$K_{eff} = \frac{\sum_{J=1}^N L_J}{\sum_{J=1}^N \left(\frac{L_J}{K_J} \right)} \quad (A.5)$$

where L_J is the height of layer J and K_J is the hydraulic conductivity of layer J .

$$K_{eff} = \frac{25 + 75}{\frac{25}{5} + \frac{75}{25}} \quad (A.6)$$

$$K_{eff} = 12.5 \text{ cm / day}$$

We can use this value and apply Darcy's law to the whole column to calculate the flux from the bottom of the column. To do this I assumed point 2 is the upper surface of the column $z_2 = 100$, $p_2 = 10$, and $H_2 = 110$ and point 1 is the bottom boundary, $z_1 = 0$, $p_1 = 0$, and $H_1 = 0$.

$$Flux = -\frac{K_{eff}}{100} (110 - 0) \quad (A.7)$$

$$Flux = -13.75 \text{ cm / day}$$

Now that we know the bottom flux we can apply Darcy's law to portion of the column and calculate the hydrostatic pressure at any point in the column such as the interface between the two soil layers.

$$J_w = K_1 \frac{(H_3 - H_1)}{(z_3 - z_1)} \quad (A.8)$$

We'll specify the interface as point 3 ($H_3 = p_3 + 25$) and the bottom of the column remains point 1 ($H_1 = 0$). The equation is then written as

$$-13.75 = -\frac{5}{25} (p_3 + 25) \quad (A.9)$$

Solving for p_3 gives a hydrostatic pressure head of 43.75 cm at the interface between the two soil types. Complete agreement between the analytical solution and the Beach-MPT model at all other locations as well.

This can be compared to the prediction made by the Beach-MPT model simulating the same soil column. The results are shown in figure A.4. The Beach-MPT model predicts the hydrostatic pressure head at the interface between the two soil types is also 43.75 cm. The hydrostatic pressures predicted by the model matches those calculated analytically at all other points as well.

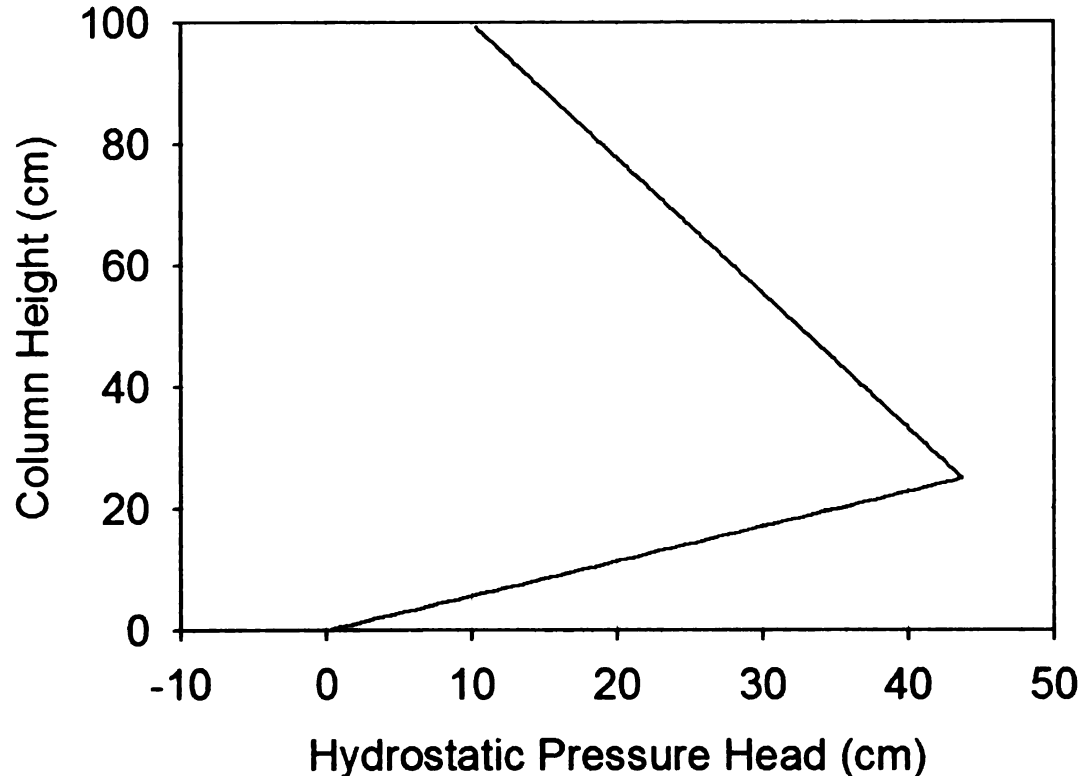


Figure A.4. The hydrostatic pressure head distribution within the sand column shown in Figure A.4 as calculated by the Beach-MPT model. The distribution matches exactly the hydrostatic pressure head calculated analytically using Darcy's law and equation A.9.

These two tests demonstrate that the equations for calculating soil water flow have been properly coded into the Beach-MPT model.

BIBLIOGRAPHY

- Ackerman, R.A. 1977. The respiratory gas exchange of sea turtle nests (*Chelonia*, *Caretta*). *Resp. Physiol.* 31:19-38.
- Ackerman, R.A. 1980. Physiology and ecological aspects of gas exchange by sea turtle eggs. *Am. Zool.* 20:275-283.
- Ackerman, R.A. 1981. Growth and gas exchange of embryonic sea turtles (*Chelonia*, *Caretta*). *Copeia* 757-765.
- Ackerman, R.A. 1997. The nest environment and the embryonic development of sea turtles. Pp. 83-106 *in* The Biology of Sea Turtles, (P.L. Lutz and J.A. Musick, eds). CRC Press, New York.
- Battino, R. 1980. Oxygen and Ozone: IUPAC Solubility Data Series Vol 7. Pergamon Press, New York.
- Bear, J. 1979. Hydraulics of Groundwater. McGraw-Hill Inc, Israel.
- Bird, R.B., W.E. Stewart, E.N. Lightfoot. 2002. Transport Phenomena, 2nd Ed. John Wiley and Sons, New York.
- Brutsaert, W. 1982. Evaporation into the atmosphere: Theory, history, and applications. D. Reidel, Boston.
- Campbell, G.S., J.D. Jungbauer, Jr., W.R. Bidlake, and R.D. Hungerford. 1994. Predicting the effect of temperature on soil thermal conductivity. *Soil Sci.* 158:307-313.
- Campbell, G.S., and J.M. Norman. 1998. An Introduction to Environmental Biophysics, 2nd ed. Springer Science, New York.
- Carslaw, H.S., and J.C. Jaeger. 1986. Conduction of Heat in Solid, 2nd ed. Oxford Science Pub, England.
- Clusella-Trullas S. 2000. Energetics during Hatchling Dispersal and the Environment of Natural and Hatchery Nests of the Olive Ridley Sea Turtle (*Lepidochelys olivacea*) at Nancite Beach, Costa Rica. M.S. Thesis. Purdue University, Fort Wayne, Ind.
- Crain, D.A., A.B. Bolten, K.A. Bjorndal. 1995. Effects of beach nourishment on sea turtles: Review and research initiatives. *Restoration Ecology* 3: 95-104.

- Crank, J. 1980. The Mathematic of Diffusion. Oxford Science Pub., England
- de Vries, D.A. 1963. Thermal properties of soils, in Physics of Plant Environment, Van Wijk, W.R. ed. North Holland Pub., Amsterdam.
- Davis, R.A., M.V. FitzGerald, J. Terry. 1999. Turtle nesting on adjacent nourished beaches with different construction styles: Pinellas County, Florida. J. Coastal Res. 15: 111-120.
- Drake, D.L. and J.R. Spotila. 2002. Thermal tolerances and the timing of sea turtle hatchling emergence. J. Therm. Biol. 27: 71-81.
- Fernandez M., L.M. Pardo and J.A. Baeza. 2002. Patterns of oxygen supply in embryo masses of brachyuran crabs throughout development: the effect of oxygen availability and chemical cues in determining female brooding behavior. Mar. Ecol. Prog. Ser. 245: 181-190.
- Freeze, R.A., and J.A. Cherry. 1979. Groundwater. Prentice-Hall, Inc. New Jersey.
- Gatti S., T. Brey, W.E.G. Muller, O. Heilmayer and G. Holst. 2002. Oxygen microoptodes: a new tool for oxygen measurements in aquatic animal ecology. Marine Biology 140: 1075-1085.
- GCE-LTER Data Portal. 2006. UGA Marine Institute Climate Monitoring. http://gce-lter.marsci.uga.edu/portal/ugami_climate.htm. Downloaded 22 November 2006.
- Glud R.N., I. Klimant, G. Holst, O. Kohls, V. Meyer, M. Kuhl and J.K. Gunderson. 1999. Adaptation, test and *in situ* measurements with O₂ microopt(r)odes on benthic landers. Deep-sea Research Part 1- Oceanographic Research Papers 46: 171-183.
- Glud R.N., J.K. Gunderson and N.B. Ramsing. 2000. Electrochemical and optical oxygen microsensors for *in situ* measurements. pp. 19-73 in *In situ* monitoring of Aquatic Systems: Chemical Analysis and Speciation. J. Buffle and G. Horvai eds. John Wiley and Sons.
- Hewavisenithi, S. and C.J. Parmenter. 2001. Influence of incubation environment on the development of the flatback turtle (*Natator depressus*). Copeia 668-682.
- Honarvar, S., M.P. O'Conner, and J.R. Spotila. 2007. Density-dependent effects on hatching success in olive ridley sea turtles. Proceedings of SICB Annual Meeting.
- Horn, R. and T. Baumgartl. 2002. Dynamic properties of soils. Pp. 17-48 in Soil Physics Companion (A.W. Warrick, ed.). CRC Press, New York.

- Incropera, F.P. and D.P. DeWitt. 2002. Introduction to Heat Transfer, 4th ed. John Wiley and Sons, New York.
- IPCC. 2001. Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report. Houghton, J.T., Y. Ding, D.J. Diggs, M, Noguer, P.J. van der Linden, X. Dai, K. Maskell, and C.A. Johnson (eds.). Cambridge University Press. Cambridge, UK and New York, NY, USA. 881pp.
- IUCN 2004. 2004 IUCN Red List of Threatened Species. <http://www.iucnredlist.org>. Downloaded on 2 February 2005.
- Kaliakin, V.N. 2002. Introduction to Approximate Solution Techniques, Numerical Modeling, and Finite Element Methods. Marcel Decker, Inc. New York, USA.
- Kam, Y. 1993. Physiological effects of hypoxia on metabolism and growth of turtle embryos. *Resp. Physiol.* 92: 127-138.
- Klimant I., V. Meyer and M. Kuhl. 1995. Fiber-optic oxygen microsensors, a new tool in aquatic biology. *Limnol. Oceanogr.* 40: 1159-1165.
- Kraemer, J. and R. Bell. 1980. Rain-induced mortality of eggs and hatchlings of loggerhead sea turtles (*Caretta caretta*) on the Georgia coast. *Herpetologica* 36: 72-77.
- Krieth, F. and M.S. Bohn. 1993. Principles of Heat Transfer, 5th ed. West Publishing Co., New York.
- Logan, D.L. 2002. A First Course in the Finite Element Method, 3rd ed. Brooks/Cole, USA.
- Maloney, J.E., C. Darian-Smith, Y. Takahashi, C.J. Limpus. 1990. The environment for development of the embryonic loggerhead turtle (*Caretta caretta*) in Queensland. *Copeia* 378-387.
- Matsuzawa, Y., K. Sato, W. Sakamoto, K.A. Bjorndal. 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. *Mar. Biol.* 140:639-646.
- McCulloch, A.D. and G. Huber. 2002. Integrative biological modeling in silico, in '*In silico*' simulation of biological processes, G. Bock and J.A. Goode, eds. John Wiley and Sons, UK.

- Meylan, A., B. Schroeder, A. Mosier. 1995. Sea turtle nesting activity in the State of Florida. Florida Marine Research Publications 52:1-51.
- Miller, K., G.C. Packard, M.J. Packard. 1987. Hydric conditions during incubation influence locomotor performance of hatchling snapping turtles. J. Exp. Biol. 127:401-412.
- Miller, J.D. 1997. Reproduction in sea turtles. Pp. 51-82 in The Biology of Sea Turtles (P.L. Lutz and J.A. Musick, eds.). CRC Press, New York.
- Monteith, J.M., and M.H. Unsworth. 1990. Principles of Environmental Physics. Elsevier Limited, UK.
- Mortimer, J.A. 1990. The influence of beach sand characteristics on the nesting behavior and clutch survival of green turtles (*Chelonia mydas*). Copeia 802-817.
- Mrosovsky, N., C.L. Yntema. 1980. Temperature dependence of sexual differentiation in sea turtles: implications for conservation practices. Biol. Conserv. 18:271-280.
- Oreskes, N., K. Shrader-Frechette, K. Belitz. 1994. Verification, Validation, and Confirmation of Numerical Models in the Earth Sciences. Science 263:641-645.
- Peck, S.L. 2004. Simulation as experiment: a philosophical reassessment for biological modeling. TREE 19: 530-534.
- Penman, H.L. 1940. Gas and vapor movements in soil. I. The diffusion of vapors through porous solids. J. Agr. Sci. 30: 437-462.
- Polley, S.L., Snyder, O.P. and Kotnour, P. 1980. A compilation of thermal properties of foods. Food Tech. 11:76-94
- Ralph C.R., R.D. Reina, B.P. Wallace, P.R. Sotherland, J.R. Spotila and F.V. Paladino. 2005. Effect of egg location and respiratory gas concentrations on developmental success in nests of the leatherback turtle, *Dermochelys coriacea*. Aust. J. Zool. 53: 289-294.
- Rhen, T., J.W. Lang. (1995). Phenotypic plasticity for growth in the common snapping turtle: Effects of incubation temperature, clutch and their interaction. Am. Nat. 146:726-747.

- Rimkus, T.A., and R.A. Ackerman. 1995. The impact of beach renourishment on the hydric climate of sea turtle nesting beaches along the Atlantic coast of Florida. Pp. 97-102 in *Proceedings of the 12th Annual Workshop on Sea Turtle Biology and Conservation* (J.I. Richardson and T.H. Richardson). NOAA Technical Memorandum, Florida.
- Romanoff, A.L. and A.J. Romanoff. 1949. *The avian egg*. John Wiley and Sons, New York.
- Schaap, M.G. and F.J. Leij. 2000. Improved prediction of unsaturated hydraulic conductivity with the Mualem-van Genuchten model. *Soil Sci. Soc. Am. J.* 64: 843-851.
- Seymour, R.S., and J.D. Roberts. 1991. Embryonic respiration and oxygen distribution in foamy and nonfoamy egg masses of the frog *Limnodynastes tasmaniensis*. *Physiol. Zool.* 64: 1322-1340.
- Seymour, R.S. and M.K. Seely. 1996. The respiratory environment of the Namib Desert Golden Mole. *J. Arid Environ.* 32: 453-461.
- Skopp, J.M. 2002. Physical properties of primary particles, in *Soil Physics Companion*, A.W. Warrick, ed. CRC Press, Boca Raton, pp 1-16.
- Steinitz, M.J., M. Salmon, J. Wyneken. 1998. Beach renourishment and loggerhead turtle reproduction: A seven year study at Jupiter Island, Florida. *J. Coast. Res.* 14: 1000-1013.
- Titus, J.G. 1998. Rising seas, coastal erosion, and the takings clause: How to save wetlands and beaches without hurting property owners. *Maryland Law Review.* 57: 1279-1399.
- Titus, J.G. and C. Richman. 2001. Maps of lands vulnerable to sea level rise: Modeled elevations along the U.S. Atlantic and Gulf coasts. *Climate Research.* 18: 205-228.
- Tracy, C.R., G.C. Packard, M.J. Packard. 1978. Water relations of chelonian eggs. *Physiol. Zool.* 51: 378-387.
- Trindell, R.N., D. Arnold, K. Moody, B. Morford. 1998. Nourished beaches and marine turtle nesting in Florida: An evaluation of recent projects. *Proc. 18th Internat. Symp. Sea Turt. Biol. Conserv.* 217-218.
- Urban-Malinga, B. and K.W. Opalinski. 1999. Vertical zonation of the total, benthic, and abiotic oxygen consumption on a Baltic sandy beach. *Oceanological Studies* 28: 85-96.

- van Genuchten, M.Th. 1980. A closed-form equation for predicting the hydraulic conductivity of unsaturated soils. *Soil Sci. Soc. Am. J.* 4:892-898.
- Wallace B.P., P.R. Sotherland, J.R. Spotila, R.D. Reina, B.F. Franks and F.V. Paladino. 2004. Biotic and abiotic factors affect the nest environment of embryonic leatherback turtles, *Dermochelys coriacea*. *Physiol. Biochem. Zool.* 77: 423-432.
- Warkentin K.M., I. Gomez-Mestre and J.G. McDaniel. 2005. Development, surface exposure, and embryo behavior affects oxygen levels in eggs of the red-eyed treefrog, *Agalychnis callidryas*. *Physiol. Biochem. Zool.* 78: 956-966.
- Weiss, R.F. 1970. The solubility of nitrogen, oxygen, and argon in water and sea water. *Deep Sea Res.* 17: 721-735.
- Yntema C.L. and N. Mrosovsky. 1980. Sexual differentiation in hatchling loggerhead (*Caretta caretta*) incubated at different controlled temperatures. *Herpetologica* 36: 33-36.

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