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Effects of transients on estimating survival and population growth in juvenile loggerhead turtles

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ABSTRACT: Population growth and annual survival of juvenile loggerhead turtles *Caretta caretta* were investigated in North Carolina using mark-recapture techniques. Lack of fit of the models employed caused us to reject the obtained estimates and led us to suspect that many loggerhead turtles were transient in the study area. We estimated apparent survival and the proportions of residents and transients. Transients represented approximately 75% of newly captured individuals captured at our study site. When transients were taken into account, apparent survival of residents increased from between 0.36 and 0.74 to 0.81. Our study highlights the need to consider the presence of transients when interpreting the results of loggerhead monitoring studies.

KEY WORDS: Mark-recapture · North Carolina · Pound nets · Sea turtles

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INTRODUCTION

For endangered and threatened species, population growth rate is of fundamental interest as a metric to evaluate the effectiveness of recovery efforts. However, in order to understand the dynamics of a population, it is first necessary to have an insight into recruitment and survival rates, in particular stage-specific survival, which are the underlying components of population growth (Fox 1993, Nichols et al. 2000). Mark-recapture studies provide a method to estimate both population growth rate and survival (Pradel 1996). When using traditional mark-recapture models, one potential cause for lack of model fit is the presence of transient individuals, which can bias estimates of survival (Pradel et al. 1997). Because transients are animals never seen again after initial capture, their probability of apparent survival is 0. Unless presence of transients is taken into account, estimates of survival will be downwardly biased.

Most studies of sea turtle population dynamics that utilize mark-recapture techniques are based on reproductive females at nesting beaches, owing to the ease of access to animals and relatively low costs (Heppell et al. 2003). However, while nesting beach studies can provide data on survival and trends in nesting populations (e.g. Frazer 1983, Heppell et al. 1996), they provide no direct information about what is occurring in stages other than the nesting population. Generally, after leaving the nesting beach as hatchlings, the juveniles of most sea turtle species spend a protracted period of time in an oceanic stage and then move to the neritic zone as larger juveniles, before finally reaching reproductive maturity; in some species such as the loggerhead turtle *Caretta caretta*, reproductive maturity may not be reached until at least 20 (Bolten 2003) to 31 years of age (Snover 2002). Given the delayed maturity of these species, a failure to monitor life-stages other than nesting females may result in decades passing before population declines are detected. The need for estimates of population status and survival from the juvenile stage classes has been identified as a research priority to improve sea turtle population modeling efforts and, ultimately, sea turtle management (Chaloupka & Musick 1996, Heppell et al. 2003). Other than research conducted on Australia's Great Barrier Reef by Chaloupka & Limpus (2002), no other studies have used mark-recapture data to estimate survival for juvenile loggerhead sea turtles in foraging areas.

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Juvenile loggerhead turtles inhabiting foraging areas along the USA Atlantic coast typically range from approximately 50 to 80 cm straight carapace length (Musick & Limpus 1997). In northern foraging areas, turtles seasonally migrate to warmer waters when water temperatures decline (Shoop & Kenney 1992, Epperly et al. 1995). While the seasonal migrations of juvenile turtles occupying these foraging areas have been well documented (Shoop & Kenney 1992, Epperly et al. 1995), knowledge of their general residence patterns, movements, and many other aspects of this life stage is limited. Such information is essential for understanding the dynamics of these neritic foraging populations, which in turn would make it possible to improve population models and to forecast population trends.

To assess population growth rate and estimate survival in Atlantic juvenile loggerheads, the National Marine Fisheries Service (NMFS) initiated a study to monitor sea turtles inhabiting North Carolina's Core Sound. Loggerhead turtles, the most abundant species in the study area, are mainly small-benthic juveniles that utilize the area as developmental habitat (Epperly et al. 1995). During their residence in Core Sound, the turtles are vulnerable to capture in pound nets set inshore of the barrier islands. Pound nets are passive, stationary fishing gear that incidentally capture turtles but allow them to surface, breathe, and be released alive (Higgins & Pearson 1928).

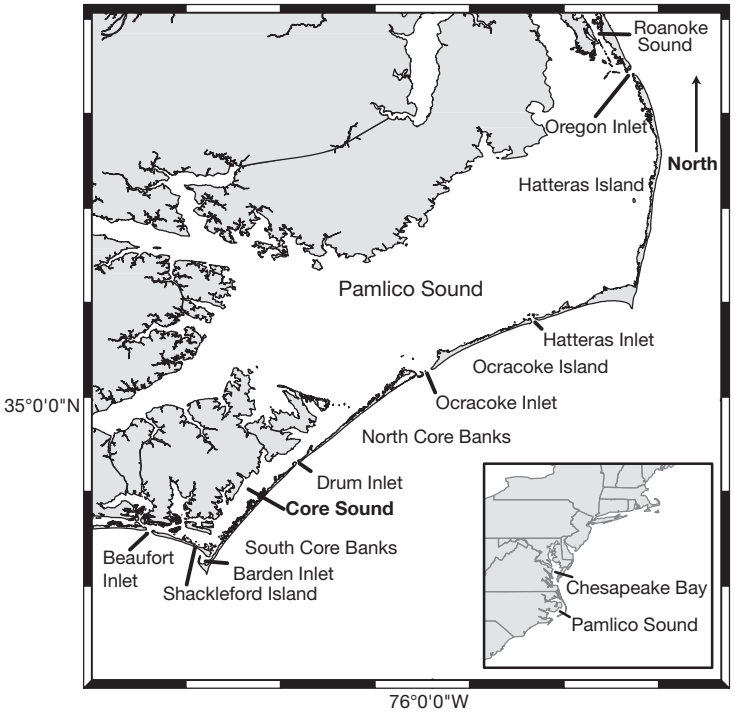

Fig. 1. Study area in central, Core Sound, North Carolina, USA

In this study, we analyzed 7 years of pound net mark-recapture data from North Carolina in order to assess annual growth in this population, and to estimate annual apparent survival, adjusted for transience. Apparent survival represents a minimum survival estimate because it does not account for emigration and, therefore, underestimates true survival (Williams et al. 2001).

MATERIALS AND METHODS

We sampled 5 to 8 pound nets encompassing a study area of 18.68 km^2 in central Core Sound, North Carolina, USA (Fig. 1), twice per week between June and August, from 1998 to 2004. Loggerhead turtles are present in Core Sound in spring, summer, and autumn (Epperly et al. 1995). Upon being brought on board, turtles were double-tagged with Inconel Style 681 tags (National Band and Tag Company[1]) applied to the trailing edge of each rear flipper. In addition, all turtles were tagged with 125 kHz unencrypted Passive Integrated Transponder (PIT) tags (Destron-Fearing) injected subcutaneously above the second-most proximal scale of the trailing margin of the left front flipper, to ensure identification of the turtle in the event that both Inconel tags were shed. Application of the 3 tags in this manner resulted in negligible (0.005%) total tag loss (Braun-McNeill et al. 2003). A unique capture history was created for each individual each year over the 7 yr.

Mark-recapture data were analyzed using Pradel's (1996) temporal symmetry approach implemented in the program MARK (White & Burnham 1999). This approach provides estimates of annual apparent survival (Φ), recapture probability (p), and population growth rate (λ) without having to estimate abundance, and assumes that both the survival and recruitment processes for the study area are representative of the entire population of interest.

Parameters can be either time dependent or constrained to a constant value that applies to all time periods. Eight models were run to account for all possible combinations of time-specific and time-invariant states of the 3 parameters (Table 2). Goodness-of-fit (GOF) of the general time-dependent model (Φ_i, p_i, λ_i) was assessed using the program RELEASE (Burnham et al. 1987). GOF tests were used to determine whether the model fitted the data and its use was appropriate. RELEASE provides 3 tests to assess fit or

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lack thereof: (1) Test 2 + 3 tests the full parameter model (time-dependent annual survival and recapture probabilities) to evaluate whether marked animals have the same recapture and survival probability, (2) Test 2 assesses whether marked animals meet the assumption of equal catchability, and (3) Test 3 tests whether all marked animals alive on occasion *i* have the same probability of surviving to *i* + 1, testing the assumption of homogeneity of survival of marked animals. In addition, there are 2 sub-tests of Test 3 that can be used to assess violations of the assumption of homogeneity of apparent survival of marked animals. Sub-test Test 3.SR evaluates whether the probability of future capture depends on whether the animal was marked on or before occasion *i*. Of those animals seen again, sub-test Test 3.SM determines if, when animals are recaptured, their recapture depends on whether they were marked on or before occasion *i*. We also used the program UCARE (Choquest et al. 2001) to implement Test 2.CT (Pradel 1993), which evaluates capture heterogeneity and temporary emigration.

The small-sample form of Akaike's Information Criterion (AIC_c) was used to rank the models and indicate which model was the most parsimonious (Hurvich & Tsai 1989, Burnham & Anderson 1992, 1998). Lower AIC_c values and higher AIC_c weights indicate a more appropriate model.

To estimate the proportion of transient individuals, the methods of Pradel et al. (1997) were employed using the program Transient-Model Survival Analysis (TMSURVIV) (Hines 1996). TMSURVIV estimates survival and probability of capture for residents and the proportion of residents among newly marked turtles, and is used when some captured animals may just be passing through (i.e. transients) and are not part of the resident population. AIC_c values and weights were used to select the most parsimonious model.

RESULTS

We captured and tagged 693 individual loggerhead turtles, ranging in size from 42.3 to 102 cm with the majority being small-benthic juveniles (mean = 63.6 ± 7.43 cm standard straight carapace length). Of these individuals, 63 were recaptured between years with 41 recaptured once, 18 recaptured twice, 2 recaptured 3 times, 1 recaptured 4 times, and 1 recaptured 5 times. No individual was captured in all 7 years.

The Pradel model with constant apparent survival, time-dependent recapture probability, and constant population growth rate was ranked as the best model (Table 1; AIC_c = 3381.7, AIC_c weight = 0.85), with the next best model having constant apparent survival and time-dependent recapture probability and population growth rate (AIC_c = 3386.0, AIC_c weight = 0.10). The time-dependent general model (Table 1) had an AIC_c of 3392.02 and an AIC_c weight of 0.005. However, the GOF test of the general model indicated an overall poor fit to the data (χ^2 = 51.35, df = 13, p < 0.001). This lack of fit provided no confidence in the predictive power of the model, and therefore no further attempts to calculate λ were made.

All animaals did not have the same probability of surviving from *i* to *i* + 1 (Test 3, χ^2 = 49.13, df = 9, p < 0.001). Newly marked individuals had a consistently lower probability of being seen again than previously marked individuals (Test 3.SR, χ^2 = 38.41, df = 5, p < 0.001). This result suggests that transients may be present, and that the occasion when marked animals were seen again depended upon when they were marked (Test 3.SM, χ^2 = 10.71, df = 4, p = 0.03). From Test 2, we did not reject the hypothesis that all marked individuals present on occasion *i* had the same probability of recapture (χ^2 = 2.23, df = 4, p = 0.69). There was no evidence of temporary emigration or trap dependence (Test 2.CT, χ^2 = 3.98, df = 4, p = 0.41). Estimates of survival obtained from the fully time-dependent Pradel model ranged from 0.38 to 0.74, while the best-ranked model estimated survival to be a time-invariant 0.55 (Table 1). However, the Pradel models were discounted because of the lack of fit to the data.

The presence of transients was confirmed using TMSURVIV (Table 2). The model which assumed constant survival, constant proportion of residents, and time-dependent probability of recapture was the highest ranked (AIC_c = 113.64, AIC_c weight = 0.90), whereas the time-dependent general model, which assumed all individuals to be residents, ranked poorly (AIC_c = 158.57,

Table 1. Estimated population parameters from Pradel's reverse-time models: (a) model (Φ_i, p_i, λ_i) AIC = 3392.02, (b) model (Φ, p_i, λ) AIC = 3381.74; Φ: apparent survival, p: recapture probability, λ: population growth rate. Values in parentheses: SE

Sample period	(a) Model Φ_i	p_i	λ_i	(b) Model Φ^a	p_i	λ^a
1	0.57 (0.19)	–	–	0.55 (0.5)	–	1.16 (0.07)
2	0.38 (0.11)	0.13 (0.06)	0.42 (0.24)		0.22 (0.06)	
3	0.67 (0.22)	0.40 (0.12)	2.20 (1.03)		0.19 (0.04)	
4	0.58 (0.21)	0.17 (0.06)	1.48 (0.81)		0.21 (0.04)	
5	0.74 (0.39)	0.12 (0.05)	1.21 (0.81)		0.17 (0.03)	
6	–	0.12 (0.06)	–	–	0.16 (0.04)	–
7	–	–	–	–	0.08 (0.02)	–

[a]Single estimate applies to periods 1 to 5

Table 2. Estimated apparent survival (Φ), probability of recapture (p), and proportion of residents using the TMSURVIV model (Transient-Model Survival Analysis). Values in parentheses: SE

Sample period	Model (Φ, p_i, Residents) Φ	p_i	Residents
1	0.81 (0.06)[a]	–	0.25 (0.04)[a]
2		0.35 (0.12)	
3		0.64 (0.11)	
4		0.38 (0.08)	
5		0.25 (0.07)	
6		0.30 (0.08)	
7	–	0.15 (0.05)	–

[a]Single estimate applies to periods 1 to 6

AIC_c weight = 0.00). Our analysis indicated that 75% of newly tagged individuals were transients (Table 2). The estimates for apparent survival (0.81) and recapture probabilities were higher when transients were taken into account, compared to estimates of 0.38 to 0.74 and 0.55 from the poorly fitting Pradel models.

DISCUSSION

Reporting on the same dataset extending between 1998 and 2001, Avens et al. (2003) found that 21% of juvenile loggerhead turtles were recaptured in subsequent years in the same general location in which they were originally caught, presumably after having migrated away from the capture area during winter months. Similarly, for the period from 1998 to 2004, we found that 75% of animals captured in the sampled nets were transients, i.e. animals available for capture only once. The high proportion of transients present in the sampled population explains the lack of fit in the Pradel models presented here. The GOF tests from the Pradel model indicated that newly marked individuals had a lower probability of being seen again, which suggested that transients were present, and was the motivating factor for the analysis using TMSURVIV. Animals captured for the first time have a much lower probability of apparent survival than residents, because transients will not be seen again and have an apparent survival probability of 0 (Pradel et al. 1997). Transients are an important consideration in survival estimates, as shown in other wildlife studies. For example, estimates of apparent survival for black-capped chickadees, another seasonal migrant, were lower for new captures because of the presence of transients (Loery et al. 1997).

Despite the high proportion of transients, we were still able to estimate apparent survival to be 0.81. However, because apparent survival does not distinguish between emigration and mortality, it represents a minimum estimate of realized survival. Thus, realized survival should be even higher because the model does not take into account emigration of turtles that leave the Pamlico-Albemarle Complex (Fig. 1) as they mature. Indeed, we rarely captured animals greater than 80 cm in the pound nets of North Carolina, indicating that larger animals may reside in other habitats or pound nets are size selective.

Previous estimates of juvenile loggerhead survival for the USA Atlantic were based on a catch-curve analysis and represented realized survival. Frazer (1987) estimated survival to be 0.68 and 0.70, whereas NMFS SEFSC (2001) estimated survival to be 0.893. However, both of these survival estimates represent the pre-1990 period, before turtle excluder devices were mandatory in the shrimp fishery; hence, survival during this time was expected to be lower than at present. Our estimate is higher than those of Frazer (1987) but lower than that of the NMFS SEFSC (2001), and again only represents a minimum estimate for the USA Atlantic because it does not account for emigration.

The high proportion of transients from our study site, which must be considered when analyzing mark-recapture data, also provides insight into the behavior of the species. Loggerhead turtles inhabiting temperate inshore foraging areas such as North Carolina undergo seasonal migrations, leaving inshore waters during late autumn/early winter and returning in spring when waters warm (Shoop & Kenney 1992, Epperly et al. 1995). As a result, animals never seen again in the sampled nets could be animals that (1) have little site fidelity and utilize neritic habitats throughout their range, (2) have some site fidelity, but were captured in the sampled nets during migrations to or from preferred sites, within or outside the Pamlico-Albemarle Complex, or (3) have site fidelity to the general area, but failed to be recaptured in the sampled nets. The GOF test does not support the contention that there is any difference in recapture probability for turtles present in the study area. We do have information on 43 of the animals that were never recaptured in this study: 21 were subsequently reported dead (12 on the banks of Core Sound or on ocean beaches in the vicinity of Core Sound, 4 elsewhere in North Carolina, 3 in Virginia, and 2 in South Carolina); 16 were recaptured—some more than once—in subsequent years either at our study site in periods other than between June and August (n = 6), or after the study between June and August 2005 (n = 3), in other Core Sound locations (n = 8), or in other North Carolina inshore waters (n = 4); and 9 animals (3 included from above) were initially captured in Core Sound (or in 1 case, in Pamlico Sound 5 km north of Core Sound) in years prior to being captured at the study site during the study period.

Chaloupka & Limpus (2002) estimated a juvenile survival rate for loggerhead turtles of 0.918 on the Great Barrier Reef, and reported a lower proportion of transients (34%) than that observed by us. Although they found evidence for loggerhead transients, their estimates of juvenile survival were not significantly altered by whether they took transients into account or not. A likely reason for the difference between apparent survival and proportion of transients in our study and that of Chaloupka & Limpus (2002) may be due to the fact that we monitored juveniles utilizing seasonal habitat, whereas their study was conducted on feeding areas occupied year-round. In addition, they had much higher recapture probabilities (0.63 to 0.82) than what we observed (0.15 to 0.64).

Whether our estimates of survival and residency can be extrapolated and applied to this juvenile stage in other areas in the Western Atlantic needs to be validated by studies in other localities. It may be reasonable to assume that it applies to similar situations where loggerhead turtles are present only seasonally (e.g. temperate waters of the western North Atlantic). Populations in the southern portion of the range, such as Florida Bay, may not have as high a proportion of transients as the water temperature would not necessitate migration from the area in the winter (Shoop & Kenney 1992, Epperly et al. 1995).

An additional question that should be addressed involves determining the natal origins of transients and residents. Recently, Bass et al. (2004) and Bowen et al. (2004) found evidence for some population structure of juvenile foraging areas, which suggests a correlation between feeding populations and adjacent nesting populations. It would be interesting to determine whether residents are more likely to be from local nesting colonies, in this case the northern loggerhead subpopulation, and whether transients are more likely to be from more distant nesting assemblages such the Florida or Yucatán sub-populations. A comparison of the genetic structure of transients versus residents may provide some insight into understanding the structure of foraging populations.

While we were able to estimate apparent survival, the lack of fit of the Pradel models and the high proportion of transients reported here may indicate that the scale of this study, limited to central Core Sound, North Carolina, was too small to extrapolate and assess the overall population growth rate for juvenile loggerhead turtles along the USA Atlantic coast. If loggerheads' use of a water body or of any particular area within the water body is not consistent among years, the use of a single sampling site would not be appropriate as an index of overall population growth. Monitoring loggerhead turtles over a larger spatial scale by establishing multiple monitoring sites along the USA Atlantic coast would provide better estimates of population growth rate, movements among seasonal foraging areas and, potentially, more precise survival estimates by reducing the effects of transients.

Despite the presence of transients in our study, we were able to estimate apparent annual survival by accounting for their presence. Our estimates are the first from mark-recapture data for juvenile loggerheads along the USA Atlantic coast, and represent minimum survival estimates for this stage. There is still a need for future studies to estimate realized survival for this stage by accounting for emigration. In addition, spatial expansion of studies in order to assess population growth of the juvenile stage would greatly improve our understanding of overall population trends and future risks.

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LITERATURE CITED

Avens L, Braun-McNeill J, Epperly S, Lohmann KJ (2003) Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). Mar Biol 143:211–220

Bass AL, Epperly S, Braun-McNeill J (2004) Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. Conserv Genet 5:783–796

Bolten AB (2003) Active swimmers–passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution, Washington, DC, p 63–78

Bowen BW, Bass AL, Chow SM, Bostrom M and 15 others (2004) Natal homing in juvenile loggerhead turtles (*Caretta caretta*). Mol Ecol 13:3797–3808

Braun-McNeill J, Avens L, Epperly SP (2003) Estimated tag retention rates for PIT and Inconel tags in juvenile loggerhead (*Caretta caretta*) sea turtles. In: Seminoff JA (ed) Proc 22nd Annu Symp Sea Turtle Biology and Conservation. NOAA Tech Memo NMFS-SEFSC-503:104

Burnham KP, Anderson DR (1992) Data-based selection of an appropriate biological model: the key to modern data analysis. In: McCullough DR, Barett RH (eds) Wildlife 2001: populations. Elsevier Science Publishers, New York, p 16–30

Burnham KP, Anderson DR (1998) Model selection and inference: a practical information-theoretic approach. Springer Verlag, New York

Burnham, KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release-recapture. Am Fish Soc Monogr 5:1–437

Chaloupka MY, Limpus CJ (2002) Survival probability estimates for the endangered loggerhead sea turtle resident in southern Great Barrier Reef waters. Mar Biol 140: 267–277

Chaloupka MY, Musick JA (1996) Age, growth, and population dynamics. In: Lutz PL, Musick JA (eds) The biology of sea turtles, Vol II. CRC Press, Boca Raton, FL, p 275–306

Choquest R, Roeboulet AM, Pradel R, Leberton JD (2001) UCARE user's guide, version 3.1. Centre d'Ecologia Fonctionelle et Evolutive, Centre National de la Recherche Scientifique, Montpellier

Epperly SP, Braun J, Veishlow A (1995) Sea turtles in North Carolina waters. Conserv Biol 9:384–394

Fox GA (1993) Life history evolution and demographic stochaticity. Evol Ecol 7:1–14

Frazer NB (1983) Survivorship of adult female loggerhead sea turtles, *Caretta caretta*, nesting on little Cumberland Island, Georgia, USA. Herpetologica 39:436–447

Frazer NB (1987) Preliminary estimates of survivorship for wild loggerhead sea turtles (*Caretta caretta*). J Herpetol 21:232–235

Heppell SS, Limpus CJ, Crouse DT, Frazer NB, Crowder LB (1996) Population model analysis for the loggerhead sea turtle, *Caretta caretta*, in Queensland. Wildl Res 23: 143–159

Heppell SS, Snover ML, Crowder LB (2003) Sea turtle population ecology. In: Lutz PL, Musick JA, Wyneken J (eds) The biology of sea turtles, Vol II. CRC Press, Boca Raton, FL, p 275–306

Higgins E, Pearson JC (1928) Examination of the summer fisheries of Pamlico and Core Sounds, NC, with special reference to the destruction of undersized fish and the protection of the gray trout *Cynnoscion regalis* (Bloch and Schneider), Appendix II. Report of the United States Commissioner of Fisheries for the Fiscal Year 1927 with Appendices. Bureau of Fisheries No. 1019:29–65

Hines JE (1996) TMSURVIV user's manual. Biological Resources Division, US Geol Surv, Laurel, MD

Hurvich CM, Tsai CL (1989) Regression and time series model selection in small samples. Biometrika 76:297–307

Loery G, Nichols JD, Hines JE (1997) Capture-recapture analysis of a wintering black-capped chickadee population in Connecticut, 1958–1993. Auk 114:431–442

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz PL, Musick JA (eds) The biology of sea turtles. CRC Press, Boca Raton, FL, p 137–163

Nichols JD, Hines JE, Lebreton JD, Pradel R (2000) Estimation of contributions to population growth: a reverse-time capture-recapture approach. Ecology 81:3362–3376

NMFS SEFSC (National Marine Fisheries Service Southeast Fisheries Science Center) (2001) Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on loggerhead and leatherback sea turtles of the western north Atlantic. NOAA Tech Memo NMFS-SEFSC-455

Pradel R (1993) Flexibility in survival analysis from recapture data: handling trap dependence. In: Leberton JD, North PM (eds) Marked individuals in the study of bird population. Birkhäuser Velag, Basel, p 29–37

Pradel R (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709

Pradel R, Hines JE, Lebreton JD, Nichols JD (1997) Capture-recapture survival models taking account of transients. Biometrics 53:60–72

Shoop CR, Kenney RD (1992) Seasonal distributions and abundances of loggerhead and leatherback sea turtles in the waters of the northeastern United States. Herpetol Monogr 6:43–67

Snover ML (2002) Growth and ontogeny of sea turtles using skeletonochronology: methods, validation and application to conservation. PhD dissertation, Duke University, Durham, NC

White GC, Burnham KP (1999) Program MARK: survival rate estimation from both live and dead encounters. Bird Study 46(Suppl):S123–S139

Williams BK, Nichols JD, Conroy MJ (2001) Analysis and management of animal populations. Academic Press, San Diego, CA

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