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A Review of the Demographic Features of Hawaiian Green Turtles (*Chelonia mydas*)

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Abstract. – This review summarizes all existing data and knowledge of the demographic variables and their stochasticity of Hawaiian green turtles. The population numbers roughly 4000 breeding females today, having rebounded from its near extinction in the early 1970s, with most of the nesting restricted to French Frigate Shoals in the remote and geologically ancient Northwestern Hawaiian Islands. A timeline is provided of the scientific monitoring for this population and associated data streams relating to morphometrics, maturity, nest dynamics, sex ratio, as well as population growth and viability.

Key Words. – Reptilia; Testudines; Northwestern Hawaiian Islands; French Frigate Shoals; nesting biology; population monitoring

Systematic studies of the green turtle (*Chelonia mydas*) in the Hawaiian Islands were initiated by the Hawaii Institute of Marine Biology in partnership with the US Fish and Wildlife Service in 1973 with annual seasonal monitoring and tagging of nesters at East Island, French Frigate Shoals (FFS) in the Northwestern Hawaiian Islands (NWHI). Subsequently, in the late 1970s, ocean capture tagging and related research of immature green turtles commenced in the Main Hawaiian Islands (MHI), expanding over time to include numerous coastal neritic sites throughout the archipelago (Balazs 1980).

Concomitantly, in 1982, the National Oceanic and Atmospheric Administration (NOAA) Marine Turtle Research Program of the Pacific Islands Fisheries Science Center (PIFSC), began a sea turtle stranding investigation. The goal of this initiative was to spatially and temporally document sea turtle strandings and necropsy dead turtles to determine cause of stranding, health status, morphometrics, gender, diet, and collect tissues for archival and various analytical purposes. In 1990, a companion program was launched to rescue, rehabilitate, and conduct clinical research on stranded turtles found treatable for return to the wild. Turtles stranding with injuries or disease deemed untreatable by veterinary evaluation were humanely euthanized and necropsied by wildlife pathologists for fresh sample collection primarily for use in research of fibropapillomatosis disease (Work et al. 2004, 2014; Chaloupka et al. 2008b). Presently, there are 7 major long-term data sets and associated sample arrays collected annually over a 24–41-yr time period housed at the PIFSC and partner organizations. These 7 broad categories consist of 1) nesting female monitoring and tagging, 2) ocean capture/basking turtle tagging, 3) strandings, 4) necropsies including pelagic turtle bycatch, 5) rehabilitation and release, 6) euthanasia, and 7) satellite tracking. Overall, as the result of these initiatives, and the commitment of time, resources, partnerships, and expertise to keep them going, the Hawaiian population is among the best studied of green turtles globally in terms of longevity, consistency of methodologies, central consolidation and coordination of data, and multidisciplinary partnerships resulting in numerous journal publications (see http://www.pifsc.noaa.gov/marine_turtle/).

Types of information that can be gained by long-term monitoring of nesting, which are difficult to determine in any other way, include an understanding of population dynamics (Richardson et al. 1999); adult female survival rates (Frazer 1983); critical fecundity factors of clutch and remigration intervals (Van Buskirk and Crowder 1994); clutch size, nest survival rates, and the population trend of adult females (Troëng and Rankin 2005); and the annual reproductive output of the population.

Although monitoring and tagging of nesting females at East Island, FFS, is the longest running green turtle research and monitoring initiative in Hawaii, the demographic features revealed by these four decades of annual surveys have not been previously presented in a unified fashion. Additionally, some components of the full data set have only recently been delineated, thereby yielding new and updated demographic variables useful to population modelers for assessment and conservation. Herein, we present a consolidated update of this information for the first time.

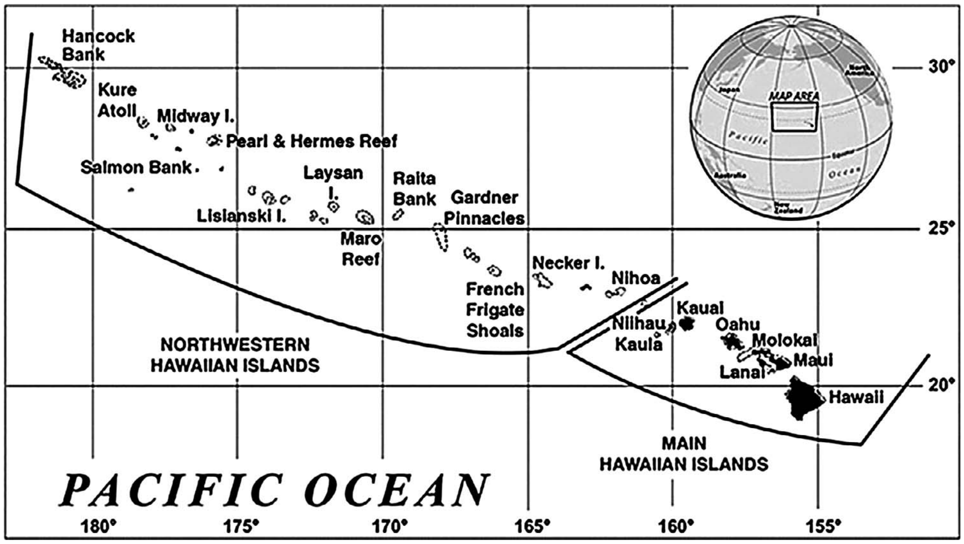

Figure 1. Hawaiian Archipelago.

Geographic and Ecological Settings of the Hawaiian Archipelago

Distant from continental land masses, the Hawaiian chain extends in a linear fashion for 2400 km across a vast and remote oceanic region of the Central North Pacific Ocean (Fig. 1).

As the most isolated island group globally, the archipelago ranges from the volcanically active island of Hawaii in the southeast at 19°N, 155°W, to diminutive Kure Atoll at the extreme northwestern end (28°N, 178°W). Known as the Main Hawaiian Islands, there are 8 large and geologically young islands (0.4–5.1 million yrs) in the southeastern segment of the chain, Hawaii, Maui, Kahoolawe, Lanai, Molokai, Oahu, Kauai, and Niihau, with resident human populations totaling approximately 1.4 million. In contrast, the Northwestern Hawaiian Islands, extending from Nihoa to Kure (Fig. 1), are geologically older (20–30 million yrs) representing small remnant tips of extinct submerged volcanoes with virtually no human habitation. Therefore, the archipelago is slowly sinking and disappearing over geologic time in the northwest, and rising and growing in the southeast.

The approximate midpoint of the Hawaiian chain is FFS, a crescent-shaped semi-atoll, 26 km from north to south, located at 24°N, 166°W, in the NWHI (Amerson 1971). The nearest island to FFS outside the immediate Hawaiian Archipelago is Johnston Atoll situated 850 km to the south at 17°N, 169°W (Amerson and Shelton 1976). Other prominent islands of substantially greater distance from FFS, but nevertheless among the nearest neighbors to the Hawaiian Archipelago, include the following: to the east, Clarion Island, Mexico (5350 km); to the south, Palmyra Atoll (2050 km); and to the southwest, Bikar in the Marshall Islands (2800 km).

The Hawaiian Archipelago, including Johnston Atoll, is inhabited by green turtles that are geographically discrete in their normal range and movements, as evidenced by comprehensive mitochondrial DNA analysis (Dutton et al. 2008; Frey et al. 2013) and mark–recapture studies using flipper tags, microchip tags (Balazs 1976, 1983; Nurzia Humburg and Balazs 2014), and satellite tracking (Balazs 1994; Balazs et al. 1994; Seminoff et al. 2015; D.M. Parker, G.H. Balazs, and M. Rice, unpubl. data, 2015). The principal nesting site of Hawaiian green turtles has been and continues to be FFS (Balazs 1976, 1980; Lipman and Balazs 1983; Kittinger et al. 2013), where more than 96% of the nesting activity occurs (Seminoff et al. 2015). Within FFS, the 5-ha East Island accounts for approximately 50% of seasonal (May through September) nesting, whereas other islets of FFS—Tern, Trig, Gin, and Little Gin—account for the remaining approximately 50% of nesting. Whale–Skate, joined by sand deposition between the former islets of Whale and Skate in the 1950s, eroded and became submerged in the mid-1990s (Baker et al. 2006).

Information from tagging at FFS and at areas in the MHI, in the NWHI to the northwest of FFS, and at Johnston Atoll, show that reproductive females and males periodically migrate to FFS for seasonal breeding (Balazs 1976, 1980, 1994). At the end of the nesting season, the turtles return to their respective foraging areas (Balazs 1994; Rice and Balazs 2008; D.M. Parker, G.H. Balazs, and M. Rice, unpubl. data, 2015; Fig. 2; http://akepa.hpa.edu/~mrice/turtle/ffsmigration/migration.html). Therefore, in the overall ecologic setting, FFS represents the prominent focal point of green turtle nesting and hatchling production in the Hawaiian Archipelago and, hence, the entire Central North Pacific Region (Wallace et al. 2010; Pilcher et al. 2012; Seminoff et al. 2015), although historically nesting was more geographically distributed throughout the Hawaiian Archipelago (Kittinger et al. 2013).

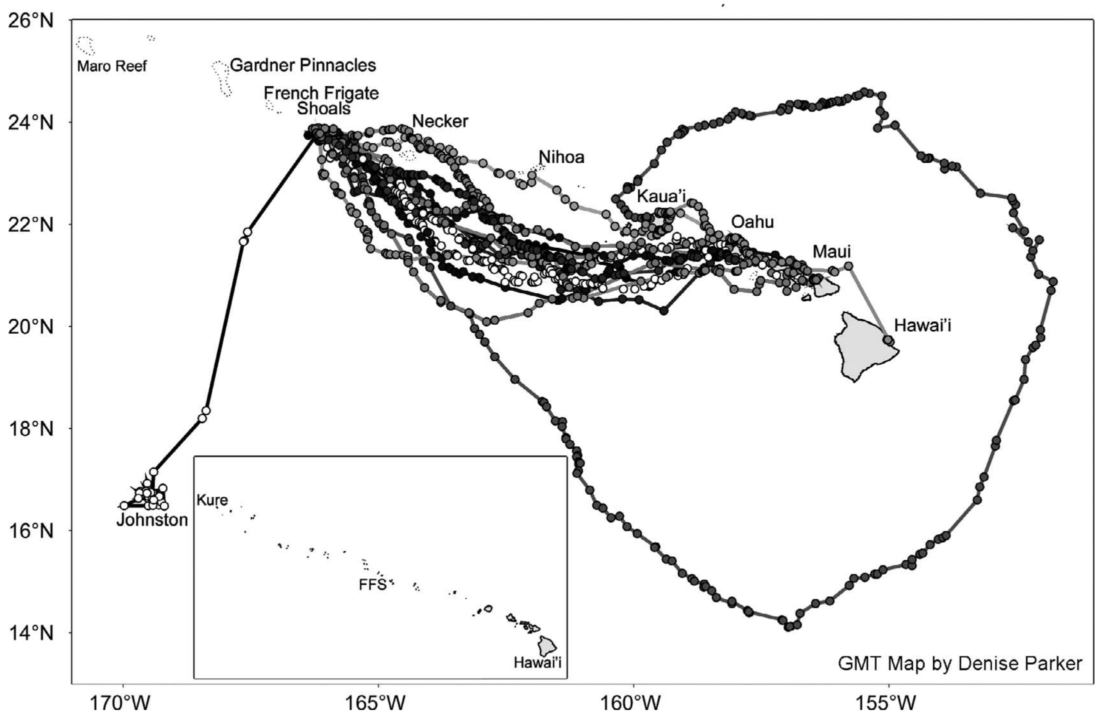

Figure 2. Post-reproductive migrations of 16 green turtles satellite tracked from French Frigate Shoals Northwestern Hawaiian Islands, 1992–1998 (D.M. Parker, G.H. Balazs, and M. Rice, unpubl. data, 2015).

METHODS

Annual surveys of the number of female green turtles coming ashore to nest each night were conducted at East Island, FFS, from 1973 to 2012 (Fig. 3). During the summer nesting season, each night females that emerged to nest were tagged and morphometric information recorded without restraint of the turtle. The standardized techniques of these surveys are detailed by Bogardus and Nurzia Humburg (2012) and Nurzia Humburg and Balazs (2014). Additionally, nesting and basking green turtles within FFS were intermittently and opportunistically tagged at islets other than East (e.g., Lautenslager 1985; Niethammer et al. 1997).

Some annual surveys were short because field personnel were not always able to remain on the island for lengthy periods because of logistics and safety considerations associated with the remoteness of the area. Consequently, in many years the surveys were an incomplete census. A Horwitz-Thompson type estimator was used to estimate total annual number of individual nesters (Wetherall et al. 1998). The sighting probability function was calibrated using entire nesting season census data derived from nightly emergence probabilities recorded for over 1100 nesters during a 5-yr full-season saturation program (May through September) conducted from 1988 to 1992 (Wetherall et al. 1998).

Maximum straight carapace length (SCL) and curved carapace length (CCL; Bolten 1999) were recorded to the nearest 0.1 cm using tree calipers and a flexible measuring tape. During 1999, nesting turtles were weighed on Tern Island to the nearest 0.1 kg using a portable tripod and scale (Pepi 2002). Double and triple tagging with alloy tags were applied to the flippers prior to 1996, and double tagging with passive integrated transponder (PIT) tags, one in each hind flipper, have been used since to positively identify each individual nester (Balazs 1999; Balazs and Chaloupka 2004, 2006). Clutch size and hatching success were estimated by direct observation including excavation of emerged nests, as described by Balazs (1980), Niethammer et al. (1997), Miller (1999), and Pepi (2002). Sand temperatures at a depth indicative of green turtle egg incubation were recorded using techniques described by Layton (2011).

Male and female sex ratio was determined from gonad examination (Work 2014) during necropsies of green turtles stranded in the MHI from 1983 to 2013 (e.g., Francke et al. 2014). This builds on earlier work of Koga and Balazs (1996), which used a shorter data set.

Somatic growth rates were calculated from turtles initially tagged at nearshore sites and later recaptured at the same sites, or while basking, or during nesting attempts. Age at maturity was then either extrapolated from these mark–recapture growth rates (e.g., Balazs 1980), estimated using skeletochronology (e.g., Zug et al. 2002), or modeled from both recaptures and skeletochronology relationships of length-to-age (e.g., Van Houtan et al. 2014).

Population growth rates were calculated from the time series of estimates of the annual abundance of nesting females at East Island, FFS. Recent assessments of loggerhead sea turtles (*Caretta caretta*) have calculated population growth using $N(\mathrm{t} + 1) = N(\mathrm{t}) + r$, where N is

Figure 3. Nesting green turtle at East Island, French Frigate Shoals, making its way back to the sea during the morning hours through a colony of Laysan and black-footed albatross (*Phoebastria* spp.). In 2012, the Hawaiian green turtle was downlisted by the International Union for Conservation of Nature (IUCN) from Endangered to their Red List category of Least Concern (see <http://www.iucnredlist.org/details/16285718/0>). Photo by Joseph Spring.

the ln-transformed annual count and r is the average rate of change (Conant et al. 2009; Van Houtan 2011). However, to keep consistency with previous green turtle studies (e.g., Chaloupka et al. 2008b), here we use regression parameters to estimate intrinsic growth from the time series of ln-transformed annual nester counts. These approaches are analogous to zero-order (loggerheads) and first-order (greens) density-dependent growth models (Van Houtan et al. 2009).

All quantitative information acquired during the course of this 40-yr study was digitized and quality checked for long-term storage and access, following the guidance by Briseno-Duenas and Abreu-Grobois (1999).

RESULTS

Demographic features for the FFS nesting colony at East Island and Tern Island were identified for 15 variables falling within 6 categories. Table 1 lists the various demographic data collected on nest dynamics and on renesting and remigration. Table 2 lists the various population demographic data on morphometrics, maturity and somatic growth, sex ratio, and intrinsic population growth. We describe these results in detail in the following sections.

Nest Dynamics. — From 1973 to 2012, 8 parameters were measured related to eggs, hatchlings, and internesting intervals of nesting green turtles at FFS (Table 1). In the early years, clutch size ($\bar{x}$ = 104 eggs), egg diameter ($\bar{x}$ = 44 mm), egg mass ($\bar{x}$ = 50 g), hatching success ($\bar{x}$ = 76.7%), emergence success ($\bar{x}$ = 70.8%), and internesting interval ($\bar{x}$ = 13.2 days) were quantified at East Island (Balazs 1980).

An in-depth study of reproductive ecology was undertaken at Tern Island from 1986 to 1991 (Niethammer et al. 1997). During those years, the earliest and latest nesting dates were 26 April and 20 October. Clutch size ($\bar{x}$ = 92.4 eggs), incubation period ($\bar{x}$ = 66 days), hatching success ($\bar{x}$ = 78.6%), and emergence success ($\bar{x}$ = 71.1%) were quantified. From 1986 to 1991, complete season nesting surveys were conducted on East Island, resulting in a complete census of the nesting population. The mean clutch frequency during those 5 yrs was 4 clutches per female (range, 1–9 clutches; Tiwari et al. 2010; this study). In 1999, Pepi (2002) conducted a full-season study on Tern Island, FFS, and obtained data on nesters and eggs. Results were similar to those of previous studies. The first nest was deposited on 13 May 1999 and the last on 29 September 1999. A mean of 2.8 clutches were laid per female (range, 1–6), and the mean internesting

Table 1. Nesting demographics of Hawaiian green turtles at their primary nesting colony, French Frigate Shoals, in the Northwestern Hawaiian Islands. Range estimates constitute 95% intervals either directly measured or calculated from standard deviations. East and Tern Islands constitute the majority of nesting at FFS. * Temperature at-depth measurements were obtained with data loggers; all other data were obtained through observations.

Variable	Mean	Range	Location	Period	Source
Nest dynamics					
Oviposition dates (nesting females)	6/15–8/1	4/26–10/20	Tern	1986–1991	Niethammer et al. 1997
Clutch size (nesting females)	104 eggs	38–145 eggs	East	1974	Balazs 1980
	92.4 eggs	33–150 eggs	Tern	1986–1991	Niethammer et al. 1997
	89.7 eggs	17–143 eggs	Tern	1999	Pepi 2002
Incubation period (nests)	64.5 d	54–88 d	East	1974	Balazs 1980
	66 d	53–97 d	Tern	1986–1991	Niethammer et al. 1997
	67 d	54–102 d	Tern	1999	Pepi 2002
Hatching success (nests)	76.7%	0–100%	East	1974–1975	Balazs 1980
	78.6%	77.5–85.1%	Tern	1986–1991	Niethammer et al. 1997
	80.6%	2–100%	Tern	1999	Pepi 2002
Emergence success (nests)	70.8%	0–97.6%	East	1974–1975	Balazs 1980
	71.1%	63.8–79.5%	Tern	1986–1991	Niethammer et al. 1997
Emergence dates (nests)	8/15–10/10	7/8–12/27	Tern	1986–1991	Niethammer et al. 1997
Temperature at-depth* (nests)	–	23.2–29.8°C	East	2003–2009	Layton 2011
Renesting and remigration					
Minimum reproductive longevity (nesting females)	8 yrs	2–38 yrs	East	1973–2013	This study
Remigration interval (nesting females)	4 yrs	2–9 yrs	East	1973–2013	This study
Internesting interval (nesting females)	13.2 d	11–18 d	East	1974–1975	Balazs 1980
	13.8 d	10–20 d	Tern	1999	Pepi 2002
Clutch frequency (nesting females)	1.8	1–6	East	1974–1975	Balazs 1980
	4	1–9	East	1988–1992	This study
	2.8	1–6	Tern	1999	Pepi 2002

interval was 13.8 d (range, 10–20 d). Each clutch contained a mean of 89.7 eggs (range, 12–143 eggs) and had a mean incubation period of 67 d with a mean hatching success of 80.6%. A sample of eggs were measured and averaged 47 mm in diameter and 52.3 g in mass.

The phenology of green turtle nesting at FFS also has been monitored. Peak oviposition spans 15 June to 1 August; however, nesting season spans late April through late October (Niethammer et al. 1997). The peak period of hatchling emergence runs from 15 August through 10 October but spans early July through late December (Niethammer et al. 1997).

Green turtles in Hawaii, like all sea turtle species, do not possess sex chromosomes but rather sex is determined from environmental temperatures. To address environmental influences on population sex ratios, Layton (2011) measured the beach and nest temperatures at Tern Island and East Island, FFS, in 2003–2004 and 2007–2009. Average nest temperatures in the middle third of the incubation period (the thermo-sensitive period when sex is determined) ranged between 23.2°C and 29.8°C. Although neither pivotal temperatures nor the transitional range of temperatures were previously established for Hawaiian green turtles, captive experiments by Layton (2011) suggest these important metrics are not significantly different from those described for other sea turtle populations. If this is true, then the pivotal sex determination temperature is near 29.0°C, and most nests at FFS are male biased. In fact, 60 of 68 (88%) nests examined by Layton (2011) were considered male biased, whereas the remaining 8 (12%) were female biased. Such a strong male bias is extremely uncommon across sampled sea turtle populations globally. As a result, it has been argued that this population may have evolved lower pivotal and transitional temperatures, in accord with the relatively cool nest temperatures. Layton's (2011) captive experiments, however, do not support this hypothesis but rather find the sex determination temperatures approximate those widely reported for other populations. Therefore, both field monitoring and experimental studies indicate that environmental conditions at FFS are producing a significantly male-biased population. However, this hypothesis is not supported by direct observations of sea turtles resulting from a robust necropsy data set (see "Sex Ratio").

Renesting and Remigration. — A mean remigration interval of 4 yrs was calculated during the study period 1973–2012 (Table 1). The range of intervals for this metric of periodicity of travel from residential foraging areas to the FFS nesting beach was 2–9 yrs.

Recapture durations, as a measure of minimum nesting longevities, were recorded by Nurzia Humburg and Balazs (2014) for 2138 turtles ranging from 2 to 38 yrs (Table 1; Fig. 4). Documentation of nesting of 20 yrs or more occurred with 155 (7.2%) of the turtles. The sole 38-yr nester was first tagged in 1973 and last seen nesting in 2011.

Morphometrics. — Four external anatomical metrics as well as body mass were recorded during the 1973–2012 study period (Table 1). From 1973 to 1979, a mean SCL of 92.2 cm and mean SCW of 71.4 cm were documented

Table 2. General population demographics of Hawaiian green turtles throughout the areas where they are measured in the Hawaiian Archipelago, including captive-raised turtles. SCL = straight carapace length, CCL = curved carapace length, SCW = straight carapace width, CCW = curved carapace width, CMR = capture–mark–recapture.

Variable	Mean	Range	Location	Period	Source
Morphometrics					
Adult females					
SCL (cm)	90.7	75–106	East	1973–2012	This study
SCL (cm)	92.2	81–106	East	1973–1979	Balazs 1980
CCL (cm)	97.0	78–113	East	1973–2012	This study
CCL (cm)	97.3	85–113	East	1973–1979	Balazs 1980
CCL (cm)	97.6	88–104	Tern	1999	Pepi 2002
SCW (cm)	71.4	60–86	East	1973–1979	Balazs 1980
CCW (cm)	91.2	80–107	East	1973–1979	Balazs 1980
CCW (cm)	90.9	82–102	Tern	1999	Pepi 2002
Mass (kg)	102.6	61–139	Tern	1999	Pepi 2002
Hatchlings					
Length (mm)	53	48–59	East	1974–1975	Balazs 1980
Length (mm)	51.1	45–57	Captive	1997–2009	This study
Mass (g)	31	25–35	East	1974–1975	Balazs 1980
Mass (g)	29	22.9–35.1	Captive	1997–2009	This study
Eggs					
Diameter (mm)	44	43–46	East	1974–1975	Balazs 1980
Diameter (mm)	47	–	Tern	1999	Pepi 2002
Mass (g)	50	45–54	East	1974–1975	Balazs 1980
Mass (g)	52.3	43–64.4	Tern	1999	Pepi 2002
Maturity—adult females					
Age at first reproduction (yrs)—CMR	23	17–28	MHI	1982–2012	Van Houtan et al. 2014
	40	35–50	All Hawaii	1973–2004	Balazs and Chaloupka 2004
Age at first reproduction (yrs)—skeletochronology	30+	35–50	MHI	1982–2002	Zug et al. 2002
Size at first reproduction (cm SCL)	89.7	82–97	East	1982–2012	Van Houtan et al. 2014
Somatic growth (cm SCL yr^{-1})					
CMR	3.8	3.0–5.0	MHI	1982–2012	Van Houtan et al. 2014
CMR	2.1	1.7–2.4	All Hawaii	1973–2004	Balazs and Chaloupka 2004
Skeletochronology	2.3	1.7–2.4	MHI	1982–2002	Zug et al. 2002
Sex ratio—female abundance (strandings) %					
Adults	61.6	57.5–64.5	All Hawaii	1982–2014	This study
Subadults	51.1	48.8–53.5	All Hawaii	1982–2014	This study
Juveniles	49.2	48.0–50.4	All Hawaii	1982–2014	This study
All age classes	51.6	50.6–52.6	All Hawaii	1975–2014	This study
All age classes	53.7	51.2–56.1	MHI	1982–1994	Koga and Balazs 1996
Intrinsic population growth—adult females %	5.4	5.0–5.8	East	1973–2012	This study
	5.7	5.3–6.1	East	1973–2003	Chaloupka et al. 2008a
	5.4	3.1–8.9	East	1973–2004	Chaloupka and Balazs 2007

(Balazs 1980). For all study years 1973–2012, mean SCL was 90.7 cm (n = 3414), and mean CCL was 97.0 cm (n = 3693). The smallest nesting female documented was SCL 74.6 cm, and the largest was SCL 105.5 cm.

During 1999, Pepi (2002), working at Tern Island, reported mean CCL of 97.6 cm (n = 44) and mean CCW of 90.9 cm (n = 38). The mean body mass of 64 nesters weighed by Pepi (2002) at Tern Island was 102.6 kg. The SCL and mass of a sample of newly emerged hatchlings recorded during 1974–1975 were $\bar{x}$ = 53 mm and $\bar{x}$ = 31 g (Balazs 1980).

Somatic Growth and Maturity. — Using skeletochronology methods to ascertain growth rates and age from growth markings on humeri cross sections, Zug et al. (2002) examined 104 green turtles from across the archipelago that ranged from 5.3 to 96 cm SCL in size. After developing several model relationships relating age and length, they suggested the age at first nesting for some individuals to be 30 or more years. These estimates are similar to those of Balazs (1980) and Balazs and Chaloupka (2004), which relied on growth rates extrapolated from observed growth over brief periods between captures of individual turtles caught repeatedly at foraging sites across the archipelago. Growth rates over these intervals were considered both size and site specific, such that growth rates generally decreased with increasing size, and growth rates were lowest in turtles from the cooler waters of the NWHI. Extrapolating these growth rates to expected size at maturity, both Balazs (1980) and Balazs and Chaloupka (2004) estimated age at first reproduction to be 35–40 yrs for the MHI but as high as 50 yrs for resident turtles at Midway and other locations in the NWHI.

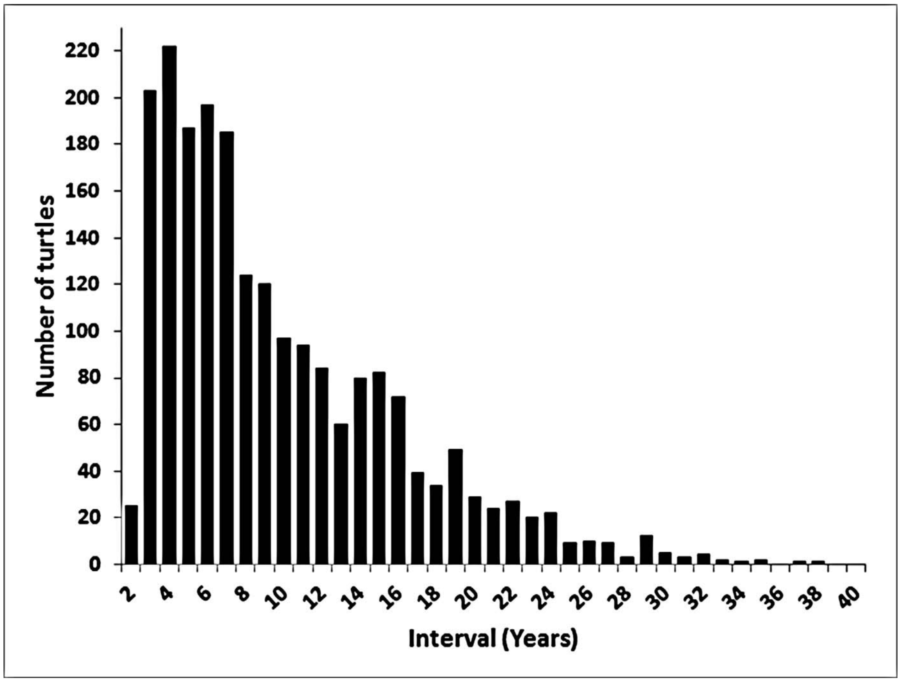

Figure 4. Recapture durations as an indication of minimum nesting life spans for green turtles nesting at French Frigate Shoals, 1973–2012 (n = 2138) (Nurzia Humburg and Balazs 2014).

Hargrove and Balazs (2011) presented data from direct tag recaptures of nesters at FFS showing that reproductive maturity can occur much earlier than previously estimated. Van Houtan et al. (2014), using a hybrid approach that employed data from skeletochronology and capture–recapture methods, also found significantly younger maturity ages. For 109 females that were first captured as juveniles or subadults in foraging grounds in the MHI, they estimated their age when first detected as putative neophyte breeders at East Island, FFS, in two ways. The first method inferred age from their measured length and using the skeletochronology-based age-to-length relationship (Zug et al. 2002). The second method used the Zug et al. (2002) model to estimate their age when first captured and then added the elapsed time between their first capture and first observed nesting. The second method resulted in younger and less variable age estimates, and a scaling rule developed from these results indicated females in this population might first breed on average at 23 yrs (95% interval, 17–29 yrs). These modeled results compared favorably with the only female in this population with a so-called living tag with a known date of birth and date of first breeding that first bred at 20 yrs. Because 85% of the turtles in the Van Houtan et al. (2014) study were captured only once on their foraging grounds, the authors suggested nearshore studies may sample an atypical type of the population that is sedentary and slow growing. As a result, growth rates from long-term monitoring of foraging grounds may have a negative bias and may overestimate maturity age.

Sex Ratio. — A total of 6616 green turtles ranging from 35 to 95 cm SCL were recorded from strandings occurring throughout the Hawaiian Islands during 1982 to May 2014. A total of 36.4% (2411) were necropsied and the gonads examined revealing that 51.0% (1229) were females and 49.0% (1182) were males. Assuming an adult size of > 81 cm SCL (Balazs 1980), 61.6% (172) of the necropsied turtles this size or greater were females, and 38.4% (107) were males, giving an adult gender ratio of 1.61:1 biased to females inferred for FFS. Necropsied turtles classified as subadults 65–81 cm SCL, a size class that might be expected to breed at FFS within 5–10 yrs, had a nearly equal female to male ratio of 1.05:1. These direct observations of gender involved a substantial data set of 2411 necropsy examinations.

Population Growth. — The 3 recent estimates of Hawaiian green turtle population growth are surprisingly similar. Using nesting data 1973–2003 and 1973–2004, Chaloupka et al. (2008b) and Chaloupka and Balazs (2007) calculated intrinsic growth at 5.7% (range, 5.3%–6.1%) and 5.4% (range, 3.1%–8.9%). Using, similar methods to the 2008 study, but expanding the analysis to nesting data from 1973 to 2012, we estimate intrinsic growth at 5.4% (range, 5.0%–5.8%). These estimates are statistically indistinguishable, indicating that the last 10 yrs have not demonstrated any slowing of population growth or negative density dependence as some predicted (e.g., Chaloupka and Balazs 2007). Using the larger 1973–2012 data set to establish growth rate parameters, Seminoff et al. (2015) performed a traditional population viability analysis (e.g., Van Houtan 2011) with these data. This study found a 0.0% probability that the population would fall below a variety of abundance thresholds that would indicate extinction risk (Fig. 5 adapted from Seminoff et al. 2015). These analyses suggest the Hawaiian green turtle population is still growing at a robust rate and underscore historical analyses (e.g., Kittinger et al. 2013; Van Houtan and Kittinger 2014) that suggest the population was significantly more abundant historically.

DISCUSSION

This article brings together current and historical demographic data for the breeding colony at FFS, a critical life-history element of the Hawaiian green turtle population. Information gaps have been filled, and the status of knowledge for the species has been advanced, as a component and comparative part of global green turtle biology (see Hirth 1997).

Demographic traits assembled herein have recently played key roles in conservation-status analyses, as reported by Seminoff et al. (2015), S. Piacenza, G. Balazs, S. Hargrove, P. Richards, and S. Heppell (unpubl. data, 2015), Pilcher et al. (2012), and Chaloupka and Balazs (2007). The need for more assessments of Hawaiian and other populations of green turtles can easily be anticipated. The magnitude of the need might be expected to increase as the present global dichotomy continues to widen between populations demonstrating encouraging signs of increasing numbers and those in decline in danger of extinction (Chaloupka et al. 2008a; Seminoff et al. 2015). The Hawaiian green turtle is presently exhibiting promising signs of recovery (Fig. 5) after 40 yrs of protection from heavy commercial harvest. However, climate change and the concomitant effects of sea level rise could potentially complicate the favorable upward trend through the potential loss of low-lying sand islets, such as East Island at FFS (Seminoff et al. 2015). Present predictions estimate a 30% loss of East Island nesting habitat by the year 2100. However, carrying capacity estimates by Tiwari et al. (2010) indicate that East Island habitat is currently hosting only 1.3%–2.0% of green turtle nestings possible before the density-dependent effects of nest destruction would manifest. In contrast, at least one of the resident nearshore foraging pastures in the Main Hawaiian Islands is already at carrying capacity in terms of algal food resources and the number of green turtles (Wabnitz et al. 2010). Although Wabnitz et al. (2010) focused on 1 site (Kaloko-Honokohau) on the Kona coast, that site is ecologically representative of green turtle foraging habitats that span 100 km of the west Hawaii Island coast. Similar observations on green turtle abundance and availability of forage have been made at 7 long-term green turtle study sites on the west coast of Hawaii Island.

With the evolving temporal and spatial collection of additional demographic information for more refined analyses, green turtles in the Hawaiian Islands can serve as an experimental model in comprehensively understanding the dynamics of a recovering sea turtle population. In addition, conservation and management practices in Hawaii founded on four decades of research findings can serve as a real-life learning ground for resident people at other insular Pacific islands interested in saving and sustaining their own charismatic and culturally important sea turtle resources.

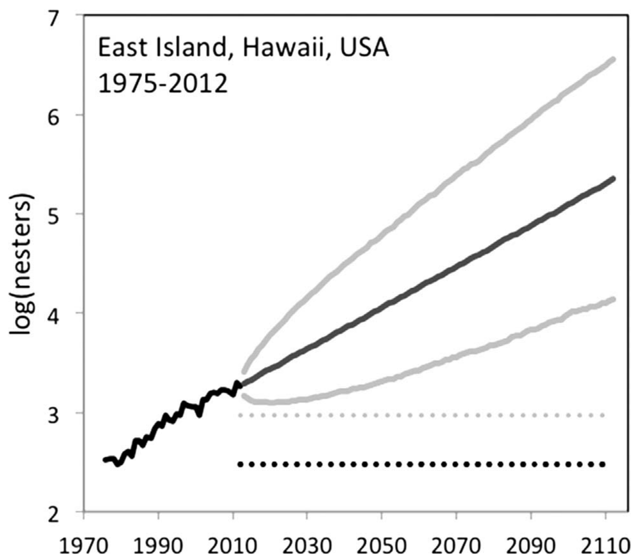

Figure 5. Stochastic Exponential Growth (SEG) Model Output for East Island, French Frigate Shoals, USA, adapted from Seminoff et al. (2015). Black line is observed data from 1973 to 2013 and the average of 10,000 simulations for 2014 and beyond; light gray lines are the 2.5 and 97.5 percentiles (serving as the 95% credible interval); gray dotted line is trend reference; and black dotted line is absolute abundance reference.

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