# A SURVEY OF THE GENETIC DIVERSITY OF THE LOGGERHEAD AND GREEN SEA TURTLES OF THE SULTANATE OF OMAN

Joshua S. Reece[1], A. Alansari[2], H. M. Kalkvik[3], A. Alkindi[2], I. Mahmoud[2], A. Y. Al Kiyumi[4], A. E. Elshafie[2], Michael P. Jensen[5], and C. L. Parkinson[3]

## ABSTRACT

The Sultanate of Oman hosts large annual nesting aggregations of up to 23,000 Loggerhead Sea Turtles (*Caretta caretta*) and 10,000 Green Sea Turtles (*Chelonia mydas*). Both populations have until now been poorly sampled (eight samples for *C. caretta* and fifteen for *C. mydas*). Genetic diversity information is needed for both species because these populations are increasingly threatened as the coastlines of Oman become more developed. It is currently unclear how diverse these rookeries are relative to other rookeries in the Atlantic, Mediterranean, Indian, or Pacific oceans. We explored mitochondrial DNA (mtDNA) diversity in 100 *C. caretta* from Masirah Island and 42 *C. mydas* from Ras al Hadd, Oman. We also analyzed *C. caretta* with four nuclear DNA (nDNA) microsatellites to investigate nuclear diversity. Loggerhead populations in Oman showed extremely low mtDNA diversity, but high nDNA diversity, suggesting isolation of genetically impoverished matrilineal lines, but relatively high male-mediated gene flow. In contrast, *C. mydas* populations in Oman consist of two clusters of distinct haplotypes that yield extremely high estimates of haplotype and nucleotide diversity relative to other global rookeries. These results describe the diversity of *C. caretta* and *C. mydas* rookeries in Oman with implications for global conservation.

**Key words:** *Caretta caretta*, *Chelonia mydas,* genetic diversity, Indian Ocean, nesting aggregation, phylogeography, rookery, sea turtles.

Published On-line: December 7, 2016
Open Access Download at https://www.flmnh.ufl.edu/bulletin/publications/
ISSN 2373-9991



[1]Department of Biology, California State University, 2555 E. San Ramon Ave, Fresno CA 93740 USA <joshua_reece@csufresno.edu>
[2]Sultan Qaboos University, Department of Biology, Al-Khod 36, Postal Code 123, Muscat, Sultanate of Oman <alansari@squ.edu.om>
[3]University of Central Florida Department of Biology, 4000 Central Florida Blvd., Orlando, FL 32816-2368 USA <kalkvik@gmail.com>
[4]Ministry of Nature Conservation, P.O. Box 323, Postal Code 113, Muscat, Sultanate of Oman <alialkiyumi@hotmail.com>
[5]Southwest Fisheries Science Center, National Marine Fisheries Service, NOAA, 8901 La Jolla Shores Drive, La Jolla, CA 92037 USA <michael.jensen@noaa.gov>

Reece, J. S., A. Alansari, H. M. Kalkvik, A. Alkindi, I. Mahmoud, A. Y. Al Kiyumi, A. E. Elshafie, Michael P. Jensen, and C. L. Parkinson. 2016. A survey of the genetic diversity of the Loggerhead and Green Sea Turtles of the Sultanate of Oman. Bulletin of the Florida Museum of Natural History 54(6):104–117.

## INTRODUCTION

Loggerhead Sea Turtles (*Caretta caretta*) are distributed globally and nest in temperate and subtropical regions of the Mediterranean, Atlantic, Pacific, and Indian oceans (Bolten and Witherington, 2003). The two largest known rookeries consist of over 10,000 females nesting per year, and are located in south Florida in the United States and on Masirah Island in Oman (Indian Ocean) (Ross, 1978; Baldwin et al., 2003; Ehrhart et al., 2003). Loggerhead Sea Turtles are threatened by global climate change, loss of nesting habitat, hunting and bycatch (Witherington, 2003; Witt et al., 2010; Reece et al., 2013). *Caretta caretta* is currently listed by IUCN (www.redlist.org) as Vulnerable, and as Threatened under the U.S. Endangered Species Act (NMFS and USFWS, 1991a). The rookery at Masirah Island, Oman, contains up to 23,000 nesting females annually on a single 10-kilometer beach (Ross, 1978; Ross and Banwari, 1982; Baldwin et al., 2003); a number comparable to the largest rookeries in the Caribbean (Ehrhart et al., 2003). Assessment of genetic diversity and genetic structure has been widely used in management of listed species (Frankham et al., 2002; Frankham, 2010). Although the south Florida *C. caretta* rookery has been extensively characterized for genetic diversity (Bowen et al., 2005; Shamblin et al., 2012, 2014), the Oman rookery has not been thoroughly surveyed for genetic diversity at mitochondrial DNA (mtDNA) or nuclear DNA (nDNA) levels (but see Bowen et al., 1994). Green Sea Turtles (*Chelonia mydas*) are also globally distributed in tropical and subtropical oceans and share many of the same threats as the Loggerhead Sea Turtle (NMFS and USFWS, 1991a, 1991b, 1998). This species is listed as Endangered by the IUCN and was recently downgraded to Threatened under the US Endangered Species Act (NMFS and USFWS, 1991a). *Chelonia mydas* nest in significant numbers in Florida, throughout the Caribbean, and Hawaii; the largest known aggregations are at Ascension Island (mid-Atlantic) and Raine Island, Australia. They also nest in significant numbers in Oman, where up to 44,000 nests (representing over 10,000 females) were recorded in 2005. Genetic data on *C. mydas* aggregations in Oman is also sparse, but include a study of four microsatellite loci to examine patterns of male-mediated gene flow (Roberts et al., 2004), an RFLP survey (Karl et al., 1992), and a mtDNA control region sequence analysis of 15 individuals (Bowen et al., 1992), all of which were used to examine global phylogeography. *Chelonia mydas* in Oman share close ties to Austral-Asian rookeries. Male-mediated gene flow occurs over much larger distances than female-mediated gene flow. However, information on comparative levels of genetic diversity for both species is lacking. The genetic diversity of *C. caretta* and *C. mydas* in Oman is of interest both for understanding biogeography and for long-term management (NMFS and USFWS, 1991a, 1991b, 1998).

We inventory and describe the population genetic diversity of the *C. caretta* rookery at Masirah Island, Oman, based on a sample of 100 nesting females, and the *C. mydas* rookery at Ras al Hadd, Oman, based on 42 nesting females. These samples more than double the most extensive sampling for both species from Oman for genetic data to date (Bowen et al., 1992; Bowen et al., 1994). We assessed genetic diversity for *C. caretta* using markers that would allow for comparison with the most extensive characterization of Atlantic rookery population genetic diversity available at the time of the study, which included a short (391 bp) fragment of the mtDNA control region and four nuclear microsatellite loci (Bowen et al., 2005). We describe mtDNA and nDNA diversities at Masirah Island relative to other rookeries globally. We assessed *C. mydas* genetic diversity based solely on mtDNA control region haplotypes comparable to those published for the Atlantic, Indian and Pacific Ocean rookeries. These data represent an important improvement over the current state of knowledge for sea turtles in Oman.

## MATERIAL AND METHODS

### Sample Collection

During summer 2004, a single researcher (JSR) collected tissues from 100 *C. caretta* adult nesting females over 10 km of northeastern Masirah Island, Oman (58.8905° N, 20.4551° E) and from

42 adult *C. mydas* over two km of Ras al Hadd, Oman (22.5080° N, 59.7643° E). We obtained tissue samples from the dorsal medial portion of the front right flipper using a six mm biopsy punch. We collected all *C. caretta* samples over the course of three nights and inspected each individual for sign of previous biopsy to avoid double sampling. In most cases, we biopsied females after they completed the nesting process, and when possible, flipper tags were applied by local Omani researchers. We sampled *C. mydas* over the course of a single evening, using the same methods to avoid double sampling of any individual. Tissue samples were stored in lysis buffer for later DNA extraction using DNeasy Tissue Kits (Qiagen).

### Mitochondrial DNA Isolation and Amplification

Because *C. caretta* rookeries were globally described by Encalada et al. (1998) based on a 391 base pair (bp) fragment of the mtDNA D-loop, we amplified this fragment using primers TCR-5 and TCR-6 (Norman et al., 1994). Subsequent to sequences being generated for this study, a longer fragment (817 bp) has been developed (Abreu-Grobois et al., 2006) that provides greater resolution (Shamblin et al., 2012). We did not use this fragment because it was not available at the time these data were generated and because the majority of studies available for comparison today used the shorter 391 bp fragment (Bowen et al., 1995; Encalada et al., 1998; Hatase, et al. 2002; Boyle et al., 2009; Garofalo et al., 2009; Chaieb et al., 2010; Shamblin et al., 2011). We evaluated *C. mydas* nesting populations at the same locus, but using a 487 bp fragment amplified by primers CR-1 and CR-2 (Norman et al., 1994) that have been used extensively to characterize *C. mydas* populations in the Atlantic Ocean (Encalada et al., 1996; Bjorndal et al., 2005, 2006), Indian (Bourjea et al., 2007) and Pacific oceans (FitzSimmons et al., 1996; Dethmers et al., 2006; Formia et al., 2006). We subjected purified DNA to polymerase chain reaction (PCR) in 25 μL reactions by denaturing at 93° C for three min, followed by 39 cycles of (1) DNA denaturing at 93° C for 30 s, (2) primer annealing at 52° C for 30 s, and (3) primer extension at 72° C for 30 s, with a final primer extension cycle at 72° C for 10 min with both positive and negative PCR controls. We visualized PCR products on an agarose gel and purified the 391 bp (*C. caretta*) and 487 bp (*C. mydas*) fragments using MinElute Gel Extraction Kits (Qiagen). We sequenced the purified products on an ABI 3100 automated sequencer in both directions following manufacturer's protocols. All mtDNA analyses were conducted in 2004 at Sultan Qaboos University in Muscat, Oman.

### Microsatellite Amplification for Loggerhead Sea Turtles

Microsatellite loci were chosen to be comparable to a previous inventory of Atlantic rookeries by Bowen et al. (2005). Additional loci have become available subsequent to the generation of the data in this study (Shamblin et al., 2009), but comparative data are not yet available for other rookeries. Carreras et al. (2007) surveyed the Mediterranean for three of the four microsatellite loci used in this study, but due to lack of the fourth microsatellite locus, these data were not included in our analyses. We used the primers CC141 (FitzSimmons et al., 1996), CC176 (Moore and Ball, 2002), CC7 (FitzSimmons, 1998), and DC107 (Bowen et al., 2005). Amplification conditions for the multiplexed microsatellites consisted of 15 μL reactions containing 0.4 units of Sigma Taq, 1.5 μL 10x reaction buffer, 1.5 mM MgCl2, 0.2 μM dNTPs, 200 nM primers and 6 ng DNA. The thermocycler programs for the PCR reactions were 93° C for 3 min, 8 cycles of 92° C for 30 s, annealing temperature for 55 s (54° C, CC141; 55° C, DC107; 56° C, CC7; 60° C, CC176), 72° C for 1 min 25 s, followed by 30 cycles of 89° C for 30 s, annealing for 55 s (52° C, CC141; 53° C, DC107; 54° C, CC7; 58° C, CC176), 72° C for 1 min 25 s, with a final extension of 72° C for 10 min. Forward primers were labeled fluorescently, and samples were genotyped on a Beckman CEQ 8000 using 20 μL dilution of PCR reactions in SLS buffer. The microsatellite fragment length was scored using CEQ 8000 software. We included the same loci as Bowen et al. (2005), and to ensure identical binning of microsatellite loci and comparability of datasets from their study and our own sampling, we acquired the original tissue samples from

eight *C. caretta* used in their study to standardize allele scoring of the microsatellite loci. The eight individuals were genotyped, and the fragment lengths acquired from our analysis were compared to those reported in Bowen et al. (2005). The eight individuals represented 31–55% of the identified alleles of the four loci from their original study. We believe this provided a sufficient sampling of alleles to ensure consistent scoring between the two microsatellite datasets and comparability of datasets. We attempted to acquire additional samples scored in the previous study, but were unsuccessful. This limitation would have no effect on estimates of diversity.

### Mitochondrial DNA Analyses

We manually edited sequence data in SEQUENCHER v.4.2 (www.genecodes.com) and aligned the sequence data in GENEDOC (Nicholas and Nicholas, 1997). Sequences from several previous studies were incorporated with our own sampling. To compare our findings with globally published estimates of *C. caretta* genetic diversity, we incorporated eight previously published global or regional surveys of major *C. caretta* nesting aggregations and eight surveys of major *C. mydas* rookeries (see results).

For both *C. caretta* and *C. mydas*, we inventoried mitochondrial haplotype diversity ($h$ [Nei, 1987]), nucleotide diversity ($\pi$ [Nei, 1987]), and average number of nucleotide differences ($k$ [Tajima, 1983]) per population for the mitochondrial control region in DnaSP v.5.0 (Rozas et al., 2003). For each of the above metrics (except $k$), we computed 1000 coalescent simulations using the coalescent calculator in DNAsp and recorded 95% confidence intervals for each metric for the Oman rookery. We then compared these distributions to the values calculated in the same way for rookeries previously surveyed. We used Tajima's $D$ (Tajima, 1989) to test the hypothesis that control region variation does not differ from neutral expectations or show evidence of large demographic shifts.

For *C. caretta*, we described nDNA diversity based on microsatellites using the program GENALEX v.6 (Peakall and Smouse, 2006) to summarize the number of alleles (A), number of effective alleles ($A_E$), mean expected heterozygosity per locus ($H_E$), mean observed heterozygosity per locus ($H_O$), and overall fit to Hardy-Weinberg equilibrium expectations. Genetic diversity at these loci was compared to previously surveyed rookeries in the western Atlantic (Bowen et al., 2005).

**Table 1.** Haplotypes and numbers of individuals for *C. caretta* and *C. mydas* sampled in Oman. Haplotype names referenced here correspond with nomenclature used by the University of the Florida Archie Carr Center for Sea Turtle Research database.

| Haplotype | Number of Individuals |
|---|---|
| ***Caretta caretta* (n = 100)** | |
| CC-Oman1 (new) | 1 |
| CC-Oman2 (new) | 1 |
| CCA11 | 98 |
| ***Chelonia mydas* (n = 42)** | |
| CM-Oman1 (new) | 1 |
| CM-Oman2 (new) | 1 |
| CMP49 | 1 |
| CMP62 | 15 |
| CMP71 | 8 |
| CMP73 | 16 |

## RESULTS

### Genomic Diversity in the Masirah Island *Caretta caretta* Rookery

We identified low mtDNA diversity in the Masirah Island *C. caretta* rookery with three mitochondrial haplotypes in 100 individuals (Table 1). The most common haplotype (CC-A11) occurred in 98 individuals. The two remaining haplotypes were novel, each found in a single individual, and were distinct from the common haplotype CC-A11 by a single transition mutation at sites 119 and 314, respectively. Haplotype diversity ($h$) for the Masirah Island *C. caretta* rookery was 0.04 (95% CI = 0.0–0.4 from coalescent simulations), which is among the lowest documented haplotype diversity for a major *C. caretta* rookery surveyed in this dataset. Nucleotide diversity ($\pi$) was 0.0001 (95% CI = 0.0–0.1) and the average number of nucleotide differences ($k$) was 0.04. Tajima's D for the Masirah Island ($D$ = -1.38) rookeries was not significant at $\alpha = 0.05$. Oman has among the lowest *C. caretta* mitochondrial DNA diversity globally (Table 2) in terms of both haplotype diversity (Fig. 1) and nucleotide diversity (Fig. 2).

No microsatellite loci deviated from H-W equilibrium at an $\alpha = 0.05$ after a Bonferroni correction. In contrast to mtDNA diversity, the Masirah Island rookery showed similar levels of nuclear marker diversity not only to the similarly sized south Florida rookery (Table 3), but also relative to the entire northwestern Atlantic aggregation combined. We compared observed and expected heterozygosity among all four microsatellite loci between Masirah and the south Florida rookery, both similarly sized, and between all northwestern Atlantic rookeries combined. Neither metric yielded significantly different comparisons (t-test, $p \geq 0.1$).

### Mitochondrial Genetic Diversity for *Chelonia mydas* at Ras al Hadd Rookery

We observed six haplotypes in 42 sampled individuals (Table 1). These haplotypes form two clusters, one that includes three haplotypes unique to Oman (CMP71, CMP73, and one novel haplotype- CM-Oman1) and separated by 14 mutational steps from a second cluster that contains three haplotypes, two unique to Oman (CMP62 and a novel haplotype CM-Oman2), and one shared between Oman and other rookeries throughout Austral-Asia (CMP49). Haplotype diversity was 0.71 (95% CI = 0.59–0.93 from 1000 coalescent simulations). Nucleotide diversity was 0.02 (95% CI = 0.01 to 0.03) and the average number of nucleotide differences was 8.6 (Table 4). Tajima's D was significant and positive ($D$ = 2.5) indicating recent population contraction. Overall, the *C.*

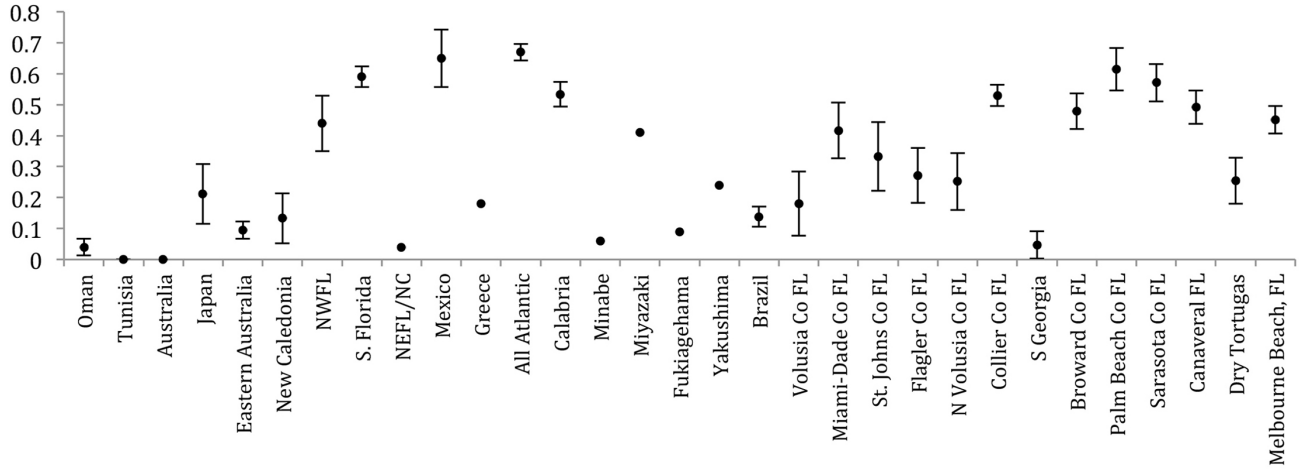


**Figure 1.** *Caretta caretta* haplotype diversity for this study (Oman) and previously published surveys of rookeries listed in Table 2. Whiskers represent standard errors where available from published studies. The abbreviations CC and CM correspond to *C. caretta* and *C. mydas*, respectively.

**Table 2.** *Caretta caretta* diversity metrics for this study and eight others. Metrics reported here include ocean basin, haplotype diversity (*h*) and standard error (SE), nucleotide diversity (π) and standard error (SE), the number of individuals sampled (n), and relevant citation.

| Rookery | Ocean Basin | *h* | SE | π | SE | n | Citation |
|---|---|---|---|---|---|---|---|
| Oman | Indian | 0.04 | 0.027 | 0.0001 | 0.00007 | 100 | This study |
| Tunisia | Mediterranean | 0 | 0 | 0 | | 16 | Chaieb et al. (2010) |
| Australia | Pacific | 0 | | 0 | | 26 | Bowen et al. (1995) |
| Japan | Pacific | 0.212 | 0.097 | 0.00277 | 0.00127 | 26 | |
| Eastern Australia | Pacific | 0.095 | 0.028 | | | 101 | Boyle et al. (2009) |
| New Caledonia | Pacific | 0.133 | 0.081 | | | 27 | |
| NWFL | Atlantic | 0.44 | 0.09 | 0.02 | 0.0035 | 42 | Encalada et al. (1998) |
| S. Florida | Atlantic | 0.59 | 0.033 | 0.0294 | 0.00096 | 50 | |
| NEFL/NC | Atlantic | 0.04 | | 0.0019 | | 105 | |
| Mexico | Atlantic | 0.65 | 0.093 | 0.0028 | 0.00054 | 20 | |
| Greece | Mediterranean | 0.18 | | 0 | | 21 | |
| All Atlantic | Atlantic | 0.67 | 0.027 | 0.023 | 0.001 | 249 | |
| Calabria | Mediterranean | 0.533 | 0.04 | | | 47 | Garofalo et al. (2009) |
| Minabe | Pacific | 0.06 | | 0.0008 | | 102 | Hatase et al. (2002) |
| Miyazaki | Pacific | 0.41 | | 0.006 | | 46 | |
| Fukiagehama | Pacific | 0.09 | | 0.0013 | | 22 | |
| Yakushima | Pacific | 0.24 | | 0.0034 | | 89 | |
| Brazil | Atlantic | 0.138 | 0.0327 | 0.000372 | 0.000606 | 190 | Reis et al. (2010) |
| Volusia Co FL | Atlantic | 0.181 | 0.104 | 0.0087 | 0.0052 | 21 | Shamblin et al. (2011) |
| Miami-Dade Co FL | Atlantic | 0.416 | 0.09 | 0.02 | 0.0109 | 22 | |
| St. Johns Co FL | Atlantic | 0.333 | 0.111 | 0.0134 | 0.0075 | 27 | |
| Flagler Co FL | Atlantic | 0.272 | 0.089 | 0.0132 | 0.0073 | 32 | |
| N Volusia Co FL | Atlantic | 0.252 | 0.092 | 0.0083 | 0.0049 | 37 | |
| Collier Co FL | Atlantic | 0.53 | 0.035 | 0.0242 | 0.0126 | 40 | |
| S Georgia | Atlantic | 0.047 | 0.044 | 0.0022 | 0.0018 | 43 | |
| Broward Co FL | Atlantic | 0.479 | 0.058 | 0.0206 | 0.0108 | 48 | |
| Palm Beach Co FL | Atlantic | 0.615 | 0.069 | 0.0169 | 0.009 | 49 | |
| Sarasota Co FL | Atlantic | 0.571 | 0.061 | 0.0232 | 0.0121 | 57 | |
| Canaveral FL | Atlantic | 0.492 | 0.054 | 0.022 | 0.0115 | 58 | |
| Dry Tortugas | Atlantic | 0.254 | 0.074 | 0.0068 | 0.0041 | 58 | |
| Melbourne Beach, FL | Atlantic | 0.451 | 0.044 | 0.0201 | 0.0105 | 106 | |

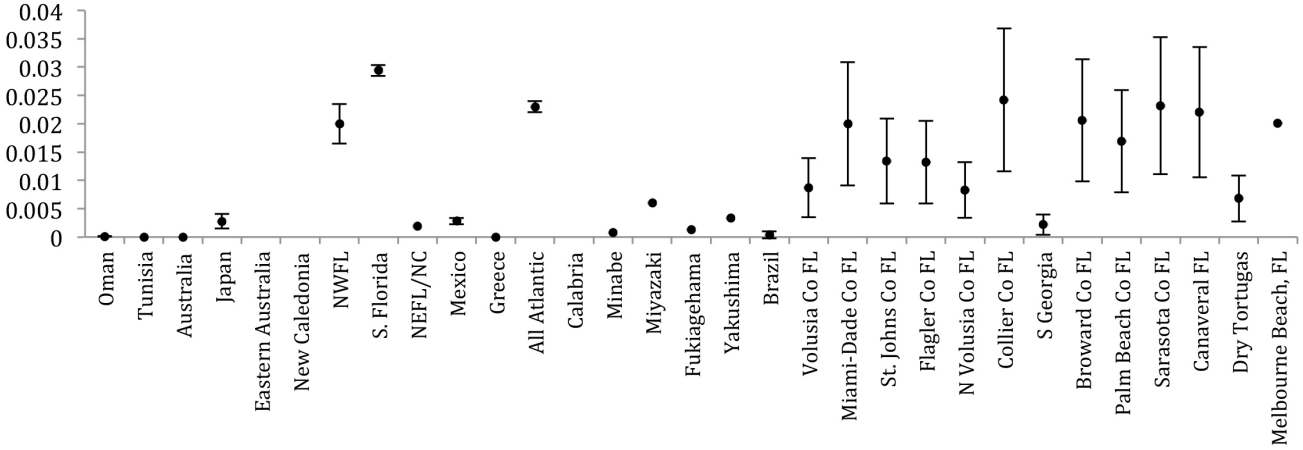


**Figure 2.** *Caretta caretta* nucleotide diversity for this study (Oman) and previously published surveys of rookeries listed in Table 2. Data represent means and standard errors where available from published studies.

**Table 3.** Microsatellite population genetic statistics for *Caretta caretta*, including the sample size (n), number of alleles (A), the effective number of alleles ($A_E$), observed heterozygosity ($H_O$), and expected heterozygosity ($H_E$). None of the comparisons observed and expected heterozygosities were significantly different at $\alpha = 0.05$.

| Population | Locus | n | A | $A_E$ | $H_O$ | $H_E$ |
|---|---|---|---|---|---|---|
| North Carolina | DC107 | 26 | 7 | 4.418 | 0.769 | 0.774 |
| | CC176 | 26 | 14 | 4.952 | 0.923 | 0.798 |
| | CC141 | 27 | 11 | 6.284 | 0.741 | 0.841 |
| | CC7 | 26 | 10 | 4.135 | 0.769 | 0.758 |
| South Carolina | DC107 | 24 | 6 | 4.299 | 0.750 | 0.767 |
| | CC176 | 24 | 12 | 4.235 | 0.750 | 0.764 |
| | CC141 | 24 | 11 | 6.261 | 0.833 | 0.840 |
| | CC7 | 24 | 11 | 4.702 | 0.875 | 0.787 |
| Georgia | DC107 | 39 | 7 | 4.261 | 0.821 | 0.765 |
| | CC176 | 39 | 15 | 5.828 | 0.872 | 0.828 |
| | CC141 | 39 | 11 | 6.364 | 0.821 | 0.843 |
| | CC7 | 39 | 12 | 5.895 | 0.872 | 0.830 |
| Florida | DC107 | 288 | 10 | 4.652 | 0.795 | 0.785 |
| | CC176 | 289 | 29 | 5.289 | 0.775 | 0.811 |
| | CC141 | 290 | 15 | 7.650 | 0.828 | 0.869 |
| | CC7 | 290 | 18 | 5.128 | 0.766 | 0.805 |
| Brazil | DC107 | 81 | 8 | 3.647 | 0.741 | 0.726 |
| | CC176 | 81 | 14 | 4.528 | 0.790 | 0.779 |
| | CC141 | 81 | 11 | 3.266 | 0.704 | 0.694 |
| | CC7 | 81 | 8 | 2.368 | 0.580 | 0.578 |
| Oman | DC107 | 115 | 15 | 2.587 | 0.583 | 0.613 |
| | CC176 | 108 | 12 | 3.283 | 0.713 | 0.695 |
| | CC141 | 112 | 11 | 6.018 | 0.839 | 0.834 |
| | CC7 | 115 | 14 | 4.606 | 0.774 | 0.783 |

**Table 4.** *Chelonia mydas* diversity metrics for this study and eight others. Metrics reported here include ocean basin, haplotype diversity (*h*) and standard error (SE), nucleotide diversity (π) and standard error (SE), number of individuals sampled (n), and relevant citation.

| Rookery | Ocean Basin | h | SE | π | SE | n | Citation |
|---|---|---|---|---|---|---|---|
| Oman | Indian | 0.706 | 0.017 | 0.0215 | 0.00133 | 42 | This study |
| Trinidade | Atlantic | 0.5046 | 0.0522 | 0.0012 | 0.0011 | 99 | |
| Atol das Rocas | Atlantic | 0.5196 | 0.0763 | 0.0012 | 0.0011 | 53 | Bjorndal et al. (2006) |
| Fernando de Noronha | Atlantic | 0.2333 | 0.1256 | 0 | 0 | 16 | |
| Tortugaro | Atlantic | 0.16 | 0.02 | 0.0034 | 0.0022 | 433 | Bjorndall et al. (2005) |
| Total NMC | Indian | 0.3964 | | 0.01962 | | 191 | |
| Total SMC | Indian | 0.3425 | | 0.0221 | | 53 | |
| Europa | Indian | 0.1174 | | 0.0076 | | 33 | |
| Juan de Nova | Indian | 0.5632 | | 0.036 | | 20 | |
| Nosy Iranja | Indian | 0 | | 0 | | 13 | |
| Mayotte | Indian | 0.4524 | | 0.0231 | | 41 | |
| Mohéli | Indian | 0.3708 | | 0.0133 | | 34 | Bourjea et al. (2007) |
| Glorieuses | Indian | 0.3441 | | 0.0168 | | 39 | |
| Cosmoledo | Indian | 0.3871 | | 0.021 | | 31 | |
| Aldabra | Indian | 0.4646 | | 0.0249 | | 26 | |
| Farquhar | Indian | 0.7143 | | 0.0342 | | 7 | |
| Tromelin | Indian | 0.241 | | 0.0132 | | 44 | |
| Total SW Indian Ocean | Indian | 0.5063 | | 0.0289 | | 288 | |
| Pacific | Pacific | 0.71 | 0.02 | 0.034 | 0.017 | 272 | |
| Indian | Indian | 0.7 | 0.03 | 0.019 | 0.01 | 107 | Dethmers et al. (2006) |
| Australasia | Indo-Pacific | 0.88 | 0.01 | 0.041 | 0.02 | 714 | |
| Southeast Asia | Indo-Pacific | 0.8 | 0.01 | 0.006 | 0.004 | 335 | |
| Cyprus | Mediterranean | 0.22 | 0.16 | 0.00042 | | 10 | |
| Florida | Atlantic | 0.56 | 0.047 | 0.0013 | | 24 | |
| Mexico | Atlantic | 0.82 | 0.058 | 0.0057 | | 20 | |
| Costa Rica | Atlantic | 0.13 | 0.11 | 0.00028 | | 15 | |
| Aves | Atlantic | 0.25 | 0.18 | 0.0053 | | 8 | |
| Surinam | Atlantic | 0.26 | 0.14 | 0.0056 | | 15 | Encalada et al. (1996) |
| Brazil | Atlantic | 0.68 | 0.085 | 0.0017 | | 16 | |
| Ascension | Atlantic | 0.35 | 0.12 | 0.00077 | | 20 | |
| Guinea Bissau | Atlantic | 0 | 0 | 0 | 0 | 19 | |
| Atlantic overall | Atlantic | 0.83 | | 0.005 | | 147 | |
| Poilão | Atlantic | 0 | 0 | 0 | 0 | 51 | |
| Ascension | Atlantic | 0.26 | 0.081 | 0.0006 | 0.0007 | 50 | |
| Bioko | Atlantic | 0.184 | 0.068 | 0.0004 | 0.0006 | 50 | |
| Principe | Atlantic | 0.533 | 0.172 | 0.0011 | 0.0012 | 6 | Formia et al. (2006) |
| São Tome | Atlantic | 0.584 | 0.127 | 0.003 | 0.0021 | 20 | |
| Comoros | Indian | 0.733 | 0.12 | 0.0261 | 0.0154 | 10 | |
| Atlantic overall | Atlantic | 0.22 | 0.041 | 0.0007 | 0.0008 | 178 | |
| Aves | Atlantic | 0.186 | 0.088 | 0.0039 | 0.0025 | | Lahanas et al. (1998) |
| Costa Rica | Atlantic | 0.1627 | 0.0231 | 0.0033 | 0.0022 | 433 | Seminoff (2002) |

*mydas* rookery in Oman appears to have relatively high haplotype (Fig. 3) and nucleotide diversity (Fig. 4) compared to other rookeries globally.

## DISCUSSION

This study represents the first detailed survey of genetic diversity in Oman's *C. caretta* and *C. mydas* rookeries. We find that mitochondrial DNA diversity in the *C. caretta* sample is low and among the lowest ever surveyed compared to similarly sized rookeries in the Atlantic (Tables 1–2; Figs. 1–2). This is despite the tremendous size of the Masirah Island rookery, which may be equal in size to the largest Atlantic *C. caretta* rookeries (Ross, 1978; Ross and Banwari, 1982; Baldwin et al., 2003; Ehrhart et al., 2003). However, nuclear diversity at four microsatellite loci is high (Table 3), suggesting an even greater discrepancy between nuclear and mitochondrial diversity than has been observed in Atlantic rookeries (Bowen et al., 2005). This disparity likely results from the effective population size differences between mtDNA and nDNA, but also from the geographic isolation of maternally-inherited mitochondrial DNA through natal homing, whereas nuclear material is exchanged through male-mediated gene flow with other rookeries. The three haplotypes we observed in Oman are closely related to one very common allele in the Atlantic (CCA1), but are at least 16 mutational steps from most remaining Atlantic haplotypes.

We surveyed *C. mydas* for mitochondrial DNA only and found levels of genetic diversity that are high relative to other rookeries in the Indian Ocean, Atlantic Ocean, or entire Austral-Asian region (Figs. 3–4). Haplotype diversity in

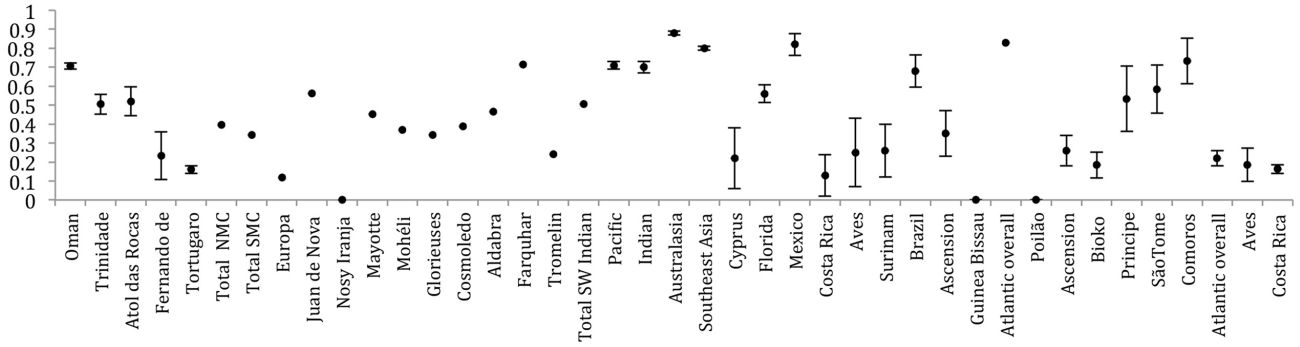


**Figure 3.** *Chelonia mydas* haplotype diversity for this study (Oman) and previously published surveys of rookeries listed in Table 4. Data represent means and standard errors where available from published studies.

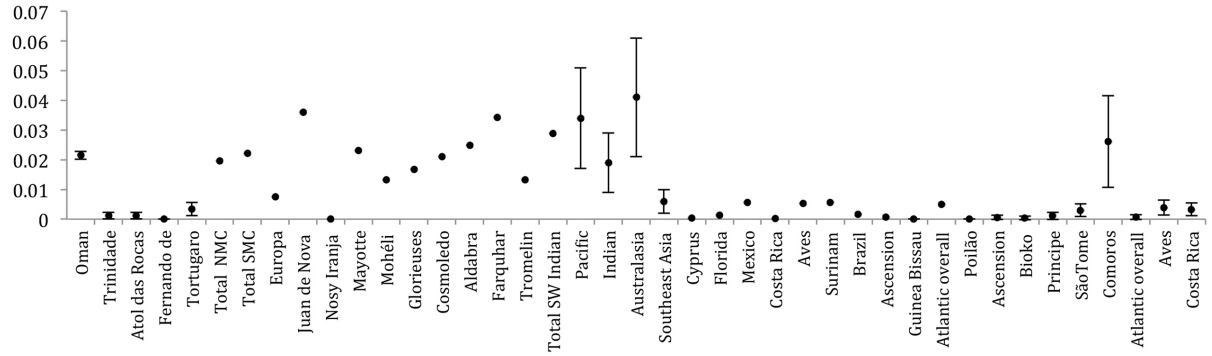


**Figure 4.** *Chelonia mydas* nucleotide diversity for this study (Oman) and previously published surveys of rookeries listed in Table 4. Data represent means and standard errors where available from published studies.

Oman (0.71) is similar to that reported for Mexico (0.82), and Brazil (0.68), and higher than rookeries in Florida (0.56) and Costa Rica (0.13), Ascension Island (0.35), and the Mediterranean (Encalada et al., 1996). Overall haplotype diversity for the Atlantic is 0.83 with nucleotide diversity lower than what we observed in Oman (see also Encalada et al., 1996; Bjorndal et al., 2005). Haplotype and nucleotide diversity also rank high relative to other rookeries sampled in the southwest Indian Ocean, which range from 0 to 0.71 for haplotype diversity and 0 to 0.03 for nucleotide diversity (the rookery at Farquhar, North of Madagascar, being the most diverse; Bourjea et al., 2007). African rookeries typically have lower levels of genetic diversity, with the exception of the Comoros ($h$ =0.733, $\pi$ = 0.026) (Formia et al., 2006). Our focus in this work is the comparative diversity of *C. mydas* rookeries in Oman, but preliminary analyses (not shown here) reveal close associations of mtDNA haplotypes and some shared haplotypes with rookeries in the southwestern Indian Ocean (Bourjea et al., 2007) and Austral-Asia (Dethmers et al., 2006). Use of microsatellite loci would make it possible to more accurately identify and estimate levels of connectivity among Oman and other rookeries throughout the Indian and Pacific Oceans. However, it is clear that Oman hosts a *C. mydas* rookery that is genetically diverse with a mixture of unique and shared mitochondrial haplotypes (Table 1). Additional sampling is warranted to provide a clearer assessment of genetic diversity in this region.

We demonstrated that Oman's *C. caretta* show low mitochondrial DNA diversity. It is unclear whether the shared haplotypes between Oman and the western Atlantic are a result of gene flow from the Indian to the Atlantic Ocean or vice versa. However, it is clear that of the two clades of *C. caretta* present in the Atlantic (Encalada et al., 1998; Reece et al., 2005; Shamblin et al. 2014), one is less diverse and shares recent ancestry with the Omani rookery. Available evidence indicates that the CCA11 lineage present in Oman may represent a recent re-invasion of the Indo-Pacific by an Atlantic lineage (see Shamblin et al., 2014). *Chelonia mydas* in Oman appear to not have suffered as severe of a population contraction and/or loss of genetic diversity as *C. caretta*. These changes are potentially mitigated by lower nest site fidelity in *C. mydas* and female-mediated gene flow with other rookeries in the Indo-Pacific and the southern Atlantic (Bourjea et al., 2007).

The *C. caretta* rookery at Masirah Island has low levels of mitochondrial DNA and high levels of nuclear DNA diversity, suggesting a recent colonization or demographic shift and/or high nest site fidelity. However, male-mediated gene flow may be substantial, allowing for an overall diverse genetic makeup of the rookery. It is unclear how unique the genetic variants that make up Oman's *C. caretta* rookery are in the Indian Ocean. Although most of the *C. caretta* nesting in Oman are concentrated at Masirah Island, other rookeries do exist elsewhere in Oman and neighboring Yemen. None has been characterized for genetic diversity.

Threats faced by Oman's rookeries include rapid coastal development and loss of dune structure due to introduced goats, which defoliate the dunes and rob them of the root structures on which the dunes depend (JSR, pers. obs.). Loss of dunes leads to urban lights being visible from the berm, which causes disorientation of adults and hatchlings (JSR, pers. obs.). *Chelonia mydas* face additional threats, including some harvesting for food, although not on a commercial level (Oman Ministry of Environment and Climatic Affairs, pers. comm.). Oman's *C. mydas* are genetically diverse. Their genetic makeup is similar to other rookeries in the Pacific and Indian Oceans, such that females may recruit to different nesting beaches over the course of their reproductive lives or these shared haplotypes may be an artifact of common ancestry. Determining the degree of connectivity among rookeries is critical for their future management. For example, the impacts of local threats to rookeries may be ameliorated or exacerbated by the degree of connectivity with surrounding rookeries. That information is necessary for conservation practitioners to develop effective management strategies. Future studies in Oman will benefit from the increased

phylogeographic resolution of longer mtDNA fragments (Abreu-Grobois et al., 2006; Shamblin et al., 2012), additional microsatellite data (Shamblin et al., 2009), and genomic advances (Tikochinski et al., 2012). Satellite tagging and physical tags will yield additional information on the movements of *C. mydas* throughout the Indo-Pacific and south Atlantic. Lastly, although this study characterized a single geographically localized rookery in Oman for each species, additional sampling and increased nuclear microsatellite sampling may yield greater insight into the management of distinct nesting beaches on a regional scale, which may or may not be genetically similar genetically to those sampled here.

## ACKNOWLEDGMENTS

Funding for this project was provided by grants to JSR from the University of Central Florida Biology Department and the Caribbean Conservation Corporation Mel Stark Award, and funds awarded to CLP from UCF startup package, NSF grant DEB–0416000, and a Florida Fish and Wildlife Conservation Commission/Caribbean Conservation Corporation License Plate Grant. Samples of Oman Loggerhead Sea Turtles were collected under permit number 09/2003 issued by the Director General of Nature Conservation, Sultanate of Oman, and CITES permit 04US076985/9 issued by the U.S. Department of Interior. Transportation, housing, collecting assistance, laboratory space and logistics of field work were provided by Sultan Qaboos University. We acknowledge Shoaib Al-Zidjali and the Hematology Department at Sultan Qaboos University Hospital for sequencing assistance. We thank the turtle rangers at Ras al Hadd and Masirah Island who provided invaluable assistance through the Department of Nature Conservation. We also thank Perran Ross for his valuable advice in preparation for this project. We thank Earl Possardt and Blair Witherington and the U. S. Fish and Wildlife Service and Nicolas Pilcher for their assistance in the field and coordination of travel. Peter Dutton and the Southwest Fisheries Science Center were instrumental in providing archived tissue samples from previous studies to standardize microsatellite scores across studies. We thank the following for helpful comments on this manuscript: Russell Blaine, Brian Bowen, Steve Carl, Todd Castoe, Nic Kooyers, John Fauth, Matt Gifford, Eric Hoffman, Allan Larson, Reed Noss, Lindsay Young, and the Fall 2005 Topics of Genomics students (University of Central Florida).

## LITERATURE CITED

Abreu-Grobois, F. A., J. Horrocks, A. Formia, P. H. Dutton, R. Leroux, X. Velez-Zuazo, L. S. Soares, and A. B. Meylan. 2006. New mtDNA D-loop primers which work for a variety of marine turtle species may increase the resolution of mixed stock analysis. Pp. 200–201 *in* M. Frick, ed. 26th Annual Symposium of Sea Turtle Biology and Conservation, Athens, Greece.

Baldwin, R., G. R. Hughes, and R. Prince. 2003. Loggerhead turtles in the Indian Ocean. Pp. 218–232 *in* A. B. Bolten and B. E. Witherington, eds. Loggerhead Sea Turtles. Smithsonian Institution Press, Washington D.C.

Bjorndal, K. A., A. B. Bolten, L. Moreira, C. Bellini, and M. Â. Marcovaldi. 2006. Population structure and diversity of Brazilian green turtle rookeries based on mitochondrial DNA sequences. Chelonian Conservation and Biology 5:262–268.

Bjorndal, K. A., A. B. Bolten, and S. Troeng. 2005. Population structure and genetic diversity in green turtles nesting at Tortuguero, Costa Rica, based on mitochondrial DNA control re-gion sequences. Marine Biology 147:1449–1457.

Bolten, A. B., and B. E. Witherington. 2003. Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, D.C. 319 p.

Bourjea, J., S. Lapegue, G. L., D. Broderick, A. Mortimer, S. Ciccione, D. Roos, C. Taquet, and H. Grizel. 2007. Phylogeography of the green turtle, *Chelonia mydas*, in the southwest Indian Ocean. Molecular Ecology 16:175–186.

Bowen, B. W., F. A. Abreu-Grobois, G. H. Balazs, N. Kamezaki, C. J. Limpus, and R. J. Ferl. 1995. Trans-Pacific migrations of the loggerhead turtle (*Caretta caretta*) demonstrated with

mitochondrial DNA markers. Proceedings of the National Academy of Sciences of the United States of America 92:3731–3734.

Bowen, B. W., A. L. Bass, L. Soares, and R. J. Toonen. 2005. Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*). Molecular Ecology 14:2389–2402.

Bowen, B. W., N. Kamezaki, C. J. Limpus, G. R. Hughes, A. B. Meylan, and J. C. Avise. 1994. Global phylogeography of the loggerhead turtle (*Caretta caretta*) as indicated by mitochondrial DNA haplotypes. Evolution 48:1820–1828.

Bowen, B. W., A. B. Meylan, J. P. Ross, C. J. Limpus, G. H. Balazs, and J. C. Avise. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46:865–881.

Boyle, M. C., N. N. FitzSimmons, C. J. Limpus, S. Kelez, X. Velez-Zuazo, and M. Waycott. 2009. Evidence for transoceanic migrations by loggerhead sea turtles in the southern Pacific Ocean. Proceedings of the Royal Society B 276:1993–1999.

Carreras, C., M. Pascual, L. Cardona, A. Aguilar, D. Margaritoulis, A. Rees, O. Turkozan, Y. Levy, A. Gasith, M. Aureggi, and M. Khalil. 2007. The genetic structure of the loggerhead sea turtle (*Caretta caretta*) in the Mediterranean as revealed by nuclear and mitochondrial DNA and its conservation implications. Conservation Genetics 8:761–775.

Chaieb, O., A. E. Ouaer, F. Maffucci, M. N. Bradai, F. Bentivegna, K. Said, and N. Chatti. 2010. Genetic survey of loggerhead turtle *Caretta caretta* nesting population in Tunisia. Marine Biodiversity Records 3:e20. doi:10.1017/S175526721000014X. accessed 15 January 2016.

Dethmers, K. E. M., D. Broderick, C. Moritz, N. N. Fitzsimmons, C. J. Limpus, S. Lavery, S. Whiting, M. Guinea, R. I. T. Prince, and R. O. D. Kennett. 2006. The genetic structure of Australasian green turtles (*Chelonia mydas*): exploring the geographical scale of genetic exchange. Molecular Ecology 15:3931–3946.

Ehrhart, L. M., D. A. Bagley, and W. E. Redfoot. 2003. Loggerhead turtles in the Atlantic Ocean: geographic distribution, abundance, and population status. Pp. 157–174 *in* A. B. Bolten and B. E. Witherington, eds. Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, D.C.

Encalada, S. E., K. A. Bjorndal, A. B. Bolten, M. M. Miyamoto, and B. W. Bowen. 1996. Phylogeography and population structure of the Atlantic and Mediterranean green turtle *Chelonia mydas*: a mitochondrial DNA control region sequence assessment. Molecular Ecology 5:473–483.

Encalada, S. E., K. A. Bjorndal, A. B. Bolten, J. C. Zurita, B. Schroeder, E. Possardt, C. J. Sears, and B. W. Bowen. 1998. Population structure of loggerhead turtle (*Caretta caretta*) nesting colonies in the Atlantic and Mediterranean as inferred from mitochondrial DNA control re-gion sequences. Marine Biology 130:567–575.

FitzSimmons, N. N. 1998. Single paternity of clutches and sperm storage in the promiscuous green turtle (*Chelonia mydas*). Molecular Ecology 7:575–584.

FitzSimmons, N. N., C. Moritz, C. J. Limpus, J. D. Miller, C. J. Parmenter, and R. Prince. 1996. Comparative genetic structure of green, loggerhead, and flatback populations in Australia based on variable mtDNA and nDNA regions. Pp. 25–32 *in* B. W. Bowen and W. N. Witzell, eds. Proceedings of the International Symposium on Sea Turtle Conservation Genetics. National Technical Information Service, Springfield, VA.

Formia, A., B. J. Godley, J. F. Dontaine, and M. W. Bruford. 2006. Mitochondrial DNA diversity and phylogeography of endangered green turtle (*Chelonia mydas*) populations in Africa. Conservation Genetics 7:353–369.

Frankham, R. 2010. Challenges and opportunities of genetic approaches to biological conservation. Biological Conservation 143:1919–1927.

Frankham, R., J. D. Ballou, and D. A. Briscoe. 2002. Introduction to Conservation Genetics. Cambridge University Press, Cambridge, UK. 644 p.

Garofalo, L., T. Mingozzi, A. Mico, and A. Novelletto. 2009. Loggerhead turtle (*Caretta caretta*) matrilines in the Mediterranean: further evidence of genetic diversity and connectivity. Marine Biology 156:2085–2095.

Hatase, H., M. Kinoshita, T. Bando, N. Kamezaki, K. Sato, Y. Matsuzawa, K. Goto, K. Omuta, Y. Nakashima, H. Takeshita, and W. Sakamoto. 2002. Population structure of loggerhead turtles, *Caretta caretta*, nesting in Japan: bottlenecks on the Pacific population. Marine Biology 141:299–305.

Karl, S. A., B. W. Bowen, and J. C. Avise. 1992. Global population genetic structure and male-mediated gene flow in the green turtle (*Chelonia mydas*): RFLP analysis of anonymous nuclear loci. Genetics 131:163–173.

Lahanas, P. N., K. A. Bjorndal, A. B. Bolten, S. E. Encalada, M. M. Miyamoto, R. A. Valverde, and B. W. Bowen. 1998. Genetic composition of a green turtle (*Chelonia mydas*) feeding ground population: evidence for multiple origins. Marine Biology 130:345–352.

Moore, M. K., and R. M. Ball. 2002. Multiple paternity in loggerhead turtle (*Caretta caretta*) nests on Melbourne Beach, Florida: a microsatellite analysis. Molecular Ecology 11:281–288.

Nei, M. 1987. Molecular Evolutionary Genetics. Columbia University Press, New York. 512 p.

Nicholas, K. B., and H. B. Nicholas. 1997. GeneDoc: A tool for editing and annotating multiple sequence alignments. http://www.cris.com/~Ketchup/genedoc.shtml accessed 1/15/2016.

National Marine Fisheries Service (NMFS), and U.S. Fish and Wildlife Service (USFWS). 1991a. Recovery Plan for U.S. Population of Atlantic Loggerhead, Washington, D.C.

National Marine Fisheries Service (NMFS), and U.S. Fish and Wildlife Service (USFWS). 1991b. Recovery plan for US population of Atlantic Green Turtle, Washington, D.C.

National Marine Fisheries Service (NMFS), and U.S. Fish and Wildlife Service (USFWS). 1998. Recovery plan for US Pacific populations of the East Pacific Green Turtle (*Chelonia mydas*), Silver Spring, MD.

Norman, J. A., C. Moritz, and C. J. Limpus. 1994. Mitochondrial DNA control region polymorphisms: genetic markers for ecological studies of marine turtles. Molecular Ecology 3:363–373.

Peakall, R., and P. E. Smouse. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. Molecular Ecology Notes 6:288–295.

Reece, J. S., T. A. Castoe, and C. L. Parkinson. 2005. Historical perspectives on population genetics of three marine turtle species. Conservation Genetics 6:235–251.

Reece, J. S., D. Passeri, L. Ehrhart, S. C. Hagen, A. Hays, C. Long, R. F. Noss, M. Bilskie, C. Sanchez, M. V. Schwoerer, B. Von Holle, J. Weishampel, and S. Wolf. 2013. Sea level rise, land use, and climate change influence the distribution of loggerhead turtle nests at the largest USA rookery (Melbourne Beach, Florida). Marine Ecology Progress Series 493:259–274.

Reis, E. C., L. S. Soares, S. M. Vargas, F. R. Santos, R. J. Young, K. A. Bjorndal, A. B. Bolten, and G. Lobo-Hajdu. 2010. Genetic composition, population structure, and phylogeography of the loggerhead sea turtle: colonization hypothesis for the Brazilian rookeries. Conservation Genetics 11:1467–1477.

Roberts, M. A., T. S. Schwartz, and S. A. Karl. 2004. Global population genetic structure and male-mediated gene flow in the green sea turtle (*Chelonia mydas*): analysis of microsatellite loci. Genetics 166:1857–1870.

Ross, J. P., and M. A. Banwari. 1982. Review of sea turtles in the Arabian area. Pp. 373–383 *in* K. A. Bjorndal, ed. Biology and Conservation of Sea Turtles. Smithsonian Institution Press, Washington D.C.

Ross, P. 1978. Marine Turtle Survey, 1977, Sultanate of Oman. Marine Turtle Newsletter 7:4–5.

Rozas, J. J., C. Sánchez-DelBarrio, X. Messeguer, and R. Rozas. 2003. DNAsp, DNA polymorphism analyses by the coalescent and other methods. Bioinformatics 19:2496–2497.

Seminoff, J. A. 2002. 2002 IUCN Red List global status assessment: Green Turtle (*Chelonia mydas*). IUCN/SSC Marine Turtle Specialist Group, Gland, Switzerland.

Shamblin, B., A. Bolten, K. Bjorndal, P. Dutton, J. Nielsen, F. Abreu-Grobois, K. Reich, B. Witherington, D. Bagley, L. Ehrhart, A. Tucker, D. Addison, A. Arenas, C. Johnson, R. Carthy, M. Lamont, M. Dodd, M. Gaines, E. LaCasella, and C. Nairn. 2012. Expanded mitochondrial control region sequences increase resolution of stock structure among North Atlantic loggerhead turtle rookeries. Marine Ecology Progress Series 469:145–160.

Shamblin, B., M. Dodd, D. Bagley, L. Ehrhart, A. Tucker, C. Johnson, R. Carthy, R. Scarpino, E. McMichael, D. Addison, K. Williams, M. Frick, S. Ouellette, A. Meylan, M. Godfrey, S. Murphy, and C. Nairn. 2011. Genetic structure of the southeastern United States loggerhead turtle nesting aggregation: evidence of additional structure within the peninsular Florida recovery unit. Marine Biology 158:571–587.

Shamblin, B. M., A. B. Bolten, F. A. Abreu-Grobois, K. A. Bjorndal, L. Cardona, C. Carreras, M. Clusa, C. Monzón-Argüello, C. J. Nairn, J. T. Nielsen, R. Nel, L. S. Soares, K. R. Stewart, S. T. Vilaça, O. Türkozan, C. Yilmaz, and P. H. Dutton. 2014. Geographic patterns of genetic variation in a broadly distributed marine vertebrate: new insights into loggerhead turtle stock structure from expanded mitochondrial DNA sequences. PLoS ONE 9:e85956. doi: 85910.81371/journal.pone.0085956.

Shamblin, B. M., B. C. Faircloth, M. G. Dodd, D. A. Bagley, L. M. Ehrhart, P. H. Dutton, A. Frey, and C. J. Nairn. 2009. Tetranucleotide markers from the loggerhead sea turtle (*Caretta caretta*) and their cross-amplification in other marine turtle species. Conservation Genetics 10:577–580.

Tajima, F. 1983. Evolutionary relationship of DNA sequences in finite populations. Genetics 105:437–460.

Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. Genetics 123:585–595.

Tikochinski, Y., R. Bendelac, A. Barash, A. Daya, Y. Levy, and A. Friedmann. 2012. Mitochondrial DNA STR analysis as a tool for studying the green sea turtle (*Chelonia mydas*) populations: The Mediterranean Sea case study. Marine Genomics 6:17–24.

Witherington, B. E. 2003. Biological Conservation of Loggerheads. Pp. 295–311 *in* A. B. Bolten and B. E. Witherington, eds. Loggerhead Sea Turtles. Smithsonian Institution Press, Washington, D.C.

Witt, M. J., L. A. Hawkes, M. H. Godfrey, and A. C. Broderick. 2010. Predicting the impacts of climate change on a globally distributed species: The case of the loggerhead turtle. Journal of Experimental Biology 213:901–911.