



## Mexican origins for the Texas green turtle foraging aggregation: A cautionary tale of incomplete baselines and poor marker resolution



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### ABSTRACT

The green turtle (*Chelonia mydas*) foraging aggregation along the Texas coast has increased dramatically in recent years, but the source populations for these turtles have not been adequately resolved. Previous mixed stock analysis (MSA) based on 490 base pair (bp) mitochondrial control region haplotypes suggested a large Florida contribution, but widespread sharing of common haplotypes among potential source populations and incomplete source population baseline data precluded precise assessment. To test the hypothesis that Texas turtles may represent proximal western Gulf of Mexico (GoM) nesting populations, we analyzed novel rookery samples from Rancho Nuevo, Tamaulipas, Mexico (RNMx) and conducted oceanic connectivity simulations. The RNMx samples yielded haplotypes CM-A1.1 and CM-A3.1 in frequencies not significantly different from those of the central eastern Florida nesting population. However, mitogenomic sequencing identified a diagnostic mitochondrial SNP (mtSNP) variant that is fixed in RNMx relative to the Florida CM-A1.1 lineage. Pairwise comparisons indicate that the Tamaulipas rookery represents a discrete population relative to those previously described in the northern Greater Caribbean, warranting recognition of a western GoM management unit (MU). Contrary to previous findings, the Florida populations were ruled out as major contributors to the Texas aggregation through screening of the mtSNP. Mixed stock analysis incorporating the mtSNP data suggested a western GoM origin for approximately 70% of the Texas foraging aggregation, with Quintana Roo contributing the majority of the remainder. Backtracking simulations within an ocean circulation model were broadly congruent with genetic results in indicating substantial probability of oceanic transport from Mexican rookeries to the Texas coast (68%) while also dismissing the possibility of transport from the eastern Florida rookeries (0%). The mixed stock analyses and backtracking simulations are consistent with previous hypotheses implicating oceanic dispersal followed by natal homing by neritic juveniles to explain juvenile green turtle distributions. In contrast to a pattern of stepping stone connectivity across the remaining northern Greater Caribbean, the Texas foraging aggregation was distinct from all others analyzed in the region, including one in the eastern GoM. This isolation highlights the significance of Texas as developmental habitat for the proposed western GoM MU and reiterates the importance of continued international cooperation to facilitate recovery of this stock. This study also underscores the importance of satisfying underlying assumptions of mixed stock analysis in order to make robust inferences of connectivity.

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### 1. Introduction

Assessing connectivity is an important consideration for management of migratory marine species with complex life histories. Despite potential for considerable dispersal and migration, many marine and anadromous taxa have discrete mating sites that create genetic structure among populations (Quinn and Dittman, 1990; Hoelzel, 1998;

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Hueter et al., 2005; Jensen et al., 2013). However, individuals from these distinct populations often mix during other parts of their life cycle, obscuring their population identity. Green turtles (*Chelonia mydas*) exhibit this complex life history. Female turtles home to natal regions to nest (Meylan et al., 1990). Hatchlings disperse from their natal beaches and spend the first few years of their lives in an epipelagic, oceanic stage (Reich et al., 2007). Juveniles recruit to neritic foraging sites, where they transition through multiple developmental habitats before ultimately selecting a foraging area to which they show high fidelity, at least in the Atlantic basin (Meylan et al., 2011; Moncada et al., 2006). Given this dispersal and migratory behavior, monitoring and management efforts require knowledge of the number of discrete nesting populations and the distribution of all life history stages from each of these populations. Because marine turtle nesting populations are structured through female natal philopatry, they are often designated as management units (MUs) on the basis of significant differentiation of maternally inherited mitochondrial DNA (mtDNA) haplotypes as outlined by Moritz (1994). Assessing stock structure and migratory connectivity have been highlighted as global research priorities for marine turtle conservation (Hamann et al., 2010).

Mixed stock analyses (MSA) based on mtDNA haplotypes provide critical linkages between foraging sites and source rookeries for juvenile green turtles. The first study in the Atlantic Ocean detected considerable Costa Rican contributions to a Bahamian foraging site, suggesting that relative rookery size might be an important predictor of foraging aggregation composition (Lahanas et al., 1998). A later study of a foraging aggregation on the east coast of Florida suggested that proximity of nesting and foraging sites might play a larger role than relative rookery sizes in determining the distribution of juveniles (Bass and Witzell, 2000). These investigators also hypothesized that the distribution of juvenile green turtles was likely influenced by dispersal away from natal rookeries via currents followed by regional natal homing as turtles migrate through neritic developmental habitats. Several subsequent studies have supported this hypothesis (Bass et al., 2006; Luke et al., 2004; Naro-Maciel et al., 2012). Increasingly sophisticated ocean circulation models have permitted more direct tests of the influence of ocean currents on dispersal of epipelagic juveniles (Putman and Naro-Maciel, 2013). However, recent research has demonstrated that even small oceanic juveniles actively affect their distribution through directed swimming behavior (Putman and Mansfield, 2015). The potential for natal homing by larger juveniles, often against prevailing currents, following recruitment to initial neritic foraging sites could contribute to incongruence between biophysical model predictions assuming passive drift and genetic MSA results. Analysis of the Barbados foraging aggregation highlights this discrepancy as backwards tracking of virtual particles from the foraging aggregation indicated contributions solely from eastern Caribbean and South Atlantic rookeries (Putman and Naro-Maciel, 2013), whereas the genetic results highlighted substantial contributions (~50%) from western and northern Caribbean rookeries (Luke et al., 2004). Ocean currents are undoubtedly critical in dispersing small juveniles. However, gaps remain in determining the effects of swimming behavior by oceanic juveniles and how mechanisms driving juvenile turtle habitat selection following initial neritic recruitment shape their distributions.

Resolving migratory connectivity for Greater Caribbean green turtles is particularly important given their conservation status. Nesting populations and foraging aggregations across the region were severely depleted by centuries of systematic harvest that expanded with European exploration and colonization in the region, resulting in extirpation of some of the largest rookeries (McClenachan et al., 2006). The foraging aggregation along the Texas coast was no exception. Green turtles were historically abundant in the state, but turtle numbers became so low that the turtle fishery and related processing industry collapsed in Texas by the dawn of the 20th century, most likely as a result of overharvest and hypothermic stunning events (Dougherty, 1984; Hildebrand, 1982). After decades of protection under the U.S. Endangered Species

Act, the aggregation of green turtles inhabiting Texas waters has increased in recent years (Shaver, 2000; Shaver et al., 2013). Green turtle catch per unit effort increased exponentially in the Lower Laguna Madre from 1991 to 2010 (Metz and Landry, 2013), suggesting a rapidly growing juvenile green turtle foraging aggregation. Based on documentation of large numbers of individuals stranded and captured during netting studies (Metz and Landry, Jr., 2013; Shaver, 1994, 2000; Shaver et al., 2013), the Laguna Madre, Mansfield Channel, and Brazos Santiago Pass in south Texas are likely among the most important developmental habitats for green turtles in the western Gulf of Mexico (GoM).

The source populations of the Texas foraging aggregation remain unresolved. A recent MSA suggested northern Greater Caribbean origins, dominated by Florida contributions (Anderson et al., 2013). However, as highlighted by the authors of that study, the findings should be interpreted with caution for two important reasons. First, one critical assumption of most mixture analysis methods is that all potentially contributing source populations have been sampled (Manel et al., 2005). This assumption is violated with respect to northern Greater Caribbean green turtles. Although the largest Mexican rookeries are represented by genetic data from Isla Cozumel and X'cabel, Quintana Roo (Encalada et al., 1996), genetic data are unavailable from regionally significant rookeries along the entire GoM coast of Mexico (NMFS and USFWS, 2015). Second, extensive marker overlap among potential source populations can introduce considerable uncertainty around their estimated contributions to mixed aggregations (Okayama and Bolker, 2005). The Texas MSA results reflect this as Florida and Quintana Roo contributions had extremely wide credible intervals that severely limited the utility of fine scale results (FL contribution: 0.8, 0.2–1.0; QR contribution: 0.2, 0–0.8; Anderson et al., 2013).

Two common 490 base pair (bp) haplotypes (CM-A1 and CM-A3) dominate the rookery profiles of Mexico, Cuba, and Florida (Encalada et al., 1996; Ruiz-Urquiola et al., 2010; Shamblyn et al., 2015a), and the scale of demographic and migratory connectivity are unresolved in many cases because of this extensive marker overlap. Recent studies incorporating additional mitochondrial markers have demonstrated increased resolution of stock structure among nesting assemblages of marine turtles. Expanding standard control region sequences to ~800 bp resulted in geographically informative subdivision of common 400–500 bp haplotypes for loggerhead turtles (*Caretta caretta*), hawksbill turtles (*Eretmochelys imbricata*), and green turtles (Dutton et al., 2014a, 2014b; LeRoux et al., 2012; Shamblyn et al., 2014). Beyond the control region, mitogenomic sequencing of green turtles carrying the common 490 bp haplotype in the eastern Caribbean (CM-A5) yielded mitochondrial single nucleotide polymorphisms (mtSNPs) that were highly informative regionally (Shamblyn et al., 2012). Incorporating mitogenomic sequencing to identify informative mtDNA polymorphism, we assessed the potential rookery sources of foraging green turtles from the Texas coast using novel baseline data from a Tamaulipas, Mexico rookery.

## 2. Methods

### 2.1. Sample collection and laboratory analysis

Tissue samples were collected from nests in Rancho Nuevo, Tamaulipas Mexico (RNMX) and from juvenile green turtles that stranded along the southern Texas coast in 1998–2002 (Table 1). Tissue was sampled from dead embryos salvaged from nests after hatchling emergence at Rancho Nuevo, taking care to only collect one sample from each nest and avoiding sampling more than one clutch from the same female. Stranded turtles ranged in size from 14.0 to 81.3 cm straight carapace length (SCL) (Supplemental Fig. 1). Because sample sizes were small for oceanic and subadult turtles, all individuals were treated as a single juvenile cohort for analyses. Samples were stored in 95% ethanol prior to DNA extraction. These samples were originally analyzed through amplification and sequencing of a 490 bp fragment of the mitochondrial

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