

Age and growth rates of Hawaiian hawksbill turtles (*Eretmochelys imbricata*) using skeletochronology

Melissa L. Snover · George H. Balazs ·
Shawn K. K. Murakawa · Stacy K. Hargrove ·
Marc R. Rice · William A. Seitz

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Abstract The Hawaiian hawksbill population has fewer than 20 females nesting per year; hence, there is a need to monitor this population closely and basic biological information on individual growth and age to maturity is critical. We present a skeletochronology analysis of Hawaiian hawksbills using humeri recovered from 30 dead stranded hawksbills, plus 10 dead hatchlings. Growth mark morphology shows readily distinguishable marks similar in appearance to other species, though some animals displayed more diffuse marks. Growth rates remained high (average 2.24–4.77 cm year⁻¹) from 20 to 80 cm straight carapace length (SCL). Hawksbills larger than 80 cm SCL had average growth rates of 0.3 cm year⁻¹. There were

few adult turtles in the sample; however, results indicate hawksbills have faster growth rates than loggerhead or green turtles, with probable average age to maturity (at size 78.6 cm SCL) occurring between 17 and 22 years.

Introduction

Individual growth rates and age at sexual maturity are critical variables for understanding the population dynamics of a species. Generally, very little information exists regarding these parameters for hawksbill turtles (*Eretmochelys imbricata*), especially for the Hawaiian population, making management decisions for this species difficult. Our ability to successfully conserve and protect these populations is important because they have been greatly diminished due to extensive hunting throughout their range, primarily for their carapaces which are used in tortoise shell jewelry and other crafts (NMFS and USFWS 1993, 1998). Hawksbill turtles are considered endangered globally under the U.S. Endangered Species Act and critically endangered on the IUCN redlist. The hawksbill population in Hawaii, an archipelago in the North Pacific, is particularly small, with fewer than 20 nesting females per year, primarily on the island of Hawaii (Seitz et al. 2012), with most nesting in Hawaii confined to the southeastern region of the Hawaiian Archipelago (Parker et al. 2009).

Neritic juvenile and adult hawksbill turtles are found primarily in tropical, coral reef habitats in the Atlantic Ocean, Caribbean Sea, Pacific Ocean, and Indian Ocean (NMFS and USFWS 1993, 1998). Globally, the average size of an adult female hawksbill is 78.6 cm straight carapace length (SCL; van Buskirk and Crowder 1994; Miller 1996). In Hawaii, the mean size of nesting females is 82.3 cm SCL (range 72–90 cm SCL; Seitz et al. 2012). Nesting occurs on

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M. L. Snover · G. H. Balazs · S. K. K. Murakawa ·
S. K. Hargrove
NOAA Fisheries, Pacific Islands Fisheries Science Center,
2570 Dole St., Honolulu, HI 96822, USA

Present Address:

M. L. Snover (✉)
Denali National Park and Preserve, P.O. Box 9, Milepost 237
George Parks Highway, Denali Park, AK 99755, USA
e-mail: melissa_snover@nps.gov

M. R. Rice
Hawaii Preparatory Academy, 65-1692 Kohala Mt. Rd.,
Kamuela, HI 96743, USA

W. A. Seitz
Hawaii Island Hawksbill Turtle Recovery Project, Pacific
Cooperative Studies Unit, University of Hawaii-Mānoa,
P.O. Box 52, Hawaii National Park, HI 96718, USA

W. A. Seitz
Hawaii Volcanoes National Park, P.O. Box 52,
Hawaii National Park, HI 96718, USA

ocean-facing beaches and, typical of most other sea turtle species, hatchling hawksbills swim directly off shore and remain pelagic for an unknown period of time, though Boulon (1994) estimated this duration at 1–3 years for turtles that recruit to neritic habitats at 20–25 cm SCL, the smallest size classes observed in coral reef habitats in the Virgin Islands.

Skeletochronology, the analysis of growth marks found in cross-sections of long bones, has been used to estimate age and growth rates in most marine turtle species: loggerhead (*Caretta caretta*; Snover and Hohn 2004; Snover et al. 2007a), leatherback (*Dermochelys coriacea*; Avens et al. 2009), green (*Chelonia mydas*; Zug and Glor 1998; Zug et al. 2002; Goshe et al. 2010), Kemp's (*Lepidochelys kempii*; Snover and Hohn 2004; Snover et al. 2007b), and olive (*Lepidochelys olivacea*; Zug et al. 2006) ridleys. The annual nature of skeletal growth marks has been validated for loggerhead (Klinger and Musick 1992; Coles et al. 2001; Snover and Hohn 2004), Kemp's ridley (Snover and Hohn 2004), and green turtles (Goshe et al. 2010, Snover et al. 2011).

Other methods have been used to estimate age and growth rates in hawksbills. Most commonly used is mark-recapture growth data (Boulon 1994; Chaloupka and Limpus 1997; León and Diez 1999; Diez and Dam 2002; Bell and Pike 2012); however, this method yields limited longitudinal data for information on individual growth. Other studies have examined the possibility of inferring age from the speckle patterns found on scutes of the carapace (Kobayashi 2000, 2001). This method is intriguing as it can be applied noninvasively to live animals; however, further validation work is needed, and its application would be limited as individual, longitudinal growth data cannot be inferred as it can be using skeletochronology (Snover et al. 2007a).

Here, we apply skeletochronology to humeri recovered from Hawaiian hawksbill turtles. We present the following: (1) characterization of the relationship between humerus diameter at the site where the bone is sectioned for skeletochronology and carapace length, (2) incorporation of this relationship into the back-calculation technique developed by Francis (1990), termed the Body Proportional Hypothesis and modified for sea turtles by Snover et al. (2007a), (3) estimates of size-at-age for 23 hawksbill turtles and for each growth mark, resulting in 120 size-at-age data points, and (4) fits of growth curves to estimate age at maturity for hawksbills in Hawaii.

Methods

We obtained humeri and carapace length measurements for 40 free-ranging hawksbill turtles found stranded dead on

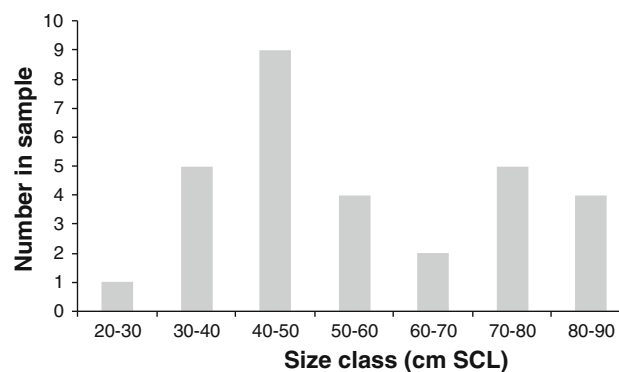


Fig. 1 Distribution of carapace lengths from dead stranded hawksbill turtles in this study, measured as straight carapace length (SCL) from notch-to-tip ($N = 30$), excluding hatchlings

beaches in Hawaii. Our sample contained 30 juvenile and adult turtles between 26.2 and 83.8 cm straight carapace length (SCL), and 10 hatchlings recovered dead from nests on Maui (Fig. 1). For size, we used the SCL measurements taken with calipers from the nuchal notch-to-the-posterior end of the posterior marginal scute (notch-to-tip). The humeri were flensed, boiled to remove remaining soft tissue and air-dried for several weeks.

Age estimation

We followed the methods of Snover and Hohn (2004) to prepare humeri for skeletochronology. Briefly, 2–3 mm cross-sections were taken from each humerus at a site just distal to the deltopectoral crest using a Buehler® isomet low-speed saw, first measuring the diameter at this location with digital calipers. These sections were fixed and decalcified in Fisher Scientific Cal-Ex II Fixative/Decalcifier (Fisher Scientific Company L.L.C.) for approximately 24 h. Sections were then mounted on a freezing-stage microtome and 25 micron sections removed. These thin sections were then placed back into the decalcifying agent for up to 12 h to complete the decalcification process. Sections were then stained with Ehrlich's hematoxylin and mounted on microscope slides in 100 % glycerin. Sections were observed and digital images captured at 40× magnification. For larger cross-sections, multiple digital images were taken, and these were stitched together using Adobe Photoshop (Adobe Systems Inc.).

In amphibians and reptiles, growth marks consist of a broad, lightly stained region followed by a thin, darkly stained line termed a line of arrested growth (LAG, Castanet et al. 1993). We counted and measured the diameter of the LAGs visible in cross-sections of each humerus from the digital images using iSolutions Lite image analysis software (IMT i-Solutions Inc.). If all or a part of the hatchling mark was visible (see the “Results” section), we determined age

through direct counts. Using information from animals for which all growth marks were visible, we developed a size-at-age relationship and used that to back-calculate the numbers of missing LAGs for larger animals where the early growth marks had been resorbed.

Validation of annual growth marks

While no direct validation was possible due to the lack of known-age individuals, three sources of indirect validation are presented. For the first method, the morphology of the growth marks is compared with that of other marine turtle species for which direct validation has been completed.

For the second method, Peabody (1961) and Castanet et al. (1993) suggest marginal increment analysis (MIA) which is a correlation between the width of the last zone formed and date of death as an indirect means of assessing that the deposition of the LAG occurs annually and at the same time of year for an individual population. Snover and Hohn (2004) applied this method to Kemp's ridleys, and we use it here with all turtles less than 60 cm SCL ($N = 17$). We quantified the width of the last zone formed by measuring the outside diameter of the whole section (D_O), and the diameter of the last-completed LAG (D_L), between the lateral edges of the bone on an axis parallel to the dorsal edge. The amount of bone growth after the last LAG ($D_O - D_L$) was plotted against the Julian stranding date, making the assumption that stranding date approximated date of death. A least-squares linear regression was fit to the data.

Finally, for the third method of indirect validation, we used data from a tagged, free-ranging Hawaiian hawksbill turtle. The Marine Turtle Research Program of the NOAA, NMFS/Pacific Islands Fisheries Science Center and the Hawaii Preparatory Academy captured, and tagged turtle Y-254 as a small juvenile at 32.9 cm SCL on October 19, 1989 (Table 1). This turtle was recaptured on January 24, 1990, measuring 36.2 cm SCL, and again on January 14, 1992, measuring 46.4 cm SCL (annual growth rate = 5.2 cm year⁻¹ using the two January capture dates). Most recently, this turtle was observed by the Hawaii Hawksbill Turtle

Table 1 Capture records for hawksbill turtle Y-254 from Kiholo and Punalu'u Bays, Island of Hawaii

Tag numbers	Date	SCL (cm)	Mass (Kg)
Y-254	10/19/1989	32.9	4.3
Y-254	1/24/1990	36.2	4.9
Y-254	1/14/1992	46.6	10.4
Y-254	4/21/1992	46.7	11.6
Y-254, 3D03	8/20/2009	76.4	–

Lengths are given as straight carapace length (SCL)

Recovery Project at Hawaii Volcanoes National Park nesting at Punalu'u Beach on the island of Hawaii on August 20, 2009, measuring 76.4 cm SCL. We use growth information from this turtle to support our findings on age and growth rates based on skeletochronology.

Back-calculation of carapace length

Diameters were measured of the total cross-section and each LAG observed in each section. We used the back-calculation methods presented in Snover et al. (2007a) to estimate carapace length at interior growth mark diameters. First we fit Eqs. 1 and 2 to the cross-section diameter and carapace length data (excluding the hatchlings) using least-squares regression to determine whether the relationship is allometric (Eq. 1) or isometric (Eq. 2).

$$L = L_{op} + b(D - D_{op})^c \quad (1)$$

$$L = L_{op} + b(D - D_{op}) \quad (2)$$

In these equations, L is carapace length (cm), D is humerus section diameter (mm), L_{op} is average hatchling carapace length, D_{op} is average hatchling humerus diameter, and b and c are fitted parameters. We used the mean carapace length and humerus diameter from the 10 hatchlings as estimates of L_{op} and D_{op} . We then used Eq. 3 to back-calculate carapace length from the diameters of the interior LAGs.

$$L = [f(D)][L_{final}][f(D_{final})]^{-1} \quad (3)$$

where $f(D)$ represents the appropriate relationship estimating carapace length from humerus diameter (Eqs. 1 or 2), $f(D_{final})$ is the same relationship estimating the final carapace length from the final humerus diameter, and L_{final} is the measured carapace length at death. We used ANOVA and Tukey's test (Zar 1999) to compare growth rates between sizes. Relationships between age and size were examined to estimate age at maturity.

Growth curve

Katsanevakis and Maravelias (2008) propose fitting multiple growth curves to size-at-age data rather than a priori selecting one (i.e., the von Bertalanffy growth function commonly used in fisheries). This approach was applied to green sea turtles by Goshe et al. (2010), and we apply it here by fitting the von Bertalanffy, logistic and Gompertz growth curves. The von Bertalanffy function is

$$L = B_0(1 - \exp(-B_1(t - B_2))) \quad (4)$$

where B_0 is the asymptotic length, B_1 is the Brody growth coefficient, and B_2 is the hypothetical age when length = 0. The equation for the logistic function is

$$L = B_0(1 + \exp(-B_1(t - B_2)))^{-1} \quad (5)$$

where B_0 is the asymptotic length, B_1 is the Brody relative growth rate parameter, and B_2 is the age at the inflection point. The equation for the Gompertz function is

$$L = B_0 \exp(-\exp(-B_1(t - B_2))) \quad (6)$$

where B_0 is again the asymptotic length, B_1 is the rate of exponential decrease of the relative growth rate with age, and B_2 is the age at the inflection point. We fit the three functions using maximum likelihood and used Akaike's information criteria (AIC) to determine the best model fit for the data.

Results

Age estimation

As discussed in the “[Validation of annual growth marks](#)” section below, we show evidence that LAGs are deposited as early as mid-February. Hawksbill turtles in Hawaii typically hatch in mid-to-late summer or into the fall, which would make the first mark occur at less than 1 year of age. Therefore, we considered the first-year mark to represent 0.75 years of age, the second mark to represent 1.75 years of age, etc. Age was estimated for the last completed LAG, and additional time was then added on to account for time of death as follows: (1) if the turtle stranded in February, March, or April, no time was added to the age estimate; (2) if the turtle stranded between May, June, or July, 0.25 year was added to the age estimate at the last growth mark; (3) if the turtle stranded between August, September, or October, 0.5 year was added to the age estimate at the last growth mark; and (4) if the turtle stranded between November, December, or January, 0.75 year was added to the age estimate at the last growth mark.

Three of the humeri had resorption cores similar in diameter to hatchling bone diameters (1.89 mm based on the 10 collected for this study); hence, it was likely that all growth marks are visible in these turtles (Fig. 2). From these bones, the first growth mark observed was a diffuse mark, similar in morphology to that observed in Kemp's ridley turtles (Fig. 2; Snover and Hohn 2004). Snover and Hohn (2004) validated this as the first-year mark in this species, and they found this mark useful in assigning age because of its distinctiveness. When a portion of the mark is still visible within the core, age can be determined from direct counts. This first-year mark was visible in 9 additional humeri, allowing the direct estimate of age for those turtles.

Age was estimated directly for these 12 turtles, ranging in size from 26.2 to 56.5 cm SCL. Using information from those ages and sizes, age was estimated for an additional 15

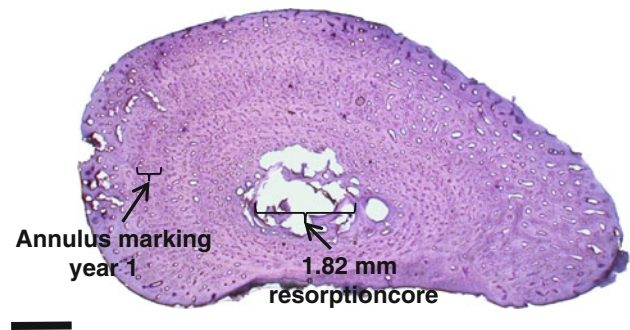


Fig. 2 Image of a humerus cross-section from a 26.2 cm SCL hawksbill turtle. The *black bar* represents 1 mm. The resorption core is 1.82 mm at the widest diameter. The *first year mark* is represented by a diffuse annuli. The stranding date for this turtle was June 17, 1993 and there were no additional growth marks visible outside of the annulus, hence this turtles was estimated at 1-year-old

turtles ranging in size from 42.0 to 83.8 cm SCL (Fig. 3). Each of these 15 turtles had interior growth marks that were back-calculated to carapace lengths within the range of the turtles whose age was estimated by direct counts. We used the confidence intervals (CI) for size-at-age to assign the most likely age to the interior growth marks. Of the remaining 3 turtles, two had indistinct growth marks that could not be quantified (46.4 cm and 83.4 cm SCL), and the other turtle (83.0 cm SCL) had too much resorption to estimate age as its interior LAGs did not correspond to the size range of the directly aged turtles.

Validation of annual growth marks

Growth mark morphology

In addition to the diffuse annuli noted above for what is likely the first-year mark, two additional growth mark morphologies were observed in cross-sections of humeri from juvenile hawksbill turtles. The most common was a thin, distinct and darkly stained LAG, which is typical of many species of amphibians and reptiles, including marine turtles (Fig. 4a; Castanet et al. 1993; Snover and Hohn 2004; Snover and Rhodin 2007). The other growth mark morphology was typically observed in larger juveniles that appeared to be undergoing rapid growth, and this was a thin, diffuse mark (Fig. 4b). Though diffused, these marks were still readily distinguishable in stained cross-sections. We also observed double, closely spaced LAGs, as described by Goshe et al. (2010). Without known-age specimens, we cannot be certain of the interpretation of these marks; however, similar, supplementary marks have been observed in Hawaiian green sea turtles (Snover et al. 2011). Therefore, we interpreted these marks as single growth marks, consistent with Goshe et al. (2010) and Snover et al. (2011), but acknowledge further validation is required to confirm this interpretation.

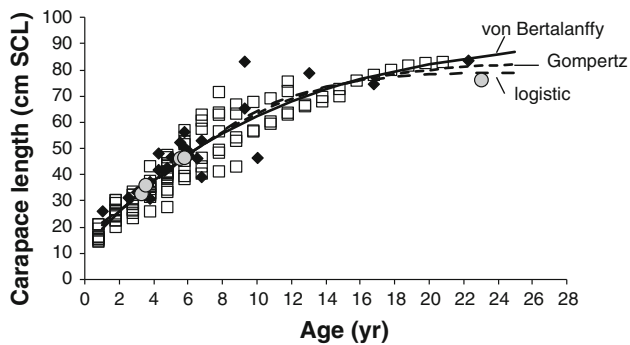


Fig. 3 Relationship between age and size for all hawksbill turtle in the sample for which age could be estimated. *Solid diamonds* represent age estimates based on actual direct growth mark counts compared to the final straight carapace length (SCL) of the turtle ($N = 24$). *Open squares* represent age and size estimated from lengths back-calculated from growth mark diameters ($N = 139$). *Gray filled circles* are the data from the tagged turtle, assuming it was 3.25 year at initial capture. *Lines* represent the means of the model fits

Marginal increment analysis

We examined the relationship between the amount of bone growth that occurred after the deposition of the most-recent (outer-most) growth mark and the outer edge of the bone, representing the time of death, for animals less than 60 cm SCL (Fig. 5). We restricted the data to this length as no significant difference in annual growth rates could be detected within these size classes, whereas significant differences were detected for larger animals. Combining years, there was a clear pattern of increasing amounts of bone growth after mid-February, which suggests that this is the approximate time of year when the LAGs are deposited for Hawaiian hawksbills.

Tagged turtle

As noted in the “Methods” section, a juvenile hawksbill turtle was captured, tagged, measured and released on October 19, 1989, and subsequently recaptured or resighted four additional times (Table 1). While the age of this turtle at first capture is unknown, three of the turtles in our sample were between 30 and 35 cm SCL with age estimated from direct counts of growth marks. Age estimates were consistent for all three of these turtles at 2.0, 3.0, and 3.75. This is also a reasonable age range for other sea turtle species in this size class based on limited tag return information from known-aged individuals (Bell et al. 2005, Caillouet et al. 2011). Based on our age estimates, the most likely age at initial capture for Y-254 was 3.25 years, though it is possible she was only 2.25 years. Based on these estimates, the age when she was observed nesting was 22.25–23.25 years. Assuming the initial age of

3.25 years, subsequent lengths and ages are consistent with what we estimated from skeletochronology (Fig. 3).

Back-calculation of carapace length

An examination of the residuals resulting from fitting Eqs. 1 and 2 to the carapace length and humerus section diameters revealed that the isometric relationship of Eq. 2 would underestimate carapace length in small turtles and overestimate the length in large turtles, similar to the findings for loggerhead turtles by Snover et al. (2007a; Fig. 6a). There is no trend in the residuals from the fit for Eq. 1 (Fig. 6b), and we therefore used that equation to back-calculate carapace length from the diameters of the interior LAGs (Fig. 6c). Combining Eqs. 1 and 3 gives the relationship used for this back-calculation

$$L = [L_{op} + b(D - D_{op})^c][L_{final}][L_{op} + b(D_{final} - D_{op})^c]^{-1} \quad (7)$$

where $L_{op} = 3.7$ cm (average of 10 hatchling carapace lengths), $D_{op} = 1.89$ mm (average of 10 hatchling humerus diameters), $b = 4.48$ and $c = 0.84$.

We used all of the back-calculated size-at-age data to estimate annual growth rates as the difference between consecutive carapace length estimates ($N = 117$; Fig. 7). Growth rates were log-transformed to normalize them and were then binned into 10 cm size categories based on the average of the start and end back-calculated lengths of the turtle for each year of growth. Based on the ANOVA test, there were significant differences in growth rates among the size classes ($F_{(7, 97)} = 12.56$, $P < 0.005$). From the Tukeys test, there were no significant differences between growth rates for size classes less than 80 cm SCL, and all growth rates for size classes between 20 and 80 cm SCL were significantly higher than those for the 80–90 cm SCL size classes. The average growth rate for size classes less than 80 cm SCL was $3.87 \text{ cm year}^{-1}$ ($SD = 2.23$; $N = 95$) and $0.30 \text{ cm year}^{-1}$ ($SD = 3.72$; $N = 9$) for size classes greater than 80 cm SCL.

Growth curve

Similar to what was observed by Snover et al. (2007b), the first year of growth for hawksbill turtles in this study was exceptional and markedly different from subsequent growth rates. Therefore, we follow Snover et al. (2007b) and fit the growth curves starting at age one. All three of the growth models fit the data well as evidenced by the narrow 95 % CI (Table 2; Fig. 3). Based on the AIC values, the von Bertalanffy function provided the best fit to the data. Based on all three models, mean age at 78.6 cm SCL (mean length of adult female hawksbills from van Buskirk and Crowder 1994) is estimated to be between 17 and 22 years.

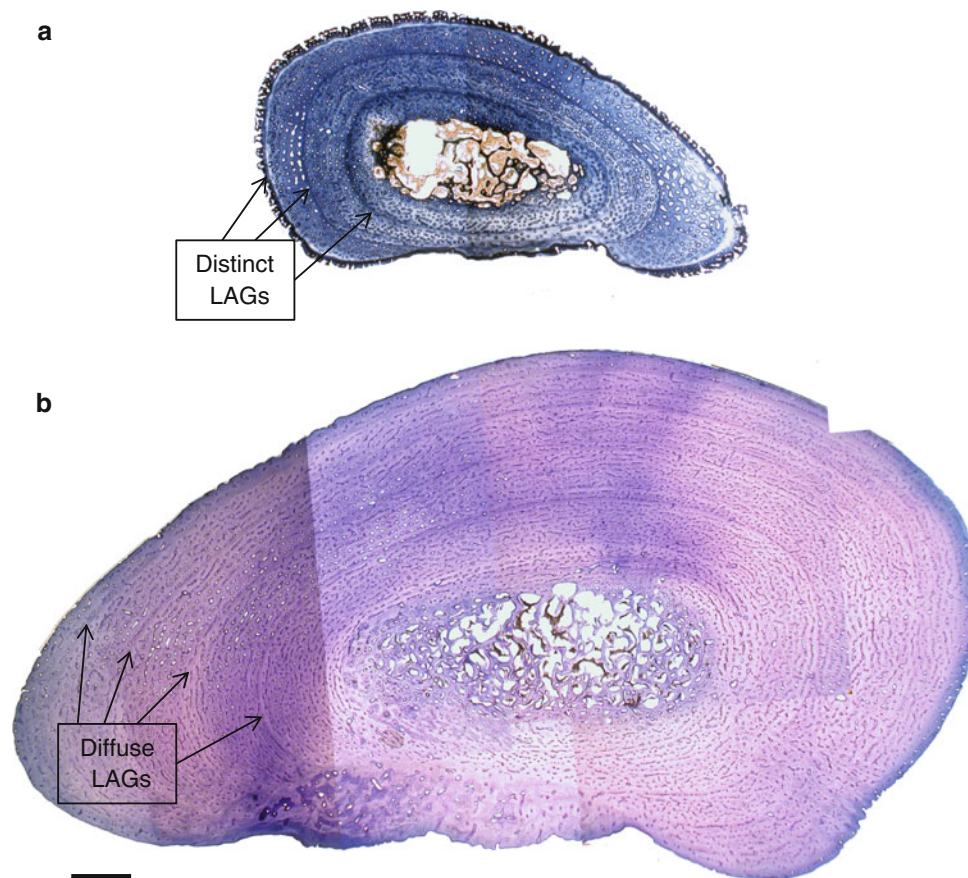


Fig. 4 Images of humeri cross-sections from **a** 47.2 and **b** 83.4 cm SCL hawksbill turtles. In **a**, sharp, distinct LAGs are demonstrated while in **b**, thin diffuse LAGs are *highlighted*. Black bar represents 1 mm

Discussion

Validation of annual growth marks

While we could not offer any direct validation of the annual nature of the growth marks in this study, we were able to present several indirect methods of validation that support this assumption. Annual marks have been validated in other species, including green turtles found in the same region (Snover and Hohn 2004, Snover et al. 2011); and the growth marks observed in this study are morphologically identical to those seen in species where the marks have been validated. There is nothing unique in regards to the life history of hawksbill turtles as compared to other species of hard-shell sea turtles (i.e., long biannual migration patterns) that would make one assume the growth marks may be different and not be annual. We also demonstrated increasing amounts of bone growth after the most recently deposited LAG with length of time between February and time of death. The clear trend in these data strongly suggests an annual pattern of growth mark deposition and that LAGs are deposited in late winter/early spring for Hawaiian hawksbills.

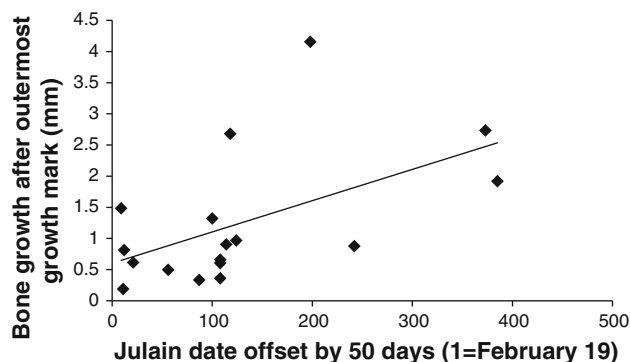


Fig. 5 Relationship between stranding date (used as a proxy for death date) and amount of bone growth in the final year of life for hawksbill turtles in Hawaii. Filled diamonds are the data ($N = 17$), solid black line is a least-squares linear regression through the data. This relationship is significant ($P < 0.05$). Julian dates have been offset by 50 days such that a Julian date of 1 represents February 19

Lastly, to support our interpretation of annual growth marks, we obtained growth records for one free-ranging hawksbill turtle that was initially captured in 1989 at 32.9 cm SCL and observed nesting in 2009 at 76.4 cm SCL. We cannot determine if 2009 was the first nesting

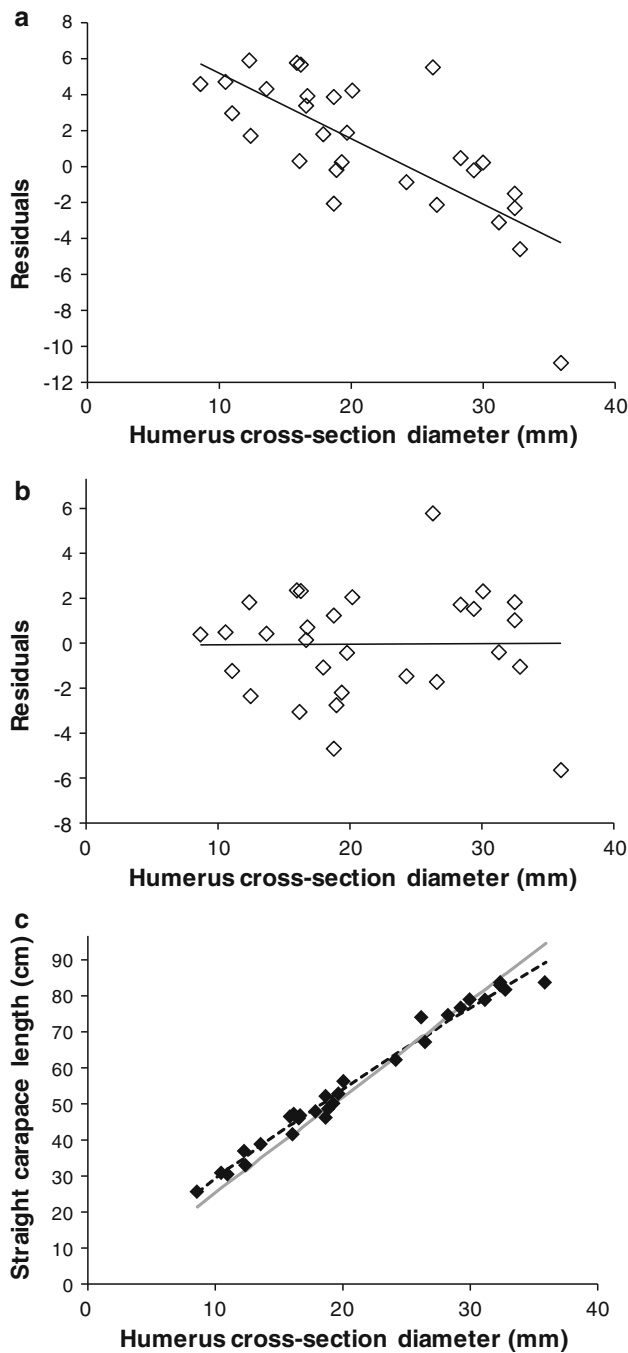


Fig. 6 Relationship between the diameter of the humerus cross-section and the carapace length of the turtle. **a** Residuals of the linear, isometric, relationship shown in *c*. *Solid line* is a least-squares linear regression through the residuals ($r^2 = 0.56$, $f_{1,27} = 34.48$, $P < 0.001$). **b** Residuals of the allometric relationship shown in *c*. *Solid line* is a least-squares linear regression through the residuals ($r^2 = 0.0$, $f_{1,27} = 0.002$, $P = 0.96$). **c** *Filled diamonds* are the data ($N = 30$), *gray solid line* is the fit of the linear relationship, *black dashed line* is the fit of the allometric relationship

year for this turtle or if it had nested previously. The turtle was recaptured and measured additional times as a juvenile, and using the capture dates of 1/24/1990 and

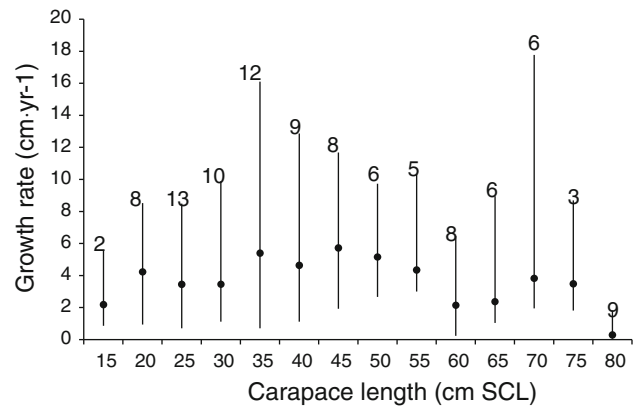


Fig. 7 Relationship between size category and annual growth rates based on back-calculated lengths from *growth mark* diameters. Growth rates were binned based on the mean of the start and end lengths. *Carapace lengths* indicate the start length of the size category. *Vertical bars* indicate the range of the data, *black dots* are the mean from the log-transformed data. *Numbers* indicate the sample size for each size class

1/14/1992 results in an average annual growth rate of 5.2 cm year⁻¹, which is consistent with the average growth rates estimated here for turtles between 35 and 45 cm SCL (3.52 cm year⁻¹; range 0.83 to 12.19 cm year⁻¹). Based on our age estimates for similar-sized turtles, this turtle was likely 2.25 or 3.25 years old at initial capture, making it 22.25–23.25 year-old at the time it was observed nesting. This estimate is a maximum age at first nesting as it is possible the turtle nested in a previous year.

Juvenile growth rates

Mean carapace length at age one (back-calculated from the diameter of the first, diffuse, annuli) was 17.5 cm SCL. This is similar to the value estimated and validated for Kemp’s ridley turtles, 20.9 cm SCL (Snover et al. 2007b), and that estimated for North Atlantic loggerheads, approximately 10–16 cm curved carapace length (Bjorndal et al. 2003) making it consistent with what is understood regarding post-hatchling growth in sea turtles. This also supports the assumption that the broad, diffuse annuli observed in cross-sections of small hawksbills in this study are likely the first growth mark, corresponding to an age of 0.75 years.

Our results indicated no significant differences in annual growth rates for juveniles ≤60 cm SCL and the average for all size classes was 4.59 cm year⁻¹ (SD = 2.04; N = 81). For juvenile hawksbills between 60 and 75 cm SCL we found an average of 2.50 cm year⁻¹ (SD = 2.38; N = 16). These growth rates are high compared to another Pacific hawksbill population in the Great Barrier Reef (Chaloupka and Limpus 1997, Bell and Pike 2012) but are similar to growth rates determined for populations of hawksbills in

Table 2 Summary of fitted parameters for three model types

Parameter	Von Bertalanffy	Logistic	Gompertz	
B_0	94.81 [83.90, 105.71]	79.41 [74.58, 84.23]	83.68 [77.64, 89.71]	
B_1	0.09 [0.07, 0.12]	0.26 [0.23, 0.31]	0.18 [0.15, 0.21]	
B_2	-1.44 [-2.07, -0.81]	4.60 [4.02, 5.17]	2.86 [2.40, 3.31]	
Model	K	AIC_c	ΔAIC	Age at 78.6 cm SCL
Von Bertalanffy	3	823.12	0	17.40 [10.72, 37.66]
Logistic	3	829.13	6.01	21.63 [13.65, -]
Gompertz	3	824.18	1.07	18.23 [12.86, -]

The 95 % CIs for each of the fitted parameters are in square brackets. K is the number of fitted parameters. The von Bertalanffy curve had the best fit with the lowest corrected Akaike's information criterion (AIC_c) value, although all of the fits were very similar as evidenced by the low ΔAIC for all models. The lower range of the 95 % CI for asymptotic length for both the logistic and Gompertz curves are lower than length at maturity (78.6 cm SCL), making it impossible to determine an upper CI for age to maturity

the Caribbean (Boulon 1994, Bjorndal and Bolten 1988, León and Diez 1999, Diez and van Dam 2002).

Chaloupka and Limpus (1997) analyzed juvenile hawksbill growth rates from a mark and recapture study in the Great Barrier Reef, Australia. They found non-monotonic patterns of growth for both males and females, with growth peaking at approximately 55 cm SCL (estimated from the reported curved carapace length) for both sexes but with higher growth rates for females (2.2 cm year⁻¹) than for males (1.7 cm year⁻¹). Similarly, Bell and Pike (2012) found growth rates between 1.25 and 0.179 cm year⁻¹ for juvenile and pubescent hawksbills. Growth rates declined to 0.90–0.17 cm year⁻¹ for adults.

Several studies have been conducted on juvenile hawksbill growth rates in the Caribbean. In a study in the U.S. Virgin Islands, Boulon (1994) reports growth rates for nine hawksbills with initial lengths of 27.4–60.7 cm SCL and recapture intervals greater than 1 year. For these turtles, the average annual growth rate was 4.01 cm year⁻¹ (SD = 1.94). León and Diez (1999) recorded 51 growth rates for 37 hawksbills with initial capture lengths of 21.0–45.2 cm SCL at foraging sites in the Dominican Republic. For 22 of these growth rates, the time-at-large was greater than 6 months and annual growth rates ranged between approximately 2 and 9 cm year⁻¹. The overall average for all growth records was 5.67 cm year⁻¹ (SD = 2.68), very similar to that found for Hawaiian hawksbills in our skeletochronology study. Diez and van Dam (2002) compared growth rates for 3 foraging sites in Puerto Rico and found substantially different growth rates in one of the sites. Juvenile hawksbills recaptured in the Mona reef and Mona cliff sites with recapture intervals greater than 0.8 year had growth rates between 2 and 4 cm year⁻¹. In contrast, hawksbills recaptured at the Monito cliff wall exhibited growth rates between 6 and 7.5 cm year⁻¹ for turtles up to approximately 40 cm SCL and growth rates decreased to 4–6 cm year⁻¹ for turtles up

to approximately 60 cm SCL. For all sites they found that growth rates were maximal at 34–35 cm SCL. Bjorndal and Bolten (1988) present data for five recaptured turtles and report annual growth rates of 15.7 and 5.9 cm year⁻¹ for turtles less than 45 cm SCL and 2.4 (average of 2 individuals) and 3.1 cm year⁻¹ for turtles greater than 60 cm SCL.

Age at maturity

While several of the turtles in our sample were adult-sized, skeletochronological examination showed evidence of decreased growth rates and compressed outer LAGs typical of adult turtles (rapprochement; Snover and Hohn 2004) in only 3 of them, measuring 81.9, 83.0 and 83.8 cm SCL, respectively, all female. Approximate age could be assigned to one of these turtles; 22.25 years (83.8 cm SCL). The low number of adult growth rates limits the usefulness of the growth curves for estimating this variable; however, the growth curves suggest Hawaiian hawksbills reach 78.6 cm SCL on average between 17 and 22 years. The lack of adult growth rates would tend to decrease the estimate of age at 78.6 cm SCL; hence, these estimates can be considered low. We estimated the recaptured turtle to be 23–24 years, and this would be a maximum age at first reproduction for this turtle given that it is uncertain whether it was her first-year nesting in 2009. Combining these lines of evidence, there is strong support that age to maturity for Hawaiian hawksbill is late teens to early twenties.

Implications for conservation

A key component of population dynamics models and population viability assessment is an understanding of age to maturity for the population or species in question, and until this information can be gained, conservation actions such as establishing reasonable recovery timeframes,

cannot be accomplished. Juvenile stage durations are also key variables to understand to focus conservation actions to achieve the highest benefit. The data presented here suggests that the pelagic stage for Hawaiian hawksbill turtles is likely quite short, with turtles as young as 1.5 years recovered as dead stranding in the nearshore habitats. This length of time is consistent with that observed for Kemp's ridley turtles (Snover et al. 2007b). The near-shore benthic habitats around the islands of the Hawaiian Archipelago are, then, the critical developmental habitats for juvenile Hawaiian hawksbills and protection from anthropogenic mortality sources such as boat strikes and bycatch in fisheries within these habitats is important to the recovery of this population.

Our estimate of age to maturity for Hawaiian hawksbills is intermediate for estimates made for other hard-shell sea turtles using skeletochronology or mark-recapture data. Average age to maturity estimates for the smaller ridley turtles (Kemp's and olive) are between 10 and 13 years (Zug et al. 2006, Snover et al. 2007b, Shaver and Wibbels 2007, Caillouet et al. 2011). Estimates of the average age to maturity for the larger loggerheads and greens are generally >25 years (Snover 2002, Zug et al. 2002, Balazs and Chaloupka 2004, Chaloupka et al. 2004, Casale et al. 2009, Goshe et al. 2010, Piovano et al. 2011). Bell et al. (2005) report 15–19 years for known-age green turtles that were tagged and released as hatchlings or yearlings at the Cayman turtle farm in the Caribbean and subsequently observed nesting or mating. The low values for age to maturity reported by Bell et al. (2005) do not contradict the other studies reporting higher average ages as these values are likely well within the range of what could be expected. For example, while our logistic curve reported an average of 17.4 years to maturity, the 95 % CI ranged from 10.7 to 37.7 years (Table 2). Individuals that mature faster in a population are more likely to be identified on nesting beaches because they have both higher survival and tag retention probabilities than turtles that are slower to mature later (Bell et al. 2005).

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