

Natal homing in juvenile loggerhead turtles (*Caretta caretta*)

Brian W. Bowen¹, Anna L. Bass², Shaio-Mei Chow³, Meredith Bostrom⁴, Karen A. Bjorndal⁵, Alan B. Bolten⁵, Toshinori Okuyama⁵, Benjamin M. Bolker⁵, Sheryan Epperly⁶, Erin LaCasella⁷, Donna Shaver⁸, Mark Dodd⁹, Sally R. Hopkins-Murphy¹⁰, John A. Musick¹¹, Mark Swingle¹², Karen Rankin-Baransky¹³, Wendy Teas⁶, Wayne N. Witzell⁶, and Peter H. Dutton⁷

¹Hawaii Institute of Marine Biology, University of Hawaii, P.O. Box 1346, Kaneohe, HI 96744 USA. E-mail: bbowen@hawaii.edu

²Department of Biology, SCA 110, University of South Florida, 4202 E. Fowler Ave., Tampa, FL 33620-5150 USA E-mail: abass@helios.acomp.usf.edu

³2500 N van Dorn St., #1620, Alexandria, VA 22302 USA E-mail: meemers333@comcast.net

⁴Division of Endocrinology and Molecular Medicine, University of Kentucky, Lexington, KY 40536-0001 USA. E-mail: mabost2@uky.edu

⁵Department of Zoology and Archie Carr Center for Sea Turtle Research, 223 Bartram Hall, University of Florida, Gainesville, FL 32611 USA. E-mail: KAB@zoology.ufl.edu, ABB@zoology.ufl.edu, tokuyama@zoology.ufl.edu, bolker@zoology.ufl.edu.

⁶National Marine Fisheries Service, Miami Laboratory, 75 Virginia Beach Drive, Miami, FL 33149 USA. E-mail: Sheryan.Epperly@noaa.gov, Wendy.Teas@noaa.gov, Wayne.Witzell@noaa.gov.

⁷National Marine Fisheries Service, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla CA 92037 USA. E-mail: Peter.Dutton@noaa.gov, Erin.Lacasella@noaa.gov

⁸National Park Service, Padre Island National Seashore, P.O. Box 181300, Corpus Christi, TX 78480-1300 USA E-mail: donna_shaver@nps.gov

⁹Georgia Department of Natural Resources, 1 Conservation Way, Brunswick GA 31520-8687 USA. E-mail: mark_dodd@mail.dnr.state.ga.us

¹⁰South Carolina Department of Natural Resources, Box 12559, Charleston, SC 29422-2559. E-mail: murphys@mrd.dnr.state.sc.us

¹¹Virginia Institute of Marine Science, Gloucester Point, VA 23062 USA. E-mail: jmusick@vims.edu

¹²Virginia Marine Science Museum, 717 General Booth Boulevard, Virginia Beach, VA 23451 USA. E-mail: mswingle@vb.gov.com

¹³68 Pebble Lane, North Falmouth, MA 02556 USA. E-mail: tscripta@aol.com

Key words: Bayesian, conservation genetics, marine turtles, mtDNA, mixed stock analysis

Left running head: Bowen et al.

Right running head: Juvenile loggerhead homing

Five tables, two figures, 8500 words

Juvenile Loggerhead Homing

ABSTRACT

Juvenile loggerhead turtles (*Caretta caretta*) from West Atlantic nesting beaches occupy oceanic (pelagic) habitats in the eastern Atlantic and Mediterranean, whereas larger juvenile turtles occupy shallow (neritic) habitats along the continental coastline of North America. Hence the switch from oceanic to neritic stage can involve a trans-oceanic migration. Several researchers have suggested that at the end of the oceanic phase, juveniles are homing to feeding habitat in the vicinity of their natal rookery. To test the hypothesis of juvenile homing behavior, we surveyed ten juvenile feeding zones across the eastern U.S. with mtDNA control region sequences (N=1437) and compared these samples to potential source (nesting) populations in the Atlantic Ocean and Mediterranean Sea (N=465). The results indicate shallow but significant population structure of neritic juveniles ($\phi_{st} = 0.0088$, $P = 0.016$), and haplotype frequency differences are significantly correlated between coastal feeding populations and adjacent nesting populations (Mantel test $R^2 = 0.52$, $P = 0.001$). Mixed stock analyses (using a Bayesian algorithm) indicate that juveniles occur at elevated frequency in the vicinity of their natal rookery. Hence all lines of evidence support the hypothesis of juvenile homing in loggerhead turtles. While not as precise as the homing of breeding adults, this behavior nonetheless places juvenile turtles in the vicinity of their natal nesting colonies. Some of the coastal hazards that impact declining nesting populations may also impact the next generation of turtles feeding in nearby habitat.

Juvenile Loggerhead Homing

Introduction

Loggerhead turtles have two distinct juvenile stages, the first being an oceanic stage after hatching (Carr 1987; Bolten 2003a). For post-hatchling turtles departing the nesting beaches of the western Atlantic, this oceanic habitat includes waters around the Azores and Madeira, the Grand Banks (Newfoundland, Canada), as well as the Mediterranean Sea (Bolten et al. 1998; Laurent et al. 1998; Bolten 2003a). Subsequent to the oceanic stage, which may span a decade (Bjørndal et al. 2000, 2003), most older juveniles enter a neritic (benthic feeding) stage, in which they consume hard-shelled invertebrates in shallow habitats of the western Atlantic (Dodd 1988; Bolten 2003b). Whereas the journey from nesting beaches to oceanic juvenile habitat is largely mediated by passive transport, the return trip may include active orientation and swimming (Bolten 2003a).

Upon reaching sexual maturity, female loggerheads make reproductive migrations to breed and nest in the vicinity of their natal beach (Bowen et al. 1993). Male loggerheads may make a similar migration to breeding areas near their natal beach (see FitzSimmons et al. 1997a, 1997b). Hence homing behavior is widely accepted for the reproductive migrations of adults, begging the question of whether juveniles also exhibit homing behavior during their trans-oceanic migration. Genetic markers hold considerable promise for addressing this issue. As a consequence of natal homing by females, most nesting populations are distinguished by differences in the frequency of mitochondrial DNA (mtDNA) haplotypes (Bowen et al. 1994; Encalada et al. 1998; Hatase et al. 2002a). It is possible to use these natural genetic “tags” to resolve the origin of feeding populations, even when the feeding population is a mixture of turtles from several source nesting populations (Bowen 1995; Bowen 2003). Mixed stock analyses have been used to monitor salmon for over 20 years (Grant et al. 1980), but this methodology has seldom been applied to other organisms (Broderick et al. 1994; Epifanio et al. 1995, Wirgin et al. 1997).

Previous mtDNA studies by Norrgard and Graves (1996), Rankin-Baransky et al. (2001), Witzell et al. (2002), Engstrom et al. (2002) and Bass et al. (2004) concluded that contributions to juvenile loggerhead habitats are influenced by the size of regional source (nesting) populations. The very large rookery in southern Florida contributes most of the neritic-stage turtles feeding along this coast, with smaller but significant contributions from the rookeries on the Yucatan peninsula, Gulf of Mexico, and the

Juvenile Loggerhead Homing

Atlantic states of Georgia, South Carolina, and North Carolina. The same mtDNA studies prompted authors to suggest that juvenile turtles may tend to feed in the vicinity of their natal nesting colony. Hence two factors have been postulated to explain the composition of juvenile loggerhead feeding populations: size of source populations and proximity to these sources. A third factor, male-biased dispersal, has been proposed for loggerhead juveniles in the Mediterranean (Casale et al. 2002).

These mtDNA surveys invoke the possibility that loggerhead turtles have two distinct homing migrations. The well known reproductive migration, that brings adults back to their ancestral breeding areas, plus a juvenile migration that brings oceanic migrants to neritic feeding habitats near their location of origin. If juvenile homing occurs in the northwestern Atlantic, how precise is this behavior? Do older juvenile turtles return to a broad region of the western Atlantic, or do they tend to recruit to feeding grounds near their rookery of origin? The latter possibility (homing towards natal location) would carry the expectation of population genetic differences among regional feeding cohorts, in parallel to the genetic differences observed between nesting populations (Bowen et al. 1993). Previous studies invoked the possibility of juvenile homing (Norrgard and Graves 1996; Rankin-Baransky et al. 2001; Witzell et al. 2002; Engstrom et al. 2002). However, all of these surveys examined a single feeding habitat. To evaluate the veracity and precision of homing, samples from multiple feeding locations across the western Atlantic are necessary.

Here we survey 1437 neritic-feeding individuals (strandings and live captures) along the Atlantic coast of North America from Texas to New England, with mtDNA control region sequences (Fig. 1). We incorporate three previous surveys of juveniles from this region (Rankin-Baransky et al. 2001; Witzell et al. 2002; Bass et al. 2004) along with complementary surveys of regional nesting females (Encalada et al. 1998; Laurent et al. 1998; Pearce 2001) to resolve the origin of neritic-feeding loggerhead populations and to assess the site fidelity of juveniles. This survey is intended to resolve a gap in loggerhead life history, but the information is relevant to conservation strategies, as thousands of juvenile loggerhead turtles are entrained in fishing gear and dredging operations. Wildlife managers need to know which breeding populations are impacted by these activities.

Juvenile Loggerhead Homing

METHODS

Nest samples were previously collected from 465 females or progeny from Quintana Roo (Yucatan Peninsula, Mexico), Bahia (Brazil), Kiparissia Bay (Greece), Turkey and the southeast U.S. during the interval 1987-1999 (Table 1; for details consult Bowen et al. 1993; Encalada et al. 1998; Laurent et al. 1998; Pearce 2001). Tissue samples (typically an egg or moribund hatchling) were the primary DNA source prior to 1993, and blood samples from nesting females (usually less than one ml) were taken in most collections after 1993, following the procedure of Owens and Ruiz (1980) and FitzSimmons et al. (1999). Precautions to ensure that nesting females were sampled only once included either 1) tagging the nesting females, or 2) sampling within a single 11 day interval. Females may nest several times in a nesting season, but rarely at intervals shorter than 11 days (Dodd 1988).

Samples of the feeding populations ($n = 1437$) were collected during the interval 1995-2001 (Table 2). Most samples were collected as tissue specimens from stranded individuals (dead and moribund turtles that wash ashore), and these are assumed to represent the local juvenile cohort (Epperly et al. 1996). Blood aliquots were collected from live individuals in North Carolina (Bass et al. 2004), and most of the specimens from SE Florida were collected in a power-plant entrainment ($n=106$; Witzell et al. 2002). Tissue specimens were stored in a saturated salt buffer (Seutin et al. 1991; Dutton and Balazs 1996). This solution has proven useful for storing specimens at room temperature for at least five years.

Size class information was not available in all cases, but the vast majority of specimens came from neritic-stage juveniles in the size range of 40-80 cm straight carapace length. Epperly et al. (1995) noted that the habitats sampled here contain few adults. However, we did not conduct internal examination of gonads, so cannot rule out the possibility that a few adults are included in our neritic-stage samples.

Genomic DNA was isolated using a phenol/chloroform procedure followed by ethanol precipitation (Hillis et al. 1996). A 391 base-pair (bp) fragment located in the control region of the mitochondrial genome was amplified with polymerase chain reaction (PCR) methodology (Mullis and Faloona 1987), using the primers TCR-5 (5'-TTG TAC ATC TAC TTA TTT ACC AC-3') and TCR-6 (5'-GTA CGT ACA AGT AAA ACT ACC GTA TGC C-3') (Norman et al. 1994). For some of the samples a 480 bp fragment of the control region was amplified with LTCM1 and HTCM1 primers from Allard et al. (1994). The PCR reactions used standard conditions (Encalada et al. 1998) with an annealing temperature of 52°C and a $MgCl_2$ concentration of 1.5 mM in 50 ul volume reactions. PCR amplifications included negative (DNA

Juvenile Loggerhead Homing

free) control reactions to guard against contamination. PCR products were purified using 30,000 MW filter units (Millipore, Inc., Bedford, MA). Cycle sequencing reactions were conducted with fluorescent dye-primer and dye-terminator technology (Applied Biosystems Inc. [ABI], Foster City, CA) and fragments were gel separated at the University of Florida DNA Sequencing Core using an automated sequencer (ABI model 373A or 377), and at the NOAA-Fisheries Molecular Genetics Laboratory at the Southwest Fisheries Science Center in La Jolla, CA (ABI models 377 and 3100). Chromatograms were aligned using Sequencher 3.1 (Gene Codes, Inc., Ann Arbor, MI). These sequences were compared to previously identified haplotypes from nesting and foraging locations (Bolten et al. 1998; Encalada et al. 1998) and were assigned haplotype numbers based on the web site maintained by the Archie Carr Center for Sea Turtle Research (<http://accstr.ufl.edu/ccmtdna.html>).

The mtDNA diversity among populations was measured with an analysis of molecular variance (AMOVA) as implemented in ARLEQUIN vers. 2.0 (Schneider et al. 2000). The same software package was used to conduct a Mantel test and to estimate haplotype diversity, nucleotide diversity, and haplotype frequencies (Nei 1987; Excoffier & Slatkin 1995). In all tests that required estimates of sequence divergence, the Tamura-Nei model of nucleotide substitutions was employed (Tamura and Nei 1993). The Mantel test is a comparison of genetic differentiation (ϕ_{st} values) among seven nesting colonies (FL-NG, FL-SG, FL-SA, FL-NA, GA, SC, NC in Table 1) along the continental coast of North America (X-matrix), and seven proximal feeding zones (Y-matrix). The correlation between these two matrices was evaluated with a permutation test as described by Smouse et al. (1986). In a related test, the frequency of the most common haplotype (CCA-1) was compared between seven nesting areas and adjacent feeding populations, calculating the standard Pearson coefficient of determination (r^2) and using a permutation test (with 30,000 permutations) to calculate two-tailed significance against a null hypothesis of $r^2 = 0$.

The availability of data from multiple mixed stocks (feeding populations) and multiple sources (nesting areas), as well as the need to account for the effects of population size, has led us to develop a variation of standard Bayesian methods for mixed stock analysis (see Pella and Masuda 2001; Bolker et al. 2003; Bass et al. 2004; Okuyama and Bolker in press). Mixed stock analysis normally estimates the proportion of the individuals in a single mixed stock contributed by each of a number of source populations. In the current analysis, where we have multiple sources and multiple mixed stocks, we compute the same parameters -- the proportion of each mixed stock contributed by each rookery -- but

Juvenile Loggerhead Homing

we are also interested in partitioning the other way, finding the fractions of the total contribution to the NW Atlantic (from each source population) that is present in each mixed stock. In particular, we want to know if rookeries contribute disproportionately to nearby feeding populations. Estimating contributions to foraging grounds separately also assumes that all foraging grounds are the same size. Even if we can say that 57% of the feeding individuals in the NE US and 69% of those in South Florida originate from the South Florida rookery, we cannot necessarily infer that more turtles from South Florida go to the South Florida foraging ground, if the northern foraging ground has a larger population. Our new method does not make this assumption.

We can estimate these parameters in a straightforward way, if we know the relative sizes of the rookeries and if we make the assumption that the total contributions of nesting populations to the combined feeding populations are proportional to their size. Essentially, if the relative sizes (and therefore overall proportional contributions) of the rookeries are known, we can derive an equation to translate between the partitioning of mixed-stock turtles according to their nesting population of origin and the partitioning of nesting population turtles according to their mixed-stock destination (Bolker et al., unpublished ms.). This procedure can then be incorporated into standard mixed-stock estimation procedures, either in a maximum-likelihood or in a Bayesian estimation framework; we have chosen a Bayesian framework because of its more accurate calculation of confidence limits (Bolker et al. 2003). We can examine the estimates from this procedure either in the traditional way, as the fractions of each mixed stock estimated to come from each source population (rookery), or, in the new way, as the fractions of the total contribution from each rookery estimated to be present in each mixed stock. The new method also adds an “unknown” category to the list of mixed stocks, to allow for the possibility that some of the sampled rookeries contribute to one or more unknown mixed stocks.

DESIGNATION OF SOURCE POPULATIONS FOR MIXED STOCK ANALYSES

Based on the population subdivisions defined by Encalada et al. (1998), Laurent et al. (1998) and Pearce (2001), the nesting samples (Table 1) were grouped into the following source populations for mixed stock analysis: 1) Florida coast in the northern Gulf of Mexico (FL-NG; n=49); 2) South Florida (SFL, n=109) combining southern Atlantic and southern Gulf coasts of Florida (FL-SA and FL-SG in Table 1); 3) northeast Florida to North Carolina (NEFL-NC; n=105), combining northern Atlantic coast of Florida,

Juvenile Loggerhead Homing

Georgia, South Carolina, and North Carolina (FL-NA, GA, SC, and NC in Table 1); 4) Dry Tortugas, FL (DT, n=58); 5) Quintana Roo, Yucatan, Mexico (MX, n=20); 6) Bahia, Brazil (BR, n=11), 7) Greece (GR, n=81); and 8) Turkey (TU; n=32). These groupings are based on statistically significant differences in haplotype frequencies. Additional population subdivisions almost certainly exist, but cannot be detected with the available mtDNA sequence information.

DESIGNATION OF FEEDING POPULATIONS FOR MIXED STOCK ANALYSIS

Juvenile populations from Texas to the northeast U.S. (Table 2) were analyzed without modification for indices of genetic diversity, haplotype frequency comparisons, F statistics, correlation coefficient, and the Mantel test. Because of the relatively sparse data from the mixed stocks, analyzing the contributions to the mixed stocks in their fully disaggregated form leads to very wide confidence limits. We estimated the contributions to each of 11 "foraging grounds" (the 10 foraging grounds represented by the different data sets in Table 2 plus an unknown foraging ground) separately, but we also lumped the results into four groups representing a northern mixed stock (N: FL-NA, GA, SC, NC, VA, NEUS in Table 2), a southern mixed stock (S: FL-SA in Table 2), and a Gulf of Mexico mixed stock (G: TX, FL-NG, FL-SG in Table 2) and an unknown mixed stock (not shown). As well as considering the basic estimate of contribution to each of the known mixed stocks, we also consider the ratio of the contributions to the total contributions to known stocks (e.g. $N/(N+S+G)$ would represent the contribution to the Northern stock relative to the combined total of Northern, Southern, and Gulf contributions). In addition, we discard "orphan" haplotypes, the haplotypes from the feeding grounds that were not detected in nesting populations (haplotypes CCA-18, 19, 22, and 23 in Table 2); these specimens provide no additional information about the contributions of nesting populations to feeding grounds. The individuals with "orphan" haplotypes (n = 4) comprise less than 1% of the overall feeding ground sample.

RESULTS

In the analysis of feeding grounds and adjacent nesting populations, we encountered 18 of the 23 haplotypes reported for Atlantic loggerhead turtles (Table 1, Table 2). Haplotype diversity in juvenile feeding populations was fairly uniform ($h = 0.555 - 0.684$) as was nucleotide diversity ($\pi = 0.0221-0.0249$). In both cases the lowest diversity estimates were from locations in Florida (Table 3).

Juvenile Loggerhead Homing

The test of population structure and natal homing in juvenile turtles consists of three classes of data analysis. The first is a comparison of haplotype distributions among 10 feeding zones along the Atlantic coast of North America, from Texas to Massachusetts. These feeding zones correspond to U.S. states and federal management regimes, including Texas, four zones around the Florida peninsula, Georgia, South Carolina, North Carolina, the seasonal feeding habitat in Virginia, and the seasonal feeding habitat from Maryland to Massachusetts (Fig. 1). Results of AMOVA indicate that juvenile turtles are not randomly distributed among these regions: $\phi_{st} = 0.0088$. This value is low on the scale of population genetic separations, but significant in permutation tests ($P = 0.016$). When we compare just the seven feeding grounds that are adjacent to continental nesting colonies (FL-NG, FL-SG, FL-SA, FL-NA, GA, SC, NC in Table 2), the corresponding values are somewhat higher: $\phi_{st} = 0.0164$ ($P < 0.006$). The same comparison with conventional F-statistics (which do not include the divergence between haplotypes) yielded a lower but significant value ($F_{st} = 0.0070$; $P = 0.035$). Hence our first conclusion is that juvenile loggerhead turtles are not distributed randomly among feeding habitats.

Our second approach is an assessment of haplotype frequencies at nesting populations compared to adjacent (juvenile) feeding populations. The frequency of the most common haplotype (CCA-1) at the seven nesting populations is significantly correlated with the frequencies at the seven adjacent feeding populations ($R^2 = 0.88$, $P = 0.049$; Fig. 2). Given that our data matrices include only seven values, the significant outcome is especially compelling. A Mantel test of genetic distances (ϕ_{st} values) among the seven nesting colonies (X-matrix) versus genetic distances among seven feeding populations (Y-matrix) is highly significant ($R^2 = 0.52$, $P = 0.001$). Approximately half of the genetic divergence among juvenile feeding populations is correlated to genetic divergence among corresponding nesting populations. These two correlation tests provide strong support for our second conclusion, that haplotype distributions in juvenile feeding populations are significantly influenced by the composition of nearby nesting populations.

Third, the results of the Bayesian mixed stock analysis show that nesting populations do indeed contribute more to neighboring mixed stocks than to distant mixed stocks (Tables 4 and 5). For most rookeries, the data are too sparse to determine destinations of neritic juveniles with certainty. The mean and median estimates of the fraction going to any one of the three (lumped) mixed stocks is close to

Juvenile Loggerhead Homing

proportional to the number of foraging grounds included in the mixed stock: $0.55=6/11$ for Northern, $0.09=1/11$ for Southern, and $0.27=3/11$ for Gulf (the denominator of 11 includes ten feeding populations plus the “other” category, not shown). Furthermore, the 2.5 and 97.5 percentiles of the posterior contribution for many of the stocks range from nearly zero to a proportional contribution above 0.5. In fact, none of the rookeries alone show “significantly” disproportionate contributions to the closest lumped mixed stocks, where we define significance as a 2.5 percentile of the relative contribution greater than 0.55, 0.09, or 0.27 respectively (according to the partitioning discussed above). Nevertheless, there are patterns in the results: the NEFL-NC appears to contribute disproportionately to the Northern mixed stock (median 0.77, 2.5 percentile 0.498, null expectation 0.55), and South Florida contributes slightly more to the Gulf mixed stock (median 0.33, 2.5 percentile 0.13, null 0.25). In the disaggregated results (treating each feeding area separately; data not shown), structure is reflected in slightly enhanced contributions (>10% over an expected proportional contribution of 9.1%) from south Florida to TX, FL-SG, GA, and VA; from Mexico to FL-NG, FL-SA, and SC; and from NEFL-NC to NC, VA, and NE-US (see Tables 1 and 2 for abbreviations).

Looking at the results in the more traditional way, as the fraction of each feeding ground population contributed by specific rookeries (Table 5), we see that the estimated contributions are (as expected) dominated by the size of the contributing rookeries: the three aggregate feeding-ground populations are estimated to have 82-90% contributions from the large rookery in South Florida. The main conclusion to draw from Table 5 is the very small contribution of rookeries outside the NW Atlantic (Greece, Brazil, and Turkey). Despite their non-negligible size, we can show that these rookeries provide at most (95% confidence limit) about one percent of the turtles in our focal mixed stocks. (Since Table 4 shows the partitioning among mixed stocks of the total contribution to NW Atlantic feeding habitats, it cannot provide this information).

The nesting colonies designated here as source populations represent most (but not all) of the known nesting effort in the Atlantic-Mediterranean system (Ehrhart et al. 2003; Margaritoulis et al. 2003). Important nesting effort occurs in Cuba, Cape Verde Islands, and along the coast of Africa, but could not be included for a variety of logistic reasons. Furthermore, additional nesting colonies may await discovery in undersurveyed regions. It is important to remember these limitations when formulating an interpretation of mixed stock analyses. However, more than 99% of the haplotypes observed in juvenile

Juvenile Loggerhead Homing

populations (excepting CC-A18, CCA-19, CCA-22, CCA-23; $n=4$) can be matched to haplotypes in nesting populations, providing at least a qualitative assurance that most of the genetic diversity is captured in the existing rookery samples.

DISCUSSION

Previous investigations have revealed that loggerhead turtles may cross entire ocean basins during their post-hatchling oceanic phase (Bowen et al. 1995, Bolten et al. 1998, Resendiz et al. 1998, Nichols et al. 2000, Alfaro-Shigueto et al. 2004). Juveniles from nesting beaches in the NW Atlantic inhabit oceanic zones around the Azores, Madeira, Grand Banks (Newfoundland, Canada), off the coast of Africa, and throughout the Mediterranean Sea (Bolten 2003a). Laurent et al. (1998) demonstrated that about half of the oceanic-stage juveniles in the Mediterranean originated on beaches of the western Atlantic. At the same time, the older neritic-stage turtles in the Mediterranean included little or no contribution from the western Atlantic (Laurent et al. 1998). In other words, by the time these Atlantic loggerheads switch from pelagic to neritic feeding, they have departed the Mediterranean and reappear in continental shelf habitats on the other side of the Atlantic. Notably, the switch from oceanic to neritic stages is not immutable, as both older juveniles and adults can return to oceanic habitats (Eckert and Martins 1989; Hatase et al. 2002b; Witzell 2002; Bolten 2003a).

Three analyses were conducted to test for population subdivisions and natal homing behavior in juvenile loggerhead turtles of the NW Atlantic: 1) an AMOVA for juvenile feeding populations ($\phi_{st} = 0.0088$; $P = 0.016$); 2) correlation statistics to compare genotype frequency differences in nesting populations versus adjacent feeding populations (Mantel $R^2 = 0.52$; $P = 0.001$), and 3) a mixed stock analysis using Bayesian methodology. All three approaches indicate a nonrandom distribution of juvenile turtles, and a significant relationship between nesting colonies and adjacent feeding populations. Collectively these analyses yield substantial evidence of natal homing in developmental migrations. Tagging studies, indicating high site fidelity in juvenile turtles on the Atlantic coast, indirectly support this conclusion (Avens et al. 2003; Hopkins-Murphy et al. 2003).

One caveat to these conclusions is that the correlation statistics are based on a subset of the entire data base, specifically the seven nesting locations along the continental coastline of the southeastern U.S. (Table 1), and their adjacent feeding populations (Table 2). A second caveat is that

Juvenile Loggerhead Homing

sampled individuals may have included a few small adults, and certainly includes a wide range of juvenile age classes, from new neritic-stage recruits to older turtles approaching maturity. A third qualification is that we have not sampled the entire range of feeding habitat in the NW Atlantic (see Engstrom et al. 2002). Given these limitations, we caution that the affinity described here between nesting colonies and adjacent juvenile feeding areas does not verifiably extend beyond the continental shelf of North America.

Population Structure and Life history implications

Subsequent to the oceanic juvenile stage, loggerhead turtles switch to primarily neritic, benthic foraging habitats. These neritic foraging habitats may be a great distance from the oceanic habitats, from Baja California to Japan, for example, or from the Azores to the eastern coast of North America. Whereas the migration to oceanic feeding areas is apparently facilitated by passive drift, the return trip may include active swimming. Once juveniles return to their region of origin and switch to benthic feeding, they may occasionally return to a pelagic feeding mode, as indicated by satellite telemetry, stable isotope ratios, and tag returns (Eckert and Martins 1989; Hatase et al. 2002b). Juvenile turtles make seasonal migrations into temperate habitats (such as the NE U.S. coast), and adults make reproductive migrations on the order of hundreds of kms (Limpus et al. 1992; Schroeder et al. 2003). We conclude that the complex life history of loggerhead turtles may include two homing migrations. The first is a migration from oceanic habitat (often thousands of kms from the nesting beach) to region of origin. The second is the cyclic reproductive migration from adult foraging habitat to courting grounds and nesting habitat.

Our analyses demonstrate that there is genetic structure among feeding ground populations and that this genetic structure is spatially correlated with the genetic structure of nesting populations. The technique that comes closest to answering our specific question -- how the contribution of rookeries to foraging grounds is partitioned -- results in wide confidence intervals, but with some consistent trends. First, there is little contribution from assayed nesting colonies outside the NW Atlantic (the parameter giving relative contributions from outside the NW Atlantic has a mean of 0.03, with an upper confidence limit of 0.11). Second, there are indications (supporting our simpler analyses of correlation in frequency of the dominant haplotype) of targeted contributions from rookeries to nearby feeding grounds, especially from south Florida rookery to foraging grounds in the Gulf of Mexico and from Atlantic rookeries (NEFL-NC) to Atlantic foraging habitat. However, no rookery-foraging ground pair actually shows significantly

Juvenile Loggerhead Homing

greater contributions than a proportional null model. Mixed stock analyses do not allow strong conclusions at this level of resolution. While this limitation can partly be overcome with more data, some of it is inherent in the overlap of haplotype profiles among rookeries and foraging grounds. We are working to incorporate spatial structure into the framework of mixed stock analysis, so that we can more powerfully test specific spatial hypotheses (Bolker et al. unpublished ms).

Marine turtles have complex population structure, with lower levels of population differentiation in nuclear DNA assays relative to mtDNA assays (Karl et al. 1992; FitzSimmons et al. 1996; 1997b; Pearce 2001; Roberts et al. 2004). Superimposed on this pattern are the life history stages of loggerhead turtles, with varying degrees of population structure. Oceanic juveniles are well mixed in the North Atlantic (Bolten et al. 1998; LaCasella et al. 2004; P. Dutton unpublished data); the neritic juveniles of the western Atlantic subsequently segregate at a low but significant level ($\phi_{st} = 0.0088$; $P = 0.016$); and corresponding nesting populations are highly structured ($\phi_{st} = 0.27$, $P < 0.001$ for the seven rookeries compared to adjacent feeding cohorts).

In this study we consider two primary influences on the distribution of neritic-stage juveniles: the size of source populations and proximity of juvenile feeding habitat to these source populations. However, additional factors are certainly to influence the distribution of juveniles. Hopkins-Murphy et al. (2003) demonstrate that larger juveniles dominate the feeding habitat in the eastern Gulf of Mexico (FL-NG and FL-SG), while smaller juveniles are more prevalent in the peripheral and seasonal habitats of the western Gulf of Mexico (TX) and the NE U.S. Analyses of haplotype distributions among size classes may prove fruitful in teasing apart these additional life-history components.

Notably, one life stage in North Atlantic loggerheads remains to be evaluated with mtDNA surveys: the adult feeding populations. Little is known about adult feeding habitats, but (for loggerheads nesting in the SE United States) they include sites along the east coast of the U.S., the Bahamas, Cuba, Gulf of Mexico, and Caribbean Mexico (Hopkins-Murphy et al. 2003; Schroeder et al. 2003). It will be informative to survey the adult cohorts and determine whether they also segregate on feeding grounds. It also would be informative to test the juvenile homing hypothesis in other regions (Mediterranean Sea, Japan), and in other sea turtle species.

Juvenile Loggerhead Homing

Conservation Implications

The finding of significant population structure in juvenile loggerhead turtles carries some implications for wildlife management. The hazards that impact breeding populations may also impact the next generation feeding in nearby waters. However, homing is not absolute and considerable movement occurs as well. The stranding data from Texas and the NE U.S., where nesting is sparse or absent, illustrate that feeding populations extend far past the regional nesting habitat (Figure 1). One consequence of this widespread foraging is that juvenile turtles originating in Yucatan Mexico are feeding in U.S. waters (Table 5). We suspect the converse is true (Table 4). This finding invokes provisions of the 1982 United Nations Convention on the Law of the Sea, in which nations that host the developmental habitat for migratory marine species hold fishing rights for these animals on the high seas (Van Dyke 1993). The 1983 U.N. Convention on the Conservation of Migratory Species (a.k.a. the Bonn Convention) prohibits taking endangered species during migrations on the high seas (Hykle 1992). Under the principles outlined in these international agreements, nations that host nesting and developmental habitats for marine turtles have some level of jurisdiction over these animals on geographically remote feeding grounds, even if those feeding grounds are within the territorial boundaries of another nation. Activities in U.S. waters can deplete an embattled rookery in Mexico, and activities in Mexico could impact threatened nesting populations in the southeastern U.S. Provisions of international law apply here.

ACKNOWLEDGEMENTS

This study was made possible by the outstanding contributions of J.C. Avise, D. Bagley, M. Camhi, R. Carthy, P. Castenada, C. Coogan, M. Duffy, K. Dwyer, L. Ehrhart, R. Ferris, L. Fisher, A. Foley, G. Garris, R. Herrera, S. Johnson, S.A. Karl, R. Klinger, R. LeRoux, L. Letson, G. Marcovaldi, M. Marcovaldi, D. Margaritoulis, R. Mezich, J. Richardson, N. Richardson, T. Richardson, B. Schroeder, S. Shea, G. Smith, J. Thome, B. Witherington, M. Zacks, and J. Zurita. For invaluable advice and assistance we thank E. Almira, D. Amorocho, R. Briseno-Duenas, M. Courtney, E. Ezcurra, N. FitzSimmons, J. Frazier, M. Harris, R. Marquez, H. Martins, C. Moritz, L. Ogren, F. Percival, S. Reynolds, S. Sadove, S. Shanker, M. Swingle, P. Taylor, C.J. Williams, Broward County Environmental Quality Control Board, Centro de Investigaciones El Colegio de la Frontera Sur (CIQRO; Mexico), The Conservancy, DNA Sequencing Core at University of Florida, Florida Dept. of Natural Resources, Florida Sea Turtle Stranding and Salvage Network, Florida Cooperative Fish and Wildlife Research Unit, Georgia Dept. of

Juvenile Loggerhead Homing

Natural Resources, Instituto Nacional de Pesca (Mexico), NOAA-Fisheries Molecular Genetics Laboratory, Projeto Tartaruga Marinha (TAMAR; Brazil), Sea Turtle Protection Society of Greece, South Carolina Dept. of Natural Resources, and the Virginia Marine Science Museum Foundation Stranding Program. We are indebted to R. Toonen for assistance with the statistical analyses, and to S. White for drafting the map. We thank L. Bernatchez and two anonymous reviewers for valuable advice and critique. Research was funded by the National Marine Fisheries Service, U.S. National Science Foundation, U.S. Fish and Wildlife Service, National Geographic Society, Turner Foundation, Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA), and private contributions.

REFERENCES

- Alfaro-Shigueto J, Dutton PH, Mangel J, Vega, D (2004) First confirmed occurrence of loggerhead turtles in Peru. *Marine Turtle Newsletter*, **103**, 7-11.
- Allard MW, Miyamoto MM, Bjorndal KA, Bolten AB, and Bowen BW (1994) Support for natal homing in green turtles from mitochondrial DNA sequences. *Copeia*, **1994**, 34-41.
- Avens L, Braun-McNeill J, Epperly S, Lohmann KJ (2003) Site fidelity and homing behavior in juvenile loggerhead sea turtles (*Caretta caretta*). *Marine Biology*, **143**, 211-220.
- Bass AL, Epperly SP and Braun-McNeill J (2004) Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. *Conservation Genetics*, In press
- Bjorndal KA, Bolten AB, Martins HR (2000) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Marine Ecology Progress Series*, **202**, 265-272.
- Bjorndal KA, Bolten AB, Dellinger T, Delgado C, Martins HR (2003) Compensatory growth in oceanic loggerhead sea turtles: response to a stochastic environment. *Ecology*, **84**, 1237-1249.
- Bolker B, Okuyama T, Bjorndal K, Bolten, A (2003) Sea turtle stock estimation using genetic markers: accounting for sampling error of rare genotypes. *Ecological Applications*, **13**, 763-775.
- Bolten AB (2003a) Active swimmers – passive drifters: the oceanic juvenile stage of loggerheads in the Atlantic system. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 63-78. Smithsonian Books, Washington, D.C.
- Bolten AB (2003b) Variation in sea turtle life history patterns: neritic versus oceanic developmental stages. In: *The Biology of Sea Turtles, Vol. 2* (eds. Lutz PL, Musick JA, Wyneken J) pp. 243-257. CRC Press, Boca Raton, FL.
- Bolten AB, Bjorndal KA, Martins HR, Dellinger T, Biscoito MJ, Encalada SE, Bowen BW (1998) Trans-Atlantic developmental migrations of loggerhead sea turtles demonstrated by mtDNA sequence analyses. *Ecological Applications*, **8**, 1-7.
- Bowen BW (1995) Tracking marine turtles with genetic markers: voyages of the ancient mariners. *BioScience*, **45**, 528-534.

Juvenile Loggerhead Homing

- Bowen BW (2003) What is a loggerhead turtle? The genetic perspective. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 7-27, Smithsonian Books, Washington, D.C.
- Bowen BW, Avise JC, Richardson JI, Meylan AB, Margaritoulis D, Hopkins-Murphy SR (1993) Population structure of loggerhead turtles (*Caretta caretta*) in the northwestern Atlantic Ocean and Mediterranean Sea. *Conservation Biology*, **7**, 834-844.
- Bowen BW, Kamezaki N, Limpus CJ, Hughes GH, Meylan AB, Avise JC (1994) Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. *Evolution*, **48**, 1820-1828.
- Bowen BW, Abreu-Grobois FA, Balazs GH, Kamezaki N, Limpus CJ, Ferl RJ (1995) Trans-Pacific migrations of the loggerhead sea turtle demonstrated with mitochondrial DNA markers. *Proceedings of the National Academy of Sciences, USA*, **92**, 3731-3734.
- Broderick D, Moritz C, Miller JD, Guinea M, Prince RJ, Limpus CJ (1994) Genetic studies of the hawksbill turtle: evidence for multiple stocks and mixed feeding grounds in Australian waters. *Pacific Conservation Biology*, **1**, 123-131.
- Carr A (1987) New perspectives on the pelagic stage of sea turtle development. *Conservation Biology*, **1**, 103-121.
- Casale P, Laurent L, Gerosa G, Argano R (2002) Molecular evidence of male-biased dispersal in loggerhead turtle juveniles. *Journal of Experimental Marine Biology and Ecology*, **267**, 139-145.
- Dodd CK Jr. (1988) Synopsis of the biological data on the loggerhead sea turtle *Caretta caretta* (Linnaeus, 1758). *United States Fish & Wildlife Service Biological Report*, **88**, 1-110.
- Dutton, PH, Balazs GH (1996) Simple biopsy technique for sampling skin for DNA analysis of sea turtles. In: *Proceedings of the Fifteenth Annual Symposium on Sea Turtle Biology and Conservation*. NOAA Technical Memorandum NMFS-SEFSC-38 (Compilers Keinath, JA, Barnard DE, Musick JA, Bell BA), pp. 78-79. National Technical Information Service, Springfield, Virginia.
- Eckert SA, Martins HR (1989) Transatlantic travel by a juvenile loggerhead turtle. *Marine Turtle Newsletter*, **45**, 15.
- Ehrhart LM, Bagley DA, Redfoot WE (2003) Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance, and population status. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 157-174. Smithsonian Books, Washington DC.
- Encalada SE, Bjorndal KA, Bolten AB, Zurita JC, Schroeder B, Possardt E, Sears CJ, Bowen BW (1998) Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean regions as inferred from mtDNA control region sequences. *Marine Biology*, **130**, 567-575.
- Engstrom TN, Meylan PA, Meylan, AB (2002) Origin of juvenile loggerhead turtles (*Caretta caretta*) in a tropical developmental habitat in Caribbean Panama. *Animal Conservation*, **5**, 125-133.
- Epifanio JM, Smouse PE, Kobak CJ, Brown BL (1995) Mitochondrial DNA divergence among populations of American shad (*Alosa sapidissima*): how much variation is enough for mixed stock analysis? *Canadian Journal of Fisheries and Aquatic Sciences*, **52**, 1688-1702.
- Epperly SP, Braun J, Veishlow A (1995) Sea turtles in North Carolina waters. *Conservation Biology*, **9**, 384-394.
- Epperly SP, Braun J, Chester AJ, Cross FA, Merriner JV, Tester PA, Churchill JH (1996) Beach strandings as an indicator of at-sea mortality of sea turtles. *Bulletin of Marine Science*, **59**, 289-297.

Juvenile Loggerhead Homing

- Excoffier L, Slatkin M (1995) Maximum likelihood estimation of molecular haplotype frequencies in a diploid population. *Molecular Biology and Evolution*, **12**, 921-927.
- FitzSimmons NN, Moritz C, Limpus CJ, Miller JD, Parmenter CJ, Prince R (1996) Comparative genetic structure of green, loggerhead, and flatback populations in Australia based on variable mtDNA and nDNA regions. In: *Proceedings of the International Symposium on Sea Turtle Conservation Genetics*. NOAA Technical Memo. NMFS-SEFSC-396 (eds. Bowen BW, Witzell WN), pp. 25-32. National Technical Information Service, Springfield, Virginia.
- FitzSimmons NN, Limpus CJ, Moritz C (1997a) Philopatry of male marine turtles inferred from mitochondrial DNA markers. *Proceedings of the National Academy of Sciences USA*, **94**, 8912-8917.
- FitzSimmons, NN, Moritz C, Limpus CJ, Pope L, Prince R (1997b) Geographic structure of mitochondrial and nuclear gene polymorphisms in Australian green turtle populations and male-biased gene flow. *Genetics*, **147**, 1843-1854.
- FitzSimmons NN, Moritz C, Bowen BW (1999) Population identification. In: *Research and Management Techniques for the Conservation of Sea Turtles* (eds Eckert KL, Bjorndal KA, Abreu-Grobois FA, Donnelly M), pp 72- 79. IUCN/SSC Marine Turtle Specialist Group Publication No. 4.
- Grant, WS, Milner GB, Krasnowski P, Utter FM (1980) Use of biochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 1236-1247.
- Hatase, H, Kinoshita M, Bando T, Kamezaki N, Sato K, Matsuzawa Y, Goto K, Omuta K, Nakashima Y, Takeshita H, Sakamoto W (2002a) Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: bottlenecks on the Pacific population. *Marine Biology*, **141**, 299-305.
- Hatase, H, Takai N, Matsuzawa Y, Sakamoto W, Omuta K, Goto K, Arai N, Fujiwara T (2002b) Size-related differences in feeding habitat use of adult female loggerhead turtles *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. *Marine Ecology Progress Series*, **233**, 273-281.
- Hillis DM, Mable BK, Larson A, Davis SK, Zimmer EA (1996) Nucleic Acids. IV. Sequencing and cloning. In: *Molecular Systematics*, 2nd edn. (eds. Hillis DM, Mable BK, Moritz C), pp. 321-384. Sinauer Associates, Sunderland, Massachusetts.
- Hopkins-Murphy SR, Owens DW, Murphy TM (2003) Ecology of immature loggerheads on foraging grounds and adults in interesting habitat in the eastern United States. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 79-92. Smithsonian Books, Washington, D.C.
- Hykle DJ (1992) The migratory species (Bonn) convention and marine turtle conservation. In: *Proceedings of the Eleventh Annual Workshop on Sea Turtle Biology and Conservation*. NOAA Technical Memo NMFS-SEFC-302 (Compilers Salmon M, Wyneken J), pp. 61-63. National Technical Information Service, Springfield Virginia.
- Karl SA, Bowen BW, Avise JC (1992) Global population structure and male-mediated gene flow in the green turtle (*Chelonia mydas*): RFLP analysis of anonymous nuclear DNA regions. *Genetics*, **131**, 163-173.
- LaCasella EL, Dutton PH, Epperly SP (2004) Genetic stock composition of loggerheads (*Caretta caretta*) encountered in the northeast Atlantic distant (NED) longline fishery using mtDNA analysis. NOAA-NMFS-SEFSC Tech Memo. *In press*
- Laurent L, Casale P, Bradai MN, Godley BJ, Gerosa G, Broderick AC, Schroth W, Schierwater B, Levy AM, Freggi D, Abd El-Mawla EM, Hadoud DA, Gomati HE, Domingo M, Hadjichristophorou M,

Juvenile Loggerhead Homing

- Kornaraky L, Demirayak F, Gautier C (1998) Molecular resolution of the marine turtle stock composition in fishery bycatch: a case study in the Mediterranean. *Molecular Ecology*, **7**, 1529-1542.
- Limpus CJ, Miller JD, Parmenter CJ, Reimer D, McLachlan N, Webb R (1992) Migration of green (*Chelonia mydas*) and loggerhead (*Caretta caretta*) turtles to and from eastern Australian rookeries. *Wildlife Research*, **19**, 347-358.
- Mullis KB, Faloona F (1987) Specific synthesis of DNA in vitro via a polymerase-catalyzed chain reaction. *Methods in Enzymology*, **155**, 335-350.
- Margaritoulis D, Argano R, Baran I, Bentivegna F, Bradai MN, Camiñas JA, Casale P, De Metrio G, Demetropoulos A, Gerosa G, Godley BJ, Haddoud DA, Houghton J, Laurent L, Lazar B. (2003) Loggerhead turtles in the Mediterranean Sea: present knowledge and conservation perspectives. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 175-198. Smithsonian Books, Washington DC.
- Nei M (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York.
- Nichols WJ, Resendiz A, Seminoff JA, Resendiz B (2000) TransPacific migration of a loggerhead turtle monitored by satellite telemetry. *Bulletin Marine Science*, **67**, 937-947.
- Norrgard JW, Graves JE (1996) Determination of the natal origin of a juvenile loggerhead turtle (*Caretta caretta*) population in Chesapeake Bay using mitochondrial DNA analysis. In: *Proceedings of the International Symposium on Sea turtle Conservation Genetics*. NOAA Technical Memo NMFS-SEFSC-396 (eds. Bowen BW, Witzell WN), pp.129-138. National Technical Information Service, Springfield, Virginia.
- Norman JA, Moritz C, Limpus CJ (1994) Mitochondrial DNA control region polymorphisms: genetic markers for ecological studies of marine turtles. *Molecular Ecology*, **3**, 363-373.
- Okuyama T, Bolker BM (2004) Combining genetic and ecological data to estimate sea turtle origins. *Ecological Applications*, In press.
- Owens DW, Ruiz GW (1980) New methods of obtaining blood and cerebrospinal fluid from marine turtles. *Herpetologica*, **36**, 17-20.
- Pearce AF (2001) Contrasting population structure of the loggerhead turtle (*Caretta caretta*) using mitochondrial and nuclear DNA markers. M.S. Thesis, University of Florida, Gainesville, 71 pp.
- Pella J, Masuda M (2001) Bayesian methods for analysis of stock mixtures from genetic characters. *Fishery Bulletin*, **99**, 151-167.
- Rankin-Baransky K, Williams CJ, Bass AL, Bowen BW, Spotila JR (2001) Origin of loggerhead turtle (*Caretta caretta*) strandings in the northwest Atlantic as determined by mtDNA analysis. *Journal of Herpetology*, **35**, 638-646.
- Resendiz A, Resendiz B, Nichols WJ, Seminoff JA, Kamezaki N (1998) First confirmed East-West trans-Pacific movement of a loggerhead turtle (*Caretta caretta*), released in Baja California, Mexico. *Pacific Science*, **52**, 151-153.
- Roberts MA, Schwartz TS, Karl SA (2004) Global population structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): analysis of microsatellite loci. *Genetics*, **166**, 1857-1870.
- Schneider S, Roessli D, Excoffier L (2000) *ARLEQUIN, Version 2.0: a Software for Population Genetics Data Analysis*. Genetics and Biometry Laboratory, University of Geneva. Switzerland.

Juvenile Loggerhead Homing

- Schroeder BA, Foley AM, Bagley DA (2003) Nesting patterns, reproductive migrations, and adult foraging areas of loggerhead turtles. In: *Loggerhead Sea Turtles* (eds. Bolten AB, Witherington BE), pp. 114-124. Smithsonian Books, Washington DC.
- Seutin G, White BN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analysis. *Canadian Journal of Zoology*, **69**, 82-90.
- Smouse PE, Long JC, Soka RR (1986) Multiple regression and correlation extensions of the mantel test of matrix correspondence. *Systematic Zoology*, **35**, 627-632.
- Tamura K, Nei M (1993) Estimation of the number of substitutions in the control region of mitochondrial DNA in humans and chimpanzees. *Molecular Biology and Evolution*, **10**, 512-526.
- Van Dyke JM (1993) International governance and stewardship of the high seas and its resources. In: *Freedom for the Seas in the 21st Century: Ocean Governance and Environmental Harmony* (eds. Van Dyke JM, Zaelke D, Hewison G), pp. 13-20. Island Press, Washington D.C.
- Wirgin II, Waldman JR, Maceda L, Stabile J, Vecchio VJ (1997) Mixed stock analysis of Atlantic coast striped bass (*Morone saxatilis*) using nuclear DNA and mitochondrial DNA markers. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2814-2826.
- Witzell WN (2002) Immature Atlantic loggerhead turtles (*Caretta caretta*): suggested changes to the life history model. *Herpetological Review*, **33**, 266-269.
- Witzell WN, Bass AL, Bresette MJ, Singewald DA, Gorham JC (2002) Origin of immature loggerhead turtles (*Caretta caretta*) from Hutchinson island, Florida: Evidence from mtDNA markers. *Fishery Bulletin*, **100**, 624-631.

Juvenile Loggerhead Homing

Table 1. **Nesting (source) populations in the Atlantic and Mediterranean**, as described in Laurent et al. (1998), Pearce (2001) with additional specimens from Encalada et al. (1998). Haplotypes described previously as "A" through "Q" have been renamed CC-A1 to CC-A17. Full sequences and haplotype designations are available at <http://accstr.ufl.edu/ccmtdna.html>. Abbreviations: FL-NG = Florida Peninsula, northern Gulf of Mexico; FL-SG = Florida Peninsula, southern Gulf of Mexico; FL-SA = Florida Peninsula, southern Atlantic coast; FL-NA = Florida Peninsula, northern Atlantic coast (Amelia Island and Jacksonville County); GA= Georgia; SC=South Carolina; NC=North Carolina; DT = Dry Tortugas; MX = Quintana Roo, Mexico; BR = Bahia, Brazil; GR = Kiparissia Bay, Greece and adjacent regions; TR = Turkey.

	FL-NG	FL-SG	FL-SA	FL-NA	GA	SC	NC	DT	MX	BR	GR	TR
CC-A1	38	20	32	14	42	20	28	4				
CC-A2	7	17	28		1			50	11		78	19
CC-A3	2	4							2			13
CC-A4										11		
CC-A5			1									
CC-A6											2	
CC-A7	2	2	1									
CC-A8									1			
CC-A9								2	1			
CC-A10								2	5		1	
CC-A11			1									
CC-A13												
CC-A14		1	1									
CC-A20		1										
Total	49	45	64	14	43	20	28	58	20	11	81	32

Juvenile Loggerhead Homing

Table 2. **Juvenile Feeding Populations**, from biopsies in North Carolina, power plant entrainment (n=106) and strandings on the coast of southern Florida, and strandings from everywhere else, as described in Rankin-Baransky et al. 2001, and Witzell et al. 2002. Full sequence descriptions are available from <http://accstr.ufl.edu/ccmdna.html>. Abbreviations: TX = Texas; FL-NG = Florida Peninsula, northern Gulf of Mexico; FL-SG = Florida Peninsula, southern Gulf of Mexico; FL-SA = Florida Peninsula, southern Atlantic coast; FL-NA = Florida Peninsula, northern Atlantic coast; GA = Georgia; SC = South Carolina; NC = North Carolina; VA = Virginia; NE U.S. = Northeast U.S. including Maryland, Delaware, New Jersey, New York, and Massachusetts.

HAPS	TX	FL-NG	FL-SG	FL-SA	FL-NA	GA	SC	NC	VA	NE U.S.
CC-A1	67	10	14	59	37	107	49	166	143	90
CC-A2	53	6	21	58	28	68	32	98	91	53
CC-A3	10	1	5	10	1	10	5	8	4	9
CC-A4								1		
CC-A5						2	1	3	1	1
CC-A6										
CC-A7	4			2		3	2	5	4	1
CC-A8		1		1			1	1		
CC-A9				4	1			1		
CC-A10	2		1	2		2	2	4	3	4
CC-A11				1		1				
CC-A13	1		2	1		2		1	2	
CC-A14	5			6	1	10	3	7	4	3
CC-A18								1		
CC-A19						1				
CC-A20			2	2	1	1			4	
CC-A22						1				
CC-A23						1				
TOTAL	142	18	45	146	69	209	95	296	256	161

Juvenile Loggerhead Homing

Table 3. **Feeding habitat diversity estimates**, including haplotype diversity (h) and nucleotide diversity (π). Abbreviations are explained in the legend to Table 1 and 2.

	HAP. DIV.	NUC. DIV.
TX	0.635 \pm 0.025	0.02442 \pm 0.01247
FL-NG	0.608 \pm 0.086	0.02475 \pm 0.01330
FL-SG	0.684 \pm 0.048	0.02214 \pm 0.01159
FL-SA	0.676 \pm 0.024	0.02492 \pm 0.01273
FL-NA	0.555 \pm 0.032	0.02380 \pm 0.01227
GA	0.630 \pm 0.024	0.02451 \pm 0.01251
SC	0.622 \pm 0.035	0.02414 \pm 0.01238
NC	0.576 \pm 0.021	0.02337 \pm 0.01193
VA	0.563 \pm 0.020	0.02339 \pm 0.01194
NE U.S.	0.579 \pm 0.028	0.02355 \pm 0.01205

Juvenile Loggerhead Homing

Table 4. **Results of mixed stock analysis:** proportions from each rookery contributed to specified feeding grounds. Abbreviations: FL-NG, northwest Florida; SFL, South Florida; NEFL-NC, northeast Florida to North Carolina; DT, Dry Tortugas; MX, Mexico; BR, Brazil; GR, Greece; TR, Turkey.

Rookery	FG	Mean	sd	2.50%	Median	97.50%
FL-NG	North	0.6202	0.1449	0.3209	0.6302	0.8707
	South	0.08726	0.07969	0.002518	0.06432	0.2973
	Gulf	0.2926	0.1376	0.07244	0.2769	0.5909
SFL	North	0.6058	0.1203	0.3674	0.6105	0.8255
	South	0.0555	0.03944	0.01028	0.04559	0.1596
	Gulf	0.3387	0.118	0.129	0.3322	0.578
MX	North	0.4828	0.1223	0.2498	0.4827	0.7207
	South	0.2091	0.1019	0.05463	0.1943	0.4441
	Gulf	0.3081	0.1148	0.1127	0.3001	0.5535
NEFL-NC	North	0.7514	0.1114	0.498	0.7653	0.9262
	South	0.02831	0.0299	7.40E-04	0.01916	0.1077
	Gulf	0.2203	0.1095	0.05372	0.205	0.4723
DT	North	0.5988	0.1463	0.3026	0.6049	0.8596
	South	0.1032	0.09249	0.002652	0.07686	0.3451
	Gulf	0.298	0.1368	0.07421	0.284	0.5925
GR	North	0.5985	0.1477	0.2962	0.6051	0.8621
	South	0.09958	0.08974	0.002792	0.07463	0.3336
	Gulf	0.3019	0.1386	0.07637	0.2885	0.603
BR	North	0.6071	0.1464	0.3076	0.6147	0.8666
	South	0.08453	0.08125	0.002017	0.05967	0.3047
	Gulf	0.3083	0.1399	0.07803	0.2952	0.6105
TR	North	0.5934	0.1484	0.2947	0.5998	0.8611
	South	0.1009	0.09136	0.002971	0.07512	0.3409
	Gulf	0.3057	0.139	0.07793	0.2921	0.6066

Juvenile Loggerhead Homing

Table 5. **Results of mixed stock analysis:** proportions of each feeding ground contributed by specified rookeries. NEFL-NC is a category combining nesting beaches from Northeast Florida, Georgia, South Carolina, and North Carolina. Other abbreviations are described in the legends to Tables 1-4.

FG	Rookery	Mean	sd	2.50%	Median	97.50%
NORTH	FL-NG	0.008292	0.002842	0.003652	0.00797	0.0148
	SFL	0.8645	0.03129	0.7909	0.8687	0.9139
	MX	0.01947	0.006148	0.009428	0.01882	0.03353
	NEFL-NC	0.1018	0.02579	0.0592	0.0989	0.1614
	DT	0.002898	0.00101	0.001259	0.00279	0.005179
	GR	0.001555	0.00155	7.91E-05	0.001094	0.005711
	BR	9.80E-04	8.82E-04	5.57E-05	7.34E-04	0.003294
	TR	5.70E-04	5.54E-04	3.11E-05	4.11E-04	0.002044
SOUTH	FL-NG	0.01674	0.01959	3.61E-04	0.01038	0.07155
	SFL	0.8215	0.07938	0.6262	0.8352	0.9367
	MX	0.103	0.04618	0.03393	0.09557	0.2122
	NEFL-NC	0.0442	0.03909	0.001333	0.03336	0.1458
	DT	0.007729	0.01019	1.31E-04	0.004337	0.03522
	GR	0.003635	0.00636	2.71E-05	0.001512	0.02036
	BR	0.001733	0.002521	1.51E-05	8.27E-04	0.008925
	TR	0.001478	0.002754	9.97E-06	5.64E-04	0.008591
GULF	FL-NG	0.008005	0.005311	0.001609	0.00677	0.02194
	SFL	0.9022	0.04311	0.7959	0.9104	0.9611
	MX	0.02521	0.0133	0.007518	0.02252	0.05865
	NEFL-NC	0.05827	0.03239	0.01363	0.05253	0.1372
	DT	0.002963	0.001972	5.90E-04	0.002512	0.007989
	GR	0.00165	0.002143	5.66E-05	9.87E-04	0.007048
	BR	0.001119	0.001428	3.48E-05	6.51E-04	0.005034
	TR	6.29E-04	8.21E-04	2.08E-05	3.76E-04	0.002792

Juvenile Loggerhead Homing



Figure 1: Map indicating the location of sampled rookeries and foraging grounds in North America. For abbreviations see Tables 1 and 2. Divisions between FL-NA and FL-SA and between FL-NG and FL-SG are indicated by dark bars at Cape Canaveral and Tampa Bay, respectively.

Juvenile Loggerhead Homing

Figure 2. Relationship between genotype frequency of haplotype CC-A1 in seven juvenile feeding areas and seven adjacent nesting beaches. The resulting correlation ($R^2 = 0.88$) is significant at $P = 0.049$.

