

Abstract—Estimates of instantaneous mortality rates (Z) and annual apparent survival probabilities (Φ) were generated from catch-curve analyses for oceanic-stage juvenile loggerheads (*Caretta caretta*) in the waters of the Azores. Two age distributions were analyzed: the “total sample” of 1600 loggerheads primarily captured by sighting and dipnetting from a variety of vessels in the Azores between 1984 and 1995 and the “tuna sample” of 733 loggerheads (a subset of the total sample) captured by sighting and dipnetting from vessels in the commercial tuna fleet in the Azores between 1990 and 1992. Because loggerhead sea turtles begin to emigrate from oceanic to neritic habitats at age 7, the best estimates of instantaneous mortality rate (0.094) and annual survival probability (0.911) not confounded with permanent emigration were generated for age classes 2 through 6. These estimates must be interpreted with caution because of the assumptions upon which catch-curve analyses are based. However, these are the first directly derived estimates of mortality and survival probabilities for oceanic-stage sea turtles. Estimation of survival probabilities was identified as “an immediate and critical requirement” in 2000 by the Turtle Expert Working Group of the U.S. National Marine Fisheries Service.

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Estimates of survival probabilities for oceanic-stage loggerhead sea turtles (*Caretta caretta*) in the North Atlantic

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A major gap in our understanding of sea turtle demography is the level of mortality—both natural and human-induced—experienced by wild populations. Lack of directly derived estimates of mortality (or survival) probabilities for the juvenile oceanic-stage in sea turtle populations is a critical source of uncertainty in development of population models and evaluation of management plans. In current population models, survival estimates for juvenile, oceanic-stage sea turtles are fitted parameters, not directly derived estimates, of survival (Chaloupka, in press; Heppell et al., in press). The Turtle Expert Working Group (2000) identified the estimation of survival probabilities as “an immediate and critical requirement.” Population models indicate that survival probability of juvenile oceanic-stage loggerhead sea turtles (*Caretta caretta*) has a substantial effect on overall population growth (Chaloupka, in press; Heppell et al., in press).

Catch-curve analyses have been used for many years to estimate survival probabilities for species harvested in commercial fisheries and, less frequently, for other species (Seber, 1982). Estimates of survival probabilities have been generated from catch-curve analyses for subadult neritic-stage populations of loggerhead sea turtles (Frazer, 1987; Epperly et al., 2001) and Kemp’s ridley sea turtles (*Lepidochelys kempii*) (Turtle Expert Working Group,

2000) based on stranding data. Catch-curve analyses confound mortality and permanent emigration, and thus generate estimates of apparent survival probability (Φ),

$$\Phi = S(1 - \text{emigration}),$$

where S = true survival probability; and
 emigration = the probability of permanent emigration.

We estimated survival probabilities (both Φ and S) for juvenile oceanic-stage loggerhead sea turtles in the waters around the Azores, a developmental habitat for the population of loggerhead sea turtles that nest on beaches in the southeastern United States (Bolten et al., 1998). We applied catch-curve analyses to two age distributions of loggerhead sea turtles.

Methods

Two size distributions were compiled for this study. The first (“total sample”) comprised 1600 oceanic-stage loggerhead sea turtles that were captured from 1984 through 1995 in the waters of the Azores. Except for a few of the smallest of these sea turtles found as stranded carcasses, they were collected in dipnets after being sighted at the surface of the ocean from the decks of a

variety of vessels. Loggerhead sea turtles captured on longline hooks were excluded from this sample to meet the requirement of equal probability of capture across the age range (see “Results” section). The turtles were measured, tagged, and released soon after capture. The juvenile loggerhead sea turtles ranged in size from 8.5 to 82.0 cm curved carapace length (mean=33.1 cm, SD=11.6) measured from the anterior point at midline to the posterior notch at midline between the supracaudals (Bolten, 1999). For 248 turtles, straight-line carapace measurements were converted to curved carapace length, as described in Bjorndal et al. (2000).

The second age distribution (“tuna sample”) was a subset of the total sample and comprised 733 loggerhead sea turtles captured by crews of commercial tuna vessels in the Azores between 1990 and 1992. We analyzed the tuna sample in addition to the total sample because the tuna sample was collected over a shorter interval (1990–92) than was the total sample (1984–95). In addition, sizes of vessels from which turtles were captured were more consistent for the tuna sample. This collaborative project with the tuna fleet is described in Bolten et al. (1993); sea turtles are not bycatch in the tuna fishery. Sea turtles were sighted at the surface while the crews were scanning for indications of tuna feeding activity. The turtles were then captured in dipnets, tagged and measured by a crew member, and released at sea. The juvenile loggerhead sea turtles ranged from 11.0 to 82.0 cm curved carapace length (mean=33.5, SD=11.2). No conversion from straight to curved measurements was required.

The size distributions were converted to age distributions by using a size-at-age function developed for this population based on a skeletochronological study (Table 1; Bjorndal et al., 2003). Catch curves were generated for each age distribution by plotting the natural log of N_x against x , where N_x is the number of turtles of age x . The catch curves were truncated by excluding age classes with fewer than five individuals, as recommended by Seber (1982). The age at which the population fully recruited to the capture method (threshold age) was identified as the age with the highest $\ln(N_x)$. Linear regression analyses of the values on the right-hand or declining slope of the distribution were used to generate estimates of total instantaneous mortality rate (Z), which is expressed on an annual basis and is the absolute value of the slope of the regression line. Annual apparent survival probability (Φ) was estimated as e^{-Z} . The statistical software S-PLUS (Guide to statistics, vol. 1, MathSoft, Seattle, WA) was used for regression analyses.

Results

The age distributions for the two samples are shown in Figure 1 and the catch curves in Figure 2. For catch-curve analyses, the age distributions were truncated to the 12-

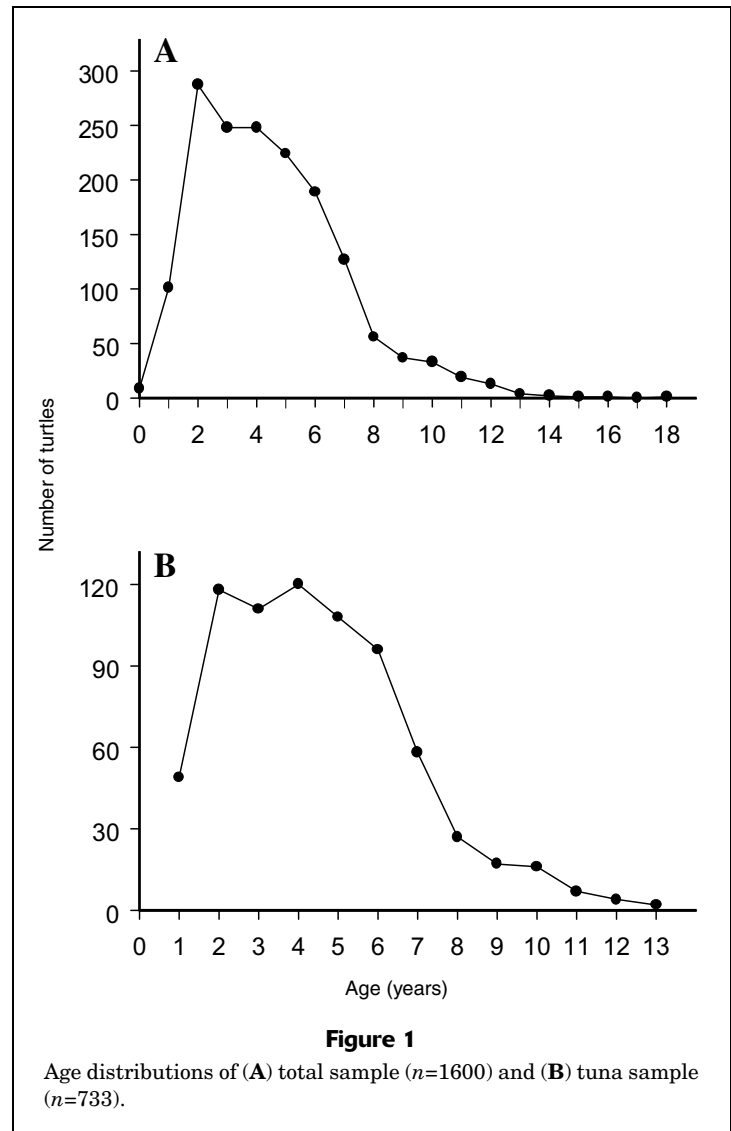


Figure 1
Age distributions of (A) total sample ($n=1600$) and (B) tuna sample ($n=733$).

year age class for the total sample and to the 11-year age class for the tuna sample because older age classes contained fewer than 5 individuals (Seber, 1982). The selection of the appropriate threshold age—the first fully recruited age class to the capture method—can be difficult but is critical for the analyses (Seber, 1982; Isaac, 1990). We designated 2 years as the threshold age for the total sample and 4 years for the tuna sample; in the tuna sample, the 4-year age class was slightly larger than the 2-year age class (120 vs. 118 turtles, Table 1).

We believe that turtles between ages 2 and 12 in the total sample and between 4 and 11 in the tuna sample meet the assumption of equal capture probability. With increase in turtle size, capture probability is a compromise; greater visibility of larger turtles is countered by greater difficulty in capturing larger turtles. Loggerhead sea turtles captured incidentally by longline vessels were excluded from our sample because there is a capture bias toward the largest size classes. The mean size of the turtles in the total sample

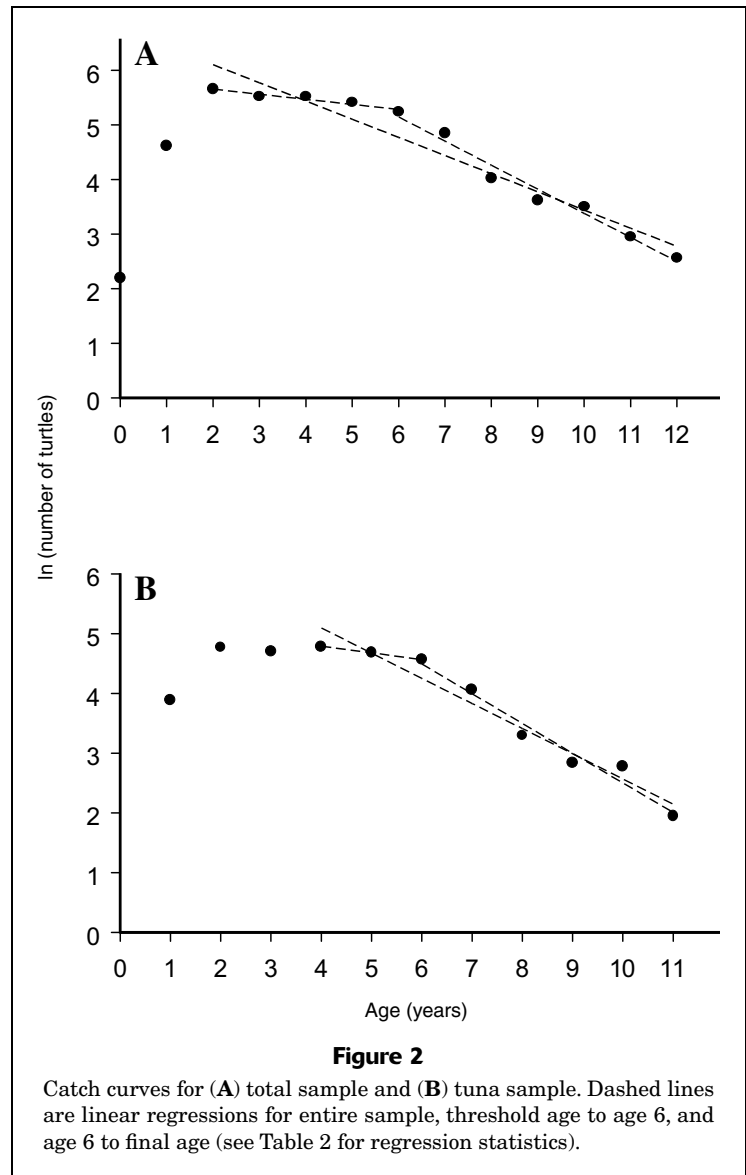
(33.1 cm) was significantly different (Kolmogorov-Smirnov test, $ks=0.6966$, $P<0.001$) from the mean size of loggerhead sea turtles caught in longline fisheries in the Azores during an experiment conducted in 2000 (49.8 cm; $n=224$; Bolten, in press).

The catch curves for both samples (Fig. 2) reveal a change in slope at age 6. The 7-year age class includes loggerhead sea turtles with curved carapace lengths >46 cm—the size at which they begin to leave oceanic habitats and recruit to neritic habitats (Bjorndal et al., 2000). Thus, the sharper decline beginning with age 7 reflects the migration of turtles out of the sampling area. Estimates of total instantaneous mortality rate (Z) and annual apparent survival probability (Φ) were generated for three age ranges for each sample: from threshold age to final age, from threshold age to pre-emigration age (6 years), and from pre-emigration age to final age. For the total sample, the age ranges were 2 to 12 years, 2 to 6 years, and 6 to 12 years, respectively; for the tuna sample, the ages were 4 to 11, 4 to 6, and 6 to 11 years (Fig. 2, Table 2).

Discussion

Estimates of mortality and survival generated from catch curves should be interpreted with caution for several reasons. First, the analysis assumes a stable age distribution, which we cannot confirm for North Atlantic loggerhead sea turtles. Second, the analysis assumes that mortality rates were consistent over the years of the study. The similarity of the mortality and survival estimates between the total sample (1984–95) and the tuna sample (1990–92) suggests that the estimates for the total sample are not greatly affected by heterogeneity among years. Third, converting size distributions to age distributions based on a size-at-age function introduces some level of error. We believe the error from our size-at-age function is small, as discussed in Bjorndal et al. (in press).

Fourth, the analysis assumes no size or age effect on mortality rates. The catch curves for both the total sample and tuna sample reveal a size or age effect with a pivot point at age 6. This size or age effect reflects the beginning of emigration out of our study area. Loggerhead sea turtles begin to leave oceanic habitats around the Azores and recruit to neritic habitats at 7 years of age, at ~ 46 cm curved carapace length (Bjorndal et al., 2000, 2003). This change in slope demonstrates the fifth difficulty in interpreting catch-curve estimates: permanent emigration and mortality are confounded in the estimates. That is, declines in numbers with age, whether they are due to emigration or mortality, are included in the estimate of mortality. The confounding of emigration and mortality can introduce a major error in estimates of mortality in populations—such as sea turtle populations in oceanic and neritic habitats—that undergo developmental migrations.



Because little permanent emigration apparently occurs before the age of 7, the survival estimates for the ages prior to 7 years are our best estimates of true survival (S). As can be seen in Table 2, the estimates of total instantaneous mortality and annual survival are similar for the two samples. We believe that the estimate of S (0.911 and 0.894, respectively, for the total sample and tuna sample) would apply to the entire life stage over the size range from 20 to 65 cm CCL for most sources of mortality other than fisheries biased to large sizes, such as longline fisheries. For predation, as sea turtles increase in size, they outgrow the prey size of some fish predators, but they also grow into the prey size of the largest predators, such as killer whales and humans (although the latter source is now very low in the Azores as a result of legislation and education [senior author, personal obs.]). Death from ingestion of or entanglement in marine debris would probably not vary substantially over this size range. However, mortality from incident-

Table 1

Size ranges of age classes and age distributions for total sample and tuna sample. CCL is curved carapace length, N_x is the number of turtles in each age class x , and YOY is young of year.

Size range (cm CCL)	Age	Total sample		Tuna sample	
		N_x	$\ln(N_x)$	N_x	$\ln(N_x)$
< 15.0	YOY	9	2.197	—	—
15.0–20.5	1	101	4.615	49	3.892
20.5–26.1	2	287	5.659	118	4.771
26.1–31.7	3	248	5.513	111	4.710
31.7–36.9	4	248	5.513	120	4.787
36.9–41.7	5	224	5.412	108	4.682
41.7–46.5	6	189	5.242	96	4.564
46.5–49.9	7	127	4.844	58	4.060
49.9–52.3	8	56	4.025	27	3.296
52.3–55.0	9	37	3.611	17	2.833
55.0–58.2	10	33	3.497	16	2.773
58.2–61.6	11	19	2.944	7	1.946
61.6–65.0	12	13	2.565	—	—

tal capture in longline fisheries in the Azores does increase with size, with the 2 to 6 year age classes experiencing very little mortality (Bolten, in press). Thus, if our estimate of S (calculated for the age classes between threshold age and age 6) were applied to the entire oceanic stage, the effect of mortality in longline fisheries, or other fisheries biased to large size classes, would be underestimated.

The estimate of 0.911 for annual survival probabilities for oceanic-stage loggerhead sea turtles in the waters of the Azores indicates high survival in this lifestage without mortality from longline fisheries. Species characterized by long life and late sexual maturity, such as loggerhead sea turtles, require very high survival throughout immature stages to maintain populations (Congdon et al., 1993; Crouse, 1999). This high probability of survival is also consistent with the theory that lower predation in oceanic habitats compared to neritic habitats is the selective pressure that maintains oceanic juvenile stages in most species of sea turtles (Bolten, 2003).

In two updated matrix models for North Atlantic loggerhead sea turtles (that differed in stage lengths), Heppell et al. (in press) derived fitted estimates of 0.745 and 0.875 for annual survival probabilities of the oceanic stage, which they defined as spanning 5 to 45 cm carapace length. Chaloupka (in press) derived an estimate of annual survival probability for oceanic-stage loggerhead sea turtles in Australia of 0.67 sampled from a logistic probability density function that ranged from 0.60 to 0.76 and had a mode at 0.67. The tuned estimate of 0.67 was derived from a stochastic simulation model that incorporated empirically based survival probability estimates for all age classes in the model except the oceanic phase (Chaloupka and Limpus, 2002; Chaloupka, in press). The estimate of 0.67 was generated for a size range from posthatchlings that have left the waters directly adjacent to the nesting

Table 2

Estimates of instantaneous mortality rates (Z) and annual apparent survival probabilities (Φ , estimated as e^{-Z}) for oceanic-stage loggerheads in the waters of the Azores generated from catch-curve analyses. r^2 (coefficient of determination) and P values are from linear regression analyses (see Fig. 2).

Age range (years)	Z	Φ	r^2	P
Total sample				
2 to 12	0.333	0.720	0.935	< 0.001
2 to 6	0.094	0.911	0.923	= 0.009
6 to 12	0.441	0.643	0.974	< 0.001
Tuna sample				
4 to 11	0.421	0.656	0.954	< 0.001
4 to 6	0.112	0.894	0.999	= 0.021
6 to 11	0.498	0.608	0.966	< 0.001

beach to subadults that begin to leave the oceanic habitats at a size of 69 cm curved carapace length (Chaloupka and Limpus, 2002).

The fitted estimates for annual survival from the Heppell et al. (in press) models and the Chaloupka (in press) model are lower than the estimates in our study, but the size ranges are different. In the Heppell et al. (in press) models and the Chaloupka (in press) model, the oceanic stage includes the posthatchling phase during which loggerhead sea turtles migrate from nesting beaches to their oceanic habitats. We could not include this early posthatchling phase in our estimates of survival of oceanic-stage loggerhead sea turtles in the waters of the Azores because many turtles in this phase

have not reached the Azores and they are younger than our threshold ages. We believe that mortality in this early transitional stage when loggerhead sea turtles first cross the Atlantic may be high. In addition to high rates of predation, winds and currents can overwhelm the swimming and orientation abilities of the posthatchling sea turtles, transporting the turtles to habitats, such as waters off the British Isles, that cannot sustain them (Carr, 1986; Hays and Marsh, 1997). Generating directly derived estimates of survival probabilities of loggerhead sea turtles younger than 2 years of age should be a high priority.

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