Herpetological Review, 2013, 44(2), 221–226.
© 2013 by Society for the Study of Amphibians and Reptiles

Estimates of Tag Loss for Loggerhead Sea Turtles (*Caretta caretta*) in the Western North Atlantic

Capture-mark-recapture (CMR) research can provide valuable information on the survival rates, movements, population sizes and trends, growth rates, demographics, and other life-history parameters of wildlife populations (Williams et al. 2002). However, in order for CMR research to be accurate in the estimation of these parameters, a reliable method needs to be used to mark animals. Nevertheless, tag or mark loss occurs since no marking system is infallible. This loss, if not accounted for, can bias estimation of population parameters and abundance (Arnason and Mills 1981; Cowen and Schwarz 2006; Frazer 1983; McDonald et al. 2003).

The inability to recognize a mark (hereafter referred to as tag loss) generally has been measured using simple models that evaluate tag retention by monitoring groups of double-tagged animals and quantifying those that were recovered with one and two tags (Seber 1982). However, the assumption that the two tags have an independent rate of loss was not found to be true for sea otters (Siniff and Ralls 1991), black bears (Diefenbach and Alt 1998), fur seals (Bradshaw et al. 2000), leatherback sea turtles (Rivalan et al. 2005), or elephant seals (McMahon and White 2009). Furthermore, Seber's (1982) model only calculates discrete rates of tag loss that might not be accurately extrapolated to the end of the

JOANNE BRAUN McNEILL[1]*
e-mail: Joanne.B.McNeill@noaa.gov
AMY M. SCHUELLER[1]
e-mail: Amy.Schueller@noaa.gov
LARISA AVENS[1]
e-mail: Larisa.Avens@noaa.gov
APRIL GOODMAN HALL[1]
e-mail: April.Goodman@noaa.gov
LISA R. GOSHE[1]
e-mail: Lisa.Goshe@noaa.gov
SHERYAN P. EPPERLY[2]
e-mail: epperlychester@gmail.com

[1]National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA
[2]National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, Florida 33149, USA
**Corresponding author*

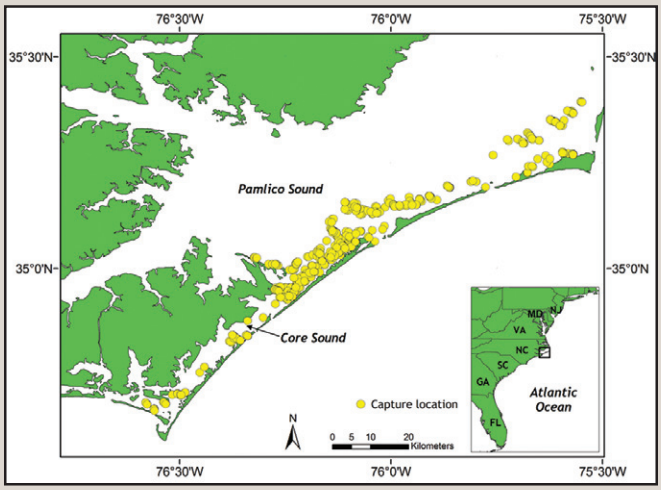

Fig. 1. Loggerhead Sea Turtles (*Caretta caretta*) were captured in fishing gear set in Core and Pamlico Sounds, North Carolina, United States. Inset shows position of main figure within the east coast of the USA.

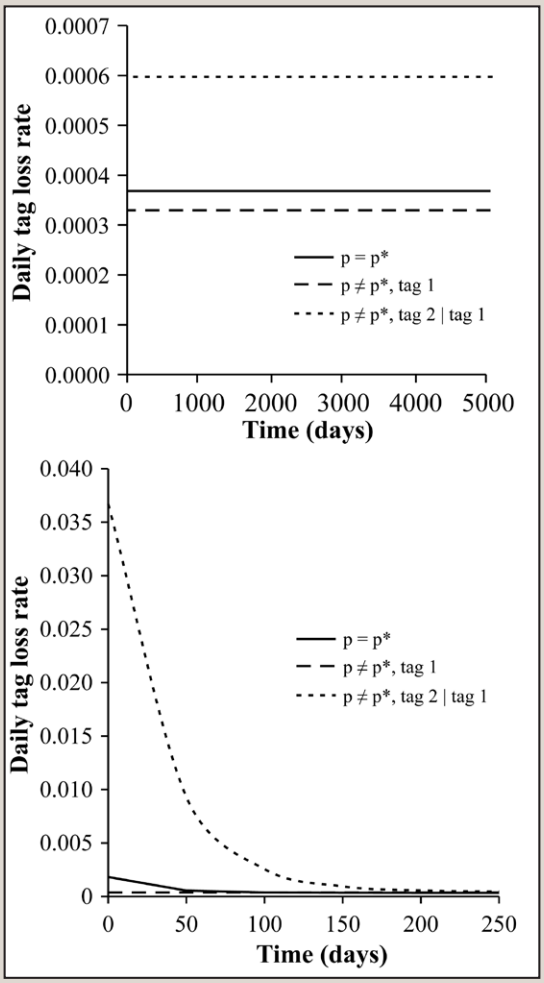

Fig. 2. Daily tag loss rate estimated for Data Set 1 (all individuals that received a PIT tag) using model A, the best fit model, which had a constant tag loss rate over time (upper panel). Daily tag loss rate estimated for Data Set 2 (only those individuals that received a PIT tag during initial capture; lower panel). The best fit model for DS2 was Model D with p ≠ p*, which resulted in model A for Inconel tag one and model D for Inconel tag two.

CMR study. Therefore, new methods were developed to address some of these limitations (Diefenbach and Alt 1998; Pistorius et al. 2000; Rivalan et al 2005; Schwartz et al. 2012). One of the models, described in Rivalan et al. (2005), takes an integrative approach that provides an estimate of tag loss rate while allowing for several tag shedding possibilities.

Loggerhead Sea Turtles (*Caretta caretta*) are long-lived, slow-growing animals that spend portions of each life stage in various oceanic and coastal environments (Meylan and Ehrenfeld 2000). In addition, they are vulnerable to many sources of mortality, most notably incidental capture in commercial fisheries (Lewison et al. 2004). Consequently, there is an urgent need to assess and protect their populations from extirpation (National Research Council 2010). Many turtles have been tagged in long-term, in-water studies so that aspects of their cryptic life history can be revealed (see Chaloupka and Musick 1996 for a review). Identification of individual sea turtles is generally accomplished through the use of metal or plastic flipper tags and Passive Integrated Transponder (PIT) tags (Balazs 1999). Efforts to develop photo identification techniques for turtle identification are also becoming more common (Lloyd et al. 2012; McDonald and Dutton 1996; Reisser et al. 2008; Schofield et al. 2008) Previous studies have attributed tag loss in sea turtles to a variety of reasons including turtle species, size of turtle, position of tag, tag material, poor application of the tag, or environment of the turtle (Alvarado 1993; Balazs 1982; Bjorndal et al. 1996; Henwood 1986; Limpus 1992; Parmenter 1993; Reisser et al. 2008; van Dam and Diez 1999).

The first objective of our study was to determine the tag loss rate of Loggerhead Sea Turtles in Pamlico and Core Sounds, North Carolina, USA. We have been double-tagging sea turtles with Inconel metal tags since 1989 and additionally tagging with PIT tags since 1995. We estimated tag loss using the maximum likelihood method in Rivalan et al. (2005), which makes two assumptions: 1) PIT tag loss is negligible and 2) the probability of a turtle not being observed again is the same for individuals tagged initially with or without a PIT tag. The second objective of our study was to determine the ramifications of the two assumptions and to explore if they were valid assumptions for our data set.

Materials and Methods.—We handled Loggerhead Sea Turtles incidentally captured in pound nets, long haul seines, and trawlers in Core and Pamlico Sounds, North Carolina, from June through December, 1989 to 2010 (Fig. 1). Core and Pamlico Sounds are a part of the Pamlico-Albemarle estuarine complex, the largest estuarine system (6630 km^2) in the southeastern United States. This system, which is bounded on the east side by the Outer Banks barrier islands, consists of lagoonal-type ecosystems that are shallow (the mean depth of Pamlico Sound is 4.5 m; Core Sound is 1.2 m), and productive (Copeland and Gray 1991; Roelofs and Bumpus 1953).

We recorded standard straight-line carapace length (SCL, notch to tip) to the nearest 0.1 cm. We applied Inconel metal alloy size 681 self-piercing tags (National Brand and Tag Company, Newport, Kentucky, USA) with approximately half the length of the tag to the trailing edge of both rear flippers, just anterior to the first large scale (Balazs 1999). We chose the rear instead of front flippers as we found some turtles were becoming entangled in the mesh of pound nets when the tag was on either front flipper (NMFS, unpubl. data). Beginning in 1995, we additionally injected unencrypted PIT tags (Destron-Fearing Corp., South St. Paul, Minnesota, USA, 125 kHz) subcutaneously approximately 1 cm anterior to the second most proximal scale of the trailing

margin of the left or right front flipper, or in the triceps superficialis muscle of the left front flipper; thus, all turtles were triple tagged beginning in 1995. We initially scanned all turtles to determine if they already had a PIT tag; if none was found, we scanned each PIT tag both before and after insertion to ensure it was functioning. After tagging, we released turtles in the vicinity of their capture locations. When a turtle was recaptured, we recorded all tags still detectable on the turtle. Only three of the recaptured turtles were recovered by researchers outside of our group who did not scan for a PIT tag, thus having a negligible effect on our results.

To determine daily tag loss rate, we used the integrative model of tag loss developed by Rivalan et al. (2005). We converted turtle capture histories so that the data provided time intervals (in days) for the following tag loss categories: N_{22} is the number of days that the recaptured turtle had retained both Inconel tags; N_{21} is the number of days during which the recaptured turtle had lost one of its Inconel tags; N_{20} the number of days during which the recaptured turtle had lost both Inconel tags (and only the PIT tag remained for identification); N_{11} is the number of days during which the recaptured turtle that had lost one of its Inconel tags was released with one tag and was recaptured still retaining that one Inconel; and N_{10} is the number of days during which the recaptured turtle that had lost one of its Inconel tags was released with one tag and was recaptured without any Inconel tags (and only the PIT tag remained for identification). For example, if a turtle was recaptured three times (first event with two tags, second event with one tag, and third event with one tag), then one would calculate the time intervals for N_{22}, N_{21}, and $N_{11.}$

The maximum likelihood method described by Rivalan et al. (2005) makes two assumptions: 1) that PIT tag loss is negligible and 2) that those individuals tagged initially without a PIT tag have the same probability of not being observed again as those individuals who initially received a PIT tag. We addressed the first assumption by calculating the percentage of recaptured turtles whose PIT tags were no longer detectable. We addressed the second assumption two different ways. First, we separated turtles into two different groups: turtles that were triple-tagged (2 Inconels and 1 PIT) and turtles that were double-tagged (2 Inconels). We compared the percent of triple-tagged turtles that were never recaptured to that of double-tagged turtles that were never recaptured to test the assumption that tag loss rate was the same for individuals in both groups. Confidence intervals for each of the proportions were calculated using Wilson's (1927) confidence interval and the confidence intervals were compared to see if they overlapped. Second, we created two data sets to see if the shape and magnitude of tag loss over time was the same when analyzing the data using the methods of Rivalan et al. (2005). The first data set (DS1) included all tagged individuals in the study who received a PIT tag at some point (N = 2811). The second data set (DS2) included only those individuals that received a PIT tag on their first capture event (N = 2606); thus, DS2 is a subset of DS1. By analyzing both data sets separately, we were able to determine if tag loss rate was affected by including those individuals that were not PIT-tagged during their initial capture event.

Each data set was then used to find daily tag loss rate, using maximum log-likelihood to find parameter values for:

$$p(t) = \frac{1-\min_t}{1+e^{(a_0(a_1-t))}} + \min_t \quad \text{where} \quad \min_t = \frac{a_4}{1+e^{(a_2(a_3-t))}}$$

where p is the probability of tag loss; t is time; and a_0, a_1, a_2, a_3, and a_4 were model parameters with standard errors being estimated with the delta method (Rivalan et al. 2005). We used the software application TAG LOSS, Version 3.2.3 (Girondot 2011).

We modeled six different tag loss patterns, which can be found in Fig. 1 of Rivalan et al. (2005):

Model A, a constant daily tag loss rate;

Model B, a linearly decreasing tag loss rate;

Model C, a high tag loss rate that decreased over time to asymptote near zero;

Model D, a high tag loss rate that decreased over time to an asymptote above zero;

Model E, a high tag loss rate that gradually decreased over time, although not as a smooth function; and

Model F, an initially decreasing tag loss rate, which began increasing after a certain period of time.

Each model was fit for each data set assuming 1) probability of tag loss was equal for both tags ($p = p^*$) and 2) probability of tag loss was different for both tags ($p \neq p^*$). Tag loss rates were estimated for Inconel tags, not PIT tags, and the probability of tag loss for the second tag was a conditional probability. We selected the best model based on the lowest Akaike's Information Criteria (AIC; Akaike 1974) values.

Results.—From 1990 to 2010, we tagged 2811 loggerheads and recaptured 585 identifiable turtles, ranging from 44.1 to 102.5 cm SCL (mean ± SE, 64.7 ± 0.3) at initial capture. Recapture intervals ranged from 1 to 4725 days (mean ± SE, 507.1 ± 29.5). We triple-tagged (2 Inconel and 1 PIT tag) 2606 loggerhead turtles, of which 2021 or 78% (95% CI: 0.76–0.79) never were recaptured. We double-tagged (2 Inconel tags) 205 loggerheads which were PIT-tagged during subsequent recaptures, and of those turtles, 172 or 84% (95% CI: 0.78–0.88) were never recaptured. Based on our data, we were not able to detect the PIT tag for 44 of the 557 recaptures that were scanned for a PIT tag, resulting in a 0.079 failed detection rate over the duration of the 15 years that we were tagging with PIT tags.

For DS1, daily tag loss rate for $p = p^*$ was estimated at 0.00037 using model A (Table 1; Fig. 2; AIC = 788.29). Daily tag loss rate for $p \neq p^*$ was estimated at 0.00033 for tag one and 0.00060 for tag two using model A (Table 1; Fig. 2; AIC = 391.15). Daily tag loss rate for $p = p^*$ using model C was a decreasing function through time starting at a high of 0.00050 on day one and decreasing as time continued (Table 1; Fig. 2b; AIC = 788.81). Daily tag loss rate for $p \neq p^*$ using model C was a decreasing function through time starting at a high of 0.00044 for tag one and 0.00143 for tag two on day one and decreasing as time continued (Table 1; Fig. 2; AIC = 777.15). When fitting models B, D, E, and F, the parameter estimates all reduced to model A as the best fit to the data.

For DS2, daily tag loss rate for $p = p^*$ was estimated at 0.00040 using model A (Table 1; Fig. 3; AIC = 770.67). Daily tag loss rate for $p \neq p^*$ was estimated at 0.00037 for tag one and 0.00058 for tag two using model A (Table 1; Fig. 3; AIC = 767.40). Daily tag loss rate for $p = p^*$ using model C was a decreasing function through time starting at a high of 0.00058 on day one and decreasing as time continued (Table 1; Fig. 3; AIC = 774.03). Daily tag loss rate for $p \neq p^*$ using model C was a decreasing function through time starting at a high of 0.00052 for tag one and 0.00122 for tag two on day one and decreasing as time continued (Table 1; Fig. 3; AIC = 767.90). Model D did not reduce to model A as in the other data set. Daily tag loss rate for $p = p^*$ started at a high of 0.0018 on day one and decreased to an asymptote of 0.00034 using model D (Table 1; Fig. 4; AIC = 757.57). Daily tag loss rate for $p \neq p^*$ reduced to a constant loss rate (model A) for tag one and remained a decreasing function with an asymptote for tag two (model D).

Table 1. Model parameter estimates (standard error) for the models that converged for each data set and the associated AIC values. Data sets are DS1, which includes all turtles marked during this study, and DS2, which includes only turtles that received a PIT tag during the initial capture event. If $p \neq p^*$, then the parameter estimates (standard errors) are listed as the parameter estimates for the first tag followed by the parameter estimates for the second tag. Parameters with dashes below them were not estimated for that specific formulation of the model.

Data set	Model	AIC	a_0	a_1	a_4
DS1	A; $p \neq p^*$	391.15	—	—	6.59×10^{-4} (5.7×10^{-5}) 1.19×10^{-3} (2.1×10^{-4})
DS1	C; $p \neq p^*$	777.15	-6.1×10^{-4} (6.57×10^{-6}) −12531.3 (138.12)	-1.1×10^{-3} (2.6×10^{-5}) −5943.0 (156.70)	—
DS1	A; $p = p^*$	788.29	—	—	7.36×10^{-4} (5.6×10^{-5})
DS1	C; $p = p^*$	788.81	-6.08×10^{-4} (5.76×10^{-6})	−12479.9 (122.68)	—
DS2	D; $p \neq p^*$	755.26	— -2.87×10^{-2} (2.9×10^{-3})	— −114.1 (16.46)	7.5×10^{-4} (6.3×10^{-5}) 8.7×10^{-4} (1.8×10^{-4})
DS2	D; $p = p^*$	757.57	-3.89×10^{-2} (1.5×10^{-3})	−167.7 (7.39)	6.8×10^{-4} (5.8×10^{-5})
DS2	A; $p \neq p^*$	767.40	— —	— —	7.4×10^{-4} (6.3×10^{-5}) 1.17×10^{-3} (1.9×10^{-4})
DS2	C; $p \neq p^*$	767.90	-7.3×10^{-4} (7.1×10^{-6}) -9.8×10^{-4} (2.2×10^{-5})	−10284.8 (113.5) −6845.6 (170.6)	—
DS2	A; $p = p^*$	770.67	—	—	8.08×10^{-4} (6.0×10^{-5})
DS2	C; $p = p^*$	774.03	-6.96×10^{-4} (6.5×10^{-6})	−10720.14 (104.82)	—

For tag one, the tag loss rate was a constant 0.00037, while for tag two, the tag loss rate started at a high of 0.0367 and declined to an asymptote of 0.00044. Model D with $p \neq p^*$ (which resulted in model A for tag one and model D for tag two) had an AIC value of 755.26. Finally, when fitting models B, E, and F, the parameter estimates all reduced to model A as the best fit to the data.

Discussion.—Careful consideration of assumptions should always be used when analyzing data. For Loggerhead Sea Turtles in North Carolina, Inconel tag loss rate estimates were different when including all individuals that were PIT-tagged in the study (DS1) than when restricting the analysis to only those that received a PIT tag during their initial capture event (DS2). Although daily tag loss rates were similar for both data sets, the first year for DS2 showed the greatest tag loss rate for the second tag, which could have an effect on tag retention rates over time. The estimation of tag loss using DS2 demonstrated that the probability of not being observed again was not the same for turtles that initially received a PIT tag as compared to those that were PIT-tagged later; therefore, the second assumption made in Rivalan et al. (2005) should be considered for other datasets that have not PIT-tagged individuals during the entire duration of their study. Additionally, a portion of turtles from DS1 could have shed their Inconel tags prior to being PIT-tagged, and thus their tag loss would not be noted, as they would not have been recognized as recaptures. We also found that the first assumption of the method was not met as PIT tag detection failure during the 15 years we used these tags was 7.9%, which was not negligible. How PIT tag loss affects the model outcomes is unknown at this point, but could be addressed by constructing a model with three different tags that can be lost at different rates. Based on these findings, we suggest that those marking turtles for mark-recapture use more than one type of tag. Furthermore, our decision to only include turtles that received a PIT tag during their initial capture event did lead to different tag loss rates over time. Thus, careful consideration of input data into the model should be used.

A constant tag loss rate, such as that found for Inconel tag one in DS2, could be an indication of well-applied tags, the effect of tag location, or the interval of recapture. We calculated a tag loss rate of 13% after one year for the first tag using model A with $p \neq p^*$ for individuals tagged in the rear flipper. In contrast, Gorham et al. (1997) calculated a tag loss rate of >50% after 440 days for loggerhead turtles tagged in the front flippers. Thus, tagging rear flippers might result in an increase in tag retention compared to tagging front flippers. However, a constant tag loss rate also could be a reflection of the long recapture intervals (2–4 years) that we recorded with some individuals. Because of a lack of data on recaptures during the time immediately following marking of these individuals, the model has little information to determine the shape of the tag loss rate function during the time interval immediately following marking. Thus, the model falls back to the simplest explanation, which is a constant tag loss rate over the entire time interval.

In our study, the daily loss rate for tag two given that tag one had been lost was a decreasing function that went to an asymptote of 0.00044. Rivalan et al. (2005) also found tag loss rate for Leatherback Sea Turtles, *Dermochelys coriacea*, in French Guiana, to be very high initially, followed by a rapidly decreasing probability of tag loss soon after application. However, they found this initial high tag loss rate for tag one while we found it to be true for tag two. They tagged the rear flippers with Monel tags and attributed tag loss over a short time scale to tagging failure caused either by human or mechanical error. Likewise, the loss of the second tag in our study could have been a result

of incorrect application of the tag or failure of the tag to lock properly. Over the course of our 21-year study, several different trained technicians applied tags, which may be responsible for some tagging failure.

Similar to Rivalan et al. (2005), we also found that the rate of losing the second tag was significantly higher given the loss of the first tag. Tissue necrosis could have increased tag loss dependency since individuals susceptible to tissue necrosis are likely to lose both tags (Rivalan et al. 2005). However, tissue necrosis may be more of a problem with leatherback turtles than with loggerhead turtles, as we did not encounter any loggerheads with tissue necrosis on our study site. Rather, a possible explanation for the tag loss dependency in North Carolina loggerhead turtles may be attributed to tagging failure as a result of human error, i.e., improper application of the tag. In other words, if the first tag was not applied correctly (either through improper technique or mechanical failure of either the tag or tag applicator), there was an increased chance that the second tag also would not be applied correctly, resulting in the second tag being lost as well.

Tag loss in sea turtles varies, depending upon turtle species, size of turtle, position of tag, tag material, environment of the turtle, and the experience of taggers (see Balazs 1982 for a summary). For example, van Dam and Diez (1999) reported an Inconel tag loss rate of 18% after 3 years for front-flipper-tagged Hawksbill Sea Turtles (*Eretmochelys imbricata*), much less than our calculated rate of 39% after 3 years, indicating that hawksbill turtles might have an overall higher tag retention rate for Inconel tags in their front flippers than loggerhead turtles tagged in their rear flippers. However, their large sub-adults and adults (>60 cm) were tagged with just external tags (no PIT tags), so the possible inability to identify recaptures due to the loss of external tags might have influenced their overall estimation of tag retention rates.

Although PIT tags have been described as being "permanent"(Gibbons and Andrews 2004), several sea turtle tagging studies, including this one, have reported a failure to detect these tags. Failure to detect PIT tags can be attributed to a variety of factors: tags can be expelled from the body or migrate internally, the PIT tag scanner or reader can fail to detect a tag that is present, or the tag itself can fail (Wyneken et al. 2010). Parmenter (1993) found an 8% failure rate of PIT tags in Flatback Turtles (*Natator depressus*) after two years, while van Dam and Diez (1999) saw up to 15% failure in their ability to detect PIT tags in hawksbill turtles after a five-year period. We failed to detect approximately 8% of the PIT tags in loggerheads over the course of the 15 years we used PIT tags. Despite this failure rate, there are many advantages to using PIT tags to mark sea turtles. Because the tags are internal, tag loss through abrasion is low to non-existent. In addition, they have very little negative impact on the turtle, including entanglement in fishing gear, provided the animal is of a sufficient size to receive the tag. Finally, although our failure rate to detect PIT tags was not negligible, it was substantially less than the tag loss rate of Inconel tags, which was about 13% each year.

To increase our tag retention rates, we followed the advice of previous researchers by applying more than one tag to each turtle, using two Inconel tags and a "permanent" PIT tag. Triple-tagging turtles in this way allowed for greater identification of recaptures and enabled us to take advantage of the benefits of using both methods of tagging. For example, metal, external tags such as Inconel tags do not require a special reader to view the tag. Additionally, the cost (US $70 for 100 tags) is substantially less than that of PIT tags (US $6–8 per tag). On the other hand, despite their higher costs and need for a reader, PIT tags are essentially permanent marks as they can potentially last for the lifetime of the animal. Therefore, we likewise recommend using PIT tags in conjunction with one or more external tags (such as Inconel) to maximize the probability of identifying a recaptured turtle.

Loggerhead Sea Turtles are a slow-growing, late-maturing species that conduct wide-ranging migrations, life-history traits that make them especially susceptible to overexploitation (National Research Council 2010). Successful management of these vulnerable populations requires an accurate accounting of their absolute abundance to properly evaluate potential impacts of management decisions (National Research Council 2010). Estimation of tag loss rates will help to correct for potential biases in models used to estimate population abundance and survival over time. This allows for increased accuracy of abundance and survival estimates used in population modeling and for management of sea turtle populations.

Acknowledgments.—We thank the many observers who have helped us to tag sea turtles throughout this long-term study and the fishermen for allowing us access to sea turtles captured in their fishing gear. The manuscript was improved by comments from M. Godfrey, A. Hohn, P. Marraro, K. Shertzer, and anonymous reviewers. Research was conducted under NMFS scientific research permit #1260 and #1551 and USFWS Permit #TE-676379. Products referenced are not endorsed by the authors or the agency they represent.

Literature Cited

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19:716–723.

Alvarado, J. 1993. Differential retention of metal and plastic tags on the black sea turtle. Herpetol. Rev. 23:23–24.

Arnason, A. N., and K. H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark–recapture experiments. Can. J. Fish. Aquat. Sci. 38:1077–1095.

Balazs, G. H. 1982. Factors affecting the retention of metal tags on sea turtles. Mar. Turtle Newsl. 20:11–14.

———. 1999. Factors to consider in the tagging of sea turtles. *In* K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly (eds.), Research and Management Techniques for the Conservation of Sea Turtles, pp. 101–109. IUCN/SSC Marine Turtle Specialist Group.

Bjorndal, K. A., A. B. Bolten, C. J. Lagueux, and A. Chaves. 1996. Probability of tag loss in green turtles nesting at Tortuguero, Costa Rica. J. Herpetol. 30:567–571.

Bradshaw, C. J. A., R. J. Barker, and L. S. Davis. 2000. Modeling tag loss in New Zealand fur seal pups. J. Agric. Biol. Environ. Stat. 5:475–485.

Chaloupka, M. Y., and J. A. Musick. 1997. Age, growth, and populations dynamics. *In* P. L. Lutz and J. A. Musick (eds.), The Biology of Sea Turtles, pp. 233–276. CRC Press, Inc., Boca Raton, Florida.

Copeland, B. J., and J. Gray. 1991. Status and trends of the Albemarle-Pamlico estuaries. Albemarle-Pamlico Estuarine Study Report 90-01. North Carolina Department of Environment, Health, and Natural Resources, Raleigh, North Carolina.

Cowen, L., and C. J. Schwarz. 2006. The Jolly-Seber model with tag loss. Biometrics 62:699–705.

Diefenbach, D. R., and G. L. Alt. 1998. Modeling and evaluation of ear tag loss in black bears. J. Wildl. Manage. 62:1292–1300.

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

Gibbons, J. W., and K. M. Andrews. 2004. PIT tagging: simple technology at its best. BioScience 54:447–454.

Girondot, M. 2011. Tag Loss, Version 3.2.3. Available at http://www.ese.u-psud.fr/epc/conservation/Girondot/Publications/Tag-Loss.html.

Gorham, J. C., M. J. Bresette, and B. D. Peery. 1997. Comparative tag retention rates for two styles of flipper tags. *In* S. P. Epperly and J. Braun (eds.), Proceedings of the Seventeenth Annual Symposium on Sea Turtle Biology and Conservation, pp. 190–193. NOAA Tech. Memo– NMFS-SEFSC-415. Available from http://www.sefsc.noaa.gov/species/turtles/techmemos.htm.

Henwood, T. A. 1986. Losses of monel flipper tags from loggerhead sea turtles, *Caretta caretta* J. Herpetol. 20:276–279.

Lewison, R. L., L. B. Crowder, A. J. Read, and S. A. Freeman. 2004. Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol. Evol. 19:598–604.

Limpus, C. J. 1992. Estimation of tag loss in marine turtle research. Wildl. Res. 19:457–469.

Lloyd, J. R., M. A. Maldonado, and R. Stafford. 2012. Methods of developing user-friendly keys to identify green sea turtles (*Chelonia mydas* L.) from photographs. Internatl. J. Zool. 2012:7.

McDonald, D. L., and P. H. Dutton. 1996. Use of PIT tags and photoidentification to revise remigration estimates of leatherback turtles (*Dermochelys coriacea*) nesting in St. Croix, U.S. Virgin Islands, 1979–1995. Chelonian Conserv. Biol. 2:148–152.

McDonald, T. L., S. C. Amstrup, and B. F. J. Manly. 2003. Tag loss can bias Jolly-Seber capture-recapture estimates. Wildl. Soc. Bull. 31:814–822.

McMahon, C. R., and G. C.White. 2009. Tag loss probabilities are not independent: assessing and quantifying the assumption of independent tag transition probabilities from direct observations. J. Exp. Mar. Biol. Ecol. 372:36–42.

Meylan, A. B., and D. Ehrenfeld. 2000. Conservation of marine turtles. In M. W. Klemens (ed.), Turtle Conservation, pp. 96–125. Smithsonian Institution Press, Washington, D.C.

National Research Council. 2010. Assessment of Sea-Turtle Status and Trends Integrating Demography and Abundance. The National Academies Press, Washington, D.C. 174 pp.

Parmenter, C. J. 1993. A preliminary evaluation of the performance of Passive Integrated Transponders and metal tags in a population study of the flatback sea turtle (*Natator depressus*). Wildl. Res. 20:375–381.

Pistorius, P. A., M. N. Bester, S. P. Kirkman, and P. L. Boveng. 2000. Evaluation of age- and sex-dependent rates of tag loss in southern elephant seals. J. Wildl. Manage. 64:373–380.

Reisser, J., M. Proietti, P. Kinas, and I. Sazima. 2008. Photographic identification of sea turtles: method description and validation, with an estimation of tag loss. End. Spec. Res. 5:73–82.

Roelofs, E. W., and D. F. Bumpus. 1953. The hydrography of Pamlico Sound. Bull. Mar. Sci. Gulf Carib. 3:181–205.

Rivalan, P., M. H. Godfrey, A. C. Prevot-Julliard, and M. Girondot. 2005. Maximum likelihood estimates of tag loss in leatherback sea turtles. J. Wildl. Manage. 69:540–548.

Schofield, G., K. A. Katselidis, P. Dimopoulos, and J. D. Pantis. 2008. Investigating the viability of photo-identification as an objective tool to study endangered sea turtle populations. J. Exp. Mar. Biol. Ecol. 360:103–108.

Schwartz, L. K., M. A. Hindell, C. R. McMahon, and D. P. Costa. 2012. The implications of assuming independent tag loss in southern elephant seals. Ecosphere 3:1–11.

Seber, G. A. F. 1982. The Estimation of Animal Abundance and Related Parameters, 2nd ed. Macmillan Publ., New York. 654 pp.

Siniff, D. B., and K. Ralls. 1991. Reproduction, survival and tag loss in California sea otters. Mar. Mamm. Sci. 7:211–229.

van Dam, R. P., and C. E. Diez. 1999. Differential tag retention in Caribbean hawksbill turtles. Chelonian Conserv. Biol. 3:225–229.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and Management of Animal Populations: Modeling, Estimation, and Decision Making. Academic Press, San Diego. 817 pp.

Wilson, E. B. 1927. Probable inference, the law of succession, and statistical inference. J. Am. Stat. Assoc. 22:209–212.

Wyneken, J., S. P. Epperly, B. Higgins, E. McMichael, C. Merigo, and J. P. Flanagan. 2010. PIT tag migration in sea turtle flippers. Herpetol. Rev. 41:448–454.