FINAL REPORT:

IDENTIFICATION OF LOGGERHEAD TURTLE (*CARETTA CARETTA*) STOCK STRUCTURE IN THE SOUTHEASTERN UNITED STATES AND ADJACENT REGIONS USING NUCLEAR DNA MARKERS

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Project number T-99-SEC-04

SUBMITTED TO THE NATIONAL MARINE FISHERIES SERVICE

May 7, 2001

CONTRASTING POPULATION STRUCTURE OF THE LOGGERHEAD TURTLE (*CARETTA CARETTA*) USING MITOCHONDRIAL AND NUCLEAR DNA MARKERS

By

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A THESIS PRESENTED TO THE GRADUATE SCHOOL
OF THE UNIVERSITY OF FLORIDA IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

UNIVERSITY OF FLORIDA

2001

ACKNOWLEDGMENTS

I gratefully acknowledge the advice and unending patience of my major advisor, Brian Bowen, and my committee members Karen Bjorndal and Mark Brenner. For enduring long hours and many insect bites on the beach, I thank D. Bagley, C. Coogan, K. Diemer, E. Dunlavey, L. Ehrhart, L. Fisher, J. Foote, M. Godfrey, L. Iocco, M. Lamont, B. Liebert, K. Moore, L. Parris, N. Price, R. Reardon and C. Vietas. For assistance in the lab, I recognize the extensive contributions of Shaio-Mei Chow and Anna Bass. Amy Ball and Michelle Zatcoff answered all my data analysis questions. Writing would not have been finished without the help (and imposed deadlines) of Joel Carlin and Steve Johnson. I am grateful to Dale Johnson for drafting all the figures and for giving me a place to stay. For invaluable contributions to the project I thank E. Almira, J.C. Avise, J. Beam, A. Bolton, R. Carthy, P. Castaneda, S.E. Encalada, A. Foley, S. Hopkins-Murphy, J.A. Huff, S.A. Karl, R.C. Klinger, A.B. Meylan, R. Mezich, N. Mrsovsky, L. Ogren, F. Percival, E. Possardt, J.I. Richardson, C.J. Sears, S. Shanker, B. Schroeder, W. Witzell, M. Zacks-Karl, and J.C. Zurita. I extend special thanks to Shirley Reynolds and the Volusia County Turtle Patrol. For logistic support I gratefully recognize Broward County Environmental Quality Control Board, the Florida Department of Natural Resources, Florida Cooperative Fish and Wildlife Research Unit, the DNA Sequencing Core at the University of Florida, and the

U.S. National Park Service. This research was funded by the National Marine Fisheries Service, the U.S. Fish and Wildlife Service, The Turner Foundation, and private contributions. My parents, Donna and David Francisco, provided moral support and kept me clothed throughout my lengthy college career. I especially thank my husband, Jeff, for believing in me and for understanding the role of the president and the elephant shoe.

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Abstract of Thesis Presented to the Graduate School
of the University of Florida in Partial Fulfillment of the
Requirements for the Degree of Master of Science

CONTRASTING POPULATION STRUCTURE OF THE
LOGGERHEAD TURTLE (*CARETTA CARETTA*)
USING MITOCHONDRIAL AND NUCLEAR
DNA MARKERS

By

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May 2001

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Mitochondrial DNA (mtDNA) and microsatellite DNA (nuclear DNA, nDNA) analyses were applied to loggerhead turtles (Caretta caretta) in the Northwest Atlantic to determine geographic boundaries of breeding aggregations, elucidate male migratory behavior and assess stock structure. The geographic boundaries of nesting aggregations were determined by analysis of 12 nesting beaches throughout Florida using maternally inherited mtDNA. Overall we observed strong population structure among nesting beaches (Φ_{ST}=0.298), but adjacent beaches were not significantly different with one exception; the offshore islands of the Dry Tortugas. Nesting site fidelity appears to operate on a scale of 100 km rather than individual beaches, consistent with the level of relocation observed in tagging studies. Genetic signatures of male migratory behavior and genetic

stock structure were analyzed using biparentally inherited nDNA applied to the 12 Florida beaches and specimens from nesting beaches in Georgia, South Carolina, North Carolina, and Brazil. The overall population structure among nesting beaches at the nDNA level was low (F_{ST} =0.0187), an order of magnitude lower than the structure found with mtDNA. Because of different inheritance dynamics of mtDNA and nDNA, these results are not conflicting, but rather show that males either are not philopatric or (more likely) they mate opportunistically during migration.

CHAPTER 1
OVERVIEW

Loggerhead turtles, *Caretta caretta*, are in the family Cheloniidae that includes five other extant species of sea turtle. Loggerheads occur around the world in temperate, tropical, and subtropical waters of the Atlantic, Pacific, and Indian Oceans. Unlike other species of sea turtle, major loggerhead nesting aggregations are generally located in warm temperate and subtropical regions except for one of the larger rookeries on Masirah Island, Oman (Dodd 1988). The U.S. hosts what is perhaps the largest nesting concentration with more than 14,000 females nesting each year from North Carolina through the Gulf Coast of Florida (Meylan et al. 1995, Ehrhart 1989, Murphy and Hopkins 1984).

Sea turtles spend their life at sea with the exception of mature females that trudge up beaches to lay eggs 2-7 times a nesting season (Dodd 1988). Females reach sexual maturity at 20-30 years of age and nest approximately every 2-3 years (Klinger and Musick, 1995, Frazer and Ehrhart, 1985). Since loggerheads spend so little time on land, most of our knowledge of sea turtle migration has come from tag-recapture studies. Tags placed on nesting females revealed that many turtles returned to the same beaches in successive years, which led to several hypotheses about the apparent nest site fidelity of sea turtles. The two most prominent were "social facilitation" and "natal homing". The social facilitation model proposed that first time nesters follow experienced females from foraging grounds to nesting beaches and imprint on that beach for

subsequent reproductive efforts (Owens et al. 1982). The natal homing theory proposes that hatchlings imprinted on their natal beaches and return to these beaches to reproduce. A direct test of these alternatives would be prohibitive, requiring thousands of hatchlings each with a tag that would persist from hatchling to adult (20-30 years). Hence a new approach was necessary to discover how females choose nesting beaches.

With the invention of polymerase chain reaction (PCR), studies involving maternally inherited mitochondrial (mt)DNA became possible and could be used to discern which hypothesis about nest site fidelity explains marine turtle behavior. If social facilitation occurs, there would be no genetic structure among regional nesting beaches, while natal homing would mandate genetic partitioning among beaches. Studies of mtDNA support natal homing in nesting green (*Chelonia mydas*, Norman et al. 1994; Encalada et al. 1996), loggerhead (Bowen et al. 1994, Encalada et al. 1998), and hawksbill turtles (*Eretmochelys imbricata*, Bass et al. 1996). Although mtDNA assays have revealed much about sea turtle life history and behavior of females, precise geographic boundaries of breeding aggregations as well as male migratory patterns and possible philopatry remain largely unknown.

Habitat destruction, commercial fisheries, and pollution have adversely affected marine turtle species worldwide. The predictability of sea turtle nesting seasons paired with the relative ease of capturing females on land has drastically reduced population sizes due to the slaughter of nesting females and collection of their eggs. Turtles are also vulnerable in the marine environment, being killed

both intentionally and incidentally by trawl, gill net, pound net, and longline fisheries. Consequently, loggerhead turtles are listed as threatened under the U.S. Endangered Species Act of 1973 and are restricted from international trade by CITES. The National Marine Fisheries Service and the U.S. Fish and Wildlife Service (1991) have formulated a recovery plan for loggerheads that outlines the need to 'define geographical boundaries of breeding aggregations' and to 'determine movements and distribution of adult males'.

To address the questions about the geographic boundaries of breeding aggregations and movements and distribution of adult males, mtDNA and microsatellite DNA (nuclear DNA) analyses were applied to loggerhead turtles in the Northwest Atlantic. The geographic boundaries of nesting aggregations were examined in an analysis of 12 nesting beaches throughout Florida using maternally inherited mtDNA. Genetic signatures of male migratory behavior and genetic stock structure were analyzed with biparentally inherited microsatellite DNA applied to the 12 Florida beaches and specimens from nesting beaches in Georgia, South Carolina, North Carolina, and Brazil.

CHAPTER 2
STOCK STRUCTURE AND NESTING SITE FIDELITY IN FLORIDA LOGGERHEAD TURTLES (*CARETTA CARETTA*) RESOLVED WITH MTDNA SEQUENCES

Introduction

The loggerhead (*Caretta caretta*) is the only marine turtle that nests primarily outside the tropics. Major nesting aggregates exist in warm temperate regions of the Atlantic, Indian, and West Pacific Oceans but are absent from the central and eastern Pacific. Despite this wide distribution, there are few large (>10,000) nesting aggregations of loggerheads. The southeastern United States from North Carolina to Florida probably encompasses the largest loggerhead nesting aggregation in the world, hosting 35-40% of the total loggerhead nesting effort (Bjorndal et al. 1983, Meylan et al. 1995). Within this region, Florida accounts for 90% of the nests, making this state a critical habitat for nesting loggerheads.

After reaching sexual maturity at an estimated 20-30 years of age (Bjorndal et al. 2000, Klinger and Musick 1995; Frazer and Ehrhart 1985), female loggerheads nest every 2-3 years on average (Bjorndal et al. 1983). Tagging studies demonstrate that females tend to return to the same beaches to nest and utilize the same foraging grounds between nesting seasons (Limpus et al. 1992). This observation prompted Carr (1967) to suggest that females are returning to their natal beach. A testable corollary of this natal homing hypothesis is genetic

partitioning between nesting areas, an expectation that has been confirmed in several sea turtle species (Bowen and Karl 1996). In particular, Bowen et al. (1993) found evidence of natal homing for loggerhead turtles in the southeastern U.S. using maternally-inherited mitochondrial DNA (mtDNA).

Encalada et al. (1998) surveyed mtDNA control region variation in ten major nesting areas in the Atlantic Ocean and Mediterranean Sea. Although sharing of haplotypes between geographic regions was observed, most nesting aggregates were genetically distinct populations. The distribution of mtDNA markers resulted in the delineation of (at least) six population genetic units, including three in the southeastern United States: (1) North Carolina, South Carolina, Georgia and northeast Florida (Atlantic coast), (2) south Florida, and (3) northwest Florida (Gulf of Mexico).

There were several gaps in coverage of nesting beaches surveyed by Encalada et al. (1998), especially in Florida where the majority of nesting occurs. Low sample size was a factor that may have limited statistical power to detect partitions among distinct nesting aggregates because, for example, this study included only six specimens from Melbourne, the center of the largest nesting aggregate (Meylan et al. 1995). As a result, the genetic assays were sufficient to show regional differentiation, but could not precisely define the boundaries of (genetically distinct) nesting populations. Therefore, a primary motivation of this study was to resolve the geographic limits of nesting populations, as defined by the nesting site fidelity of female loggerheads. Schroth et al. (1996) reported evidence of population structure on a scale of 100 kilometers in the

Mediterranean. In contrast, nesting aggregates in North Carolina, South Carolina, and Georgia U.S.A. separated by hundreds of km of coastline, are monotypic in terms of mtDNA control region sequences, indicating very close relationships and no detectable population structure (Encalada et al. 1998). FitzSimmons et al. (1996) demonstrated population structure between nesting colonies in eastern and western Australia, but low detected variation precluded a more detailed analysis. Hence the geographic limits of nesting populations remain controversial.

To accomplish the genetic test of nesting site fidelity, we conducted a survey of mtDNA sequence diversity throughout the Florida peninsula, including 12 locations with samples sufficient for population-level analyses. In addition to the 101 Florida samples analyzed by Encalada et al. (1998) we sampled more beaches and increased sample sizes for some of the larger nesting aggregates (N=274). The Dry Tortugas was also sampled since these islands lay on the outer fringes of the Florida peninsula.

To conduct a hierarchical analysis of genetic variance, nesting beach samples were divided into the four zones previously defined by management personnel (Meylan et al. 1995): northeast Florida, southeast Florida, southwest Florida, and northwest Florida (the panhandle) (Fig. 1). We chose these zones as an objective starting point for evaluating hypotheses about geographic subdivisions because they are approximately concordant with biogeographic boundaries (see Fig. 1 legend). The larger sample size allowed us to conduct an

analysis of molecular variance to determine if the zones correspond to a hierarchical structure of genetic diversity.

This research has several implications for loggerhead biogeography and natural history, but it is also relevant to the conservation of this threatened species. Since loggerhead turtles have natal homing behavior, a decimated nesting population in one area may not be replenished by turtles from other areas. Distinguishing the number and size of nesting populations, and the precision of natal homing, are necessary prerequisites for informed management decisions.

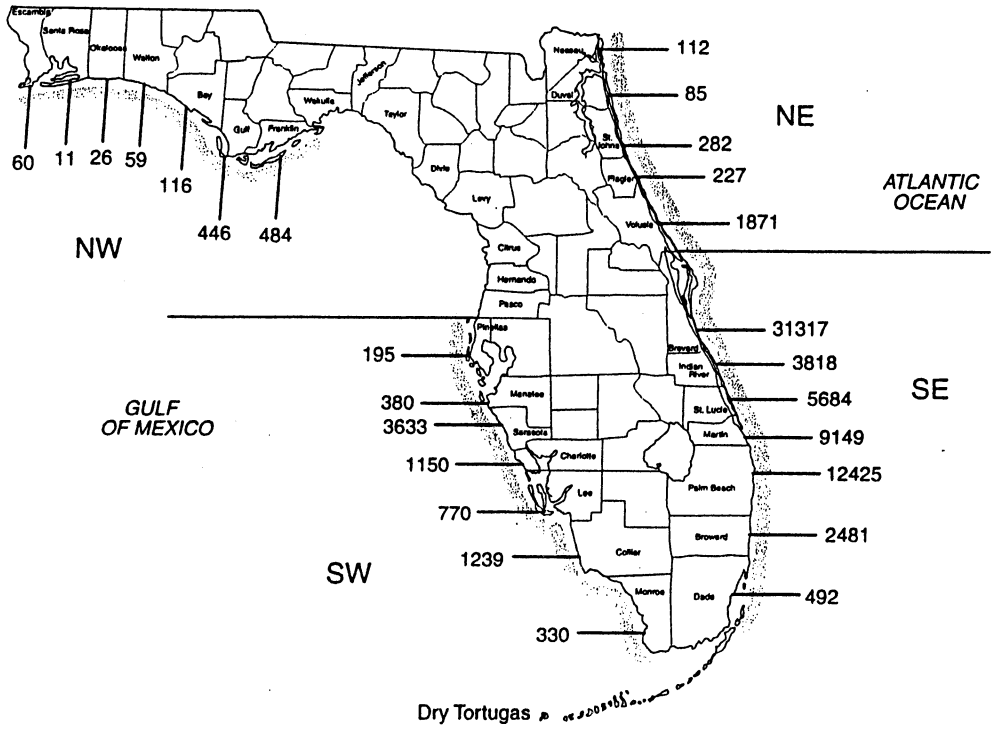

Figure 1. Management zones of Florida and number of nests per year averaged over the last three years for each county (www.fmri.usf.edu/turtle/nesting/default.htm). These four zones are separated by recognized marine biogeographic barriers. In the case of NE vs. SE, and NW vs. SW, management zones are separated by biogeographic boundaries between temperate and subtropical zones with borders at Cape Canaveral and Tampa Bay (Briggs 1974, Avise 1992). The division between SE and SW is the freshwater outflow of the Everglades as such outflows are recognized distribution breaks for coastal marine organisms (Muss et al. 2001). However, the distribution of loggerhead nesting straddles the Cape Canaveral boundary and possibly the Everglades boundary such that biogeographic zones defined for other marine organisms may not strictly apply to marine turtles (see discussion).

Materials and Methods

Sample Collection

Samples from 173 nesting females were obtained between 1995 and 1999 from four regions of Florida: 1) northeast Florida (NEFL): Volusia County (VC, n=49); 2) southeast Florida (SEFL): Melbourne Beach (MB, n=40); 3) southwest Florida (SWFL): Dry Tortugas (DT, n=58), Sarasota County (SC, n=19); and 4) northwest Florida (NWFL): Cape San Blas (CSB, n=7). Tissue from moribund hatchlings, embryos, and skin biopsy punches were placed in 15 mL of a saturated salt (NaCl) buffer (Amos and Hoelzel, 1991) and stored at room temperature. Blood samples were obtained from the dorsal cervical sinus of nesting females following the procedure of Owens and Ruiz (1980) with 1 mL of blood placed in 9 mL of lysis buffer (Fitzsimmons et al. 1999) and stored at room temperature. Precautions were taken to ensure that individual females were sampled only once. These precautions included 1) tagging the sampled females, and 2) sampling within the 11-15 day renesting interval. Females may nest several times in a nesting season, but rarely at intervals shorter than 11 days; (Dodd 1988).

These samples are added to the data from 101 Florida nesters previously analyzed by Encalada et al. (1998). Locations previously sampled were 1) NEFL: Amelia Island (AI, n=12); 2) SEFL: Melbourne Beach (MB, n=6), Hutchinson Island (HI, n=9) and Port Everglades (PE, n=10); 3) SWFL: Key

Island (KI, n=15) and Sarasota County (SC, n=10); and 4) NWFL: Eglin Air Force Base (EAFB, n=21), Tyndall Beach (TB, n=7), and St. Joseph (SJ, n=11).

Data Collection

Whole genomic DNA from tissue and blood samples was isolated using phenol/chloroform extractions 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 CR-1 (5'-TTG TAC ATC TAC TTA TTT ACC AC-3') and CR-2 (5'-GTA CGT ACA AGT AAA ACT ACC GTA TGC C-3') (Norman et al. 1994). The annealing temperature was 52°C with 1.5 mM $MgCl_2$ in 50 µl volume reactions. All PCR amplifications contained a negative control (DNA free) reaction to guard against contamination. PCR products were purified using 30,000 MW filter units (Millipore, Inc.). Cycle sequencing reactions were conducted with Big Dye technology (ABI Inc.), and fragments were gel separated at the University of Florida DNA Sequencing Core using an automated sequencer (373A and 377, ABI). Chromatograms were checked against computer base calls to ensure accuracy and then aligned using Sequencher 3.1. These sequences were compared to previously identified haplotypes from nesting and foraging locations (Encalada et al. 1998, unpublished data) and were assigned corresponding haplotype letter designations.

Data Analysis

The distribution of sequence variation among populations was determined using ARLEQUIN ver. 1.1 (Schneider et al. 1997) which correlates genotype distances at various hierarchical levels with Φ-statistics. For the purposes of this study, Φ_{ST} measures the proportion of genetic diversity within a nesting beach relative to the entire data set. Φ_{CT} is the proportion of genetic diversity within the four management regions defined above relative to the entire data set, and measures the proportion of genetic variation among groupings of nesting beaches. Φ_{SC} measures the proportion of variation among nesting beaches within a region. The significance of Φ-statistics was assessed by comparison to values generated from 1023 random permutations of sequences among populations. The groupings used for the hierarchical AMOVA included variations on the classification scheme defined by management personnel (NE, SE, SW, NW; Meylan et al. 1995), such as including the Dry Tortugas in the SW group, treating the Dry Tortugas as a separate entity, and combining the SE and SW zones because they were not significantly different in some analyses (see legend Table 3).

The amount of sequence variation within nesting populations was summarized as haplotype diversity (*h*) and nucleotide diversity (π, the average number of pairwise nucleotide differences per site; Nei 1987) calculated with ARLEQUIN. Genetic heterogeneity among nesting beaches was also assessed by chi-square tests of haplotype frequencies. Values were compared to distributions obtained by randomizing individuals among populations using Monte-Carlo resampling (Rolf & Bentzen 1989), as implemented in CHIRXC

(Zaykin and Pudovkin 1993). Estimates of migration (Nm, number of migrants between nesting beaches per generation) were calculated based on Φ_{ST} estimates using the equation $Nm= [1- \Phi_{ST}]/[2 \Phi_{ST}]$.

Results

A 380 bp fragment of the mtDNA control region (removing 11 ambiguous bp at the ends of the 391 bp fragment) was aligned for all sequences. Eleven haplotypes were present among the 274 sequences analyzed (Table 1). All of the haplotypes correspond to previously reported sequences from *C. caretta*, but two of the haplotypes (K and M) were previously observed in specimens from foraging grounds (Bolten et al. 1998, Laurent et al. 1998), and haplotype CC20 had been observed only in a turtle stranded in Georgia (unpublished data).

Nucleotide diversity within populations was high (π=0.022 ± 0.011), as was the nucleotide diversity for all populations together (π=0.032 ± .016). This was due to the presence of two phylogenetically distinct clusters of haplotypes (Encalada et al. 1998). The average value for within population haplotype diversity was high (h=0.460) and ranged from 0.000 to 0.714 (Table 1).

Haplotypes A and B accounted for 91.6% of the individuals sampled, but the distribution of these two haplotypes was not uniform across Florida (Fig. 2). For example, haplotype B was present in 21% of the turtles in NEFL, 40% in SEFL, 65% in SWFL and 15% in NWFL. Haplotype A shows the opposite trend, occurring 72% of the time in NEFL, 53% in SEFL, 24% in SWFL, and 78% in NWFL.

Table 1. Distribution of mtDNA haplotypes for Florida loggerheads and within-nesting beach haplotype diversity (*h*) and nucleotide diversity (π). Top row contains original haplotype designations, with haplotype designations according to Laurent et al. (1998) below.

Location	A	B	C	E	G	I	J	K	M	N	CC20	Total	*h*	π
Laurent et al. (1998)	C1	A1	A3		A7	A4	A2		A8	C3				
NE														
Amelia Island	12											12	0.000	0.0000
Volusia County	32	13	1				2		1			49	0.511	0.0256
SE														
Melbourne Beach	25	17			1			1		1	1	46	0.579	0.0271
Hutchinson Island	4	5										9	0.556	0.0301
Port Everglades	3	6		1								10	0.600	0.0253
SW														
Dry Tortugas	4	50				2	2					58	0.254	0.0076
Key Island	5	9	1									15	0.562	0.0262
Sarasota County	15	8	3		2					1		29	0.663	0.0291
NW														
Cape San Blas	4	3										7	0.571	0.0310
St. Joseph's	9	2										11	0.327	0.0178
Tyndall Air Force Base	4	1	1		1							7	0.714	0.0329
Eglin Air Force Base	19	1			1							21	0.186	0.0102

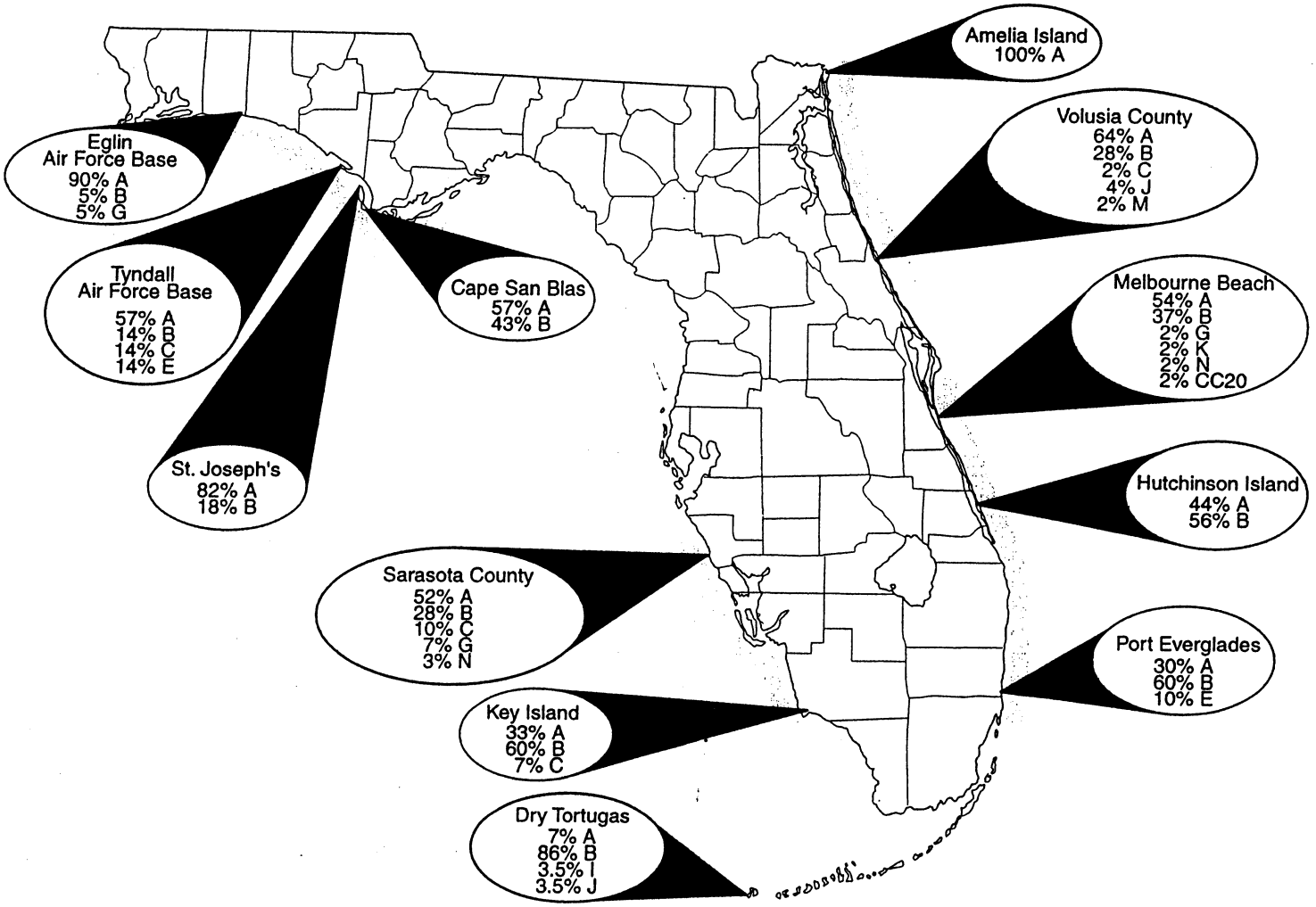

Figure 2. Mitochondrial control region haplotype frequencies for loggerhead turtles from twelve nesting beaches in Florida. Dark borders indicate the four biogeographic regions.

Chi-square analysis of overall haplotype frequencies showed highly significant population differentiation (χ^2 =183.1, P< 0.005) among the 12 nesting locations identified in Table 1. Pairwise comparisons between the four zones were significant (all P< 0.008), with the exception of the two most distant zones (NE and NW, see below). Comparisons between adjacent nesting sites were not significant except for the Dry Tortugas versus the adjacent mainland localities (Key Island and Port Everglades). Chi-square analysis of haplotype frequencies for 66 pairwise comparisons yielded significant differences in 23 cases (Table 2). Migration estimates between sample sites ranged from Nm = 0.07 to infinity (Table 2).

In the AMOVA comparison of sample sites (without regard to management zones), 29.8% of haplotypic diversity was distributed among nesting beaches, a value that is highly significant (P<0.001). Hierarchical analysis of populations partitioned among zones revealed that 68.4% of haplotypic diversity was within nesting sites, 15.8% was distributed among populations within the four zones, and 15.8% was distributed among the zones (Table 3, comparison F). The partitions within and between populations are significant (AMOVA: Φ_{ST} =0.316, P<0.001; Φ_{SC} =0.188, P<0.001), but the variation between zones does not depart significantly from a random distribution (Φ_{CT} =0.158, P=0.179). However, when we group the two southern regions (SE and SW) all the Φ values are significant (Table 3, comparison I).

Table 2. Above diagonal: pairwise haplotype frequency comparisons based on χ^2 statistics, using the Monte Carlo procedure. Numbers in parentheses indicate *P*-values for each comparison (significant values in bold). Below diagonal: migration rates based on Φ_{ST} estimator.

Populations	AI	VC	MB	HI	DT	PE	KI	SC	CSB	SJ	TAFB	EAFB
Amelia Island		5.77 (0.25)	8.59 (0.14)	8.75 **(0.01)**	48.8 **(0.00)**	12.32 **(0.00)**	12.71 **(0.00)**	8.79 (0.05)	6.11 **(0.04)**	2.39 (0.23)	6.11 **(0.04)**	1.22 (1)
Volusia County	1.89		9.31 (0.16)	3.33 (0.51)	47.08 **(0.00)**	10.35 (0.11)	7.47 (0.14)	9.86 (0.08)	1.21 (0.79)	1.51 (0.87)	10.43 (0.12)	8.80 (0.064)
Melbourne Beach	1.32	High		1.57 (0.73)	38.59 **(0.00)**	1.57 (0.74)	6.79 (0.46)	7.61 (0.23)	0.67 (1)	3.02 (0.71)	10.32 (0.16)	10.12 **(0.03)**
Hutchinson Island	0.41	20.1	High		10.71 **(0.039)**	1.18 (1)	0.80 (1)	3.05 (0.51)	0.25 (1)	3.04 (0.16)	4.49 (0.19)	10.29 **(0.00)**
Dry Tortugas	0.07	0.43	0.57	0.74		11.62 **(0.05)**	12.67 **(0.02)**	41.7 **(0.00)**	14.7 **(0.02)**	33.98 **(0.00)**	33.98 **(0.00)**	57.1 **(0.00)**
Port Everglades	0.22	2.42	4.80	High	2.17		2.19 (0.78)	7.91 (0.13)	1.67 (0.78)	5.97 **(0.04)**	6.38 (0.17)	15.22 **(0.00)**
Key Island	0.32	2.88	5.91	High	1.69	High		5.12 (0.29)	1.39 (0.78)	6.13 **(0.03)**	5.30 (0.13)	16.01 **(0.00)**
Sarasota County	1.04	High	High	High	0.59	9.10	12.2		1.91 (0.87)	3.76 (0.49)	1.12 (0.95)	9.20 **(0.03)**
Cape San Blas	0.63	High	High	High	0.38	21.3	High	High		1.29 (0.35)	3 (0.54)	6.37 **(0.04)**
St. Joseph	4.00	High	8.35	2.22	0.15	0.85	1.03	5.47	17.5		3.54 (0.47)	1.97 (0.67)
Tyndall Air Force Base	0.65	High	High	High	0.38	20.8	High	High	High	17.0		5.04 (0.14)
Eglin Air Force Base	High	3.82	2.28	0.77	0.11	0.39	0.49	1.73	1.61	High	1.63	

Table 3. AMOVA analyses for loggerhead populations of Florida to test for the geographic grouping that best explains the distribution of genetic diversity. Variance components are among populations (AP, where populations are individual nesting beaches), among groups (AG, where groups are biogeographic zones), among populations within groups (AP/WG) and within populations (WP). This table includes nine tests. Test of grouping A is within and among the 12 nesting beaches, Test of grouping B is within and among biogeographic zones NE, NW, SE, SW including the Dry Tortugas, Test of grouping C is within and among the four biogeographic zones with the Dry Tortugas as a separate category, Test of grouping D is within and among biogeographic zones and the Dry Tortugas combining SE and SW into a single "S" category, Test of grouping E is within and among biogeographic zones with Dry Tortugas included in S, Test F is a three-tiered analysis of variation within biogeographic zones between biogeographic zones and overall using the same groupings as B, Test G is a three-tiered test of grouping C, Test H is a three-tiered test of grouping E, and Test I is a three tiered test of grouping D.

Divisions	Variance Component	Variance	% Total	Φ-statistics	P
A	AP	1.97	29.84	Φ_{ST}=0.298	P<0.001
	WP	4.63	70.16		
B	AG	1.59	23.51	Φ_{ST}=0.235	P<0.001
	WG	5.18	76.49		
C	AG	1.91	28.41	Φ_{ST}=0.284	P<0.001
	WG	4.82	71.59		
D	AG	2.13	30.72	Φ_{ST}=0.307	P<0.001
	WG	4.81	69.28		
E	AG	1.63	23.04	Φ_{ST}=0.230	P<0.001
	WG	5.44	76.96		
F	AG	1.07	15.82	Φ_{SC} =0.187	P<0.001
	AP/WG	1.07	15.81	Φ_{ST} =0.316	P<0.001
	WP	4.62	68.37	Φ_{CT} =0.158	P=0.179
G	AG	1.60	23.74	Φ_{SC} =0.098	P<0.001
	AP/WG	0.50	7.48	Φ_{ST} =0.312	P<0.001
	WG	4.63	68.78	Φ_{CT} =0.237	P=0.064
H	AG	1.15	16.33	Φ_{SC} =0.211	P<0.001
	AP/WG	1.24	17.69	Φ_{ST} =0.340	P<0.001
	WG	4.63	65.98	Φ_{CT} =0.163	P=0.126
I	AG	1.93	27.86	Φ_{SC} =0.073	P<0.001
	AP/WG	0.37	5.32	Φ_{ST} =0.332	P<0.001
	WG	4.63	66.82	Φ_{CT} =0.279	P=0.018

Discussion

Populations of *Caretta caretta* are believed to be declining worldwide (Dodd 1988) such that Florida is an important reservoir of Atlantic nesting effort. To make informed management decisions about this species, geographic delineation of reproductive units is necessary. Loggerhead rookeries are spatially structured along matrilines, due to female nest site fidelity, and this indicates demographic autonomy among nesting colonies (Avise 2000), regardless of the level of gene flow mediated by males. Therefore management units are defined by female nest site fidelity.

Analysis of mtDNA variance within and among populations reveals high levels of genetic partitioning. Over the entire state of Florida, nearly 30% of the total molecular variance was a result of variation among the twelve sampled nesting beaches (Φ_{ST} =0.298, P<0.001) (Table 3). This value indicates strong population structure across Florida. However, the results from the chi-square analysis revealed there were no statistically significant differences between most adjacent populations.

Chi-square analysis also revealed no statistically significant differences between many distant populations. Migration estimates of Nm<4 generally indicate that gene flow is too low to homogenize populations (Birky et al. 1983). By this criterion, 33 of 66 Nm pairwise estimates fell below the critical threshold (Table 3). Of the remaining 33 estimates (Nm >4), 15 involve comparisons from opposite sides of the peninsula. The most extreme example is Amelia Island and Eglin Air Force Base, which are separated by over 1600 km of coastline.

How can we reconcile the strong overall population structure with the apparent genetic homogeneity of widely separated locations? Some long-term tagging studies have shown that there is occasional movement between nesting beaches (Bjorndal et al. 1983). Long distance relocations of nesting females could explain the high migration estimates between populations on opposite sides of the peninsula. However, most documented relocation events occur between adjacent nesting beaches involving a few tens of km, with more distant relocations occurring much less frequently (Richardson 1982).

Given the pattern of strong population structure revealed by Φ- statistics, and considering the life history characteristics of loggerhead turtles, a second explanation bears consideration. The similarity of the haplotype distributions between widely separated nesting beaches may be a remnant of historical lineage sorting, rather than an indication of present day migration. During the Wisconsin glaciation 24,000-10,000 years ago, loggerheads may have nested in south Florida but almost certainly not through the remainder of the current nesting range in Florida (see Hedgpeth 1954). Loggerheads require sand temperature of at least 25° C to nest (Dodd 1988); therefore the majority of the Florida peninsula has been amenable to nesting for less than 10,000 years. After the Wisconsin glaciation, loggerhead turtles evidently colonized up the coasts of Florida but have not had sufficient time to differentiate into highly isolated nesting colonies. Hence the observed population structure is shallow (in an evolutionary framework), encompassing less than 600 loggerhead generations. Considered in this historical context, the similarity of widely

separated locations is very likely a result of genetic drift during colonization northward from an ancestral population to the south.

Encalada et al. (1998) hypothesized that the break between populations on the Atlantic coast would occur somewhere between Amelia Island and Cape Canaveral, the location of a widely recognized biogeographic break between tropical and warm-temperate biota (Avise 1992). Volusia County nesting beaches lie within this region, and biogeographic considerations would indicate that they are affiliated with the nesting groups to the north. However the corresponding haplotype distribution is not easily affiliated with populations to the north or south. Chi-square analysis indicates that Amelia Island (to the north) and Volusia County are not differentiated (P=0.25), but this could be due to the low sample size from Amelia Island (n=12). When Amelia Island samples are grouped with the samples from adjacent Georgia barrier islands to the north (as suggested by Encalada et al. 1998) Volusia County is significantly different (P<0.01, data not shown). Volusia was not statistically differentiated from Melbourne Beach to the south (P=0.16), but this region has intermediate haplotype frequencies and may not belong to either the Amelia Island or Melbourne management units. In contrast, the Dry Tortugas is a highly distinct population, as indicated by significant χ^2 values in all pairwise comparisons with no migration estimates greater than Nm=0.74.

Based on the overall pattern of mtDNA distributions in Florida, we did not find differentiation on a scale of tens of km. We begin to find differences in comparisons across distances greater than 100 km. Tag returns are consistent

with this scale for management units; Richardson (1982) reports 20% nesting crossover between adjacent barrier islands in Georgia but only a 2-4% crossover involving more distant barrier islands along the Georgia coast. Based on these findings we conclude that natal homing occurs with the precision of tens of km. As a first approximation for defining management units, we suggest a scale of 100 km between discontinuous nesting habitats. In terms of Florida management units the SE and SW regions are not significantly different and perhaps should be combined into a single unit. The revised three regions (NE, S, and NW) plus the Dry Tortugas constitute management units that would protect the majority of genetic diversity indicated by mtDNA surveys.

Genetic diversity in mtDNA should not be the sole criterion for defining management units; demographic trends have to be taken into account, as well as the risk of extirpation for individual areas. For example, the Dry Tortugas is already protected as a National Park while other areas (such as Volusia County, which includes the tourist resort of Daytona Beach) are highly susceptible to human impacts that may be detrimental to sea turtle survival.

CHAPTER 3
MIGRATORY BEHAVIOR AND SITE FIDELITY IN MALE LOGGERHEAD TURTLES (*CARETTA CARETTA*) IN THE NORTHWEST ATLANTIC USING NUCLEAR DNA MARKERS

Introduction

Complex animal behaviors such as sex-biased dispersal or philopatry may be revealed by multi-locus population genetic studies. For example, population structure based on mitochondrial markers may differ from the structure defined using nuclear markers, due to the different inheritance mechanisms of these two genomes (Karl and Avise 1992). Mitochondrial DNA (mtDNA) is maternally inherited (passed from mother to offspring) without recombination, while nuclear DNA (nDNA) is biparentally inherited and undergoes recombination. Discordance between population structure detected with mtDNA and nDNA assays is indicative of sex-specific dispersal, as has been demonstrated in marine mammals, e.g. humpback whales (Baker et al. 1998). However, the unusual life history of marine turtles may provide the starkest examples: cases in which female matrilines are highly structured and nuclear lineages have no population structure.

The loggerhead turtle (*Caretta caretta*) is distributed worldwide, inhabiting coastal temperate, tropical, and subtropical waters of the Atlantic, Indian and Pacific oceans. Females nest primarily on warm temperate beaches and after a 50-60 day incubation, hatchlings enter the surf to begin a pelagic phase where

they drift passively in ocean currents for five or more years (Carr 1986, Bjorndal et al. 2000). Advanced juveniles (or subadults) leave the pelagic habitat and recruit to shallow coastal feeding grounds. Upon reaching sexual maturity at an estimated 20-30+ years of age (Bjorndal et al. 2000, Klinger and Musick 1995), adult loggerheads leave the foraging grounds and travel tens to thousands of kilometers to mating and nesting grounds. Results from mark and recapture studies indicate that the majority of females return to the same nesting beach for subsequent nesting efforts (Carr 1986) and both sexes return to the same feeding grounds after reproductive migrations (Limpus et al. 1992).

Molecular techniques have enabled researchers to elucidate life history characteristics of marine turtles that would have taken decades of field studies, if they could be done at all. Surveys of the maternally inherited mtDNA genome have demonstrated natal homing in several sea turtle species, including green (*Chelonia mydas*; Bowen et al., 1992, Norman et al., 1994, Encalada et al., 1996), hawksbill (*Eretmochelys imbricata*; Bass et al. 1996), leatherback (*Dermochelys coriacea*; Dutton et al., 1999) and loggerhead turtles (Bowen et al., 1993, Francisco et al., submitted). Foraging ground studies utilizing mtDNA have linked adult and juvenile turtles to their corresponding rookeries (Broderick et al., 1994, Bowen et al., 1996, Lahanas et al., 1998) and have documented developmental migrations that span the Atlantic and Pacific oceans (Bowen et al., 1995, Bolten et al., 1998).

These mtDNA studies have been instructive, but they pertain predominantly to the female (egg-producing) lineages. Informed management

requires knowledge of male dispersal and philopatry as well. Specifically, wildlife managers need to know the migratory behavior of males and what effects their behavior has on the overall population structure. A few studies have examined biparentally inherited nuclear DNA (nDNA) loci in sea turtles. Peare and Parker (1996) analyzed minisatellite DNA in nesting green turtles and found genetic structure on the scale of a few kms in Tortuguero, Costa Rica but not in Melbourne Beach, Florida. Although this study looked at nDNA, the goal was to investigate the precision of female philopatry. Schroth et al. (1996) compared mtDNA and RAPD (random amplified polymorphic DNA) profiles in nesting loggerheads from the eastern Mediterranean and found that male-mediated gene flow was insufficient to prevent genetic subdivisions among neighboring rookeries. Karl et al. (1992) surveyed anonymous nDNA loci and demonstrated that male green turtles might provide an occasional avenue of gene flow between nesting colonies. Only one study to date has examined male-mediated gene flow using microsatellites; Fitzsimmons et al. (1997b) surveyed Australian green turtles and found that widely separated nesting aggregates were genetically distinct populations, although low levels of gene flow were detected. An interesting exception involved two nesting populations that overlap on migratory corridors or feeding grounds. Nuclear gene flow was found to be extensive between these two locations, despite a nearly fixed difference in mtDNA haplotypes (Fitzsimmons et al. 1997b).

Microsatellite DNA assays are generally considered to be the most sensitive population genetic marker for detecting fine scale population structure

(Goldstein and Pollack 1997). Microsatellites are preferred over RAPDs because each set of primers amplifies a single locus that contains a simple repeat motif. Variation in the number of repeats (such as CA7 or CA9) is responsible for the observed allelic diversity. The popularity of these genetic markers led to the development of statistical methods based on explicit models of microsatellite evolution (Goldstein et al., 1995, Slatkin et al., 1995).

Our analyses of loggerhead microsatellite loci allows for a comparison to studies using mtDNA alone and therefore an elucidation of the degree of male-mediated gene flow among nesting populations. Analysis of nuclear DNA can also reveal information on stock structure, effective population size, levels of inbreeding within small nesting populations, and can prevent some common pitfalls in stock definition (Bowen, 1997). This type of information is important for the resolution of management units and can greatly enhance the scientific foundations of recovery plans.

Materials and Methods

Sample Collection

We obtained 462 *Caretta caretta* specimens from 22 sites throughout the southeast U.S. and two additional sites in Brazil between 1995 and 1999 (Fig. 1). Tissue from moribund hatchlings, embryos and skin biopsy punches were placed in 15 ml of a saturated salt buffer (Amos and Hoezel, 1991), and stored at room temperature. Blood samples were obtained from the dorsal cervical sinus of nesting females following the procedure of Owens and Ruiz (1980) and were

stored in a 9:1 lysis buffer-to-blood ratio at room temperature (Fitzsimmons et al. 1999). Whole genomic DNA was isolated according to Hillis et al (1996) using a standard phenol chloroform extraction and ethanol precipitation.

Microsatellite Library

Microsatellite library construction was accomplished using the strategy of Kandpal et al. (1994). Genomic DNA from two different locations were combined, digested with Sau3AI, and fractionated on a 1.2% agarose gel. The 400- to 1500 bp region was excised from the gel, and purified using the QIAquick Gel Extraction Kit (Qiagen, Valencia, CA). The purified DNA was ligated to Sau3AI linkers using T4DNA ligase. Excess linkers were removed by gel electrophoresis, and the 400-1500 bp region was recovered using the QIAquick Gel Extraction Kit. One microgram of ligated DNA was denatured and then hybridized in solution to a biotinylated probe (5'-(CA15TATAAGATA-biotin-3'). The hybridized fragments were captured using VECTREX Avidin D (Vector Laboratories, Burlingame, CA) following the manufacturers instructions.

Enriched DNA fragments were amplified by polymerase chain reaction (PCR) with Sau-L-A primer (5'-GCGGTACCCGGGAAGCTTGG-3'). PCR parameters (1.5 mM $MgCl_2$, 100 uM dNTPs each, 0.5 uM primer, 2.5 U Taq in a 50 uL rxn 94 °C for 3 min initial denaturation, (94 °C 1 min, 68 °C 1 min, 72 °C 2 min) 25 cycles, 72 °C for 10 min final amplification). The PCR product was ligated to the pCR2.1 vector from the TOPO-TA cloning kit (Invitrogen, Carlsbad, CA), transformed into competent *E. coli* INValphaF cells and plated onto LB-ampicillin (50 ug/mL) agar plates.

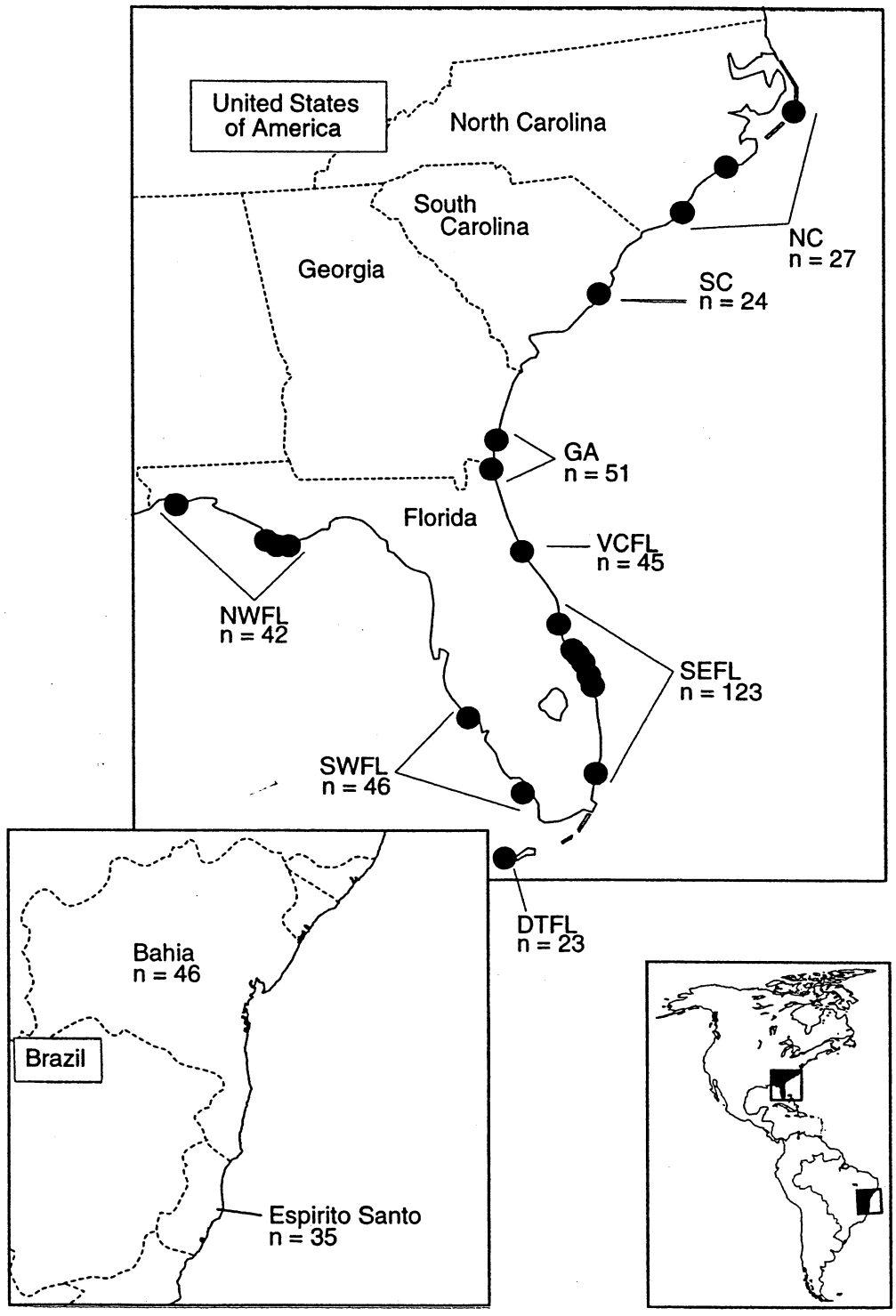

Figure 3. Collections sites and analysis groupings for *C. caretta* samples from the southeast U.S. and Brazil.

Bacterial clones were screened by direct colony lifts using nylon hybridization membranes (Micron Separations, Inc, Westboro, MA), hybridized with a (CA)n probe (Lifecodes Corp, Stamford, CT), and developed with Lumi-phos 480 (modified dioextanes). The membranes were exposed to x-ray film that was visually inspected for microsatellite positive clones. Positive clones were cultured overnight in 3 mL of LB-Amp (Luria broth with 100 uL/mL Ampicillin). The cultured cells were pelleted and plasmids purified using the Qiagen Miniprep Kit. A dot blot was performed on each sample to confirm the presence of CA repeats.

Plasmids positive for CA repeats were sequenced by the DNA Sequencing Core at the University of Florida. Oligonucleotide primers were designed in the regions flanking the repeats using Oligo Primer Analysis software (Molecular Biology Insights, Inc., Cascade, CO).

Microsatellite Amplification

Four microsatellite loci (dinucleotide repeats) previously shown to be polymorphic in loggerheads plus one locus developed for this project were used for population analysis: CC141 and CC7 (Fitzsimmons 1996, 1998); Ccar176 (Moore 2000); DC107 (Dutton, pers comm.); and CCM2 (this study). One primer from each locus was fluorescently labeled with either 6-Fam or Tet (CyberSyn, Lenni, PA). The loci were amplified in 10 uL reactions containing 25-50 ng of DNA, 1x Promega PCR buffer, 0.2 mM each dNTP, 0.375 - 1.125 mM $MgCl_2$, 0.4 U Promega Taq, and 8 pmol of each primer. The cycling parameters used were: one cycle of denaturation at 93 °C for 3 min, followed by 6 cycles of denaturation

at 92 °C for 30s, annealing at 60 °C (Ccar176), 58 °C (CCM2), 56 °C (CC141, CC7), 55 °C (DC107) for 55s, 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 1 min 25 s, followed by a final extension at 72 °C for 10 min. PCR products were analyzed either by the Iowa State University Sequencing Facility with an ABI 377 or on an ABI 310 automated sequencer (Applied Biosystems Inc., Foster City, CA) in the Dept. of Fisheries and Aquatic Sciences at the University of Florida.

Data Analysis

Allele designations were assigned using Genescan Analysis software (Perkin-Elmer Corp., Foster City, CA). Population subdivisions were determined a priori based on previous mtDNA studies. The localities were initially partitioned into ten groups: 1) North Carolina (n=27); 2) South Carolina (n=24); 3) Georgia plus adjacent Amelia Island, Fl (n=51); 4) Volusia County (n=45); 5) Southeast Florida (SEFL; n=123) from Cape Canaveral to Port Everglades; 6) Dry Tortugas, Florida (DTFL; n=23); 7) Southwest Florida (SWFL; n=46) from the Everglades to Tampa Bay; 8) Northwest Florida (NWFL; n=42) the Panhandle; 9) Bahia, Brazil (n=46); 10) Espirito Santo, Brazil (n=35). Since we found no significant differences between northern and southern sample sites in Brazil (separated by no more than 1000 kms) they were subsequently grouped together for all statistical tests.

Tests for departure from Hardy-Weinberg equilibrium (HWE), differences in allelic counts among localities, and pairwise tests for population differentiation

using allele frequencies were conducted using GENEPOP version 3.1 (Raymond and Rousset 1995). P-values were calculated with a Markov chain-randomization (Guo and Thompson 1992). Fisher's method, which assumes statistical independence across loci, was used to combine test results for allelic counts among localities for all five loci (Raymond and Rousset 1995).

Estimates of population structure were made using both the infinite-alleles (IAM) and the stepwise mutation (SMM) evolutionary models. The extent of population subdivision under the IAM was examined with an analysis of molecular variance (AMOVA) using ARLEQUIN ver 2.0 (Schneider et al. 2000). This program package calculates F-statistics (Wright 1965) utilizing the methodology of Weir and Cockerham (1984). F statistics are used to partition the genetic variation within populations (F_{IS}) and between populations (F_{ST}) (populations have been determined a priori based on geographic or other criteria). Slatkin's (1995) R_{ST} was used to quantify genetic differentiation under the SMM. RSTCALC (Goodman 1997) was used to calculate p, an estimator of R_{ST} that takes into account differences in variation among loci and differences in sample size among populations. The significance of these estimates was evaluated by describing the null distribution of pairwise F_{ST} or pairwise p-values (R_{ST}) under the assumption of panmixia by 1000 permutations of genotypes between populations, or genotypes across population strata.

Results

In screening for new microsatellite loci, a total of 25 positive clones were sequenced. Of these 25, three had no microsatellite array, 12 did not contain enough flanking region for primer design, and primers were designed for the remaining ten. Four of the loci were monomorphic, and five of the primer pairs did not amplify reliably despite repeated optimization attempts (Table 1). The remaining locus was used in this study, in addition to the four loci characterized in previous studies.

High levels of polymorphism were observed at all five loci (Table 2). The number of distinct alleles observed per locus ranged from 10 for CCM2 to 29 for Ccar176 with an average of 16.8. Gene diversity (H_e) ranged from 74.5% (CCM2) to 86.5% (CC141) and averaged 79.6%. The observed heterozygosities (H_o) were also high with values greater than 72% at all five loci (Table 2). In all cases alleles varied by increments of 2bp, consistent with characterization of a CA motif.

Table 4. Primer sequences, annealing temperatures (T_a), size of amplified product and observed heterozygosity (H_o) for microsatellite primer pairs developed.

Locus	Primer Sequence	T_a (°C)	Size (bp)	H_o
CCM1	F: GCC ACT CAT CAC ATT GCC TCA TT R: ACA GAC TCC CCA CAG CCA CCT C	57	237	0
CCM2	F: TGG CAC TGG TGG ATT R: TGA CTC CCA AAT ACT GCT	58	169-195	0.72
CCM3	F: GCC GTT GAG AGA GCC AC R: TGT GTG CCA GCC AAT AGG	54		?
CCM4	F: ATG CCC GCT CAA CAC TTC R: TCT GCC GTT GAG AGA GCC	56		?
CCM5	F: TGC CGT TGA GAG AGC CA R: TTG TGT TGT GTG CCA GCC	60	170	0
CCM6	F: TAA GTG GTT GTA AAT GTG R: TGC CTT GCT AGT GAC	51		?
CCM7	F: CGG GAA GCT TGG AGG TG R: GCT TCC GGC TCG TAT GTT	56	228	0
CCM8	F: TCA TTA CAT TGC CTC ATT R: TAC TTC CCC AGA CAG ACA	53	117	0
CCM9	F: TGA AGT GCA TTG AGG R: CAT GTG GCC CTT GAT	55		?
CCM10	F: GTT CAA GCG ATT CTC R: GAT CCG AGC TCG GTA	60		?

Table 5 *Caretta caretta*. Summary statistics for five microsatellite locievaluated [product size in basepairs, number of alleles (*k*), gene diversity(aka expected heterozygosity, H_e), and observed heterozygosity (H_o)].

Locus	Product size (bp)	*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

Allelic counts were similar at all localities (Fisher's method $\chi^2 = 96.30$, df = 90, P = 0.31). The size-frequency distributions of microsatellite alleles varied among the nine populations (Figs. 2-6). For loci Ccar176, CC141 and CC7 the allelic distributions were skewed to the left (Figs. 4-6), and locus DC107 was skewed slightly to the right (Fig. 2). Allele distributions for the Brazilian population showed reduced diversity (relative to the southeast U.S.) with a single allele occurring at over 50% frequency at three of the five loci [allele 185 at locus CCM2 (Fig. 3), allele 192 at locus CC141 (Fig. 5), and allele 219 at locus CC7 (Fig. 6)].

In tests of Hardy Weinberg equlibrium three of 45 population/locus combinations (Volusia County, FL/CC7, P = 0.02, Dry Tortugas, Fl/CC141, P = 0.02, and Northwest FL/CC141, P = 0.03) deviated significantly from expected values (95% confidence level)(Table 3). In all three cases this indicated a lower than expected heterozygosity. The departure from Hardy-Weinberg equilibrium was not significant at the table wide level when Fisher's method was used to combine the 45 independent tests (P = 0.31).

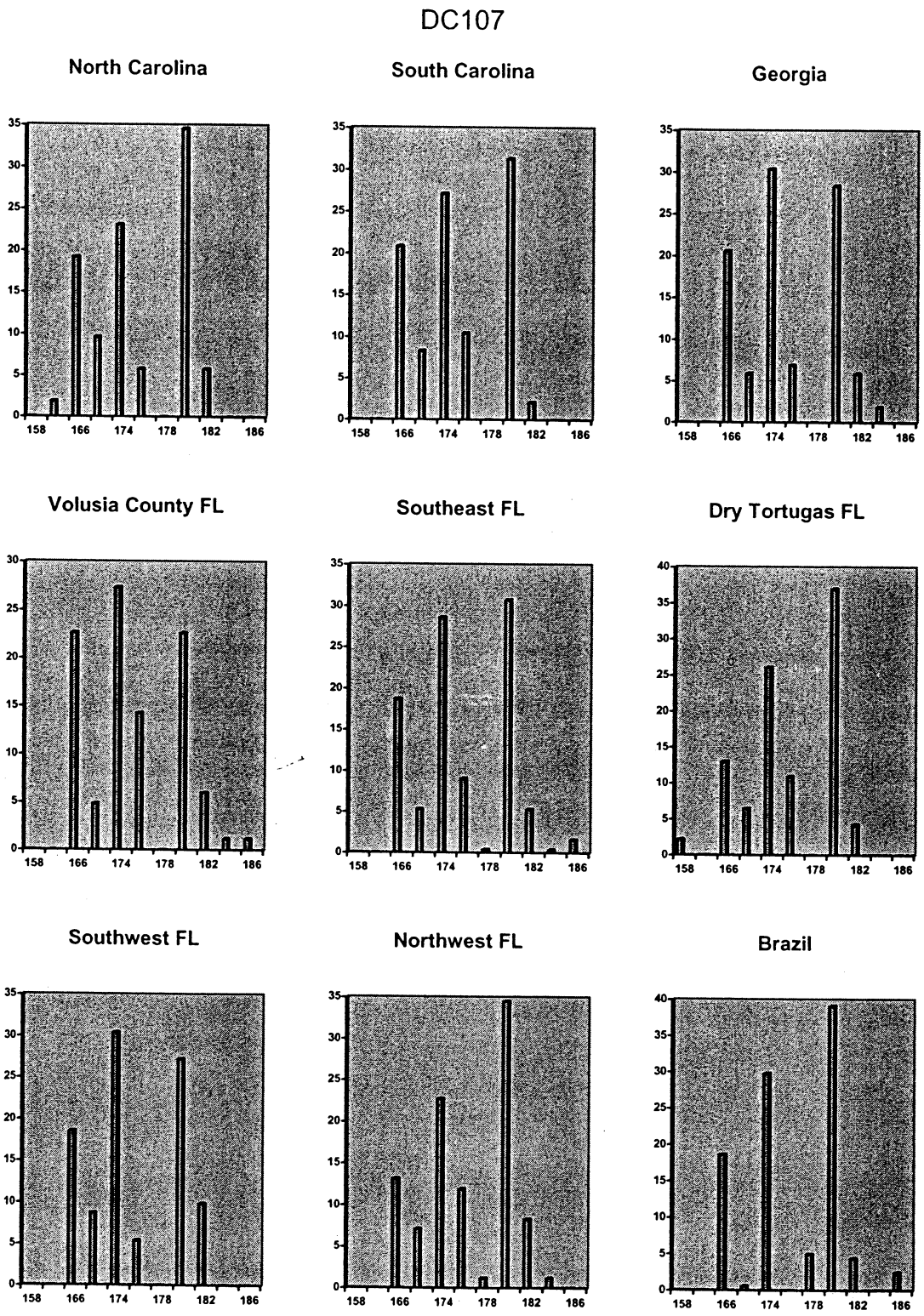

Figure 4. *Caretta caretta*. Histograms of allele frequencies (%) at microsatellite locus DC107 for the nine sampling locations. X-axis alleles in base pairs, Y-axis allele frequencies.

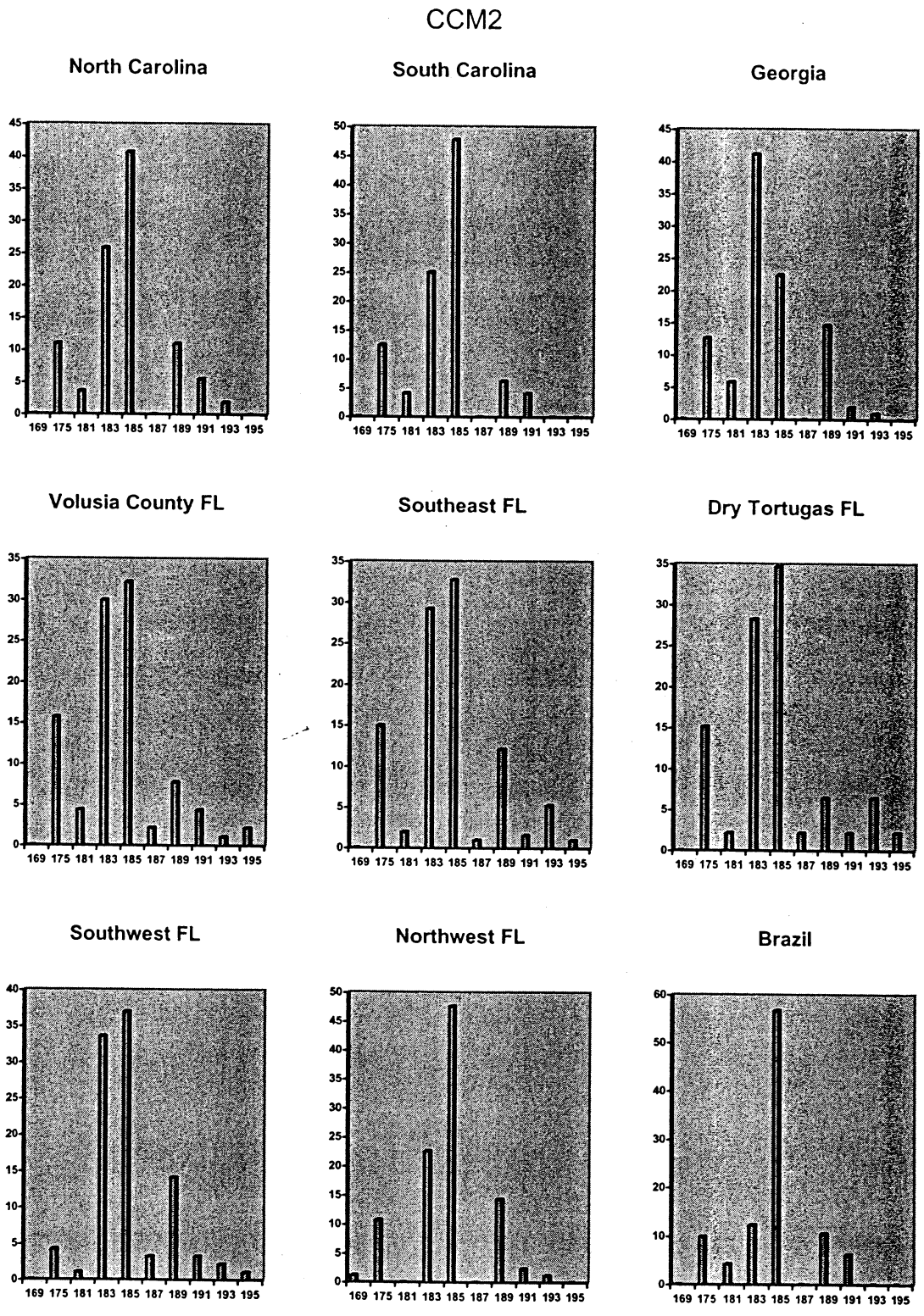

Figure 5. *Caretta caretta*. Histograms of allele frequencies (%) at microsatellite locus CCM2 for the nine sampling locations. X-axis alleles in base pairs, Y-axis allele frequencies.

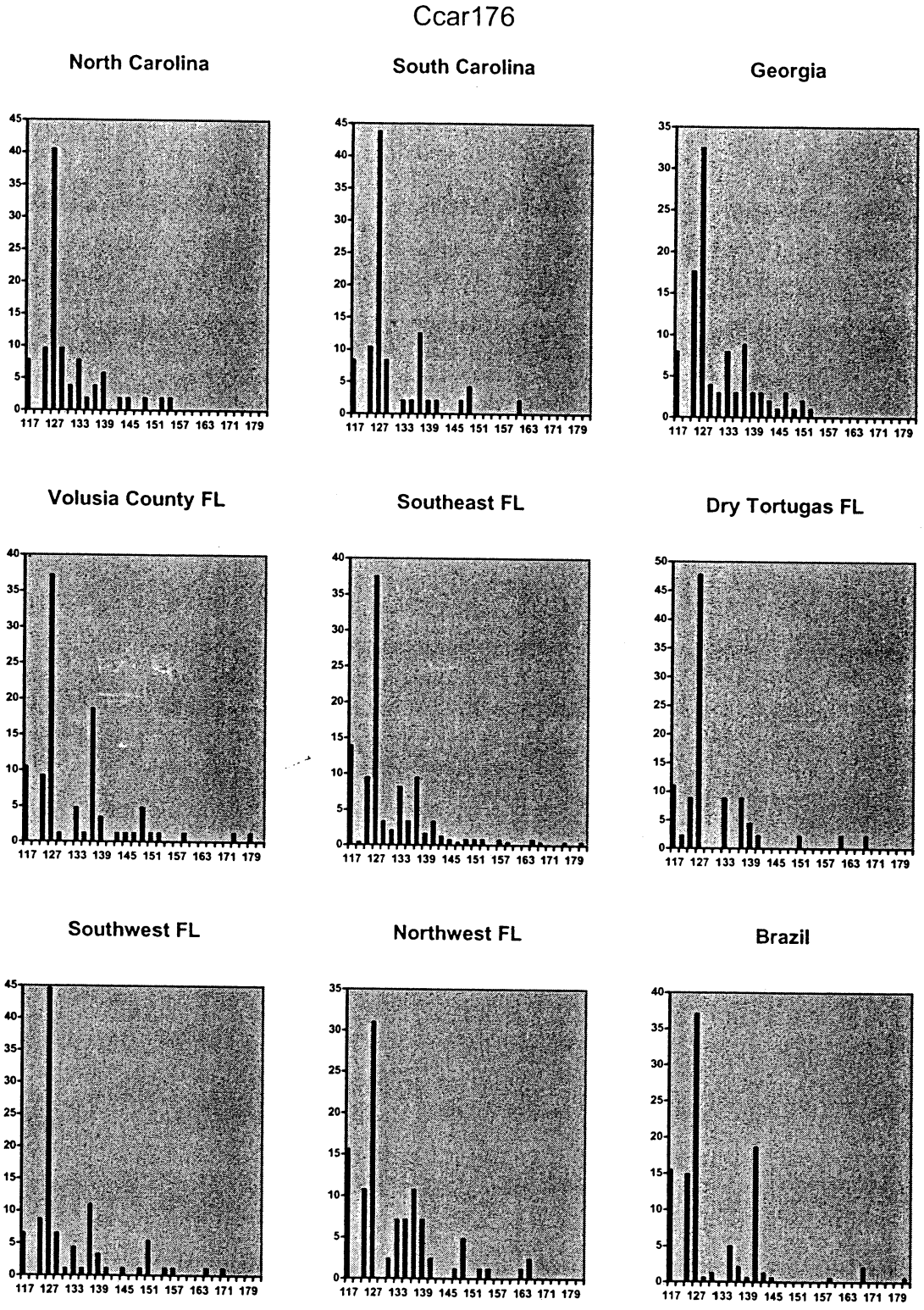

Figure 6. *Caretta caretta*. Histograms of allele frequencies (%) at microsatellite locus Ccar176 for the nine sampling locations. X-axis alleles in base pairs, Y-axis allele frequencies.

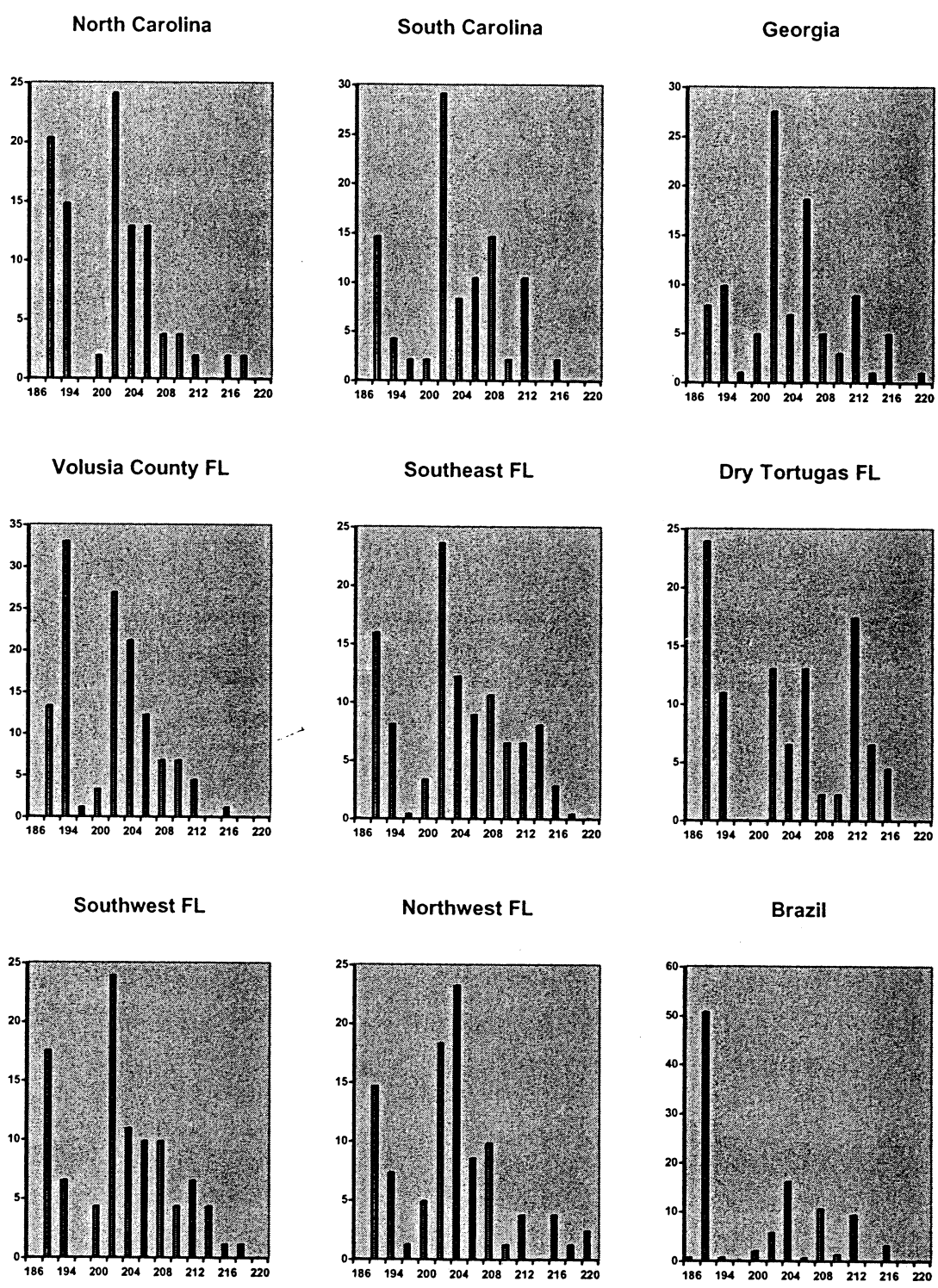

Figure 7. *Caretta caretta*. Histograms of allele frequencies (%) at microsatellite locus CC141 for the nine sampling locations. X-axis alleles in base pairs, Y-axis allele frequencies.

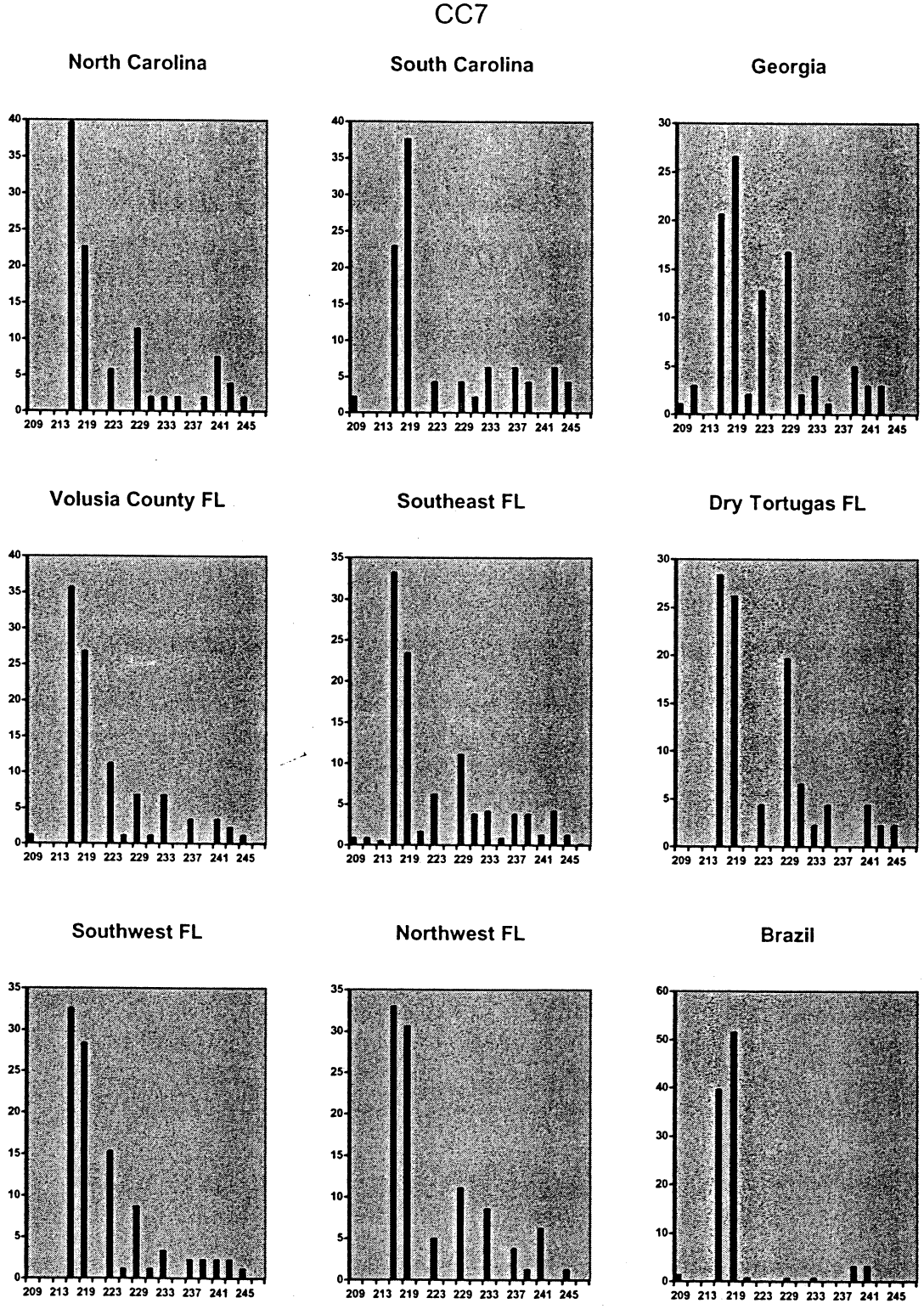

Figure 8. *Caretta caretta*. Histograms of allele frequencies (%) at microsatellite locus CC7 for the nine sampling locations. X-axis alleles in base pairs, Y-axis allele frequencies.

Table 6. *Caretta caretta*. Number of samples (N), alleles (k), gene diversity (H_e), and observed heterozygosity(H_o) for each population and each locus (* allelic frequencies significantly out of Hardy-Weinberg equilibrium based on exact tests ($p<0.05$).

	DC107	CCM2	Ccar176	CC141	CC7	Mean *k* Mean H_e
NC						
N	26	27	26	27	26	
k	7	7	14	11	10	9.8
H_e	0.7888	0.7512	0.8137	0.8537	0.7730	0.7961
H_o	0.7692	0.7037	0.9231	0.7407	0.7692	
SC						
N	24	24	24	24	24	
k	6	6	12	11	11	9.2
H_e	0.7837	0.6995	0.7801	0.8582	0.8041	0.7851
H_o	0.7500	0.75	0.75	0.8333	0.8750	
GA						
N	51	51	51	51	51	
k	7	7	16	13	13	11.2
H_e	0.7800	0.7451	0.8455	0.8618	0.8443	0.8153
H_o	0.8039	0.7451	0.902	0.7843	0.8627	
VCFL						
N	42	45	43	45	45	
k	8	9	17	11	12	11.4
H_e	0.8058	0.7795	0.8098	0.8477	0.7868	0.8059
H_o	0.7619	0.8	0.7674	0.7778	0.6667*	
SEFL						
N	123	123	123	123	122	
k	9	9	23	13	17	14.2
H_e	0.7779	0.7679	0.8158	0.8717	0.8146	0.8096
H_o	0.7967	0.7561	0.7642	0.8780	0.7869	
DTFL						
N	23	23	23	23	23	
k	7	9	11	10	10	9.4
H_e	0.7768	0.7826	0.7488	0.8744	0.8203	0.8006
H_o	0.6957	0.6957	0.6087	0.7391*	0.7391	
SWFL						
N	46	46	46	46	46	
k	6	9	17	13	12	11.4
H_e	0.7917	0.7332	0.775	0.8803	0.7883	0.7937
H_o	0.8043	0.7826	0.7391	0.8913	0.6957	
NWFL						
N	42	42	42	41	41	
k	8	7	15	13	9	10.4
H_e	0.7955	0.6976	0.8526	0.8738	0.7811	0.80001
H_o	0.8571	0.6905	0.8810	0.7561*	0.9024	
BR						
N	80	81	81	81	81	
k	7	6	14	11	8	9.2
H_e	0.7198	0.6398	0.7840	0.6981	0.5829	0.6849
H_o	0.75	0.5926	0.7901	0.7037	0.5679	

Excess homozygosity for all loci combined, as quantified by the correlation of alleles within individuals (F_{IS}) was not significantly different from zero (Table 4). None of the 90 exact tests for linkage-disequilibrium resulted in significant values.

Table 7. *Caretta caretta* Population structure on the coasts of the southeast U.S. and Brazil.*,** P<0.01 and P<0.001 respectively.

Locus	F_{IS}	F_{ST}	R_{ST}
DC107	-0.0123	0.0004	-0.0043
CCM2	0.0133	0.0232**	-0.0014
Ccar176	0.0173	0.0092	-0.0063
CC141	0.0444	0.0372**	0.0362**
CC7	0.0246	0.0212**	0.0014**
Total	0.0179	0.0189*	0.0057*

Pairwise tests for genetic differentiation using allele frequencies show that the Brazilian turtles are genetically distinct from all other populations surveyed here (Table 5). Considering just the southeast U.S., genetic differentiation was observed between the Dry Tortugas and three other locations at locus CC141 (Table 5). In comparing Georgia to other locations, nine of 35 pairwise tests showed significant genetic differentiation (Table 5).

Table 8. *Caretta caretta*. Results of pairwise tests of genic (allelic) differentiation between populations at each locus.NS (not significant) **,*** P<0.05, p<0.001 respectively.

Comparison	DC107	CCM2	CCAR176	CC141	CC7
NC vs SC	NS	NS	NS	NS	NS
NC vs GA	NS	NS	NS	NS	NS
NC vs VC	NS	NS	NS	NS	NS
NC vs SEFL	NS	NS	NS	NS	NS
NC vs DTFL	NS	NS	NS	NS	NS
NC vs SWFL	NS	NS	NS	NS	NS
NC vs NWFL	NS	NS	NS	NS	NS
NC vs BR	***	NS	***	***	***
SC vs GA	NS	**	NS	NS	**
SC vs VCFL	NS	NS	NS	NS	NS
SC vs SEFL	NS	NS	NS	NS	NS
SC vs DTFL	NS	NS	NS	NS	NS
SC vs SWFL	NS	NS	NS	NS	NS
SC vs NWFL	NS	NS	NS	NS	NS
SC vs BR	***	NS	***	***	***
GA vs VCFL	NS	NS	NS	**	**
GA vs SEFL	NS	NS	NS	**	NS
GA vs DT	NS	NS	NS	NS	NS
GA vs SWFL	NS	**	NS	NS	NS
GA vs NWFL	NS	**	NS	**	**
GA vs BR	***	***	***	***	***
VCFL vs SEFL	NS	NS	NS	NS	NS
VCFL vs DTFL	NS	NS	NS	***	NS
VCFL vs SWFL	NS	NS	NS	NS	NS
VCFL vs NWFL	NS	NS	NS	NS	NS
VCFL vs BR	***	***	***	***	***
SEFL vs DTFL	NS	NS	NS	**	NS
SEFL vs SWFL	NS	NS	NS	NS	NS
SEFL vs NWFL	NS	NS	NS	NS	NS
SEFL vs BR	***	***	***	***	***
DTFL vs SWFL	NS	NS	NS	NS	NS
DTFL vs NWFL	NS	NS	NS	**	NS
DTFL vs BR	***	***	***	***	***
SWFL vs NWFL	NS	NS	**	NS	NS
SWFL vs BR	***	***	***	***	***
NWFL vs BR	***	**	***	***	***

Pairwise F_{ST} values (the proportion of diversity among populations) were calculated and compared to R_{ST}, an analogue of F_{ST}, to estimate levels of genetic

differentiation for microsatellite loci (Table 6). Georgia had sigificant F_{ST} estimates in six out of eight comparisons (the exceptions being North Carolina and the Dry Tortugas) while the only significant R_{ST} values were in comparisons of Brazil vs. the southeast U.S. locations (Table 6). However, the R_{ST} values for Brazil vs. North Carolina and Brazil vs. the Dry Tortugas were not significant (p= 0.46 and p= 0.095, respectively). The R_{ST} estimate for overall comparisons was lower than the corresponding F_{ST} estimate (0.0057 and 0.0189, respectively). Estimates of F_{ST} and R_{ST} for each locus at all localities ranged from 0.004 to 0.0372 and -0.0063 to 0.0362 respectively (Table 4). Single locus F_{ST} estimates for three loci (CCM2, CC141, CC7) were significantly greater than zero as was the combined estimate for all loci (F_{ST} = 0.0189) whereas only CC141 and CC7 had significant single locus R_{ST} estimates and the combined estimate was significant (R_{ST} = 0.0057)(Table 4).

Table 9. *Caretta caretta*. F_{ST} (below diagonal) and Slatkin's analogous R_{ST} (above diagonal) between all pairs of populations. *,** P<0.05 and P<0.001 respectively calculated from 1000 random permutations.

	NC	SC	GA	VCFL	SEFL	DTFL	SWFL	NWFL	Brazil
NC		-0.0020	0.0114	0.0026	-0.0005	-0.0093	0.0026	0.0036	-0.0012
SC	-0.0015		-0.0138	-0.0103	-0.0061	-0.0172	0.0034	-0.0015	0.0269*
GA	0.0800	0.0108*		-0.0043	-0.0014	-0.0122	0.0115	0.0012	0.0365*
VCFL	-0.0003	0.0017	0.0076*		-0.0000	-0.0081	0.0029	0.0005	0.0262*
SEFL	-0.0033	0.0012	0.0057*	0.0007		-0.0109	0.0027	-0.0025	0.0144*
DTFL	-0.0046	0.0012	0.0075	0.0078	-0.0007		-0.0073	-0.0139	0.0118
SWFL	-0.0039	-0.0027	0.0055*	0.0002	-0.0002	0.0004		-0.0005	0.0214*
NWFL	-0.0029	0.0020	0.0215**	0.0062	0.0048	0.0052	0.0066*		0.0179*
Brazil	0.0429**	0.0396**	0.0812**	0.0594**	0.0489**	0.0437**	0.0501**	0.0346**	

Discussion

Surveys of nesting loggerhead turtles with mtDNA have shown population structuring, consistent with female natal homing (Bowen and Karl 1996). Francisco et al. (submitted) found high levels of population structure over the state of Florida based on mtDNA haplotypes (Φ_{ST} = 0.298). However, the same populations have much less population structuring at five nuclear loci. When five Florida populations along with North Carolina, South Carolina, Georgia and Brazil were analyzed using microsatellites, the comparable population statistics were more than an order of magnitude lower (F_{ST} = 0.0189). Previous studies have reported incongruence between mitochondrial and nuclear based variation, e.g. in trout (Bernatchez and Osinov 1995), the African elephant (Nyakaana and Arctander 1999) and Dall's porpoise (Escorza-Trevino and Dizon 2000). These studies explained the apparent discrepancies as differences in the inheritance dynamics as well as different modes and rates of mutation between the two types of genetic markers.

The discrepancy between mtDNA and microsatellite data indicates that male loggerheads provide an avenue for gene flow among matrilineally-structured nesting colonies. To reconcile the mtDNA and nDNA data, three classes of explanations bear consideration. First, perhaps male loggerheads are not philopatric and they migrate to non-natal breeding aggregations. Fitzsimmons et al. (1997a) sampled male green turtles on courtship areas and compared the mtDNA frequencies to those of the nesting females in those areas. They found that the haplotype frequencies were comparable between the sexes

indicating that males were returning to the vicinity of their natal site to breed. Since the life history characteristics of these two species are similar we suspect that these findings may also pertain to loggerheads, and provisionally discount the hypothesis that males are not philopatric.

The second possibility is that males are philopatric to natal sites for breeding, but they also mate opportunistically, copulating with receptive females on feeding grounds or in migratory corridors (Bowen 1997). Male Australian green turtles were found to migrate more frequently to breeding grounds than females and had a tendency to inhabit foraging grounds closer to the nesting habitat (Fitzsimmons et al. 1997b). Females may be intercepted by males during reproductive migrations, especially if they pass through nonnatal courting areas.

A third alternative is that only a percentage of males are philopatric. Genetic studies of weakfish (an estuarine-spawning marine fish) utilizing allozymes and mtDNA found no genetic differentiation among spawning populations (Crawford et al., 1989, Graves et al., 1992). However, Thorrold et al. (2001) used geochemical signatures in otoliths and found that spawning site fidelity ranged from 60 to 81%. The majority of male loggerheads may be philopatric to natal sites, but this fidelity may not be detected in nDNA assays as it would only take a few strays to homogenize populations.

Results from pairwise tests of allelic frequencies (Table 5) and pairwise F_{ST}'s (but not R_{ST})(Table 6) revealed significant differences between Georgia and most other southeast U.S. populations. These results are intriguing because Georgia is not obviously more isolated or distant than the other U.S. populations.

In principle it is possible that Georgia turtles are resident year-round, although adults are only documented to occur in Georgia's coastal waters from May to October with any regularity (Ruckdeschel et al. 2000). Another alternative is that Georgia turtles have different migratory routes than other turtles and thereby avoid inter-rookery gene flow. This could be tested with satellite transmitters. A third possibility, prompted by the R_{ST} results (Table 6), is that the significant F_{ST} values do not reflect a biological phenomenon, but are an artifact of our analysis. However, spurious values would be expected to be scattered throughout the data set, not aligned with comparisons of Georgia versus elsewhere. The explanation for the Georgia findings is not clear at this time.

The difference between Brazilian and U.S. loggerheads represents the deepest genetic partition observed in our study. Analysis of mtDNA revealed no shared haplotypes between the two countries (Encalada et al. 1998, unpub data) and analysis of nuclear loci found significant allele frequency shifts. These differences highlight a cryptic aspect of the life history of loggerhead turtles. Juvenile loggerheads have been shown to cross both the North Atlantic and North Pacific oceans during developmental migrations (Bolton et al., 1998, Bowen et al., 1995), but they may only rarely cross between northern and southern hemispheres (Bowen et al. 1995). The significant population differentiation between northern and southern ocean basins in the Atlantic indicates that reproductive migrations do not span the equator and there do not appear to be avenues for routine gene flow between these locations.

CHAPTER 4
CONCLUSIONS

Conservation Implications

Loggerhead turtles have complex population structure. Population genetic theory, particularly the rules of inheritance, predict that such an outcome is possible (Avise 2000). The conservation ramifications are incompletely understood, but two conclusions are possible at this time: first, the occurrence of male-mediated gene flow does not change the status of rookeries as distinct management units (MUs). MU's as defined by Moritz (1994) are 'populations with significant divergence of allele frequencies at nuclear or mitochondrial loci'. mtDNA studies have shown that nesting populations have significant haplotype frequency differences and, regardless of the level of philopatry in males, the female (egg-laying) lineages are clustered by nesting beach fidelity. Because maternally inherited mtDNA is an indicator of historical female reproductive success, as noted by Avise (1995, 2000), the strong matrilineal population structure implies independent recruitment and demographic autonomy. Second, the interconnectivity of nesting populations in the southeast U.S. through male-mediated gene flow has some positive aspects in terms of conservation and management. Many of the nesting populations in the southeast U.S. are relatively small, especially in the Florida panhandle, Georgia, South Carolina and North Carolina. For these nesting aggregates, male-mediated gene flow

indicates that reduced genetic diversity in small populations is not a compelling issue. In typical small, isolated populations, genetic diversity is quickly lost by bottlenecks, low effective population size, and genetic drift. Loss of genetic diversity may retard a population's response to challenges such as disease, habitat degradation, climate changes or other perturbations, consequently the population is more susceptible to extinction. Small loggerhead nesting aggregates may not be susceptible to these problems as male-mediated gene flow can maintain high levels of nuclear DNA diversity in small nesting aggregates.

Finally, these findings indicate that nesting populations of the northwest Atlantic are not evolutionarily significant units (ESU's) defined as 'reciprocally monophyletic for mtDNA alleles and showing significant divergence of allele frequencies at nuclear loci' (Moritz 1994). Under this definition it may be possible to define ESU's as clusters of rookeries within ocean basins but certainly not at the scale of individual nesting aggregations. An exception to this generalization may be when only one nesting aggregate occurs in an ocean basin, in which case the ESU may be a single population.

Prospectus

Several research challenges lie ahead. First, it is desirable to test the alternatives we used to explain male-mediated gene flow. This can be initiated with mtDNA and microsatellite surveys of courting grounds, to assess the degree of male philopatry. Additional studies of the Georgia rookery are necessary to determine if some special life history attribute underlies the finding of genetic

distinctiveness. Finally, satellite telemetry may reveal the extent of overlap and contact between reproductive populations on foraging grounds. An appropriate balance of field and lab studies will be necessary to illuminate the reproductive behaviors of these enigmatic marine reptiles.

APPENDIX A
MITOCHONDRIAL DNA HAPLOTYPES

Table A. Mitochondrial DNA haplotypes for 274 *Caretta caretta* from Florida.

Sample	Location	Haplotype
CC244	Florida, Amelia Island	A
CC245	Florida, Amelia Island	A
CC246	Florida, Amelia Island	A
CC247	Florida, Amelia Island	A
CC248	Florida, Amelia Island	A
CC249	Florida, Amelia Island	A
CC250	Florida, Amelia Island	A
CC251	Florida, Amelia Island	A
CC252	Florida, Amelia Island	A
CC253	Florida, Amelia Island	A
CC255	Florida, Amelia Island	A
CC256	Florida, Amelia Island	A
CC1679	Florida, Volusia County	A
CC1680	Florida, Volusia County	A
CC1682	Florida, Volusia County	A
CC1684	Florida, Volusia County	B
CC1685	Florida, Volusia County	B
CC1686	Florida, Volusia County	A
CC1687	Florida, Volusia County	J
CC1690	Florida, Volusia County	A
CC1692	Florida, Volusia County	B
CC1693	Florida, Volusia County	A
CC1694	Florida, Volusia County	A
CC1695	Florida, Volusia County	B
CC1696	Florida, Volusia County	A
CC1698	Florida, Volusia County	B
CC1699	Florida, Volusia County	B
CC1700	Florida, Volusia County	A
CC1701	Florida, Volusia County	A
CC1702	Florida, Volusia County	A
CC1703	Florida, Volusia County	A
CC1704	Florida, Volusia County	A
CC1705	Florida, Volusia County	A
CC1707	Florida, Volusia County	A
CC1709	Florida, Volusia County	A
CC1711	Florida, Volusia County	A
CC1712	Florida, Volusia County	A
CC1713	Florida, Volusia County	B
CC1714	Florida, Volusia County	B
CC1715	Florida, Volusia County	A
CC1717	Florida, Volusia County	A

Table A--continued.

Sample	Location	Haplotype
CC1719	Florida, Volusia County	A
CC1722	Florida, Volusia County	B
CC1728	Florida, Volusia County	A
CC1729	Florida, Volusia County	C
CC1733	Florida, Volusia County	A
CC1734	Florida, Volusia County	M
CC1737	Florida, Volusia County	A
CC1738	Florida, Volusia County	A
CC1740	Florida, Volusia County	A
CC1745	Florida, Volusia County	B
CC1746	Florida, Volusia County	A
CC1748	Florida, Volusia County	B
CC1750	Florida, Volusia County	A
CC1752	Florida, Volusia County	B
CC1754	Florida, Volusia County	A
CC1755	Florida, Volusia County	A
CC1756	Florida, Volusia County	A
CC1758	Florida, Volusia County	B
CC1759	Florida, Volusia County	J
CC1760	Florida, Volusia County	A
CC2466	Florida, South Melbourne Beach	B
CC2467	Florida, South Melbourne Beach	B
CC2468	Florida, South Melbourne Beach	B
CC2469	Florida, South Melbourne Beach	A
CC2470	Florida, South Melbourne Beach	B
CC2471	Florida, South Melbourne Beach	A
CC2472	Florida, South Melbourne Beach	B
CC2473	Florida, South Melbourne Beach	A
CC2474	Florida, South Melbourne Beach	B
CC2475	Florida, South Melbourne Beach	G
CC2476	Florida, South Melbourne Beach	A
CC2477	Florida, South Melbourne Beach	K
CC2478	Florida, South Melbourne Beach	A
CC2479	Florida, South Melbourne Beach	A
CC2480	Florida, South Melbourne Beach	B
CC2481	Florida, South Melbourne Beach	A
CC2482	Florida, South Melbourne Beach	A
CC2483	Florida, South Melbourne Beach	B
CC2484	Florida, South Melbourne Beach	B
CC2485	Florida, South Melbourne Beach	A
CC2505	Florida, North Melbourne Beach	B
CC2506	Florida, North Melbourne Beach	B
CC2507	Florida, North Melbourne Beach	A
CC2508	Florida, North Melbourne Beach	A
CC2509	Florida, North Melbourne Beach	A
CC2510	Florida, North Melbourne Beach	A
CC2511	Florida, North Melbourne Beach	B
CC2512	Florida, North Melbourne Beach	A
CC2513	Florida, North Melbourne Beach	A
CC2514	Florida, North Melbourne Beach	N
CC2515	Florida, North Melbourne Beach	A
CC2516	Florida, North Melbourne Beach	A
CC2517	Florida, North Melbourne Beach	A
CC2518	Florida, North Melbourne Beach	CC20

Table A--continued.

Sample	Location	Haplotype
CC2519	Florida, North Melbourne Beach	B
CC2520	Florida, North Melbourne Beach	B
CC2521	Florida, North Melbourne Beach	A
CC2522	Florida, North Melbourne Beach	A
CC2523	Florida, North Melbourne Beach	B
CC2524	Florida, North Melbourne Beach	B
CC282	Florida, Melbourne Beach	B
CC283	Florida, Melbourne Beach	A
CC289	Florida, Melbourne Beach	A
CC290	Florida, Melbourne Beach	A
CC295	Florida, Melbourne Beach	A
CC301	Florida, Melbourne Beach	A
CC49	Florida, Hutchison Island	A
CC50	Florida, Hutchison Island	B
CC51	Florida, Hutchison Island	B
CC53	Florida, Hutchison Island	B
CC322	Florida, Hutchison Island	A
CC323	Florida, Hutchison Island	B
CC324	Florida, Hutchison Island	A
CC325	Florida, Hutchison Island	A
CC326	Florida, Hutchison Island	B
CC90	Florida, Broward, Port Everglades	B
CC91	Florida, Broward, Port Everglades	A
CC92	Florida, Broward, Port Everglades	B
CC93	Florida, Broward, Port Everglades	A
CC94	Florida, Broward, Port Everglades	B
CC95	Florida, Broward, Port Everglades	B
CC96	Florida, Broward, Port Everglades	B
CC97	Florida, Broward, Port Everglades	A
CC98	Florida, Broward, Port Everglades	E
CC99	Florida, Broward, Port Everglades	B
CC1762	Florida, Dry Tortugas	B
CC1763	Florida, Dry Tortugas	B
CC1764	Florida, Dry Tortugas	B
CC1765	Florida, Dry Tortugas	B
CC1766	Florida, Dry Tortugas	J
CC1768	Florida, Dry Tortugas	B
CC1769	Florida, Dry Tortugas	B
CC1770	Florida, Dry Tortugas	B
CC1771	Florida, Dry Tortugas	B
CC1773	Florida, Dry Tortugas	B
CC1774	Florida, Dry Tortugas	B
CC1775	Florida, Dry Tortugas	B
CC1776	Florida, Dry Tortugas	B
CC1778	Florida, Dry Tortugas	B
CC1779	Florida, Dry Tortugas	B
CC1780	Florida, Dry Tortugas	B
CC1783	Florida, Dry Tortugas	B
CC1784	Florida, Dry Tortugas	B
BCC114	Florida, Dry Tortugas	B
BCC115	Florida, Dry Tortugas	J
BCC116	Florida, Dry Tortugas	B
BCC117	Florida, Dry Tortugas	B
BCC118	Florida, Dry Tortugas	B

Table A--continued.

Sample	Location	Haplotype
BCC119	Florida, Dry Tortugas	B
BCC120	Florida, Dry Tortugas	B
BCC121	Florida, Dry Tortugas	B
BCC122	Florida, Dry Tortugas	B
BCC123	Florida, Dry Tortugas	B
BCC124	Florida, Dry Tortugas	B
BCC125	Florida, Dry Tortugas	B
BCC126	Florida, Dry Tortugas	B
BCC127	Florida, Dry Tortugas	A
BCC128	Florida, Dry Tortugas	B
BCC129	Florida, Dry Tortugas	B
BCC130	Florida, Dry Tortugas	A
BCC131	Florida, Dry Tortugas	B
BCC132	Florida, Dry Tortugas	B
BCC133	Florida, Dry Tortugas	B
BCC134	Florida, Dry Tortugas	A
BCC135	Florida, Dry Tortugas	A
BCC136	Florida, Dry Tortugas	B
BCC137	Florida, Dry Tortugas	B
BCC138	Florida, Dry Tortugas	B
BCC139	Florida, Dry Tortugas	B
BCC140	Florida, Dry Tortugas	B
BCC141	Florida, Dry Tortugas	B
BCC142	Florida, Dry Tortugas	B
BCC143	Florida, Dry Tortugas	B
BCC144	Florida, Dry Tortugas	B
BCC145	Florida, Dry Tortugas	B
BCC146	Florida, Dry Tortugas	B
BCC147	Florida, Dry Tortugas	I
BCC148	Florida, Dry Tortugas	B
BCC149	Florida, Dry Tortugas	I
BCC150	Florida, Dry Tortugas	B
BCC151	Florida, Dry Tortugas	B
BCC152	Florida, Dry Tortugas	B
BCC153	Florida, Dry Tortugas	B
CC54	Florida, Key Island	B
CC55	Florida, Key Island	B
CC56	Florida, Key Island	B
CC57	Florida, Key Island	B
CC58	Florida, Key Island	B
CC59	Florida, Key Island	B
CC60	Florida, Key Island	A
CC61	Florida, Key Island	C
CC62	Florida, Key Island	A
CC63	Florida, Key Island	A
CC64	Florida, Key Island	B
CC65	Florida, Key Island	A
CC66	Florida, Key Island	B
CC67	Florida, Key Island	A
CC68	Florida, Key Island	B
CC333	Florida, Sarasota County	B
CC334	Florida, Sarasota County	A
CC335	Florida, Sarasota County	A
CC336	Florida, Sarasota County	A

Table A--continued.

Sample	Location	Haplotype
CC337	Florida, Sarasota County	C
CC338	Florida, Sarasota County	A
CC339	Florida, Sarasota County	B
CC340	Florida, Sarasota County	A
CC341	Florida, Sarasota County	B
CC342	Florida, Sarasota County	G
CC1540	Florida, Sarasota	A
CC1541	Florida, Sarasota	B
CC1542	Florida, Sarasota	A
CC1543	Florida, Sarasota	A
CC1544	Florida, Sarasota	C
CC1545	Florida, Sarasota	A
CC1546	Florida, Sarasota	A
CC1547	Florida, Sarasota	A
CC1548	Florida, Sarasota	B
CC1549	Florida, Sarasota	A
CC1550	Florida, Sarasota	A
CC1552	Florida, Sarasota	A
CC1553	Florida, Sarasota	G
CC1554	Florida, Sarasota	N
CC1555	Florida, Sarasota	C
CC1556	Florida, Sarasota	A
CC1557	Florida, Sarasota	B
CC1558	Florida, Sarasota	B
CC1559	Florida, Sarasota	B
CC1786	Florida, Cape San Blas	A
CC1787	Florida, Cape San Blas	A
CC1788	Florida, Cape San Blas	B
CC1789	Florida, Cape San Blas	B
CC1790	Florida, Cape San Blas	A
CC1791	Florida, Cape San Blas	B
CC1792	Florida, Cape San Blas	A
CC475	Florida, St. Joesph's	B
CC476	Florida, St. Joesph's	A
CC477	Florida, St. Joesph's	A
CC478	Florida, St. Joesph's	A
CC479	Florida, St. Joesph's	A
CC480	Florida, St. Joesph's	A
CC481	Florida, St. Joesph's	A
CC483	Florida, St. Joesph's	A
CC484	Florida, St. Joesph's	A
CC486	Florida, St. Joesph's	B
CC487	Florida, St. Joesph's	A
CC278	Florida, Tyndall Air Force Base	A
CC469	Florida, Tyndall Air Force Base	G
CC470	Florida, Tyndall Air Force Base	C
CC471	Florida, Tyndall Air Force Base	A
CC472	Florida, Tyndall Air Force Base	A
CC473	Florida, Tyndall Air Force Base	B
CC474	Florida, Tyndall Air Force Base	A
CC266	Florida, Eglin Air Force Base	G
CC267	Florida, Eglin Air Force Base	A
CC268	Florida, Eglin Air Force Base	A
CC450	Florida, Eglin Air Force Base	A

Table A--continued.

Sample	Location	Haplotype
CC451	Florida, Eglin Air Force Base	A
CC452	Florida, Eglin Air Force Base	A
CC453	Florida, Eglin Air Force Base	A
CC454	Florida, Eglin Air Force Base	A
CC455	Florida, Eglin Air Force Base	A
CC456	Florida, Eglin Air Force Base	A
CC458	Florida, Eglin Air Force Base	A
CC459	Florida, Eglin Air Force Base	A
CC460	Florida, Eglin Air Force Base	A
CC461	Florida, Eglin Air Force Base	A
CC462	Florida, Eglin Air Force Base	A
CC463	Florida, Eglin Air Force Base	B
CC464	Florida, Eglin Air Force Base	A
CC465	Florida, Eglin Air Force Base	A
CC466	Florida, Eglin Air Force Base	A
CC467	Florida, Eglin Air Force Base	A
CC468	Florida, Eglin Air Force Base	A

APPENDIX B
NUCLEAR DNA GENOTYPES

Table B. Multi-locus genotypes for all 462 turtles. 0 indicates alleles that did not amplify.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC302	North Carolina, Topsail Beach	174/180	183/183	129/145	206/206	217/223
CC303	North Carolina, Topsail Beach	166/166	175/189	125/127	206/218	217/241
CC304	North Carolina, Topsail Beach	174/182	185/185	127/153	192/204	219/231
CC305	North Carolina, Topsail Beach	166/172	183/185	117/127	202/206	217/241
CC307	North Carolina, Topsail Beach	166/180	189/191	127/143	194/200	217/241
CC308	North Carolina, Topsail Beach	176/180	183/185	127/155	194/210	219/243
CC310	North Carolina, Topsail Beach	172/180	183/185	127/131	204/212	223/229
CC312	North Carolina, Camp Lejuene	180/180	185/185	129/133	192/210	217/233
CC313	North Carolina, Camp Lejuene	166/180	175/185	137/139	194/194	217/241
CC320	North Carolina, Caswell Beach	164/172	183/191	0/0	202/202	217/217
CC512	North Carolina, Bald Head Island	166/182	183/185	127/129	194/208	217/229
CC513	North Carolina, Bald Head Island	176/180	185/185	127/129	192/194	219/229
CC514	North Carolina, Bald Head Island	174/180	181/185	117/131	192/192	217/219
CC515	North Carolina, Bald Head Island	0/0	185/193	127/137	202/202	217/219
CC516	North Carolina, Bald Head Island	166/174	185/189	127/133	202/206	219/219
CC517	North Carolina, Bald Head Island	174/182	183/189	129/133	192/204	219/223
CC518	North Carolina, Bald Head Island	172/180	185/185	125/127	204/204	217/235
CC519	North Carolina, Bald Head Island	174/180	175/185	127/127	192/202	245/0
CC520	North Carolina, Cape Lookout	180/180	175/185	117/127	192/216	217/217
CC521	North Carolina, Cape Lookout	166/174	175/183	127/127	204/206	217/229
CC522	North Carolina, Cape Lookout	174/180	183/191	125/133	192/202	217/217
CC523	North Carolina, Cape Lookout	180/180	175/183	127/149	202/202	239/243
CC524	North Carolina, Cape Lookout	166/174	181/185	125/127	194/202	219/219
CC525	North Carolina, Cape Lookout	180/180	183/185	125/139	192/206	219/229
CC526	North Carolina, Cape Lookout	166/176	185/185	127/139	204/208	217/217
CC527	North Carolina, Cape Lookout	174/174	189/189	127/135	194/202	217/229
CC528	North Carolina, Cape Lookout	172/174	183/183	117/127	192/202	217/219
CC201	South Carolina, Cape Romaine	174/180	183/189	127/127	206/212	217/219
CC202	South Carolina, Cape Romaine	166/182	175/183	127/127	192/194	217/233
CC203	South Carolina, Cape Romaine	176/176	175/183	127/149	192/212	223/239
CC204	South Carolina, Cape Romaine	166/180	185/185	127/127	192/202	219/237
CC205	South Carolina, Cape Romaine	174/180	181/185	135/137	202/208	219/219
CC206	South Carolina, Cape Romaine	174/180	183/185	127/137	204/208	219/233
CC207	South Carolina, Cape Romaine	180/180	185/189	129/129	202/212	219/237
CC208	South Carolina, Cape Romaine	174/176	185/185	127/137	202/206	217/219
CC209	South Carolina, Cape Romaine	166/180	175/183	117/117	192/216	217/229
CC210	South Carolina, Cape Romaine	174/180	175/185	127/133	204/204	217/219
CC211	South Carolina, Cape Romaine	166/166	185/185	127/161	202/206	223/243
CC212	South Carolina, Cape Romaine	172/172	183/185	125/127	198/202	219/219
CC213	South Carolina, Cape Romaine	166/172	175/183	125/127	192/210	219/243

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC214	South Carolina, Cape Romaine	166/174	181/183	127/129	202/208	219/245
CC215	South Carolina, Cape Romaine	174/176	183/185	127/137	206/212	217/243
CC216	South Carolina, Cape Romaine	174/180	183/191	127/139	202/202	219/219
CC217	South Carolina, Cape Romaine	174/180	185/185	117/147	208/208	217/237
CC218	South Carolina, Cape Romaine	174/180	185/189	129/149	194/202	217/219
CC219	South Carolina, Cape Romaine	166/180	175/185	117/127	204/206	217/233
CC220	South Carolina, Cape Romaine	176/180	185/185	125/137	202/202	217/219
CC221	South Carolina, Cape Romaine	174/174	183/185	125/137	202/208	219/231
CC222	South Carolina, Cape Romaine	166/166	185/185	127/141	192/200	209/217
CC223	South Carolina, Cape Romaine	172/180	185/191	127/127	208/212	229/245
CC224	South Carolina, Cape Romaine	174/180	183/185	125/127	192/202	219/239
CC14	Georgia; Cumberland Island	166/166	183/185	125/143	204/208	217/229
CC16	Georgia; Cumberland Island	166/180	183/189	125/127	194/212	229/243
CC17	Georgia; Cumberland Island	174/180	175/183	125/127	202/202	217/239
CC18	Georgia; Cumberland Island	172/174	183/189	125/143	202/208	229/233
CC19	Georgia; Cumberland Island	166/176	183/185	129/137	202/202	209/217
CC20	Georgia; Cumberland Island	174/180	175/183	117/127	202/202	217/219
CC21	Georgia; Cumberland Island	174/174	183/183	127/147	202/202	217/229
CC22	Georgia; Cumberland Island	174/174	175/183	125/125	198/212	219/219
CC23	Georgia; Cumberland Island	172/174	183/189	131/137	194/202	229/229
CC100	Georgia; Cumberland Island	166/180	189/189	127/147	194/212	223/243
CC101	Georgia; Cumberland Island	174/180	183/183	125/127	200/210	217/219
CC102	Georgia; Cumberland Island	176/180	183/183	127/129	200/202	223/229
CC103	Georgia; Cumberland Island	174/180	175/185	133/139	192/206	229/231
CC104	Georgia; Cumberland Island	174/174	183/185	125/127	194/206	221/233
CC105	Georgia; Cumberland Island	166/174	183/189	125/127	206/206	219/219
CC106	Georgia; Cumberland Island	180/182	181/185	125/137	206/208	217/223
CC107	Georgia; Cumberland Island	180/182	181/181	125/137	206/216	217/223
CC108	Georgia; Cumberland Island	180/180	175/185	137/141	194/204	219/229
CC109	Georgia; Cumberland Island	174/180	189/191	125/151	202/216	217/239
CC110	Georgia; Cumberland Island	166/174	175/183	127/147	192/202	219/223
CC114	Georgia; Cumberland Island	166/180	183/185	117/145	202/206	229/241
CC115	Georgia; Cumberland Island	174/174	183/185	127/131	204/212	223/229
CC116	Georgia; Cumberland Island	166/174	183/185	117/127	210/212	219/223
CC117	Georgia; Cumberland Island	180/184	175/185	127/129	194/206	219/241
CC118	Georgia; Cumberland Island	172/176	185/189	125/133	206/206	219/233
CC119	Georgia; Cumberland Island	180/180	189/191	127/137	200/204	217/219
CC120	Georgia; Cumberland Island	166/180	175/185	135/149	192/202	217/219
CC121	Georgia; Cumberland Island	174/180	175/185	127/127	202/212	223/231
CC122	Georgia; Cumberland Island	174/180	175/183	117/139	194/206	217/219
CC123	Georgia; Cumberland Island	166/180	175/181	127/127	202/216	219/223
CC124	Georgia; Cumberland Island	166/176	175/193	127/127	202/202	233/239
CC125	Georgia; Cumberland Island	174/184	183/183	127/127	206/212	217/217
CC126	Georgia; Cumberland Island	174/176	185/185	125/127	206/212	219/229
CC127	Georgia; Cumberland Island	166/172	181/183	131/135	200/202	211/219
CC128	Georgia; Cumberland Island	174/180	183/183	117/127	192/200	211/217
CC129	Georgia; Cumberland Island	174/180	185/185	133/137	194/206	219/223
CC130	Georgia; Cumberland Island	166/174	183/189	127/151	202/208	211/219
CC131	Georgia; Cumberland Island	166/172	185/189	125/127	202/216	219/219
CC132	Georgia; Cumberland Island	166/182	183/185	129/133	202/204	217/219
CC244	Florida, Amelia Island	176/180	183/189	133/153	202/202	217/219
CC245	Florida, Amelia Island	174/180	175/183	137/139	208/216	217/239
CC246	Florida, Amelia Island	174/174	183/189	117/137	206/220	229/243
CC247	Florida, Amelia Island	174/182	183/185	125/127	192/214	217/229

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC248	Florida, Amelia Island	182/182	183/189	133/141	194/210	223/235
CC249	Florida, Amelia Island	166/166	183/183	127/133	204/204	219/241
CC250	Florida, Amelia Island	166/172	183/183	127/141	192/192	217/219
CC251	Florida, Amelia Island	166/180	183/189	125/127	192/202	223/223
CC252	Florida, Amelia Island	166/180	185/185	127/135	194/202	229/239
CC253	Florida, Amelia Island	176/180	181/183	125/127	206/206	221/229
CC255	Florida, Amelia Island	174/180	183/183	117/133	206/212	217/229
CC256	Florida, Amelia Island	174/180	183/185	117/127	202/206	219/219
CC1679	Florida, Volusia County	174/174	185/185	137/137	204/204	217/219
CC1680	Florida, Volusia County	174/176	183/185	127/149	202/206	219/223
CC1682	Florida, Volusia County	174/180	175/181	117/127	198/202	219/243
CC1690	Florida, Volusia County	166/180	187/189	117/117	206/210	217/219
CC1692	Florida, Volusia County	174/176	175/183	127/127	202/208	241/241
CC1693	Florida, Volusia County	0/0	183/183	127/145	192/208	217/217
CC1694	Florida, Volusia County	174/180	183/185	0/0	192/192	219/219
CC1695	Florida, Volusia County	166/180	185/185	127/139	202/206	217/227
CC1696	Florida, Volusia County	180/180	175/185	125/137	202/204	217/245
CC1698	Florida, Volusia County	180/180	183/183	117/135	202/210	219/237
CC1699	Florida, Volusia County	174/174	183/185	133/137	192/200	217/217
CC1700	Florida, Volusia County	166/174	195/195	127/143	194/202	209/217
CC1701	Florida, Volusia County	0/0	175/185	0/0	192/204	217/217
CC1702	Florida, Volusia County	166/176	183/191	117/127	194/206	219/219
CC1703	Florida, Volusia County	180/180	183/185	127/179	210/212	223/229
CC1704	Florida, Volusia County	166/176	185/189	127/153	192/212	233/237
CC1705	Florida, Volusia County	166/174	183/185	125/125	204/210	217/229
CC1707	Florida, Volusia County	166/180	183/183	127/127	202/204	217/223
CC1708	Florida, Volusia County	166/180	185/185	127/151	200/206	219/219
CC1709	Florida, Volusia County	172/180	181/183	127/139	202/204	219/223
CC1711	Florida, Volusia County	176/180	183/193	127/133	202/206	217/223
CC1712	Florida, Volusia County	166/174	175/181	127/137	202/208	217/233
CC1713	Florida, Volusia County	180/180	175/183	125/149	206/208	219/233
CC1714	Florida, Volusia County	174/176	175/185	127/137	194/206	217/229
CC1715	Florida, Volusia County	0/0	175/183	117/125	192/192	217/217
CC1717	Florida, Volusia County	166/180	181/183	127/129	192/212	219/233
CC1719	Florida, Volusia County	166/176	185/191	127/149	202/202	217/229
CC1720	Florida, Volusia County	166/174	175/191	127/159	202/204	219/219
CC1728	Florida, Volusia County	174/174	185/191	127/127	192/210	219/219
CC1729	Florida, Volusia County	174/174	175/185	127/127	192/208	217/217
CC1733	Florida, Volusia County	166/180	183/185	117/127	202/212	223/223
CC1734	Florida, Volusia County	172/176	185/185	139/147	204/208	217/229
CC1737	Florida, Volusia County	172/176	185/189	125/127	204/210	217/217
CC1738	Florida, Volusia County	166/184	185/189	137/175	202/204	219/233
CC1740	Florida, Volusia County	174/174	183/189	127/137	202/202	217/217
CC1745	Florida, Volusia County	166/186	183/185	133/137	202/206	217/243
CC1746	Florida, Volusia County	176/182	183/189	127/137	202/202	217/219
CC1748	Florida, Volusia County	166/182	183/187	127/127	204/204	217/233
CC1750	Florida, Volusia County	174/180	183/185	137/137	206/216	217/219
CC1752	Florida, Volusia County	166/174	175/185	117/127	202/202	217/223
CC1754	Florida, Volusia County	172/182	175/185	125/133	204/204	231/237
CC1755	Florida, Volusia County	166/174	185/185	125/149	204/206	223/241
CC1756	Florida, Volusia County	176/176	183/189	127/137	204/204	217/219
CC1758	Florida, Volusia County	166/182	175/183	137/137	192/200	223/229
CC1759	Florida, Volusia County	174/182	175/183	117/137	202/204	219/219
CC2466	Florida, Melbourne Beach	174/180	175/185	127/135	208/214	217/229

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC2467	Florida, Melbourne Beach	166/174	175/189	117/135	204/206	217/243
CC2468	Florida, Melbourne Beach	174/182	183/185	117/137	202/204	219/239
CC2469	Florida, Melbourne Beach	166/180	183/189	135/141	202/212	219/219
CC2470	Florida, Melbourne Beach	180/182	185/193	127/145	192/204	217/219
CC2471	Florida, Melbourne Beach	180/186	185/185	125/127	194/194	223/235
CC2472	Florida, Melbourne Beach	166/174	183/185	127/181	202/210	217/219
CC2473	Florida, Melbourne Beach	174/180	183/189	127/127	192/212	209/217
CC2474	Florida, Melbourne Beach	166/172	183/185	129/137	202/204	217/237
CC2475	Florida, Melbourne Beach	172/174	175/185	127/127	192/212	217/239
CC2476	Florida, Melbourne Beach	174/180	185/185	125/127	192/202	219/223
CC2477	Florida, Melbourne Beach	174/180	183/183	125/125	204/214	219/231
CC2478	Florida, Melbourne Beach	166/166	183/183	127/127	192/208	229/245
CC2479	Florida, Melbourne Beach	180/182	185/185	127/135	202/204	223/229
CC2480	Florida, Melbourne Beach	174/174	183/185	127/151	206/206	217/217
CC2481	Florida, Melbourne Beach	174/180	175/183	127/129	194/202	217/229
CC2482	Florida, Melbourne Beach	180/180	183/183	125/145	202/202	217/229
CC2483	Florida, Melbourne Beach	174/174	183/183	125/129	194/202	217/217
CC2484	Florida, Melbourne Beach	166/174	185/185	117/133	202/202	229/229
CC2485	Florida, Melbourne Beach	174/180	175/183	127/141	194/210	219/219
CC2505	Florida, Melbourne Beach	166/186	185/185	127/137	202/206	217/229
CC2506	Florida, Melbourne Beach	166/174	175/183	117/117	206/208	217/219
CC2507	Florida, Melbourne Beach	166/182	185/185	117/125	208/216	219/237
CC2508	Florida, Melbourne Beach	174/180	183/189	125/135	202/210	217/233
CC2509	Florida, Melbourne Beach	166/176	185/185	127/141	204/206	223/229
CC2510	Florida, Melbourne Beach	172/174	183/183	117/137	202/206	217/219
CC2511	Florida, Melbourne Beach	180/182	183/185	125/125	202/212	209/217
CC2512	Florida, Melbourne Beach	174/186	175/185	127/137	202/202	217/223
CC2513	Florida, Melbourne Beach	166/180	183/185	127/139	200/210	219/223
CC2514	Florida, Melbourne Beach	166/180	183/193	133/137	202/212	217/219
CC2515	Florida, Melbourne Beach	172/180	175/185	117/127	208/212	231/231
CC2516	Florida, Melbourne Beach	174/180	175/185	127/127	192/202	219/223
CC2517	Florida, Melbourne Beach	174/182	183/189	125/127	202/210	219/233
CC2518	Florida, Melbourne Beach	166/180	175/185	127/169	192/206	219/223
CC2519	Florida, Melbourne Beach	176/176	185/193	137/167	200/202	231/245
CC2520	Florida, Melbourne Beach	166/180	175/193	117/117	200/202	217/219
CC2521	Florida, Melbourne Beach	174/180	195/195	117/141	194/210	217/247
CC2522	Florida, Melbourne Beach	166/180	175/193	127/135	192/192	219/231
CC2523	Florida, Melbourne Beach	174/180	175/185	127/127	194/202	217/233
CC2524	Florida, Melbourne Beach	174/174	175/183	117/131	194/202	217/217
CC282	Florida, Melbourne Beach	174/182	175/175	117/127	192/206	219/229
CC283	Florida, Melbourne Beach	174/176	175/185	127/137	202/212	217/235
CC289	Florida, Melbourne Beach	172/174	183/189	117/127	202/218	211/219
CC290	Florida, Melbourne Beach	180/180	183/185	127/127	202/206	211/219
CC295	Florida, Melbourne Beach	166/176	183/189	137/139	204/208	217/219
CC301	Florida, Melbourne Beach	176/180	183/189	127/127	202/208	229/229
CC2538	Florida, Carlin Park	174/180	175/185	117/125	204/208	219/237
CC2539	Florida, Carlin Park	176/180	189/189	117/127	202/202	219/241
CC2540	Florida, Carlin Park	174/180	175/183	133/137	192/204	217/229
CC2541	Florida, Carlin Park	166/182	183/185	133/137	192/204	229/231
CC2542	Florida, Carlin Park	180/180	183/185	117/127	202/208	217/229
CC2543	Florida, Carlin Park	166/176	183/185	127/127	202/204	217/239
CC2544	Florida, Carlin Park	166/180	185/185	125/153	204/208	219/243
CC2545	Florida, Carlin Park	176/180	183/185	117/127	204/206	217/219
CC2546	Florida, Carlin Park	172/174	183/183	127/127	202/212	217/219

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC2547	Florida, Carlin Park	166/174	175/183	127/137	202/204	221/239
CC2548	Florida, Carlin Park	166/176	185/189	127/127	202/210	217/217
CC2550	Florida, Carlin Park	180/180	189/189	127/157	202/202	217/219
CC2551	Florida, Carlin Park	176/176	175/183	117/117	202/204	221/229
CC2552	Florida, Carlin Park	174/174	183/185	127/133	208/208	219/231
CC2553	Florida, Carlin Park	166/166	183/185	127/127	192/194	217/219
CC2554	Florida, Coral Cove	174/180	175/185	127/133	192/198	217/229
CC2555	Florida, Coral Cove	174/174	183/189	125/125	204/216	217/217
CC2556	Florida, Coral Cove	180/180	175/189	117/127	192/202	217/223
CC2557	Florida, Coral Cove	174/180	181/185	127/141	192/212	217/219
CC2558	Florida, Coral Cove	166/176	183/185	127/137	212/216	217/217
CC2559	Florida, Coral Cove	174/176	183/185	137/143	200/206	217/217
CC2560	Florida, Coral Cove	166/174	185/193	127/129	192/202	219/237
CC2561	Florida, Coral Cove	172/176	185/191	117/125	210/212	217/229
CC2562	Florida, Coral Cove	166/172	185/185	127/149	206/216	217/229
CC2563	Florida, Coral Cove	174/174	183/183	137/177	212/212	217/219
CC2564	Florida, Coral Cove	166/174	189/189	125/143	206/210	217/217
CC2565	Florida, Coral Cove	180/182	183/189	137/143	194/208	223/233
CC2566	Florida, Coral Cove	174/182	183/185	127/149	204/212	217/243
CC2567	Florida, Coral Cove	166/166	175/185	117/127	192/204	217/229
CC2568	Florida, Coral Cove	174/180	183/185	127/127	194/204	219/245
CC2569	Florida, Coral Cove	172/174	183/185	119/127	202/204	219/223
CC2570	Florida, Coral Cove	176/180	189/189	127/157	194/208	217/233
CC2571	Florida, Coral Cove	166/180	175/193	117/131	200/200	217/241
CC2572	Florida, Jensen Beach	166/180	183/185	131/133	202/210	217/217
CC2585	Florida, Jensen Beach	166/180	175/185	127/127	210/216	217/217
CC2586	Florida, Jensen Beach	174/176	183/183	129/141	194/216	223/239
CC2587	Florida, Jensen Beach	166/174	183/189	125/127	206/208	219/219
CC2588	Florida, Jensen Beach	174/174	185/189	117/127	192/192	239/239
CC2589	Florida, Jensen Beach	166/166	175/183	127/127	194/202	217/219
CC2590	Florida, Jensen Beach	166/180	185/187	117/117	208/216	217/217
CC2591	Florida, Jensen Beach	176/178	185/193	117/117	200/206	211/243
CC2592	Florida, Jensen Beach	174/180	175/175	127/137	194/202	217/217
CC2593	Florida, Jensen Beach	166/180	175/189	117/133	192/212	217/217
CC2594	Florida, Normandy Beach	166/182	183/185	117/133	192/192	219/219
CC2596	Florida, Normandy Beach	174/180	183/193	127/127	206/210	217/219
CC2597	Florida, Normandy Beach	172/180	185/193	127/129	192/202	233/233
CC2598	Florida, Normandy Beach	166/174	185/185	127/127	192/208	219/229
CC2599	Florida, Normandy Beach	176/182	183/185	127/133	206/208	219/243
CC2600	Florida, Normandy Beach	180/184	185/189	125/141	194/206	223/243
CC2601	Florida, Normandy Beach	174/180	185/193	133/135	192/194	219/237
CC2602	Florida, Normandy Beach	176/180	189/189	127/131	202/204	219/229
CC2603	Florida, Normandy Beach	174/180	185/187	125/159	192/210	219/239
CC2604	Florida, Normandy Beach	174/180	183/185	125/127	192/200	219/239
CC2605	Florida, Normandy Beach	172/174	175/175	127/127	204/210	217/243
CC2606	Florida, Normandy Beach	180/180	183/185	117/137	202/204	213/221
CC2607	Florida, Normandy Beach	174/180	175/183	127/135	192/202	221/233
CC2608	Florida, Normandy Beach	174/180	183/183	133/167	192/202	217/243
CC49	Florida, Hutchison Island	180/180	183/185	133/133	194/202	229/243
CC50	Florida, Hutchison Island	166/180	185/191	127/141	192/210	237/237
CC51	Florida, Hutchison Island	174/180	175/185	125/133	192/204	217/219
CC52	Florida, Hutchison Island	172/174	183/185	127/137	206/212	219/231
CC53	Florida, Hutchison Island	166/166	185/185	117/137	194/208	217/217
CC321	Florida, Hutchison Island	174/174	181/183	127/127	192/208	229/229

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC322	Florida, Hutchison Island	172/180	181/183	125/133	194/208	217/223
CC323	Florida, Hutchison Island	182/186	175/181	129/137	202/202	219/231
CC324	Florida, Hutchison Island	166/180	181/183	127/133	202/204	237/241
CC325	Florida, Hutchison Island	176/180	183/191	137/153	192/202	219/219
CC326	Florida, Hutchison Island	174/180	183/185	127/133	192/202	217/237
CC90	Florida, Port Everglades	174/180	183/193	133/139	204/206	217/233
CC91	Florida, Port Everglades	174/180	189/191	127/129	204/206	229/243
CC92	Florida, Port Everglades	166/174	189/193	127/151	208/208	229/231
CC93	Florida, Port Everglades	166/174	185/189	127/127	202/208	219/233
CC94	Florida, Port Everglades	174/180	175/185	127/139	192/208	217/217
CC95	Florida, Port Everglades	180/180	183/185	127/131	192/208	217/219
CC96	Florida, Port Everglades	180/180	185/185	117/133	192/210	217/219
CC97	Florida, Port Everglades	174/176	175/183	127/127	202/204	217/219
CC98	Florida, Port Everglades	180/180	185/189	137/147	192/204	217/223
CC1762	Florida, Dry Tortugas	174/176	175/187	127/169	202/202	219/235
CC1763	Florida, Dry Tortugas	174/180	175/185	125/125	194/202	217/229
CC1764	Florida, Dry Tortugas	180/180	183/191	127/127	192/210	217/217
CC1765	Florida, Dry Tortugas	174/176	175/185	127/137	192/212	219/219
CC1766	Florida, Dry Tortugas	172/174	185/193	125/133	192/194	217/229
CC1767	Florida, Dry Tortugas	174/180	189/193	127/127	192/192	219/233
CC1768	Florida, Dry Tortugas	174/182	185/185	127/141	192/212	219/223
CC1769	Florida, Dry Tortugas	166/174	185/195	127/133	214/214	217/241
CC1770	Florida, Dry Tortugas	180/180	183/183	117/119	192/194	217/217
CC1771	Florida, Dry Tortugas	174/174	183/185	117/133	204/214	217/231
CC1772	Florida, Dry Tortugas	180/180	185/185	127/137	194/202	219/243
CC1773	Florida, Dry Tortugas	158/182	183/183	127/133	206/206	235/241
CC1774	Florida, Dry Tortugas	166/180	183/183	117/117	192/202	223/245
CC1775	Florida, Dry Tortugas	166/174	183/185	127/127	206/206	217/231
CC1776	Florida, Dry Tortugas	176/180	175/185	127/137	208/216	219/229
CC1777	Florida, Dry Tortugas	166/180	185/189	127/127	212/212	219/229
CC1778	Florida, Dry Tortugas	172/180	175/183	127/127	192/212	219/219
CC1779	Florida, Dry Tortugas	176/176	183/193	117/137	194/206	217/229
CC1780	Florida, Dry Tortugas	172/174	183/185	125/139	202/206	217/229
CC1781	Florida, Dry Tortugas	180/180	183/189	139/161	204/216	219/231
CC1782	Florida, Dry Tortugas	180/180	175/175	127/151	204/212	229/229
CC1783	Florida, Dry Tortugas	166/174	185/185	127/127	192/212	219/229
CC1785	Florida, Dry Tortugas	166/180	181/185	127/127	192/212	217/217
CC54	Florida, Key Island	166/172	181/187	127/137	202/208	217/219
CC55	Florida, Key Island	174/174	183/185	127/167	202/204	223/239
CC56	Florida, Key Island	180/180	183/185	127/127	192/202	217/233
CC57	Florida, Key Island	174/180	183/189	125/127	202/202	217/219
CC58	Florida, Key Island	174/180	185/185	127/129	204/208	223/223
CC59	Florida, Key Island	166/180	175/183	127/137	206/206	223/223
CC60	Florida, Key Island	174/180	183/183	127/127	194/212	217/231
CC61	Florida, Key Island	176/180	185/189	127/137	192/204	219/229
CC62	Florida, Key Island	172/174	183/185	117/137	192/206	219/219
CC63	Florida, Key Island	166/172	183/185	127/149	188/192	223/229
CC64	Florida, Key Island	166/174	185/185	131/151	194/200	217/219
CC65	Florida, Key Island	166/172	183/185	127/127	212/214	217/243
CC66	Florida, Key Island	166/182	185/189	127/127	212/214	217/239
CC67	Florida, Key Island	174/180	185/185	127/127	192/202	217/219
CC68	Florida, Key Island	166/180	183/191	137/171	194/202	219/233
CC333	Florida, Sarasota	166/166	183/189	127/129	202/208	217/227
CC334	Florida, Sarasota	180/182	185/189	125/155	192/202	217/233

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC335	Florida, Sarasota	180/182	185/195	125/129	202/208	217/217
CC336	Florida, Sarasota	172/176	185/189	125/127	204/208	219/219
CC337	Florida, Sarasota	172/176	185/191	117/135	192/202	217/217
CC338	Florida, Sarasota	174/174	185/189	117/117	200/202	219/223
CC339	Florida, Sarasota	174/182	185/189	127/145	202/214	223/223
CC340	Florida, Sarasota	180/180	185/185	127/151	206/208	217/217
CC341	Florida, Sarasota	174/174	183/193	127/127	210/216	217/229
CC342	Florida, Sarasota	166/174	187/189	127/151	202/204	217/223
CC1540	Florida, Sarasota	174/180	183/185	127/127	210/212	217/241
CC1541	Florida, Sarasota	166/174	183/191	137/141	192/210	217/217
CC1542	Florida, Sarasota	174/180	183/187	125/157	202/208	219/223
CC1543	Florida, Sarasota	176/180	183/193	127/127	202/212	219/243
CC1544	Florida, Sarasota	166/174	183/185	125/129	192/192	217/219
CC1545	Florida, Sarasota	166/174	183/185	127/133	202/206	217/237
CC1546	Florida, Sarasota	166/182	183/185	127/127	206/218	217/229
CC1547	Florida, Sarasota	166/174	183/183	133/151	194/208	219/245
CC1548	Florida, Sarasota	172/174	185/185	125/129	206/214	223/229
CC1549	Florida, Sarasota	172/174	183/183	117/137	192/202	217/217
CC1550	Florida, Sarasota	176/182	185/189	127/133	192/194	219/223
CC1551	Florida, Sarasota	174/180	185/189	127/137	200/206	217/217
CC1552	Florida, Sarasota	166/182	185/189	125/127	204/204	219/223
CC1553	Florida, Sarasota	174/180	183/183	133/151	202/204	229/241
CC1554	Florida, Sarasota	166/180	183/185	127/139	192/200	219/229
CC1555	Florida, Sarasota	180/182	183/185	117/139	192/202	219/229
CC1556	Florida, Sarasota	174/180	175/183	127/137	202/202	217/219
CC1557	Florida, Sarasota	180/180	175/183	127/129	204/212	217/237
CC1558	Florida, Sarasota	174/174	175/185	127/127	192/208	219/219
CC1559	Florida, Sarasota	180/180	183/185	137/139	202/206	219/219
CC1560	Florida, Sarasota	174/182	183/185	127/127	194/210	219/219
CC1786	Florida, Cape San Blas	166/174	175/185	117/117	200/202	219/241
CC1787	Florida, Cape San Blas	174/176	189/189	127/127	202/206	219/219
CC1788	Florida, Cape San Blas	176/180	183/189	135/137	208/212	223/233
CC1789	Florida, Cape San Blas	172/182	183/183	125/127	198/202	217/219
CC1790	Florida, Cape San Blas	180/182	183/185	125/149	208/208	217/219
CC1791	Florida, Cape San Blas	174/182	175/189	117/137	192/204	217/217
CC1792	Florida, Cape San Blas	166/180	183/185	135/137	208/218	217/229
CC475	Florida, St. Joesph's	176/180	175/185	117/117	192/192	217/237
CC476	Florida, St. Joesph's	172/180	183/185	127/127	192/216	223/245
CC477	Florida, St. Joesph's	176/182	185/185	133/149	192/208	219/229
CC478	Florida, St. Joesph's	172/174	189/189	147/149	204/206	217/237
CC479	Florida, St. Joesph's	180/180	183/185	125/131	194/208	217/219
CC480	Florida, St. Joesph's	166/174	185/185	127/131	200/202	217/229
CC481	Florida, St. Joesph's	180/182	185/189	127/139	206/212	229/237
CC483	Florida, St. Joesph's	174/180	175/185	117/125	204/206	217/219
CC484	Florida, St. Joesph's	174/180	185/185	125/127	204/204	217/219
CC486	Florida, St. Joesph's	180/180	183/185	127/127	204/204	219/223
CC487	Florida, St. Joesph's	180/180	169/189	127/155	202/210	217/223
CC269	Florida, Tyndall Air Force Base	174/180	185/185	117/127	206/206	219/233
CC278	Florida, Tyndall Air Force Base	174/180	183/189	117/125	192/202	217/229
CC281	Florida, Tyndall Air Force Base	174/180	183/185	133/153	192/204	219/233
CC469	Florida, Tyndall Air Force Base	174/180	185/193	133/137	200/208	217/241
CC470	Florida, Tyndall Air Force Base	174/178	183/185	127/137	192/204	217/219
CC472	Florida, Tyndall Air Force Base	172/176	185/185	133/163	194/202	219/241
CC267	Florida, Eglin Airforce Base	174/180	185/185	127/135	202/204	217/233

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC268	Florida, Eglin Airforce Base	180/180	185/185	117/137	194/212	217/239
CC450	Florida, Eglin Airforce Base	172/180	175/189	117/127	204/204	217/219
CC451	Florida, Eglin Airforce Base	166/180	185/185	125/167	194/194	219/229
CC452	Florida, Eglin Airforce Base	180/184	183/185	125/127	202/204	219/219
CC453	Florida, Eglin Airforce Base	166/180	175/185	137/167	200/202	217/229
CC454	Florida, Eglin Airforce Base	174/180	185/185	127/135	204/220	217/219
CC455	Florida, Eglin Airforce Base	166/176	175/189	127/133	192/194	217/219
CC456	Florida, Eglin Airforce Base	174/176	183/191	127/135	204/220	219/233
CC459	Florida, Eglin Airforce Base	166/182	175/185	117/127	204/204	223/229
CC461	Florida, Eglin Airforce Base	166/180	183/185	117/127	202/202	217/219
CC462	Florida, Eglin Airforce Base	166/174	175/183	127/135	202/216	219/229
CC463	Florida, Eglin Airforce Base	166/176	183/189	133/137	202/204	217/219
CC464	Florida, Eglin Airforce Base	176/182	183/185	127/141	192/192	217/217
CC465	Florida, Eglin Airforce Base	166/172	183/185	117/127	202/208	217/241
CC466	Florida, Eglin Airforce Base	180/180	185/185	127/141	204/216	217/241
CC467	Florida, Eglin Airforce Base	174/174	183/185	137/149	192/206	219/233
CC468	Florida, Eglin Airforce Base	174/176	185/191	125/137	0/0	0/0
CC805	Brazil, Bahia	174/180	183/185	117/127	192/204	219/219
CC806	Brazil, Bahia	166/166	183/185	125/125	192/202	217/217
CC807	Brazil, Bahia	166/180	185/185	127/137	192/192	217/219
CC808	Brazil, Bahia	174/180	185/185	125/141	192/192	219/239
CC809	Brazil, Bahia	174/174	185/185	117/127	192/202	217/219
CC810	Brazil, Bahia	174/180	185/189	127/141	192/216	219/219
CC811	Brazil, Bahia	174/174	183/185	127/143	192/208	219/219
CC812	Brazil, Bahia	178/178	183/191	127/141	192/212	219/239
CC813	Brazil, Bahia	166/180	185/185	127/141	192/212	219/219
CC814	Brazil, Bahia	166/186	191/191	127/141	192/202	217/219
CC815	Brazil, Bahia	166/166	185/189	117/127	192/192	219/219
CC816	Brazil, Bahia	166/180	185/185	127/135	192/204	219/219
CC817	Brazil, Bahia	174/180	185/185	117/141	192/208	219/219
CC818	Brazil, Bahia	174/180	185/185	127/127	192/192	209/217
CC819	Brazil, Bahia	180/182	175/175	117/135	192/200	217/219
CC820	Brazil, Bahia	166/182	181/189	117/127	192/204	217/217
CC821	Brazil, Bahia	174/180	175/183	125/125	192/192	217/219
CC822	Brazil, Bahia	166/180	185/185	127/127	192/212	219/239
CC823	Brazil, Bahia	174/180	185/189	127/141	204/210	239/241
CC824	Brazil, Bahia	174/182	175/185	117/127	208/216	217/219
CC825	Brazil, Bahia	172/180	185/189	117/127	192/194	217/219
CC826	Brazil, Bahia	174/180	185/185	127/127	192/192	219/219
CC827	Brazil, Bahia	166/180	183/185	117/141	192/208	219/219
CC828	Brazil, Bahia	174/174	185/189	137/141	192/192	219/219
CC829	Brazil, Bahia	180/182	185/185	127/131	192/208	217/219
CC830	Brazil, Bahia	178/180	185/189	125/127	192/192	217/219
CC831	Brazil, Bahia	180/180	183/185	127/135	192/206	217/241
CC832	Brazil, Bahia	180/180	185/189	125/141	192/192	219/219
CC833	Brazil, Bahia	166/180	183/189	125/141	208/212	219/219
CC834	Brazil, Bahia	174/180	185/185	117/127	202/208	217/217
CC835	Brazil, Bahia	174/180	185/185	125/169	204/212	219/219
CC836	Brazil, Bahia	166/182	175/183	127/159	192/208	217/219
CC837	Brazil, Bahia	166/180	185/185	135/141	192/216	217/219
CC838	Brazil, Bahia	166/180	185/185	127/127	204/212	217/217
CC839	Brazil, Bahia	174/184	183/185	117/127	192/192	219/219
CC840	Brazil, Bahia	166/178	175/191	117/125	192/192	217/219
CC841	Brazil, Bahia	180/180	185/185	117/141	204/204	217/219

Table B--continued.

Sample	Location	DC107	CCM2	Ccar176	CC141	CC7
CC842	Brazil, Bahia	180/180	181/185	127/127	192/192	217/217
CC843	Brazil, Bahia	174/180	175/181	127/141	192/212	217/239
CC844	Brazil, Bahia	166/174	185/189	117/135	204/208	219/219
CC845	Brazil, Bahia	174/180	181/185	127/127	204/204	219/219
CC846	Brazil, Bahia	174/174	185/185	127/135	192/192	217/217
CC847	Brazil, Bahia	174/180	185/191	127/139	192/204	219/219
CC848	Brazil, Bahia	174/180	185/189	131/143	192/204	217/219
CC849	Brazil, Bahia	180/186	175/185	125/137	192/204	217/219
CC850	Brazil, Bahia	166/174	185/185	127/127	202/210	217/217
CC851	Brazil, Espirito Santo	174/180	181/191	127/127	192/192	217/219
CC852	Brazil, Espirito Santo	166/178	175/185	127/141	192/212	217/219
CC853	Brazil, Espirito Santo	174/180	185/185	117/127	202/204	217/219
CC854	Brazil, Espirito Santo	174/174	183/185	127/141	204/208	217/219
CC855	Brazil, Espirito Santo	174/180	175/185	127/141	192/212	217/219
CC856	Brazil, Espirito Santo	174/180	175/185	127/141	192/204	217/219
CC857	Brazil, Espirito Santo	178/178	189/189	117/125	186/192	219/233
CC858	Brazil, Espirito Santo	174/180	175/183	127/127	192/204	219/241
CC859	Brazil, Espirito Santo	174/180	183/185	127/127	192/208	217/219
CC860	Brazil, Espirito Santo	174/180	189/191	117/141	202/208	217/219
CC861	Brazil, Espirito Santo	174/180	185/185	117/125	202/212	217/219
CC862	Brazil, Espirito Santo	174/180	183/183	125/127	192/204	217/219
CC863	Brazil, Espirito Santo	166/174	175/181	117/127	192/192	217/219
CC864	Brazil, Espirito Santo	166/174	185/189	117/125	204/208	217/217
CC865	Brazil, Espirito Santo	180/180	185/185	117/117	192/192	219/219
CC866	Brazil, Espirito Santo	166/180	185/185	125/125	200/204	219/219
CC867	Brazil, Espirito Santo	166/174	185/191	141/141	192/202	217/217
CC868	Brazil, Espirito Santo	166/180	185/185	141/141	192/192	219/219
CC869	Brazil, Espirito Santo	174/174	183/185	127/141	204/216	217/221
CC870	Brazil, Espirito Santo	174/174	185/185	135/169	208/212	217/217
CC871	Brazil, Espirito Santo	166/174	185/185	125/169	192/204	217/219
CC872	Brazil, Espirito Santo	174/182	175/185	117/145	192/204	217/217
CC873	Brazil, Espirito Santo	166/186	175/185	125/129	192/212	217/217
CC874	Brazil, Espirito Santo	180/180	183/185	141/181	192/212	217/229
CC875	Brazil, Espirito Santo	174/182	185/185	125/127	192/208	217/219
CC876	Brazil, Espirito Santo	180/180	185/185	127/141	192/192	217/217
CC877	Brazil, Espirito Santo	166/180	183/185	117/141	192/216	219/219
CC878	Brazil, Espirito Santo	166/166	185/185	125/135	192/212	219/241
CC879	Brazil, Espirito Santo	180/180	175/183	127/141	192/208	209/219
CC880	Brazil, Espirito Santo	180/180	185/185	125/127	200/208	217/219
CC881	Brazil, Espirito Santo	166/180	183/189	127/127	192/192	217/219
CC882	Brazil, Espirito Santo	178/180	185/185	125/141	192/192	217/219
CC883	Brazil, Espirito Santo	178/180	181/185	125/127	204/204	217/241
CC884	Brazil, Espirito Santo	180/186	189/191	127/141	192/212	219/219
CC885	Brazil, Espirito Santo	174/180	185/191	117/127	192/192	217/219

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