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NOTE

Estimating carrying capacity at the green turtle nesting beach of East Island, French Frigate Shoals

Manjula Tiwari[1,*], George H. Balazs[2], Stacy Hargrove[2]

[1]Marine Turtle Ecology and Assessment Program, Protected Resources Division, Southwest Fisheries Science Center, NOAA-National Marine Fisheries Service, La Jolla, California 92037, USA

[2]Marine Turtle Research Program, Pacific Islands Fisheries Science Center, NOAA-National Marine Fisheries Service, Honolulu, Hawaii 96822, USA

ABSTRACT: Many sea turtle populations are at a fraction of their historical abundance, and understanding ecological processes, under current and climate change scenarios, is critical for establishing recovery goals. In the Hawaiian Islands, the nesting population of the green turtle *Chelonia mydas* on East Island, French Frigate Shoals, has been recovering at a rate of 5.7% per year. Climate change models, however, predict a loss in nesting habitat on East Island of up to 30% due to sea level rise by 2100. Therefore, the objective of the present study was to determine the carrying capacity of East Island for hatchlings and nesting females under current conditions and predictions of sea level rise. In the simulation model, density-dependent nest destruction was the primary factor regulating population size. Carrying capacity was reached between 1.9 and 2.1 million hatchlings at current conditions; carrying capacity was approached when 80 000 to 120 000 nests were laid on the beach, representing 20 000 to 30 000 nesting females. With a rise in sea level, carrying capacity was reached when 60 000 to 100 000 nests were laid on the beach. The current mean estimate of 390 nesting females per year, over the past 10 yr, at East Island represents 1.3 to 2% of the females that would nest at carrying capacity. The beach at East Island is well below carrying capacity and is capable of supporting a larger nesting population. However, the availability of suitable coastal habitats may play a bigger role in regulating the Hawaiian green turtle population than available nesting habitat.

KEY WORDS: Carrying capacity · Green turtles · *Chelonia mydas* · Nesting · Climate change · French Frigate Shoals · Hawaii

INTRODUCTION

Populations of green sea turtles *Chelonia mydas* have declined worldwide, and many populations are considered to be at a fraction of their historical abundance and environmental carrying capacity (Jackson et al. 2001, Seminoff 2004, Tiwari et al. 2006). However, recent analyses of global trends in green turtle nesting populations demonstrated a promising, and sometimes remarkable, increase over the past decades at several nesting rookeries (Bjorndal et al. 1999, Seminoff 2004, Troëng & Rankin 2005, Broderick et al. 2006, Chaloupka et al. 2008). Among the rookeries that have responded positively to long-term protection is the green turtle population on East Island in French Frigate Shoals (Balazs 1976), which lie within the remote Northwestern Hawaiian Islands (Fig. 1), an area designated as the Papahanaumokuakea Marine National Monument in 2007. Prior to the mid 20th century, green turtles were heavily exploited for their eggs and meat in the Hawaiian Islands, and their nesting habitats destroyed, resulting in a severe population decline (Balazs 1980, Balazs & Chaloupka 2004a). However, protection was strengthened in the late 1970s by the State of Hawaii and the US Endangered Species Act (Bennett & Keuper-Bennett 2008), and the green turtle population has since been recovering rapidly at a rate of 5.7% per year (Balazs & Chaloupka 2006, Chaloupka et al. 2008) over the past 35 yr.

Although green turtles nest throughout the Northwestern Hawaiian Islands, about 90% of the nesting takes place in French Frigate Shoals (Balazs 1980).

*Email: manjula.tiwari@noaa.gov

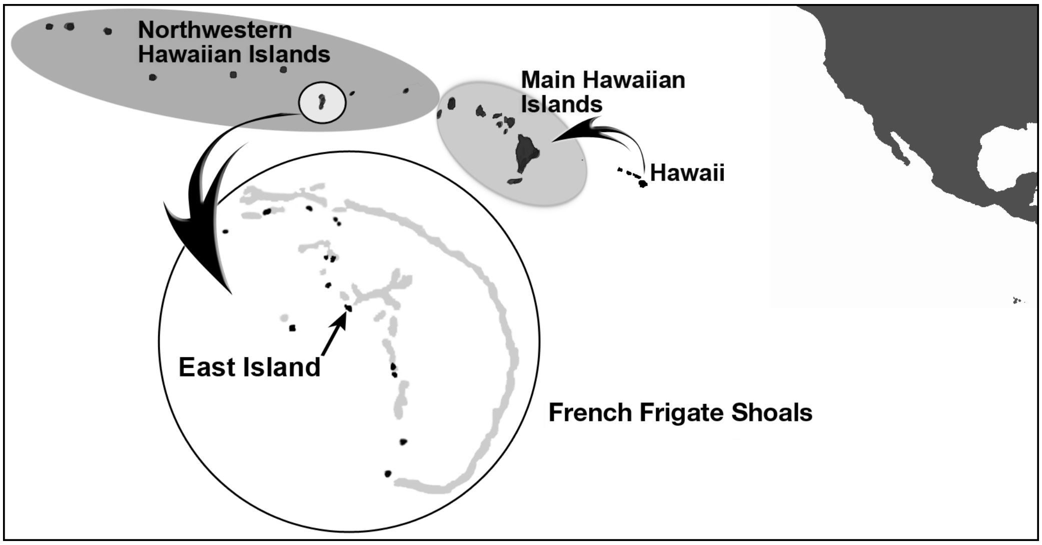

Fig. 1. Hawaiian archipelago and the location of French Frigate Shoals and East Island

Within this atoll, approximately 55% of the nesting takes place on East Island (Fig. 1), where data collection was initiated in the 1970s (Balazs 1980, Balazs & Chaloupka 2004a). Evidence from tagging and radio telemetry work indicates that females nesting on East Island maintain strong nesting fidelity and rarely nest on any of the other islands (Balazs 1980, Dizon & Balazs 1982). Green turtles migrate from throughout the Hawaiian archipelago to French Frigate Shoals to breed (Balazs 1976, 1980), and the numerous foraging aggregations are composed of one genetic stock and form a distinct regional population (Dutton et al. 2008). With increased nesting on East Island and decreased observations of turtles that have not been previously tagged, it has been suggested that the population may be approaching carrying capacity in the coastal foraging habitats (Balazs & Chaloupka 2004a, Chaloupka & Balazs 2007). However, the carrying capacity of the finite beaches of French Frigate Shoals remains to be determined.

Furthermore, loss of nesting habitat from climate change-related sea level rise has been predicted for many beaches worldwide (Fish et al. 2005, Baker et al. 2006, Fuentes et al. 2010). In the Northwestern Hawaiian Islands, sea level rise due to climate change and the natural subsidence of the northwestern segment of the archipelago over geologic time are of growing concern. Baker et al. (2006) estimated a loss in terrestrial habitat between 3 to 75% under various scenarios of sea level rise. Models predicted that, of the islands evaluated within French Frigate Shoals, East Island would persist the longest (Baker et al. 2006), suggesting that East Island may play an even greater role for green turtle nesting in the Hawaiian Islands.

Increased nesting densities on East Island would result in density-dependent changes in the nesting environment (Honarvar et al. 2008) and in density-dependent factors such as nest destruction by nesting females and disease regulating population size. Females have been observed to destroy incubating nests during their nesting process on East Island (Balazs 1980). When a turtle crawls up a beach to nest, she clears the sand around her with her flippers creating a body pit, and then excavates the nest chamber, deposits her eggs, and covers up and camouflages the nest; at high nest densities nearby incubating nests are often destroyed by a nesting turtle (Girondot et al. 2002, Caut et al. 2006, Tiwari et al. 2006). As destroyed eggs accumulate in the sand, increased microbial activity may increase mortality within incubating nests (Cornelius et al. 1991, Marcovaldi et al. 1999, Phillott & Parmenter 2001). Density-dependent predation on nests (Tiwari et al. 2006) would not apply to East Island because of the absence of predators (Balazs 1980).

Thus, the objective of the present study is to determine the carrying capacity of East Island for hatchlings and nesting females under current conditions and the predictions of reduced nesting habitat due to sea level rise; carrying capacity is defined as the maximum number of hatchlings that can be produced in a season (Tiwari et al. 2006). Given the relatively rapid increase in the nesting population and its distinct genetic and ecological importance, evaluating the carrying capacity of key habitats and understanding ecological processes, under current scenarios and the predictions of climate change, are critical for updating and achieving recovery goals for this species (National Marine Fisheries Service and US Fish and Wildlife Service 1998).

MATERIALS AND METHODS

French Frigate Shoals is a 35 km long crescent-shaped atoll consisting originally of 11 islands (Amerson 1971) and currently of 8 emergent islands and 2 volcanic outcrops. Islands within the atoll differ in substrate, and East Island is characterized by a calcareous substrate composed of coarse to fine fragments of coral, coralline algae, mollusks, humus, and barnacles (Balazs 1980, Mortimer 1990). Green turtle nesting extends from May to September (Balazs 1980), and annual surveys of nesting females have been conducted on East Island since 1973. For most of these 37 seasons, night surveys have been conducted for a few weeks during the peak nesting months to count and tag turtles. Saturation surveys were conducted from 1988 to 1992, during which time the entire nesting season was monitored (Wetherall et al. 1998). Recent analyses of population trends for 30 and 32 yr of nesting have been presented by Balazs & Chaloupka (2004a) and (2006), respectively. Here we add nesting female estimates for the years 2005 to 2009, and present an updated graphical overview of the nesting trend for the past 37 yr.

Carrying capacity at East Island was determined by using the simulation model described by Tiwari et al. (2006) to estimate carrying capacity at the green turtle nesting beach in Tortuguero, Costa Rica. The model was modified to simulate processes that affect hatchling emergence on East Island. Given the remoteness of French Frigate Shoals and the difficulties of extensive monitoring and data collection, including potential conflicts with the critically endangered Hawaiian monk seal *Monachus schauinslandi*, limited data are available to estimate East Island model parameters. Several life history parameters are estimated from in-depth studies on East Island during the 1970s (Balazs 1980).

In the present simulation model, all available area on the island was considered suitable for nesting, as turtles have been observed to scatter their nests randomly throughout the island (G. H. Balazs unpubl. data). The available nesting area of 30 865 m^2 was determined by taking the average of the mean low water line and the spring high tide as estimated by Baker et al. (2006) for East Island and subtracting the unsuitable nesting habitat, which consists of a permanent wooden platform (7.5 m^2) and a rock pile (27.1 m^2). The number of nests present on the beach on each day (t) can be summarized by the equation:

$$\text{Nests}_t = \text{Nests}_{(t-1)} - F_t + N_t - H_t$$

On each day (t) for 174 d, the model simulated a random value (according to the descriptions given below) for the number of nests completely destroyed by nesting females (F), the number of nests deposited each day (N), and the number of nests hatched (H). Erosion was considered to be negligible in this model as it occurs towards the end of the season, and only at one end of East Island; this would result in lowering hatchling output and its significance would depend on the timing and intensity of the erosion. No mammalian nest predators are present on East Island, and although 2 species of ghost crabs (*Ocypode ceratophthalmus* and *O. laevis*) are found on the island, neither has been observed depredating incubating eggs (Balazs 1980).

Only nesting in the main months (15 May to 31 August) was considered in the model, but the model was run until early November (t = 174 d) to allow all nests laid in August to complete their average incubation period of 65 d, which was estimated by Balazs (1980) and is similar to the mean incubation duration of 66 d estimated on Tern Island in French Frigate Shoals (Niethammer et al. 1997). The number of nests laid each day (N) was drawn from a Poisson distribution whose mean was the product of the total number of nests laid in the season and the mean proportion of nests laid on that day, which was determined from the average proportion of nests laid on each day between 1988 and 1992; these were the only years for which saturation surveys were carried out. Temporal patterns of nesting appear not to have changed radically over the past 37 yr (G. H. Balazs pers. obs.). An average clutch size of 104 eggs, estimated by Balazs (1980), was assigned to each nest.

The expected probability of a nest being destroyed by a nesting female is summarized by the equation $1 - e^{-AD}$, where A is the area of destruction and D is nest density (nests m^{-2} on East Island) at time of nest destruction. The area within which a female is likely to destroy another nest during her nesting process was determined from body pits excavated by nesting green turtles on East Island during the 2009 nesting season. This area on East Island measured on average 1.33 × 1.5 m, which corresponds to an area of 2.0 m^2, and was assumed to be circular. Therefore, in the present study, the number of nests destroyed by each female (F) on each day was drawn from a Poisson distribution with a mean defined as 2.0 m^2 × the current nest density on the beach. A female was allowed to destroy more than one nest, but the total number of nests destroyed could not exceed the total number of nests in the beach. The fraction of the nest destroyed by a nesting female varied from a few eggs to most of the eggs; a random fraction of eggs selected from a uniform distribution was subtracted from the clutch. Eggs remaining in partially destroyed nests were allowed to complete the 65 d of incubation and hatch (according to rules given below) and removed from the model on the day they hatched. Nests that were completely destroyed were removed from the model on the day they were destroyed.

Hatchling output on each day (t) is summarized by the equation:

$$\text{Hatchlings}_t = \sum_{i=1}^{E_t} (CS \times P_t)$$

where hatchling emergence from nests successfully completing incubation (E) is determined by multiplying the number of eggs or clutch size (CS) in each nest ready to hatch (i) by a proportion (P) randomly selected from a beta distribution with shape parameters 1.73 and 0.7. These parameters were calculated from hatchling emergence data collected by Balazs (1980) on East Island. Nests partially destroyed by nesting females were subjected to a similar random reduction of eggs because a female's disturbance of the area while nesting may increase risks for incubating nests from increased microbial activity due to broken eggs and from changes in the environmental conditions of nests (Tiwari et al. 2006). The simulation model was run from an estimate of at least 1000 nests on East Island in recent years up to 200 000 nests.

Finally, to determine the sensitivity of the model to small changes in parameters, a 20% increase in mortality during incubation was integrated into the model. To incorporate projections of maximum sea level rise by Baker et al. (2006) at East Island, the model was subsequently run with a 30% reduction in available nesting area (21 865 m^2). Increasing sea levels may also increase the water table on the island, thereby drowning nests. Therefore, model output was also evaluated with a 20% increase in mortality during incubation in addition to the 30% reduction in available nesting area. These simulations were also run for nest numbers on East Island from 1000 up to 200 000 nests. The R software (R Development Core Team 2009) was used to run the models.

RESULTS

Inclusion of nesting data from 2005 to 2009 demonstrated that the nesting population is continuing to grow with the greatest number of turtles over the 37 sampling seasons nesting in 2008 (Fig. 2). In the simulation model, carrying capacity was reached between 1.9 and 2.1 million hatchlings under current conditions; carrying capacity was approached when 80 000 to 120 000 nests were laid on the beach (Fig. 3), which represents 2.6 to 3.9 nests m^{-2} if nests were uniformly distributed on the beach. The number of nests destroyed by nesting females in the model was approximately 26 per 1000 nests laid on the beach, consistent with the number of nests observed being destroyed by nesting females at the peak of the season in 2008 when the maximum number of nests was laid on East Island (Fig. 2). For a 20% increase in mortality during incubation, hatchling output decreased and carrying capacity was reached between 1.5 and 1.6 million hatchlings; carrying capacity was approached when at least 80 000 to 120 000 nests were placed on the beach.

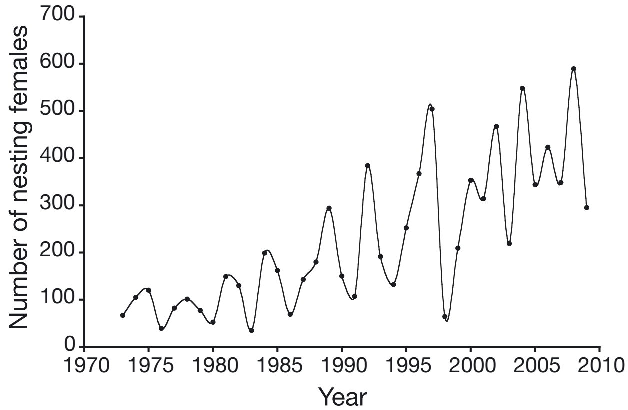

Fig. 2. *Chelonia mydas.* Estimated number of green turtles nesting on East Island, French Frigate Shoals, 1973–2009

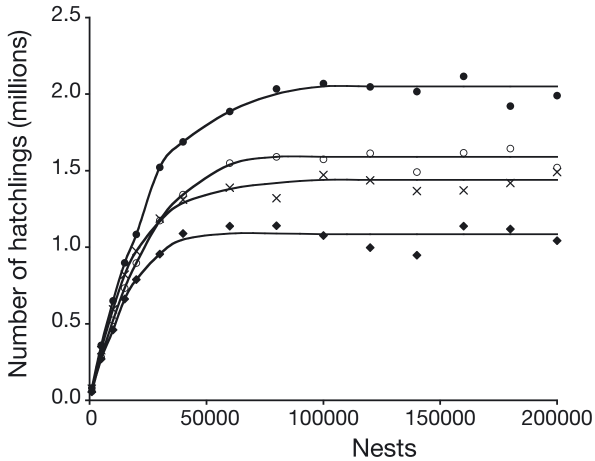

Fig. 3. *Chelonia mydas.* Number of hatchlings produced at East Island under different scenarios incorporated in the simulation model: current situation (●), current situation with 20% increase in mortality during incubation (○), sea level rise and reduced nesting habitat (×), and sea level rise and reduced nesting habitat with 20% increase in mortality during incubation (◆)

With sea level rise and a reduction in available nesting habitat, carrying capacity was between 1.3 and 1.6 million hatchlings (Fig. 3). When a 20% increase in mortality during incubation was applied to this model, hatchling output decreased; carrying capacity was between 0.9 and 1.1 million hatchlings (Fig. 3). With a rise in sea level, carrying capacity was reached when 60 000 to 100 000 nests were laid on the beach.

DISCUSSION

Although once seriously depleted due to widespread exploitation within the Hawaiian Islands (Balazs 1980), the green turtle stock in French Frigate Shoals has been making an impressive comeback. With the absence of major predators on the islands, the main factors regulating hatchling output would be intraspecific destruction of eggs, as suggested by other researchers (Bustard & Tognetti 1969, Girondot et al. 2002, Tiwari et al. 2006, Mazaris et al. 2009), increased microbial activity resulting from a higher nutrient load after a certain nest density threshold is reached (Cornelius et al. 1991, Tiwari et al. 2006), as well as changes in the incubation environment. Honarvar et al. (2008) demonstrated experimentally that increasing the density of olive ridley *Lepidochelys olivacea* nests resulted in lower hatching success possibly due to higher temperatures, higher carbon dioxide levels, and lower oxygen levels. Tiwari et al. (2006) found that below-beach-surface predation, erosion, and beach flooding affected green turtle hatchling production at Tortuguero, Costa Rica, in a density-independent manner. Density-independent effects of erosion and severe tidal inundation are considered negligible during the main season on East Island; however, climate change forecasts suggest an increase in the intensity of these factors (Hawkes et al. 2009).

The beach at East Island appears to be well below its carrying capacity. If mean clutch frequency for green turtles nesting on East Island is 4 (estimated from saturation surveys during 1988–1992; G. H. Balazs unpubl. data) and the mean number of females nesting in the past 10 yr is 390 (estimated from values in Fig. 2), then the current mean nesting population represents 1.3 to 2 % of the 20 000 to 30 000 females that would deposit 80 000 to 120 000 nests on East Island at carrying capacity. Similarly, in the Caribbean, the current green turtle population is estimated to represent only 3 to 7 % of pre-exploitation levels (Jackson et al. 2001). If mature females comprise 0.6 % of a green turtle stock (Chaloupka & Balazs 2007), then 20 000 to 30 000 females represent stocks of 3.3 to 5 million green turtles. While 20 000 to 30 000 females in a population falls well within acceptable estimates for some of the other large green turtle populations (Bjorndal et al. 1999, Limpus et al. 2003, Seminoff 2004) and East Island appears capable of supporting this larger nesting population, the green turtle population in French Frigate Shoals may be regulated by availability of food and refugia in suitable coastal habitats. Chaloupka & Balazs (2007) estimated carrying capacity of the current coastal habitat to be 73 600 green turtles and the current stock to be at 83 % of carrying capacity. Wabnitz (2010) also demonstrated that the green turtle foraging population at the Kaloko-Honokohau National Historical Park had reached carrying capacity. Furthermore, a decline in growth rates of immature green turtles at the foraging grounds while population abundance has been increasing suggests local density-dependent effects (Balazs & Chaloupka 2004b). Under this scenario, East Island will successfully support increased nesting when carrying capacity is reached in the coastal habitat and if other traditional nesting areas are inundated by sea level rise. Over geological timescales sea turtles rookeries have undergone many changes resulting in colonization of new areas (Bowen et al. 1992). Nevertheless, new findings suggest that most low-lying atoll islands may either remain stable or increase in area (Webb & Kench 2010) despite climate change-induced changes in sea level. In the end, the coastal habitats may play a bigger role in regulating the Hawaiian green turtle population than available nesting habitat.

However, the estimates of carrying capacity in the coastal habitat and the percentage of mature females present in the population (Chaloupka & Balazs 2007) are based on limited data and inferences that have raised concerns because of their management implications (Snover 2008). Additional assessments will be necessary when more data on age and size class composition, rates of predation, and productivity of the foraging habitats become available for the Hawaiian stock. Also, impacts of climate change on the ecology and structure of key habitats, sex ratios, as well as distribution, behavior, and diet will need to be evaluated (Hawkes et al. 2009).

Given the genetic and ecological importance of the Hawaiian stock (Chaloupka & Balazs 2007, Dutton et al. 2008), the ongoing debate on the reinstatement of indigenous hunting rights in the Hawaiian Archipelago (Chaloupka & Balazs 2007), and the ambiguous impacts of climate change (Baker et al. 2006, Hawkes et al. 2009), an ecosystem-based assessment of the population is needed to understand the adaptability and resilience of the green turtle population within a fluctuating ecosystem. This is particularly important for devising meaningful and adaptive ecosystem-based conservation and management strategies.

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