

# Mixed stock analyses indicate population-scale connectivity effects of active dispersal by surface-pelagic green turtles

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**ABSTRACT:** Dispersal is a fundamental driver of population dynamics and connectivity in marine organisms but is often poorly characterized due to the cryptic nature of pelagic life stages. The initial 'lost year' model proposed for surface-pelagic juvenile marine turtles assumed that they passively drifted following a brief swim-frenzy stage. However, mounting evidence indicates that these juveniles engage in directed swimming that affects their trajectories. Dispersal modeling (DM) offers an inferential approach to estimate distributions and connectivity, but model validation remains challenging with sparse empirical data. We sequenced mitochondrial DNA from 121 surface-pelagic juvenile green turtles *Chelonia mydas* collected in the northern Gulf of Mexico (GoM) from 2009 to 2015 and conducted mixed stock analyses (MSAs) to compare contribution estimates with published DM predictions assuming passive drift. MSA indicated that a large majority of juveniles originated from local nesting populations within the GoM, with contributions markedly divergent from published DM predictions assuming passive drift. DM predictions for western GoM rookeries fell well below their MSA 95 % credible intervals (DM: 2 %, MSA point estimates: 49–58 %), whereas the DM predictions for Caribbean Mexico (Quintana Roo) were larger than the MSA 95 % credible intervals (DM: 51–65 %, MSA point estimates: ≤5 %). Therefore, directed swimming by surface-pelagic green turtles, recently demonstrated via telemetry, likely has profound consequences for their dispersal at the population scale. These results emphasize the value of additional *in situ* studies of this life stage, as well as the need to integrate swimming behavior into DM to refine fine-scale predictions.

**KEY WORDS:** Connectivity · Mixed stock analysis · Dispersal · Behavior · *Chelonia mydas* · Deepwater Horizon

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## INTRODUCTION

Characterizing the scale of population connectivity in marine organisms represents a challenging but critically important aspect of resolving their life history and population dynamics. Many benthic marine

species disperse via a pelagic larval stage. Genetic studies of these species have often detected little to no structure between populations separated by hundreds or thousands of kilometers, consistent with expectations of demographically open populations connected by extensive larval dispersal from mixed

pools (Cowen & Sponaugle 2009). However, biophysical modeling has highlighted the importance of self recruitment and suggested relatively constrained connectivity, often mediated by active larval movement (Cowen et al. 2006). Similarly, surface-pelagic juvenile dispersal in marine turtles was initially hypothesized as a passive process (Carr 1986), but this dispersal paradigm has begun to shift away from viewing these juveniles as passive drifters, and increasingly recognizes the potential importance of active dispersal through directed swimming. In marine turtles, dispersal does not result in contemporary population connectivity, because females recruit to their natal regions for nesting in demographically discrete management units (MUs) or genetic stocks (Jensen et al. 2013). Nonetheless, dispersal from natal beaches determines the possible extent of surface-pelagic juvenile distribution and initial neritic recruitment sites for each MU. Therefore, characterizing the dispersal of these juveniles is fundamental for refining the spatial ecology of, and determining anthropogenic threats for, each genetic stock.

Carr (1986, 1987) proposed a 'lost year' model during which loggerhead turtle *Caretta caretta* hatchlings depart their natal beaches in the Northwest Atlantic, swim to the Gulf Stream, and are then passively transported by the North Atlantic Gyre as surface-pelagic juveniles. This population remains the best-studied example of this life stage in marine turtles and has served as a model for neonates of the species that undergo a surface-pelagic stage (Bolten 2003). Beyond the brief swim-frenzy period in which hatchlings swim offshore from their natal beaches (Wyneken & Salmon 1992), their distribution and behavior during the surface-pelagic stage remain poorly described in most species and populations. Despite initial hypothesized expectations of passive drift, mounting evidence has suggested that oriented swimming may play a crucial role in the dispersal process. Post-hatchling loggerheads observed in downwelling lines near the Gulf Stream off east-central Florida, USA, were inactive while associated with *Sargassum*, but captured turtles oriented and swam towards floating material following release (Witherington 2002). These observations prompted the hypothesis that surface-pelagic loggerheads function as facultatively active or 'smart' drifters, capable of short periods of oriented swimming when floating material becomes dispersed and extensive oriented swimming to prevent transport onshore or into cold waters (Witherington 2002). Laboratory studies have demonstrated that loggerhead turtles are capable of perceiving magnetic cues that could

serve as latitudinal and longitudinal proxies to facilitate long-distance navigation (Lohmann & Lohmann 1994, Putman et al. 2011). Dispersal simulations for Northwest Atlantic loggerhead turtles have suggested that even brief bouts of directed swimming in response to magnetic navigational cues can dramatically influence the trajectories and distribution of surface-pelagic juveniles (Putman et al. 2012, Scott et al. 2012). This directed swimming behavior has recently been demonstrated for surface-pelagic juvenile loggerhead turtles in the South Atlantic via drifter deployment alongside satellite-tagged turtles (Mansfield et al. 2017).

Genetic mixed stock analyses (MSAs) of surface-pelagic loggerhead turtles by-caught in long-line fisheries have indicated trans-basin dispersal within the North Atlantic, North Pacific, and South Pacific (Bowen et al. 1995, Bolten et al. 1998, Boyle et al. 2009). MSA of recently recruited neritic juvenile green turtles in Cape Verde provided evidence of some degree of trans-basin dispersal in the North Atlantic (Monzón-Argüello et al. 2010). However, green turtles recruit to neritic foraging areas at much smaller sizes than loggerhead turtles (e.g. Kubis et al. 2009, Avens et al. 2013), implying a considerably shorter surface-pelagic stage for green turtles and likely more constrained dispersal. A sample of 9 surface-pelagic green turtles from Japanese waters was consistent with Japanese origins (Hamabata et al. 2016). However, this sample was comprised of 8 dead-stranded turtles and 1 cold-stunned individual in coastal waters, so it may not be representative of typical surface-pelagic green turtle behavioral and distribution patterns. The logistical difficulty of collecting a robust sample size from surface-pelagic juveniles *in situ* has thus far prevented application of MSA for this life stage in green turtles.

Dispersal modeling (DM) provides an inferential approach that alleviates the logistical challenge of direct interception of surface-pelagic juveniles. These simulations, which predict transport within an ocean circulation model, can highlight pathways and potential high-density hotspots (Putman & Naro-Maciel 2013). DM of surface-pelagic marine turtles suggested that approximately 175 000 green turtles may have traveled in the vicinity of the *Deepwater Horizon* spill site, with roughly 50% of these originating from Caribbean Mexico (Quintana Roo) rookeries, with a significant portion of the remainder from Costa Rican rookeries (Putman et al. 2015). DM is capable of predicting dispersal across broad regions with virtual sample sizes impossible to achieve with *in situ* studies, but genetic data from surface-pelagic

green turtles, needed to test model assumptions, have been lacking. Moreover, recent evidence from paired drifter and satellite telemetry data indicates that surface-pelagic green turtles engage in directed swimming that affects their trajectories relative to expectations under passive drift (Putman & Mansfield 2015). How this individual behavior may scale up to affect population-level distributions has not yet been assessed.

The primary objective was to determine the origins of surface-pelagic juvenile green turtles sampled in the northern Gulf of Mexico (GoM) through MSA. In order to test whether contributions were consistent with expectations of dispersal assuming passive drift, we compared MSA contribution estimates with those from published DM analyses. To our knowledge, this analysis represents the first population-scale genetic assessment of dispersal of surface-pelagic green turtles relative to predictions assuming passive drift, and represents the most robust *in situ* genetics sample of this green turtle life stage collected to date globally.

## MATERIALS AND METHODS

### Sample collection and laboratory analysis

We collected skin tissue samples from surface-pelagic juvenile green turtles in the northern GoM from 2009 through 2015 (see Table S1 in the Supplement at [www.int-res.com/articles/suppl/m601p215\\_supp.xlsx](http://www.int-res.com/articles/suppl/m601p215_supp.xlsx)). Details of search and capture methodology are provided in descriptions of 2 efforts to quantify turtle abundance via surface-pelagic (*Sargassum*) drift habitat surveys, one in the northern and eastern GoM (Witherington et al. 2012), and one in the northern GoM following the *Deepwater Horizon* oil spill (McDonald et al. 2017). For the former, transects were conducted offshore of Venice, Louisiana (VEN), and the Florida ports of Apalachicola (APL) and Pensacola (PEN) (Fig. 1). For the latter, a larger area was surveyed (Natural Resource Damage Assessment *Deepwater Horizon* response survey area, NRDA; Fig. 1). Turtles were captured via dipnet and individually identified

through insertion of passive integrated transponders into the front flipper. All sampled individuals were collected from *Sargassum* habitat and were  $\leq 30$  cm straight carapace length. Each genetic sample consisted of a 4 mm biopsy taken from the distal rear flipper. Samples were stored in 95% ethanol prior to DNA extraction.

An 817 bp fragment of the mitochondrial control region was amplified using primers LCM15382 and h950 and sequenced using LCM15382 and internal sequencing primer Cm1820 (Shamblin et al. 2015a). Following control region sequencing, all individuals carrying haplotype CM-A1.1 were sequenced as previously described for mitochondrial single nucleotide polymorphism (mtSNP) 12 958 in the ND5 gene using PCR primers CM12751F-CM13064R and sequencing primer CM12781 to distinguish between Tamaulipas and Florida lineages (Shamblin et al. 2017).

### Genetic analyses

Sequences were aligned, edited, and compared to previously described haplotypes using the program

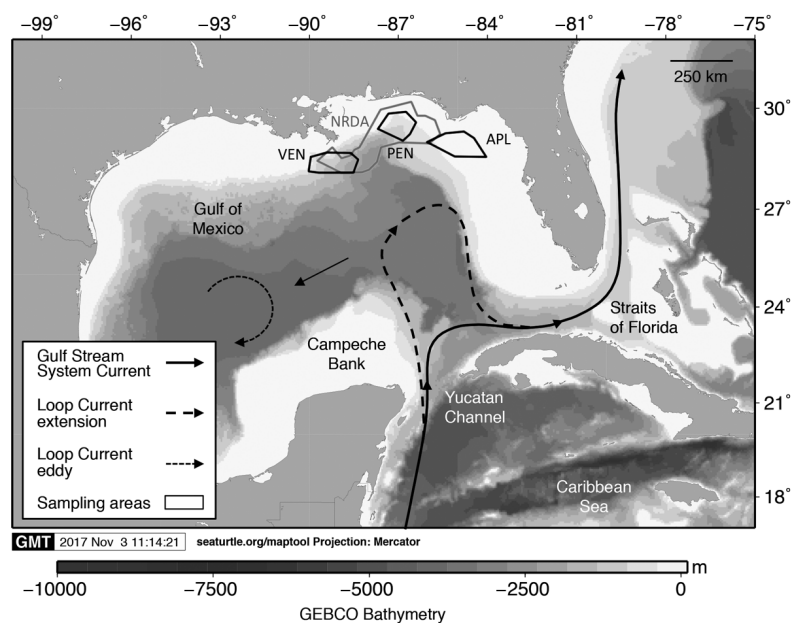


Fig. 1. Distribution of surface-pelagic juvenile green turtles *Chelonia mydas* sampled for genetics along with variation in the position of the Loop Current in the Gulf of Mexico. A typical eddy is included to demonstrate the scale and movement following detachment. Sampling areas for surface-pelagic juveniles are indicated based on the surveying effort and ports. Smaller surveys areas are associated with Florida Fish and Wildlife Research Institute sampling offshore of VEN: Venice, Louisiana; PEN: Pensacola, Florida; APL: Apalachicola, Florida. NRDA represents the larger Natural Resource Damage Assessment *Deepwater Horizon* response survey area

Sequencher 5.0 (Gene Codes). Sequences were assigned haplotype designations after nomenclature published on the Archie Carr Center for Sea Turtle Research (ACCSTR) website (<http://accstr.ufl.edu/resources/mtdna-sequences/>). Population structure between the surface-pelagic sample and 7 Greater Caribbean neritic juvenile foraging aggregations (Table S2) was tested using haplotype frequency-based pairwise  $F_{ST}$  comparisons and analysis of molecular variance (AMOVA) as implemented in Arlequin version 3.5 (Excoffier & Lischer 2010). Comparisons were tested using 490 and 817 bp control region haplotype data as available. Significance values for AMOVA were obtained from 10 000 permutations, and p values were corrected for multiple tests using a false discovery rate approach (Benjamini & Yekutieli 2001).

Stock contributions to the surface-pelagic juvenile samples were estimated through Bayesian many-to-one MSA implemented in the program BAYES (Pella & Masuda 2001). Spatial and temporal sample subsets were typically too small to be analyzed independently. However, we considered both the comprehensive sample ( $n = 121$ ) and those collected only during 2010 ( $n = 34$ ) to facilitate a more direct comparison with the DM results that focused on the *Deepwater Horizon* spill during that year. Nine 'upstream' Greater Caribbean nesting populations were considered as potential source stocks: Aves Island, Venezuela (AVES); Suriname (SURN); Tortuguero, Costa Rica (TORT); Western Bay of Campeche (Tamaulipas/Veracruz), Mexico (WBCMX); Eastern Bay of Campeche (Campeche/Yucatán), Mexico (EBCMX); Cayo Arcas, Mexico (CAMX); Scorpion Reef, Mexico (SRMX); Quintana Roo, Mexico (QRMX); and southwestern Cuba (SWCB) (Fig. 2, Table S2).

The central eastern Florida (CEFL) and southern Florida (SOFL) MUs were not considered as potential sources for several reasons. First, genetic evidence does not support the presence of CEFL Florida juveniles in the sample. All CM-A1.1 surface-pelagic juveniles carried mitogenomic haplotype CM-A1.1.1 (see 'Results'), which was previously identified from

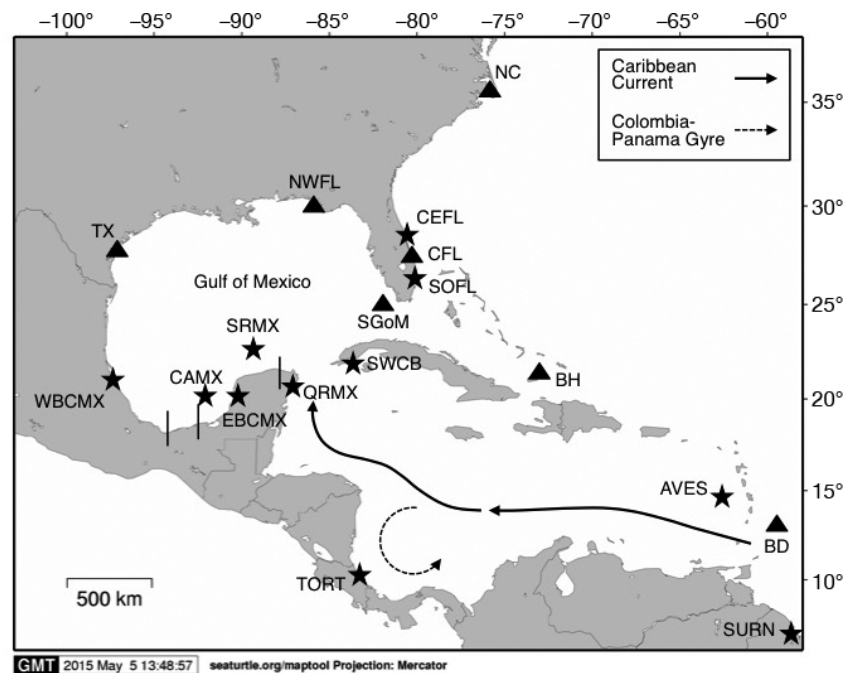


Fig. 2. Green turtle nesting populations (stars) and neritic juvenile foraging aggregations (triangles) in the Greater Caribbean region. Nesting stocks are AVES: Aves Island, Venezuela; SURN: Suriname; TORT: Tortuguero, Costa Rica; WBCMX: Western Bay of Campeche (Tamaulipas/Veracruz), Mexico; EBCMX: Eastern Bay of Campeche (Campeche/Yucatán), Mexico; CAMX: Cayo Arcas, Mexico; SRMX: Scorpion Reef, Mexico; QRMX: Quintana Roo, Mexico; SWCB: southwestern Cuba; CEFL: central eastern Florida. Juvenile foraging aggregations are BD: Barbados; TX: Texas, USA; NWFL: northwestern Florida, USA; SGOM: southern Gulf of Mexico (Everglades and Dry Tortugas), Florida, USA; BH: Bahamas; CFL: central Florida, USA; NC: North Carolina, USA

the Rancho Nuevo, Tamaulipas, Mexico, rookery (Shamblin et al. 2017). Conversely, none carried the variant identified in all Florida-nesting CM-A1.1 turtles sampled to date (CM-A1.1.2), which comprises 59% of the CEFL sample (Shamblin et al. 2017). Second, the major rookeries along Florida's east coast are 'downstream' of the surface-pelagic habitats in the GoM, which would require pelagic juveniles to swim against the Gulf Stream to enter the GoM via the Straits of Florida. Average recorded swim speeds for neonate green turtles during their frenzy period range from 1.57 to 2.25 km h<sup>-1</sup> (Frick 1976, Pilcher & Enderby 2001), whereas the average velocity of the Gulf Stream is 6.4 km h<sup>-1</sup> and may attain speeds as high as 9 km h<sup>-1</sup> at the surface (NOAA 2018). Third, as the juveniles were estimated to be 1 to 2 yr old at capture (Witherington et al. 2012), there would be insufficient time for Florida juveniles to make a full circuit of the North Atlantic gyre and enter the GoM via the Yucatán Current as surface-pelagic juveniles. Finally, *Sargassum* distribution patterns

suggest that entry into the GoM by Florida surface-pelagic juveniles following even a partial circuit into the Sargasso Sea is highly unlikely. *Sargassum* is present throughout much of the North Atlantic gyre and North Equatorial Recirculation Region (NERR). However, drifter data have indicated the presence of discrete blooms originating in the GoM and NERR, with no connectivity between the Sargasso Sea and Caribbean Sea (Gower & King 2011, Franks et al. 2016). Mitochondrial and chloroplast genomic analyses confirmed the genetic distinction of *Sargassum* clones sampled near Bermuda in the Sargasso Sea versus St. Croix (Amaral-Zettler et al. 2017). Given that Florida green turtles are *Sargassum* associates throughout their surface-pelagic stage (Witherington 2002, Witherington et al. 2012), the apparent lack of *Sargassum* movement from the Sargasso Sea into the Caribbean Sea suggests limited potential for this dispersal pathway.

MSAs were based primarily on 490 bp control haplotype data. Additional variation has been detected in the 817 bp sequences for CM-A5 and CM-A18, and these data were incorporated because baselines were complete across potential source stocks. Variation in 817 bp sequences for CM-A1 was not considered in MSAs because baseline data were not available for SWCB. A total of 300 000 Markov Chain Monte Carlo steps were run for 9 chains, with the first 50% of each run discarded as de-memorization (burn-in) steps, to ensure convergence as indicated by Gelman-Rubin shrink factors of <1.2 (Pella & Masuda 2001). Stock contributions were estimated using uninformative priors (1) and relative stock size-weighting priors (2) (Table S3). Estimated nesting female abundance was used to scale relative rookery sizes (Seminoff et al. 2015). Using hatchling production numbers from Putman et al. (2015), which were also based primarily on population and reproductive estimates from Seminoff et al. (2015), for relative size-weighting of stocks would have facilitated more direct comparisons between MSA and DM estimates. However, this approach was not feasible due to differences in how some rookeries were treated (splitting versus combining) and because Yucatán state was not included in DM analyses. Using estimated female abundance required fewer simplifying assumptions and facilitated incorporation of updated data where needed. Nonetheless, the differences in weighting schemes between methodologies for rookeries included in the MSA were small (e.g. QRMX DM weight of 0.09, MSA weight of 0.11) and not expected to substantially affect comparisons.

## MSA and DM comparisons

We qualitatively compared MSA results with those from DM that estimated the abundance and sources of surface-pelagic green turtles at the *Deepwater Horizon* spill site in 2010 (Putman et al. 2015). These models incorporated 3 different surface-pelagic juvenile annual survival rates (25, 81.7, and 94%) to generate a range of abundance estimates. Putman et al. (2015) considered 24 different nesting sites as potential sources. Several of these were not included in MSA because genetic data were unavailable or because their haplotypes were not present among the surface-pelagic sample. Based on DM assuming passive drift, these excluded rookeries had minor contributions (<5% cumulatively). To more explicitly compare contributions from only those stocks included in MSA, we recalculated the proportional DM contributions assuming that only this subset contributed (Table S4).

## RESULTS

### Haplotypes and structure

Thirteen control region haplotypes were present in the GoM surface-pelagic juvenile sample (Table 1). A single individual carried CM-A47.1, known only from the insular Campeche Bank rookery of CAMX (Millán-Aguilar 2009). Two individuals carried CM-A27, which has been described from SWCB and the insular SRMX rookery off the Yucatán coast (Millán-Aguilar 2009, Ruiz-Urquiola et al. 2010). Two haplotypes thus far endemic to QRMX (CM-A22 and CM-A26, Pérez-Ríos 2008) were recorded in a single individual each. A novel haplotype was designated CM-A77.1 (GenBank accession no. MH025958). It differs from CM-A1.1 by a G to A substitution at position 386 in the 817 bp alignments. Of 53 CM-A1.1 individuals analyzed for mtSNP 12958, all represented the conserved CM-A1.1.1 variant previously described from Rancho Nuevo, Mexico, and absent from Florida MUs (Shamblin et al. 2017).

Temporal structure was not apparent in the surface-pelagic sample (AMOVA  $F_{ST} = 0.007$ ,  $p = 0.347$ ). Analysis of 490 bp haplotypes indicated the presence of significant structure among Greater Caribbean juvenile aggregations (AMOVA  $F_{ST} = 0.074$ ,  $p < 0.0001$ ). The GoM pelagic juveniles were distinct from all neritic juvenile aggregations characterized in the Greater Caribbean region with the exception of Texas (TX), southern GoM (SGoM), and North

Table 1. Mitochondrial haplotypes for northern Gulf of Mexico surface-pelagic juvenile green turtles ( $n = 121$ ). Sampling location codes are defined in Fig. 1. Haplotype names with single suffixes represent 817 bp sequences. Haplotype names with 2 suffixes represent 817 bp plus mitogenomic single nucleotide polymorphism sequences for CM-A1.1 individuals

	2009 PEN	2010 NRDA	2011 APL	2011 PEN	2011 NRDA	2012 PEN	2013 VEN	2014 PEN	2014 VEN	2015 VEN	Total
CM-A1.1.1	2	12	2	3	17	2	2	3	2	8	53
CM-A1.2		1									1
CM-A1.3		1									1
CM-A1.4							1				1
CM-A3.1	1	19	5		8	1	5	1	5	4	49
CM-A5.1					2	1	1				4
CM-A18.1			1	1					1		3
CM-A18.2				1	1		1				3
CM-A22.1				1							1
CM-A26.1					1						1
CM-A27.1					1				1		2
CM-A47.1		1									1
CM-A77.1					1						1

Carolina (NC) (Table S5). When only aggregations with 817 bp haplotype data were considered, structure was also evident (AMOVA  $F_{ST} = 0.067$ ,  $p < 0.0001$ ). With 817 bp haplotype data, the surface-pelagic sample was significantly different from TX and SGoM (Table S5).

### MSAs

WBCMX contributed the largest share of individuals to the comprehensive GoM pelagic aggregation (53–58%), with similar point estimates and credible intervals across both models considered (Fig. 3A, Table S6). EBCMX and TORT were the next most likely sources, but with considerable uncertainty given variable point estimates across models and credible intervals passing through or near 0. Contribution estimates for these stocks were highly sensitive to the size-weighting prior. EBCMX point estimates were 24% assuming uniform priors (MSA-1) versus 0% in the weighted run (MSA-2), whereas TORT was 0% in MSA-1 and 27% in MSA-2. QRMX contribution point estimates were small ( $\leq 5\%$ ), but the credible intervals suggested that 11–14% contributions could not be excluded. The insular Campeche Bank stocks of CAMX

and SRMX had small point estimates assuming uninformative priors (2 and 9%, respectively), but 0% estimates using weighted priors.

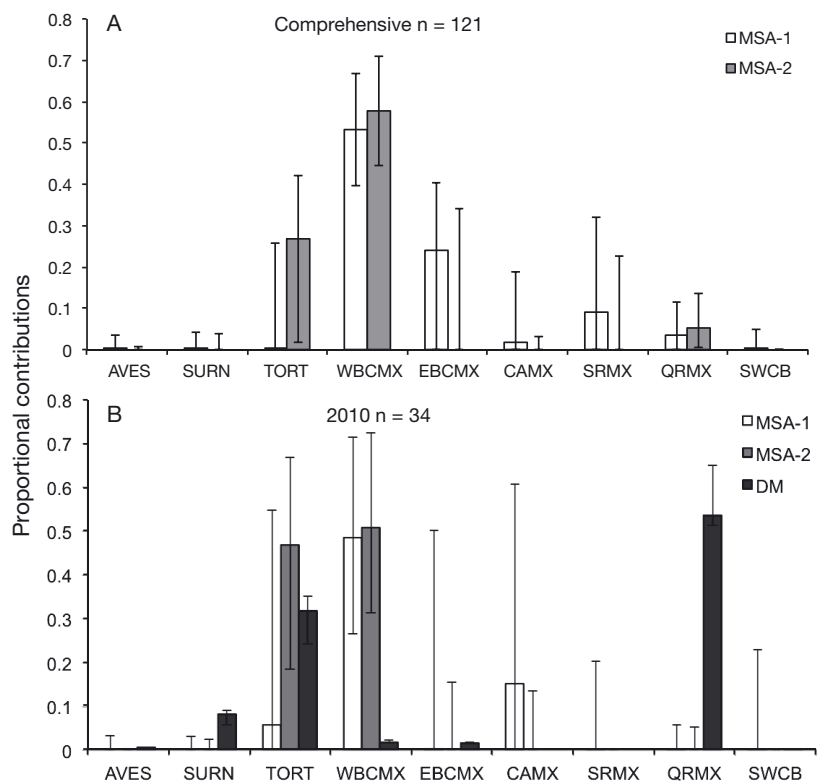


Fig. 3. Median proportional stock contribution estimates to the northern GoM surface-pelagic juvenile green turtle aggregation. Stock abbreviations are explained in Fig. 2. Mixed stock analysis (MSA)-1 assumed uniform priors. MSA-2 included relative population sizes as priors. MSA error bars represent 95% credible intervals. Dispersal modeling (DM) error bars represent the range of Putman et al. (2015) results obtained assuming minimum (25%) and maximum (94%) values of surface-pelagic stage survival

MSA results for samples collected in 2010 in the vicinity of the oil spill ( $n = 34$ ) also yielded primary WBCM<sub>X</sub> contributions (~50%; Fig. 3B). There was considerable uncertainty with respect to other sources given the lack of any informative CM-A5 and CM-A18 individuals in the sample (Table S7). TORT contributions were highly sensitive to priors (6 and 47%, based on uniform and weighted priors, respectively). By virtue of the presence of CM-A47 in the sample, the estimated CAM<sub>X</sub> contribution was modest with uniform priors (15%) but nil with weighted priors. QRM<sub>X</sub> point estimates were essentially 0, with small upper credible limits (5–6%).

### MSA and DM comparisons

MSA and DM analyses were consistent in suggesting the presence of individuals from TORT and not supporting significant contributions from AVES (Fig. 3B). However, estimated contributions from SURN, WBCM<sub>X</sub>, EBCM<sub>X</sub>, and QRM<sub>X</sub> were markedly divergent between the 2 methodologies (Fig. 3B, Table S7). Across a broad range of surface-pelagic survival assumptions, DM-predicted contributions from the Mexican GoM states (Tamaulipas, Veracruz, and Campeche) were small (3–4%) relative to substantial QRM<sub>X</sub> predictions (51–65%). Conversely, cumulative MSA-1 point estimates for the Mexican GoM stocks accounted for the majority of surface-pelagic juveniles (51–88%) across the various models and datasets, whereas the signal from QRM<sub>X</sub> was weak ( $\leq 5\%$ ). Similarly, the contribution from Suriname suggested by DM (6–9%) was not supported by the MSA. The SURN, WBCM<sub>X</sub>, and QRM<sub>X</sub> estimates were sufficiently disparate that the DM predictions fell outside their 95% credible interval ranges from MSA.

## DISCUSSION

The surface-pelagic sample carried haplotypes consistent with nearly exclusive western and northern Greater Caribbean origins. Although significantly different from both, the surface-pelagic sample was more similar to TX neritic juveniles than SGoM neritic turtles. This similarity, along with the large estimated contributions from WBCM<sub>X</sub> to both, implies that some proportion of WBCM<sub>X</sub> neonates disperse across the GoM and may recruit to distant neritic foraging areas prior to returning to neritic foraging sites near their natal rookeries, consistent with

hypothesized natal homing behavior by neritic juveniles (Luke et al. 2004, Bass et al. 2006). This connectivity is reinforced by a tag return that indicated east-to-west migration (from the Florida panhandle to southern Texas) by a neritic juvenile green turtle in the GoM (Foley et al. 2007). The uniform prior MSA runs suggested substantial contributions by Mexican GoM stocks (64–88%), with WBCM<sub>X</sub> as the single largest contributor in weighted MSA runs as well (51–58%). Caribbean Mexico (QRM<sub>X</sub>) contributions were negligible across all models and data considered ( $\leq 5\%$ ). Given that these MSA estimates contrast sharply with DM predictions, what factors might account for this incongruence?

### Loop Current dynamics and sampling considerations

The Gulf Stream System (GSS), the western boundary current of the North Atlantic subtropical gyre, dominates the surface current dynamics in the Northwest Atlantic Ocean. The Loop Current functions as the GoM portion of the GSS, originating at the Yucatan Channel and flowing into the eastern GoM prior to exiting via the Straits of Florida as the Florida Current (Fig. 1). The distribution of the Loop Current can vary markedly with respect to how far into the GoM it intrudes. When retracted, the Loop Current takes on a 'port-to-port' configuration in which the current runs nearly directly from the Yucatan Channel to the Straits of Florida (Chérubin et al. 2005). When extended, the Loop Current may reach 29°N and separate from the GSS, leading to the formation of anticyclonic eddies (Chérubin et al. 2005). These eddies may detach and reattach to the main current or drift westward and southward, a process termed ring shedding (Oey et al. 2003). Ring shedding occurs at irregular intervals and is driven by seasonal shifts in relative wind forcing in the Caribbean Sea and GoM (Chang & Oey 2012). The timing of this process relative to the hatching season for QRM<sub>X</sub> green turtles each year could have a marked annual effect on the proportion of individuals from this stock that is retained within the GoM. Despite this potential for annual variation, no correlation between ring shedding and Caribbean contributions was apparent. Although inter-annual variation should be further explored, MSA-estimated QRM<sub>X</sub> contributions from 2010 samples were nil, suggesting that annual variation is not likely to explain the discrepancies between DM and overall MSA estimates.

All individuals included in the present study were captured in *Sargassum* habitat over the continental shelf or slope waters. This sampling scheme should not affect comparisons with DM analyses given that the oil spill extent used in modeling was confined to the same region (Putman et al. 2015). Although significant temporal structure was not detected, the qualitative variation among annual samples does suggest some degree of variation in the amount of admixture from GoM sources across years. Combining these disparate annual samples, as well as focusing sampling in summer, may have resulted in an aggregate sample that was not entirely representative of the region across all years studied. Even so, genetic sampling each year fell within the April through August particle release period for 2010 DM for 104 of the 121 surface-pelagic juveniles. Therefore, seasonal sampling constraints are unlikely to account for differences between DM and MSA estimates. The detection of informative haplotypes most likely from the Campeche Bank stocks of CAMX and SRMX (CM-A47 and CM-A27, respectively), each 2 orders of magnitude smaller than QRMX, also suggest that sampling error is unlikely to explain the strong discrepancies between DM and MSA estimates.

#### Caveats with interpretation of MSA

Inferences of primary contributions from WBCMX and small contributions from QRMX were robust across all data and models considered, but estimates for other stocks should be interpreted with caution. Sharing of haplotypes CM-A1, CM-A3, and CM-A5 among potential source stocks contributed to highly variable point estimates and broad credible intervals for some stocks. Poor marker resolution was particularly evident in the sensitivity of point estimates for TORT and EBCMX to MSA priors. This was not surprising, given that their haplotype profiles are dominated by CM-A3 (91 and 85%, respectively). Use of rookery-scaling priors is a common practice in marine turtle MSA, particularly when marker resolution is poor. This approach is intuitive in minimizing unrealistic contributions from small stocks, but likely underestimated true contributions from small MUs (and overestimated those from large MUs) in the case of the GoM surface-pelagic juveniles. Small point estimates from CAMX and SRMX generated from MSA-1, reasonable given the presence of endemic haplotype CM-A47 and rare CM-A27 in the surface-pelagic sample, were not detected in

MSA-2. The small estimated contributions from QRMX, despite its size and proximity to the sampling area, along with the presence of CM-A47 and CM-A27, suggest that actual TORT and EBCMX contributions may fall closer to MSA-1 estimates than those from MSA-2. The lack of any CM-A18 and CM-A5 individuals in the 2010 sample prevented further refinement of contribution estimates for that dataset.

#### Caveats with DM assumptions

DM abundance estimates of loggerhead and green turtles at the *Deepwater Horizon* spill site assuming passive drift were generally consistent with survey-based abundance estimates (Putman et al. 2015). In contrast, initial DM estimates assuming passive drift for Kemp's ridley *Lepidochelys kempii*, a species with primary nesting beaches in Tamaulipas and Veracruz, were 2 orders of magnitude low relative to survey-based estimates (Putman et al. 2015). This discrepancy may point to a 'west-to-east effect' that was not adequately captured in the models, given that DM also considerably underestimated western GoM green turtle contributions relative to MSA estimates.

Although this study represents the first comparison of MSA and DM estimates for surface-pelagic green turtles, both genetic and DM approaches have been independently applied in assessing dispersal of surface-pelagic loggerheads. Genetic analyses indicated trans-basin dispersal of surface-pelagic loggerheads in the North Atlantic, North Pacific, and South Pacific (Bowen et al. 1995, Bolten et al. 1998, Boyle et al. 2009), and subsequent DM assuming passive drift supported these dispersal patterns (Mansfield & Putman 2013). These approaches also corroborated the dispersal of South African surface-pelagic juveniles from the Indian Ocean into the South Atlantic basin (Reis et al. 2010, Mansfield & Putman 2013, Shamblin et al. 2014). However, these techniques were not congruent with respect to estimates of broader connectivity across the Indian Ocean and South Atlantic. DM assuming passive drift suggested retention of juveniles from Oman within the northwestern Indian Ocean and retention of juveniles from Western Australia within the eastern Indian and southern Pacific basins (Mansfield & Putman 2013). In contrast, genetic analyses supported the possible linkage of a significant proportion of the Brazilian surface-pelagic aggregation to these distant rookeries (15 and 26%, respectively; Reis et al. 2010, Shamblin et al. 2014).



MSA of recently recruited neritic juvenile green turtles in Cape Verde suggested substantial trans-Atlantic dispersal from Suriname (Monzón-Argüello et al. 2010), a connection that was not supported by DM assuming passive drift (Putman & Naro-Maciel 2013). Conversely, MSA of SGoM neritic juveniles did not detect the Suriname contributions predicted by DM (Naro-Maciel et al. 2017), consistent with genetic estimates for the GoM surface-pelagic juveniles in the present study. Active swimming by Suriname post-hatchlings to attain favorable currents to reach Cape Verde, and therefore avoid the North-west Atlantic, was invoked to explain this discrepancy (Naro-Maciel et al. 2017). Similarly, DM assuming passive drift suggested the likely retention of Guinea Bissau neonate green turtles in western Africa, with no possibility of connectivity with juvenile foraging aggregations in Brazil (Putman & Naro-Maciel 2013). However, subsequent genetic analyses with improved Guinea Bissau rookery sampling suggested substantial east-to-west dispersal across the Central and South Atlantic (Patricio et al. 2017). Together with the present study, these examples jointly suggest that patterns of connectivity for surface-pelagic juveniles can be markedly different from those modeled under the assumption of passive drift.

We propose that directed swimming by surface-pelagic juveniles, sufficient to affect their dispersal, best explains the discrepancies between DM assuming passive drift and MSA estimates. Recent evidence from paired drifter and satellite telemetry data indicates that surface-pelagic juvenile green turtles engage in directed swimming behavior that affects their trajectories relative to expectations under passive drift (Putman & Mansfield 2015). The MSA results support a population-level consequence of this behavior. The Yucatan Current, encountered by neonate turtles departing from Quintana Roo beaches, is a strong, nearshore boundary current similar to the Florida Current that occurs off the major marine turtle nesting beaches on Florida's Atlantic coast. If post-hatchling QRMX green turtles engage in directed swimming behavior similar to that hypothesized for North Atlantic loggerhead turtles (Putman et al. 2011, 2012), then the majority of these would remain entrained within the GSS and quickly traverse the GoM en route to the Atlantic coast of Florida and possibly beyond. A similar scenario may be likely for surface-pelagic juveniles entering the GoM from the remainder of the Caribbean Sea, if these juveniles are not yet ready to recruit to neritic foraging sites.

### Refining inferences of connectivity

DM and MSA approaches each have relative strengths and weaknesses. Despite uncertainties about the influence of directed swimming on the distribution of surface-pelagic juveniles, DM with the assumption of passive drift can provide a sound null hypothesis of passive oceanic dispersal and distribution (Putman & Naro-Maciel 2013). Likewise, even with marker resolution caveats, MSA can be useful in highlighting deviations from expectations under various modeling scenarios. Results from these complementary approaches would benefit from refinement with additional data. Transmitter mass constraints have historically limited use of satellite tracking in surface-pelagic juvenile marine turtles, but this approach has increasingly been applied to better understand this cryptic life stage with the availability of smaller, lighter transmitters and modified attachment techniques (Mansfield et al. 2012, 2017, Briscoe et al. 2016). Tracks of surface-pelagic Kemp's ridley and green turtles fitted with satellite tags in the northern and eastern GoM suggested species- and location-specific differences in oriented swimming behavior (Putman & Mansfield 2015), indicating that strategically satellite-tagging surface-pelagic juveniles likely to represent different genetic stocks would better reveal population-specific movement patterns. As miniaturization of transmitters advances, opportunities to track hatchlings directly from their natal beaches might one day dramatically improve our understanding of turtle behavior and the dispersal process. Having baseline behavioral data for the major stocks would facilitate incorporation of these data into DM, as Putman et al. (2015) previously proposed. Fully integrating data on sea-surface circulation, swimming behavior, and *Sargassum* habitat distribution using higher-resolution satellite imagery will be challenging, but these inputs offer the best opportunity to model fine-scale distribution patterns.

Several steps are necessary to improve the resolution of genetic assessments of green turtle stock structure and migratory connectivity in the Greater Caribbean region. Filling sampling gaps and generating 817 bp haplotype data for all rookeries is an important first step. Incorporation of the CM-A1.1 mtSNP data was useful in excluding major CEFL contributions, but baseline data for this marker are needed for SWCB and all Mexican stocks. Extensive marker overlap among stocks indicates that screening of additional genetic markers is warranted. CM-A3 is the most numerically abundant and geographi-

cally widespread haplotype in the Greater Caribbean region. Mitogenomic sequencing of CM-A1, CM-A3, and CM-A5 individuals representing each genetic stock may yield additional population informative variation, as previously demonstrated for southern Caribbean CM-A5 lineages (Shamblin et al. 2012). A mitochondrial short tandem repeat (mtSTR) has also proven useful in subdividing common green turtle control region haplotypes (Tikochinski et al. 2012) and discerning fine-scale structure that was not apparent using the traditional markers (Shamblin et al. 2015b, Tikochinski et al. 2018). This marker should be applied across Greater Caribbean rookeries to assess the potential for increased stock structure resolution.

### Conservation implications

The MSA results provide context on the origins of surface-pelagic juveniles in the northern GoM, valuable information for assessing the effects of mortality factors. Surface-pelagic juveniles in the *Sargassum* community are susceptible to anthropogenic threats, particularly interactions with marine debris and petroleum (Witherington et al. 2012). Ingested plastics comprised approximately 12 to 27% of the dry mass of lavage and fecal samples, respectively, collected from surface-pelagic green turtles foraging in *Sargassum* habitat off the coast of Florida (Witherington et al. 2012). In addition to the impaction threat, plastic ingestion can also contribute to dietary dilution (McCauley & Bjorndal 1999) and facilitate absorption of endocrine-disrupting and toxic compounds (Cole et al. 2011).

Their small size and habitat use also likely make post-hatchlings and surface-pelagic juveniles the most susceptible life history stages to fouling by petroleum (Witherington et al. 2012). Of 574 surface-pelagic juveniles captured during *Deepwater Horizon* rescue operations, 220 were green turtles (McDonald et al. 2017). Only a small portion of the oil spill footprint was accessible by rescuers, and an estimated 148 000 surface-pelagic green turtles were present in the area during the duration of the spill (McDonald et al. 2017). MSA results suggest that rather than broadly impacting green turtle populations across the Atlantic, the *Deepwater Horizon* spill primarily affected local stocks within the GoM. This discrepancy between DM and MSA contributions is of conservation concern given the smaller and more vulnerable populations of all GoM stocks relative to QRMX, particularly the insular Campeche Bank

rookeries of CAMX and SRMX. How oil spill-related mortality in a single surface-pelagic juvenile cohort will affect recruitment into these breeding populations is unclear, but the MSA contribution estimates provide context for future nesting trend analyses in these stocks. Although ocean currents undoubtedly play a major role in determining the dispersal patterns for surface-pelagic juveniles, the MSA results suggest that DM would benefit from incorporation of additional parameters, particularly swimming behavior. Our results further highlight the importance of continued *in situ* studies to better characterize the green turtle surface-pelagic life history stage.

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