

**An Assessment of Loggerhead Sea Turtles to Estimate Impacts of Mortality Reductions
on Population Dynamics**

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July, 2009
NMFS Southeast Fisheries Science Center Contribution PRD-08/09-14

INTRODUCTION

In April of 2009 the NMFS Southeast Regional Office (SERO) requested from the Southeast Fisheries Science Center (SEFSC) a population assessment of loggerhead sea turtles of the western North Atlantic (April 23, 2009 memo from Roy Crabtree, Regional Administrator to Bonnie Ponwith, Center Director). The assessment was needed to complete a new biological opinion that will evaluate the effect of the continued authorization for the Gulf of Mexico federal reef fish fishery under the Reef Fish Fishery Management Plan (FMP), including new management measures proposed in Amendment 31. Those new measures are intended to reduce sea turtle bycatch in the commercial bottom longline segment of the fishery. More specifically, SERO requested a model that assesses the effects of variability and changes in vital rates (*e.g.*, survival rates) on population projections for loggerhead sea turtles. For example, they wanted to answer questions such as what happens to population growth rates when management changes affect vital rates. This question is of pressing concern given the recent declines in the number of loggerhead nests in the Southeast U.S. (Witherington et al. 2009, Turtle Expert Working Group [TEWG] 2009). The present document describes a demographic matrix model and analyses designed to address these questions.

A number of matrix-based demographic models for loggerhead sea turtles have been constructed and analyzed for insights into what matrix elements could be subjected to management. Crouse et al. (1987) showed that management focusing on survival of large juveniles would have the greatest proportional effect on long-term population growth rate, supporting the first regulations for turtle excluder devices (TEDs) (Dep. of Commerce 1987). Subsequent work (Crowder et al 1994, Heppell et al. 2003, NMFS SEFSC 2001) increased awareness of the value of turtle excluder devices in the shrimp fishery, and most recently led to the requirement for TEDs with large escape openings (Dep. of Commerce 2003a). Only one other trawl fishery in the U.S. Atlantic - the winter trawl fishery for summer flounder in the Mid Atlantic - is required by federal regulations to use TEDs (Dep. of Commerce 1996), but the agency is considering extending TED regulations to other trawl fisheries (Dep. of Commerce 2007b). Restrictions have also been placed, or are being proposed, in the following non-trawl U.S. fisheries of the Atlantic and Gulf of Mexico to minimize the impact on the neritic/benthic sea turtles by reducing the number of interactions and/or reducing mortality resulting from interactions: scallop dredges (Dep. of Commerce 2008a), Chesapeake Bay pound nets (Dep. of Commerce 2004a), gillnets used in the monkfish (Dep. of Commerce 2002b), shark (Dep. of Commerce 2002a, 2003b; Dep. of Commerce 2007a), and flounder fisheries (Dep. of Commerce 2005), and hook and line gear used in the shark (Dep. of Commerce 2002a, 2007a, 2008b) and reef fish fisheries (Dep. of Commerce 2006, Dep. of Commerce 2009). The most recent stock assessment (NMFS SEFSC 2001) examined the loggerhead population with regard to mortality due to pelagic longline fisheries, and culminated in regulations aimed at reducing mortality of oceanic/pelagic juveniles (Dep. of Commerce 2004b). This assessment does not explicitly incorporate any of the above management actions, but these many actions certainly have perturbed the population from any stasis.

We used the basic age/stage structure of the all female demographic model of NMFS SEFSC (2001), also described in Heppell et al. (2003), with updated parameters and reasonable ranges of

those parameters, then stochastically constructed demographic matrices to look at possible population trajectories, ranges of possible long-term population growth rates, and the possible effect of changes in mortality on those rates. The NMFS SEFSC (2001) model was based on four size-based life stages: pelagic juveniles, small benthic juveniles, large benthic juveniles, and adult. These stages were then converted to an age-based model for pelagic, small benthic, and large benthic animals, and combined with a five reproductive stage model for adults. Adult reproductive stages were defined as the years between nesting seasons, allowing the incorporation of a 5 year limited frequency distribution of annual re-nesting events (“remigration”) [See Heppell et al. (2003) for details]. In NMFS SEFSC (2001) pelagic stage survival was a parameter solved for by the demographic model, using 3 different starting (pre-1990) hypothesized population growth rates and 4 growth models, yielding 12 possible values, some of which were impossible (survival > 1.0). Our model differs somewhat from NMFS SEFSC (2001): we changed stage definitions (therefore stage durations and annual survival are not directly comparable to the previous model) and we used empirically based estimates for some parameters, expert opinion for others, and a combination of these for others. We also attempted to account for parameter uncertainty, and considered 5 management units (and added a parameter to describe movement between management units). We randomly selected parameter values from several hypothesized distributions of each parameter, and produced frequency distributions of adult female loggerhead population sizes, then created demographic matrices and either produced population trajectories, frequency distributions of the dominant eigenvalues (long term population growth rates), or solved for benthic survival needed to produce matrices with positive long term population growth rates. The MatLab code and associated input files are available, along with this document, at www.sefsc.noaa.gov/seaturtleunpublishedreports.jsp

PARAMATERIZATION

We created parameter sets that sought first to bound the annual mean value of each demographic parameter (‘low’ and ‘high’ values) and identify a point estimate – a nominal value. Development of this Nominal parameter set was our initial attempt at a set of reasonable reference parameter values. Each input parameter is discussed below. For the basic demographic matrix defined by NMFS SEFSC (2001), parameters are stage specific survival and duration, and a suite of fecundity parameters. We used nest counts by management unit to generate adult female population estimates and we created hypothesized movement rates between management units. We attempted to identify the range of population values for each and, when possible, indicate alternative values to indicate central tendencies (see section on Parameter Uncertainties below). The low, Nominal, and high estimates for parameters represented either: a) point estimates and 95% confidence intervals, b) point estimates with expert opinion of the range, c) estimates based on the midpoint between adjacent parameters, or d) expert opinion for the first two years of pelagic survival and movement between management units. The values sometimes represented individual variation, rather than the population’s demographic variability. We were unable to separate sampling variance from demographic variance, thus increasing the uncertainty throughout.

Management Units

The recent recovery plan for the Western North Atlantic population of loggerheads described 5 recovery units (NMFS and USFWS 2008). We use those same recovery unit definitions herein. TEWG (2009) suggested that the Cay Sal Bank, Bahamas rookery cannot be distinguished from the Dry Tortugas based on genetics. Thus, they grouped Cay Sal with the Dry Tortugas recovery unit, rather than with the Greater Caribbean recovery unit:

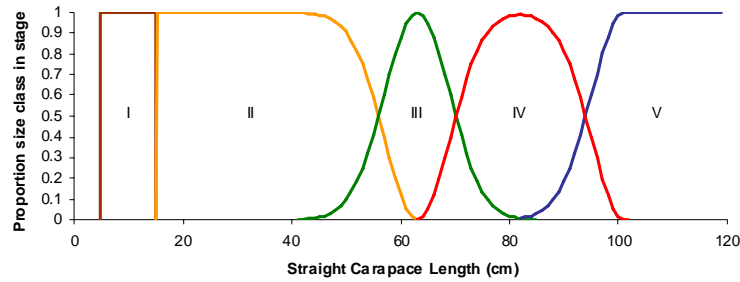
1. Northern U.S. Subpopulation (Florida/Georgia border through southern Virginia)
2. Peninsular Florida Subpopulation (Florida/Georgia border through Pinellas County, Florida)
3. Northern Gulf of Mexico Subpopulation (Franklin County, Florida through Texas)
4. Dry Tortugas Subpopulation (islands located west of Key West, Florida; TEWG (2009) included Cay Sal Bank, Bahamas)
5. Greater Caribbean Subpopulation (all other nesting assemblages within the Greater Caribbean, Mexico through French Guiana, The Bahamas, Cuba, Lesser Antilles, and Greater Antilles, including or excluding Cay Sal Bank.

Life Stages

We described and parameterized the life history of Western North Atlantic loggerheads as six stages and converted them to the 4 stages needed to maintain the structure of NMFS SEFSC (2001). TEWG (2009) provided the 5 stage definitions below, and we attempted to follow that same structure and remain compatible with the previous models and available data., but combined and re-divided the first two stages into three stages (“phases” below) because of available data. For continuity with past models we retain the labels of the past [provided in brackets after each definition]. The reader is referred to the TEWG report for a full description of these stages. Each stage can be described on the basis of length distributions approximating a normal distribution and on the basis of habitat.

- I. Egg, Hatchling, and Post-Hatchling through first year: <15 cm straight carapace length (SCL) [Young-of-Year]
- II. Juvenile (1), exclusively oceanic: 15-63 cm SCL [pelagic juvenile]
- III. Juvenile (2), small, oceanic or neritic: 41-82 cm SCL [small benthic juvenile]
- IV. Juvenile (3), large, oceanic or neritic: 63-100 cm SCL [large benthic juvenile]
- V. Adult: 82 cm SCL and larger [adult]

Figure 1. Conceptual model of size distributions for each life stage of the loggerhead turtle.
(from TEWG 2009)



Stage Duration

We do not have subpopulation-specific growth rates. Hence, stage durations for each subpopulation and the whole Western North Atlantic population are based on a single set of values.

Exclusively Oceanic Juveniles

Pelagic Juvenile (Stage I and Stage II of TEWG 2009)

The exclusively oceanic Stage II was combined with Stage I and then was divided into 3 phases: Ages 0-1 (2 yr), Ages 2-5 (4 yr) and Ages ≥ 6 (variable). These subunits were based on the availability of empirical survival estimates and the vulnerability of the last phase to pelagic longlines (see below). The duration of the entire stage was based on two sources (described below), both of which had some foundation in skeletochronology using stained sections (unstained sections tend to underestimate the number of annual marks; Goshe et al. in review):

(1) Bjorndal et al.'s (2000) von Bertalanffy growth curve, which was based on size frequency data. Later, the same authors reported that the average age of a 46 cm CCL juvenile, based on growth marks in humerus sections (7 yr), was comparable to the average age based on the size frequency data (6.5 yr), thereby corroborating the prior method (Bjorndal et al. 2003b). The TEWG (2009) applied a normal probability distribution to the sizes associated with the transition from Pelagic Juveniles (Stage II) to Small Benthic Juveniles (Stage III). We then applied the growth curve of Bjorndal et al. (2000) to the size distribution's midpoint $\pm \sigma$ [52 cm SCL \pm 3.2; SCL was converted to CCL using equation (1) of Bjorndal et al. (2000) because their von Bertalanffy growth equation was based on curved length], yielding a low estimate (10 years), a point estimate (11 years), and a high estimate (12 years).

(2) Snover's (2002) estimate of the average duration of the stage and its reported variance, which were based on bone sections. She regressed humerus section width vs. carapace length and back-calculated the regressions for individual growth trajectories and reported an average age-at-settlement of 14.8 yr \pm 3.3 SD. The range of settlement was 9-24 years.

The first method yielded a duration of 10 years for a low and the second method yielded a duration of 18 years (14.8+3.3 yr) for a high for our parameter range. We used the mean of the two midpoints as our Nominal value: 13 years. The durations of the first two phases were

constant (2 and 4 years, respectively). The duration of the 3rd phase varied as a function of the total stage duration (Table 1).

Table 1. Stage duration estimates (years) for phases of the Pelagic Juvenile Stage of loggerhead sea turtles.

Phase	Low	Nominal	high
1	2	2	2
2	4	4	4
3	4	7	12

Neritic or Oceanic Juveniles

We based our stage durations of neritic and oceanic juveniles (Small Benthic Juveniles and Large Benthic Juveniles) on skeletochronology of stained sections. Low, Nominal, and high estimates of length (midpoint $\pm \sigma$, based on a normal probability distribution provided by TEWG 2009) were converted to age using the von Bertalanffy growth curve described by Snover (2002), which was based on humerus sections. Bjorndal et al. (2001) also reported von Bertalanffy equations based on size frequency data. Their results yield durations for both the Small Benthic Juvenile and for Large Benthic Juvenile stages each about 2 years longer than Snover's equations would predict. Braun-McNeill et al. (2008) reported growth rates, based on a relatively large number of measured marked and recaptured animals (n=160), as even slower (average of 17.4 yr for 50-80 cm SCL). Skeletochronology may bias stage durations low due to occurrence of zero growth rates, which have been reported for some individuals in mark-recapture studies but would be difficult to detect in skeletochronology.

Small Benthic Juveniles (Stage III of TEWG 2009)

The stage was described as 63 cm SCL \pm 6. The population mean stage durations ranged from 9 to 12 years, with 10 chosen as our Nominal value (Table 2).

Large Benthic Juveniles (Stage IV of TEWG 2009)

This stage was described as 82 cm SCL \pm 6.5. The population mean stage durations ranged from 4 to 12 years, with 7 chosen as our Nominal value (Table 2)

Table 2. Stage durations (years) for immature loggerhead sea turtles.

Stage	Low	Nominal	High
Pelagic Juvenile (II)	10	13	18
Small Benthic Juvenile (III)	9	10	12
Large Benthic Juvenile (IV)	4	7	12

The above stage durations for immature loggerhead sea turtles yielded an average age at maturity ranging from 23 to 42 years, with a Nominal value of 30 years (Table 2).

Survival Rates

We do not have subpopulation-specific survival rates for juvenile stages, but do for adults in two of the subpopulations. Hence, juvenile survival rates for each subpopulation and for the whole

population are based on a single set of values. Where they exist, we used empirical estimates of survival and selected recent estimates over old estimates to account for the many management perturbations which presumably have resulted in a change in survival rates.

Pelagic Juvenile (Stage II of TEWG 2009)

Phase 1. We have no empirical survival estimates for the first two years of the pelagic juvenile stage. Using a demographic model, Heppell et al. (2005) solved for the survival rate of Kemp’s ridleys (*Lepidochelys kempii*) during their pelagic stage, which is about 2 yr in duration. They reported a survival rate of 0.37 for model runs using 12 years as the age at maturity, which was considered to be the most representative for Kemp’s ridley; the estimate for 10 years as the age of maturity, the best model fit for TEWG (2000), was 0.31. Because Kemp’s ridleys and loggerhead sea turtles share the pelagic habitat, we used 0.37 as the survival rate for loggerheads for their first two years in the water (Table 3). We set the low and high estimates at 0.37 ± 0.1 , based on expert opinion.

Phase 2. Bjorndal et al. (2003a) reported apparent annual survival rates for ages 2-6 based on all available samples and for ages 4-6 based on a subset of sampling data. Even though their analysis was hampered by unequal cohort sizes, there were no alternative sources of empirical survival estimates. Thus, we used the mean of their two estimates as our Nominal value (Table 3). We calculated confidence intervals of their estimates using the raw data provided in Table 1 of their publication. The total sample provided the largest confidence intervals which were used to represent the low and high estimates for the population.

Phase 3. While Bjorndal et al. (2003a) provided survival estimates for older oceanic juveniles in this stage, their analysis was hampered by emigration and unequal cohort sizes, which could not be accounted for in the catch-curve analysis used to generate their estimates. Sasso and Epperly (2007) provided estimates for animals $\geq \sim 6$ years old. Their estimate was used as the Nominal value in our analysis, along with their 95% confidence intervals as the low and high estimates (Table 3).

Table 3. Survival rate estimates for the Pelagic Juvenile Stage of loggerhead sea turtles.

Phase	Low	Nominal	High
1	0.300	0.370	0.500
2	0.870	0.900	0.950
3	0.557	0.814	0.939

Annual pelagic survival rate (Table 4) for the matrix was calculated as the geometric mean of survival rates in the three phases (Table 3) weighted by their respective stage durations (Table 1) or

$$\text{Pelagic survival} = \left(\prod_i s_i^{d_i} \right)^{\frac{1}{\sum_i d_i}} .$$

Small Benthic Juvenile (Stage III of TEWG 2009).

Frazer (1983) estimated juvenile survival from a catch curve of stranded and trawl-caught animals, converting size to age. In models developed since, many have used his estimate for small neritic juveniles (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2003, NMFS SEFSC 2001, Snover 2002), or recalculated survival from a catch curve based on more recent strandings (NMFS SEFSC 2001), or used an apparent survival rate (Hedges 2007). Frazer's estimate reflected pre-TED conditions. There are two recent and similar empirical estimates of survival for the small benthic juvenile stage. One is the apparent survival rate (Sasso et al. 2006) used by Hedges (2007) and the other is a realized survival rate (Braun-McNeill et al. 2007). Both are based on animals marked and recaptured in Core Sound, North Carolina. For our Nominal value we used the realized survival rate and the 95% confidence intervals for the low and high values (Table 4).

Large Benthic Juvenile (Stage IV of TEWG 2009).

There are no empirical estimates of survival for this stage. Frazer (1983) estimated survival of the largest juveniles as a mean of small benthic juvenile survival rate (see above) and adult survival rate (see below). Others have used this same method to generate a mean survival rate for large juveniles (Crouse et al. 1987, Crowder et al. 1994, Heppell et al. 2003, NMFS SEFSC 2001, Snover 2002). On two occasions, the same value used for small benthic juveniles also was applied to large benthic juveniles (NMFS SEFSC 2001, Hedges 2007). The range of values used to date is 0.74 to 0.89. Here we follow Frazer's lead and for the Nominal value use the average of the small juvenile survival rate and the adult survival rate for the entire population, as the difference in the two rates is small ($\Delta=0.01$). We use the lower of the two minimum estimates as the low estimate for the population and likewise use the higher of the two maximum estimates as the high survival rate estimate for the population of large juveniles (Table 4).

Table 4. Survival rates for immature loggerhead sea turtles.

Stage	Low	Nominal	High
Pelagic Juvenile (II)	0.588	0.744	0.878
Small Benthic Juvenile (III)	0.740	0.830	0.890
Large Benthic Juvenile (IV)	0.740	0.835	0.925

Adults

Northern U.S. Subpopulation. Richardson (1982) and Frazer (1983) provided estimates of adult survival based on nesting females on Little Cumberland Island, Georgia. Frazer's estimate was used in all models through 2005. NMFS SEFSC (2001) used a Jolly-Seber model to estimate adult survival on two beaches (Wassaw Island, Georgia and Melbourne Beach, Florida) and averaged those with Frazer's estimate for two of their models. However, these data violate the assumptions of the Jolly-Seber model as loggerheads do not nest every year and are therefore not available for recapture every year. Frazer's estimate represents the pre-listing conditions of the species. More recently, Hedges (2007) estimated survival for adult females nesting on Baldhead Island, North Carolina (0.853), and TEWG (2009) provided survival estimates for Wassaw Island nesters (0.81). A time effect was not detected for Wassaw Island and the estimate was identical to Frazer's old estimate of 0.8091 for nearby Cumberland Island, perhaps because TEDs that protected large loggerheads were not required until 2003. For our purpose, we

averaged the Hedges and TEWG estimates for our Nominal value and used the maximum range of the original estimates as the low and high values (Table 5).

Greater Caribbean Subpopulation. The TEWG (2009) provided the first estimate for survival of nesting females in the Quintana Roo, Mexico rookery. That point estimate (0.85) and its 95% confidence limits were used as the Nominal, low, and high values, respectively (Table 5).

Peninsular Florida Subpopulation. There are two estimates of survival for adult females nesting on Melbourne Beach, Florida. In the first case (NMFS SEFSC 2001) the estimate (0.83) was inappropriately calculated (see discussion above). In the second (TEWG 2009), the estimate (0.73) is likely biased low because it was based on a study that was not a dedicated mark-recapture study and the rate of interception of turtles was very low. Hence, we are not using either estimate, and the survival rate for this subpopulation defaulted to the overall population values (see below).

Western North Atlantic Population, Peninsular Florida Subpopulation, Dry Tortugas Subpopulation, and Northern Gulf of Mexico Subpopulation. For the overall population survival rate estimate we used the average of the Northern U.S. and Greater Caribbean subpopulation estimates for the Nominal value, and the maximum range of the original pair of estimates as our low and high values for adult survival (Table 5).

Table 5. Survival rates for adult loggerhead sea turtles, by management unit.

Subpopulation	Low	Nominal	High
Northern U.S.	0.770	0.832	0.925
Peninsular Florida	0.770	0.841	0.925
Northern Gulf of Mexico	0.770	0.841	0.925
Dry Tortugas	0.770	0.841	0.925
Greater Caribbean (Yucatán)	0.810	0.850	0.880
<i>Western North Atlantic pop.</i>	<i>0.770</i>	<i>0.841</i>	<i>0.925</i>

Fecundity Parameters

The fecundity term (F) in the pre-breeding census based matrix (NMFS SEFSC 2001) was:

$$F = \text{nests per female} * \text{eggs per nests} * \text{egg survival} * \text{proportion of female offspring} * \text{pelagic juvenile stage survival}$$

Below we provide the subpopulation-specific parameters.

Nests per female per season (clutch frequency)

Females lay multiple clutches of eggs during one nesting season. There are many sources of information on nests per female as indicated by the compilation of Schroeder et al. (2003). These were based on observations on the beach, sometimes corrected based on interesting intervals. Murphy and Hopkins (2004) estimated the mean nests per female to be 4.1, based on the distribution of the number of nests over time and an average interesting interval. Recently,

there have been two studies that did not require repeated interception of the animals on the beach; both studies used satellite telemetry. Scott (2006) telemetered animals nesting early in the season on the barrier islands of Georgia. He provided an estimate of 4.5 nests per female in the 2005 season (n = 12). A similar study was conducted on Florida’s southwest coast (Tucker 2009). Tucker provided an estimate of 5.5 nests per female (n=34, A.D. Tucker, Mote Marine Lab, Mote Marine Lab, personal communication). Interestingly, he determined that about half the nesting emergences occurred outside the beaches being monitored. Thus, it appears that previous estimates of nests per female might be biased low. Alternatively, animals which begin nesting early in the season might lay more nests per female than the population average. The consequence of using an estimate that might be biased high would be to underestimate the nesting population, the most conservative approach, but it would also inflate the long term population growth rate.

Thus, we use Scott’s estimate for the Northern U.S. subpopulation and Tucker’s estimate for the Peninsular Florida subpopulation and the mean of the two is the default for the other subpopulations and for the whole population (Table 6). We use the minimum and maximum nests per female reported in both studies as the low and high values, realizing that these represent individual, not population variation, and are without a temporal component.

Table 6. Nests per female of loggerhead sea turtles, by management unit.

Subpopulation	Low	Nominal	High
Northern U.S.	4	4.5	6
Peninsular Florida	2	5.5	8
Northern Gulf of Mexico	2	5	8
Dry Tortugas	2	5	8
Greater Caribbean (Yucatán)	2	5	8
<i>Western North Atlantic pop.</i>	2	5	8

Eggs per nest (clutch size)

The number of eggs laid in a nest varies.

Northern U.S. Subpopulation. Data exist for several beaches of the Northern U.S. subpopulation and mean annual eggs per nest appears to have declined over time at all locations. The largest rookery in the region is on Cape Island, S.C. The Cape Romain National Wildlife Refuge provided annual mean eggs per nest for 1981-2008 for Cape Island (Sarah Dawsey, Cape Romain National Wildlife Refuge, personal communication). We calculated mean eggs per nest for 2000-2008: mean=119, range of annual means=114-124). Wassaw Island data were provided also (Kris Williams, Caretta Research Project, personal communication) and the mean eggs per nest for 2001-2008 was 114 (range 107-125). Hedges (2007) reported that mean eggs per nest was 118 eggs for Baldhead Island. Thus, to represent the northern subpopulation, we used the range reported among all the beaches, and use 119 as our Nominal value in recognition of Cape Island’s much greater size as a rookery relative to the other two beaches.

Peninsular Florida Subpopulation. The largest rookery in the western North Atlantic is in Brevard County, Florida. We were provided annual mean eggs per nest for 1992-2007 for a 40.5

km stretch of high density nesting beach in Brevard County (Lew Ehrhart and Bill Redfoot, Univ. Central Florida, personal communication). They did not observe a decline in mean eggs per nest over the period and thus, our calculations of mean (as the Nominal value), low, and high are based on the entire period (the ranges are identical whether the time period is 1992-2007 or 2001-2007 and the mean differs by only 1 egg) (Table 7). We also were provided data for Casey Key, on Florida's west coast, and the mean eggs per nest there is 10 eggs less. We did not include the Casey Key data in our calculations because of that large difference in mean eggs per nest and because the rookeries along the east coast represent a much greater proportion of the subpopulation's nesting activity. We note that the range in annual mean eggs per nest reported for Brevard County encompasses the range reported for Casey Key, differing only in the minimum (Casey Key's minimum is 1 less egg than Brevard County's minimum).

Northern Gulf of Mexico Subpopulation. Lamont et al. (1998) reported the annual mean number of eggs per nest for Cape San Blas, Florida for 1994-1997. We averaged those estimates for the Nominal value (Table 7).

Dry Tortugas Subpopulation. Van Houtan and Pimm (2006) reported the annual mean eggs per nest for the Dry Tortugas, 1996-2004. We averaged those estimates for the Nominal value (Table 7).

Greater Caribbean Subpopulation. Annual estimates of mean eggs per nest in Quintana Roo, 1996-2006, were provided by Julio Zurita (Comité de Protección Marinas en Quintana Roo, personal communication). We averaged those estimates for the Nominal value (Table 7).

Western North Atlantic Population. The Nominal value is the mean of the values of all subpopulations and the low and high represent the range in annual mean eggs per nest observed across all subpopulations (Table 7).

Table 7. Eggs per nest of loggerhead sea turtles, by management unit.

Subpopulation	Low	Nominal	High
Northern U.S.	107	119	125
Peninsular Florida	95	112	117
Northern Gulf of Mexico	89	100	112
Dry Tortugas	96	102	105
Greater Caribbean (Yucatán)	103	112	117
<i>Western North Atlantic</i>	89	109	125

Egg survival

Not all eggs hatch and not all hatchlings emerge from the nest. Egg survival is the proportion of eggs laid that yield emerged hatchlings. The weighted (by annual number of nests) mean of annual estimates was used for the Nominal value and the low and high were based on the observed annual rates (Table 8).

Northern U.S. Subpopulation. We obtained raw data for Wassaw Island (Kris Williams, Caretta Research Project, personal communication) for 1973-2008 and calculated egg survival. Data prior to 1979 were censored because most nests had been depredated. We did not use Baldhead Island data in the calculations for this subpopulation because it appears that lost nests were not included in past presentations of the data (Hawkes et al. 2005, Hedges 2007) and thus reported egg survival would be biased high.

Peninsular Florida Subpopulation. Annual estimates of egg survival, 2001-2008, were provided by the Florida Fish and Wildlife Conservation Commission, and are based on a relatively new program that has protocols for sampling design and nest-by-nest reporting (Anne Meylan, FFWCC, personal communication).

Northern Gulf of Mexico Subpopulation. Annual estimates of egg survival, 2001-2008, were provided by the Florida Fish and Wildlife Conservation Commission, and are based on a relatively new program that has protocols for sampling design and nest-by-nest reporting (Anne Meylan, FFWCC, personal communication).

Dry Tortugas Subpopulation. Reported estimates of annual egg survival in the Dry Tortugas, 1996-2004, do not include lost nests (Van Houtan and Pimm 2006). However, other information was provided so that we can estimate the true egg survival for some years and observe that it is about 90% of that reported; we adjusted all the reported annual rates accordingly.

Greater Caribbean Subpopulation. Annual estimates of egg survival in Quintana Roo 1996-2006 were provided by Julio Zurita (Comité de Protección Marinas en Quintana Roo, personal communication).

Western North Atlantic Population. We note that 4 of the 5 subpopulations had very similar Nominal values ($\Delta=0.04$), with the Northern U.S.' success rate substantially higher. Thus, the Nominal value for the Western North Atlantic population was set equal to the average of the 4 subpopulations, which is the same value calculated for the Peninsular Florida subpopulation, where the majority of nests are laid. The population's low and high values were based on the range observed across all 5 subpopulations.

Table 8. Egg survival of loggerhead sea turtles, by management unit.

Subpopulation	Low	Nominal	High
Northern U.S.	0.47	0.71	0.80
Peninsular Florida	0.42	0.53	0.67
Northern Gulf of Mexico	0.11	0.50	0.70
Dry Tortugas	0.27	0.54	0.69
Greater Caribbean (Yucatán)	0.18	0.54	0.71
<i>Western North Atlantic pop.</i>	<i>0.11</i>	<i>0.53</i>	<i>0.80</i>

Proportion of Female Offspring

We used the range of proportion female offspring reported in NMFS SEFSC (2001) (0.35-0.80), and consistent with all models prior to that analysis, used a 1:1 sex ratio as our Nominal value (Table 9). TEWG (2009) discussed sex ratios across stages and regions and through time, and reports that although there appears to be a strong female bias in the juvenile stages, the proportion of females in the adult stage appears to be about 0.5.

Table 9. Proportion female offspring of loggerhead sea turtles.

	Low	Nominal	High
Proportion Female	0.35	0.5	0.8

Remigration Intervals (Inter-seasonal Nesting Intervals)

Females rarely nest in consecutive years. Thus, fecundity must be adjusted for non-nesting turtles. The inter-seasonal nesting intervals are variable, even for a given female. The observed intervals (Table 10) are not suitable for use in the model because those represent turtles surviving and nesting, and turtles with inherently longer intervals have a lower probability of surviving to nest again than turtles with shorter remigration intervals. Frazer (1984) adjusted the remigration intervals observed on Little Cumberland Island by his point estimate of survival in the adult population. We did the same, using a range of annual survival rates, in 0.05 increments, to encompass the 95% confidence intervals of estimated survival rates in each subpopulation: 0.75, 0.80, 0.85, 0.90, 0.95 (0.80-0.90 for Greater Caribbean). Thus, each observed array (an array is a frequency distribution of re-nesting events, see Table 10) yielded up to 5 adjusted arrays; the Nominal parameter set used the array resulting from adjustment with the survival rate closest to the point estimate for the subpopulation (Table 5). We pooled all the arrays for the Western North Atlantic population; subpopulations without observed distributions defaulted to the same as used for the entire population. The mean remigration intervals ranged from 2.9 to 3.7 yr for the Northern U.S. subpopulation and 2.7 to 2.9 yr for both Peninsular Florida and the Greater Caribbean subpopulations. Data sources were Richardson (1982) for Little Cumberland Island, Kris Williams (Caretta Research Project, personal communication) for Wassaw Island, Hedges (2007) for Baldhead Island, Bjorndal et al. (1983) for Melbourne Beach, and Julio Zurita (Comité de Protección Marinas en Quintana Roo, personal communication) for Quintana Roo.

Table 10. Observed remigration intervals of loggerhead sea turtles, uncorrected for mortality, by management unit and beach location.

Remigration Interval (yr)	Subpopulation				
	Northern U.S.			Peninsular Florida	Greater Caribbean
	Little Cumberland Island, Ga.	Wassaw Island, Ga.	Baldhead Island, N.C.	Melbourne Beach, Fla.	Quintana Roo, Mex.
1	0.04	0.004	0.040	0.019	0.093
2	0.43	0.189	0.312	0.466	0.432
3	0.36	0.320	0.496	0.348	0.306
4	0.13	0.187	0.088	0.130	0.093
5+	0.04	0.151	0.064	0.037	0.076
Average	2.70	2.85	2.82	2.70	2.63

Movement

We set the proportion of nesting females that move between management units to range from 1 in 10,000 to 1 in 1 million (Table 12) based on anecdotal reports of females moving between management units and as initial values to determine if movement would have an effect in a multi-management unit dynamical model. Bowen (2003) discussed 11 cases of females that were known to nest in one management unit to be found nesting in another management unit over a 7 year period, but as will be noted below, movement in this model had little effect. Even if we have underestimated the movement rates, we retrospectively assume they will have no appreciable effect on the results as presented here.

Number of Nests

The number of nests was used, in part, to estimate the current population size of adult females for each subpopulation. We used the minimum count for the period 2004-2008, or if unavailable, the most recent nest count data available (Table 11). We chose to use a minimum to obtain the most conservative estimate of total nest counts from which to base conservative female population size estimates. This information was obtained from the recent loggerhead recovery plan (NMFS and USFWS 2008), TEWG (2009), Florida Fish and Wildlife Conservation Commission (2009), SWOT (2006-2007), Addison and Morford (1996), and personal communication from Julio Zurita (Comité de Protección Marinas en Quintana Roo).

Table 11. Number of nests in Western North Atlantic population of loggerhead sea turtles. Minimum annual number of nests, except where noted here, are from the period 2004-2008. The most recent data are from 2008 for the mainland U.S. subpopulations, and the Quintana Roo, Mexico, rookery. Dry Tortugas data are from 2004 and Cay Sal Bank data are from 1995. Greater Caribbean data, except for Quintana Roo, Mexico, are based on SWOT (2006-2007), and mostly are from 2005. Note that the 2008 count for Northern Gulf of Mexico is only for the Florida Panhandle and that the minimum for 2004-2008 is for the Florida Panhandle and Alabama; the total nests in the Gulf of Mexico outside Florida is negligible (<50 nests/year).

Subpopulation	Minimum 2004-2008	Most recent data
Northern U.S.	1804	6976
Peninsular Florida	44512	60465
Northern Gulf of Mexico (Fla. and Ala. only)	605	919
Dry Tortugas		
Dry Tortugas	159	159
Greater Caribbean		
Quintana Roo, Mexico	1172	2137
W. Caribbean (excl. Quintana Roo)	~85	~85
Northern Caribbean	~215	~215
Southern Caribbean	~150	~150
Eastern Caribbean	negligible	negligible
Cay Sal Bank*	~500	~500
<i>Western North Atlantic population</i>	<i>49202</i>	<i>71606</i>

*included with Dry Tortugas by TEWG (2009) but not in the recovery unit definitions by NMFS and USFWS (2008)

Parameter Uncertainty

We attempted to develop a single set of parameters with associated distributions, but given the disparate types of data, and an inability to accurately assess the relative quality, we were unable to settle on a single best set of parameters and associated distributions. We created parameter sets that sought first to bound the annual mean value of each demographic parameter ('low' and 'high' values) (see above), then either made no assumptions about parameter distribution by using a uniform distribution to select from the parameter range, or examined the effect of different point estimates of central tendency with variable strength of the 'peak' of distributions (see Figure 2). We implemented the latter utilizing the point estimate as an approximation of the mean with a standard deviation (SD) error equal to the parameters range divided by a shape parameter (s):

$$SD \sim (\text{parameter range})/s$$

We examined model runs for all distributions with our shape parameter (s) between 2 and 8. This resulted in an approximate analog of the coefficient of variation of between 6.25% and 50% for affected parameters which we felt covered a reasonable range of possible shapes of parameter distributions (see Figures 2 and 3). We considered uniform distributions for all parameters plus truncated beta distributions for all survival and proportion parameters, and truncated normal distribution for all but the movement and remigration intervals. We used truncated distributions to keep all parameters within the high and low limits we set. Second, we developed two alternative sets of point estimates to the Nominal: Alternative U and Alternative W, named arbitrarily. By Nominal we mean the first set of estimates that we used (see details below) as a reference to define other alternative parameter sets, which are defined in the following paragraph. None of these should be interpreted as a best set of estimates.

Development of the Nominal parameter set (see sections above and summarized in Table 12) was our initial attempt at a set of reasonable reference parameter values to use to demonstrate the effects of the strength (value of shape parameter) and type of parameter distribution (uniform, truncated normal, or truncated beta) on output. The two alternative parameter sets moved the value of most (except stage durations, see below) of the Nominal parameters $\frac{1}{4}$ of the distance to either of the endpoints of that parameter's range that resulted in the same directional effect on the dominant eigenvalue. In other words, all parameters within an alternative (U or W) either increase (Alternative W) or decrease (Alternative U) the dominant eigenvalue. In the case of stage durations, we used the age of first reproduction as the measure of distance. Because stage duration was non-continuous we usually only moved it one unit in either direction, and in one case we did not move the stage duration parameter value to avoid setting the parameter at its end point. This resulted in an approximate $\frac{1}{4}$ distance for Alternative W, and exactly a $\frac{1}{4}$ distance for Alternative U, although for any individual parameter the move was not $\frac{1}{4}$ of the distance (see Table 12). This procedure resulted in sets of distributions that are, in our opinion, representative of a range of relatively small collective changes to parameter sets that could be reasonably chosen as alternative Nominal sets. Figures 2c and 3a-c shows this for the distributions when using shape parameter 8. We chose this shape parameter for illustration here and in subsequent examples because the effect of truncation on the distribution is apparently negligible (see Figures 2c and 3a-c). We truncated distributions at our specified low and high range endpoints to keep

all parameters within our argued limits (see below), but this does not mean that we feel parameters do not or may not lie outside of these endpoints.

Table 12. All demographic parameters except remigration interval (see Table 10) for the Western North Atlantic loggerhead population and for individual management units. Table lists annual population mean for each parameter's Nominal, low, and high estimates, the range midpoint, the alternative hypothesized point estimates (Alt-U and Alt-W), and associated hypothesized distribution types (Figures 2 and 3). Alternatives to the midpoint include the Nominal values reported above and movement of that point of central tendency lower (Alt-U) and higher (Alt-W). See text for more details. Abbreviations for the management units are: "FL" for Peninsular Florida, "NR" for Northern U.S., "GC" for Greater Caribbean, "NG" for Northern Gulf of Mexico, and "DT" for Dry Tortugas. Parameter sets Alt-U, Nominal, and Alt-W were used in model runs with a specified shape parameter (see text) Model runs using uniform distribution effectively used the range midpoint as the mean. Limits of the uniform or truncated distributions are specified as low and high.

Parameter	Low	Alt-U	Midpoint	Nominal	Alt-W	High	Distribution type
Pelagic duration	10	14	14	13	12	18	Uniform/ truncated normal
Small benthic duration	9	11	10.5	10	10	12	Uniform/ truncated normal
Large benthic duration	4	8	8	7	6	12	Uniform/ truncated normal
Pelagic survival	0.588	0.705	0.733	0.744	0.777	0.878	Uniform/ truncated beta
Small benthic survival	0.740	0.808	0.815	0.830	0.845	0.890	Uniform/ truncated beta
Large benthic survival	0.740	0.812	0.833	0.835	0.858	0.925	Uniform/ truncated beta
w. N. Atl. Adult survival	0.770	0.823	0.848	0.841	0.862	0.925	Uniform/ truncated beta
FL adult survival	0.770	-	0.848	0.841	-	0.925	Uniform/ truncated beta
NR adult survival	0.770	-	0.848	0.832	-	0.925	Uniform/ truncated beta
GC adult survival	0.810	-	0.845	0.850	-	0.880	Uniform/ truncated beta
NG adult survival	0.770	-	0.848	0.841	-	0.925	Uniform/ truncated beta
DT adult survival	0.770	-	0.848	0.841	-	0.925	Uniform/ truncated beta
w. N. Atl. Nests per female	2	4.25	5	5	5.75	8	Uniform/ truncated normal
FL nests per female	2	-	5	5.5	-	8	Uniform/ truncated normal
NR nests per female	4	-	5	4.5	-	6	Uniform/ truncated normal
GC nests per female	2	-	5	5	-	8	Uniform/ truncated normal
NG nests per female	2	-	5	5	-	8	Uniform/ truncated normal
DT nests per female	2	-	5	5	-	8	Uniform/ truncated normal
w. N. Atl. eggs per nests	89	104	107	109	113	125	Uniform/ truncated normal
FL eggs per nests	95	-	106	112	-	117	Uniform/ truncated normal
NR eggs per nests	107	-	116	119	-	125	Uniform/ truncated normal
GC eggs per nests	103	-	110	112	-	117	Uniform/ truncated normal
NG eggs per nests	89	-	100.5	100	-	112	Uniform/ truncated normal
DT eggs per nests	96	-	100.5	102	-	105	Uniform/ truncated normal
w. N. Atl. egg survival	0.11	0.425	0.465	0.53	0.603	0.82	Uniform/ truncated beta
FL egg survival	0.42	-	0.545	0.53	-	0.67	Uniform/ truncated beta
NR egg survival	0.47	-	0.635	0.71	-	0.8	Uniform/ truncated beta
GC egg survival	0.18	-	0.445	0.54	-	0.71	Uniform/ truncated beta
NG egg survival	0.11	-	0.405	0.5	-	0.7	Uniform/ truncated beta
DT egg survival	0.27	-	0.48	0.54	-	0.69	Uniform/ truncated beta
Proportion female	0.35	0.463	0.575	0.5	0.575	0.8	Uniform/ truncated beta
Movement probability	0.000001	-	0.0000505	-	-	0.0001	Uniform

Figure 2: Frequency distribution for Nominal parameter set (Table 12) for the Western North Atlantic loggerhead population showing the types of distribution shapes examined. Note that the uniform distributions for the parameters are not illustrated, except for remigration intervals.

a) Shape parameter = 2

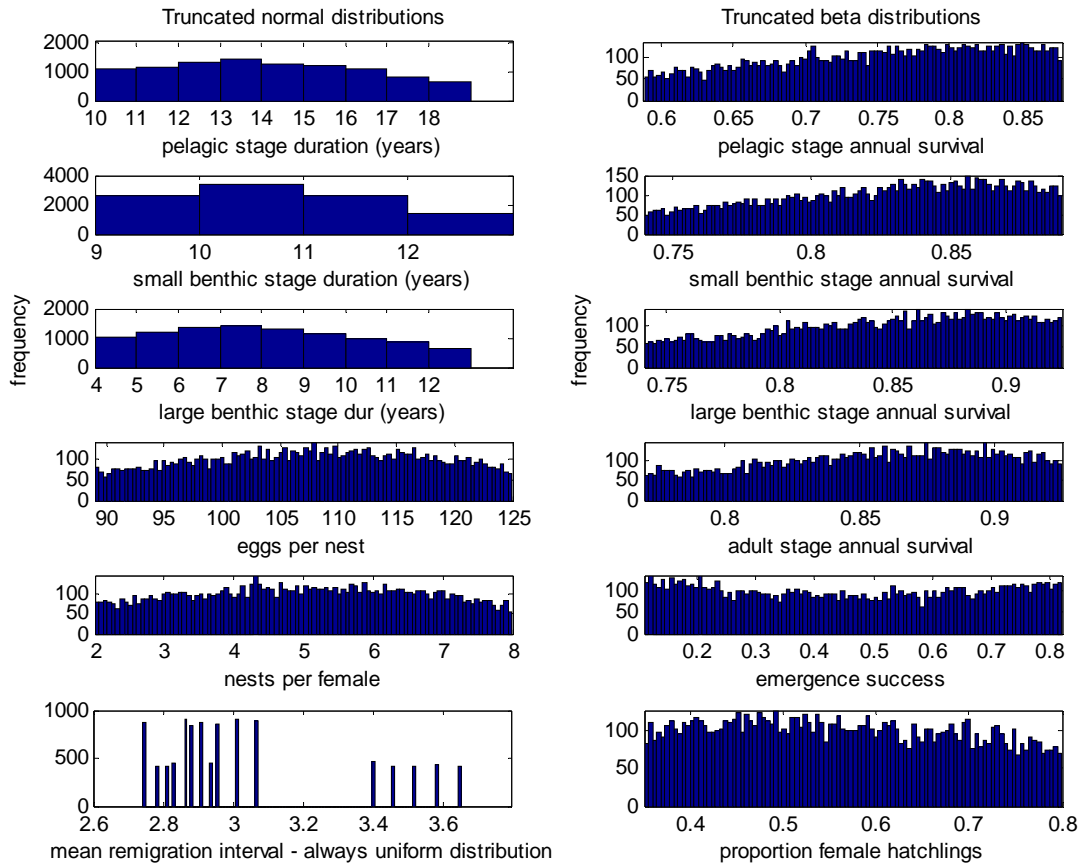


Figure 2 cont.

b) Shape parameter = 4

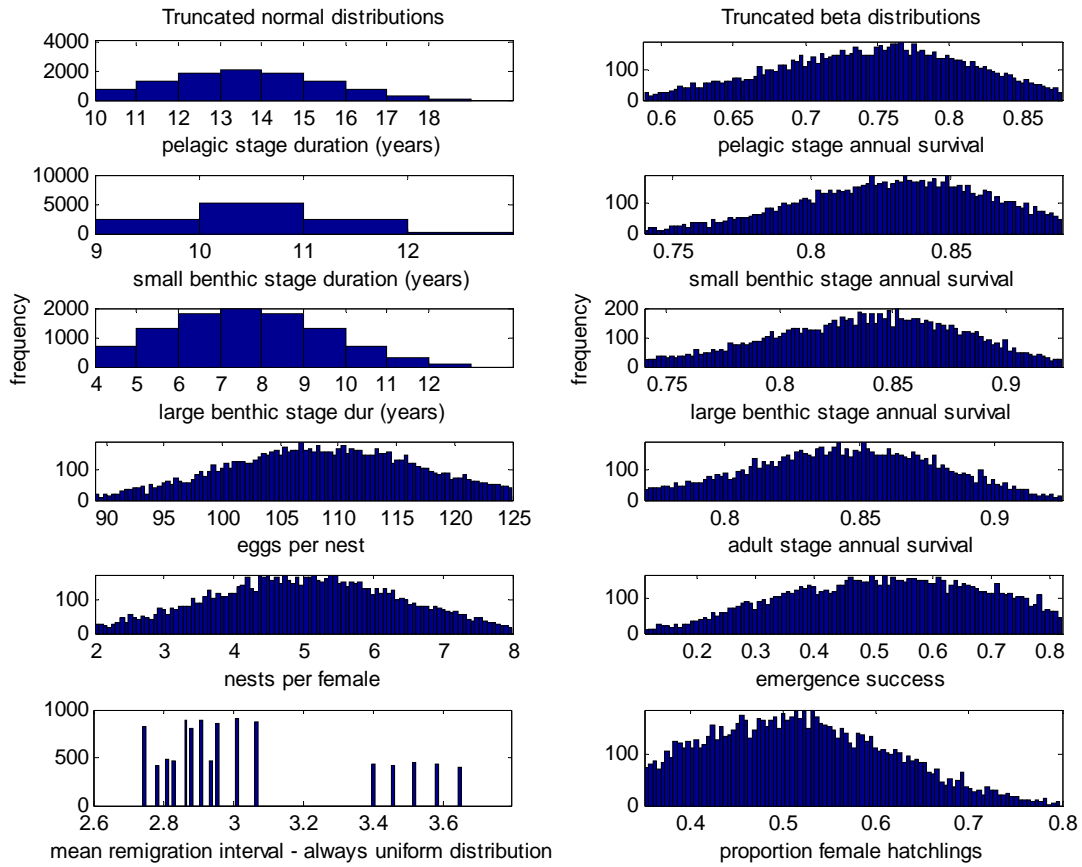


Figure 2 cont.

c) Shape parameter = 8

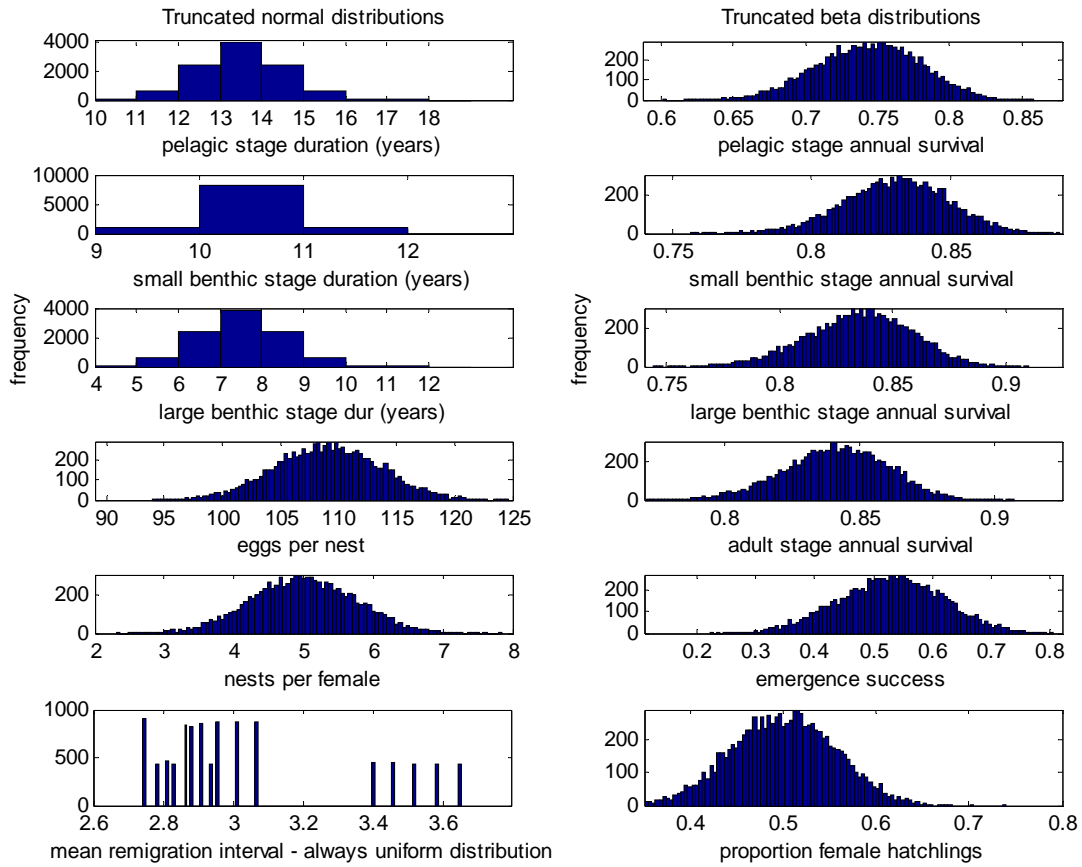


Figure 3: Frequency distributions for shape = 8 for Alternatives U and W for the Western North Atlantic loggerhead population (Table 12) showing the shift in a parameters central tendency dependent upon selection of parameter sets.

a) Alternative U, shape parameter = 8 (compare to Figure 2c)

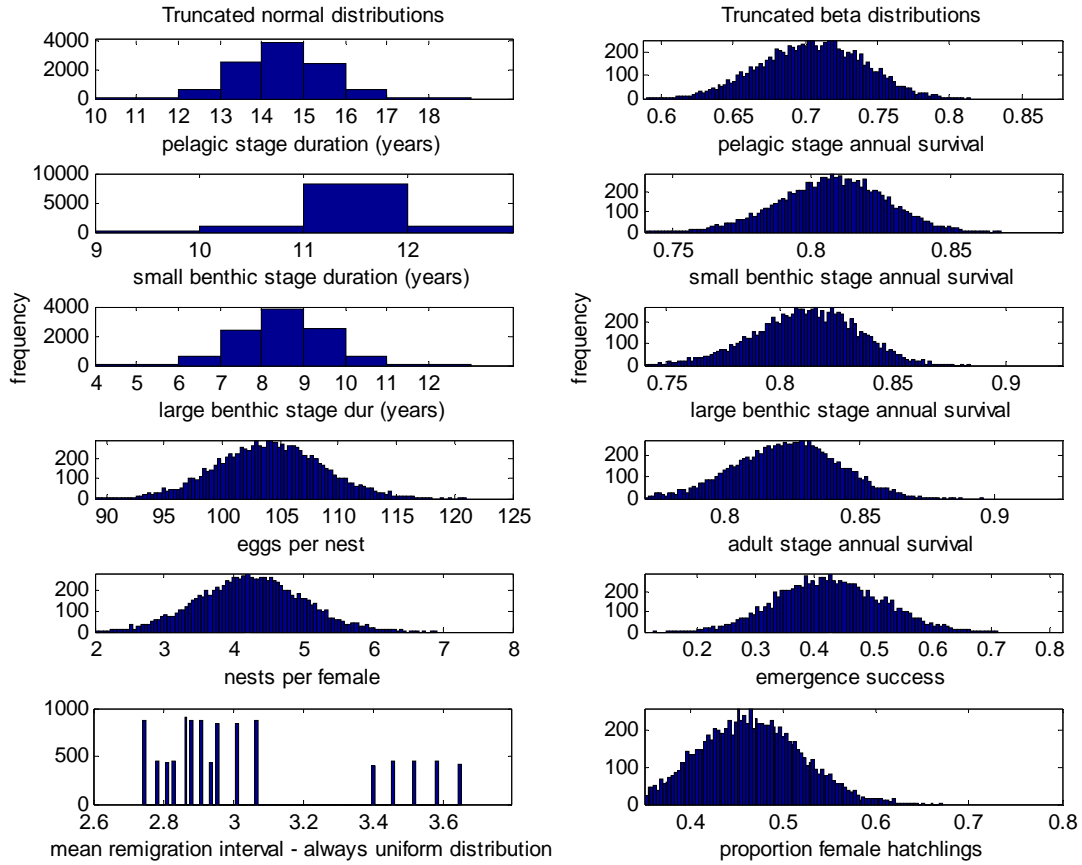
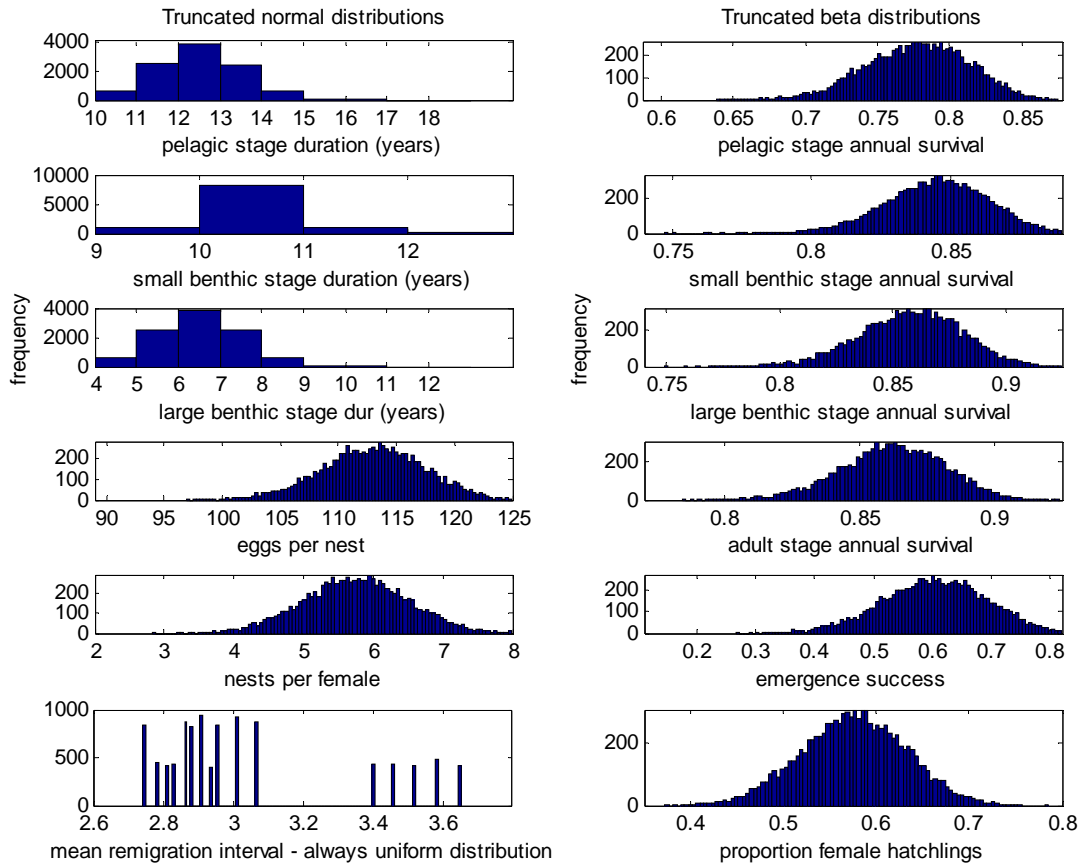


Figure 3 cont.

b) Alternative W, shape parameter = 8 (compare to Figure 2c)



POPULATION ESTIMATES

We estimated current population sizes for adult female loggerhead sea turtles for each management unit and for the total western North Atlantic (Table 13 and Figure 4a-e). We used the general method developed by the Leatherback Turtle Expert Working Group (TEWG 2007), modifying their equation X.1 by removing the proportion female term:

$$\text{Adult Females} = (\text{nests}/(\text{nests per female})) * \text{remigration interval}$$

and used this to create estimates of female population size and to initialize population projections. We simplified the number of assumptions and reduced uncertainty in our estimates by using the minimum total nest counts for the last 5 years (Table 11), resulting in what we consider a set of reasonably conservative female population estimates. Nests per female values were chosen from Table 12, depending upon parameter sets and distribution types. Remigration intervals were taken as the mean from our randomly selected frequency distribution as explained above in that section. One set of distributions of population estimates by management unit and the total Western North Atlantic population are provided in Figure 4a-e. We consider these to be a reasonably conservative set of estimates as we used the minimum nest count in the last 5 years, combined with remigration intervals selected randomly from a uniform distribution, and nests per female using our truncated normal distribution with shape parameter = 2, which is nearly a uniform distribution (see Figure 2a). These are but one set of possible estimates. By using the uniform distribution and our truncated distributions with shape parameter = 2, we make minimal assumptions about the distribution of our parameters. We believe that fewer assumptions produce a more conservative estimate than estimates made with more assumptions.

The estimated number of adult females for the management units ranged from a minimum of 55 females for the U.S. segment of the Dry Tortugas subpopulation to a maximum of 65,001 females for the Peninsular Florida subpopulation (Table 13). We conservatively estimated the median size of the adult female population of the Western North Atlantic population to be 30,050 females (Table 13). The choice of the parameter set (Alternative U, Nominal, or Alternative W) for nests per female (Table 12) had little effect on the median size of the Western North Atlantic population. For example, we estimated a median population size of 31,579 females when using a truncated normal distribution with shape parameter = 2 for nests per female with Alternative U, a median size of 28,388 females when using a truncated normal distribution with shape parameter = 2 for nests per female with Alternative W, and a median size of 29,694 females when using a uniform distribution for nests per female. These differences are likely due to stochasticity in the model, rather than choice of distribution or parameterization.

Population estimates are for all adult females nesting in the western North Atlantic, based primarily on the U.S. nesting beaches. Additional beaches from the Yucatán, Cay Sal Bank, and others (Table 11) have been included, but still the results are a slight underestimate of total nests because we are unable to collect complete counts for many non-U.S. nesting beaches. We do assume that because Yucatán and Cay Sal Bank are currently only about 3% of the total nests counted, additional nests from non-U.S. beaches would contribute little to the total population estimate.

Table13. Conservative estimate of adult female population sizes for each U.S. management unit of loggerhead sea turtles and for the Western North Atlantic population. These results were based on a truncated normal distribution with shape parameter = 2 for nests per female and the Nominal parameter set.

Subpopulation	Percentiles of Distribution						maximum
	Minimum	2.5	25	50	75	97.5	
Peninsular Florida	15247	16025	19420	24276	32972	56420	65001
Northern U.S.	862	910	1063	1176	1288	1538	1646
Northern Gulf of Mexico	207	225	289	367	500	840	1104
Dry Tortugas	55	59	76	97	132	219	288
<i>Western North Atlantic.</i>	16847	18333	23608	30050	40641	68192	89649

Figure 4. Frequency distributions of adult female loggerhead population sizes based on conservative parameter values for each U.S. management unit and for the total Western North Atlantic population. Estimates mostly are based on the minimum available total nest counts from years 2004-2008 (Table 11), and 10,000 random selections of nests per female, using the Nominal parameter set (Table 12) and a truncated normal distribution with shape parameter = 2 and mean remigration intervals from a uniform distribution.

a) Peninsular Florida

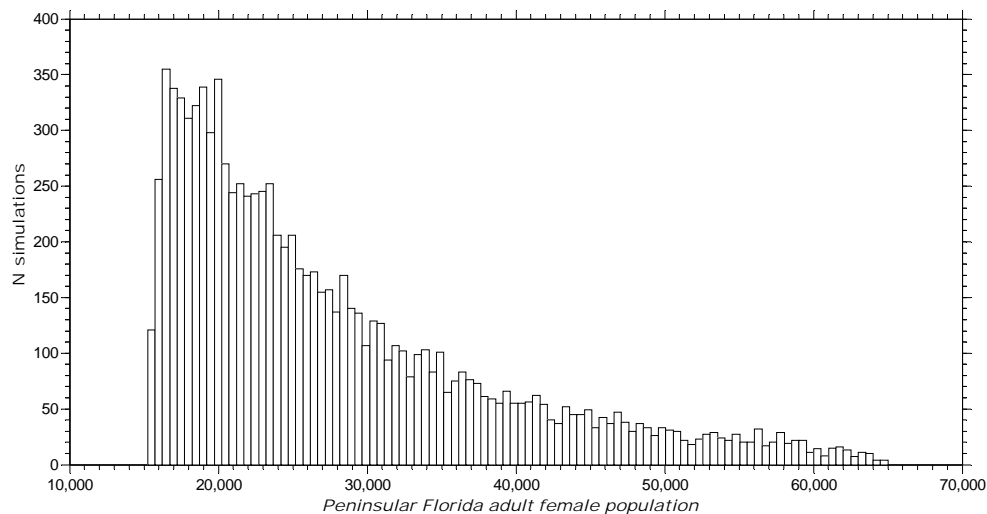
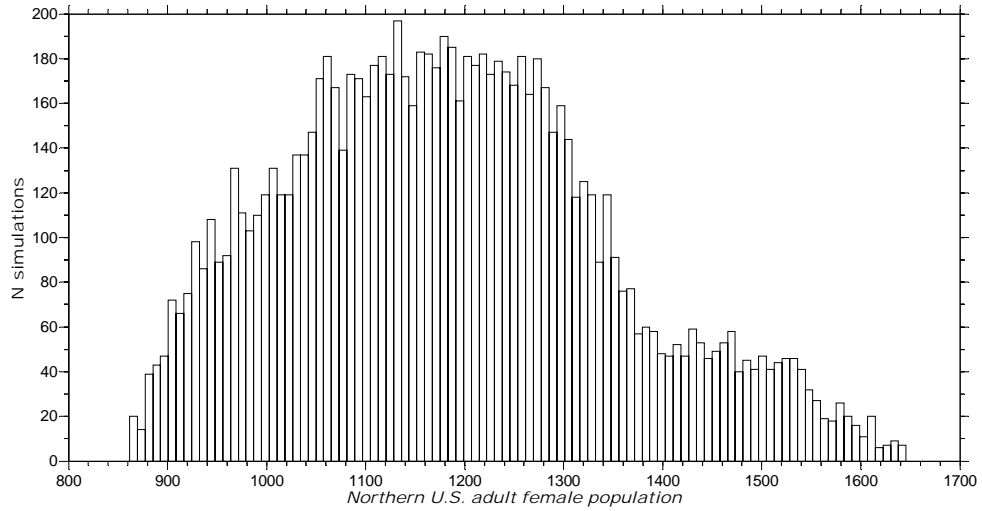


Figure 4 cont.

b) Northern U.S.



c) Northern Gulf of Mexico

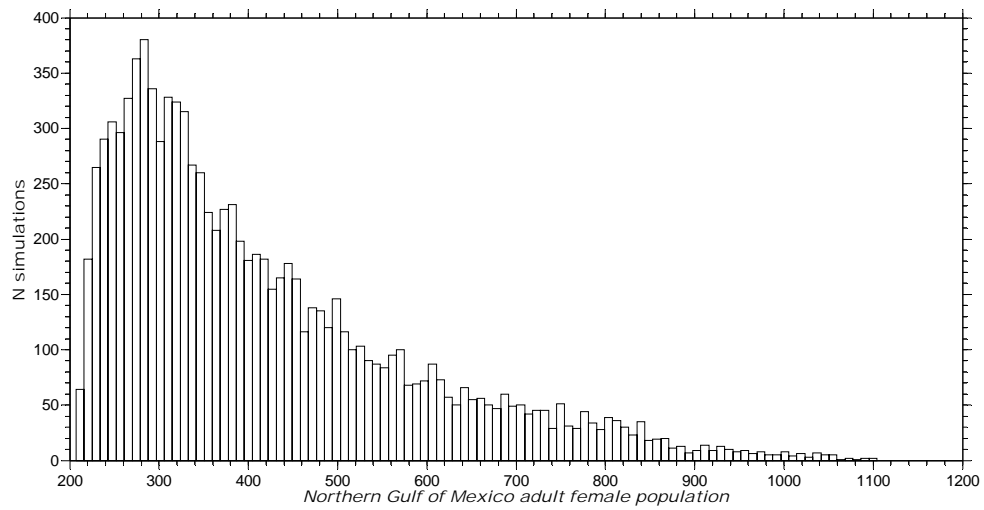
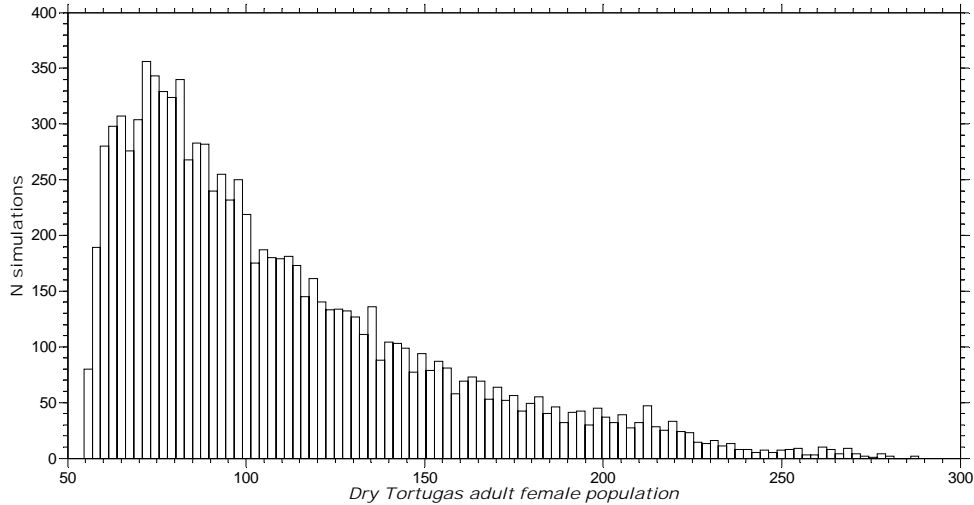
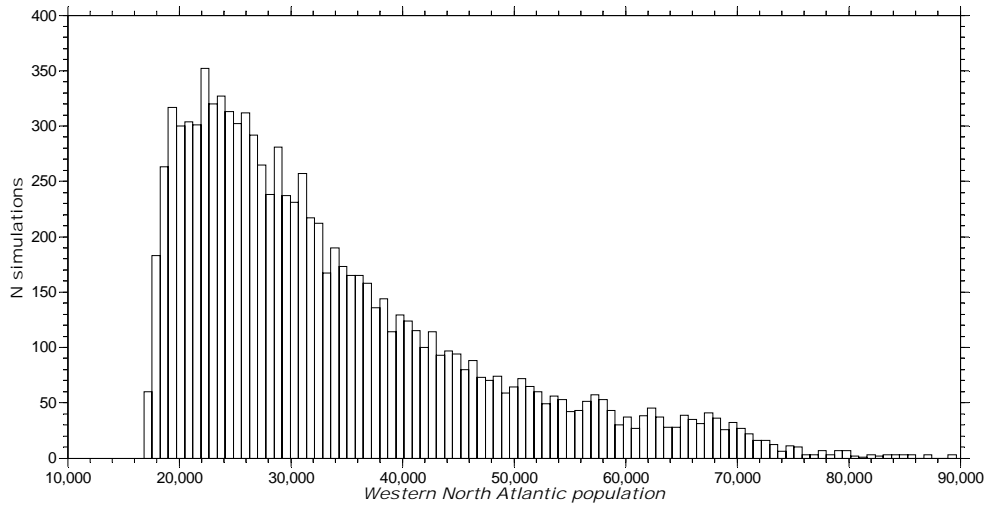


Figure 4 cont.

d) Dry Tortugas (U.S. only)



e) Western North Atlantic



POPULATION TRAJECTORIES

Our initial task was to construct a population viability analysis for the Western North Atlantic population, taking into account the relative effect of each of the 5 management units and the effect of reductions in benthic mortality. To do this we needed movement rates between management units. There are no data specifically to parameterize this, so we used expert opinion based on anecdotal reports of nesting females moving between populations. As discussed above,

we had generated demographic parameters for each management unit. The general idea was to use the parameter uncertainty to describe environmental variation; unfortunately this is not possible because much of the uncertainty in published parameters was likely due to sampling variance rather than environmental variance. Therefore stochastic runs of the model represent our uncertainty in stock assessment based on all factors: parameter uncertainty due to sampling variation, environmental variation in demographic parameters, and variation in anthropogenic impacts

For all simulated trajectories, the general procedure was first to randomly select parameter values from the appropriate parameter set, construct the initial matrix, fix the stage duration parameters (so that matrix size could not change during an individual simulated trajectory), then initialize population size by first estimating female population size, and use the matrix to estimate stable age/stage distribution to populate the remaining ages. At each subsequent time step of an individual simulation we randomly chose new demographic parameter values, except for stage duration, inserted new parameters into the projection matrix, and projected the population to the next time step.

In the 5 management unit model we allowed movement between units, either as a proportion of management unit nest count sizes, or independent of nest count size. The movement parameter was selected using a uniform distribution (Table 12). Neither case made much practical difference in model runs, and the magnitude of the movement parameter also made little difference. This was due to the similarity in demographic parameters between management units, so much so that all management units followed nearly identical trajectories. Because of this result, combined with the fact that we cannot determine the proportional effect of a given management option on any individual management/recovery unit, we did not pursue further work on this segment of the model and instead focused our work on a single Western North Atlantic population.

Our predicted female population size estimates appear to be distributed lognormally (Figure 4e), a typical property of stochastic projections (Caswell 2001). This means that for a population projection, it can be a bit misleading to look only at the 95% confidence intervals; therefore we show a series of contour lines and the absolute model maximum and minimum (Figure 5).

Population trajectories for Western North Atlantic adult females (Figure 5a-d) were created to predict future stock sizes from our initial population estimates (see examples in Figure 4a-e and Table 13 for shape parameter = 2). We present these for each of our Nominal and alternative parameter sets using shape parameter = 8 and with the uniform distribution applied to all parameters. We used uniform distribution to represent the least restrictive assumption and shape parameter = 8 to minimize complications due to truncation of distributions and to show the effect of the various parameter sets (Alternative U, Nominal, and Alternative W). Each plot shows the quartile, 95%, and absolute limit contour lines of the projected population distribution. In general the predicted population size was very sensitive to the choice of parameter set, sometimes yielding growing populations (Figure 5c) and sometimes yielding declining populations (Figure 5a, b and d). We were unable to establish relative probabilities among the trajectories.

Figure 5. Distribution contours for a range of population trajectories for our parameter sets Alternative U, Nominal, and Alternative W, all using shape = 8 and for the uniform distribution.

a) Alternative U, shape parameter = 8

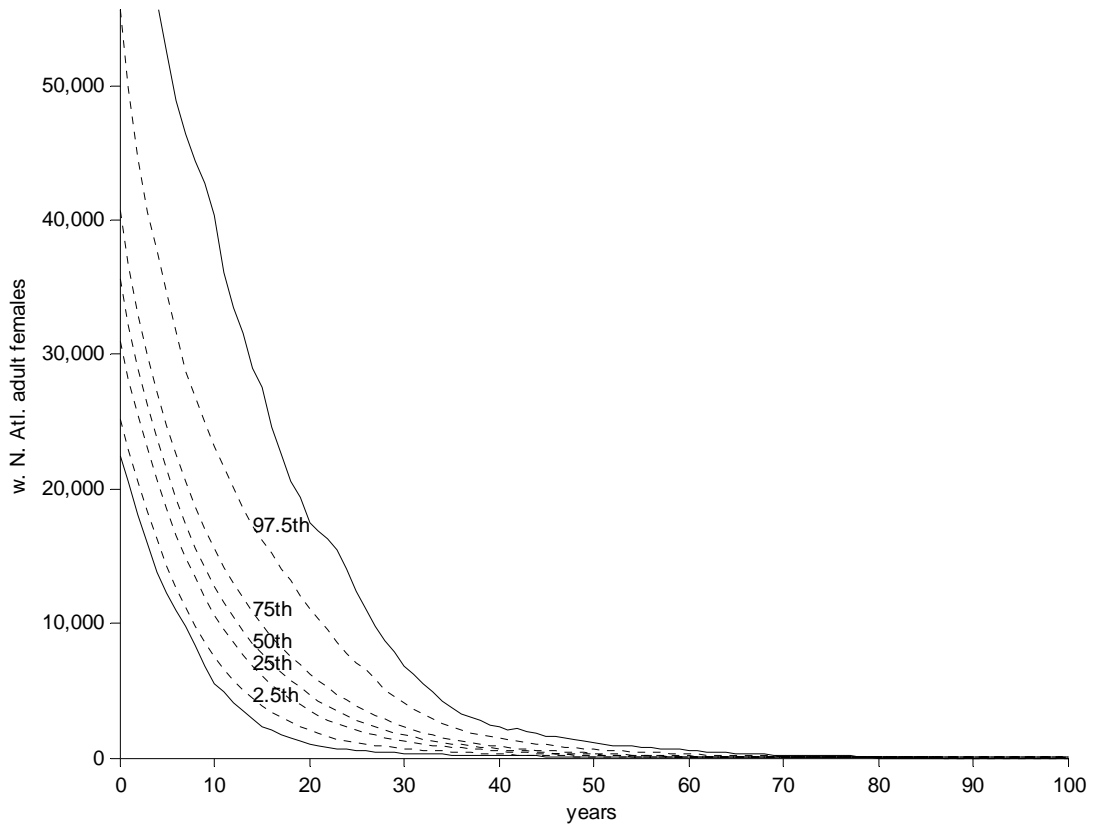


Figure 5 cont.

b) Nominal parameter set, shape parameter = 8

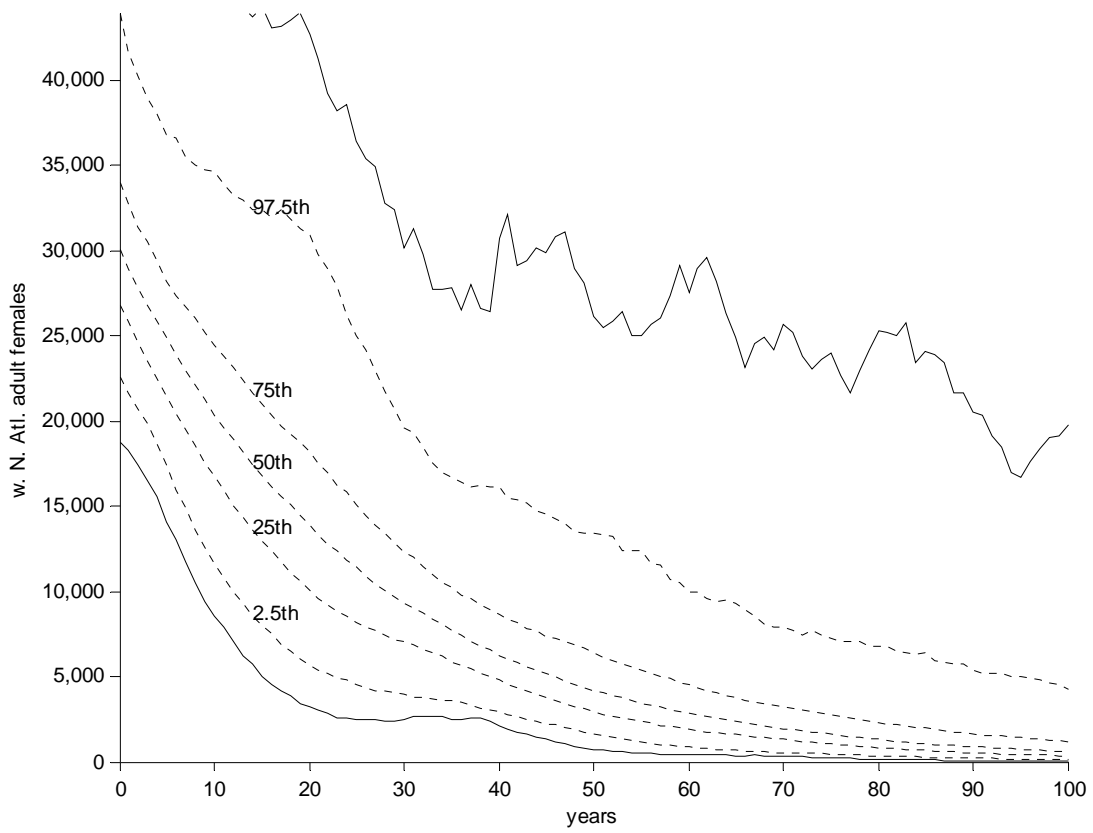


Figure 5 cont.

c) Alternative W, shape parameter = 8

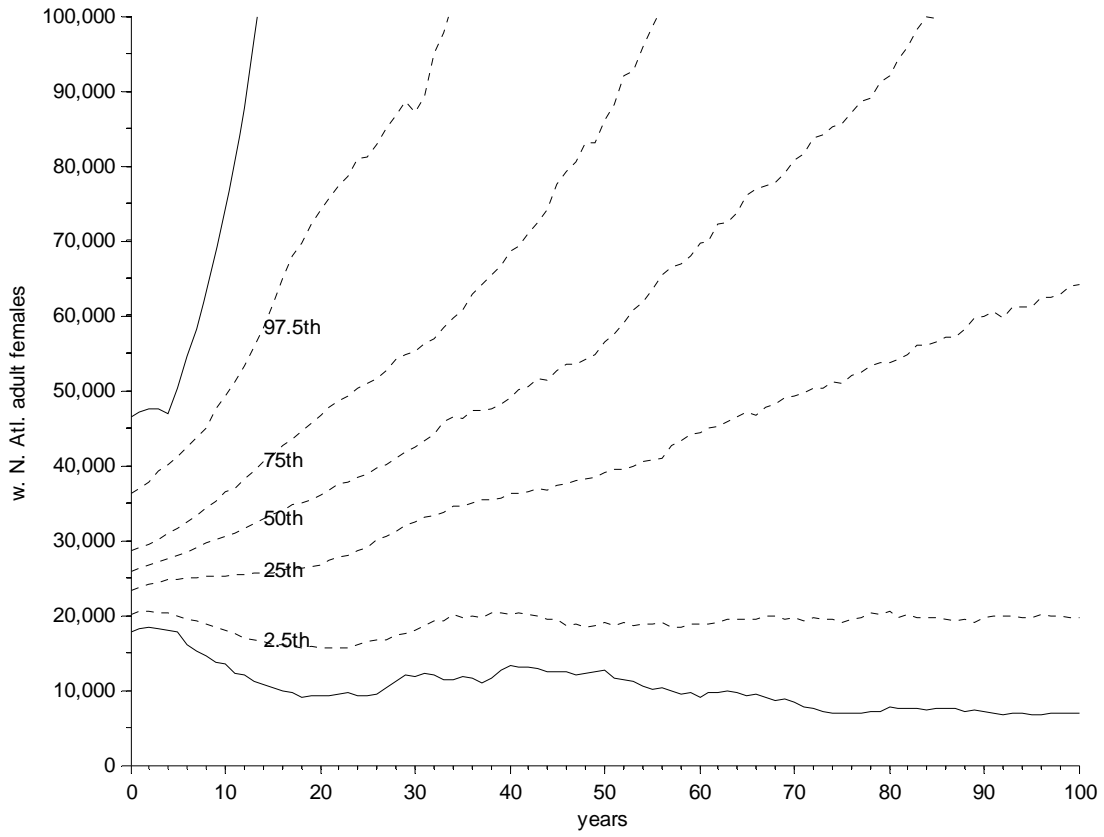
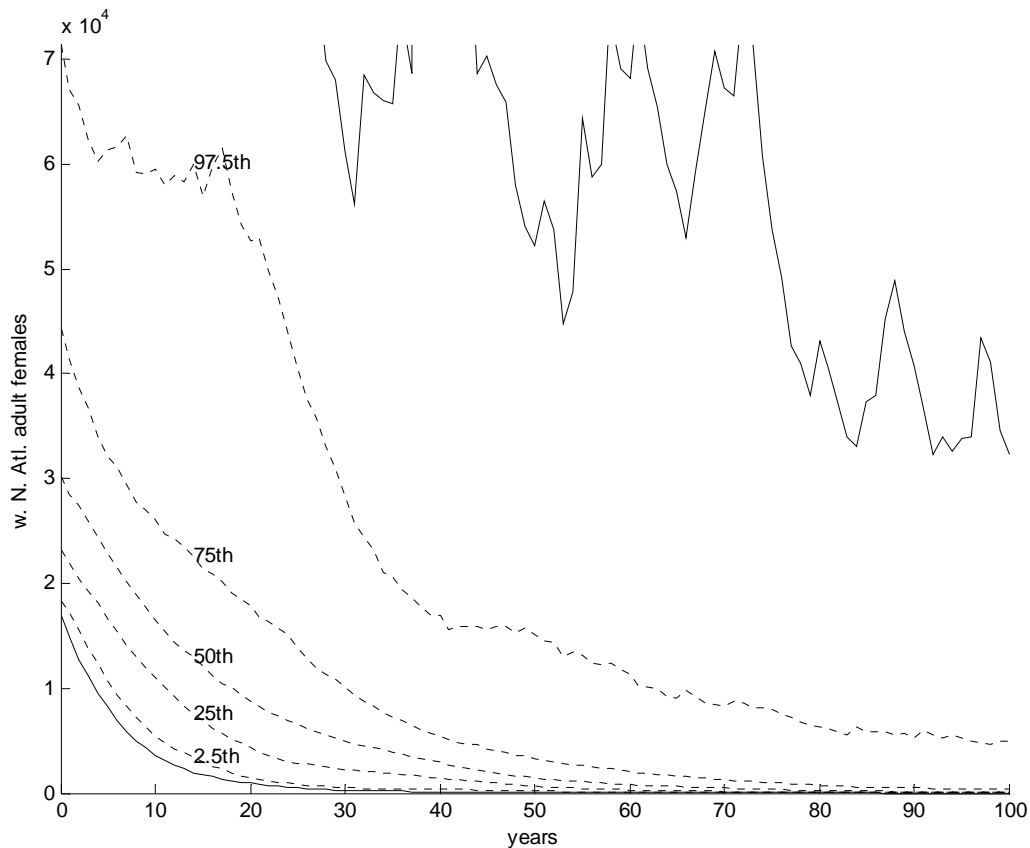


Figure 5 cont.

d) Uniform parameter distribution



ASYMPTOTIC POPULATION GROWTH RATE

We also used our stochastic matrix model to examine the range of predicted asymptotic long term population growth rates as predicted from the dominant eigenvalue of each of the randomly generated matrices. The dominant eigenvalue from the matrix is considered a good predictor of the long term population growth rate (see Caswell 2001). For a population to be growing at a value determined by the dominant eigenvalue, one assumes that a population has reached a stable stage or age distribution and that all life history parameters are constant. For loggerhead sea turtles, which we assume are not at their stable age distribution due to the multitude of perturbations the population has been subjected to, it would presumably take multiple generations to reach this dynamic equilibrium point (100 or more years from the present) in an age-based model. The utility of examining the long term population growth rate is in determining what management could do to affect this theoretical long term population growth rate, not in making short term conjectures of expected population growth rates. We provide frequency distributions of the randomly generated dominant eigenvalues, rescaled to % change per year for the parameter sets Alternative U, Nominal, and Alternative W, at shape parameter = 8 (Figure 6a-c) and for the uniform distribution for comparison (Figure 6d). While it is hard to say what reasonable long term population growth rates for loggerhead sea turtles might be, it is

difficult to imagine that they extend beyond +/- 10%. Annual rates of decline reported to date for various rookeries in the Western North Atlantic population have been about 5% or less (Frazer 1983, Hopkins-Murphy et al. 2001, NMFS and USFWS 2008, TEWG 2009, Witherington et al. 2009). Our predicted distributions for parameter sets Alternative U (Figure 6a) and when using a uniform distribution for all parameters (Figure 6d) contain a large proportion of population growth rate predictions that extend beyond - 10%, suggesting that many parameter combinations are not particularly reasonable. Part of the reason for this may be that our parameter selections do not take into account possible correlations in vital rates. There is no reason to assume that vital rates vary independently of each other but, in the absence of data on parameter correlations, we did not create hypothesized correlations to examine this.

Figure 6. Frequency distributions of dominant eigenvalues rescaled to annual % change in population size from 1000 random parameter selections using each of our parameter sets (Alternative U, Nominal, and Alternative W) with shape parameter = 8, and using the uniform distribution.

a) Alternative U, shape parameter = 8

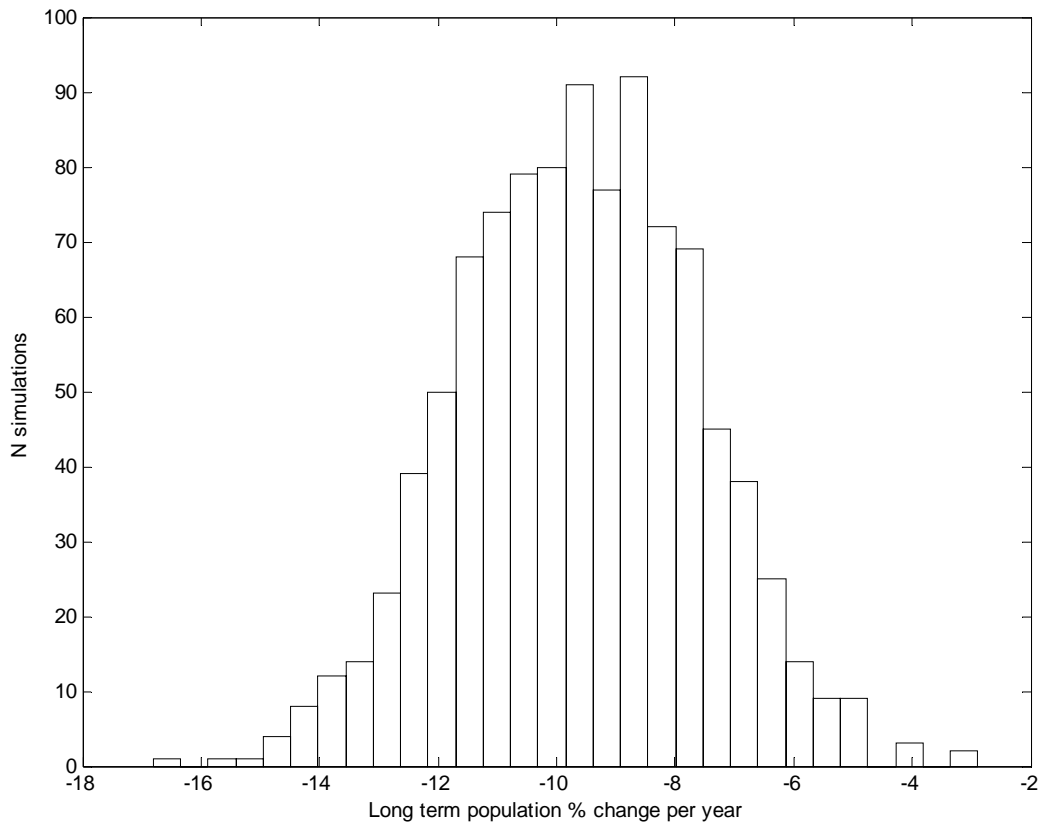


Figure 6 cont.

b) Nominal, shape parameter = 8

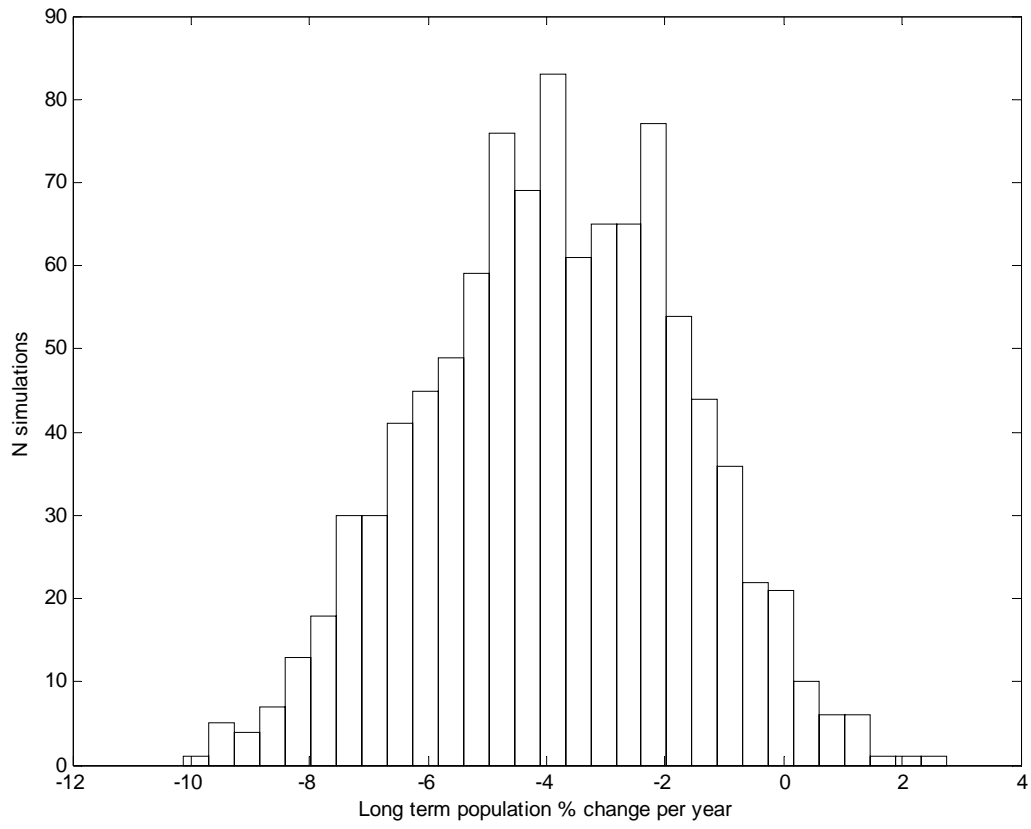


Figure 6 cont.

c) Alternative W, shape parameter = 8

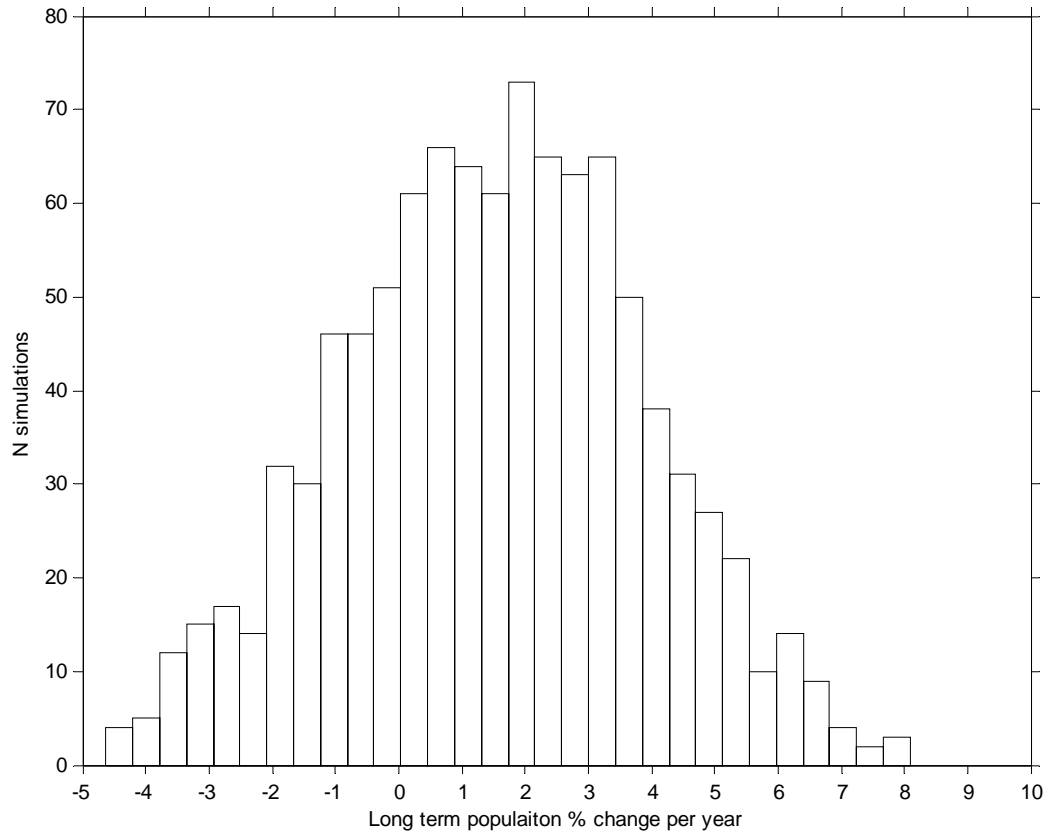
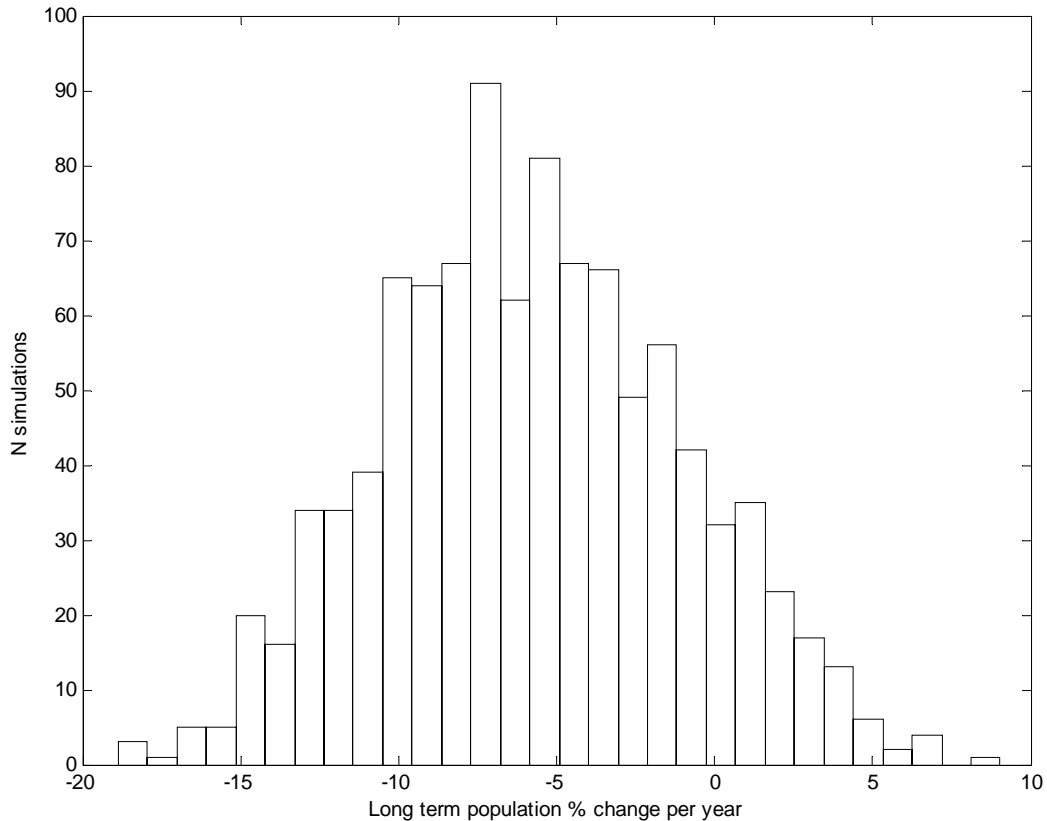


Figure 6 cont.

d) Uniform parameter distribution

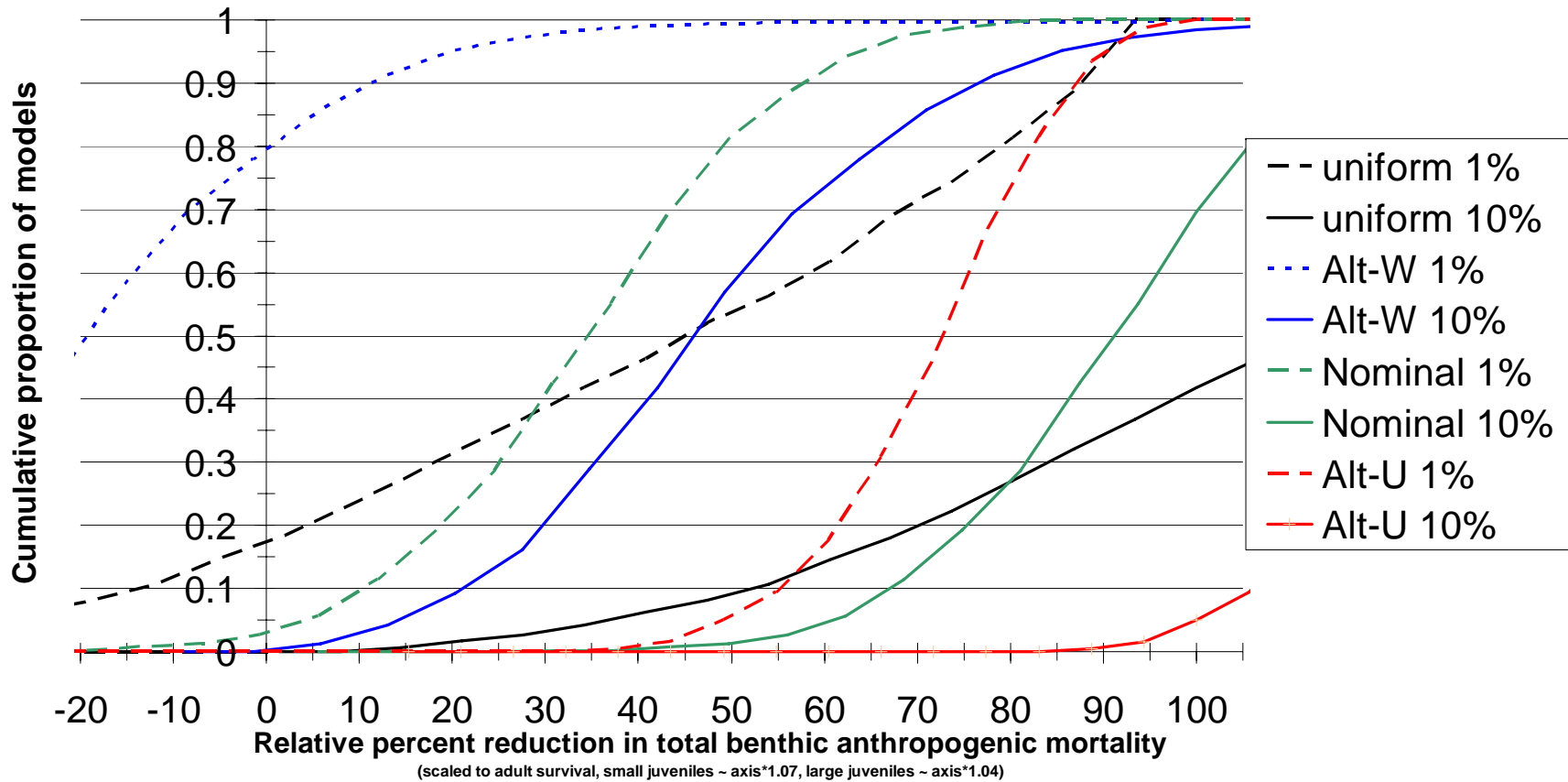


ESTIMATING THE EFFECT OF MANAGEMENT ACTIONS

To examine the effect of altering benthic survival rates, we used our randomly selected parameter sets to solve for the combined benthic survival that yielded a dominant eigenvalue > 1.0 and < 1.001 (population growth rate of 0%, approximately population stasis). To do this we set large juvenile and small juvenile survival equal to a proportion of adult survival as determined from the Nominal parameter set (Table 12), and solved for all three simultaneously while the dominant eigenvalue ~ 1.00 . After determining a set of 1000 benthic survival solutions, we converted survival to mortality, binned the results, subtracted a hypothesized level of natural mortality from each of the bins, and rescaled the bins to a relative percent change in anthropogenic mortality to either the range midpoint when using the uniform distribution or the point estimate from the parameter sets Alternative U, Nominal, or Alternative W (Table 12). Natural mortality was set at either what we consider the absolute lower or upper limit of 1% or 10%, respectively, for all three benthic stage survival rates. The upper limit was based on the fact that to date all empirical estimates of total mortality for these stages are $< 17\%$ (Tables 4 and 5)

and we surmise that the majority of that mortality is anthropogenic. The lower limit is theoretical - there must be some natural mortality. We believe the true value lies somewhere within this range and likely varies by stage (small benthic juvenile, large benthic juvenile, adult). After collecting this frequency distribution of solutions, we then summed each bin to approximate a cumulative frequency distribution of relative anthropogenic benthic mortality reduction solutions that resulted in long term population growth rates greater than or equal to 0% (Figure 7). In general, this type of figure could be useful for management in that it could be used to indicate the relative amount of anthropogenic benthic mortality needed to reach a growing population under different assumptions. We have plotted a range of these cumulative frequency distribution curves, from 1% to 10% natural mortality combined with either the uniform distribution for all parameters, or for each of our parameter sets Alternative U, Nominal, or Alternative W, each using a shape parameter = 8. We are not able to provide a probabilistic statement associated with each type of run, but any one of these can be used individually if one is willing to accept the assumptions made for each parameter set and associated distribution. We recommend taking a conservative position, which suggests at the extreme, given the uncertainty in the alternative models alone (Figure 7), that 100% reduction in anthropogenic mortality on benthic stage loggerheads is not only needed, but might have only a minimal effect on long term population projections. While the most conservative approach would be a 100% reduction in benthic anthropogenic mortality, management may also need to look elsewhere to reduce sources of anthropogenic mortality on other life stages in order to have a recovering Western North Atlantic population. However, given the proximity of the Gulf of Mexico reef fish fishery to the Northern Gulf subpopulation, it is possible that this small population is being disproportionately affected by the fishery, and a 100% reduction in only that fishery's effort may have a greater positive effect on this subpopulation. Additional research is necessary to determine if the reef fish fishery is disproportionately impacting any one subpopulation.

Figure 7. Relative percent reduction in anthropogenic mortality of benthic stage loggerhead sea turtles needed to achieve a stable or growing population for each of our parameter sets and associated distributions (see Table 12), at either 1% (dotted lines) or 10% (solid lines) natural mortality. All parameter sets distributions used shape parameter = 8 (see Figures 2c, and 3a-b). Note that the x-axis is scaled to adult mortality, and all lines are approximate due to the stochastic nature of the simulations and should be considered accurate to about +/- 5 units in both dimensions (see text).



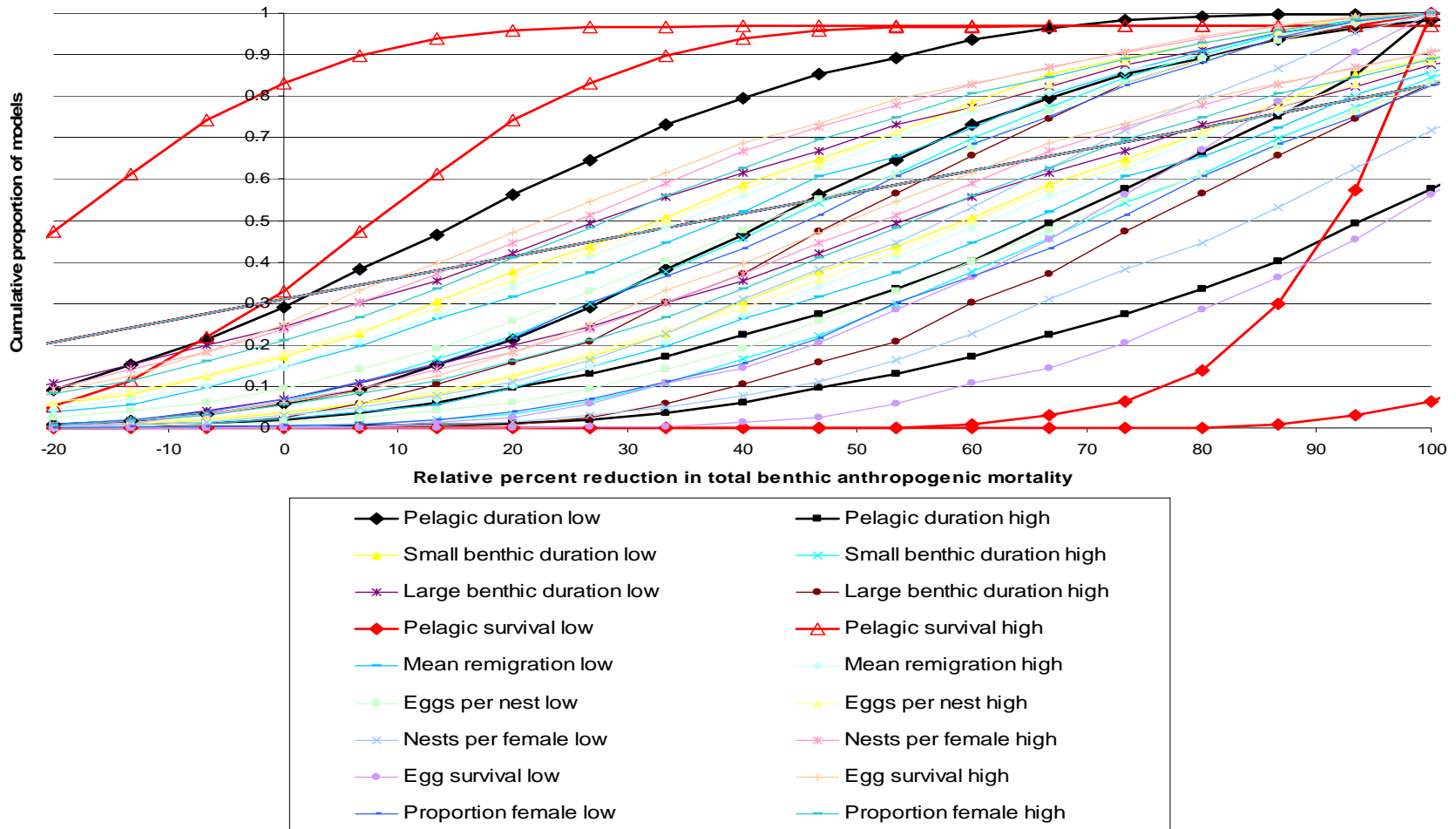
SENSITIVITY ANALYSIS

We performed an individual parameter perturbation (Bartell et al. 1986) as a way of ranking parameters for research priorities (Jackson et al. 2000) to help reduce uncertainty in future population assessments of loggerhead sea turtles in the western North Atlantic. We collected all parameter realizations from a set of 10,000 stochastic calculations of the dominant eigenvalue using our Nominal parameter set at shape parameter = 4, and regressed each parameter against the dominant eigenvalue output (Morris and Doak 2002). We then ranked the parameters by the magnitude of the adjusted R^2 of the significant regressions (Table 14). This result shows that pelagic stage survival had the largest effect on the dominant eigenvalue. Pelagic stage survival explained 67% of the variance in model output, with the next most important parameter explaining only 11% of variance in model output (Table 14). To further demonstrate this effect, we made multiple runs of the model using the Nominal parameter set, holding each parameter constant at either its low or high value while allowing all other parameters to vary randomly. We show the effect of these perturbations on the necessary reduction in anthropogenic mortality in Figure 8. This figure makes clear that: 1) pelagic survival is the most sensitive parameter and 2) the model output is very uncertain given our parameter limits because nearly all the decision space is occupied.

Table 14. Parameters in order of relative importance to population growth rate from 10,000 runs of the stochastic model based on simple regression of each parameter on asymptotic population growth rate (dominant eigenvalue). Order determined by the magnitude of the adjusted R^2 of the significant regressions.

Adj R^2	Parameter
0.673	pelagic survival
0.107	pelagic stage duration
0.066	small benthic survival
0.042	egg survival
0.038	adult survival
0.020	large benthic survival
0.019	large benthic stage duration
0.017	nests per female
0.004	eggs per nest
0.003	proportion female
n.s.	small benthic stage duration
n.s.	mean remigration interval

Figure 8. Sensitivity to individual parameter range of the relative percent reduction in anthropogenic mortality of benthic stage loggerhead sea turtles needed to achieve a stable or growing population for an alternative that was approximately our Nominal parameter set with shape parameter = 4 (see Table 12), at either 1% (upper line in a set) or 5% (lower line of a set) natural mortality. Note that the x-axis is scaled to adult and large juvenile mortality, and all lines are approximate due to the stochastic nature of the simulations, and should be considered accurate to about +/- 5 units in both dimensions (see text).



DISCUSSION, CONCLUSIONS, AND RECOMMENDATIONS

Overall, with the available data, we have been unable to rigorously describe the distribution of parameters and to set limits on the parameters. We accepted published values when available, or created our own estimate with the most recent available data. In one case we had to borrow a parameter from another model of a similar species, Kemp's ridley. The borrowed parameter was itself a heuristic estimate generated from a model, not an empirical estimate. We had hoped that despite these problems some clear patterns and possible limits would emerge. Unfortunately this was not the case. Our sensitivity analysis, looking at the sensitivity of model output to the available range for parameters, shows clearly that a very large range of possibilities exist, and we were unable to describe the probabilities of any of these possibilities within this range. Substantial work is needed in this arena.

Furthermore, the analyses presented here (and in previous matrix models of loggerhead sea turtles of the western North Atlantic) are based upon the assumption that the population is at its stable age/stage distribution. It is unlikely that loggerhead populations are at their stable age/stage distribution given the number of perturbations they have undergone (*e.g.*, historical harvest and fishery-related mortality, then listing in 1978 with many different management actions taken since to minimize those impacts). A population of long-lived organisms, like loggerhead sea turtles, far from its stable stage distribution, may exhibit transient dynamics that make predicting near-term (within the next 100 years) population size difficult, and could mask the effects of any management actions for a very long time. Crowder et al. (1994) modeled a single perturbation (TED implementation) and demonstrated the transitory response in the number of nesting loggerhead turtles in a hypothetical population. Similar responses were demonstrated for southeast U.S. loggerheads (NMFS SEFSC 2001).

Any selection of a single set of parameters, including the midpoints, means, ranges, and associated distributions, from within the host of published and unpublished values that exist is a difficult enterprise. We have been unable to associate probabilistic statements with our various parameter sets and can only put forth minimally supported parameter sets, and supply analyses such as the well described matrix models (*e.g.*, Caswell 2001). The interpretation of these models has usually been meant to be heuristic. Despite this, many have mistakenly assumed that past models themselves show a declining population and that the analyses demonstrate what will happen if a change is effected in a parameter. The real usefulness of such models is if the population is reasonably well represented by the parameters and the model, then general trends and important life history stages to be affected by management or targeted for research can be indicated by the model.

Individual parameter perturbation (sensitivity analysis) indicates that model output is most sensitive to pelagic survival, followed by pelagic stage duration (Table 14). It suggests a ranking of research priorities to most efficiently narrow the range of uncertainty in loggerhead population assessment. First, we need to devote more time and resources to the development of improved stock assessment models of sea turtles. Then, more in-water capture-recapture and telemetry studies (both fisheries independent and fisheries dependent) are needed to improve our estimates of pelagic survival and growth (stage duration), by management unit. After these, it would make

sense to increase telemetry on nesting females to look at survival and nests per female, as well as site fidelity and habitat use and to derive empirical estimates of large benthic survival and stage duration, by management unit.

All example figures were our attempt to bound the total output. In general this was accomplished by using the full range of each parameter set, combined with hypothesized distributions. The outer limits of all ranges could have been used as extremes, but nearly the entire state-space of most figures, and in particular the management based question results, are nearly completely filled by only using the parameter sets Alternative U, Nominal, and Alternative W. These make the point convincingly that it does not take much adjustment to parameters to get dramatically different results.

Concluding that any single result is “the best available science” would be a gross simplification of this assessment. This model cannot effectively address any specific question of what the effect of mortality in a given fishery might be without making very large assumptions that are difficult to justify. Overall, our results suggest that any decisions about specific management actions to reduce benthic anthropogenic impacts, beyond total elimination of anthropogenic impacts, cannot be based on this analysis. What this assessment can contribute is some general patterns (see below) and focus our research efforts:

- 1) The loggerhead adult female population in the western North Atlantic ranges from 20,000 to 40,000 or more, with a large range of uncertainty in total population size.
- 2) Predicting future populations of loggerhead sea turtles is very uncertain due in part to large uncertainty in our knowledge of loggerhead life history.
- 3) Fine-scale questions such as impacts of individual fisheries (for example “How much will it help population recovery of loggerhead sea turtles to reduce bycatch in the GOM reef fish fishery?”) cannot be resolved by the model given the high degree of uncertainty in model parameters.
- 4) Any reductions in mortality will improve the long term outlook for loggerhead sea turtles, but at one extreme, even elimination of anthropogenic benthic mortality may be insufficient to reverse a population decline, if it exists.

ACKNOWLEDGEMENTS

We would like to thank the many researchers who provided us raw or summary data, or assisted us in other ways: David Addison, Alan Bolten, Sarah Dawsey, Lew Ehrhart, Rachel King, Kate Mansfield, Anne Meylan, Bill Redfoot, Tony Tucker, Kris Williams, and Julio Zurita. We also thank Tomo Eguchi and Heather Hass for their reviews of the draft report. We also thank Jacob Richards for the “W” – double respect to you.

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