CONSERVATION IMPLICATIONS

OF COMPLEX POPULATION STRUCTURE

IN THE LOGGERHEAD TURTLE (*CARETTA CARETTA*)

FINAL REPORT TO THE SEATHEAST FISHERIES SCIENCE CENTER

REQUISITION NFFN7020-4-00050

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SEPTEMBER 15, 2004

ABSTRACT

Complex population structure can result from sex-biased gene flow, or from populations overlap during migrations. Loggerhead turtles (*Caretta* caretta) have both traits, providing an instructive case history for wildlife management. Based on surveys of maternally-inherited mtDNA, post-hatchlings in oceanic habitats of the North Atlantic show no population structure between eastern and western Atlantic ($\phi_{st} < 0.001$; $P = 0.919$), subadult cohorts in coastal habitat show low but significant population structure among locations ($\phi_{st} = 0.01$, $P < 0.005$), and nesting colonies along the southeast coast of the United States have strong population structure ($\phi_{st} = 0.42$, $P < 0.001$). Thus the level of population structure increases through progressive life history stages. In contrast, a survey of (biparentally inherited) microsatellite DNA show no significant population structure ($R_{st} < 0.005$) across the same nesting colonies. These results indicate that loggerhead females home faithfully to their natal nesting colony, but males provide an avenue of gene flow between regional nesting colonies, probably via opportunistic mating in migratory corridors. As a result, all breeding populations have similar levels of microsatellite diversity ($H_e = 0.785 – 0.815$), alleviating concerns about inbreeding and loss of genetic diversity in the smaller rookeries. Under a conventional interpretation of the nuclear DNA data, the entire southeast U.S. would be regarded as a single management unit, yet the mtDNA data indicates multiple isolated populations. As a consequence of this complex population structure, each life stage requires a different management strategy. Perturbations to pelagic juveniles will have a diffuse impact on West Atlantic nesting colonies, mortality of subadults will have a more

focused impact on nearby breeding populations, and disturbances to adults will have pinpoint impact on corresponding breeding populations.

INTRODUCTION

Population resolution is a cornerstone of species management. Isolated populations (or management units, MUs; Moritz 1994) are typically characterized by differences in key demographic features, including age structure, survivorship, fecundity, and sex ratio. These populations will prosper or perish without significant input from other populations, providing a compelling mandate for an independent management program. Such populations are also the potential wellsprings of future biodiversity (Bowen 1998).

Prior to the availability of genetic assays, population resolution was accomplished primarily with mark/recapture studies, direct observation, or geographic inference. Allozyme and mtDNA assays provided more efficient means to resolve populations, but always with a gap between population structure in the genetic sense (which requires fewer than four effective migrants per generation) and population structure in the management sense (which can allow dozens of migrants without compromising demographic independence). Microsatellite surveys are beginning to close this gap, as multilocus assignment tests can resolve population members even under conditions of moderate gene flow (Rannala & Mountain 1997; Cornuet et al. 1999; Goudet et al. 2002).

In migratory animals, the resolution of populations can be confounded by two factors:

1) Geographic overlap, in which demographically-independent populations mingle at feeding habitats or during migratory phases. Examples of population overlap can be found in migratory birds (Wenink and Baker 1996; Wennerberg 2001),

fishes (Grant et al. 1980; Wirgin et al. 1997), mammals (Baker et al. 1994; 1998), and reptiles (Bowen et al. 1996; Bolten et al. 1998). A critical question in these cases is whether populations exchange gametes during intervals of population overlap.

2) Sex-biased dispersal, in which gene flow between populations is accomplished primarily by one gender. For many mammals and birds, males disperse prior to reproduction, while females are philopatric to natal area (Greenwood 1980). In plant species, male dispersal via pollen far exceeds the relatively sedentary movements of seeds (Ennos 1994; Oddou-Muratorio et al. 2001). For the purposes of this paper, it is important to note that genetic exchange does not require dispersal of individuals between populations, but can occur when migratory populations come into contact.

Cases of population overlap and sex-biased dispersal abound, and collectively may encompass a majority of migratory species. From a wildlife management perspective, stock integrity can ebb and flow on a seasonal basis, or at different life-history stages. The philopatry of females can be countered by opportunistic mating by males, so that each gender yields a different measure of genetic isolation. This is known as complex population structure (Bowen 1997), and the corresponding management implications have seldom been addressed.

In the last two decades, gender-specific genetic markers have been profitably applied to resolve sex-specific dispersal (Mossman and Wassner 1999). In pine trees, for example, the mitochondrial genome is maternally inherited (through seeds), the chloroplast genome is paternally inherited (through pollen), and the nuclear genome has

the usual biparental (diploid) inheritance (Mogensen 1996). In bivalves of the genus *Mytilus*, males and females maintain distinct mtDNA lineages that are highly divergent (Stewart et al. 1995). Genomes with different inheritance pathways will have different responses to dispersal, selection, lineage sorting, population crashes, and isolation events. Therefore each class of markers can provide unique insights. For example, male dispersal will be recorded in surveys of the sex (Y) chromosome of mammals, but will have no impact on the genetic architecture registered in maternally inherited mtDNA. For this reason, the Y chromosome has proven useful for tracking male-mediated dispersals for *Homo sapiens* (Zegura et al. 2004), while mtDNA has illuminated female dispersal (Bonatto and Salzano 1997).

Loggerhead turtles (*Caretta caretta*) have both population overlap and sex-biased dispersal, and therefore may be especially useful for dissecting the conservation implications of complex population structure. This migratory marine reptile has 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 northwestern Atlantic, this oceanic habitat extends from the Grand Banks (Newfoundland, Canada) to the Azores and Madeira, as well as the Mediterranean Sea (Bolten et al. 1998; Laurent et al. 1998; LaCasella et al. 2004). Older juveniles return to the shallow coastal waters of the western Atlantic, where they switch to benthic feeding and consume hard-shelled invertebrates (Bolten 2003b; Hopkins-Murphy et al. 2003). Upon reaching sexual maturity, female loggerheads make cyclic 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).

In order to resolve the conservation implications of complex population structure, here we assemble loggerhead genetic data from three previously published surveys of North Atlantic populations, and an unpublished thesis. These studies include mtDNA data for oceanic juveniles (N = 455; Bolten et al. 1998, LaCasella et al. 2004), coastal subadults (N = 1437; Bowen et al. 2004), nesting females (N = 514; Encalada et al. 1998; Bowen et al. 2004), and nuclear DNA data (microsatellite loci) for nesting females (N = 463; Pearce 2001).

METHODS

Sample collections were made in the interval 1989-2003. The nesting populations that are the primary focus of this study are located in the southeast U.S. from North Carolina to the northern Gulf of Mexico (Fig. 1) plus an "outgroup population" in Bahia, Brazil. Prior to the advent of polymerase chain reaction methodology, samples from the nesting beaches consisted of whole eggs and moribund hatchlings. Subsequently, specimens from nesting beaches and feeding areas were collected as small blood aliquots (usually less than one ml) or tissue biopsy plugs. Rookery sample sizes and location data are summarized in Table 1.

Rookery sample sizes range from N = 11 for the mtDNA survey of Bahia, Brazil, to N = 123 for the microsatellite survey of southeastern Florida (Table 1). Details of the sample collections and mtDNA analyses are available in Bowen et al. (1993, 1994, 2004) and Encalada et al. (1998). Corresponding information for feeding populations is available in Bolten et al. (1998), Bowen et al. (2004), and LaCasella et al. (2004).

In brief, a 391 base-pair (bp) fragment located in the control region of the mitochondrial genome was amplified with polymerase chain reaction (PCR) methodology using primers described by Allard et al. (1994) and Norman et al. (1994; Table 2). Resulting sequences 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 rookery locations (Table 1) include the same groupings as in the mtDNA survey (Bowen et al. 2004) with two modifications: 1) The Georgia nesting colony is grouped with Jacksonville County in the northeastern corner of Florida. With the exception of one individual, these two adjacent locations have the same haplotype at 100% frequency. 2) The nesting population in Volusia County, Florida (Vo-FL in Fig. 1) is added as a distinct category. Previously there has been some question about whether this area comprises a distinct management unit, or whether it represents an area of overlap between nesting colonies to the north and south (Encalada et al. 1998). These two modifications make the groupings for mtDNA analysis concordant with the groupings for microsatellite analysis.

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 estimate haplotype diversity and nucleotide diversity (Nei 1987; Excoffier & Slatkin 1995). In all tests that required estimates of sequence divergence, we used the Tamura-Nei model of nucleotide substitutions which was designed for control region sequences (Tamura and Nei 1993).

The microsatellite data include two loci developed by FitzSimmons (1998; CC7 and CC141), one locus developed by Moore (2000; CC7), and one locus developed for leatherback turtles (DC107; P. Dutton, pers comm.). One additional locus was developed specifically for this microsatellite study (CCM2), and details of the lab procedures are available in Pearce (2001; Table 2). In brief, genomic DNA was digested with *Sau*3AI and resulting fragments were separated on a 1.2% agarose gel. Fragments in the size range of 400-1500 bp were ligated to *Sau*3AI linkers and purified with a QIAquick Gel Extraction Kit (Qiagen Corp, Valencia, CA). Fragments containing microsatellite loci were identified by hybridization with biotinylated probes containing a CA_{15} repeat. Enriched DNA fragments were amplified with Sau3AI primer and cloned with the TOPO-TA cloning kit (Invitrogen, Carlsbad, CA). Clones were screened again by hybridization with a CA probe. Plasmids that tested positive for CA repeats were sequenced, and primers were designed for flanking regions with the software package Oligo Primer Analysis (Molecular Biology Insights, Cascade, CO).

Polymerase chain reactions for the microsatellites included an initial denaturation step at 93 °C for three min, followed by six cycles of denaturation at 92 °C for 30s, annealing at 55-60 °C for 55s (see Table 2 for primer-specific annealing temperatures), and extension at 72 °C for 1 min 25 s, followed by 30 cycles of denaturation at 89 °C for 30s, annealing at 2 °C lower than previous cycle for that primer pair, and extension at 72 °C for one min 25 s, finishing with extension at 72 °C for 10 min.

GENEPOP vers. 3.1 was used to conduct an exact test for Hardy-Weinberg equilibrium at each locus (Raymond and Rousset 1995). Tests for population subdivision were made with both the infinite allele model, using F_{st} as implemented in

Arlequin vers. 2.0, and the stepwise mutation model, using R_{st} as implemented in RstCALC (Slatkin 1995, Goodman 1997). Significance of F statistics was evaluated with a randomized distribution of outcomes based on 1000 permutations.

RESULTS

Most of the mtDNA results are previously published or in press, and details are available in Bowen et al. (1993, 1994, 2004), Encalada et al. (1998), and Bolten et al. (1998). Haplotype and nuclear DNA diversities are detailed in Table 3 and Table 4.

There are 24 mtDNA haplotypes identified from feeding and nesting habitats of the Atlantic, and their distribution indicates three levels of population structure, corresponding to three life-history stages (Fig. 2). First, the pelagic juvenile populations that inhabit the eastern Atlantic (Azores and Madeira, N = 131) and western Atlantic (Grand Banks, N = 324) are not significantly different ($\phi_{st} < 0.001$; $P = 0.919$), based on our reanalysis of the data in Bolten et al. (1998) and LaCasella et al. (2004). Second, the subadults that feed along the coast of North America (N = 1437) have low but significant population structure ($\phi_{st} = 0.0088$, $P = 0.016$). Third, the nesting colonies of the West Atlantic are highly structured, with $\phi_{st} = 0.428$ ($P < 0.001$) for the nine sample locations in Table 1, or $\phi_{st} = 0.420$ ($P < 0.001$) for the eight locations in the southeastern U.S.

Volusia County, the area of possible overlap between nesting colonies to the north and south, has a highly significant difference from Georgia and northeast Florida ($\phi_{st} = 0.306$; $P < 0.001$), but is not significantly different from the rookery to the south ($\phi_{st} = 0.014$; $P = 0.178$).

The microsatellite data are from an unpublished thesis (Pearce 2001). To develop additional microsatellite loci for loggerhead turtles, 25 clones were sequenced,

and 10 of these had both the repeat sequence and sufficient flanking region for primer design. Nine of these 10 candidates proved to be either monomorphic in initial screening, or would not amplify consistently (Pearce 2001). Hence one new locus was developed (CCM2) and analyzed along with four previously characterized loci (Table 2; DC107, Ccar176, CC141, and CC7; FitzSimmons 1998; Moore 2000; P. Dutton pers. comm.).

All five loci showed high levels of polymorphism with 10-29 alleles (Table 4), and mean gene diversities per location ranging from H_e = 0.685 (Bahia) to H_e = 0.815 (Georgia). Observed heterozygosities per locus were also high, ranging from H_o = 0.568 (CC7 in Bahia) to H_o = 0.923 (Ccar176 in North Carolina) (Table 3). All alleles were distinguished by increments of 2 bp, in keeping with the CA motif of the five loci. Departures from Hardy-Weinberg equilibrium were detected in three of forty five tests, an outcome that was not significant in an exact test (P = 0.31).

Population subdivisions based on R_{st} values were not significant for any of the pairwise comparisons across the eight nesting populations in the southeast U.S., but six of the eight comparisons to Brazil were significant (Table 5). This contrasts sharply with the mtDNA surveys across the same nine locations, in which 29 of 36 pairwise comparisons were significant (Table 5). For the entire data set, R_{st} = 0.0055 ($P < 0.05$) and F_{st} = 0.0189 ($P < 0.05$) compared to mtDNA ϕ_{st} = 0.428 ($P < 0.001$). For the southeastern U.S., R_{st} < 0.001 (N.S.) compared to mtDNA ϕ_{st} = 0.420 ($P < 0.001$).

DISCUSSION

Migratory marine animals often have complex population structure, in which populations overlap during migrations, or sex-biased dispersal is detected. In global surveys of the sperm whale (*Physeter macrocephalus*), significant population structure is recorded in mtDNA sequence comparisons (G_{st} = 0.03, P < 0.001; Lyrholm and Gyllensten 1998), but not in microsatellite (nuclear DNA) comparisons (G_{st} = 0.001, P = 0.232; Lyrholm et al. 1999). A similar pattern is apparent in humpback whales (*Megaptera novaengliae*; Baker et. al. 1994; 1998; Palumbi and Baker 1994), bottlenose dolphins (*Terciops aduncus*; Möller and Beheregaray 2004), and Dall's porpoises (*Phocoenoides dalli*; Escorza-Trevino & Dizon 2000). In a multilocus survey of the white shark (*Carcharodon carcharias*), the mtDNA data indicated strong population structure (F_{st} = 0.81 between South African and Australia) while a microsatellite survey reveals no significant structure (Pardini et al. 2001). In these cases, male-mediated gene flow can readily explain the lower population structure registered in the nuclear genome relative to the mitochondrial genome.

In the first global genetic survey of a sea turtle (green turtle; *Chelonia mydas*), Karl et al. (1992) reported low population structure in single copy nuclear DNA (Atlantic F_{st} = 0.130, Indo-Pacific F_{st} = 0.126), relative to a parallel survey of mtDNA (Atlantic G_{st} = 0.63, Indo-Pacific G_{st} = 0.71; Bowen et al. 1992). This finding is confirmed with microsatellite assays across the same range (Atlantic F_{st} = 0.038, Indo-Pacific F_{st} = 0.024; Roberts et al. 2004). The conclusion of male mediated gene flow in *Chelonia mydas* is supported by comparative surveys of mtDNA and microsatellites in the West Pacific and Indian Ocean (FitzSimmons et al. 1997b). This case is especially notable

because males still show philopatry to breeding areas adjacent to the nesting habitat (FitzSimmons et al. 1997a).

In every case that has been resolved to date, sea turtles register lower population genetic structure in nuclear DNA assays relative to mtDNA (FitzSimmons 1996, Schroth et al. 1996, Pearce 2001). This trend reaches an extreme in the comparison of loggerhead nesting colonies of the northwestern Atlantic: population structure is high in mtDNA assays (F_{st} = 0.42, P < 0.001) and effectively absent in microsatellite assays (R_{st} < 0.001).

Loggerhead Life History and Population Genetics

Hatchling loggerhead turtles leave the nesting beaches of the NW Atlantic and subsequently occupy oceanic (pelagic) habitats in the NW Atlantic, NE Atlantic, and Mediterranean. These juvenile populations are well mixed, with no significant differences in haplotype composition between the western Atlantic (Grand Banks; LaCasale et al. 2004) and the eastern Atlantic (Azores and Madiera; Bolten et al. 1998) (ϕ_{st} < 0.001). Contributions to these juvenile populations are roughly proportional to the size of source (nesting) populations (Bolten et al. 1998; LaCasale et al. 2004)

After about a decade of this oceanic phase (Bjorndal et al. 2000), larger juvenile turtles switch to shallow (neritic) habitats along the continental coastline of North America (although this switch is not immutable, as subadults and adults can switch back to pelagic feeding; Witzell 2002; Hatase et al. 2002a). Hence the transition from juvenile to subadult phases can involve an trans-oceanic migration (Bowen et al. 1995), and recruitment to the same coastline that hosts the familial nesting beaches (Bolten 2003b). At this stage, subadult turtles are not uniformly distributed along the eastern

coast of North America (ϕ_{st} = 0.01, P< 0.005), and haplotype frequency differences are significantly correlated between coastal feeding populations and adjacent nesting populations (Mantel test R^2 = 0.52, P = 0.001; Bowen et al. 2004). Hence genetic data indicate that the subadult populations are not a random mix, but are homing to their region of origin, a conclusion supported by tag recapture data (Avens et al. 2003). This behavior is not as precise as the homing of breeding adults, as indicated by the ϕ_{st} values and the occurrence of subadult turtles far outside the range of nesting habitat (Ehrhart et al. 2003; Hopkins-Murphy et al. 2003), from Texas to the northeast U.S. (Fig. 1). Nonetheless, this behavior places subadult turtles at elevated frequencies in the vicinity of their natal nesting colonies.

Additional mtDNA studies indicate that contributions to subadult habitats are influenced by the size of regional source (nesting) populations (Norgard and Graves 1996, Rankin-Baransky et al. 2001, Engstrom et al. 2002, Witzell et al. 2002). The very large rookery in southern Florida contributes most of the subadult turtles feeding along this coast, with additional contributions from the rookeries at the Yucatan peninsula, Dry Tortugas, Gulf of Mexico, and the Atlantic states of Georgia, South Carolina, and North Carolina.

While the composition of juvenile populations in the North Atlantic can be explained by the size of source (nesting) populations, the composition of subadult populations is guided by two influences: the size of source populations and proximity to these source populations. A third factor, male-biased dispersal, has been proposed for juvenile loggerheads in the Mediterranean (Casale et al. 2002).

After another decade (or more) in subadult habitat, the turtles switch to adult habitat which is largely unknown, but suspected to include the Caribbean basin. As a consequence of natal homing behavior of loggerhead females, most nesting populations are distinguished by differences in the frequency of mtDNA haplotypes (Bowen et al. 1994; Encalada et al. 1998; Hatase et al. 2002b).

Population overlap in loggerhead turtles

The mtDNA surveys indicate no genetic structure among juvenile (oceanic) populations, and low population structure among subadult (coastal) populations (Figure 2). Based on the surveys of the nesting colonies, we know that the lack of population subdivisions at pre-adult stages is due to mixing of turtles from multiple isolated breeding populations. Three lessons are apparent:

1) **Genetic surveys of migratory species on feeding grounds or migratory corridors may be misleading**. The analyses on loggerhead sea turtles on feeding grounds indicate low or no population structure, because these are mixes of several breeding populations. The same conditions may apply to widely distributed fishes, including migratory sharks, billfish, and tunas. Surveys of adults are very valuable in the context of global phylogeography, but may miss the regional population structure that is relevant to management.
2) **Different management regimes are appropriate at different life stages.** For loggerhead turtles, disturbances to the juvenile populations will have a diffuse impact on nesting colonies across the North Atlantic (and possibly the Mediterranean). The large FL-SA population, with perhaps 70% of the nesting effort in this region, will absorb 70% of the disturbances to juvenile populations.

In contrast, disturbance to the subadult populations will have a more direct impact on nearby nesting colonies. Perhaps half of the subadults feed near their natal rookery, so that disturbances here will have a strong impact on local nesting populations. This must elevate the conservation priorities for habitat in the vicinity of small and dwindling nesting colonies. Finally, disturbance to the adult populations will yield pinpoint damage to the corresponding nesting colony. In these circumstances, depletion of breeding and nesting habitat has a direct impact on the local population.

3) **Ecosystem-based protection is not sufficient to manage migratory marine species.** One of the most promising advances in marine conservation is the development of marine protected areas (MPAs) on an ecosystem scale (Palumbi 2001; Norse and Crowder 2004; Sobel and Dahlgren. 2004). Recent field studies have confirmed the efficacy of MPAs for these ecological goals (Roberts et al. 2002; Friedlander et al. 2004), but do not fully address the needs of migratory species. The genetic surveys of juvenile loggerhead turtles confirm suspected links between nesting colonies in the West Atlantic and distant feeding populations in the North Atlantic and Mediterranean Sea (Carr 1987; Bolten et al. 1998; Laurent et al. 1998; LaCasella et al. 2004). These ocean-wide connections raise doubts about the efficacy of protecting specific ecosystems as a management option for loggerhead turtles and other migratory species. For an animal that begins life on a Florida beach, feeds as a juvenile in the East Atlantic and Mediterranean, forages in Florida as a subadult, and feeds in the Caribbean as an adult, what ecosystem protection will suffice? In the case of migratory

species, the solution is not ecosystem protection alone, but taxon specific protection of vulnerable life stages (Bowen and Roman 2004). In sea turtles this clearly includes nesting beaches and juvenile feeding habitat, for whales it must include the calving grounds in bays and other sheltered coastal areas, in marine fishes it will include spawning aggregates and coastal nurseries.

Sex-biased gene flow in loggerhead turtles

The microsatellite surveys indicate no population structure among nesting colonies of the southeast U.S. Taken alone, these data would mandate that these nesting colonies are a single management unit. Yet the surveys of mtDNA in nesting colonies indicate strong population structure. Two lessons can be drawn from these data:

4) **Concerns about inbreeding and corresponding loss of genetic diversity are alleviated for the smaller nesting colonies in the southeastern United States**. A key feature of loggerhead population structure is the differences in diversity indices for nesting populations. The mtDNA diversity varies tremendously among nesting colonies of the southeastern U.S. (h = 0.000 – 0.664) while the corresponding measure for microsatellites is remarkably uniform (H_e = 0.785 – 0.815; Table 3). There is considerable debate about what measures of genetic diversity are relevant for "healthy" populations (Lande and Shannon 1996; DeWoody and DeWoody 2004), but it is clear from the microsatellite survey that the smallest and the largest nesting colonies in the southeast US have comparable levels of nuclear DNA diversity. This alleviates the management concern about loss of the genetic diversity (in small populations) that is most directly relevant to genetic health.

5) **Male-mediated gene flow does not detract from the classification of breeding areas as independent populations**. For this point, it is helpful to consider the extremes of gender-specific extirpation. For the small breeding population that nests on the Florida panhandle, what would happen if all the males were eliminated? The nesting population would continue, because some of the females were inseminated before arriving at the breeding/nesting habitat. In contrast, what would happen if the females were eliminated? The nesting population would be extinct. Females are the essential vessels that transmit the threads of life from generation to generation. Their site fidelity defines nesting populations, regardless of male behavior.

Perhaps the most important lesson from these studies are that nuclear DNA surveys (allozymes, microsatellites, etc.) can be positively misleading for migratory species with complex population structure. A management plan based on nuclear DNA data would indicate a single management unit for loggerhead turtles of the southeastern U.S., a disastrous premise. The mtDNA surveys can also be misleading if applied at the junctions where populations overlap on feeding or migratory areas. For example, genetic surveys of loggerhead juveniles indicate a single panmictic population, obscuring the true structure of subadults and nesting adults. Many of the genetic surveys of tunas, billfishes, and sharks are based on adults sampled on feeding habitat, and many of these surveys indicate very low population structure. When the same species are surveyed in nursery habitats, much stronger population structure may emerge. To define populations and management units, it is not sufficient to survey these

animals in coastal feeding habitat. Migratory marine animals must be surveyed at the source, the breeding/nesting habitat in the case of sea turtles, the calving grounds in the case of whales, or the spawning/nursery habitat in the case of fishes.

ACKNOWLEDGEMENTS

This study was made possible by outstanding contributions from A.L. Bass, K.A. Bjorndal, A.B. Bolten, S.-M. Chow, P. Dutton, S. Epperly, S.A. Karl, R. Klinger, E. LaCasella, G. Marcovaldi and M. Marcovaldi. The microsatellite data was produced by A. Pearce in an unpublished thesis. For advice and field assistance we thank E. Almira, D. Amorocho, J. Avise, D. Bagley, G. Balazs, A. Ball, M. Bostrom, M. Camhi, R. Carthy, P. Castaneda, M. Chaloupka, R. Chapman, C. Coogan, M. Courtney**,** K. Diemer, M. Dodd, E. Dunlavey, L. Ehrhart, S. Encalada, L. Fisher, N. FitzSimmons, A. Foley, J. Foote, J. Frazier, M. Godfrey, S. Grant, M. Harris, S. Hopkins-Murphy, A. Huff, L. Iocco, S. Johnson, N. Kamezaki, E. LaCasella, M. Lamont, B. Liebert, A. Meylan, R. Mezich, J. Musick, L. Ogren, T. Okuyama, L. Parris, F. Percival, E. Possardt, N. Price, R. Reardon, S. Reynolds, J. Richardson, N. Richardson, J. Roman, S. Shanker, P. Taylor, W. Teas, J. Thome, W. Witzell, S. Woodley-Miller, M. Zacks, M. Zatcoff, and J. Zurita. For logistic support we thank the Archie Carr Center for Sea Turtle Research, Broward County Environmental Quality Control Board, Florida Department of Natural Resources, Florida Cooperative Fish and Wildlife Research Unit, Georgia Department of Natural Resources, NOAA-Fisheries Molecular Genetics Laboratory, North Carolina Department of Natural Resources, Projeto Tartaruga Marinha (TAMAR; Brazil), South Carolina Department of Natural Resources, the Volusia County Turtle Patrol, the DNA Sequencing Core at the University of Florida, and the U.S. National Park Service. We thank S. White for drafting Figure 1. Research was funded by the U.S. National Marine Fisheries Service, U.S. National

Science Foundation, U.S. Fish and Wildlife Service, National Geographic Society, Turner Foundation, and private contributions.

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FIGURE LEGENDS

Figure 1. Map of North America, with surveyed nesting locations for the loggerhead turtle indicated as Florida northern Gulf (FL-NG), Florida southern Gulf (FL-SG), Dry Tortugas (FL-DT), Florida southern Atlantic (FL-SA), Florida Volusia County (FL-VC), Florida northern Atlantic (FL-NA), Georgia (GA), South Carolina (SC) and North Carolina (NC). Subadult feeding populations range from Texas to the northeastern states (NE US). In the analyses of nesting populations, the FL-NA sample is combined with the adjacent GA sample, based on geographic proximity and extensive sharing of a single mtDNA haplotype.

Figure 2. A model of loggerhead population structure in the North Atlantic, using three hypothetical rookeries designated by red, green and black icons. The mtDNA data indicate a stepwise increase in population structure through juvenile, subadult, and adult stages. In the juvenile stage, turtles from all three rookeries intermingle, and no population structure is apparent between eastern and western edges of the North Atlantic Gyre. In the subadult stage, turtles tend to recruit to neritic feeding habitat in the vicinity of their natal rookery, inducing low but significant population structure. In the adult turtles, females (and possibly males) have high site fidelity to breeding/nesting habitat, inducing strong population structure.

Table 1. **Sample sizes for nesting populations in the southeastern U.S. and Bahia, Brazil**, as described in Bowen et al. (2004) for the mtDNA control region survey, and Pearce (2001) for the five microsatellite loci. Abbreviations: FL-NG = Florida Peninsula, northern Gulf of Mexico; FL-SG = Florida Peninsula, southern Gulf of Mexico; FL-DT = Dry Tortugas at the southern end of the Florida Keys; FL-SA = Florida Peninsula, southern Atlantic coast; FL-VC = Volusia County, Florida (north of Cape Canaveral); GA= Georgia and adjacent Jackson County, FL (FL-NA in Figure 1); SC=South Carolina; NC=North Carolina; BA = Bahia, Brazil.

Locus	FL-NG	FL-SG	FL-DT	FL-SA	FL-VC	GA	SC	NC	BA
mtDNA	49	45	58	64	49	43	20	28	11
DC107	42	46	23	123	42	51	24	26	80
CCM2	42	46	23	123	45	51	24	27	81
Ccar176	42	46	23	123	43	51	24	26	81
CC141	41	46	23	123	45	51	24	27	81
CC7	41	46	23	122	45	51	24	26	81

Table 2. **Primer sequences and annealing temperatures** (t) for the mtDNA control region and the five microsatellite loci used to survey loggerhead nesting colonies (Norman et al. 1994; FitzSimmons 1998; Pearce 2001; and unpublished data from N. FitzSimmons and P. Dutton).

Locus	Forward Primer	Reverse Primer	t(^{0}C)
mtDNA	TTGTACATCTACTTATTTACC AC	GTACGTACAAGTAAAACTACC GTATGCC	52
DC107			55
CCM2	TGGCACTGGTGGATT	TGACTCCCAAATACTGCT	58
Ccar176	GGCTGGGTGTCCATAAAAGA	TTGATGCAGGAGTCACCAAG	60
CC141			56
CC7	TGCATTGCTTGACCAATT AGTGAG	ACATGTATAGTTGAGGAG CAAGTG	56

Table 3. **Genetic diversity indices for nesting populations in the southeastern U.S. and Bahia, Brazil**, as described in Bowen et al. (2004) for the mtDNA control region survey, and Pearce (2001) for five microsatellite loci. Asterix indicate significant departures from Hardy–Weinberg equilibrium. Location abbreviations as in Table 1. Asterics indicate three departures from Hardy-Weinberg equilibrium, based on exact tests ($P < 0.05$).

Nesting Beach	mtDNA *h*	DC107 H_e/H_o	CCM2 H_e/H_o	Ccar176 H_e/H_o	CC141 H_e/H_o	CC7 H_e/H_o
FL-NG	0.383	0.796 0.857	0.698 0.691	0.853 0.881	0.874 0.756*	0.781 0.902
FL-SG	0.664	0.792 0.804	0.733 0.783	0.775 0.739	0.880 0.891	0.788 0.696
FL-DT	0.254	0.777 0.696	0.783 0.696	0.749 0.609	0.874 0.739*	0.820 0.739
FL-SA	0.567	0.778 0.797	0.768 0.756	0.816 0.764	0.872 0.878	0.815 0.787
FL-VC	0.511	0.806 0.762	0.780 0.800	0.810 0.767	0.848 0.778	0.787 0.667*
GA	0.035	0.780 0.804	0.745 0.745	0.846 0.902	0.862 0.784	0.844 0.863
SC	0.000	0.784 0.750	0.700 0.750	0.858 0.833	0.858 0.833	0.804 0.875
NC	0.000	0.789 0.769	0.751 0.704	0.814 0.923	0.854 0.741	0.773 0.769
BA	0.000	0.720 0.750	0.640 0.593	0.784 0.790	0.698 0.704	0.583 0.568

Table 4. **Summary statistics for the five microsatellite loci used to survey loggerhead turtle nesting colonies** (from Pearce 2001): Size = allele size in bp, k = number of alleles, H_e = mean gene diversity (or mean expected heterozygosity) per locus, and H_o = mean observed heterozygosity per locus.

Locus	Size	k	H_e	H_o
DC107	158-186	11	0.7742	0.7834
CCM2	169-195	10	0.7452	0.7208
Ccar176	117-181	29	0.8134	0.7930
CC141	186-220	16	0.8651	0.8004
CC7	209-247	18	0.7802	0.7473
Mean		16.8	0.7956	0.7690

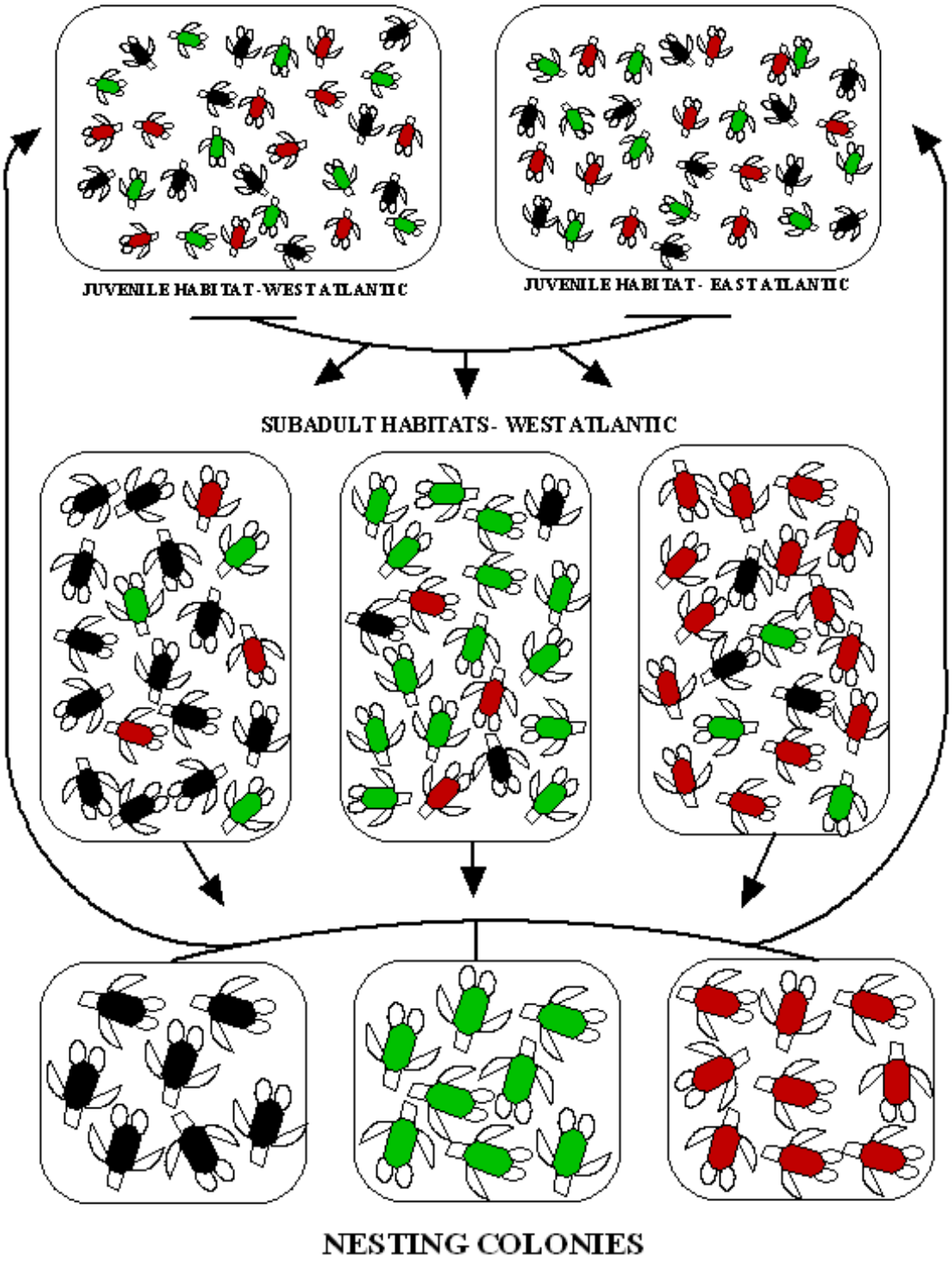
Table 5. Genetic partitions among eight nesting populations in the southeast U.S. plus Bahia, Brazil. Above the diagonal are partitions based on five microsatellite loci (R_{st} values) from Pearce (2001), below the diagonal are partitions based on mtDNA sequence comparisons (ϕ_{st} values) from Bowen et al. (2004) with additional unpublished data. On the diagonal are nucleotide diversity values (π values, in bold) for each nesting population. Significant values ($P < 0.05$) based on permutation tests are indicated with asterics. Abbreviations are defined in Table 1.

	FL-NG	FL-SG	FL-DT	FL-SA	FL-VC	GA	SC	NC	BA
FL-NG	**0.0192**	-0.0005	-0.0139	-0.0025	0.0005	0.0012	-0.0015	0.0036	0.0179*
FL-SG	0.1645*	**0.0276**	-0.0073	0.0027	0.0029	0.0115	0.0034	0.0026	0.0214*
FL-DT	0.6682*	0.3252*	**0.0073**	-0.0109	-0.0081	-0.0122	-0.0172	-0.0093	0.0118
FL-SA	0.1050*	-0.0100	0.3787*	**0.0268**	0.0000	-0.0014	-0.0061	-0.0005	0.0144*
FL-VC	0.0151	0.0491	0.5338*	0.0135	**0.0247**	-0.0043	-0.0103	0.0026	0.0262*
GA	0.1747*	0.5123*	0.9039*	0.4123*	0.3060*	**0.0018**	-0.0138	0.0114	0.0365*
SC	0.1372*	0.4272*	0.8910*	0.3479*	0.2436*	-0.0225	**0.0000**	-0.0020	0.0269*
NC	0.1592*	0.4601*	0.9004*	0.3734*	0.2711*	-0.0138	0.0000	**0.0000**	-0.0012
BA	0.2171*	0.3542*	0.8612*	0.2974*	0.2356*	0.7667*	1.0000*	1.0000*	**0.0000**

Figure 1.

North America
NE US
VA
NC
SC
GA
AL
MS
LA
TX
FL-NA
Vo-FL
FL-NG
FL-SA
FL-SG
FL Bay
Dry Tortugas
Mexico
Yucatan
Quintana Roo

Figure 2


JUVENILE HABITAT-WEST ATLANTIC
JUVENILE HABITAT- EAST ATLANTIC
SUBADULT HABITATS- WEST ATLANTIC
NESTING COLONIES