

# Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage

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**ABSTRACT:** The pelagic juvenile stage of sea turtles is poorly studied. We present a growth model and estimates for duration of the pelagic juvenile stage for loggerhead sea turtles *Caretta caretta* in the North Atlantic based on length-frequency analyses and sizes of young-of-the-year stranded in the Azores. The size-specific growth model is a monotonic, nonlinear, declining function. The growth model is consistent with growth rates calculated from recaptures of tagged loggerheads. Loggerheads leave the pelagic habitat and recruit to neritic habitats over a range of sizes from 46 to 64 cm curved carapace length (CCL). From this size range and the growth model, we estimate the duration of the pelagic stage varies from 6.5 to 11.5 yr. Nonparametric smooths of the size frequency distributions of loggerheads in pelagic (n = 1692) and neritic (n = 1803) habitats intersect at 53 cm CCL, which is equivalent to an 8.2 yr duration for the pelagic stage. More growth data from loggerheads < 2 yr old would strengthen the database for our growth model and perhaps lengthen our estimates of the duration of the pelagic stage. Incorporating our estimates for duration of the pelagic juvenile stage into the stage-based population model developed for North Atlantic loggerheads would have a major effect on estimates of population growth.

**KEY WORDS:** Azores · Length-frequency analysis · Loggerhead sea turtles · Pelagic stage · Somatic growth

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## INTRODUCTION

The early juvenile stages of all species of sea turtles, except *Natator depressus*, apparently occupy the pelagic habitat in the open ocean. This pelagic juvenile lifestage has been poorly studied, largely because the distribution of pelagic stage turtles is poorly known (Bolten & Balazs 1995). Large numbers of small loggerheads occupy the surface waters in the eastern Atlantic, and Brongersma (1972) suggested these pelagic loggerheads are derived from western Atlantic nesting beaches. The size range of pelagic loggerheads around the Azores fits the missing size range from the neritic habitats of western Atlantic waters

(Carr 1986, Bolten et al. 1993). Based largely on this size distribution, Carr (1986) developed the hypothesis that after hatchling loggerheads emerge from the nesting beaches in the southeastern USA, they become incorporated in the North Atlantic Gyre, are carried to the eastern Atlantic, and eventually, after an unknown period, recruit to neritic habitats in the western Atlantic. This proposed movement pattern was confirmed by comparisons of mtDNA sequences of pelagic loggerheads in the eastern Atlantic with those from Atlantic and Mediterranean nesting populations (Bolten et al. 1998).

Knowledge of the duration of the pelagic juvenile stage is critical for the development of population models and estimating juvenile survivorship (Crouse et al. 1987, Crowder et al. 1994). Population models are valuable tools for identifying critical life stages for

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management and for evaluating effects of anthropogenic mortality on population growth and viability. Young loggerheads in the pelagic habitat are vulnerable to predation and may suffer substantial mortality as a result of incidental capture in longline fisheries (Bolten et al. 1994) and ingestion of and entanglement in marine debris (Carr 1987). Growth rates have been calculated from recaptures of a few tagged individual loggerheads in pelagic waters of the North Atlantic (Eckert & Martins 1989, Bolten et al. 1990, 1992, Bjørndal et al. 1994), and preliminary estimates of 10 to 12 yr for the duration of the pelagic stage of loggerheads in the North Atlantic have been made (Bolten et al. 1994, 1995). However, a rigorous analysis of the duration of the pelagic stage has not been conducted.

In 1990, we initiated a collaborative effort with the commercial fishing fleets, sport gamefishing industry, and ecotourism industry in the Azores to tag and measure pelagic juvenile sea turtles (Bolten et al. 1993). This program has yielded data that can be used to estimate growth rates and the duration of the pelagic stage through analysis of length-frequency distributions and recapture of tagged loggerheads.

Analysis of length-frequency distributions has been used for many years to estimate growth rates, age structure, and mortality in fish and invertebrate populations (Ricker 1975, Hilborn & Walters 1992). Length-frequency analysis relies on the assumption that length frequencies have modes, each of which represents a single age class. When the modes are identified, the mean length of each age class in a population can be determined, and growth models may be fit to the lengths-at-age data. In most cases, the von Bertalanffy model has been used. The accuracy of length-frequency analysis (using the program MULTIFAN) for predicting number of age classes was tested in a population of green turtles *Chelonia mydas* in the southern Bahamas for which growth rates had been measured in a long-term mark and recapture study (Bjørndal & Bolten 1995, Bjørndal et al. 1995). MULTIFAN successfully estimated the number of age classes in this population.

In this paper, we estimate growth rates of pelagic juvenile loggerheads in the North Atlantic from length-frequency analyses employing MULTIFAN software and from recaptures of tagged turtles. We also estimate the duration of the pelagic juvenile stage for this population.

## MATERIALS AND METHODS

**Data collection.** We have employed a number of methods to capture *Caretta caretta* in the waters around the Azores. Most turtles have been captured

with the cooperation of the commercial tuna fleet based in the Azores. This traditional hook- and line-fishery relies on 'fishing the birds'—that is, the fishermen watch for aggregations of birds feeding at the surface that often indicate areas where schools of tuna are driving small fish to the surface. While scanning for such activity, the fishermen often see turtles floating at the surface and can motor up to them and catch them with dipnets. Turtles have also been captured incidentally in longline fisheries and caught by hand or with dipnets by individuals engaged in sport gamefishing and the ecotourism industry of whale-watching. A few loggerheads used in this study had stranded on the coast of Faial, Azores.

The tuna fishermen and some of our other collaborators tagged the turtles at sea by attaching to each front flipper a Monel metal tag (Style 681, National Band and Tag, Newport, Kentucky, USA) stamped with an identification number, a return address, and an offer of a reward for sending information about the turtle. Curved carapace length (CCL) was measured from the anterior point at midline (nuchal scute) to the posterior notch at midline between the supracaudals. Turtles were released soon after capture.

Other collaborators brought turtles to the office of the Department of Oceanography and Fisheries, University of the Azores, in Horta. These turtles were tagged with plastic jumbo roto tags (Dalton Supplies Ltd, Oxfordshire, England) stamped with the same information as the metal tags. A series of measurements was taken on these turtles, including straight carapace length notch-to-tip (SCLnt, measured from the anterior point at midline [nuchal scute] to the posterior tip of the supracaudals), minimum straight carapace length (SCLmin, measured from the anterior point at midline [nuchal scute] to the posterior notch at midline between the supracaudals), and CCL measured as described above. These measurements were used to generate equations for converting among the 3 carapace-length metrics using linear regression.

We have received reports of recaptures of tagged loggerheads. Only reports that included a measure of carapace length taken by a biologist, fisheries officer, or fisherman trained in measuring sea turtles have been used in this study. Growth rates were calculated for those recaptures with intervals between tagging and recapture >1 yr. Shorter intervals were excluded to minimize errors in growth rate estimation for turtles yet to undergo a full year of growth (Chaloupka & Musick 1997).

**Data analyses.** Length-frequency analyses were conducted with the software MULTIFAN (Version 32(f) modified to include 30 age classes: Otter Research Ltd. 1992). The MULTIFAN program simultaneously analyzes multiple samples of length-frequency data using

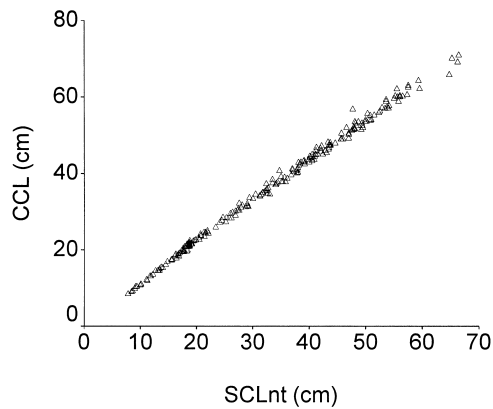


Fig. 1. *Caretta caretta*. Relationship of curved carapace length (CCL) and straight carapace length notch-to-tip (SCLnt) for 248 loggerheads captured in waters around Azores (linear regression,  $p < 0.001$ ,  $R^2 = 0.997$ )

nonlinear statistical modeling and robust parameter estimation to estimate the number of significant age classes in the sample population and the parameters of the von Bertalanffy growth model (Fournier et al. 1990, 1991). Log-likelihood objective functions are compared using maximum-likelihood analyses to determine the parameter set for the von Bertalanffy model with the best fit. The MULTIFAN program has the assumptions that (1) growth is described by a von Bertalanffy growth curve (parameterization of the von Bertalanffy growth equation is derived in Schnute and Fournier [1980]), (2) samples represent the structure of the population, (3) recruitment occurs in seasonal pulses, (4) the lengths of animals in each age class are normally distributed, and (5) the standard deviations of the lengths are a simple function of the mean length-at-age.

MULTIFAN requires that initial values for the following parameters be specified as starting points for the iterations: expected number of age classes, expected initial  $K$  values (the intrinsic growth rate in the von Bertalanffy equation), mean length of the mode representing the youngest age class, standard deviation of a distinct mode, and month in which youngest animals recruit to the population. We estimated initial values for age classes as varying between 2 and 21 yr, and for  $K$  as 0.05, 0.1, and  $0.5 \text{ yr}^{-1}$ . Initial estimate for the mean length of youngest age class was 13 cm CCL. The initial standard deviation of mode width was estimated as 1.5 cm. Because there was a significant trend in standard deviation of length-at-age with increasing length, this parameter was included in the model.

Each length-frequency sample must have a sufficient number of turtles to represent the length distribution of the population, and must be from a sufficiently short sampling period to avoid substantial growth

within the sampling period. For our analyses, we divided our samples into months and selected the 8 mo with the largest number of turtles: May ( $n = 68$ ), June ( $n = 76$ ), July ( $n = 73$ ) and September ( $n = 57$ ) 1990, and May ( $n = 57$ ), June ( $n = 80$ ), July ( $n = 76$ ), and August ( $n = 87$ ) 1991. CCL ranged from 10 to 64 cm in these samples.

Statistical analyses were conducted with the Statistical Package for the Social Sciences (SPSS; Version 9.0). A compound running-median-smoother (4253H-twice; see Velleman & Hoaglin 1981) was used to smooth the size frequency distributions of the pelagic ( $n = 1692$ ) and neritic ( $n = 1803$ ) loggerhead samples. The estimated size and age at which the two smooths intersected was then used to derive an estimate of the pelagic stage duration.

## RESULTS

Equations were needed to convert SCLnt or SCLmin to CCL because only SCL measurements were available for some *Caretta caretta*. Based on measurements of 248 loggerheads ranging in CCL from 8.5 to 70.9 cm (Fig. 1), the following equations were estimated:

$$\text{CCL} = 1.388 + (1.053)(\text{SCLnt}) \quad (1)$$

and

$$\text{CCL} = 1.226 + (1.076)(\text{SCLmin}) \quad (2)$$

For both equations,  $p < 0.001$  and  $R^2 = 0.997$ .

A total of 1692 loggerheads with a range of CCL from 8.5 to 82.0 cm were measured in the waters around the Azores. The CCL distribution of the pelagic population (left-hand curves of Fig. 2) is based on CCL measurements of 1341 loggerheads and conversion from SCL measurements for 351 loggerheads using Eqs. (1) & (2).

Growth data are available for 10 loggerheads with reliable carapace length measurements at initial capture and recapture (Table 1, Fig. 3). Growth rates for 4 of these turtles have been reported previously: the growth rate for K5583 was reported as  $3.7 \text{ cm yr}^{-1}$  SCL (Bolten et al. 1992), which differs from the value of  $4.4 \text{ cm yr}^{-1}$  CCL reported here because in 1992 the conversion from CCL (for which the turtle was measured) to SCL (in which we calculated the growth increment) was based on limited data for small loggerheads and yielded a poor estimate of SCL; the growth rate for BP2267 was reported as  $3.5 \text{ cm yr}^{-1}$  SCL (Bjorndal et al. 1994), similar to the value of  $3.6 \text{ cm yr}^{-1}$  CCL reported here. Estimates of growth rates are also available for a captive-reared loggerhead (BP749) that was released in Brazil and recaptured in the Azores (Bolten et al. 1990) and for a loggerhead (PPD122) that was tagged along the coast of Florida and recaptured in the

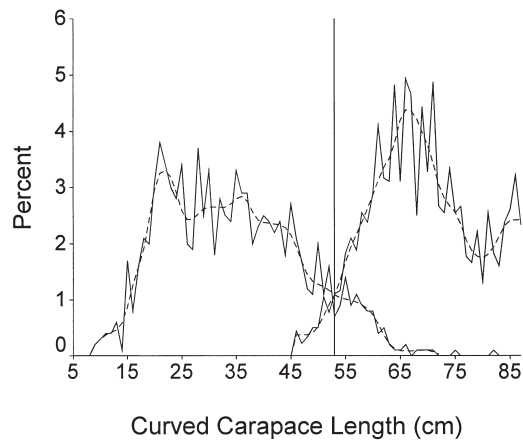


Fig. 2. *Caretta caretta*. Size-frequency distributions of loggerheads captured in waters around Azores (pelagic, left-hand curves, n = 1692) and loggerheads stranded in southeastern USA (neritic, right-hand curves, n = 1803; from Bjorndal, Bolten, Koike, Schroeder, Teas & Witzell unpubl. data). Percentages were calculated within each population. Dashed lines: compound running-median smooths (4253H-twice); vertical reference line: intersection at 53 cm CCL between smooths of pelagic and neritic size-frequency distributions

Azores (Eckert & Martins 1989). We calculated growth rates for 6 loggerheads that have not been reported previously.

In addition to recapture of tagged turtles, a stranding event allowed us to estimate growth rates of very small loggerheads. Following a storm, 6 loggerheads with CCL from 9.1 to 10.8 cm (mean 9.9 ± 0.7 SD) stranded alive or fresh-dead on 7/8 February 1990 at Porto Pim on the island of Faial in the Azores. On 25 January

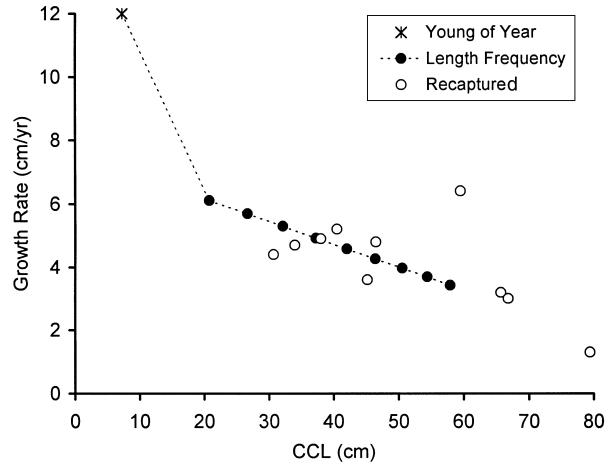


Fig. 3. *Caretta caretta*. Size-specific growth rate function of loggerhead turtles estimated from stranded young-of-year and length-frequency analyses. Growth rates of 10 recaptured, tagged loggerheads are also plotted. CCL = mean of initial and recapture CCL measurements

1993, a 10.4 cm CCL loggerhead stranded at Porto Pim. If we assume that these turtles were young-of-the-year, the average hatching date for these individuals would have been 1 September of the previous year with a mean CCL of 4.65 cm (Hirth 1980, B. E. Witherington pers. comm.), yielding a mean growth rate of 1 cm CCL month<sup>-1</sup>.

The best fit for the length-frequency analyses generated estimates for the von Bertalanffy growth model of  $K = 0.072 \pm 0.003 \text{ yr}^{-1}$  and asymptotic CCL ( $L_{\infty}$ ) = 105.5 ± 2.7 cm. Ten age classes were identified, with the mean CCL of the first and last age classes esti-

Table 1. *Caretta caretta*. Growth rates of recaptured loggerheads. Habitat 1, 2: habitat type of initial capture and recapture, respectively. CCL 1, 2: curved carapace length at initial capture and recapture, respectively

Tag No.	Habitat:		CCL (cm):		Interval (d)	Growth rate (cm yr <sup>-1</sup> )
	1	2	1	2		
Strandings	Nesting beach	Pelagic	4.65	9.9	160	12.0 <sup>a</sup>
K5583	Pelagic	Pelagic	19.3	42.0	1868	4.4 <sup>b</sup>
A4837	Pelagic	Pelagic	26.0	42.0	1233	4.7
A4821	Pelagic	Neritic	28.0	48.0	1504	4.9
BP749	Captive	Pelagic	31.9	49.0	1206	5.2 <sup>c</sup>
BP2267	Pelagic	Pelagic	40.5	49.8	950	3.6 <sup>d</sup>
BP624	Pelagic	Pelagic	41.0	52.0	828	4.8
A7951	Pelagic	Neritic	45.0	74.0	1647	6.4
BP683	Pelagic	Pelagic	60.4	70.9	1210	3.2
N5921	Pelagic	Neritic	64.0	69.6	680	3.0
PPD122	Neritic	Pelagic	78.4	80.4	552	1.3 <sup>e</sup>

<sup>a</sup>Mean values for 6 turtles stranded at Porto Pim, Faial, Azores; see 'Results' for explanation  
<sup>b</sup>Bolten et al. (1992); value different than in publication because of different conversion equation, see 'Results' for explanation  
<sup>c</sup>Bolten et al. (1990)  
<sup>d</sup>Bjorndal et al. (1994) reported 3.5 cm yr<sup>-1</sup> for this individual  
<sup>e</sup>Eckert & Martins (1989)

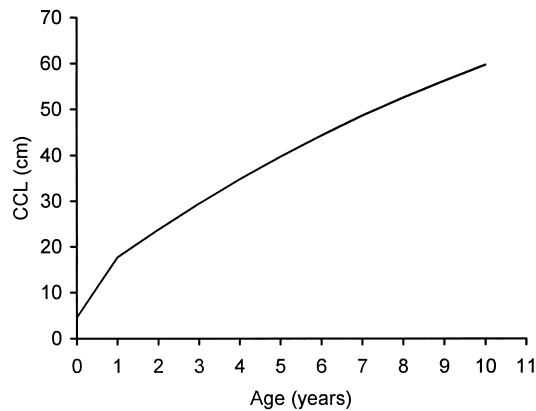


Fig. 4. *Caretta caretta*. Age-specific growth model generated from length-frequency analyses and stranded young-of-year

mated as  $17.7 \pm 0.1$  cm and  $59.7 \pm 0.1$  cm, respectively, based on the size range in our sample population. Growth rates for the 9 intervals between the 10 age classes were calculated (Fig. 3). The observed growth rates of recaptured loggerheads, except for Turtle A7951, fall close to the MULTIFAN growth curve.

## DISCUSSION

### Growth rates

The growth model (Fig. 4) is based on the growth rates estimated for the stranded young-of-the-year *Caretta caretta* for Age 1 turtles and on the von Bertalanffy model generated by length-frequency analyses for Ages 2 through 10. This model represents a monotonic, nonlinear, declining function for CCL-specific growth rates (Fig. 3), as opposed to the monotonic, linear, declining function of the von Bertalanffy model. Our estimate of 1 yr for the first age class is based on an initial size of 4.65 cm CCL at hatching and a growth rate of  $12 \text{ cm yr}^{-1}$  based on stranded young-of-the-year. This growth rate estimate of  $1 \text{ cm mo}^{-1}$  is consistent with the observations of changes in size of post-hatchling loggerheads captured off the coast of Florida during the months following emergence from the nesting beach (B. E. Witherington pers. comm.). We hope to confirm this estimate with a study under way employing skeletochronology.

Concerns about the application of the von Bertalanffy model to sea turtle populations have been discussed (Bjorndal & Bolten 1988a, Chaloupka & Musick 1997, Day & Taylor 1997). A major concern is the use of the von Bertalanffy model to extrapolate outside the size range of the study, which has been a common practice to estimate age at sexual maturity in sea turtle

populations. However, within a growth phase that exhibits monotonic decline—that is for a given size range of a population with similar habitats and diet that has declining growth rates with increasing body size—the von Bertalanffy model may provide reasonable estimates of growth rates and number of age classes. Green turtles in the southern Bahamas have a monotonic nonlinear declining function for SCL-specific growth rates in a size range of 30 to 70 cm SCL as determined from nonlinear regression of mark-recapture data (Bjorndal et al. 2000). Length-frequency analyses using a von Bertalanffy model (MULTIFAN software) yielded the same estimates as the nonlinear regression analysis for growth rates and number of age classes between 30 and 70 cm for that population (Bjorndal et al. 2000).

Use of the von Bertalanffy model within the studied size range is further supported by the similarity between growth rates generated from the growth model and those calculated from recaptures of tagged turtles, except for 1 outlier (A7951) (Fig. 3). There is some variation in the growth rates calculated for individuals, which is not surprising. First, sea turtles are known to exhibit great variation in individual growth rates (Bjorndal & Bolten 1988a, Chaloupka & Limpus 1997). Second, many of the estimates are based on long time intervals (Table 1) during which the turtles grew substantially and probably experienced changing growth rates. For example, K5583 was at large for 5.1 yr and grew from 19.3 to 42.0 cm CCL. Third, 3 of the loggerheads were recaptured in neritic habitats, and we cannot determine how much of the interval between capture and recapture was spent in pelagic or neritic habitats. Ontogenetic habitat shifts are maintained in populations because they confer an advantage, usually an increase in growth rate and/or survival (Werner & Gilliam 1984). Data for loggerheads and green turtles suggest that growth rates may change substantially when sea turtles move among habitats (Bjorndal, Bolten & Chaloupka unpubl. data).

Growth rates of pelagic and neritic loggerheads in the Atlantic are summarized in Table 2. We have not made statistical comparisons among the values in Table 2 because of lack of variance estimates and because of small sample sizes. Growth rates of pelagic loggerheads in the North Atlantic are similar to, or perhaps greater than, those of pelagic loggerheads in the North Pacific (Table 2). Water temperatures in the 2 regions are similar. In the waters around the Azores, mean surface temperature in winter is  $16^{\circ}\text{C}$  and in summer  $22^{\circ}\text{C}$  (M. Alves pers. comm.). Surface water temperatures at capture sites for 12 pelagic loggerheads in the North Pacific ranged between  $17$  and  $20^{\circ}\text{C}$  at time of capture (Zug et al. 1995). Neritic loggerheads in the warmer waters of Florida and the

Table 2. *Caretta caretta*. Growth rates (mean, range or  $\pm$  SD, [n] when available) for straight carapace lengths (SCL, cm yr<sup>-1</sup>) of non-captive loggerheads in pelagic habitats and Atlantic neritic habitats. LF: length-frequency analysis; MR: mark-recapture; SC: skeletochronology

SCL (cm)	Pelagic			Neritic				
	N. Atlantic <sup>a</sup>		N. Pacific <sup>b</sup>	VA, USA <sup>c</sup>		GA, USA <sup>d</sup>	FL, USA <sup>e</sup>	Bahamas <sup>f</sup>
	LF	MR	SC	MR	SC	SC	MR	MR
20–30	5.3	4.2	4.5	–	–	4.0	–	–
	–	–	–			3.4–4.9		
		(1)	–			(3)		
30–40	4.6	4.7	4.1	–	–	3.4	–	–
	–	4.5–5.1	–			1.9–7.0		
	–	(3)	–			(10)		
40–50	3.9	4.0	–	–	5.3	3.6	–	15.7
	–	3.4–4.6	–		$\pm 2.8$	2.6–4.3		14.8–17.2
	–	(2)	–		(6)	(9)		(3)
50–60	3.1	6.1	–	3.0	5.3	3.3	7.4	–
	–	–	–	$\pm 0.1$	$\pm 1.4$	1.7–5.2	$\pm 1.4$	–
	–	(1)	–	(2)	(13)	(8)	(2)	–
60–70	–	2.9	–	1.5	5.3	2.9	6.0	–
		2.8–3.0	–	$\pm 1.2$	$\pm 1.6$	2.2–4.1	$\pm 2.3$	–
		(2)	–	(9)	(29)	(6)	(7)	–

<sup>a</sup>This study; CCL converted to SCL using Eq. (1); total LF sample = 574  
<sup>b</sup>Zug et al. (1995), total SC sample = 12, as summarized in Parham & Zug (1997)  
<sup>c</sup>Virginia, USA; Klinger & Musick (1995)  
<sup>d</sup>Georgia, USA; Parham & Zug (1997) and Zug (pers. comm.)  
<sup>e</sup>Florida, USA; Mendonça (1981)  
<sup>f</sup>Great Inagua, Bahamas; Bjorndal & Bolten (1988b)

Bahamas appear to grow more rapidly than those in more northern areas. More data on growth rates of loggerheads in a variety of habitats are needed to evaluate polyphasic growth in loggerheads (Chaloupka 1998).

#### Duration of pelagic stage

To calculate the duration of the pelagic stage for North Atlantic loggerheads, one must determine the size at which the turtles leave the pelagic habitat and recruit to neritic habitats. Clearly this habitat shift occurs over a range of sizes (Fig. 2). A relatively sharp decline in the pelagic distribution, probably representing the first major departure of loggerheads from the pelagic habitat, occurs at approximately 46 cm CCL. Almost all loggerheads have left the pelagic habitat by 64 cm CCL. When the size-frequency distribution of pelagic turtles is compared with that of neritic turtles, the smooths intersect at 53 cm CCL. The distribution of neritic turtles is derived from measurements of 1803 loggerheads recovered in the southeast US by the Sea Turtle Salvage and Stranding Network (Bjorndal, Bolten, Koike, Schroeder, Teas & Witzell unpubl. data).

If the point of intersection at 53 cm CCL is used as an estimate of the size at which loggerheads recruit to

neritic habitats (Fig. 2), the duration of the pelagic stage, estimated from our growth model and defined as the time from when the hatchling entered the ocean, is 8.2 yr. If 46 to 64 cm CCL is used as the range during which most of the loggerheads leave the pelagic habitat, the duration of the pelagic stage ranges from 6.5 to 11.5 yr. These estimates are based on the assumption that loggerheads, for the first year of life, maintain a growth rate of 1 cm mo<sup>-1</sup> estimated for the first 5 mo of life from the stranded young-of-the-year loggerheads. If growth rates slow during the second half of the first year, which is not unlikely, durations of the pelagic stage would be increased by perhaps 0.5 to 1 yr. Earlier, based on preliminary analyses of smaller sample sizes (Bolten et al. 1994, 1995), we estimated a longer duration of the pelagic stage of about 10 to 12 yr, with 50 cm SCL (~54 cm CCL) as the upper limit of the pelagic stage.

A stage-based population model has been developed for North Atlantic loggerheads and applied to management issues (Crouse et al. 1987, Crowder et al. 1994). The durations of the first 2 stages of their population model—eggs/hatchlings and small juveniles up to 58.0 cm SCL (= 62.5 cm CCL)—were estimated as 1 and 7 yr, respectively. Our growth model estimates a longer duration for the first 2 stages; a 62.5 cm CCL turtle would be 11.0 yr old. Increasing the duration of

the first 2 stages by 3 yr (or 38%) in the population model has a substantial effect on estimates of population growth (M. Chaloupka & S. Heppell pers. comm.).

The duration of the pelagic stage for Pacific loggerheads may well be longer than that of Atlantic loggerheads. Growth rates of North Pacific pelagic loggerheads apparently are equivalent to or slower than those of Atlantic loggerheads (Table 2). Zug et al. (1995) estimated that a 46.6 cm SCL (ca 51 cm CCL) loggerhead in the North Pacific was 10 yr old, based on skeletochronology of 12 loggerheads. Chaloupka (1998) reanalyzed the data presented in Zug et al. (1995) and estimated that a loggerhead with a 42 to 43 cm CCL would be 6.5 yr old. Both these estimates suggest slower growth rates than our estimate of 6.5 yr for a 46 cm CCL Atlantic loggerhead. In addition, Pacific loggerheads recruit to neritic habitats at a larger size than Atlantic loggerheads, which would lengthen the duration of the pelagic stage. Loggerheads recruit to neritic habitats in Queensland, Australia, at a minimum size of 70 cm CCL (Limpus et al. 1994). A loggerhead recaptured in Queensland waters 15.2 yr after being notched as a hatchling had a CCL of 75.6 cm (Limpus et al. 1994), suggesting a duration of the pelagic stage of 10 to 15 yr (M. Chaloupka pers. comm.).

#### Age at sexual maturity

In another study based on length-frequency analyses employing MULTIFAN, the interval from 46 to 87 cm CCL for neritic subadult loggerheads in the southeast USA (right-hand curves of Fig. 2) has been estimated to represent 20 age classes (Bjorndal, Bolten, Koike, Schroeder, Teas & Witzell unpubl. data). The upper limit of 87 cm CCL was used to exclude all adults based on Witherington (1986), who reported that 88 cm CCL was the smallest of 119 nesting loggerheads at Melbourne Beach, Florida. Adult loggerheads were excluded from the sample to avoid obscuring size-class modes in the size-frequency distribution. Because loggerheads essentially stop growing at sexual maturity and because they attain sexual maturity at a range of sizes (Frazer & Ehrhart 1985), the age classes—or modes—above the minimum size at sexual maturity are obscured and cannot be distinguished in length-frequency analyses.

If this estimate of 20 age classes is added to the 6.5 yr estimate for age of 46 cm CCL loggerheads, 26.5 yr are required for loggerheads to grow from hatchlings to 87 cm CCL. The estimate of an age of 26.5 yr at 87 cm CCL should not be used as an estimate of age to sexual maturity. Many loggerheads will reach sexual maturity at lengths much greater than 87 cm, and, because

growth rates are slow in these large sub-adults (Parham & Zug 1997), the average age to sexual maturity would be substantially greater than the average age to 87 cm CCL.

A range of estimates from 10 to 30 yr has been generated for age at sexual maturity in North Atlantic loggerheads (summarized in Parham & Zug 1997). Our estimate of 26.5 yr of age for an 87 cm sub-adult supports the conclusion of Frazer & Ehrhart (1985) and Parham & Zug (1997) that age at sexual maturity is probably closer to 30 yr, if not greater.

#### Conclusion

The best estimate for the duration of the pelagic stage of North Atlantic loggerheads is 8.2 yr for loggerheads that leave the pelagic at 53 cm CCL. Estimates of the duration of the pelagic stage range from 6.5 to 11.5 yr for loggerheads that leave the pelagic at 46 or 64 cm CCL, respectively. These estimates are derived from a combination of length-frequency analysis and data from stranded young-of-the-year loggerheads, and are consistent with growth rates calculated from recaptures of tagged loggerheads. More data on growth rates of loggerheads <2 yr old would refine our estimates. We hope that a skeletochronology study now under way will provide these data. Future research should examine the mechanisms that regulate the departure of loggerheads from pelagic habitats and recruitment to neritic habitats.

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