AN INDIVIDUAL BASED LARVAL DISPERSION MODEL FOR THE HAWAIIAN HAWKSBILL SEA TURTLE IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

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The Hawaiian hawksbill sea turtle (*Eretmochelys imbricata*) is a critically endangered species, with an observed adult female population of approximately 6-20, nesting each year at known nesting sites on the big island of Hawaii. To create efficient management strategies for the survival of the species, a better understanding of habitat selection in the early stages of the hawksbill’s life is needed. We investigate an individual-based, advection-diffusion, larval transport model, as it applies to the Hawaiian hawksbill population in the greater Hawaiian Archipelago. The model considers the release time and location, size, foraging behavior, and geographic location of the hawksbill hatchlings first three years of life, over a six year period of study, and how their habitat selection may be affected by the geostrophic currents, sea surface temperatures, and chlorophyll-a concentrations that they encounter. Results indicate that the inclusion of simple behavior rules significantly ($p < 0.01$) increases retention, exposure to higher sea surface temperatures, and exposure to higher chlorophyll-a concentrations. Statistical analysis suggests a need to consider all three environmental parameters of the ocean surface currents, sea surface temperature, and chlorophyll-a concentration to better predict the resulting distribution of the individuals.
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This adventure with Sea Turtles began on a trip to Maruata, Mexico. I had the privilege of spending a week there seeing firsthand the relationship that a small community can have with wildlife conservation. I spent my evenings there passing an English/Spanish dictionary back and forth with a young man who shared with me the things that he had learned about the turtles. At night we would all watch as the nesting females would come ashore and lay their nests. My last day there, a stranded and apparently hooked Leatherback washed up on shore. I was beginning to think. On the flight home, as well as the weeks that followed, I was bombarded with information related to the plight of the sea turtles. Following this I transferred to Humboldt State as an undergraduate, was introduced to the Masters in Mathematical Modeling program, and the pieces just seemed to fit.

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Summary of Distribution Models
INTRODUCTION

With the exception of the Arctic, sea turtles inhabit all of the earth’s oceans. The life cycle of sea turtles consists of a sequence of migrations. From terrestrial nests on ocean-facing beaches, hatchlings make their way to the ocean, eventually swimming to the circulatory ocean surface currents which take them into the pelagic ocean. As juveniles and subadults, these turtles then migrate to shallow water feeding areas located up to thousands of miles from their home nesting sites. Adult females migrate back to their natal beaches to nest, after which they return to their own feeding areas. The study of sea turtles provides an opportunity to understand how the oceans are navigated by such species, and the role that the environmental conditions of the ocean play in such movement.

All seven of the earth’s sea turtle species are listed as endangered or threatened as defined by the 1973 Endangered Species Act (U.S. Congress, 1973). The sea turtle population has continued to plummet, and according to Minasian (2004), some species of sea turtles may face extinction within the next 10 years. One such species facing extinction due to human presence is the hawksbill (*Eretmochelys imbricata*). In the Pacific, the hawksbill is harvested for meat, eggs and tortoiseshell, as well as having incidental mortalities due to commercial fisheries (NMFS, 1998). The Hawaiian population of hawksbill is highly endangered, with a breeding population of approximately 20-30 adult females total (Seitz, et al., 2006, 2008). However this number may be lower, with many of the females nesting at multiple sites annually. Threats to the recovery of this population include the loss of nesting and foraging habitat, and nest predation. In the marine environment, Hawaiian hawksbills are also subject to near-shore
tourist development such as resorts, marinas, and aquatic recreational activities (NMFS, 1998). Very little information on habitat use by Hawaiian hawksbills is available. Recognizing potential habitat use during the turtles’ oceanic stage could then help government agencies such as the National Oceanic and Atmospheric Administration (NOAA) to understand possible fishery interactions as well as probable juvenile, neritic (i.e. post-oceanic) habitat locations.

Our study is focused on the first three years of the hawksbill’s life. Due to the small population of the hawksbill, in some cases we will need to access data for turtles biologically similar to the hawksbill, (i.e. green and loggerhead). Particularly this is true during the oceanic stage, for which very little information is currently available.

Figure 1: Primary nesting locations of the Hawaiian hawksbill, Halape and Apua Point.
In Hawaii, hawksbills primarily nest on beaches of the Big Island, with most of these sites located along the southern coast. Two of these sites Halape and Apua Point (Figure 1) are in the Hawaii Volcanoes National Park (Balazs et al., 1992, Katahira et al., 1994). Since 1989, a partnership between Hawaii Volcanoes National Park and U.S. Fish and Wildlife Service has been in place to protect and monitor these and other beaches. By 2006 as a result, a total of 73 nesting turtles had been tagged, 618 nests had been protected, and over 67,000 hatchlings had reached the Pacific Ocean since the program began (Seitz, et al., 2006).

Nesting hawksbills lay their eggs beneath the sand along the shoreline. Nests incubate for about 60 days prior to hatching. The average hawksbill clutch size varies amongst the literature, ranging from 130 (Maragos, 1991) to 150 eggs per clutch (Corliss et al., 1989). The mean hatching success on most unharmed nests is approximately 80% (Witzell, 1983, Corliss et al., 1989), but a wide range of success is known to occur (NMFS, 1998). Although the species has varying breeding seasons, the hatching season for the Hawaiian hawksbill population extends from July to December each year (Seitz, et al., 2006, 2008). Upon hatching, a clutch of hawksbill hatchlings will reach the surface of the sand and scurry towards the shore. Hawksbill hatchlings are preyed upon by various species of crabs and fish (Witzell, 1983).

The “lost year” has been a thorn in the sides of sea turtle researchers since the term was first coined by Archie Carr in the 1980s. Observations of early juvenile hawksbills in the pelagic environment are quite rare. *Sargassum*, is a genus of brown seaweed, abundant throughout the globe. Research suggests that in the time following the initial frenzy to reach the deep ocean, hawksbill hatchlings actively pursue floating mats of *Sargassum*, where they will remain motionless for extended periods of time (Carr, 1987). The juveniles are assumed to remain pelagic until they are then observed in near
shore habitats, by which time they are measuring in size of at least 26 cm straight carapace length (SCL) (Snover, et al., 2009).

Very little is known of hatchling behavior for the Pacific population of hawksbill. Although during this “lost” first year their whereabouts are unknown (Carr, 1986), the direction and velocity of the ocean currents near Pacific nesting sites should suggest the direction and distance traveled by the hawksbill hatchlings (NMFS, 1998), perhaps due to the hatchlings’ limited swimming ability that keeps them passively in the ocean currents.

The Ocean Surface Current Analyses – Real time project (OSCAR) is a collaboration of various National Oceanic and Atmospheric Administration (NOAA), Florida universities, and other research facilities. The OSCAR project provides regularly updated satellite-based maps of the ocean surface currents at a detailed resolution. The satellite data is initially acquired by the 2001 launched Jason-1 satellite, in the form of altimeter surface height data, and vector wind data. The data are then processed to provide estimated ocean surface current velocities, in vector form with 5 day averages and a spatial resolution of 1 degree of the earth in units of \( m/s^2 \) (Bonjean, Lagerloef, 2002).

Evidence indicates that the hawksbill turtle is an omnivorous scavenger (Witzell, 1998). Although little is known of the diet of juvenile hawksbills, captive hatchlings have been observed nibbling on seaweed (Deraniyagala, 1930, 1939). Many pelagic records for early hawksbill juveniles indicate an association with floating mats of \textit{Sargassum} seaweed (Carr, 1987, Redfoot et al., 1985, Limpus et al., 1994, Parker, 1995). \textit{Sargassum} was also found in the digestive tracts of four juvenile hawksbills that were stranded dead on Florida beaches (Meylan, 1984).

Recent studies involving remotely sensed data (i.e. satellite tracking) have indicated links between the habitat selection of juvenile loggerhead, a related species, to
concentrations of chlorophyll-a, as well as sea surface temperature (SST) (Polovina, et al., 2000, 2006). Satellite tracking of 43 juvenile loggerheads in the western North Pacific identified a foraging hotspot for Pacific loggerheads, in what is called the Kuroshio Extension Current (KEC), which is characterized by warm and cold surface currents during the fall, winter and spring (Polovina, 2006). It is during this time that the KEC waters contain high surface chlorophyll-a. The loggerheads often stay in this region feeding for months at a time. They are observed moving north during the summer up to 600 km from the center of the KEC into what is known as the Transition Zone Chlorophyll Front. Nine juvenile loggerhead turtles were tracked by satellite telemetry over the latitudinal band of about 28°–40°N (Polovina, Kobayashi, 2000). Against prevailing currents the turtles tended towards fronts characterized by SST between 17°C and 20°C. This appears to explain why incidental catch rates of loggerheads in the Hawaii longline fishery are highest when lines are set at these temperatures (Polovina, Kobayashi, 2000). More recently, McCarthy et al. (2010) observed, for pelagic loggerhead in the North Atlantic, foraging behavior in chlorophyll-a frontal zones. All ten of the tracked individuals were shown to forage along edges of areas with high chlorophyll-a.

For over 20 years the Advanced Very High Resolution Radiometer (AVHRR) Pathfinder SST Program has provided scientists with remotely sensed SST data. By 2009 the program had become a joint effort between the National Oceanic Data Center (NODC) and the University of Miami. AVHRR SST data is currently available with a resolution of up to 1 km on a daily time scale. The NASA Goddard Earth Sciences Distributed Active Archive Center (GES DAAC) provides Moderate Resolution Imaging Spectroradiometer (MODIS) science data products. Ocean products include
concentrations of chlorophyll, pigment and coccolithophores, fluorescence, absorptions and primary productivity (Savtchenko, et al., 2004). The chlorophyll-a concentration data is provided at a resolution of 1 degree of the earth, on a weekly scale, measured in $mg/m^3$.

Very little is known regarding growth rates of juvenile hawksbill. Age and growth estimates have been based on growth rates of benthic juveniles (Boulan, 1994). However growth rates vary geographically amongst populations. More recently the application of Skeletochronology has allowed scientists to estimate carapace lengths using growth marks within the bone leading to estimates of growth rates for the Hawaiian hawksbill (Snover, et al., 2009).

At some point in their maturation, juvenile hawksbills switch from a pelagic surface feeder, to a benthic reef feeder (Limpus, 1992). It is not clear when and how a juvenile chooses such a suitable benthic feeding area. However, Limpus (1992) observed a minimum size of 35 cm curved carapace length (CCL) for juvenile hawksbills located at a specific southern Great Barrier Reef feeding area, near Australia. An approximate minimum size of 25 cm CCL was calculated for a population of juvenile foraging hawksbills at Mona Island (Puerto Rico), with a single modal range of 23.9 – 59.3 cm for 42 of the 48 wild-caught individuals, the remaining six animals being significantly larger (63.1 – 87.3 cm CCL) (van Dam, Diez, 1994).
MODELING EFFORTS

Over the last thirty years, researchers have modeled sea turtle populations and their response to varying management strategies. However, an effective strategy has yet to be found and adopted internationally to address the issue of dangerously declining sea turtle populations.

Individual-based modeling is a recent and powerful tool in population modeling. By looking at the way individuals of a species interact with each other as well as their environment, a greater understanding of how the ecological system works can be discovered. Such models can make better predictions for populations with smaller numbers as large scale deterministic models (e.g. integrodifference) may fail. Individual-based models (IBM) have been used to study other species of sea turtles. An IBM pilot study for the life cycle of the loggerhead sea turtle suggests the following parameters to be considered: temperature preferences (for habitat classification), metabolic rates (bioenergetics), sensory abilities (environmental interactions), feeding, diet & gut function (bioenergetics), swimming speed (bioenergetics/movement), growth rates (bioenergetics, movement, reproduction), nesting ground (reproduction), age/length at maturity (reproduction), reproductive output (nesting frequency, clutch/egg size), and mortality rates for juveniles (population dynamics, selection pressure) (Kirby, unpublished).

Mazaris et al. (2005), when studying which environmental factors are associated with turtle migration, provides a similar IBM for Mediterranean loggerhead populations. Sensitivity analysis results indicate that under constant fecundity pelagic juvenile mortality has the greatest effect on future population size, and that unlike previous studies
have indicated, the egg survival rate does have a significant effect on the outcome of the species when fecundity is variable.

In 2007 Kobayashi and Polovina produced the model upon which our work will be based. Their model was an individual-based, advection-diffusion model used to examine larval transport and retention of deep ocean species in their early life stages. In advection-diffusion modeling, for transport of individuals, the model considers the advective movement of individuals based on the large scale movement of the surrounding fluid by way of the ocean surface currents, and the stochastic eddy diffusion of the individuals from a higher to lower concentration. Additionally, their model is suitable as it integrates remotely sensed oceanographic conditions, and can be modified to take into account the importance of early life physiological fitness as addressed through the use of remotely sensed Sea Surface Temperature (SST) and chlorophyll-a data. The results indicate that loss of larval retention, defined as those individuals remaining in the area of study, depended primarily on larval duration, that winter spawning maximizes chlorophyll-a exposure, and that island effects need to be considered. “Computer simulation may be a useful approach towards understanding important aspects of early life history and adult spawning ecology.” (Kobayashi, Polovina, 2007). Although the model assumes passive drift, the importance of larval physiological fitness is addressed through tabulation of SST and chlorophyll-a. Through this model we will attempt to simulate the passive drift that first year hawksbills may experience as they leave the nesting site located at 19.1°N, 155.5°W on the Island of Hawaii. Additionally by keeping track of the turtles’ SST and chlorophyll-a exposure, we hope to suggest likely migration routes through the first three years of life.

IBMs can be quite complex. Grimm (1999) suggests that this complexity can be assessed merely by the full number of parameters the model uses. One criticism that
Grimm suggests is the lack of analytical tools for use in the understanding of such models. Computer-based spatial statistics are recently developed techniques which we may use to analyze the results of the models. By considering the location of the individuals as a two-dimensional point process, our goal is to estimate parameters of the distribution of such a point process (Baddeley, 2008).

In this work, we modify the model presented by Kobayashi and Polovina (2007). The IBM will simulate the passive drift migration, physiological fitness, and growth of several cohorts of juvenile hawksbill sea turtles over three year simulations. In order to describe the pelagic behavior of the hawksbill turtle, we will discuss the remotely sensed oceanographic conditions of sea surface currents, SST, and chlorophyll-a that will be considered in this model. The literature indicates these to be strong indicators of turtle physiological fitness and migration. Furthermore we will explain the use of computer simulated, individual-based modeling, using the Overview, Design concepts, Details (ODD) format, and use of spatial statistics for model analysis.
METHODS

Grimm et al. (2010) provides a detailed description of individual-based simulation models, and describes a specific protocol in which such models could be presented. This protocol, the Overview, Design concepts, Details (ODD) protocol, provides a structure to develop and interpret individual-based models. ODD consists of seven elements of which the first three provide an overview, the fourth element explains general concepts underlying the model’s design, and the remaining three elements provide details. In the Overview phase of the model we state our purpose, and present our state variables and scales. In the Design concepts phase we present concepts related to the overall design of the model, and in the Details phase we discuss initialization, input, and submodels that occur. The model is implemented in the programming environment NetLogo 4.1 with Matlab R2009B used for data conversion, and R 10.1 used for statistical analysis.

Overview

Purpose

The models are developed to describe the spatial distribution of the individuals after 3 years of movement under various environmental conditions and behavior assumptions, and to identify possible environmental indicators of the resulting population density of those individuals remaining in the area of study (i.e. retained).

State Variables and Scale

We model the greater Hawaiian Archipelago, including the Johnston Atoll to the southwest (Figure 2). The region is defined by latitude 10.5°N - 35.5°N, and longitude 169.5°E – 145.5°W. The habitat is characterized by geostrophic currents, sea surface winds, sea surface temperature (SST), and chlorophyll-a concentration. The region is
modeled by a 451 by 251 two dimensional grid space, with each patch defined as one-tenth of a degree in both the latitudinal and longitudinal directions.

The individuals to be modeled are the Hawaiian hawksbill juveniles, characterized by their release date and location, current geographic location, age, size, swimming speed, swimming direction, and accumulated exposure to SST and chlorophyll-a concentration. The model will utilize a 6 year period of data (2002-2007), with simulations modeling 3 year intervals. Each simulation will consist of 1000 individuals. Individual’s states are updated on a daily time step, while the habitat updates every 5 days.

Figure 2: Approximate Area of Study.
**Process overview and scheduling**

In this order, on each simulated day, the following actions are executed:

- Turtle’s size is updated as a function of time.
- Turtle’s swimming rate is updated as a function of turtle size.
- Turtle’s geographic location is updated (model dependent).
  - Passive drift, considered the null model.
  - Indirect fitness seeking, behavior model.
- Retention of the individuals is checked.
- SST and chlorophyll-a values are tabulated for retained individuals.
- Completion time of simulation is checked.
- Updating of environmental variables occurs on each fifth simulated day.

The details for these processes is provided in the section “Submodels” below.

**Design concepts**

**Basic Principles**

The model, developed from an advection-diffusion model, is modified to incorporate optimization of environmental parameters in order to model behavior, and results are analyzed using maximum likelihoods.

**Emergence**

From the initial conditions of the given model, the inclusion of behavior, and day/year of release, the spatial distribution of the individual hawksbill emerges.

**Adaptation**

In the passive drift model, the turtles make no decisions as their movement is entirely determined by the remotely sensed ocean surface currents. In the behavior model,
hawksbills adapt their movement to the environmental parameters of the patches including and surrounding their individual locations. The direction and distance in which an individual travels at each time step was determined by a list of procedures which was modeled to maximize their quality of habitat.

Objectives
The objective of the individuals in the behavior model is to remain in quality habitat as often as possible. In so doing, the individuals increase their exposure to high levels of chlorophyll-a, while maintaining an SST exposure level that reflects being in habitat with SST greater than 20 degrees Celsius. We assume this as indirect fitness seeking. No explicit measure of fitness is considered for the individuals.

Learning
Due to the continuously changing environment, as well as the large scale ocean surface current driven advection-diffusion in the modeling, hawksbill hatchling/juvenile learning was not considered in either model.

Prediction
The prediction of future events was not considered in either model. To do so we would have to assume that the individuals have a precise sense of their geographic location as well as a sense of the day of the year.

Sensing
It is assumed that for each time step, the individuals in the behavior model know the environmental parameters of SST and chlorophyll-a for the nine patches surrounding and including the individuals’ current locations.
Interaction

Due to the expansiveness of the ocean, as well as the abundance of resources, the likelihood of turtle interactions is minimal. Interaction among individuals in the model was therefore not considered in either model.

Stochasticity

The initial release of the individuals was constructed within the grid space as a bivariate normal distribution with a standard deviation of 11 kilometers. This distribution was assumed to reflect the spatial variability that occurs as the individuals make their initial frenzy from the shore to the open ocean. The advection-diffusion movement described by both models utilizes stochasticity to reflect the small scale eddy diffusivity. This random fluctuation in movement occurs at each time step.

Collectives

As no interaction among individuals was modeled, and since the modeling only describes the movement of hawksbills during their initial life stage, groupings or collectives of individuals were not considered in either model.

Observation

The output of both models consists of the following: the number of individuals which remain in the study region which we define as being retained, the number of individuals that left the study region to the north, south, east, and west, the average accumulated SST and chlorophyll-a values to which an individual was exposed throughout the duration of the simulation.

Both models consider the habitat characteristics the turtles encounter, by use of remotely sensed SST and chlorophyll-a data. SST and chlorophyll-a concentrations are used as indicators of quality habitat where the turtles will actively forage. These characteristics define the quality of habitat for the turtles. Every 5 days the model will
update the individual turtle’s overall encountered SST and chlorophyll-a concentrations. In the passive drift model, these values are merely calculated and upon completion of simulation, averaged for use in data processing and spatial statistics. In the behavior model the SST and chlorophyll-a concentrations are used to determine the direction in which the individuals will actively forage.

Details

Initialization

The release site in both models, Kau Forest Reserve (19.1N, 155.5W), located on the big island of Hawaii, acts as the initial location where the hawksbill hatchlings are introduced to the currents. This location includes Kamehame, Ninole, and Punaluu; known nesting sites for Hawaiian hawksbill (Seitz, et al., 2006, 2008).

At the beginning of each simulation the models generate 1000 individuals. Individuals begin with a straight carapace length (SCL) of 3.96 cm (Dobbs, et al., 1999). For the behavior model, the initial swimming speed of the turtles is zero.

Input

External environmental input to the model includes the remotely sensed chlorophyll-a, SST, and the OSCAR sea surface current data sets (see Appendix A). The data covers the dates 5/1/2002 to 4/30/2008, updated every 5 days, and spanning from 169.5° E to 145.5° W, 10.5° N to 35.5° N.

The area of study as previously defined is generated as a 451 x 251 grid. For each of the three data sets, Matlab was used to linearly interpolate the data from its native spatial resolution of 1 degree of the earth into a spatial grid of 451 x 251 patches, with each patch length representing 0.1 degrees of the earth. Timescales for the remotely sensed AVHRR SST and MODIS chlorophyll-a data were linearly interpolated as well.
from their native weekly time scale, to the same 5 day intervals in which the OSCAR data natively provided. The SST and chlorophyll-a data has the additional complication that in many cases values were missing in the data. These data then were smoothed by taking a latitudinal average of each missing value and replacing each missing data values with its latitudinal average. Such an averaging will naturally introduce errors. However we argue that by the seasonal nature of the data, both SST and chlorophyll-a exhibit a pattern of approximate latitudinal uniformity, thus justifying the averaging. Text files were produced by Matlab upon which the Individual-based modeling software Netlogo 4.1 would read and process as the models describe.

Every five days the model will update the environmental parameters of each patch. This interval is chosen to coincide with the update schedule of the remotely sensed environmental data the models utilize. This includes the linearly-interpolated, ocean surface current vectors, SST, and chlorophyll-a concentrations.

*Submodels*

We treat the processes of growth and movement as submodels.

*Growth and swimming speed*

The individuals grow in size based on growth rates observed from skeletochronology for Hawaiian hawksbill hatchling/juveniles in nature (Snover, et al., 2009) The model will consider turtle growth to be homogeneous and linear, with constant growth rates for year one, and years two/three respectively.

The growth rate of the turtles is modeled by fitting observed length measurements. The turtle size is defined by their straight carapace length (SCL), which refers to the straight length of the carapace, measured with calipers from the nuchal notch to the posterior-most scute. The hatchling carapace lengths were measured from dead stranded turtles throughout the main Hawaiian Islands by the Sea Turtle Stranding and
Salvage Network of the NOAA/NMFS/Pacific Islands Fisheries Science Center, Marine Turtle Research Program (Snover, per comm.). The mean and range lengths observed were 16.8 (14.4 – 19.3) cm their first year, 21.1 (17.8 – 25.2) cm. their second year, and 24.3 (18.4 – 31.4) cm. their third year. The models consider this growth in \( \text{cm/day} \), to be a piecewise continuous linear function with separate growth rates for year one, and years two and three. Growth is considered uniform across all the individuals and the size of the individuals is updated daily.

The swimming speed of the individuals is modeled using the limited available information. While little observational data exists regarding the active swimming speed of the hawksbill, 11 km/day as an average maximum juvenile swimming speed is an acceptable estimate that has been observed by use of satellite monitoring. The behavior model assumes a swimming ability to be limited by size in order to make assumptions about the individual’s active foraging movement. A daily swimming speed of 11 km/day reflects the speed of the largest of individuals (24 cm) as they end their 3 year simulation. This value was assumed based on the lone reported adult hawksbill migration speed of 17.8 km/day (de Silva, 1995), which did not consider the effects of wind and ocean currents. The swimming speed for individuals was then scaled linearly to reflect their relative size. The behavior model assumes swimming speed increases linearly by the following equation.

\[
\text{swimming speed} = 0.0412 \cdot SCL \frac{\text{patch lengths}}{\text{day}}
\]

Where SCL represents straight carapace length, measured in cm, and 1 patch length is 11.1 km.
Movement.

Daily motion of the individuals is modeled in two contrasting ways. In the first (passive drift) model the individual’s location is updated by an advection-diffusion model (Kobayashi, Polovina, 2007), which uses the remotely sensed OSCAR data for the ocean surface current vector components. This model acts as the null model. The passive drift model does not take into consideration the effect that individual growth and swimming speed may have upon an individual’s location.

In the second (behavior) model, foraging behavior of the individual hawksbill is added to the passive drift model as indirect fitness seeking. In the behavior model, the SCL of the turtle determines the active swimming speed of the individual. This swimming speed is a linear function with respect to size of the individuals. The behavior model additionally incorporates this active swimming speed and direction in determining the geographic location of the individual hawksbill. As the turtles in both models are subject to the ocean currents, it is entirely possible that their path may take them into deep ocean habitats outside of the study region. Both models keep track of individuals’ locations to ensure that any individual that leaves the study region will be removed from the simulation.

Both models on a daily time scale update the location of the individuals. The passive drift, advection-diffusion equations for the model are:

\[
x_{t+\Delta t} = x_t + \left[ u_{(x,y,t)} \Delta t + \epsilon \sqrt{D \Delta t} \right] / \cos(y_t)
\]

\[
y_{t+\Delta t} = y_t + \left[ v_{(x,y,t)} \Delta t + \epsilon \sqrt{D \Delta t} \right]
\]

where \( x \) represents longitude, \( y \) represents latitude, \( t \) represents time in days, \( u \) represents the east/west component of the current speed, \( v \) represents the north/south component of the current speed, \( \cos(y_t) \) adjusts distance by latitude to account for the spherical
coordinate system, \( \epsilon \) a normal (mean 0, standard deviation 0.1) random variate, and \( D \) is the eddy diffusivity coefficient (500 m\(^2\)/sec) (Kobayashi, Polovina, 2007).

In the behavior model, we additionally assume that early juvenile hawksbills actively seek out areas of high chlorophyll-a concentrations, an indicator of food productivity (Polovina, et al., 2001), as well as actively pursue habitat which is warm (SST > 20\(^\circ\)C) (McMahon, Hays, 2006). The individuals choose where to move based on the state of the 9 patches that include the current patch and the eight surrounding patches. If an individual is in a patch with SST greater than 20\(^\circ\)C, it will then seek the patch that is greater than 20\(^\circ\)C with the greatest chlorophyll-a concentration. If an individual is located at a patch less than 20\(^\circ\)C such an individual will also seek out the patch that is greater than 20\(^\circ\)C with the greatest chlorophyll-a concentration. If no such patch is greater than 20\(^\circ\)C, the individual will seek the patch with the greatest sea surface temperature. This process is summarized in Figure 3.

With behavior included the model takes on the following form:

\[
\begin{align*}
    x_{t+\Delta t} &= x_t + [u^\text{Current}(x,y,t) \Delta t + \epsilon \sqrt{D\Delta t}] / \cos(y_t) + s_t u^\text{swim}(x,y,t) \\
    y_{t+\Delta t} &= y_t + [v^\text{Current}(x,y,t) \Delta t + \epsilon \sqrt{D\Delta t}] + s_t v^\text{swim}(x,y,t)
\end{align*}
\]

with the additional vector components of \( u^\text{swim}(x,y,t) \) and \( v^\text{swim}(x,y,t) \) describing the active foraging behavior direction in the horizontal and vertical respectively, and \( s_t \) representing the swimming speed measured in km/day.
Figure 3: Flow Chart of Modeled Foraging Behavior.
Spatial Statistics

The Netlogo-R extension (Theile, Grimm, 2010) allows for Netlogo to interface through the system shell to run commands native to the R computing environment. The spatial statistics library (spatstat) for R is then used to compute second degree spatial polynomials used to model the spatial point pattern of the individuals upon the completion of each simulation.

The second degree population distribution models used are variations of a base second degree polynomial intensity \( z(x,y) \) that considers the latitude and longitude values for the study region. Four subsequent intensity models \( z(x,y,...) \), consider the averaged values for the last fifty days of each simulation for SST, chlorophyll-a, magnitude of the ocean surface currents, and the inclusion of all 3 parameters, respectively.

\[
\begin{align*}
z(x,y) &= \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 \\
z(x,y,X_1) &= \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 + \beta_6 \cdot X_1 \\
z(x,y,X_2) &= \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 + \beta_7 \cdot X_2 \\
z(x,y,X_3) &= \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 + \beta_8 \cdot X_3 \\
z(x,y,X_1,X_2,X_3) &= \beta_0 + \beta_1 x + \beta_2 y + \beta_3 x^2 + \beta_4 xy + \beta_5 y^2 + \beta_6 \cdot X_1 + \beta_7 \cdot X_2 + \beta_8 \cdot X_3 + \beta_9 \cdot X_1 \cdot X_2 \cdot X_3
\end{align*}
\]

where \( X_1, X_2, X_3 \) represent SST, chlorophyll-a, and the magnitude of the currents respectively, \( \beta_0 \) is an intercept, and \( \beta_1\ldots \beta_9 \) are coefficients. The models are summarized in Table 1.
<table>
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<th>currents</th>
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</table>

Table 1: Summary of Distribution Models.
RESULTS

Variation in retention is observed with a low of 20/1000 individuals (October, 2002 release, passive drift) to a high of 1000/1000 individuals (September, 2002/2004 release, behavior). In every case, the retention of the behavior model significantly exceeds that of the passive drift model for the same day of release ($p < 0.01$). None of the individuals leave the system to the north or south in any of the simulations. Most simulations result in the loss of individuals predominately to the east, yet for those released September 2003, under the behavior model, the number of individuals leaving the study region to the west is greater. Retention decreases throughout the 6 months of simulated releases for 2002 and 2003. In 2004, retention is consistently high with for the behavior model 5 out of 6 months having retention greater than 900/1000 individuals (Figure 4, panels a, b).

Three observable patterns of distribution for the individuals are presented (Figures 5, 6, and 7). Most passive drift model simulations resulted in the individuals distributed in the region North-east of the main Hawaiian Islands, with most individuals lost to the east (Figure 5). For most behavior model simulations, the distribution of the individuals is centered north of the main Hawaiian Islands (Figure 6). For the September, 2003 released, behavior model, the individuals settle west of the main Hawaiian Islands with much of the loss in retention occurring to the west of the North western Hawaiian Islands (Figure 7). We aggregated separately the distribution data across all simulations for passive drift, and behavior respectively to illustrate the regularity of the distribution patterns (Figure 8). Also of note was that none of the individuals across all simulations settle within the 200 km square centered at Johnston Atoll.
Daily SST and chlorophyll-a concentration exposures were tabulated for each individual for the duration of each simulation (Figure 4, panels c-f). For SST, QQ-plots show the data to be normal, and two-sample t-tests were performed. In all but 3 of the 18 months of release (August, 2002, October, 2003/2004), the SST concentration for individuals in the behavior model is significantly different from those in the passive drift model ($p < 0.01$). Of these 15 months of release, in all but one month’s simulated releases (November, 2002), the tabulated SST exposure is significantly higher for the behavior model, ($p < 0.01$) (See Figure 9, panel a.). For chlorophyll-a concentrations, the behavior model data is not normal. A permutation test was then performed on the two models for each month of release. In all 18 months of release, the average daily chlorophyll-a concentration is significantly higher for the behavior model than for the passive drift model ($p < 0.01$) (Figure 9, panel b.).

For each simulation, maximum likelihood estimation was used to construct polynomial models $M_{ijk}$ (Table 1) predicting the population distribution of the individuals after three years. AIC weights were calculated for each of the models. For the passive drift movement model, model $M_{111}$ is the dominant model for 9 of the 18 months of release, while no model is significantly dominant for 4 of the 18 months of release. For the behavior model, population distribution model $M_{111}$ is the dominant model in all but one month of release (September, 2003).
Figure 4: For each year of release (○-2002, ▲-2003, ■-2004) and for each month of release, the number of individuals retained for passive drift (a.) behavior (b.), average daily SST (°C) encountered for passive drift (c.) behavior (d.), and average daily chlorophyll-a (mg/cm^3) encountered for passive drift (e.), behavior (f.).
Figure 5: Population intensity distribution of individuals released August, 2002, passive drift, as predicted by the 5 distribution models. ● indicates the location of release.
Figure 6: Population intensity distribution of individuals released December, 2004, behavior, as predicted by the 5 distribution models. ● indicates the location of release.
Figure 7: Population intensity distribution of individuals released September, 2003, behavior, as predicted by the 5 distribution models. ● indicates the location of release.
Figure 8: Population intensity distribution aggregated across all years and months of release for passive drift (panel a.) and behavior (panel b.) as predicted by the distribution model $M_{000}$. ● indicates the location of release.
Figure 9: Box and whisker plots comparing the average daily SST exposure (a.) and the average daily chlorophyll-a exposure (b.) across all years and months of release for the passive drift and behavior models.
DISCUSSION

The results suggest a significant effect the assumed behavior rules in the behavior model have in both the retention of individuals and exposure to SST/chlorophyll-a. By the inclusion of simulated behavior, the turtles used higher quality habitat than in the passive drift model. Additionally the resulting distribution model $M_{111}$ as the dominant model for 26/36 total simulations indicates the need to consider all three of the environmental parameters of currents, SST, and chlorophyll-a to accurately describe the predicted distribution. Comparing visually (Figure 6) the models $M_{000}$ and the dominant model $M_{111}$ illustrates how model $M_{111}$ more accurately describes the patchiness of the distribution resulting from the advection-diffusion model. First attempts at modeling the distribution included linear models including the environmental parameters as well as models including only the environmental parameters. None of these early models had AIC weights that accurately described the distribution as well as the presented models $M_{ijk}$.

On August 28th, 2003, Hurricane Jimena formed in the eastern Pacific. Jimena travelled west, just south of the main Hawaiian islands, until dissipating into a tropical storm on September 3rd, crossing the international dateline on September 5th. It could be easily suggested that the drastically different results in our model for the September, 2003 release (Figure 7) are a direct result of hurricane Jimena.

These results suggest that species managers should sample for Hawaiian hawksbill in the region northeast of the main Hawaiian islands. The results indicate that both passive drift and behavior movement models were consistent in producing distributions of individuals centered to the northeast.
Recent results (Mansfield, Wyneken, 2011) of satellite tagged, lab reared, neonate loggerheads in the Atlantic have indicated that the “lost year” passive drift assumption may need reconsideration. Further exploration of behavior rules could become increasingly more beneficial as more information is obtained regarding hatchling/juvenile biology and behavior.

The predicted distribution of the individuals in the passive drift model suggests a need to consider the Pacific Trash Vortex as a location that the Hawaiian hawksbill neonates may end up. The Pacific Trash Vortex is described as the area between $135^\circ W$ to $155^\circ W$ and $35^\circ N$ to $42^\circ N$ (Dautel, 2009). The Vortex contains a high concentration of plastics and other waste products trapped within the current system known as the North Pacific Gyre. Of concern is the possibility of these plastics ending up in the stomachs of sea turtles as well as other marine wildlife.

The model has many directions we’d like to see actualized. The very nature of Agent-based models would encourage us to explore further behavior rules, perhaps to consider biological features such as cold-freezing, or other hawksbill specific biological processes as they become better understood.

While we chose to end simulations after 3 years, this should be considered a minimum as it is not known how long hawksbill will spend in the deep ocean prior to settling in a shallow feeding area. The model could explore longer simulations and would merely need to incorporate more years of remotely sensed data. Additionally, while we chose the specific 6 year period of 2002-2008, simulating other years of data may very well provide different results in terms of retention, and final distribution of the individuals.

The release site of the individuals we chose $19.1^\circ N, 155.5^\circ W$, was assumed to describe the turtles nesting at the known nesting sites of Kamehame, Ninole, and
Punalu‘u. Other suspected nesting sites on the island include Manuka, Humuhumu point, and Kahakahakea (Seitz, 2010). Having the model explore simulated releases at these and other sites may suggest that the predicted distribution of the individuals upon completion of the 3 years is significantly different among turtles from varying release sites.

The spatial linear interpolation of the OSCAR data was performed to provide better resolution for the individuals movement as the native temporal resolution of 5 days would in many cases move the individuals a great distance, perhaps bypassing an entire current stream that at a finer resolution would take them in a different direction. Testing the significance of the linear interpolation should still be performed. While linear interpolation of the data did provide an increased degree of detail in the movement pattern of the individuals. The execution speed of the model is greatly reduced as the native spatial environment would have been only 46 x 26 patches, where each patch represents 1 degree of the earth.

We chose to program the advection-diffusion model as presented by Polovina and Kobayashi (2007). With respect to specifically the \( \cos \) term, this showed to greatly decrease the execution speed of the model. If alternatively the \( \cos \) term were to be incorporated during the initial Matlab created text files, perhaps execution speed of the simulation may increase.

As the behavior model proceeds through time, the turtles increase their ability to maximize their quality of habitat. Their size, which determines their active swimming speed, allows them to reach habitat that is counter to the direction and speed in which the ocean currents would have them move. Furthering on this concept, additional patterns of distribution may result from the inclusion of direct fitness seeking, determined by the exposure of the individuals to quality habitat.
With many of the simulations resulting in a majority of the turtles leaving the area of study to the east, and such a small number of turtles encountering patches west of the North western Hawaiian Islands, a shift of the study region 10 degrees east may result in simulations with an increase in retention. This could then potentially increase the ability of the model to determine hotspots of population density. Currently many of the simulations result in the predicted location of maximum distribution positioned outside the region of study.

While the results indicated a lack of individuals within the 200 km square centered at Johnston Atoll, it would be interesting to track individuals which encounter patches located within the 200 km square throughout their migration. Perhaps by increasing the size of the region which we determine to be settlement at Johnston Atoll different results may occur.

The relationship between the growth of the individuals and age could be better assumed by way of some non-linear function. Ideally this could be modeled to incorporate stochasticity to reflect the variability in the size of individuals.

While we assumed the turtles in the behavior model would seek to maximize their chlorophyll-a exposure by actively swimming to locations containing high concentration, the literature indicates an attraction of the turtles to chlorophyll fronts. These chlorophyll fronts can be characterized by locations in which the difference between chlorophyll concentrations of neighboring locations is large. The model could easily incorporate this relationship by taking a difference quotient for neighboring patches and having the individuals seek out patches in which the magnitude of the difference quotient is greatest.

Many of the parameters in the model would benefit from some form of sensitivity analysis. These include the parameters of diffusivity coefficient, initial release distribution, release location, and swimming speed. A preliminary look at swimming
speed indicated that with a maximum daily average swimming speed of 5.5 km/day significant increases in retention can be observed.
REFERENCES


