Modeling Sea Turtle Maturity Age from Partial Life History Records[1]

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Abstract: In the absence of direct observations, demographic traits such as age and reproductive status may be modeled through proxies. We examined 35 yr of over 10,000 captures of Hawaiian green turtles (*Chelonia mydas*) and compared results from skeletochronology studies with mark-recapture records. For 109 turtles that were captured as juveniles and later observed nesting, we estimated maturity age first from skeletochronology-based models of age to length and second by estimating age at first capture using skeletochronology and then adding the time elapsed to first nesting. The second method involving mark-recapture gave younger and less variable age estimates. From these data we developed a scaling rule that calculates that females first bred at 23 yr (95% interval: 16.8–28.1). This result was corroborated by tag returns in the Caribbean and Hawai'i showing that green turtles first nest at 16–20 yr. We validated this approach using life table models, successfully reconstructing four decades (1973–2012) of nesting surveys at East Island, French Frigate Shoals. We then compared our results with observed somatic growth rates, which suggest that nearshore studies may sample an atypical subset of the population that is chronically sedentary and slow growing. When exact life history traits are unknown, we recommend consulting multiple lines of evidence and independently validating proxy studies.

Demographic traits are important for assessing the long-term viability of wildlife populations (May 1976, Pimm 1991, Sæther and Bakke 2000, Williams et al. 2001). This is especially true for sea turtles (Crouse et al. 1987, Chaloupka and Musick 1997, Heppell 1998), whose populations consist of slow-growing, low-trophic-level consumers that reportedly take several decades to mature (Conant et al. 2009, Bjorndal et al. 2010, Jones et al. 2011, Bjorndal et al. 2013). Describing these life history characteristics accurately is crucial for understanding how anthropogenic and natural forces regulate sea turtle populations, both historically and today (Van Houtan and Halley 2011, Van Houtan and Kittinger 2014).

Despite their demonstrated value, such data are often difficult to obtain empirically. For most sea turtle populations, tracking individuals longitudinally from hatchling emergence to breeding is logistically challenging. Large geographic distances, sometimes spanning an entire ocean basin, may separate juvenile foraging grounds and adult breeding sites (Carr et al. 1978, Bowen et al. 1995, Benson et al. 2011). In addition, low survivorship to maturity requires an immense and continuous hatchling tagging effort monitoring for adult returns. An ongoing 20-yr project, for example, tagged nearly 190,000 turtle hatchlings before observing mature individuals first return years later to breed (Zurita et al. 2011). In Hawai'i, only one green turtle has been tracked throughout its development, from hatching to breeding in the wild. On 7 September 1980, turtle no. 5690 emerged from

her nest at French Frigate Shoals (FFS) in the Northwestern Hawaiian Islands (NWHI), was captively reared for 1 yr, and released into the wild at 21.7 cm straight carapace length (SCL). On 17 July 2000, no. 5690 was first observed nesting on Maui, at 19.9 yr of age and 92.5 cm SCL (Balazs et al. 2005). Though immensely important, such direct observations are unfortunately rare.

Age and reproductive status, as a result, are often inferred from empirical proxies. Such methods involve tissue stable isotope analysis, laparoscopic exams, morphometric measurements, mark-recapture, and skeletal demarcations (Snover 2002, Zug et al. 2002, Miller and Limpus 2003, Reich et al. 2007), or may be modeled at the population level from environmental data (Van Houtan and Halley 2011, Scott et al. 2012). Of these techniques, skeletochronology has been widely employed to estimate both age and growth rates for turtles in lieu of direct observations. For green turtles, skeletochronology methods suggest that breeding begins at 35–50 yr of age (Bjorndal et al. 1998, Zug et al. 2002, Goshe et al. 2010). Maturity estimates based on growth rates from nearshore captures are similar (Balazs 1980, Balazs and Chaloupka 2004a), with one estimate in the East Pacific population of 90–200 yr (Green 1993). These numbers exceed estimates for other sea turtle species (Zug et al. 1997, Zug et al. 2006, Van Houtan and Halley 2011, Jones et al. 2012, Snover et al. 2013) and are many times higher than estimates for captive green turtle populations (Bjorndal et al. 2013). Although skeletochronology may provide information on demographic traits that are otherwise difficult to obtain directly, established concerns with the method suggest that it should be independently validated (Chaloupka and Musick 1997, Bjorndal et al. 1998, Snover 2002, Snover et al. 2011).

In this study we developed methods that estimate age at maturity from partial observation records to calculate population-level estimates of age at first reproduction (AFR). We examined capture records from Hawaiian green turtles first captured on their foraging grounds and then later observed nesting. This population presents a unique opportunity to examine such issues because these turtles are genetically and geographically isolated in the archipelago (Dutton et al. 2008) and have been actively studied since the 1960s. We employed a variety of analytical techniques including nonparametric locally weighted regressions, generalized linear models, maximum likelihood estimation, and life table analysis. We compared skeletochronology-based age estimates with models that incorporate the elapsed time between the release and the first observed breeding. Using mark-recapture records that incompletely span individual life histories, we were therefore able to develop a scaling rule that estimates AFR for the population. Finally, we assessed the biological realism of our result through matrix simulations, reconstructing the last 40 yr of empirical nesting observations with different AFR values.

MATERIALS AND METHODS

Beginning in 1973, green turtles were captured on their foraging grounds at nearshore sites in the Main Hawaiian Islands, NWHI, and at Johnston Atoll, the geographic extent of the Hawaiian population (Balazs 1980, Balazs and Chaloupka 2004a). Turtles were measured and marked variously with flipper tags, biotelemetry devices, passive integrated transponders, and shell etchings. Previously marked turtles were later observed nesting by National Marine Fisheries Service (NMFS) survey crews at East Island, FFS (Balazs 1976, Balazs and Chaloupka 2004b), and opportunistically at other sites. From the standardized monitoring effort (average 29 days yr^{-1}) and the reported island fidelity of nesters (Niethammer et al. 1997) we considered individuals never before seen nesting to be putative neophyte breeders. Further details on monitoring and survey efforts are provided elsewhere (Balazs 1976, Balazs and Chaloupka 2004a, b).

We estimated AFR for each previously tagged neophyte nester using two formulae:

$$Y_s = S_i(x) = a_i(x - x_i)^3 + b_i(x - x_i)^2 + c_i(x - x_i) + d_i \quad (1)$$

$$Y_r = Y_s + (t_2 - t_1) \quad (2)$$

where Y_s is age calculated from the skeletochronology-derived relationship of SCL (x) and age, a method and model produced by Zug et al. (2002). Here, $S_i(x)$ is a cubic smoothing spline of age in years where the parameters a, b, c, and d are fit locally in a piecewise polynomial (Quinn and Keough 2002), and i (1, . . . , n) represents different terms in each parameter or variable series. (A variety of nonparametric regression smoothing techniques [Cleveland and Devlin 1988, Härdle 1990] give similar results.) When x is measured at first nesting, Y_s equals AFR. In the second method, we calculated AFR (Y_r) by adding the elapsed time between the release date (t_1) and the first nesting (t_2) to the age at release, the latter calculated from the turtle's measured length at release and equation (1). The smaller a turtle is at first capture, the more its estimated age relies on observed time. Therefore, because Y_r incorporates real calendar time in estimating AFR it can be used to assess, at least partially, Y_s, which relies wholly on bone-based methods (Plate I).

Next we developed a scaling rule to estimate AFR independent of skeletochronology. To do this, we first grouped turtles into 10 cm size classes (measured at initial capture) and fit probability models to the histograms of Y_s and Y_r. Detecting a positive skew in the resulting probability distributions, we fit normal and gamma probability density functions to the data (Pitman 1993). We selected model parameters using a maximum likelihood estimator and ranked models using an Akaike Information Criterion, similar to previous studies (Van Houtan et al. 2007, Van Houtan et al. 2010*a*). The highest-ranked models provided the distribution's variance and the AFR values at which 50%, 2.5%, and 97.5% of the cumulative observations fall below. The latter two values constitute the 95% credible interval for AFR, the former is the modeled median. Because Y_r apparently increases based on size at first capture, suggesting an artifact from skeletochronology, we plotted first capture size against the 50% probability values for Y_r for each class. Next we extrapolated a linear model of these data to hatchling size (Balazs 1980) to achieve a theoretically unbiased population-level AFR estimate, and

generated 95% intervals using JMP (SAS Institute Inc. 2012). Considering the data another way, we checked the method just described by fitting a curvilinear model through the raw time elapsed between capture and nesting ($t_2 - t_1$) plot against size at first capture. Here, however, we included the at-large data (released at 21.7 cm, 18.9 yr in the wild before observed nesting) from the only female Hawaiian green turtle tracked throughout ontogeny. We again extrapolated this model to hatchling size to infer on population-level AFR.

Finally we ran population simulations to reconstruct the observed 40 yr nesting time series from East Island, FFS (Balazs and Chaloupka 2004*b*), given the different AFR estimates. We built discrete stage-structured life tables based on egg production and considering annual survival uniquely for hatch year, pelagic juveniles, neritic juveniles, neritic subadults, and breeding adult turtles:

$$
\begin{bmatrix}
m_{1,1} & m_{2,1} & \cdots & m_{1,s} \\
m_{2,1} & m_{2,2} & \cdots & m_{2,s} \\
\vdots & \vdots & \ddots & \vdots \\
m_{s,1} & \cdots & \cdots & m_{s,s}
\end{bmatrix}
\begin{bmatrix}
n_1 \\ n_2 \\ \vdots \\ n_s
\end{bmatrix}_t
=
\begin{bmatrix}
n_1 \\ n_2 \\ \vdots \\ n_s
\end{bmatrix}_{t+1}
\quad (3)
$$

where the above population projection matrix incorporates fecundity, survival, and growth (Lefkovitch 1965). Here, s is the number of distinct life stages (for our study $s = 5$), and n_t is the total abundance of individuals in all life stages at time t. Because we are interested in AFR, our models compared $n_5/2$ (the total abundance of breeding females) with the nesters observed at East Island for each calendar year.

To do this we used Monte Carlo techniques to optimize neritic survival rates for each AFR estimate, produce a time series of $n_5/2$, and rank the model results as an Akaike Information Criterion (AIC$_c$) corrected for small samples:

$$
AIC_c = n \cdot \left[2\ln(D) + \frac{1 + (k-1)/n}{1 - (k+1)/n} \right] \quad (4)
$$

where k is the number of model parameters, n is the series length, and D is the mean square

deviation between the data and the model (Hurvich et al. 1998). We used nest survey counts from 1973 to 2012 from East Island, FFS (e.g., Balazs and Chaloupka 2004b), and estimated nesting from 1900 to 1972 as an annual 4% decrease given chronic harvest pressure (Kittinger et al. 2013, Van Houtan and Kittinger 2014). For our models, we considered clutch size of 92.4 eggs, clutch frequency of 4, 0.71% emergence success rates, and a 50:50 population sex ratio (Balazs 1980, Niethammer et al. 1997, Tiwari et al. 2010). Life stage transitions were from the skeletochronology of age to size (Plate I) and were proportionally adjusted for the earlier onset of maturity.

Because no empirical values are available for survival rates of Hawaiian green turtles, we set hatch year survival at 0.35 and pelagic juvenile survival at 0.80. Hatch year survival is the literature average, but pelagic juvenile survival was slightly higher than previous estimates (Crouse et al. 1987, Snover 2002, Jones et al. 2012) because Hawaiian green turtles have negligible interactions with pelagic fisheries, in comparison with other sea turtle species (Wallace et al. 2010). We considered two survivorship regimes for neritic stages: before and after federal and state protections went into effect in Hawai‘i in 1978. Before protection, Hawaiian green turtles were harvested for subsistence and in a small-scale commercial fishery (Van Houtan et al. 2013). Because all demographic stages were harvested (Van Houtan and Kittinger 2014) we equated all neritic survival rates across stages before 1978 (and capped those at 0.80) but allowed all neritic survival rates to vary after legal protection. We optimized the model for each AFR scenario (i.e., $Y_s = 41$ and $Y_r = 23$) but ran each AFR scenario for each optimization. This yielded four model outputs: both AFR scenarios optimized for Y_s, and both scenarios optimized for Y_r. Green turtles in Hawai‘i have a 4-yr remigration interval (G.H.B., unpubl. data) so we compared $n_5/2$ as described earlier with the total nesters observed in the most recent 4 yr of East Island surveys: a population running sum (Holmes 2001).

RESULTS

From 1984 to 2011, we documented 109 neophyte nesters that were previously tagged on their foraging grounds during 1977–2004 (four of these turtles were not measured at first nesting). At first capture 42% of these recaptures were juveniles, 49% were subadults, and 9% were nonbreeding adults, according to established size categories (Balazs 1980). Average size at first nesting was 89.7 cm (SD = 3.9, range = 80.5–100.1) SCL. Nine of the nesters were opportunistically documented at irregularly surveyed locations in the NWHI (two at Lisianski Island, seven at Tern Island, FFS), and one was located in a heavily populated area on Maui. Simple comparisons of the two methods for estimating age reveal differences that prompt more detailed analysis. Using skeletochronology (Y_s, Method 1), the average AFR was 41.3 yr (var. = 69, range = 27–60), similar to previous estimates for this population (Balazs and Chaloupka 2004a). However, the mark-recapture technique (Y_r, Method 2) gave an average of 36.2 yr (var. = 19, range = 28–45). Table 1 provides the full list of model results including parameters and 95% intervals.

Plate II shows that when compared with skeletochronology, our mark-recapture method consistently gave a younger and less variable estimate of age. From skeletochronology, the 50% cumulative probabilities of the highest-ranked models of AFR were 43, 41, 40, 41, and 44 yr, respectively, for the size at first capture groups of 40, 50, 60, 70, and 80 cm. From the mark-recapture method, the same results were 31, 35, 36, 38, and 41 yr, respectively. Based on comparisons within size class of these results alone, skeletochronology methods appear to overestimate AFR by 3–12 yr. Our AFR estimates that incorporate real time are not only younger, they are also less variable. The average width of the 95% confidence intervals for the skeletochronology distributions of AFR was 33 yr (range = 29–43), but it was less than half that (14 yr [range = 10–21]) for the mark-recapture distributions of AFR. This is illustrated in Plate II: the distributions of Y_r have more distinct peaks than the distributions of Y_s. These

TABLE 1

Full Results from the Maximum Likelihood Estimation Parameters and Probability Models

1st Capture Size (cm)	*n*	Aging Method	Fitted Model	AFR (yr)	95% Interval	Parameters		Var	ΔAIC
						Scale	Shape		
40–49	14	Skeletochronology	Gamma	43.2	25.2–68.1	16.0	2.70	121	−2.5
50–59	21	Skeletochronology	Gamma	41.3	28.0–58.0	29.6	1.41	59	−0.9
60–69	27	Skeletochronology	Gamma	39.9	27.2–56.0	29.9	1.35	54	−2.5
70–79	31	Skeletochronology	Gamma	40.7	27.8–57.0	30.3	1.36	56	−1.1
80–89	11	Skeletochronology	Gamma	43.8	28.5–63.7	24.3	1.83	81	−1.1
40–87	104	Skeletochronology	Gamma	41.3	27.1–59.5	25.5	1.64	69	−10.8
40–49	14	Mark-recapture	Gamma	31.4	26.6–36.6	149.9	0.21	7	0.5
50–59	21	Mark-recapture	Gamma	34.8	28.9–41.3	121.4	0.29	10	0.1
60–69	29	Mark-recapture	Gamma	35.5	29.7–41.9	130.7	0.27	10	0.1
70–79	34	Mark-recapture	Gamma	38.2	31.7–45.4	119.8	0.32	12	−1.4
80–89	11	Mark-recapture	Gamma	40.7	30.9–52.3	56.3	0.73	30	−1.1
40–87	109	Mark-recapture	Gamma	36.2	28.3–45.2	70.2	0.52	19	−5.2

Note: This table provides technical details from the probability model fits to the age at first reproduction (AFR) estimates shown in Plate II. "1st Capture Size" is the straight carapace length (SCL) of the turtles when first captured on foraging grounds, "*n*" is the number of individuals in this size class, and "Aging Method" refers to the aging techniques described in Plate I. "Fitted Model" refers to the probability distribution used in the MLE estimator. AFR here is the 50% inverse cumulative distribution function value, and "95% Interval" is the 2.5% and 97.5% values. We list the scale (θ) and shape (k) parameters for each model fit. Though we have 109 turtles for comparison, five were not measured when first seen nesting.

narrower AFR ranges more accurately reflect the observed phenotypic plasticities for maturity age across taxa (Stearns and Koella 1986). So although individuals born the same year might vary in their times to maturity, it is unlikely that variation would span 40 yr.

Because our mark-recapture models still contain a skeletochronology component (Plate I), they require further interpretation. Highlighted by the gray box in Plate II, mark-recapture AFR estimates increase in proportion to their size at release. In other words, nesters appear older simply because they are larger when previously caught. Because age at first capture is based on skeletochronology models, these data indicate mark-recapture-based age estimates increase proportionally to how much skeletochronology is used. Plate III*A* formally tests this by plotting the mark-recapture AFR estimate for each size class against average first capture length. A linear model of these data ($F_{1,4} = 78.1$, $R = 0.98$, $P = 0.003$) confirms this concern. The scaling rule developed from this model (Plate III*A*) calculates that turtles first captured as hatchlings would first nest at 22.5 yr. The scaling rule theoretically provides an unbiased population-level inference on AFR. (An analogous model developed from a model of first capture size and Y_s incidentally has no statistical relationship [$F_{1,4} = 0.0003$, $R = 0.01$, $P = 0.99$].)

As a reference point, it is worth comparing this result of AFR = 23 to the only female green turtle in Hawai'i with a complete life history record. The scaling rule developed from our Method 2 estimates that this turtle is 22.5 yr old, with a 0.075% probability that it is <20 yr of age. By comparison, the scaling rule developed from Method 1 (that relies solely on skeletochronology) estimates that no. 5690 is 41.7 yr old with a 0.00% probability that it would be <20. For this turtle, our model is 17 yr closer to the actual AFR than the skeletochronology estimate and suggests that 1 in 13 turtles would first breed by that age. The skeletochronology method says that such a young AFR is basically impossible. As a comparison with our Method 2, Plate III*B* plots the curvilinear relationship between the raw time at large and size at release. Here, we highlight in red the nesters documented on irregularly surveyed NWHI locations. Extrapolating this model to hatchling size

TABLE 2

Full Results from the Life Table Model Reconstructions

Aging Method	AFR (yr)	Life Stage	Cohort Years	Survival –1977	Survival 1978–	2009–2012 Nesters	RMSE	ΔAIC	Model Rank
CMR model	23	Hatch year	1	*0.350*	0.350	2,311	54	0	1
		Pelagic juvenile	2–3	*0.800*	0.800				
		Neritic juvenile	4–10	*0.799*	*0.824*				
		Subadult	11–22	0.799	*0.876*				
		Breeding adult	23–	0.799	*0.930*				
Skeletochronology	41	Hatch year	1	*0.350*	0.350	2,005	144	90	2
		Pelagic juvenile	2–7	*0.800*	0.800				
		Neritic juvenile	8–20	*0.800*	*0.967*				
		Subadult	21–40	0.800	*0.980*				
		Breeding adult	41–	0.800	*0.980*				
CMR model	23	Hatch year	1	0.350	0.350	29,573	534	480	4
		Pelagic juvenile	2–3	0.800	0.800				
		Neritic juvenile	4–10	*0.800*	*0.967*				
		Subadult	11–22	0.800	*0.980*				
		Breeding adult	23–	0.800	*0.980*				
Skeletochronology	41	Hatch year	1	*0.350*	0.350	58	185	131	3
		Pelagic juvenile	2–7	*0.800*	0.800				
		Neritic juvenile	8–20	*0.799*	*0.824*				
		Subadult	21–40	0.799	*0.876*				
		Breeding adult	41–	0.799	*0.930*				

Note: Here we present model details and results for four life table analyses assuming two estimates of age at maturity. We incorporate relevant nesting characteristics from the literature to generate annual egg production at East Island, French Frigate Shoals, from 1900 to 2012 (see Materials and Methods). We model five discrete life stages and provide duration and fitted survival rates for each. "Survival –1977" is the regime during the harvest period, "Survival 1978–" is during the period of active conservation management. "2009–2012 Nesters" is the model result for running sum of 2009–2012 nesting, with the actual value being 1,855. RMSE is root-mean-square error. ΔAIC values and Model Rankings are provided. ***Bold italicized*** values are fitted values; other vital rates are fixed or dependently related (see Materials and Methods).

(5.3 cm), again simulating a wild hatchling, estimates AFR is 23.3 yr, close to our estimates using Method 2.

Next we assessed different AFR estimates by reconstructing 40 yr of nesting observations at the principal rookery. The highest-ranked life table model is when neritic survival is optimized for 23 yr to maturity (Plate IV). Under this scenario, survival pre-1978 is 0.80 for all neritic stages, and after protection in 1978 survival increases to 0.82, 0.88, and 0.93 for neritic juveniles, subadults, and adults, respectively. These vital rates are realistic for an actively protected population with minimal anthropogenic mortality. In Plate IV results of this model are plotted against the observed nesting from 1973 to 2012, demonstrating remarkable agreement. When models optimize survival rates for 41 yr to maturity, neritic survival rates become unrealistically

high. When AFR = 41, neritic survival during the harvest period is again 0.80 and after conservation protection climbs to 0.97–0.98 for all neritic stages. These values far exceed published sea turtle survival rates (Crouse et al. 1987, Snover 2002). Table 2 provides full model details and results, including vital parameters and AIC_c values.

DISCUSSION

Our analysis of AFR in Hawaiian turtles provided several significant results. First, methods using real time from mark-recapture efforts gave younger and less variable age estimates (Plate II, Table 1). This suggests that skeletochronology overestimates sea turtle age, especially in larger turtles. Second, our mark-recapture records estimated that Hawaiian green turtles began nesting at 23 yr

(Plate III), approximately half the age of previous estimates for this population. Third, this younger age at maturity seems to uniquely be able to explain the observed 40-yr nesting recovery population trend (Plate IV). We discuss these results and their implications here.

First, our results are corroborated in Atlantic green turtles. Using skeletochronology to calculate age from measurement data (our Method 1, Plate I), in a recent paper Goshe et al. (2010) calculated that females from Yucatán, Mexico, population mature at 42 yr. However, a recent study by Zurita et al. (2011) reported that hatchlings from that population return on average at 16 yr (range: 12–20 yr), 26 yr earlier than the skeletochronology estimate. A similar mark-recapture project in the Cayman Islands also observed green turtles first nesting at 15–19 yr (Bell and Parsons 2002, Bell et al. 2005). In both the Cayman and Yucatán projects, hatchlings captively reared for 1 yr before release returned 2–3 yr in advance of released hatchlings. This earlier maturity equals the 3-yr difference in Hawai'i between turtle no. 5690 and our Y_r of 23 yr (Plate III*A*). For green turtles in the Caribbean and Hawai'i, then: (1) mark-recapture-based estimates of maturity are near 20 yr, (2) skeletochronology estimates are 40 yr or more, and (3) 1 yr captive rearing minimally advances AFR.

To first breed at 23 yr Hawaiian green turtles would grow on average 3.8 cm yr^{-1}. We make this calculation by dividing the growth from hatchling (5.3 cm SCL) to first breeding size (89.7 cm SCL) by Y_r. This value exactly equals the 3.8 cm yr^{-1} growth of no. 5690 observed from its release from captivity to its first observed nesting (including the captive year, cumulative growth was 4.4 cm yr^{-1}). Similar calculations from the Caribbean studies mentioned earlier give growth rates for Yucatán and Cayman neophyte nesters of 6.2 and 6.3 cm yr^{-1}, respectively. A subsequent analysis of the Cayman project data calculated average growth rates of wild turtles at 6–7 cm yr^{-1} over development, but as high as 13–14 cm yr^{-1} (Bell et al. 2005). A separate study of 47 captive female Atlantic green turtles from distinct populations yielded higher growth rates of 7–13 cm yr^{-1} throughout ontogeny (Bjorndal et al. 2013). Further, four captively reared Hawaiian green turtles reached 53.0 cm SCL in 6.0 yr, averaging 9.0 cm yr^{-1} growth during that time (Balazs 1980).

Although it is unsurprising that Hawaiian turtles may grow more slowly than Caribbean populations (Balazs 1980, Van Buskirk and Crowder 1994), such wild growth rates exceed those observed in Hawai'i (Balazs 1980, Balazs and Chaloupka 2004*a*). There are at least four explanations for these differences. First, neritic studies miss the earliest life stage where growth rates are highest (Chaloupka and Musick 1997, Jones et al. 2011). Though such growth rates do not persist throughout development, neritic studies a priori omit the rapid growth in early juvenile development. Second, 83% (91/109) of the putative neophyte nesters we report here were captured only once before nesting. In-water surveys in Hawai'i, by contrast, repeatedly capture the same individuals at local foraging grounds for decades. Growth rates are calculated from such chronically recaptured turtles (Balazs 1980, Balazs and Chaloupka 2004*a*). We propose that such studies may sample a unique subset of chronically sedentary and slow-growing turtles that are not indicative of the entire population. Less sedentary turtles or those that do not reside in the shallow back-reef habitat where surveys occur (Van Houtan and Kittinger 2014), by contrast, are not well represented. Third, several neritic capture sites in Hawai'i are in poor-quality habitat (Balazs 1980, Wabnitz et al. 2010) causing particularly slow growth rates (Balazs and Chaloupka 2004*a*). These habitats are not indicative of the Hawaiian archipelago and population as a whole. Fourth, neritic studies include turtles afflicted with the tumor-forming disease fibropapillomatosis (Van Houtan et al. 2010*b*), which can inhibit growth (Chaloupka and Balazs 2005, Goshe 2009). Nesting turtles, however, are almost entirely disease free (Balazs and Chaloupka 2004*b*). Given these issues, our estimate of 3.8 cm yr^{-1} growth from hatchling to maturity is plausible and was observed in the only Hawaiian green turtle tracked throughout ontogeny.

Forty years of nesting monitoring in Hawai'i also supports our results. If our AFR estimate is accurate, models that optimize vital rates to first breeding age to 23 yr will produce realistic survival rates and outperform models fitted to the later-onset maturity as suggested by skeletochronology studies. This is exactly what happens. Our life table analysis calculates neritic survival rates between 0.82 and 0.93 from 1978 to 2012, assuming females begin breeding at 23 yr. This model also produces a nesting time series consistent with observed counts (Plate IV). Models with sexual maturity at 41 yr do not perform as well (Table 2) but, crucially, require unrealistically high neritic survival rates (0.97–0.98) never before seen. Of note, our life table models do not consider density dependence factors. However, if increased population density restricted available resources and inhibited development, we would expect slowed growth and delayed maturity over the course of our study. We found no evidence to support this. No statistical relationship exists between first nesting date and either Y_r [$F_{1,103} = 0.9$, $R = -0.09$, $P = 0.34$] or Y_s [$F_{1,103} = 0.9$, $R = -0.09$, $P = 0.35$]. As it stands, the population of green turtles in Hawai'i rebounded from its near extinction more quickly than anticipated. This may be a result of the younger AFR we report here and seems improbable given a later onset of maturity. For example, if this population matured at 41 yr, the first fully protected population cohort would not breed until 2019. This means the population recovery observed at East Island to date (Plate IV) would be completely from increased survivorship of neritic juveniles and subadults and bears no recursive relationship to the observed increase in nesting. This achievement requires unprecedented annual survival.

To this point, we have not considered that our nesting surveys may have missed prior nesting events, inflating our estimate of the time between release and first nesting, and Y_r as a result. Plate III*B* highlights 10 of the 109 turtles sighted opportunistically, not at the index site of East Island, FFS. Turtle no. 5690 nested on a popular beach on West Maui, and it is unlikely that a previous nesting went undetected. The other nine, however, nested at remote sites in the NWHI. It is likely that these turtles nested before detection. Six of these nine points, for example, are above the model fit line, with two being borderline outliers. Although this subset of the data is not large enough to consider separately, it may suggest a bias. Nonetheless, it communicates that field monitoring efforts may have missed nesting events, especially at irregularly monitored sites but also at the index site. Monitoring at East Island only spanned the entire nesting season from 1988–1992, and averaged 29 days yr^{-1} over the entire monitoring period. (It is for this reason that raw counts of nester abundance are statistically corrected for partial effort [Wetherall et al. 1998].) Missing prior nesting events would bring our AFR estimates lower (removing the nine points brings the AFR estimate down to 22.4 yr), further away from skeletochronology estimates. Turtles larger than 80 cm SCL are considered adults, moreover, and could have nested before they were initially tagged in their foraging grounds in the Main Hawaiian Islands. Conversely, Plate III*B* does report that the range of AFR values could include turtles above 30 yr of age, however improbable.

How do we reconcile our results with skeletochronology estimates? One explanation is that sea turtle bones exhibit subannual markings. Fish otoliths can accrue daily accretion marks, and such analyses often validate skeletal growth using radiocarbon dating (Andrews et al. 2011). Latitude could also be influential. Green turtles are generally restricted to tropical and subtropical waters, which have less-pronounced phenologies compared with temperate zones, making environmental stressors less distinct (Bjorndal et al. 1998, Worbes 1999). A recent analysis sought to address such concerns, using oxytetracycline to validate annual bone markings (Snover et al. 2011). The results were ambiguous. Of the seven turtles examined, four had fibropapillomatosis. One of these diseased turtles exhibited semiannual bone marks, which the authors attributed to stress from snorkeling tourists (Snover et al. 2011). Annual marks were found in the three remaining turtles, comprising two juveniles and one subadult (range: 46–70 cm SCL). These three turtles
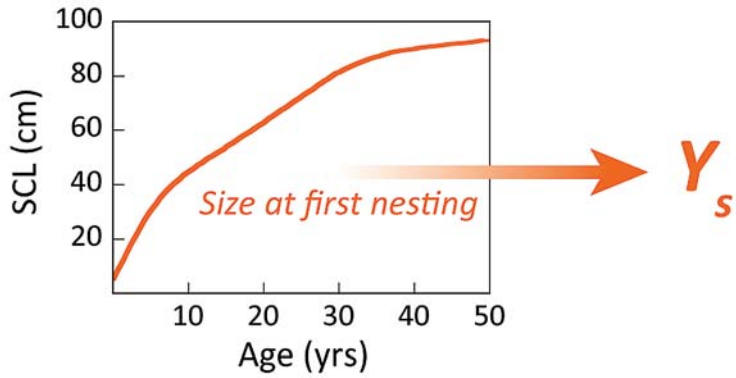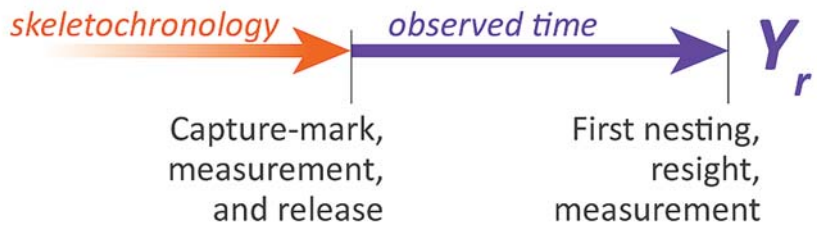
PLATE 1. Methods to estimate sea turtle maturity. We estimated age at first reproduction (AFR) for 109 Hawaiian green sea turtles that were first captured as juveniles and later recaptured after purportedly first nesting. Method 1 calculates AFR from measured female length at first nesting. The line plot shows the skeletochronology-derived relationship of length and age from a previous study (Zug et al. 2002). Method 2 uses the skeletochronology plot to estimate age of turtles at first capture added to the elapsed time to first nesting record to estimate AFR. Because the second method incorporates real time, it can be used to assess the accuracy of skeletochronology.
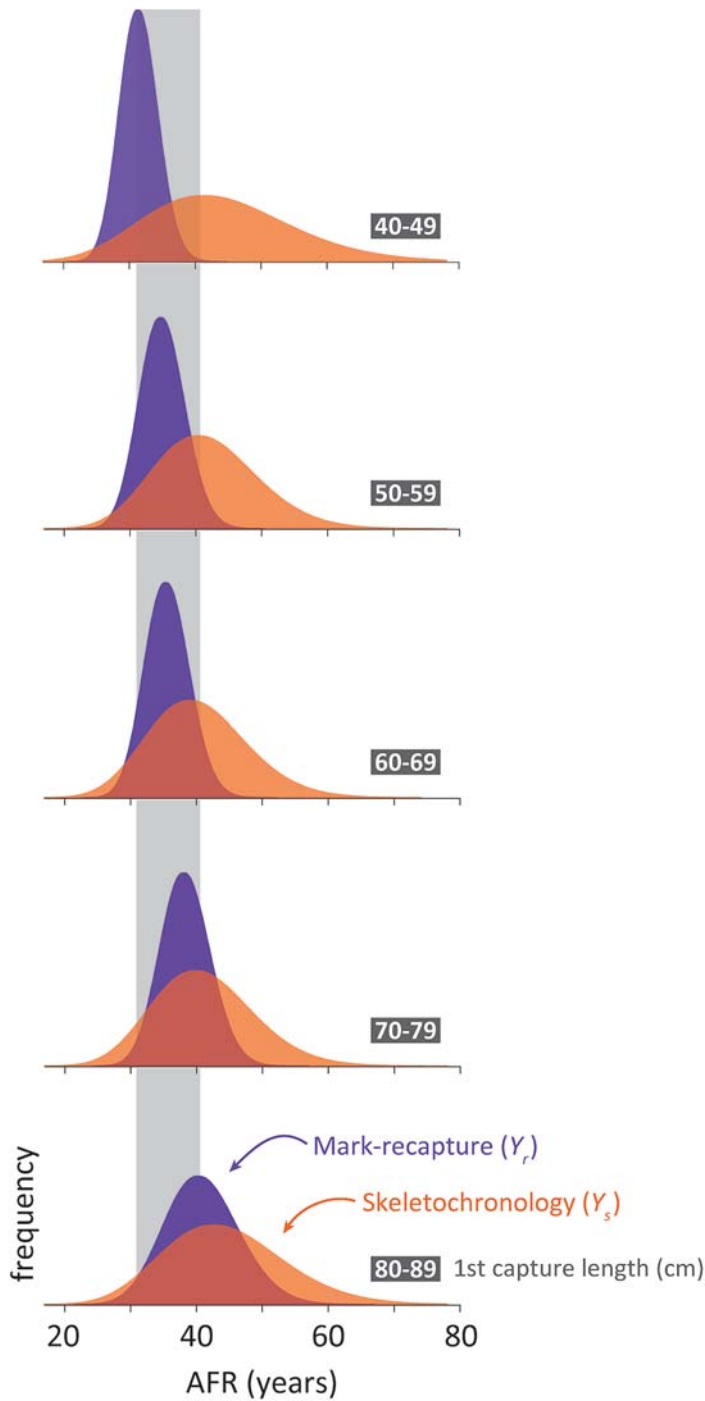
PLATE II. Mark-recapture based methods give younger and less variable age estimates of AFR. Probability distributions for mark-recapture (purple) and skeletochronology (orange) estimates of AFR, grouped according to size at first capture (labeled dark gray boxes). These curves show that mark-recapture estimates are consistently younger and less variable, suggesting that skeletochronology systematically overestimates age. Because our mark-recapture method employs both skeletochronology and observed time, the extent to which each is used may reveal a population AFR estimate. Light gray band across all panels highlights the migration in the peak distribution of Y_r.
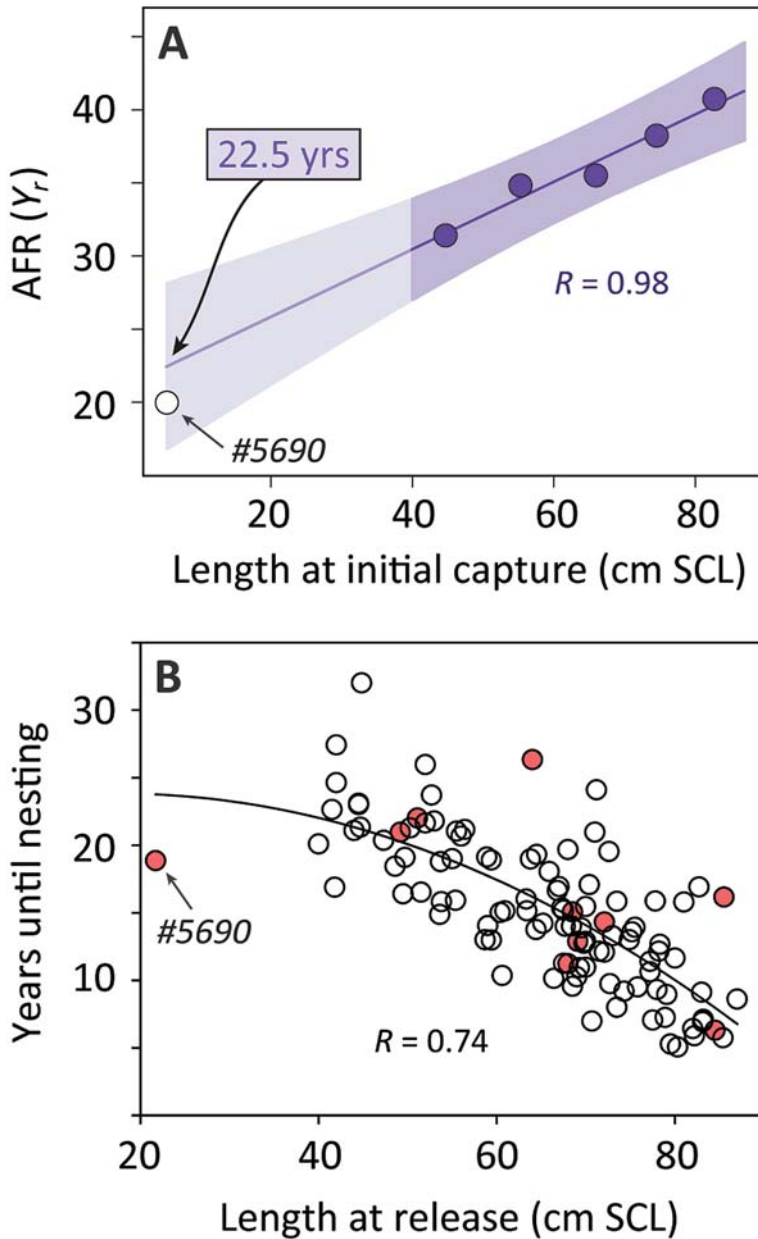
PLATE III. Hawaiian green turtles may reach maturity at 23 yr, significantly sooner than previous estimates. *A*, The 50% inverse cumulative probabilities for Y_r (purple circles) plotted against the average first capture size, for each size class shown in Plate II. Solid purple line is a linear model fit, light line is its projection beyond the empirical bounds to hatchling size, with the shaded area being the 95% interval. This scaling rule proposes that turtles observed over their entire maturity period will first breed at 22.5 yr. For comparison, we plot no. 5690 (white circle, not included in the model), the only wild Hawaiian green turtle whose hatching and first nesting date are precisely known. No. 5690 first nested at 19.9 yr, within the confidence limits for our model estimate. The skeletochronology AFR estimate (Y_s) for this turtle was 41.7 yr, more than twice the actual age. *B*, Alternatively, plotting raw time elapsed between release and first nesting produces a model that estimates AFR is 23.3 yr. Red circles highlight putative neophyte nesters from irregularly surveyed locations. Nine of these turtles nested in remote NWHI atolls and could have nested previously undetected.
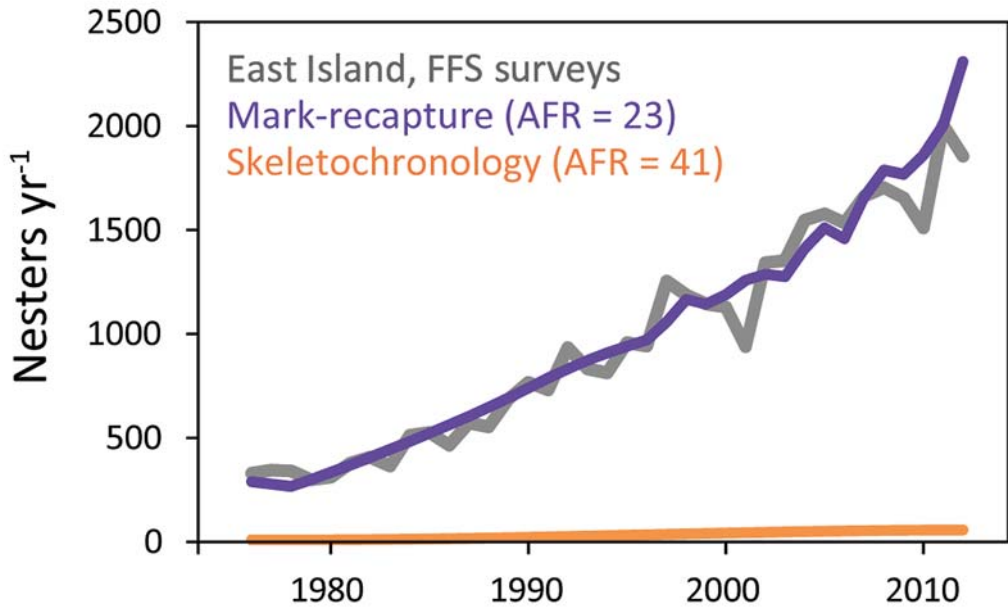
PLATE IV. Nesting population reconstructions given different age estimates. Here we compare nester surveys at French Frigate Shoals, Northwestern Hawaiian Islands, to life table model reconstructions. The increasing survey trend documents the ongoing population increase since the prohibition of harvests and implementation of protections during 1974–1978. Purple line is the fitted model considering age at maturity of 23 yr, producing survival rates in neritic life stages from 0.78 to 0.90 (selected by the model). For comparison, the orange line uses the same vital rates but assumes a maturity of 41 yr. Gray line is a 4-yr running sum of the survey counts, accounting for remigration intervals, to give a full picture of the standing population of breeding females. For full model results, see Table 2.

are restricted to one section of the population's growth curve (Plate I), so it is speculative whether the findings translate to either neonates or breeding adults. Different life stages are subject to unique physiological stresses and environments that affect growth. Young juveniles, for example, reside in pelagic ecosystems whose productivity shows dramatic spatiotemporal fluctuations (Van Houtan and Halley 2011). Adults uniquely face the metabolic demands of migration to breeding areas, yolk formation, and nesting.

Along these lines, a recent study of Hawaiian green turtles found no statistical relationship between turtle length and bone demarcations (Murakawa 2012). In that study 99 turtles from 36 cm to 98 cm SCL were examined, and it was reported that subadults had the most growth marks and mature adults often had fewer than juveniles. This highlights the role of bone resorption corrections in skeletochronology estimates. Aside from subannual demarcations, skeletochronology may separately inflate age estimates by overcorrecting for missing growth lines. Skeletal aging for sea turtles is estimated not simply by tabulating the number of bone marks but by supplementing the empirical count to correct growth marks lost to marrow resorption (Chaloupka and Musick 1997, Zug et al. 2002, Goshe et al. 2010). These various correction factors can account for >95% of the total skeletal age estimate for green turtles (Murakawa 2012). Because resorption increases with age, correction factors are increasingly relevant in older turtles, perhaps explaining the increasing bias we detected (Plates II, III*A*).

There is much debate about sea turtle age to maturity. The evidence presented here brings maturity age estimates for green turtles more in line with those for other sea turtle species. Though estimates vary, most studies of leatherback (*Dermochelys coriacea*) and various hard-shell species estimate that sexual maturity occurs at 10–30 yr (Zug et al. 1997, Zug et al. 2006, Jones et al. 2011, Van Houtan and Halley 2011, Snover et al. 2013). Our estimate of 23 yr for Hawaiian greens and the 15–20 yr reported for Caribbean recapture studies (Bell and Parsons 2002, Bell et al. 2005, Zurita et al. 2011) are within this range.

These estimates contrast with the bone-based estimates of >40 yr (Zug et al. 2002, Goshe et al. 2010). In a similar comparison with Atlantic leatherbacks, DNA analyses indicated that AFR values ranged from 9 to 15 yr (Dutton et al. 2005), and skeletochronology estimates were roughly twice that at 25–29 yr (Avens et al. 2009). We therefore suggest consulting multiple lines of evidence for life history parameters of such importance for management. Bomb radiocarbon dating (Andrews et al. 2011), stable isotope analysis (Hatase et al. 2002, Reich et al. 2007), and climate studies (Van Houtan and Halley 2011) may also shed light on time to maturity. Our results should be tempered against the possibility that our study represents only the first and youngest group of nesters and that subsequent monitoring over longer time scales may document substantially older neophyte breeders. Time will tell. However, the younger age to maturity seems uniquely able to explain the past four decades of nesting surveys and recovery (Plate IV, Table 2). Above all, these results demonstrate once again the critical importance of long-term monitoring as the fundamental basis of population ecology and conservation management (Pimm 1991).

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