El Colegio de la Frontera Sur

Estructura genética y conectividad migratoria de las tortugas carey y verde en la Península de Yucatán

Tesis

presentada como requisito parcial para optar al grado de Doctora en Ciencias en Ecología y Desarrollo Sustentable con orientación en Conservación de la Biodiversidad

Por

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And the turtles, of course... all the turtles are free, as turtles and maybe, all creatures should be.

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Resumen

El objetivo de este estudio fue analizar la diversidad y estructura genética de las colonias de anidación y de las agregaciones de forrajeo de las tortugas carey (*Eretmochelys imbricata*) y verde (*Chelonia mydas*), e identificar los patrones de conectividad migratoria entre hábitats de anidación y de forrajeo en la Península de Yucatán, y en la región del Atlántico. Mediante el análisis de las secuencias del fragmento largo de la región control del ADNmt se determinó la composición haplotípica de las colonias de anidación y agregaciones de forrajeo, resaltando la presencia de haplotipos endémicos para las poblaciones de ambas especies en la Península de Yucatán.

En las colonias de anidación de tortuga carey, se evidenció diferenciación genética entre las localidades de Campeche *vs* Yucatán-Quintana Roo, mientras que en la de tortuga verde, la diferenciación fue significativa entre el Golfo de México *vs* el Caribe Mexicano. Con respecto a las agregaciones de forrajeo, en ambas especies se identificó homogeneidad genética dentro de las localidades del Caribe Mexicano, debido a la influencia de la Corriente de Yucatán, que facilita el transporte de individuos a lo largo de la costa de Quintana Roo en dirección norte. Los patrones de conectividad migratoria difirieron entre ambas especies, la agregación de forrajeo de tortuga carey en el Golfo de México se compone de individuos provenientes de colonias locales, mientras que en el Caribe Mexicano se identificó la presencia de tortugas provenientes de colonias foráneas, como Puerto Rico, Barbados y Brasil, las cuales probablemente fueron transportadas por las corrientes marinas. Por el contrario, las agregaciones de forrajeo de tortuga verde en el Caribe Mexicano se componen de individuos de las colonias del Golfo de México y del Caribe Mexicano, lo que podría indicar que los juveniles eligen áreas de alimentación cercanas a su playa natal.

Palabras clave: Diferenciación genética, análisis de stock mezclados, *Eretmochelys imbricata*, *Chelonia mydas,* haplotipos

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CAPÍTULO I

INTRODUCCIÓN GENERAL

1.1 Generalidades

Las tortugas marinas son un grupo de vertebrados cuya historia evolutiva se remonta a más de 100 millones de años (Bowen y Karl 2007). El grupo comprende siete especies de dos familias: Cheloniidae (presentan carapacho óseo cubierto por escudos) que incluye a la tortuga carey (*Eretmochelys imbricata* [Linnaeus, 1766]), golfina (*Lepidochelys olivacea* [Eschscholtz, 1829]), caguama (*Caretta caretta* [Linnaeus, 1758]), verde (*Chelonia mydas* [Linnaeus, 1758]), lora (*Lepidochelys kempii* [Garman, 1880]), y a la tortuga aplanada (*Natator depressus* [Garman, 1880]); y Dermochelyidae (tienen un carapacho córneo), cuyo única especie existente es la tortuga laúd (*Dermochelys coriacea* [Vandelli, 1761]) (Márquez 1996).

En los sistemas marinos, estas especies desempeñan funciones ecológicas de importancia en su rol como consumidores, presas y competidores, además proveen sustrato para organismos epibiontes, transportan cantidades importantes de nutrientes provenientes de las zonas de alimentación a las playas de anidación y pueden modificar la estructura física de los ecosistemas marinos (Bjorndal y Jackson 2002). La diversidad y sucesión en los arrecifes coralinos del Caribe dependen de la competencia por espacio entre las esponjas y los corales escleractinios (Bjorndal y Jackson 2002); a menudo las esponjas son el competidor superior, por lo que la depredación por las tortugas carey tiene un papel importante en regular las poblaciones de esponjas y mantener el funcionamiento óptimo de estos ecosistemas (van Dam y Diez 1997).

Las tortugas marinas se distribuyen en todas las cuencas oceánicas; sin embargo, algunas especies ocupan hábitats con diferentes características físicas y biológicas dependiendo de su comportamiento migratorio y de sus requerimientos alimenticios (Márquez 1990, Abreu-Grobois 2016). La tortuga carey prefiere hábitats cercanos a zonas tropicales, mientras que la tortuga laúd se distribuye en aguas más frías, cercanas a latitudes subpolares (Meylan y Meylan 2000). A excepción de la tortuga lora, que se distribuye exclusivamente en el norte del Golfo de México (Tamaulipas y la costa oriental de EUA), y la tortuga aplanada,

que es una especie endémica de la plataforma continental australiana, las tortugas marinas presentan una distribución circumglobal (Meylan y Meylan 2000). En México, se ha reportado la anidación de seis especies en ambos litorales y se han identificado áreas de alimentación en las zonas costeras del Pacífico, Golfo de México y Caribe Mexicano (Márquez 1996).

1.1.1 Ciclo de vida

Las tortugas marinas se caracterizan por ser longevas y tener tiempos tardíos de maduración sexual, lo que implica que su ciclo de vida es muy largo (Márquez 1996). Desde su eclosión hasta la etapa adulta, experimentan cambios ontogénicos en el uso de hábitats, los cuales comprenden playas de anidación, corredores migratorios, hábitats de desarrollo y zonas de alimentación oceánicas y costeras (Seminoff et al. 2008).

Durante el periodo de incubación (el cual puede durar entre 45 y 60 días dependiendo de la especie), una de las fases más importante del desarrollo embrionario es la determinación sexual, la cual depende de la temperatura de incubación (Abreu-Grobois 2016). Una vez que transcurre el periodo de desarrollo embrionario, los neonatos eclosionan y mediante un proceso de facilitación social se estimulan unos a otros para ascender a la superficie del nido (Abreu-Grobois 2016). Posterior a la emergencia del nido, y durante su desplazamiento hacia el mar, ocurre un fenómeno conocido como impronta, en el cual las crías reconocen ciertas características fisicoquímicas de su playa natal y graban información geomagnética que favorece el regreso de las hembras a su playa de origen (Brothers y Lohmann 2015). Durante las primeras horas de vida, las pequeñas tortugas nadan frenéticamente hacia mar abierto; este frenesí natatorio continúa hasta que las crías agotan sus reservas energéticas (vitelo), para después ser transportadas a través de las corrientes, las cuales permiten su dispersión hasta zonas de convergencia oceánica (Whiterington et al. 2012, Abreu-Grobois 2016).

En la zona oceánica, se inicia la fase juvenil, la cual puede dividirse en dos etapas: oceánica y costera (Abreu-Grobois 2016). Durante la fase oceánica, las tortugas

utilizan diferentes hábitats de desarrollo (Carr 1978), sin embargo es una etapa poco conocida por lo que se le denomina como el año perdido (Carr 1986). Estudios posteriores aclararon que esta etapa puede durar varios años dependiendo de la especie y la región donde se localizan las poblaciones (Musik y Limpus 1997, Reich et al. 2007). Recientemente, el desarrollo de modelos de circulación oceánica, ha permitido determinar que los patrones de migración de los juveniles, no dependen exclusivamente de las corrientes oceánicas, y que el comportamiento de nado activo (aunque relativamente débil) puede orientar el movimiento y la distribución de los juveniles en las zonas oceánicas (Putman y Mansfield 2015).

Los juveniles de tortugas laúd y golfina, completan su desarrollo en zonas oceánicas, mientras que las tortugas carey, verde, caguama y lora, después de permanecer en zonas oceánicas de alimentación, se reclutan en agregaciones de forrajeo en zonas costeras, generalmente cercanas a su playa natal (Bolten 2002, Naro-Maciel et al. 2012). Los juveniles tardíos pueden utilizar secuencialmente diferentes hábitats de desarrollo o bien mostrar algún grado de filopatría a áreas de forrajeo, dicho comportamiento se define como la preferencia de los juveniles para alimentarse en zonas costeras cercanas a la playa donde nacieron. Durante esta etapa, las tortugas pueden establecer áreas de residencia permanente, a las cuales regresarán después de subsecuentes migraciones reproductivas (Márquez 1996, Broderick et al. 2007, Gaos et al. 2017).

Las tortugas marinas alcanzan la madurez sexual entre los 20 y 40 años, dependiendo de la especie y región, lo cual marca el inicio de la etapa reproductiva (Bowen y Karl 2007). En esta etapa, hembras y machos realizan migraciones periódicas entre zonas costeras de alimentación y de reproducción cercanas a las playas donde nacieron (Abreu-Grobois 2016). Este rasgo conductual, denominado filopatría natal, es una característica particular de la historia de vida de las tortugas marinas y ha sido particularmente documentado en las hembras (Lee et al. 2007). Sin embargo, evidencia genética ha mostrado que los machos de *C. mydas* también presentan algún grado de filopatría natal (FitzSimmons et al. 1997). No obstante, algunos machos pueden interceptar a las

hembras y aparearse durante las migraciones hacia las zonas de reproducción (Owens et al. 1982). Después del proceso reproductivo, las hembras continúan la migración hacia las playas de anidación para integrarse a las colonias de anidación, mientras que los machos regresan a sus zonas de forrajeo o permanecen en las cercanías (Abreu-Grobois 2016).

Una vez fertilizados los huevos, las hembras llegan a las playas a realizar sucesivas puestas durante la temporada de anidación (Abreu-Grobois 2016). Durante las diferentes oviposiciones, las hembras regresan a zonas de resguardo cercanas a las playas llamadas sitios interanidatorios (Abreu-Grobois 2016). Cuando finaliza la temporada reproductiva, las hembras post-anidantes realizan migraciones hasta sus áreas de forrajeo, para regresar a reproducirse en un periodo de 1-5 años dependiendo de la especie, edad, así como de la cantidad y calidad de alimento disponible en sus áreas de forrajeo (Abreu-Grobois 2016).

1.2 Descripción de las especies

1.2.1 Tortuga carey (*Eretmochelys imbricata*)

Se caracteriza por una disposición de los escudos del carapacho en forma imbricada o sobrepuesta, lo cual es un rasgo diagnóstico que da origen a su nombre científico (Cuevas 2016). Su carapacho es elíptico, con los bordes de los escudos costales aserrados; los adultos presentan un patrón de coloración de manchas radiales ámbar, rojizas y negras en cada escudo, y las crías se caracterizan por una coloración marrón oscuro, tanto en el carapacho como en el plastrón (Márquez 1996).

La distribución de esta especie está restringida a zonas arrecifales de mares tropicales y subtropicales de los océanos Atlántico, Pacífico e Índico (Mortimer y Donnelly 2008). Las poblaciones más abundantes se localizan en el Caribe y en el Atlántico occidental, desde el este de Florida hasta la costa sur de Brasil (Mortimer y Donnelly 2008). En México, la actividad anidatoria se ha registrado en ambos litorales; sin embargo, la Península de Yucatán (principalmente Campeche y

Yucatán), alberga una de las poblaciones de anidación de tortuga carey más grande del Gran Caribe (Garduño-Andrade et al. 1999). En esta región, que abarca playas que se localizan entre Isla Contoy y Ciudad del Carmen, se registra un promedio de anidaciones anuales menor a 100 nidos en playas de baja anidación, de 200 a 400 nidadas en playas de actividad media, y más de 500 nidos en playas con alta densidad de anidación (Abreu-Grobois et al. 2005, Cuevas 2016).

Estudios de marca-recaptura y de telemetría satelital, han permitido identificar zonas de agregación de juveniles, sub-adultos y adultos en las aguas costeras de la Península de Yucatán (González-Garza et al. 2008, Cuevas et al. 2012). En Campeche, se han identificado importantes zonas de forrajeo dentro de la Laguna de Términos, Cayo Arcas, Cayo Arena, Punta Xen, Reserva de la Biósfera de los Peténes y Ría Celestún (Guzmán et al. 2003). En Yucatán, los Bajos de Sisal, el Parque Nacional Arrecife Alacranes, San Felipe, El Cuyo y Ría Lagartos, se han identificado como áreas de alimentación de juveniles (Garduño-Andrade et al. 1999, Cuevas et al. 2007); mientras que en Quintana Roo, la zona costera de Chiquilá, Isla Contoy, Isla Mujeres, Cozumel, Punta Herrero, Banco Chinchorro e Xcalak proveen un hábitat de alimentación idóneo para las tortugas carey (Cuevas 2016, Herrera-Pavón, com. pers.).

Se ha mostrado que la Península de Yucatán es un importante corredor migratorio para las tortugas carey. Cuevas y colaboradores (2010) reportaron, con base en estudios de telemetría satelital, que las hembras que anidan en playas de Campeche migran hacia el oriente de la Península de Yucatán para llegar a zonas de alimentación en el Caribe Mexicano, y hembras que anidan en el norte de Quintana Roo y oriente de Yucatán, se desplazan hacía los sitios de alimentación localizados en el noreste del Golfo de México. Adicionalmente, se ha identificado el movimiento de hembras que anidan en el litoral del Golfo de México hacia zonas de alimentación en Florida, Cuba, Belice y Honduras (Cuevas et al. 2008, 2012, Vázquez-Cuevas 2015).

La sobreexplotación de adultos y huevos para el consumo y comercialización, el uso de los escudos para la fabricación de piezas de joyería y ornamentos, la degradación de los hábitats de anidación y alimentación, la mortalidad causada por la pesca incidental, entre otros factores, han ocasionado la disminución de las poblaciones de tortuga carey en las principales cuencas oceánicas (Mortimer y Donelly 2008). Análisis realizados en 25 sitios índices mostraron una tendencia decreciente en el número de hembras anidantes durante las últimas tres generaciones (Mortimer y Donelly 2008). Ante este panorama, la tortuga carey fue catalogada, desde 1996, como una especie en peligro crítico por la Unión Internacional para la Conservación de la Naturaleza (IUCN por sus siglas en inglés) y este estatus se mantiene hasta la actualidad (IUCN 2018). En México, la NOM-059-SEMARNAT-2010 declara a la tortuga carey como una especie en peligro de extinción, es decir que el tamaño de sus poblaciones en el territorio nacional ha disminuido drásticamente, lo que compromete su viabilidad biológica.

1.2.2 Tortuga verde (*Chelonia mydas*)

La tortuga verde (Golfo de México) o blanca (Caribe Mexicano) presenta un carapacho ovalado y liso con cuatro pares de escudos costales y cinco centrales (Pritchard y Mortimer 2000). Los patrones de coloración cambian con respecto al estadio, las crías son negras con una ligera línea blanca en la orilla del caparazón y aletas, los individuos inmaduros presentan coloración café con vetas radiales, y en adultos se torna a un color verde olivo o grisáceo (Delgado-Trejo 2016).

Esta especie tiene una distribución circumglobal en aguas tropicales y subtropicales de los océanos Atlántico, Índico y Pacífico, así como el Mar Mediterráneo (Seminoff 2004). En el Atlántico occidental y Caribe hay cinco importantes poblaciones de hembras anidantes: Tortuguero (Costa Rica), Península de Yucatán (México), Isla de Aves (Venezuela), Reserva de Galibi (Surinam) e Isla Trinidad (Brasil) (NMFS 2007). En la Península de Yucatán, las playas más importantes se encuentran en Quintana Roo, desde Punta Venado hasta la Reserva de la Biósfera de Sian Ka’an (Delgado-Trejo 2016).

En las costas de Campeche y Yucatán, los programas de marcaje y datos de telemetría satelital han identificado que la zona de Peténes-Celestún es un hábitat de alimentación costera utilizado por hembras post-anidantes de la región (CONANP 2011, Cuevas et al. 2012). De igual manera, se han localizado zonas de alimentación de relevancia ecológica para colonias de anidación regionales en Cayo Arcas y Arrecife Alacranes (Millán-Aguilar 2009, CONANP 2011). En el Caribe Mexicano, se han identificado praderas de pastos marinos (principalmente *Thalassia testudinum*) que sirven como zonas de forrajeo de tortuga verde cerca de Isla Contoy, Cozumel, Punta Sacrificio, Akumal, Xcalak y Banco Chinchorro (CONANP 2011, Herrera-Pavón com. pers.). También se han identificado sitios de reproducción en Cabo Catoche, Isla Contoy e Isla Mujeres (Cuevas et al. 2012, Herrera-Pavón, com. pers.) y se ha definido que el noreste de la Península de Yucatán funciona como un importante corredor migratorio para individuos que se desplazan hacia los cayos de Florida (Cuevas et al. 2012).

Al igual que otras especies de tortugas marinas, las poblaciones de tortuga verde han disminuido drásticamente como consecuencia de la sobreexplotación de huevos y adultos, de la captura incidental ocasionada por las pesquerías, de la degradación y pérdida de hábitats críticos, entre otros factores (Seminoff 2004). Ante estas amenazas, se ha registrado una disminución de hembras anidantes en las últimas tres generaciones (Seminoff 2004), y desde 1996 se catalogó a *C. mydas* como una especie en peligro de extinción por la UICN (IUCN 2018). En México, la tortuga verde está enlistada como una especie en peligro de extinción, en la NOM-059-SEMARNAT-2010.

1.3 El ADN mitocondrial como herramienta molecular

El ADN mitocondrial (ADNmt) es una molécula circular cerrada covalentemente, con una longitud aproximada de entre 16-20 kilobases (1 kb = 1000 pares de bases). Contiene 37 genes: 22 codificantes para ARN de transferencia (ARNt), 2 para ARN ribosomal (ARNr) y 13 para ARN mensajero (ARNm) que codifican para subunidades enzimáticas involucradas en la síntesis de ATP (Avise et al. 1987).

En células animales, el ADNmt contiene genes interrumpidos y las secuencias inter-genéticas están ausentes o son escasas; sin embargo, presenta una sección llamada región control (Moritz et al. 1987). En los vertebrados, la región control tiene una longitud aproximada de 0.8 kb y contiene un bucle de desplazamiento o D-Loop, que controla los procesos de replicación y transcripción de la molécula (Moritz et al. 1987).

Desde la década de los 70's, el ADNmt ha sido una poderosa herramienta utilizada en estudios de estructura poblacional, flujo génico, hibridación, biogeografía, filogeografía y filogenia entre especies (Vázquez-Domínguez 2007). El ADNmt tiene una alta tasa de sustitución de nucleótidos comparada con el ADN nuclear (ADNn), probablemente como consecuencia de mecanismos ineficientes de reparación, al proceso oxidativo característico de las mitocondrias o a que carece de histonas asociadas, las cuales conservan y restringen la evolución del ADNn (Avise 2009). Debido a esta alta variabilidad, la comparación de distintas regiones de secuencias de ADNmt puede proporcionar información valiosa acerca de los niveles de divergencia poblacional (Moritz et al. 1987). Otra característica distintiva del ADNmt es que se transmite exclusivamente por herencia materna, de modo que adquiere un carácter no-recombinante (Avise et al. 1987). Las secuencias variantes del ADNmt, conocidos como haplotipos, permiten identificar linajes matrilineales, es decir, genealogías trazadas por ancestros femeninos y compartidas en la población actual, así como la distribución geográfica de estos linajes (Avise 2000).

En tortugas marinas, el tamaño aproximado del genoma mitocondrial completo de las siete especies oscila entre 16,281 y 16,719 pb (Duchene et al. 2012). Kumazawa y Nishida (1999) reportaron que el mitogenoma de *Chelonia mydas* comprende ~16,497 pb y comparte la misma organización de genes con otros vertebrados. En el caso de *Eretmochelys imbricata*, Hernández-Fernández et al. (2017), reportaron que el genoma mitocondrial completo comprende una longitud aproximada de 16,386 pb. Otra característica del ADNmt de las tortugas marinas son las bajas tasas de variabilidad y diferenciación, con respecto a lo reportado en otras especies de vertebrados (Avise et al. 1992). Encalada y colaboradores

(1996) reportaron una tasa de cambio evolutivo de 0.012-0.024 sustituciones por locus por millón de años para secuencias de ADNmt de tortuga verde del Atlántico y Mediterráneo, mientras que otro estudio en poblaciones de África estimaron una tasa mutacional de 0.01751 sustituciones por locus por millón de años (Formia et al. 2006).

Las secuencias de la región control han sido ampliamente utilizadas como marcadores moleculares en estudios de genética poblacional y filogeografía de todas las especies de tortugas marinas, así como para determinar el origen de los individuos que componen las agregaciones de forrajeo (e.g. Encalada et al. 1996, Engstrom et al. 2002, Bowen y Karl 2007, Blumenthal et al. 2009, Leroux et al. 2012, Naro-Maciel et al. 2014, Gaos et al. 2017, Shamblin et al. 2018).

1.4 Estructura genética de las colonias de anidación

La estructura genética se define como la manera en la que la variabilidad genética se distribuye dentro y entre los individuos agrupados en escalas espaciales jerárquicas (Lowe et al. 2004). La diferenciación genética es una función inversa al flujo génico y juega un papel importante en la diversificación y adaptación de las poblaciones (Slatkin 1987). El desarrollo de herramientas moleculares ha permitido inferir que la estructura genética poblacional de las especies marinas comúnmente presenta patrones complejos, los cuales son resultado de las interacciones entre factores contemporáneos (e.g. historia de vida, rasgos conductuales, organización social, patrones de corrientes oceánicas, entre otros; Whitehead 1998, White et al. 2010) e históricos (e.g. barreras antiguas al flujo génico, polimorfismos ancestrales; Hewitt 2004, Piñeros y Gutiérrez-Rodríguez 2017).

En las poblaciones de tortugas marinas el grado de estructuración genética depende en gran medida del complejo ciclo de vida, que se caracteriza por la filopatría natal de las hembras, el flujo génico mediado por los machos y el traslape de las poblaciones en las zonas de alimentación y corredores migratorios (Wallace et al. 2010). La filopatría natal de las hembras representa el principal

promotor de la diferenciación genética en las poblaciones de anidación (Reece et al. 2005). Cuando las hembras regresan fielmente a su playa natal, cada población anidante conserva una firma genética única transmitida por la herencia materna del ADNmt, lo cual resulta en poblaciones altamente diferenciadas (Bowen y Karl 2007). Por lo tanto, la estructura de las poblaciones anidantes refleja divergencias significativas en las frecuencias haplotípicas del ADNmt y cada población puede ser considerada como una unidad demográficamente distinguible, denominada Unidad de Manejo (UM), lo que permite definir apropiadamente la escala geográfica a la cual se realizarán las actividades de monitoreo y manejo de las poblaciones (Moritz 1994).

Además de la influencia de la filopatría natal de las hembras en la estructura genética actual de las poblaciones de anidación, los procesos históricos, como las fluctuaciones climáticas del Pleistoceno, las barreras ancestrales al flujo de genes y la subdivisión poblacional, han afectado los patrones de estructura genética de las poblaciones de anidación de diversas especies de tortugas marinas (Reece et al. 2005). Algunos estudios genéticos sugieren que durante en Pleistoceno (2.5 millones de años-14,000 años) las variaciones climáticas originaron cambios en el nivel del mar, lo que probablemente generó diversos patrones de distribución de la variabilidad genética en las poblaciones de tortugas marinas (Encalada et al. 1996, Reece et al. 2005, Naro-Maciel et al. 2010). Los periodos de ascenso favorecieron procesos de expansión de las poblaciones y generaron intercambio genético, mientras que el descenso del nivel del mar propicio contracción poblacional, lo que originó el aislamiento genético de las poblaciones (Piñeros y Gutiérrez-Rodríguez 2017).

Al final del Pleistoceno, durante el último máximo glacial (~18,000 años atrás), el avance de las capas de hielo continentales y el descenso del nivel del mar (incluso hasta ~100 m por debajo de los niveles actuales) redujeron la disponibilidad de hábitats de anidación y alimentación adecuados para algunas especies (carey, verde y caguama), como consecuencia, algunas poblaciones fueron confinadas a zonas ecuatoriales, las cuales sirvieron como refugios (Encalada et al. 1996, Reece et al. 2010). Posteriormente, durante los periodos interglaciares se

colonizaron nuevos hábitats de anidación y alimentación localizados a mayor latitud, lo cual influyó en los patrones actuales de estructura genética en las colonias de anidación (Encalada et al. 1996). Algunos autores han propuesto la existencia de refugios glaciares en el Caribe y Brasil para poblaciones de tortuga verde (Reece et al. 2005, Naro-Maciel et al. 2014), y en México y sur de Florida para poblaciones de tortuga caguama (Reece et al. 2005).

1.5 Estructura genética de las agregaciones de forrajeo

En las agregaciones de forrajeo, las migraciones a larga distancia son una característica importante de la historia de vida de las tortugas marinas que influye en la estructura genética (Read et al. 2015). Aunque los patrones de corrientes oceánicas facilitan la migración de los juveniles hacia sitios de desarrollo y alimentación, recientemente se ha demostrado que el comportamiento de nado activo también juega un importante papel en la dispersión de los juveniles (Putman y Mansfield 2015, Shamblin et al. 2018). Además, las migraciones periódicas de los adultos hacia zonas de reproducción y alimentación permiten el flujo de genes provenientes de distintas colonias de anidación para originar grupos de alimentación con un acervo genético mezclado y donde convergen individuos de distintos estados ontogénicos (Read et al. 2015, Gaos et al. 2017). En este sentido, Engstrom y colaboradores (2002) proponen que los patrones de dispersión característicos de las tortugas marinas permiten la mezcla de individuos de distintas colonias de anidación, lo cual se refleja en baja o nula estructura genética de las agregaciones de forrajeo, y denominaron a este modelo como ‘sopa de tortugas’.

Por otro lado, se ha documentado que durante la etapa juvenil, algunas especies, como la tortuga carey, verde, y caguama, presentan algún grado de filopatría a determinadas zonas de alimentación (Naro-Maciel et al. 2012, Gaos et al. 2017). En el Caribe, se reportó que las agregaciones de alimentación de tortuga carey se conformaban principalmente por juveniles nacidos en playas cercanas, es decir elegían alimentarse ‘cerca de casa’, lo cual da evidencia de que la estructura de

las agregaciones de alimentación se correlaciona con la composición genética de las colonias de anidación cercanas (Bowen et al. 2007). Este rasgo conductual, asociado a determinados patrones de corrientes oceánicas, puede originar que la composición de las agregaciones de forrajeo dependa casi exclusivamente del reclutamiento de individuos de determinadas colonias de anidación, lo que genera un modelo llamado 'grupos de tortugas', y da evidencia de una fuerte estructuración genética (Engstrom et al. 2002, Blumenthal et al. 2009).

1.6 Conectividad entre colonias de anidación y agregaciones de forrajeo

La conectividad es un concepto que define el movimiento o intercambio de organismos entre hábitats geográficamente distintos (Bjorndal y Bolten 2008), y es un factor crítico que determina diversos procesos ecológicos y evolutivos que aseguran la persistencia de las especies y el mantenimiento de la biodiversidad en los ecosistemas (Lowe y Allendorf 2010). En especies migratorias, evaluar la conectividad es especialmente complejo, debido a que se desplazan grandes distancias usando diferentes áreas para desarrollarse, reproducirse o alimentarse (Tikochinski et al. 2018). En este sentido, el ciclo de vida de las tortugas marinas, caracterizado por las migraciones ontogénicas entre diferentes hábitats, hace que entender la ecología espacial y el grado de conectividad migratoria entre las colonias de anidación y la relación de éstas con las agregaciones de forrajeo sea un aspecto fundamental en la investigación y conservación de estas especies (Rees et al. 2016). El uso de programas de marca-recaptura, telemetría satelital y análisis de isótopos estables son metodologías que se han utilizado para evaluar el movimiento contemporáneo de los individuos, mientras que las herramientas moleculares permiten dilucidar los procesos históricos que determinan la distribución y conectividad actual de las poblaciones (Komoroske et al. 2017, Tikochinski et al. 2018). Desde el punto de vista genético, la conectividad se define como el grado en el que el flujo génico afecta los procesos evolutivos dentro de las subpoblaciones y evita los efectos de la deriva génica y de la endogamia, y generalmente es inferida a través del grado de la diferenciación genética estimado

por los valores del índice de fijación F_{ST} (Lowe y Allendorf 2010, Tikochinski et al. 2018).

En este contexto, el uso de marcadores moleculares (como el ADNmt) permite la identificación de firmas únicas en cada colonia de anidación que sirven para determinar el origen de los individuos en las poblaciones mezcladas (agregaciones de forrajeo) (Bolker et al. 2007). El análisis de stocks mezclados (MSA mixed stock analyses, Pella y Masuda 2001) es una herramienta basada en un enfoque bayesiano que permite determinar qué fracción de los individuos en un acervo genético mezclado provienen de determinada población fuente (Bolker et al. 2007).

No obstante, la precisión de este análisis depende de al menos tres factores claves: (1) un muestreo representativo de la mayoría de las posibles colonias fuente, (2) tamaño de muestra adecuado de la población mezclada y (3) evidente diferenciación genética entre las poblaciones fuente. Adicionalmente, se ha recomendado utilizar el tamaño de la colonia de anidación (número de hembras o nidos/año) como una covariante ecológica que permite ponderar la contribución potencial de las colonias, bajo el supuesto que ésta es proporcional al tamaño de la colonia (Bolker et al. 2007, Komoroske et al. 2017). Diversos estudios realizados en poblaciones de tortugas marinas han utilizado las frecuencias haplotípicas de las colonias de anidación para definir el origen de los individuos que conforman las agregaciones de forrajeo e identificar la conectividad entre estos, así como los posibles corredores migratorios (e.g. Proietti et al. 2014, Naro-Maciel et al. 2017, Shamblin et al. 2018).

1.7 Estudios genéticos en las tortugas carey y verde en la Península de Yucatán

El primer estudio que evaluó la diversidad y estructura genética en las poblaciones de tortuga carey en la Península de Yucatán utilizó un fragmento corto de 384 pb de la región control del ADNmt en hembras anidantes de Holbox (Quintana Roo), lo que permitió identificar los haplotipos Q y P (Bass et al. 1996). Posteriormente,

Díaz-Fernández y colaboradores (1999) mejoraron la resolución del marcador molecular, al aumentar la longitud del fragmento a ~480 pb se identificaron sitios polimórficos adicionales en el haplotipo Q y se subdividió en dos variantes: MX1 y MX2, mientras que el haplotipo P fue denominado MX3, los cuales fueron reportados en colonias de anidación de Las Coloradas (Yucatán) y en individuos colectados en un grupo de forrajeo al norte de Río Lagartos. Abreu-Grobois et al. (2003) caracterizaron 11 colonias de anidación en Campeche, Yucatán y norte de Quintana Roo mediante un fragmento de 620-675 pb de ADNmt, este estudio reveló una significativa diferenciación genética entre las colonias de Campeche y Yucatán/Quintana Roo. Finalmente, Leroux et al. (2012) reexaminaron las muestras utilizadas en un estudio previo (Bass et al. 1996), utilizando un fragmento largo de ~740 pb y concluyeron que las colonias de anidación de la Península de Yucatán representan una sola unidad de manejo. Con respecto a las agregaciones de forrajeo, González (2003) determinó que aproximadamente el 98 % de los individuos colectados en grupos de forrajeo de Campeche son originarios de colonias locales, principalmente provenientes de playas campechanas.

Con respecto a la tortuga verde, Encalada y colaboradores (1996) evaluaron genéticamente las principales colonias de anidación del Atlántico mediante un fragmento de ~487 pb de ADNmt; para la población de anidación de México (únicamente X'cacel e Isla Contoy, Quintana Roo) identificaron siete haplotipos. En estudios subsecuentes, se determinó la dominancia del haplotipo CM-A3 en las colonias del Golfo de México y Caribe Mexicano, y se detectó la presencia de haplotipos endémicos en las colonias de Quintana Roo (Pérez-Ríos 2008, Millán-Aguilar 2009). Con respecto a las agregaciones de alimentación identificadas en la Península de Yucatán, no han sido caracterizadas genéticamente, por lo que se desconoce la composición y conectividad de estos grupos en esta región del Caribe.

Si bien, es cierto que diversos estudios han abordado la composición genética de las colonias de anidación de las tortugas carey y verde en la Península de Yucatán, el uso de fragmentos cortos del ADNmt y/o el muestreo poco representativo a lo largo de toda la distribución geográfica de las especies, podría

generar sesgos en los análisis e inferir conclusiones parciales. Para resolver la cuestión de la resolución del marcador molecular, se estandarizaron cebadores (oligonucleótidos utilizados en amplificación de ADN) que permiten obtener un fragmento de mayor longitud en ambas especies de tortugas marinas (Abreu-Grobois et al. 2006), lo que permite identificar mayor variación nucleotídica y resolver la estructura genética a una escala geográfica más fina.

1.8 Implicaciones para el manejo y conservación

Las estrategias de manejo y conservación generalmente se basan en categorías discretas, definidas como especies; sin embargo, la mayoría de éstas están altamente estructuradas en poblaciones que precisan ser consideradas como unidades intraspecíficas que representan una diversidad genética única para fines de conservación (Coates et al. 2018). En este sentido, las unidades de conservación son definidas como múltiples niveles jerárquicos por debajo del nivel de especie que permiten priorizar las acciones de conservación (Komoroske et al. 2017); no obstante, definir la resolución de las unidades de conservación no es una tarea sencilla y requiere comprender los alcances de los programas de manejo y conservación, considerar el ciclo de vida y las potenciales amenazas que enfrentan las poblaciones (Wallace et al. 2010). La unidad de manejo (UM), definida bajo el criterio propuesto por Moritz (1994) es la unidad básica de conservación y generalmente es el reflejo de la diferenciación genética entre subpoblaciones. Además, la UM es el eje central en el manejo de las poblaciones silvestres y es crucial para determinar la escala geográfica del monitoreo y regular los efectos de la actividad humana en la abundancia de las poblaciones y especies (Palsbøll et al. 2007).

La definición de UM en poblaciones de tortugas marinas, principalmente en colonias de anidación, se ha basado en criterios genéticos (Casale y Mariani 2014, Shamblin et al. 2017). Sin embargo, la integración de otras herramientas, como telemetría satelital y estudios de marca-recaptura, pueden complementar la información biológica y ecológica que permita facilitar la definición robusta de las

unidades de conservación para tortugas marinas a múltiples escalas (Wallace et al. 2010). En un contexto global, Wallace y colaboradores (2010) propusieron el concepto de unidad regional de manejo (RMU, regional management units), que define segmentos de una población que presentan suficiente variabilidad genética para retener el potencial evolutivo de las poblaciones, y en la mayoría de los casos, agrupan varias UM. Las RMUs permiten evaluar y priorizar las acciones y estrategias de conservación a una escala geográfica amplia, por encima de las poblaciones de anidación, pero por debajo del nivel de especie.

Por otro lado, evaluar la conectividad entre colonias de anidación y grupos de forrajeo, así como determinar la ecología espacial, permite la identificación de áreas geográficas de importancia para las poblaciones de tortugas marinas (Godley et al. 2010) o bien, proponer acciones ante amenazas específicas (FitzSimmons y Limpus 2014). Por ejemplo, las áreas de forrajeo donde posiblemente convergen múltiples especies o diversos acervos genéticos pueden coincidir con importantes zonas de pesca comercial, lo que podría representar un impacto negativo en el reclutamiento de individuos a los grupos reproductivos o a las colonias de anidación a mediano o largo plazo (Tikochinski et al. 2018). Esto enfatiza que las acciones de conservación no deben limitarse a la fase reproductiva ni a las áreas de anidación, sino además, dirigir la protección a los hábitats marinos, en los cuales las tortugas marinas pasan la mayor parte de su ciclo de vida, y de esta manera, se podrá asegurar la persistencia de estas especies a largo plazo.

Justificación

La Península de Yucatán es una región que alberga poblaciones de anidación representativas de las tortugas carey y verde, además de que se han identificado diversas áreas de forrajeo y reproducción, así como un importante corredor migratorio. Pese a la importancia biológica y ecológica de la región para la conservación de las tortugas marinas, gran parte de los esfuerzos se han centrado en la conservación de los hábitats de anidación (principalmente en el manejo de

hembras reproductoras y crías). Sin embargo, en las zonas costeras de alimentación, el estudio de juveniles y adultos (especialmente de los machos) se ha abordado de manera muy limitada, debido a las dificultades que representa el monitoreo marino. Sin embargo, en años recientes se han aumentado los esfuerzos para realizar monitoreo marino de forma sistemática y regular en la Península de Yucatán, lo cual ha permitido desarrollar diversos estudios, que proporcionan nueva información sobre la composición y rutas migratorias de las tortugas que se alimentan en aguas mexicanas del Caribe y Golfo de México.

De acuerdo a lo antes planteado, es evidente la necesidad de (1) caracterizar genéticamente a las colonias de anidación y agregaciones de alimentación de las tortugas carey y verde en la región de la Península de Yucatán, utilizando el fragmento largo de la región control del ADNmt, así como aumentar el número de muestras respecto a estudios anteriores; (2) definir la estructura genética de las colonias de anidación y agregaciones de forrajeo de tortugas carey y verde e (3) identificar la conectividad migratoria entre hábitats de anidación y de forrajeo a escala local y regional. Al integrar estos aspectos, el presente trabajo permitirá sustentar, con bases científicas, la definición de UM para la implementación de las estrategias de manejo y conservación de las especies involucradas, lo cual contribuirá a la protección de los distintos hábitats favoreciendo el funcionamiento óptimo de los ecosistemas de importancia biológica y ecológica de la región.

Objetivo general

Determinar la diversidad y estructura genética de las colonias de anidación y de las agregaciones de forrajeo de las tortugas carey y verde, e identificar la conectividad migratoria entre colonias de anidación y grupos de forrajeo en la Península de Yucatán, por medio del fragmento largo de la región control del ADNmt.

Objetivos particulares

- Estimar la diversidad genética en las principales colonias de anidación y agregaciones de forrajeo de las tortugas carey y verde en la Península de Yucatán.

- Determinar los patrones de estructura genética de las colonias de anidación y grupos de forrajeo de las tortugas carey y verde en la Península de Yucatán.

- Definir el origen natal de los individuos que conforman las agregaciones de forrajeo de las tortugas carey y verde en la región del Golfo de México y Caribe Mexicano.

- Estimar la contribución de las tortugas carey y verde nacidas en la Península de Yucatán a las agregaciones de forrajeo del Atlántico.

- Delimitar las unidades de manejo para las tortugas carey y verde en la Península de Yucatán, con el fin de analizar sus implicaciones en el manejo y conservación de estas especies en la región.

Hipótesis

- La diversidad genética de las colonias de anidación de las tortugas carey y verde será baja; mientras que en las agregaciones de alimentación se reportarán valores altos de diversidad genética.

- La diferenciación genética entre las colonias de anidación de las tortugas carey y verde será evidente; no obstante en las agregaciones de forrajeo de las tortugas carey y verde la diferenciación genética será muy baja.

- Las agregaciones de forrajeo de las tortugas carey y verde en la Península de Yucatán estarán compuestas principalmente por individuos

provenientes de colonias de anidación foráneas, apegándose al modelo de “sopa de tortugas”.

- Las tortugas carey y verde nacidas en las colonias de anidación de la Península de Yucatán contribuirán sustancialmente a diversas agregaciones de forrajeo en el Atlántico.

- Las secuencias largas de la región control del ADNmt permitirán mejorar la precisión de la identificación de unidades de manejo en las colonias de anidación y agregaciones de forrajeo en la Península de Yucatán.

CAPÍTULO II

GENETIC STRUCTURE, ORIGIN, AND CONNECTIVITY BETWEEN NESTING AND FORAGING AREAS OF HAWKSBILL TURTLES OF THE YUCATAN PENINSULA. A STUDY FOR CONSERVATION AND MANAGEMENT

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GENETIC STRUCTURE, ORIGIN, AND CONNECTIVITY BETWEEN NESTING AND FORAGING AREAS OF HAWKSBILL TURTLES OF THE YUCATAN PENINSULA. A STUDY FOR CONSERVATION AND MANAGEMENT

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ABSTRACT

1. Anthropogenic activities have led marine turtle populations to a large decline. The complex life cycle (e.g., female philopatry, hatchling migration, adult movements between breeding and foraging areas) make it difficult to understand some biological aspects or human impacts on their populations. In this sense, the genetic tools play a major role to understanding population dynamic and improve conservation and management strategies.
2. Using the mtDNA control region, this study examines the composition, population structure, and connectivity between rookeries and foraging aggregations, in addition to their relationship with Atlantic rookeries and foraging areas of the hawksbill turtle in the Yucatan Peninsula.
3. Haplotype composition of rookeries showed EiA22, EiA39 and EiA41 as endemic haplotypes and revealed a segregation between Gulf of Mexico, and Yucatan and Quintana Roo rookeries, defining two Management Units. Foraging aggregations present 15 haplotypes, some common for Atlantic and others for Mexican rookeries. Considering the Gulf of Mexico *vs* the Mexican Caribbean, significant population genetic structure was revealed, inferring a differential recruitment of hawksbill turtles.
4. Rookery-centric mixed-stock analysis (MSA) reveals a high contribution of Mexican turtles to local foraging aggregations, principally in the Gulf of Mexico. Foraging-ground-centric MSA showed that the Gulf of Mexico foraging aggregation is predominantly composed of individuals from local rookeries, while Mexican Caribbean foraging groups have a mixed composition with individuals

from Barbados, Brazil, and Puerto Rico rookeries. The connectivity between rookeries and foraging aggregations suggest that the ocean currents and swimming behaviour influence the distribution of hawksbill turtles.

5. Our results highlighted the importance in identifying Management Units in nesting and foraging areas to develop monitoring and management programs in an appropriate geographic scale. In addition, understanding turtle habitats connectivity will allow for prioritized conservation actions considering particular threats, emphasizing both national and international collaborations for conservation of this endangered species.

Keywords

Eretmochelys imbricata, mtDNA haplotypes, genetic diversity, Mexico, mixed-stock analysis

1. INTRODUCTION

Marine turtles are challenged by numerous threats throughout the world. Many anthropogenic factors (e.g., overexploitation of meat and eggs, bycatch, marine pollution, plastic bags/debris among others), as well as some stochastic factors, have contributed to their decrease in numbers, particularly impacting nesting areas and foraging habitats (Bjorndal, & Jackson 2003; Rodríguez-Zárate, Rocha-Olivares, & Beheregaray, 2013; Huang, 2015). Climate change has also been found to contribute to a loss of biodiversity (Ceballos et al., 2015), and represents a major risk for marine turtles (Hawkes, Broderick, Godfrey, & Godley, 2009), which represent emblematic species that have experienced a significant population decline.

The vulnerability of marine turtles is mainly due to their habitats are distributed over a wide geographic area, and they present complex life cycles (natal philopatry, male-mediated gene flow, long-distance migrations, among others) generating complex population structure patterns (Wallace et al., 2010). Natal philopatry is a life-history strategy in which an individual returns to its natal area to reproduce (Putman et al., 2014); this behaviour suggests that nesting population will be distinguishable by a unique genetic signature of mitochondrial DNA (mtDNA) that is inherited from females to their offspring (Bowen & Karl, 2007). This results in highly structured populations such that each "regional nesting population" functions as an independent demographic unit (Bowen et al., 1994). These populations fit the concept of 'Management Units' (MUs; populations with significant divergence of allele frequencies at nuclear or mitochondrial loci) as defined by Moritz (1994), who emphasized that MUs allow to define an appropriate geographic scale for the

monitoring and management of populations. Understanding boundaries of nesting populations and the connections between them are priority research topics (Wallace et al., 2010). The use of molecular markers, as mtDNA control region, have shown sufficient power to resolve genetic differentiation among rookeries (Komoroske, Jensen, Stewart, Shamblin & Dutton, 2017), especially using primers developed to obtain a large fragment of this region and improve the detection and resolution of genetic structure (Abreu-Grobois et al., 2006).

Genetic composition of foraging aggregations is highly influenced by juvenile migration during post-hatchling toward epipelagic habitats, but also of adults between foraging and breeding habitats, generating the presence of individuals from multiple genetic stocks in a foraging aggregation (Read et al., 2015). These complex ontogenetic migrations, in addition to ocean currents, and migratory and swimming behaviours, greatly influence the composition of foraging aggregations (Blumenthal et al., 2009; Putman & Mansfield, 2015). In this context, knowledge related to connectivity between foraging aggregations and rookeries is a key component for delineating management strategies and protecting critically endangered marine turtle species. Furthermore, the definition of specific mtDNA haplotypes for each rookery can be used to determine the composition of foraging aggregations through the Bayesian method of mixed stock analyses (MSA) (Bowen & Karl, 2007).

The hawksbill turtle, *Eretmochelys imbricata* L. 1766 (Testudines, Cheloniideae), is a critically endangered species widely distributed throughout tropical and subtropical waters in the Atlantic and Pacific Oceans (Leroux et al., 2012) with important rookeries in the

wider Caribbean and Atlantic. In Mexico, the Yucatan Peninsula hosts the largest nesting population of the hawksbill turtle in the Atlantic, and several shallow coastal habitats are reported as foraging areas (Garduño-Andrade, Guzmán, Miranda, Briseño-Dueñas, & Abreu-Grobois, 1999).

The first genetic study on the hawksbill rookeries in the Caribbean, using a 384 bp mtDNA fragment, identified 21 haplotypes and concluded that six out of seven studied populations were isolated breeding populations (Bass et al., 1996). Subsequently, the number of haplotypes increased by improving the resolution of the molecular marker to a 480 pb fragment (Díaz-Fernández et al., 1999). Finally, Leroux et al. (2012) used a longer mtDNA fragment (~740 pb) to improve the resolution of the genetic structure of Caribbean populations. Genetic studies suggest that Mexican rookeries belong to a unique MU (Bass et al., 1996; Díaz Fernández et al., 1999; Leroux et al., 2012); however, this conclusion could be the result of sampling too few rookeries without considering other representative rookeries in the region. Analysis based on tag returns suggests that the Yucatan Peninsula rookeries form two nesting groups: (1) the north-east group and (2) the south-west group (González-Garza et al., 2008). This differentiation was confirmed by a genetic study using a 620-675 bp fragment on 11 rookeries of the Yucatan Peninsula defining two similar MUs: (1) Campeche, and (2) Yucatan and north of Quintana Roo (Abreu-Grobois et al. 2003).

The composition of hawksbill turtle foraging groups in the Atlantic has been previously analysed, and it has demonstrated that foraging aggregations showed low but significant genetic structure (Bowen et al., 2007; Proietti et al., 2014). To explain this genetic differentiation in the foraging aggregations, Engstrom, Meylan and Meylan (2002)

proposed that the dispersal during the pelagic stage provides the potential to thoroughly mix turtles from different rookeries, then the recruitment in pelagic habitats reflects this mixture, and called this model 'turtle soup'. On the other hand, when the oceanographic or behavioural factors lead to disproportionate contributions of nesting areas to pelagic habitats, the foraging aggregations appeared to be regionally constrained, hence that will experience major levels of proximate or local recruitment, designating this model as 'turtle groups' (Engstrom et al., 2002; Blumenthal et al., 2009). These patterns depend on several factors such as life-history stage, migratory and swimming behaviours, and ocean currents (Putman & Mansfield, 2015). A genetic study carried out by González (2003) suggests that 98% of turtles in the foraging aggregations of Campeche originate from Campeche rookeries. With the exception of the study of González (2003), other foraging aggregations in this region have not yet been genetically evaluated.

The knowledge of genetic stocks (MUs) and foraging aggregations, and the connectivity between them, is of great importance for conservation and management actions directed at marine turtle populations. Moreover, in this context and when considering the lack of information in the Yucatan Peninsula, the inclusion of data from several rookeries and new information from foraging aggregations in the region is essential. To reduce this gap in knowledge, the larger (~740 bp) fragment of mtDNA control region was used to assess the hawksbill turtle haplotype composition in the Yucatan Peninsula to obtain small-scale resolution, considering data from several rookeries and new information from foraging aggregations. Particularly, we addressed the following questions: (1) Will the use of a larger mtDNA fragment allow to reveal the population genetic structure at the small-scale for rookeries in the Yucatan Peninsula and, increase the number of previously established

MUs?; (2) Can foraging aggregations in the Yucatan Peninsula be defined in MUs?; (3) Does the composition of the Yucatan Peninsula foraging aggregations fit the "turtle soup" or "turtle groups" model?; (4) What is the contribution of Mexican turtles to Atlantic foraging aggregations?; (5) What are the implications of our results on hawksbill turtle management and conservation programs in the region?

2. METHODS

2.1 Ethics statement

All activities of capture, tagging, sampling, and transport of biological samples performed during this study were authorized by the Dirección General de Vida Silvestre-SEMARNAT under the permits SGPA/DGVS/08106/14, SGPA/DGVS/08337/15, and SGPA/DGVS/06013/16. Individuals were handled by a qualified team following the ethics protocol suggested by Ehrhart and Ogren (1999). Moreover, this research was approved by the Comité de Ética para la Investigación (CEI) of El Colegio de la Frontera Sur.

2.2 Sample collection

Tissue samples were collected in the Yucatan Peninsula, located in south-east Mexico separating the Gulf of Mexico and the Caribbean Sea, from 2013 through 2016 on four index nesting beaches (these beaches host an important proportion of the overall nesting population and, consequently, monitoring should reflect the population pattern for all beaches within the defined region; SWOT, 2011), and five foraging aggregations (Table 1). Samples from rookeries were obtained during night oviposition monitoring, while individuals were captured in the foraging aggregations using nets, snorkeling, or SCUBA

diving during population monitoring projects. All individuals were measured (curved carapace length: CCL) (Bolten, 1999) and marked with inconel tags (National Band and Tag Co. 681) to avoid resampling. Tissue samples were obtained from the right fin using a biopsy punch (3mm diameter), and then preserved in a salt-saturated 20% DMSO solution at 4°C until molecular analysis (Velez-Zuazo et al., 2008).

2.3 Laboratory methods

Genomic DNA isolation was conducted using the Wizard® Genomic DNA Purification Kit (PROMEGA) following the animal tissue protocol. A 740 bp fragment of the mtDNA control region was amplified using the primers LCM15382 (5'-GTCTAACCCTAAAGCATTGG-3') and H950g (5'-GTCTCGGATTTAGGGGTTT-3') (Abreu-Grobois et al., 2006) as described in Shamblin et al. (2015). PCR products were evaluated through electrophoresis in 2% agarose gel in 1X TAE buffer using a 100 bp DNA ladder (PROMEGA) as reference. Amplified fragments were sent to MACROGEN (Seoul, Korea) for purification and sequencing.

2.4 Data analysis

2.4.1 Haplotype characterization and genetic diversity

Sequences were edited and aligned using BIOEDIT 7.2.5 (Hall, 1999), and classified according to the Atlantic hawksbill haplotypes database (Abreu-Grobrois pers. comm, May 2017). Analyses were processed using the longer DNA fragment, and the EiAXX nomenclature for the Atlantic haplotypes was used (Leroux et al., 2012). Genetic diversity parameters were assessed for rookeries and foraging aggregations by haplotype (*h)* and

nucleotide (π) diversity for each locality and over the whole dataset (called global value) using ARLEQUIN 3.5 (Excoffier & Lischer, 2010).

2.4.2 Population genetic structure

Genetic differentiation was estimated for rookeries and foraging aggregations in ARLEQUIN 3.5, through estimates of pairwise fixation indices (F_{ST}) using haplotype frequencies (Tillett, Meekan, Field, Thorburn, & Ovenden, 2012). Furthermore, we conducted a Spatial Analysis of Molecular Variance (SAMOVA 2.0; Dupanloup, Schneider, & Excoffier, 2002). This approach defines groups of populations that are maximally differentiated from each other, and assigns populations to new groups (*K*) with the premise that they must be geographically adjacent and genetically homogeneous (Dupanloup et al., 2002). We assessed the most likely number of groups (*K)* corresponding to the highest percentage of variation among groups tested, ranging from 2 to 3 for rookeries, and 2 to 4 for foraging aggregations.

2.4.3 Mixed stock analysis

A many-to-many Bayesian MSA was performed using the "mixstock" package in *R* 3.4.1 (Bolker, Okuyama, Bjorndal, & Bolten, 2007) to estimate the contribution from main hawksbill turtle rookeries from the Atlantic to foraging aggregations in the Yucatan Peninsula (foraging-ground centric analysis), and to assess to which Atlantic foraging aggregations a turtles born in a Yucatan Peninsula rookery would migrate (rookery-centric analysis). We considered haplotype frequencies from rookeries and foraging grounds only characterized by the 740 bp fragment, including 15 rookeries and 16 foraging aggregations

from the Atlantic obtained from published data and new genetic information from four rookeries (n = 104 individuals) and five foraging aggregations (n = 123 individuals) of the Yucatan Peninsula. Additionally, the nesting population size (number of nests per year per rookery) was included in the analysis as an ecological covariate assuming that potential contribution is proportional to the relative size of the rookery. References for haplotype and nesting size data can be founded in Table S1 and S2 in Supporting Information.

3. RESULTS

3.1 Haplotypes characterization and genetic diversity

Sequencing data revealed sixteen haplotypes in rookeries and foraging aggregations from the Yucatan Peninsula (Table 2, Figure 1). Rookeries exhibited five haplotypes with the highest occurrence of haplotype EiA23 (68%), followed by EiA41 (17%), and < 7% for each of the remaining haplotypes. In the foraging aggregations, 15 haplotypes were identified with the highest occurrence of haplotype EiA01 (39%), followed by haplotypes EiA23 and EiA11 (15.4% and 13.8%, respectively), 8% each for haplotypes EiA39 and EiA41, and others (< 3%).

In the Yucatan Peninsula rookeries, haplotype diversity ranged from 0.225 (Holbox) to 0.454 (Chenkan) with a global value of 0.504 (SD 0.052), whereas the nucleotide diversity ranged from 0.0005 (Holbox and El Cuyo) to 0.0006 (Chenkan and Las Coloradas) with a global value of 0.0011 (SD 0.0009). Foraging aggregations of the Yucatan Peninsula exhibited a haplotype diversity from 0.607 (Banco Chinchorro) to 1.000 (Xcalak) with a

global value of 0.794 (SD 0.027), and a nucleotide diversity from 0.0028 (Punta Xen) to 0.0177 (Xcalak) with a global value of 0.0070 (SD 0.0030) (Table 3).

3.2 Genetic structure

Pairwise F_{ST} showed genetic differences between the rookeries from the Yucatan Peninsula with a significant separation of the Campeche rookery from Yucatan and Quintana Roo rookeries (Table 4). These results were confirmed by the SAMOVA analysis which indicates that the maximal differentiation for the Yucatan Peninsula rookeries were two groups (Campeche *vs* Yucatan and Quintana Roo; Table S3 in Supporting Information). Pairwise F_{ST} showed differences between Gulf of Mexico and Mexican Caribbean foraging aggregations, and a genetic homogeneity among all Caribbean foraging grounds (Table 5). SAMOVA analysis confirmed the previously defined grouping (Gulf of Mexico *vs* Mexican Caribbean; Table S4 in Supporting Information).

3.3 Mixed stock analysis

3.3.1 Foraging-ground-centric MSA

The natal origins of 117 individuals (95%) from foraging aggregations of the Yucatan Peninsula were identified, and six individuals (5%) presented three orphan haplotypes: EiA36 (n =1) (foraging aggregations from Mona Island, Puerto Rico; Velez-Zuazo et al., 2008), EiA63 (n = 4) (GenBank: KC196498.1), and EiA83 (n = 1) (GenBank: KC196502.1). The two samples obtained in Xcalak presented orphan haplotypes that were not previously reported in rookeries from the Atlantic basin; considering the bias that this could introduce in the MSA, we omitted these samples as suggested by Bolker et al. (2007).

MSA analysis showed that (i) the foraging aggregation of the Gulf of Mexico (Punta Xen locality) is composed principally of individuals from regional rookeries with a high contribution from Campeche (Chenkan, 29%), and less from Yucatan and Quintana Roo rookeries (Holbox, El Cuyo, and Las Coloradas between ~10 and 20% each) (Figure 2a); and (ii) all foraging aggregations from the Mexican Caribbean (Isla Contoy, Cozumel, and Banco Chinchorro) showed contributions from the furthest rookeries such as Barbados Leeward (~20 to 30% to each foraging aggregation) and Brazil (Bahia and Pipa, between 10-20% from each), and a smaller contribution from Puerto Rico (~ 10%) (Figure 2b). While, Isla Contoy showed an important contribution from Holbox and El Cuyo rookeries (close to 10% each one), and Cozumel reported a relevant contribution from El Cuyo (~10%). All other contributions are less than 5%. Complete foraging-ground-centric MSA outputs are presented in Figure S1 in Supporting Information.

3.3.2 Rookery-centric MSA

Results of rookery-centric MSA analysis showed the rookeries contribution from the Yucatan Peninsula to Mexican foraging aggregations (Figure 2c): Campeche (Chenkan locality) contributes mainly to Punta Xen and Isla Contoy (~30% and ~10%, respectively), and Yucatan and Quintana Roo rookeries contribute in lower proportions to Punta Xen (~10% each). In addition, Mexican rookeries contribute to foraging aggregations in the Atlantic region (Figure 2d): Campeche (Chenkan locality) contributes to Florida foraging grounds (Palm Beach, ~20%, and Key West, ~10%), whereas contributions of Chenkan to all other foraging aggregations are less than 10%. El Cuyo rookery (Yucatan) contributes mostly to the foreign foraging aggregations of Turks and Caicos (~20%), and Cuba (Jardines del Rey locality, ~10%). Finally, Holbox and Las Coloradas rookeries contribute

predominantly to foraging aggregations of Florida (Palm Beach and Key West, ~20% and ~10%, respectively). Complete rookeries-centric MSA outputs are presented in Figure S2 in Supporting Information.

4. DISCUSSION

4.1 Rookeries

Although the genetic composition of hawksbill nesting population from the Yucatan Peninsula has been previously evaluated, the use of different fragments length or few localities (Bass et al., 1996; Leroux et al., 2012) leads to incomplete conclusions. This study reveals a more representative genetic study of the principal rookeries on the Yucatan Peninsula using the longer fragment of mtDNA control region as well as an increase in sample size regarding previous studies.

The only study in Mexico that used the large mtDNA fragment was Leroux et al. (2012) who identified four haplotypes (EiA22, EiA23, EiA41, and EiA43). We confirmed the high frequencies of haplotypes EiA22, EiA23, and EiA41, characteristic for the Yucatan Peninsula rookeries, and a low frequency of haplotype EiA43, which is a haplotype found in Puerto Rico and Nicaragua rookeries (Leroux et al., 2012), showing that the EiA43 haplotype could be considered as a non-Mexican haplotype. Furthermore, we confirmed the presence of the haplotype EiA39 (previously identify by Abreu-Grobois et al., 2003) only in the Campeche nesting area. This support that haplotypes EiA22, EiA39, and EiA41 are endemic to the Yucatan Peninsula, making them useful for identifying the presence of Mexican hawksbill turtles in foraging aggregations from the Atlantic (Abreu-Grobois et al., 2003). The high proportion of endemic haplotypes was reported by Reece, Castoe, &

Parkinson (2005) in other hawksbill nesting populations, and could be explained considering the historical patterns of gene flow among populations. These authors suggested that Mexican rookeries have been isolated from eastern Caribbean rookeries because of historical processes as the emergence of the Campeche Bank and the Florida Shelf during the Pleistocene that decreased the gene flow across the Caribbean populations (Reece et al., 2005). The high endemicity of haplotypes, the low number of samples per site, and the low historical gene flow in the Yucatan Peninsula rookeries are also reflected in the low genetic diversity parameters (haplotype and nucleotide) reported in this study compared with those reported for the Caribbean hawksbill rookeries (Leroux et al., 2012).

Interestingly, a segregation in dominant haplotype composition between the Gulf of Mexico (EiA39 and EiA41) and the northern Yucatan Peninsula (EiA23 and EiA22) has been observed, which could reflect the high level of philopatry of hawksbill turtle (Reece et al., 2005). Finally, our study reveals the origin of the orphan haplotype EiA24, previously identified in foraging aggregations of Campeche (González, 2003) and Cuba (Pérez-Bermúdez et al., 2017). As this haplotype was observed on Mexican rookeries, it is likely that these foraging individuals migrated from Mexico. This demonstrates the importance of increased sampling, using longer mtDNA fragment to strengthen the genetic data, on Atlantic rookeries to identify orphan haplotypes from foraging aggregations in order to produce an improved map of movements of hawksbill turtles in the Atlantic.

A significant genetic structure is evident at a small geographic scale, differentiating the Campeche rookery from Yucatan rookeries. This may be due to the differential segregation of haplotypes at the region, most probably resulting from the high degree of female

philopatry combined with the influence of the complexity of current patterns (Caribbean, Yucatan, and Loop Currents) in the region as well as the semi-enclosed nature of the Gulf of Mexico (Collard & Ogren, 1990; Bowen et al., 2007; Briones-Fourzán, Candela, & Lozano-Álvarez, et al. 2008; Carrillo, Johns, Smith, Lamkin, & Largier, 2015). This fine scale structure is not uncommon for sea turtle rookeries and has been observed in hawksbill turtles at the Barbados coast (Browne, Horrocks, & Abreu-Grobois, 2010) and loggerhead turtles, *Caretta caretta*, in Florida (Bowen & Karl, 2007). Our study, although not including all the Yucatan Peninsula rookeries, provides genetic evidence for the definition of two MUs, as proposed in a previous study (Abreu-Grobois et al., 2003).

4.2 Foraging aggregations

Although some of the 15 haplotypes identified in Mexican foraging aggregations are common in the Atlantic rookeries (EiA01, EiA02, EiA03, EiA09, EiA11; Leroux et al., 2012), the remainder are exclusive of Mexican rookeries (EiA22, EiA23, EiA39, EiA41) suggesting regional contributions between rookeries and foraging aggregations. Additionally, the two new orphan haplotypes (EiA63 and EiA83) identified in the Mexican Caribbean, show that the rookery sample size analysed before was insufficient to detect genetic differences at small-scale or that small nesting populations have not yet been sampled (Bolten et al., 1998), highlighting the importance of continued rookery sampling.

Haplotype diversity was high, and our values were similar to other foraging aggregations in the Atlantic (Sao Pedro and Sao Paulo, Brazil h= 0.644, Proietti et al., 2014; Leeward coast, Tobago h= 0.838, Cazabon-Mannette, Browne, Austin, Hailey, & Horrocks, 2016), which could result from the influence of oceanic current patterns (Bass, Epperly, & Braun-

McNeill, 2006). The Caribbean Current characterized by seasonal and temporal variations can affect the movement of individuals at the early life stages; moreover, this complex current system could allow turtles from differing natal origins access to Mexican foraging aggregations (Bass et al., 2006; Blumenthal et al., 2009). The high haplotype diversity reported for Xcalak was probably overestimated due to the very low number of samples. Mexican foraging aggregations shown low nucleotide diversity compared with other localities from the Atlantic (Jardines del Rey, Cuba, $\pi = 0.04$, Pérez-Bermúdez et al., 2017; Ascension Island, $\pi = 0.01$, Putman et al., 2014), this seems to be consistent due to high genetic structure among populations and low genetic distance among haplotypes (Reece et al., 2005).

When considering Gulf of Mexico *vs* Mexican Caribbean, our study showed a significant genetic structure for foraging aggregations, which indicates differential recruitment of hawksbill turtles between both regions. The Mexican Caribbean seems to be influenced by the mixing of individuals during their pelagic stage (Bass et al., 2006; Velez-Zuazo et al., 2008), while self-recruitment is notable in the Gulf of Mexico (Bowen et al., 2004) as a resulting effect of the Loop Current, and the rings associated with it, which retain turtles in the Gulf of Mexico (Collard & Ogren, 1990).

4.3 Mixed-stock analysis

4.3.1 Foraging-ground-centric MSA

Using the longer mtDNA fragment, the foraging-ground-centric MSA allowed a more accurate evaluation of the contribution of the Atlantic rookeries to the Mexican foraging areas. The Gulf of Mexico (Campeche) foraging aggregations showed an almost exclusive

contribution from Mexican hawksbill rookeries, thus fitting the "turtle groups" model (Blumenthal et al., 2009) as previously suggested by Díaz-Fernández et al. (1999). This could be a result of the proximity between nesting and foraging areas (Luke, Horrocks, Leroux, & Dutton, 2004) or the fact that juveniles recruit in coastal habitats close to their natal rookery after oceanic migration suggesting a philopatric behaviour (Bowen et al., 2004, 2007). However, a more plausible explanation is the influence of complex currents system in the semi-enclosed Gulf of Mexico. Blumenthal et al. (2009) proposed the hatchling drift model based on the patterns of particles distribution released in genetically characterized rookeries to analyze the influence of ocean currents on the passive dispersal of hawksbills in the Caribbean. Their results indicated that the particles released from the Yucatan Peninsula rookeries (north of Yucatan Peninsula and Campeche) were largely entrained into the Gulf of Mexico because the influence of the Loop Current and the eddies associated. This hatchling drift model supports the “turtle groups” model to explain the composition of the Gulf of Mexico foraging aggregation (Collard & Ogren, 1990; Engstrom et al., 2002; Blumental et al., 2009).

On the other hand, the Mexican Caribbean foraging areas showed a completely different origin. The three foraging areas analysed presented a main contribution from Barbados Leeward, Brazil, and Puerto Rico, in concordance to the “turtle soup" model. The hatchling drift model, proposed by Blumenthal et al. (2009), showed that some particles released in Mona Island (Puerto Rico) and Barbados rookeries were transported eastward by the Caribbean Current. Furthermore, the connection between Caribbean and Brazil hawksbill populations has been confirmed by drifter trajectories and tag returns (Lima, Melo, Severo, & Barata, 2008; Proietti et al. 2014). Consequently, the ‘turtle soup’ model could be

explained by ocean current patterns that favor connectivity of hawksbill populations into the Atlantic basin. The possible pathway of foreigner hawksbills to Caribbean Mexican foraging areas could be through the Caribbean Current, which originates in the North-Brazil Current, continues along great anticyclonic gyres through the Lesser and Greater Antilles, enters the Guiana Current and ultimately flows into the southern Caribbean Sea (Fratantoni, 2001). Inside the Caribbean Sea, turtles born in Brazil, Puerto Rico and Barbados would continue their route crossing the Cayman Basin, and go toward north of the Yucatan Current that impinges on Banco Chinchorro and Cozumel along the Quintana Roo coast (Carrillo et al., 2015). Oceanic currents are clearly fundamental to understanding sea turtle movements, but different authors would also argue in favour of active swimming behaviour being important in the success of juvenile turtles reaching their final destinations (Putman et al., 2014; Shamblin, Witherington, Hirama, Hardy, & Nairn, 2018).

4.3.2 Rookery-centric MSA

The rookery-centric MSA reveals the high contribution of hawksbill turtles born in the Yucatan Peninsula rookeries to Mexican foraging areas, and mainly in the Gulf of Mexico foraging area (30% from Campeche rookery, and 10% from each of the northern Yucatan Peninsula rookeries). This could be explained by the fact that hatchlings remain at development sites (i.e., oceanic or neritic zones providing adequate food resources, essentially for young sea turtle; Meylan & Meylan, 2000) within the Gulf of Mexico, suggesting a high level of self-recruitment in Mexican foraging areas. However, even if self-recruitment is common in marine turtles (Bowen et al., 2004), external factors such as oceanic currents could influence the connectivity between rookeries and foraging aggregations in this region. The Loop Current and its associated cyclonic gyres act as the

principal mechanism to transport hatchlings born in the Yucatan Peninsula into the Gulf of Mexico where they can remain for several months or even years (Collard & Ogren, 1990). Additionally, the size distribution (21-60 cm CCL) of hawksbill turtles found in the coastal waters of Campeche with Mexican haplotypes suggests that these individuals have been recruited from nearby rookeries and, consequently, have spent their entire pelagic development period in the Gulf of Mexico (Collard & Ogren, 1990; Garduño-Andrade et al., 1999).

Another important destination for Mexican hawksbill turtles is Florida. The complex pattern and combination of different currents (Yucatan, Loop, and Florida; Molinari & Morrison, 1988) could explain the connectivity between Mexican rookeries and south-eastern Florida foraging aggregations, where hatchling turtles use the currents for passive transport combined with swimming behaviour (Putman & Mansfield, 2015). Furthermore, the shallow waters of Florida appear to provide adequate habitat for the development of small hawksbills (20-26 cm SCL; Gorham et al., 2014).

One locality north of the Yucatan Peninsula (El Cuyo) showed a high contribution to the Cuba, Turks and Caicos Islands foraging aggregations, probably due to the presence of the haplotype EiA24. Pérez-Bermúdez et al. (2017) identified Barbados as the most important source of hawksbill contributions to Cuban foraging aggregations, followed by Puerto Rico and Mexico. However, as haplotype EiA24 had been considered as an orphan haplotype, the identification of the source rookery may be biased, and the conclusions of this study are probably unrealistic. Our study identified one individual with the rare haplotype EiA24 at the El Cuyo rookery, and considering the high frequencies of this

haplotype in the Cuba foraging aggregation, the contribution of Mexican rookeries to Cuban foraging aggregation will likely result in a different scenario than proposed by Pérez-Bermúdez et al. (2017) (Figure S3 in Supporting Information). This emphasizes the need to increase sampling in Mexican rookeries to possibly increase detection of haplotype EiA24, improving MSA resolution. Our results clearly show the connectivity between foraging aggregations from north-west Cuba and Mexican rookeries, and corroborate that the north coast of Cuba is an important migratory pathway for turtles moving to habitats on the southern Cuban shelf or to coastal waters of other countries (Moncada et al., 2006). Finally, our study confirms the large contribution Mexican rookeries make to the Turks and Caicos Islands foraging aggregations as previously suggested (Proietti et al., 2014; Pérez-Bermúdez et al., 2017).

4.4 Conservations implications

The conservation and management of the hawksbill turtle represents a great challenge as a result of its circumglobal distribution, long distance migrations, complex life-history, as well as the sharing of its resources on a wide geographical scale. The identification of which rookery groups compose a genetic stock, as well as which nearshore and oceanic habitats are utilized by a population, are fundamental aspects to developing long-term effective management strategies (FitzSimmons & Limpus, 2014). In this context, genetic tools are very useful in providing knowledge about marine turtle movements and highlighting the implications for the conservation of this species.

In Mexico, the hawksbill turtle is a priority species for conservation, making it the focus of many efforts to recover their populations (Hernández-Cortés, Nuñez-Lara, Cuevas, &

Guzmán-Hernández, 2018). Genetic information obtained in this study has identified two MUs in the Yucatan Peninsula, helping to establish the monitoring strategies and conservation purposes at an appropriate geographic scale to preserve the genetic stock with consideration to the specific threats in each MUs. Some protected nesting beaches of the northern Yucatan Peninsula are in danger of habitat loss or degradation due to the increasing pressure of urbanistic and touristic activities; so it is necessary to implement strategies that will help regulate the zoning to ensure the conservation of those areas (CONANP, 2016). In Campeche, nesting and foraging areas of hawksbill turtles represent a unique genetic stock for the Atlantic populations. However, this region has not yet been categorized as Protected Natural Areas, increasing the vulnerability of this already declining turtle species, hence it is imperative that these critical zones be protected under a federal decree (CONANP, 2009).

The genetic data, combined with the tagging and telemetry data, can provide important information to prioritize actions based on threats for nesting and foraging areas (FitzSimmons & Limpus, 2014). Our results showed that the majority of Mexican hatchings and juveniles that compose the Gulf of Mexico foraging aggregation where they are at risk from incidental catch. Indeed, artisanal fishing represents a significant threat for sea turtles in all of the Yucatan Peninsula region, as potential bycatch hotspots coincide with their important foraging grounds and migratory pathways (Cuevas, Guzmán-Hernández, Uribe-Martínez, Raymundo-Sánchez, & Herrera-Pavon, 2018). Moreover, the inappropriate fishing practices with artisanal longlines and gillnets are lethal for the sea turtles; in this sense, it is fundamental to establish collaborations with local fisherman to implement voluntary and official strategies as delimitation of no-take areas, temporal

restrictions, and low-bycatch fishing practices for the protection of sea turtles in the Yucatan Peninsula (Cuevas et al., 2018). In addition, our results emphasize the importance of conserving the Mexican foraging areas, especially along the Caribbean coasts, as critical habitats for hawksbill turtles migrating from international rookeries. For example, Cozumel Island is an important foraging area for juveniles (33-81 cm CCL) from Brazil, Barbados, and Puerto Rico. However, recent analysis at Cozumel (Cedeño-Vázquez, pers. comm. November 2017) have detected heavy metals and organochlorine contaminants which could affect the quality of foraging habitats and consequently some vital functions of sea turtles (van de Merwe, Hodge, Olszowy, Whittier, & Lee, 2010). Against this background, an effective coastal management strategy needs to be implemented based on identification and monitoring of the pollution source, established prevention, and mitigation measures (e.g., develop and maintain adequate wastewater treatment infrastructure, regulate sewage discharges, protect the remaining mangrove ecosystems) to reduce contamination of the Mexican Caribbean coastal zone (Metcalfe et al., 2011). This demonstrates the significance of mapping and understanding the connectivity network among rookeries and foraging aggregations of hawksbill turtles in the Atlantic region in order to determine and evaluate the interconnected impacts. Proietti et al. (2014) indicated that the foraging aggregations of hawksbills in Brazil are composed mainly of turtles from Brazilian rookeries; however, our results show that hawksbills born in Brazil also migrate to the Mexican Caribbean for feeding, so the threats affecting juveniles in the Mexican foraging aggregations could affect adult populations in Brazil. This emphasizes the importance of international collaboration in achieving effective management and conservation actions, such as reinforced monitoring of marine habitats quality, fishing control in hotspots of turtle migration and feeding areas,

and monitoring of the habitat quality, among others to protect this emblematic species in the Atlantic region.

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TABLE 1 Sample sites for hawksbill turtles from rookeries and foraging aggregations in the Yucatan Peninsula, Mexico. Abbreviations for localities (Abbrev), number of sampled turtles (N), geographic coordinates (GC).

Locality/State	Abbrev	N	CG	Collect season
Rookeries				
Chenkan/Campeche	CK	22	19°06” N, 91°01”W	2015-2016
El Cuyo / Yucatán	CU	24	21°30” N, 87°40” W	2016
Las Coloradas / Yucatán	CL	25	21°36” N, 87°58” W	2016
Holbox / Quintana Roo	HX	33	20°57” N, 87°25” W	2016
Foraging aggregations				
Punta Xen / Campeche	PX	43	19°09” N, 90°54” W	2013-2015
Isla Contoy / Quintana Roo	IC	7	21°30” N, 86°55” W	2015-2016
Cozumel / Quintana Roo	CO	37	20°18” N, 87°01” W	2014-2016
Banco Chinchorro / Quintana Roo	BC	34	18°29” N, 87°25” W	2014, 2016
Xcalak / Quintana Roo	XC	2	18°20” N, 87°40” W	2016

TABLE 2 Haplotype frequencies based on the ~740 bp control region fragment for hawksbill turtles from rookeries and foraging aggregations in the Yucatan Peninsula, Mexico. For localities abbreviations see Table 1.

Haplotypes			**Rookeries**						**Foraging aggregations**						
384 bp[a]	480 bp[b]	740 bp[c]	CK	CU	CL	HX	Total	%	PX	IC	CO	BC	XC	Total	%
A	CU1	EiA01	-	-	-	-	-	-	2	4	22	20	-	48	**39.0**
A	CU1	EiA51	-	-	-	-	-	-	-	-	2	-	-	2	1.6
alpha	G	EiA02	-	-	-	-	-	-	-	-	-	2	-	2	1.6
B	E	EiA03	-	-	-	-	-	-	-	-	-	1	-	1	0.8
F	C	EiA09	-	-	-	-	-	-	1	-	2	-	-	3	2.4
F	PR1	EiA11	-	-	-	-	-	-	2	2	5	8	-	17	**13.8**
Q	MX1	EiA23	-	21	21	29	71	**68.2**	17	-	1	1	-	19	**15.4**
Q	MX1	EiA41	15	1	1	1	18	**17.3**	9	1	-	-		10	8.1
Q	MX2	EiA24	-	1	-	-	1	0.96	2	-	1	-	-	3	2.4
Q	MX2	EiA43	-	-	-	-	-	-	-	-	1	-	-	1	0.8

[a]Bass et al. 1996
[b] Díaz-Fernández et al. 1999
[c] Leroux et al. 2012

P	MX3	EiA22	-	1	3	3	7	6.7	-	-	-	-	-	-	-
	q	EiA39	7	-	-	-	7	6.7	10	-	-	-	-	10	8.1
	n	EiA36	-	-	-	-	-	-	-	-	-	-	1	1	0.8
		EiA58	-	-	-	-	-	-	-	-	1	-	-	1	0.8
		EiA63	-	-	-	-	-	-	-	-	-	-	1	1	0.8
		EiA83	-	-	-	-	-	-	-	-	2	2	-	4	3.2
	Total		22	24	25	33	104	100	43	7	37	34	2	123	100

TABLE 3 Haplotype (*h*) and nucleotide (π) diversity from rookeries and foraging aggregations of *Eretmochelys imbricata* from the Yucatan Peninsula. Number of turtles sampled (N), standard deviation (SD), segregating sites (S), and number of haplotypes (N hap).

Localities	N	*h* (SD)	π (SD)	S	N hap
Rookeries					
Chenkan, Campeche (CK)	22	0.454 (0.077)	0.0006 (0.0006)	1	2
El Cuyo, Yucatan (CU)	24	0.239 (0.112)	0.0005 (0.0005)	3	4
Las Coloradas, Yucatan (CL)	25	0.290 (0.109)	0.0006 (0.0006)	2	3
Holbox, Quintana Roo (HX)	33	0.225 (0.091)	0.0005 (0.0005)	2	3
Total / Global value	104	0.504 (0.052)	0.0011 (0.0009)	4	5
Foraging aggregations					
Punta Xen, Campeche (PX)	43	0.756 (0.040)	0.0028 (0.0018)	13	7
Isla Contoy, Quintana Roo (IC)	7	0.666 (0.159)	0.0084 (0.0052)	12	3
Cozumel, Quintana Roo (CO)	37	0.633 (0.085)	0.0068 (0.0038)	15	9
Banco Chinchorro, Q. Roo (BC)	34	0.607 (0.077)	0.0068 (0.0038)	12	6
Xcalak, Quintana Roo (XC)	2	1.000 (0.500)	0.0177 (0.0180)	13	2
Total / Global value	123	0.794 (0.027)	0.0070 (0.0030)	19	15

TABLE 4 Pairwise F_{ST} comparison for hawksbill turtle rookeries in the Yucatan Peninsula, Mexico. F_{ST} values (below the diagonal) and *p*-value (above the diagonal). Chenkan (CK), El Cuyo (CU), Las Coloradas (CL), and Holbox (HX). Significant values are in bold.

Rookeries	CK	HX	CU	CL
CK	-	**< 0.001**	**< 0.001**	**< 0.001**
HX	0.673	-	0.846	0.990
CU	0.651	0.000	-	0.837
CL	0.626	0.000	0.000	-

TABLE 5 Pairwise F_{ST} comparisons for hawksbill turtle foraging aggregations in the Yucatan Peninsula, Mexico. F_{ST} values (below diagonal) and *p*-value (above diagonal). Campeche locality: Punta Xen (PX); Quintana Roo localities: Isla Contoy (IC), Cozumel (CO), Banco Chinchorro (BC), and Xcalak (XC). Significant values are in bold.

Foraging aggregations	PX	BC	CO	IC	XC
PX	-	**< 0.001**	**< 0.001**	**< 0.001**	**0.018**
BC	0.279	-	0.567	0.927	0.144
CO	0.269	0.000	-	0.702	0.108
IC	0.222	0.000	0.000	-	0.108
XC	0.192	0.000	0.000	0.000	-

FIGURE 1 Geographic distribution of haplotype frequencies (~740 bp fragment) at rookeries and foraging aggregations from the Yucatan Peninsula. Rookeries (circles) and foraging aggregations (squares). Campeche localities: Chenkan (CK), and Punta Xen (PX); Yucatan localities: El Cuyo (CU), Las Coloradas (CL), and Holbox (HX); and Quintana Roo localities: Isla Contoy (IC), Cozumel (CO), Banco Chinchorro (BC), and Xcalak (XC).

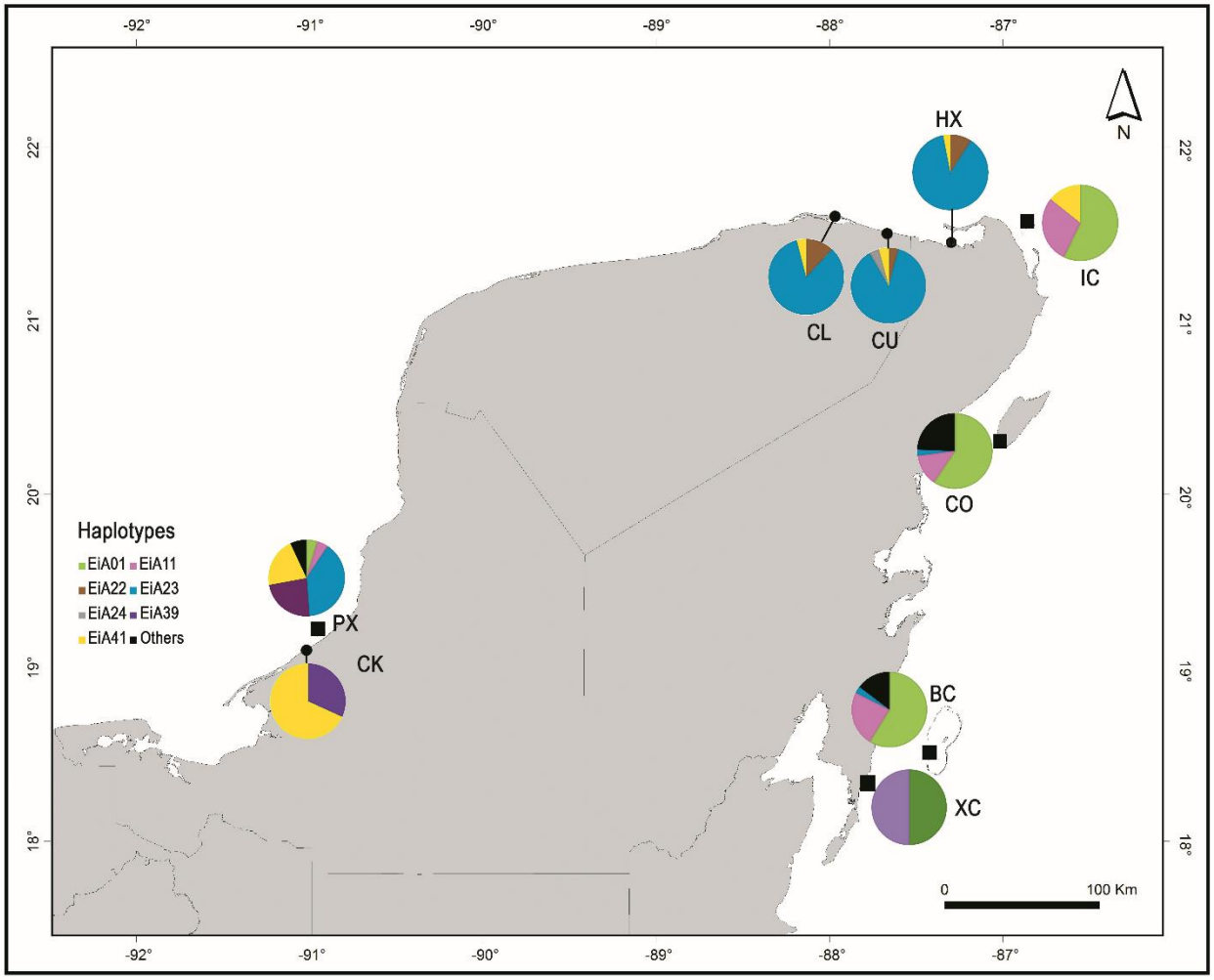
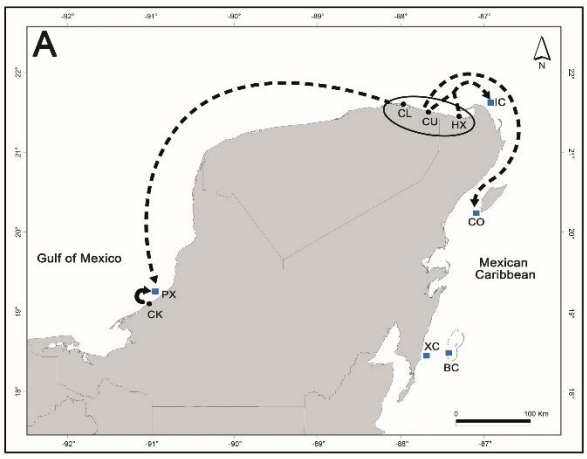
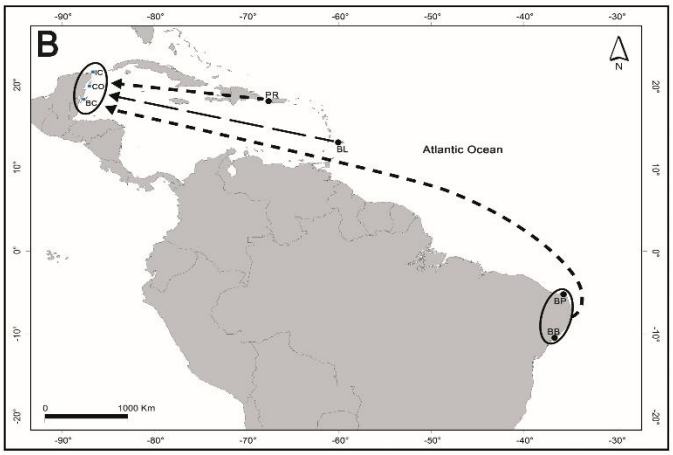


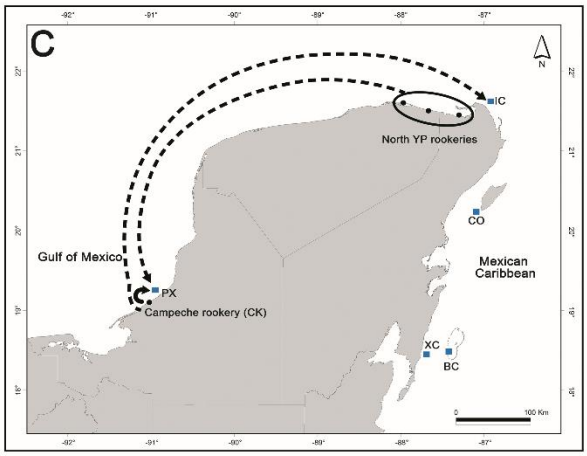
FIGURE 2 Many-to-many MSA result for Mexican hawksbill turtles. Rookeries (circles) and foraging aggregations (squares). **Foraging-ground centric**: (A) hawksbill rookeries in the Yucatan Peninsula region (CK = Chenkan, CU = El Cuyo, CL = Las Coloradas, and HX = Holbox) that contribute to the Mexican foraging aggregations (PX = Punta Xen, IC = Isla Contoy, CO = Cozumel, BC = Banco Chinchorro, XC = Xcalak), and (B) principal hawksbill rookeries in the Atlantic region (PR = Puerto Rico, BL = Barbados Leeward, BP = Brazil Pipa, BB = Brazil Bahia) that contribute to the Mexican foraging aggregations. **Rookery-centric**: (C) contribution of the Mexican rookeries to foraging aggregations in the Yucatan Peninsula region, and (D) contribution of the Mexican hawksbill turtles to foraging aggregations in the Atlantic region (KW = Key West Florida, PB = Palm Beach Florida, JR = Jardines del Rey Cuba, TC = Turks and Caicos). Mean percentage of the contributions (based in MSA results) are indicated by typography of arrows: short dashed line represents 10-19%, large dashed line represents 20-29%, and solid line shows a contribution above 30%.

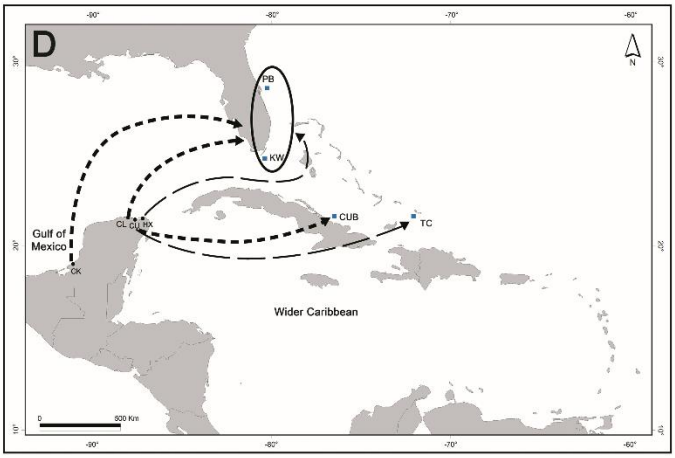
Foraging-ground-centric MSA





Rookery-centric MSA





SUPPORTING INFORMATION

Information about all localities considered in the many-to-many rookeries MSA (Table S1) and foraging aggregations MSA (Table S2) from the Atlantic; SAMOVA analysis for rookeries (TableS3) and foraging aggregations (Table S4); Foraging ground-centric many-to-many MSA estimates for the Atlantic foraging aggregations (Figure S1), Rookey-centric many-to-many MSA estimates for the Atlantic rookeries (Figure S2) and Foraging ground-centric MSA for Jardines del Rey (Cuba) without the haplotype EiA24 (Figure S3). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Table S1. Information about all localities considered in the many-to-many MSA for the Atlantic hawksbill rookeries. We considered only studies using the longer haplotype (~740 pb).

Locality/ Country (abbreviation)	Rookery size (nest/yr)	N	N Hap	*h*	π	References for haplotype frequencies	References for rookery size
Rookeries							
Chenkan, MX(CK)	338	22	2	0.454	0.0006	This study	Guzmán-Hernández pers. comm. Sep. 2017
Cuyo, MX (CU)	549	24	4	0.239	0.0005	This study	PRONATURA Península de Yucatán A.C pers. comm. Oct. 2017
Coloradas, MX (CL)	297	25	3	0.290	0.0006	This study	Cuevas et al. 2010
Holbox, MX (HX)	628	53	4	0.225	0.0005	This study/Leroux et al 2012	PRONATURA Península de Yucatán A.C pers. comm. Oct. 2017
Antigua (AN)	203	72	3	0.504	0.0179	Leroux et al. 2012	Velez-Zuazo et al. 2008
Barbados, Leeward (BL)	1504	54	1	0.000	0.0000	Browne et al. 2010	Velez-Zuazo et al. 2008
Barbados, Windward (BW)	150	30	3	0.476	0.0086	Browne et al. 2010	Velez-Zuazo et al. 2008
Brazil, Bahia (BB)	1345	66	4	0.362	0.0007	Lara Ruiz et al. 2006	Marcovaldi et al. 2007
Brazil, Pipa (BP)	1222	27	2	0.359	0.0005	Vilaça et al 2013	Santos et al. 2007
Costa Rica (CR)	25	60	7	0.655	0.0240	Leroux et al. 2012, ,	Velez-Zuazo et al. 2008
Cuba (CB)	130	70	5	0.213	0.0167	Leroux et al. 2012	Velez-Zuazo et al. 2008
Guadeloupe (GP)	151	74	4	0.131	0.0033	Leroux et al. 2012	Kamel & Delcroix 2009
Nicaragua (NIC)	205	95	5	0.612	0.0186	Leroux et al. 2012	Lagueux et al. 2003
Puerto Rico (PR)	740	109	7	0.600	0.0098	Velez-Zuazo et al. 2008	Velez-Zuazo et al. 2008
USVI (VI)	158	67	6	0.430	0.0101	Leroux et al. 2012	Velez-Zuazo et al. 2008
Dominican Republic Saona (DS)	100	15	5	0.089	0.0021	Carreras et al. 2013	Revuelta et al. 2012
Dominican Republic Jaragua (DJ)	15	33	6	0.054	0.0029	Carreras et al. 2013	Revuelta et al. 2012
Principe (PI)	125	20	1	0.000	0.0000	Monzón-Argüello et al. 2011	ATM 2014
Tobago (TO)	96	40	6	0.594	0.0063	Cazabon-Mannette et al. 2016	SOS 2015

1 N: Number of sampled turtles; N Hap: Number of haplotypes identified; *h*: haplotype diversity; π: nucleotide diversity

Table S2. Information about all localities considered in the many-to-many MSA for the Atlantic hawksbill foraging aggregations. We considered only studies using the longer haplotype (~740 pb).

Locality/ Country (abbreviation)	N	N Hap	*h*	π	References for haplotype frequencies
Foraging aggregations					
Punta Xen, MX (PX)	43	7	0.756	0.0028	This study
Isla Contoy, MX (IC)	7	3	0.666	0.0084	This study
Cozumel, MX (CO)	37	9	0.633	0.0068	This study
Banco Chinchorro, MX (BC)	34	6	0.607	0.0068	This study
Xcalak, MX (XC)	2	2	1.000	0.0177	This study
Jardines del Rey, CU (JR)	93	17	0.825	0.0435	Pérez-Bermúdez et al. 2017
Mona Island, PR (MI)	177	25	0.743	0.0068	Velez-Zuazo et al. 2008
Cape Verde Islands (CV)	28	6	0.529	0.0168	Monzón-Arguello et al. 2010
Turks and Caicos (TC)	38	8	Not available (NA)		Richardson et al. 2009
Palm Beach, Florida (PB)	112	17	NA		Wood et al. 2013
Key West, Florida (KW)	50	12	NA		Gorham et al. 2014
Ascencion (AS)	18	4	0.333	0.0148	Putman et al. 2014
Principe (PN)	80	3	0.143	0.0045	Monzón-Arguello et al. 2011
São Pedro and São Paulo, BR (BrP)	12	4	0.644	NA	Prioetti et al. 2014
Ceará coast, BR (BrC)	22	3	0.249	NA	Prioetti et al. 2014
Bahia coast, BR (BrB)	32	5	0.432	NA	Prioetti et al. 2014
Abrolhos Park, BR (BrA)	65	5	0.213	NA	Prioetti et al. 2014
Brazil South (BrS)	22	2	0.434	NA	Prioetti et al. 2014
Noronha/Rocas, BR (BrN)	94	11	0.516	0.0093	Vilaça et al. 2013
Tobago Leeward (TL)	17	7	0.838	0.0078	Cazabon-Mannette et al. 2016
Tobago Windward (TW)	47	8	0.588	0.0061	Cazabon-Mannette et al. 2016

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Table S3. SAMOVA analysis for rookeries of hawksbill turtle in the Yucatan Peninsula, Mexico. Localities from Campeche: Chenkan (CK), localities from Yucatan: El Cuyo (CU), Las Coloradas (CL), and localities from Quintana Roo: Holbox (HX).

Two groups: 1) CK, and 2) CU, HX, and CL					
Source of variation	**df**	**Sum of squares**	**Variance components**	**Percentage of variation**	***p* value**
Among groups	1	21.19	0.60	74.34	<0.001
Among populations within groups	2	0.13	-0.00	-0.68	<0.001
Within populations	100	21.55	0.21	26.34	<0.001
Total	103	325.38	3.19		
Three groups: 1) CK, 2) CU, and 3) HX and CL					
Among groups	1	21.29	0.34	62.22	<0.001
Among populations within groups	2	0.03	-0.00	-1.16	<0.001
Within populations	100	21.55	0.21	38.93	<0.001
Total	103	42.88	3.19		

Table S4. SAMOVA analysis for foraging aggregations of hawksbill turtle in the Yucatan Peninsula, Mexico. Localities from Campeche: Punta Xen (PX), and localities from Quintana Roo: Isla Contoy (IC), Cozumel (CO), Banco Chinchorro (BC), and Xcalak (XC).

Two groups: 1) Gulf of Mexico (PX), and 2) Mexican Caribbean (IC, CO, BC, XC)					
Source of variation	**df**	**Sum of squares**	**Variance components**	**Percentage of variation**	***p* value**
Among groups	1	80.42	1.45	42.39	<0.001
Among populations within groups	3	2.47	-0.07	-2.25	<0.001
Within populations	118	242.47	2.05	59.86	<0.001
Total	122	325.38	3.43		
Three groups: 1) XC, 2) PX, and 3) IC, CO and BC					
Among groups	2	82.14	1.38	41.20	<0.001
Among populations within groups	2	0.765	-0.07	-2.21	<0.001
Within populations	118	242.47	2.05	61.00	<0.001
Total	122	325.38	3.43		
Four groups: 1) PX, 2) IC, 3) CO and BC, and 4) XC					
Among groups	3	82.57	1.18	37.15	<0.001
Among populations within groups	1	0.33	-0.04	-1.52	<0.001
Within populations	118	242.47	2.05	64.38	<0.001
Total	122	325.38	3.19		

Figure S1. Foraging ground-centric many-to-many MSA estimates for Atlantic foraging aggregations. Source rookeries: AN = Antigua, BB = Brazil Bahia, BL = Barbados Leeward, BP = Brazil Pipa, BW = Barbados Winward, CB = Cuba, CK = Chenkan (MX), CL = Las Coloradas (MX), CR = Costa Rica, CU = El Cuyo (MX), DJ = Dominican Republic Jaragua, DS = Dominican Republic Saona, GP = Guadeloupe, HX = Holbox (MX), NIC = Nicaragua, PI = Principe, PR = Puerto Rico, TO = Tobago, VI = Virgin Island US.

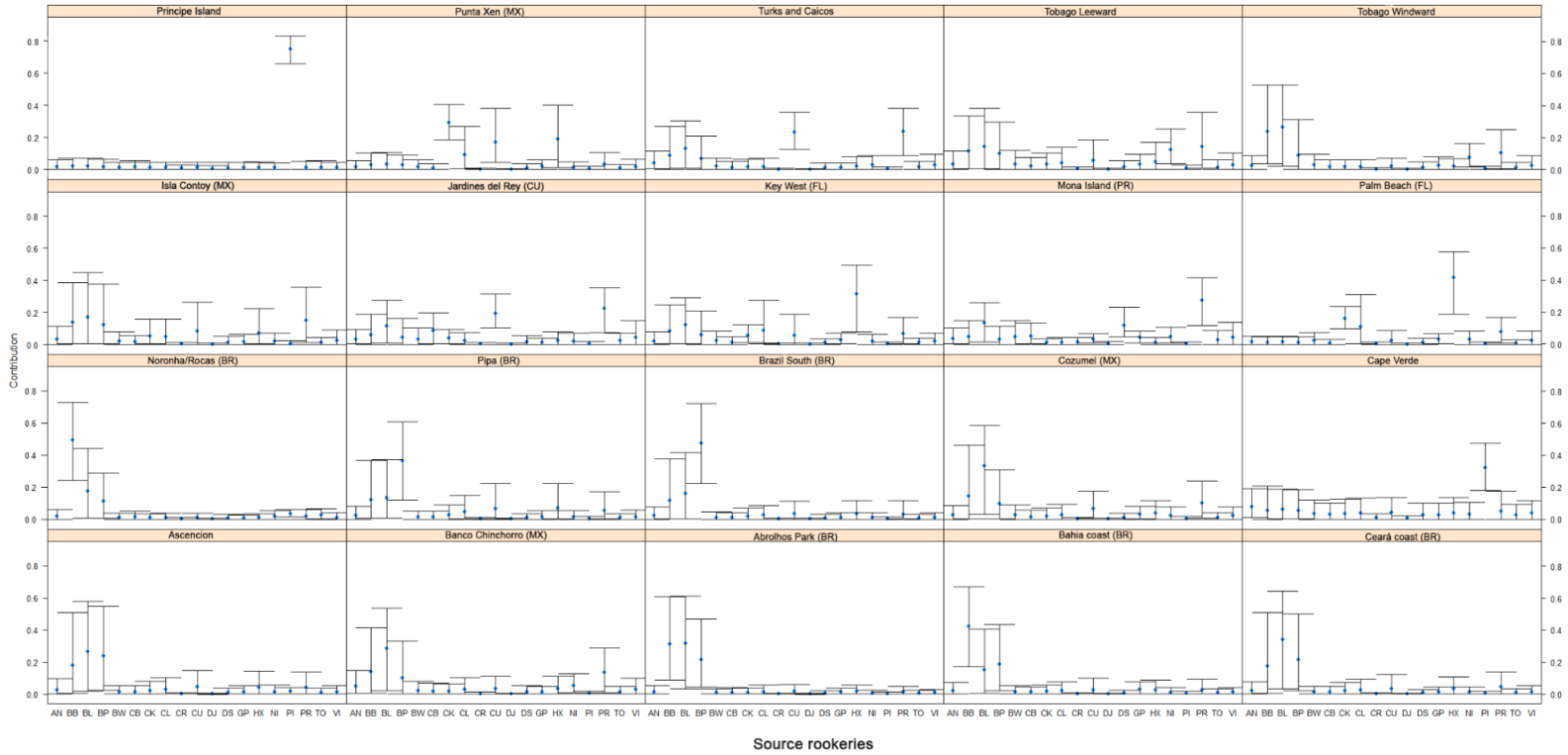


Figure S2. Rookery-centric many to many MSA estimates for Atlantic rookeries. Foraging Aggregations: As = Ascencion, BC = Banco Chinchorro (MX), BrA = Abrolhos Park (Brazil), BrB = Bahia (Brazil), BrC = Ceará Coast (Brazil), BrN = Noronha/Rocas (Brazil), BrP = São Pedro and São Paulo (Brazil), BrS = Brazil South, CO= Cozumel (MX), CV = Cape Verde Island, IC=Isla Contoy (MX), JR = Jardines del Rey (Cuba), KW = Key West (Florida), MI = Mona Island (Puerto Rico), PB = Palm Beach (Florida), PN = Principe, PX = Punta Xen (MX), TC = Turks and Caicos, TL = Tobago Leeward, TW = Tobago Winward, Unk = unknown

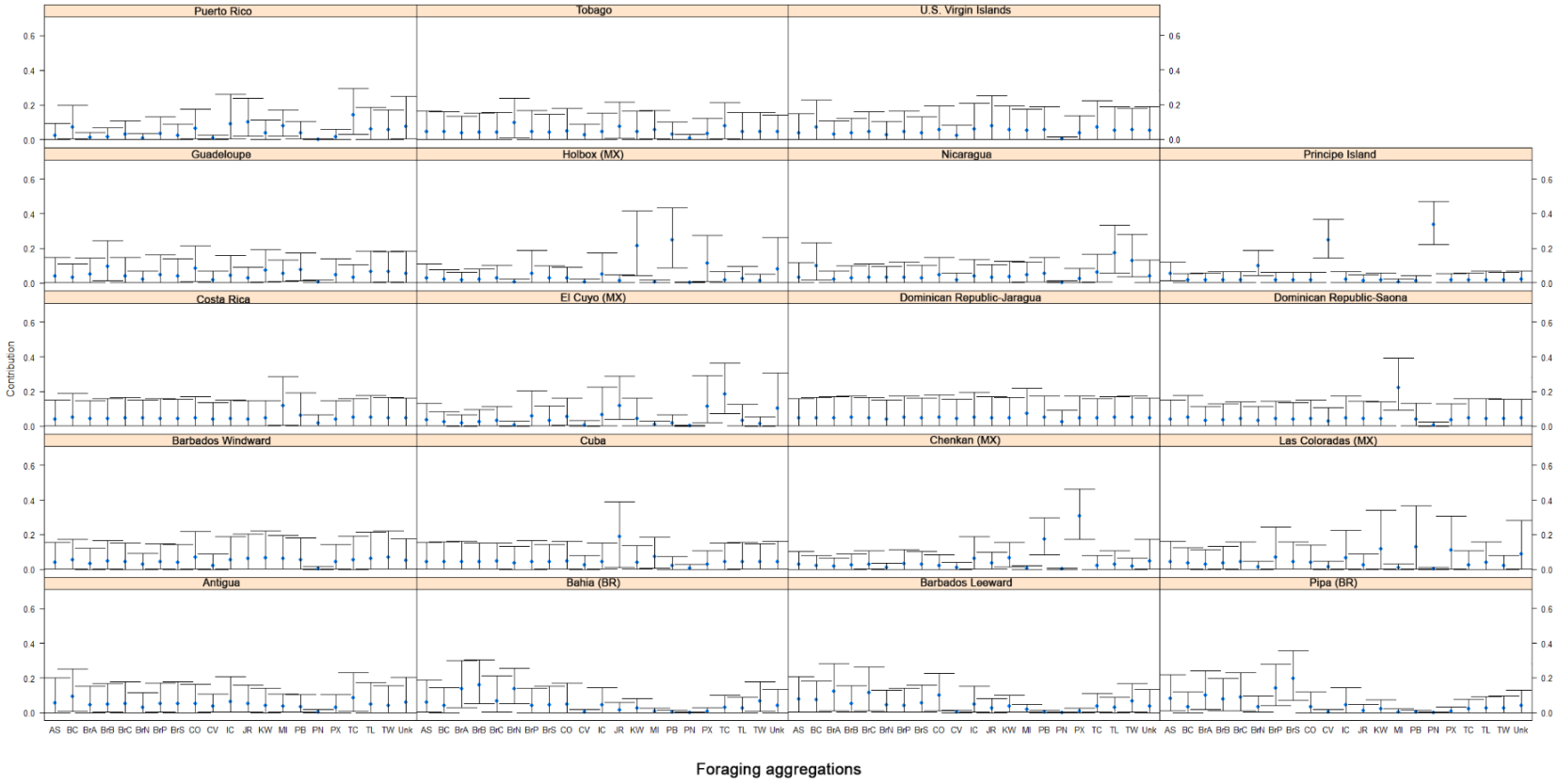
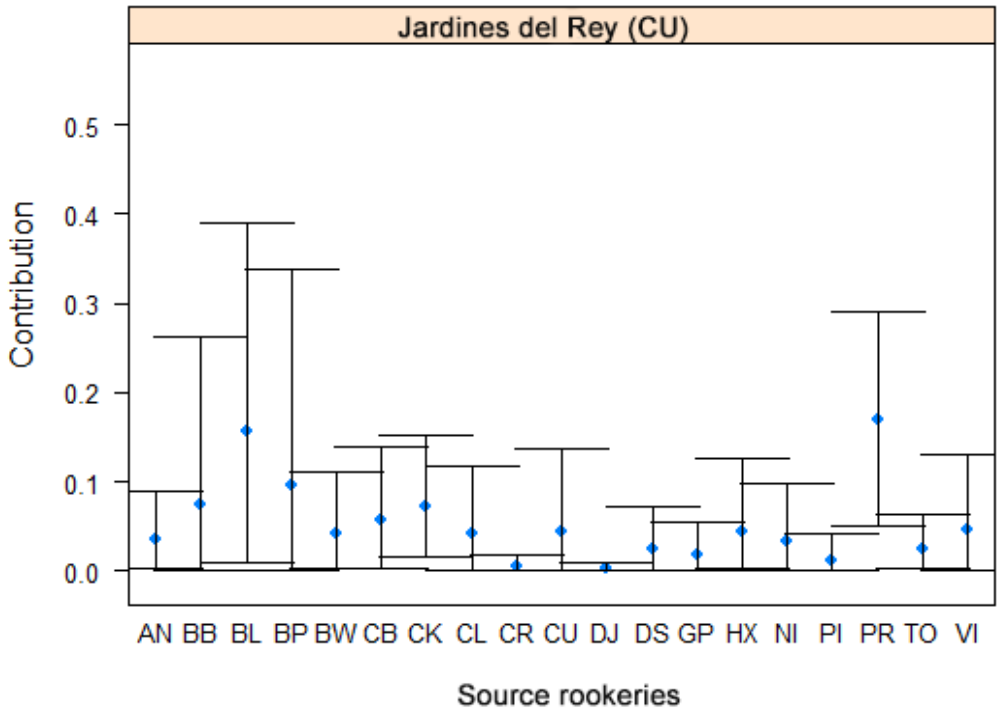


Figure S3. Foraging ground-centric many-to-many MSA estimates without haplotype EiA24 for Jardines del Rey, Cuba foraging aggregation. Source rookeries: AN = Antigua, BB = Brazil Bahia, BL = Barbados Leeward, BP = Brazil Pipa, BW = Barbados Winward, CB = Cuba, CK = Chenkan (MX), CL = Las Coloradas (MX), CR = Costa Rica, CU = El Cuyo (MX), DJ = Dominican Republic Jaragua, DS = Dominican Republic Saona, GP = Guadeloupe, HX = Holbox (MX), NIC = Nicaragua, PI = Principe, PR = Puerto Rico, TO = Tobago, VI = Virgin Islan



CAPÍTULO III

GENETIC STRUCTURE, DEMOGRAPHIC HISTORY AND MIGRATORY CONNECTIVITY OF MEXICAN GREEN TURTLE ROOKERIES AND FORAGING AGGREGATIONS IN THE YUCATAN PENINSULA

Artículo sometido para su publicación en la revista *Biodiversity and Conservation.*

Biodiversity and Conservation

GENETIC STRUCTURE, DEMOGRAPHIC HISTORY, AND MIGRATORY CONNECTIVITY OF MEXICAN GREEN TURTLE ROOKERIES AND FORAGING AGGREGATIONS IN THE YUCATAN PENINSULA

--Manuscript Draft--

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Abstract:	The green turtle undertakes long-distance migrations among nesting and foraging areas resulting in complex patterns of genetic structure and migratory connectivity. We used the mtDNA control region (~817 bp) to evaluate the genetic architecture of representative rookeries and foraging aggregations and identified migratory connectivity among green turtle populations from the Yucatan Peninsula and Gulf of Mexico. The Yucatan Peninsula rookeries presented the common haplotypes from the Great Caribbean region and six endemic haplotypes. Significant differentiation was revealed among southeastern Gulf of Mexico and Mexican Caribbean rookeries. Genetic composition of Mexican Caribbean foraging aggregations showed dominance of CM-A3.1 and CM-A1.1, and no significant genetic structure was detected within Mexican Caribbean foraging aggregations; however, when considering the Gulf of Mexico localities, significant genetic structure was revealed. Mix-stock analysis indicates a high contribution of local rookeries to Mexican Caribbean foraging aggregations and a substantial contribution of Quintana Roo rookeries to southern Florida foraging groups. Demographic analysis suggests that the genetic partition of rookeries is a result of contemporary processes such as natal homing and influence of ocean current patterns of the Yucatan Peninsula; however, high endemism in Mexican Caribbean rookeries could suggest that refugial population during the last glacial

	period could have include these rookeries. Furthermore, as with the connectivity patterns among rookeries and foraging groups, the mixing structure of foraging aggregations within the Mexican Caribbean is a consequence of the dynamic of oceanic currents along the Quintana Roo coast and Gulf of Mexico.
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GENETIC STRUCTURE, DEMOGRAPHIC HISTORY AND MIGRATORY CONNECTIVITY OF MEXICAN GREEN TURTLE ROOKERIES AND FORAGING AGGREGATIONS IN THE YUCATAN PENINSULA

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ABSTRACT

The green turtle undertakes long-distance migrations among nesting and foraging areas resulting in complex patterns of genetic structure and migratory connectivity. We used the mtDNA control region (~817 bp) to evaluate the genetic architecture of representative rookeries and foraging aggregations and identified migratory connectivity among green turtle populations from the Yucatan Peninsula and Gulf of Mexico. The Yucatan Peninsula rookeries presented the common haplotypes from the Great Caribbean region and six endemic haplotypes. Significant differentiation was revealed among southeastern Gulf of Mexico and Mexican Caribbean rookeries. Genetic composition of Mexican Caribbean foraging aggregations showed dominance of CM-A3.1 and CM-A1.1, and no significant genetic structure was detected within Mexican Caribbean foraging aggregations; however, when considering the Gulf of Mexico localities, significant genetic structure was revealed. Mix-stock analysis indicates a high contribution of local rookeries to Mexican Caribbean foraging aggregations and a substantial contribution of Quintana Roo rookeries to southern Florida foraging groups. Demographic analysis suggests that the genetic partition of rookeries is a result of contemporary processes such as natal homing and influence of ocean current patterns of the Yucatan Peninsula; however, high endemism in Mexican Caribbean rookeries could suggest that refugial population during the last glacial period could have include these rookeries. Furthermore, as with the connectivity patterns among rookeries and foraging groups, the mixing structure of foraging aggregations within the Mexican Caribbean is a consequence of the oceanic currents dynamic along the Quintana Roo coast and Gulf of Mexico.

KEY WORDS

Chelonia mydas, Management unit, mtDNA haplotypes, Mixed stock analysis, Genetic conservation, Mexico.

INTRODUCTION

The understanding of the genetic diversity distribution over small and wide geographical scales, as well as the processes influencing the genetic differentiation and interconnectivity among natural populations are important steps for successful species conservation (Avise 2000). In marine populations, the complex patterns of genetic diversity and its distribution among populations at a given time is not only the result of contemporary factors (e.g., behaviour, oceanographic features, dispersal capabilities; White et al. 2010; Piñeros and Gutierrez-Rodríguez 2017), but also reflects the footprints of historical processeses (e.g., patterns of historical population subdivision, long-distance dispersal, restricted gene flow, large-scale climatic fluctuations; Hewitt 2000). Consequently, the analysis of genetic structure provides a powerful tool for the detection of historic events producing contemporary genetic architecture and connectivity among populations (Bay et al. 2004).

Complex genetic population structure is common in marine organisms (White et al. 2010, Limborg et al. 2012), and results from mechanisms, such as long-distance dispersal connecting populations at large scale (oceanic basins) or the restriction of gene flow as a consequence of contemporary and historical processes (Palumbi 1994; Bay et al. 2004). Marine turtles are long-living vertebrates characterized by a complex genetic structure as a consequence of natal homing and natal site fidelity behaviors, long-distance migrations, and overlap populations in foraging areas and migratory corridors (Wallace et al. 2010). Natal homing and nest site fidelity represent the principal promoters of genetic differentiation and matrilineal lineage structure of the nesting populations (Bowen et al.

1992; Lee et al. 2007). Matrilineal structure reflects a significant divergence of mtDNA haplotype frequencies between nesting populations, to the extent that each could be considered as demographically distinct and functionally independent entities termed Management Units (MU; Moritz 1994; Shamblin et al. 2011).

Although many life-history characteristics are shared by marine turtles, contemporary genetic structure of rookeries differs among species and could reflect historical processes (Reece et al. 2005). During the Pleistocene, climatic variations resulted in sea-level changes that generated both population expansion (increases in sea-level favored genetic exchange) and contraction (reductions in sea-level resulted in genetic isolation) (Piñeros and Gutierrez- Rodríguez 2017) that could have originated in diverse patterns in the genetic diversity distribution of marine turtle species (Reece et al. 2005). Particularly, for tropical marine turtle species, the Pleistocene climatic changes caused subdivision and contraction of populations, but not yet enough to strongly erode genetic diversity (Reece et al. 2005). Dutton et al. (1999) proposed that in the tropical and subtropical regions, glacial periods reduced the availability of nesting habitats, thus confining the rookeries to equatorial refugia. Furthermore, extinctions and recolonization events during climatic oscillations could have prevented accumulation of extensive mutational separation, and accordingly, genetic differentiation among rookeries (Reece et al. 2005).

In foraging aggregations, long-distance migrations are an important life-history trait of marine turtles that influence genetic structure (Jensen et al. 2013). The juveniles disperse to oceanic or coastal feeding zones, helped by oceanic currents and swimming behavior (Putman and Mansfield 2015; Read et al. 2015), while adults migrate among reproductive

and forging areas, resulting in a 'mixed stock' composed of individuals from multiple rookeries and the ontogenetic stage (Jensen et al. 2013; Naro-Maciel et al. 2014). Factors such as nesting population size, geographic distance from source rookeries, natal foraging philopatry of juveniles (behaviour by which there is recruitment of juveniles to neritic waters near their natal beaches), and ocean currents likely influence foraging aggregation composition (Gaos et al. 2017; Naro-Maciel et al. 2017).

The green turtle, *Chelonia mydas* L. 1766 (Testudines, Cheloniidae) presents a circumglobal distribution, principally in tropical and subtropical waters of the Atlantic, Indian and Pacific oceans, in addition to the Mediterranean Sea (Seminoff et al. 2015). Due to a global decrease in population, *C. mydas* was classified under the category "endangered" (IUCN 2018). In Mexico, nesting activity have been reported in the Gulf of Mexico and in the Mexican Caribbean; the Yucatan Peninsula nesting population (including the states of Campeche, Yucatan, and Quintana Roo; Seminoff et al. 2015) is one of the five most important within the western Atlantic/Caribbean region (NMFS 2007).

The use of molecular markers has allowed an understanding of the geographical patterns of genetic diversity resulting from contemporary and historical processes (Diniz-Filho et al. 2008). In sea turtles, uniparental inheritance and non-recombining of mitochondrial DNA (mtDNA) has enabled the identification of matrilineal lineages in nesting populations (specifically genealogies traced by female ancestors back through time and shared by all individuals in contemporary populations), as well as their geographical distribution (Avise 2000). Several genetic studies in the Atlantic region have focused on understanding the relationship between genetic lineages and their geographic locations, providing insights of

140 the genetic structure of green turtle rookeries (Encalada et al. 1996; Reece et al. 2005;
141 Naro-Maciel et al. 2010). First analyses based on short fragments of mtDNA control region
142 (~486 bp) detected wide-scale genetic differentiation, with the separation of two lineages in
143 Atlantic nesting colonies: (1) Western Caribbean and Mediterranean Sea, and (2) Eastern
144 Caribbean, South Atlantic and West Africa (Lahanas et al. 1994; Encalada et al. 1996).
145 Despite evident wide-scale genetic segregation in this region, the fact that some mtDNA
146 haplotypes (based on the ~486 bp fragment) are widespread distributes and reported in high
147 frequencies among nesting populations, generated unclear genetic differentiation on a
148 geographical small-scale (Shamblin et al. 2017). The development of new primers has
149 allowed a longer fragment of mtDNA control region (~817 bp; Abreu-Grobois et al. 2006)
150 which has improved the resolution of genetic structure at a finer scale (Shamblin et al.
151 2015a). Additionally, determining whether haplotype sharing represents a historical genetic
152 signature or contemporary connectivity is the key to clarifying demographic processes and
153 connectivity of green turtle nesting populations of the Atlantic (Shamblin et al. 2015b).
154
155 The overlap of haplotypes among rookeries could lead to uncertain estimations of rookery
156 source contributions to mixed foraging aggregations obtained through the Bayesian mixed-
157 stock analysis (MSA; Bolker et al. 2007). Recent studies have evaluated the composition of
158 foraging aggregations in the northern region of the Gulf of Mexico (Naro-Maciel et al.
159 2017; Shamblin et al. 2017; 2018) and have highlighted some limitations for genetic
160 characterization of the green turtle foraging aggregations in this region such as: (1)
161 sampling gaps and underrepresentation of the source population baseline data for the ~817
162 bp mtDNA haplotypes for several rookeries from the Caribbean region (e.g., Mexico and
163 Cuba), and (2) based on ~486 bp fragment, two haplotypes (CM-A1 and CM-A3) dominate

164 the genetic profiles of the Gulf of Mexico rookeries (Mexico, Cuba, and Florida; Encalada
165 et al. 1996; Ruiz-Urquiola et al. 2010; Shamblin et al. 2015a).
166
167 In the Mexican green turtle rookeries, genetic composition has been defined by short
168 fragment of mtDNA control region (~486 bp). The Yucatan Peninsula rookeries showed a
169 high frequency of CM-A3 in the majority of localities sampled (Encalada et al. 1996;
170 Pérez-Ríos 2008; Millán-Aguilar 2008). Additionally, the endemic haplotypes CM-A22
171 and CM-A26 (Pérez-Ríos 2008) were reported in Mexican Caribbean localities while in the
172 Gulf of Mexico rookeries, the haplotypes CM-A27 and CM-A47 were identified (Millán-
173 Aguilar 2009). Furthermore, the coast of the Yucatan Peninsula has been identified as
174 providing important feeding areas for immature green turtles (CONANP 2012); however,
175 until now, these foraging aggregations have not been genetically characterized, leaving
176 unknown the origin or migratory pathways used by these juveniles.
177
178 In view of the aforementioned, the aim of this study is to evaluate the genetic structure of
179 rookeries and foraging aggregations of green turtles from the Yucatan Peninsula and
180 identify the migratory connectivity among foraging aggregations and source rookeries for
181 the green turtles of the Mexican Caribbean and Gulf of Mexico. To address this issue, we
182 used a ~817 bp fragment of mtDNA control region to characterize representative rookeries
183 from the Yucatan Peninsula region and foraging aggregations from the Mexican Caribbean,
184 with the following specific objectives: (i) to improve the knowledge of the green turtle
185 rookeries from the Yucatan Peninsula based on the larger mtDNA fragment, allowing an
186 improved insight of the magnitude of genetic variation among rookeries while building an
187 enhanced genetic dataset for the southeastern Gulf of Mexico and the Mexican Caribbean

188 rookeries, (ii) to define the genetic structure of rookeries from the Yucatan Peninsula, and
189 infer the influence of historical processes and/or contemporary connectivity on the genetic
190 architecture of Yucatan Peninsula green turtle rookeries, (iii) to determine the natal sources
191 of green turtles that compose the foraging aggregations of the Mexican Caribbean and to
192 evaluate the migratory connectivity among the Gulf of Mexico region, and finally (iv) by
193 resolving the fine-scale genetic structure for rookeries and foraging aggregation in the
194 Yucatan Peninsula, we are able to identify management units for the Yucatan Peninsula
195 green turtle populations with the future aim of defining management and conservation
196 priorities for this species.
197

198 # MATERIALS AND METHODS

199

200 **Sample collection**

201

202 A total of 165 tissue samples were obtained from females nesting at nine rookeries along
203 the Yucatan Peninsula coast, Mexico during May-October 2015 and 2016 (Fig 1a and Table
204 1), and 168 samples were collected in six foraging aggregations at the Mexican Caribbean
205 during water-monitoring activities using nets, snorkeling, or SCUBA diving (Fig 1b and
206 Table 1). Tissues were obtained from the edge of the front flipper using a 3 mm biopsy
207 punches and preserved in a salt-saturated 20% DMSO solution (Shamblin et al. 2012) at
208 4°C until molecular analysis. All individuals were measured (curved carapace length: CCL)
209 (Bolten 2000) and marked with inconel tags (National Band and Tag Co. 681) on the right
210 flipper for identification and to avoid duplicate samples.

Laboratory analysis

Genomic DNA was extracted using the Wizard® Genomic DNA Purification Kit (PROMEGA) following the animal tissue protocol. Polymerase chain reaction (PCR) amplifications of a ~817 bp fragment of the mtDNA control region were conducted using the primers LCM15382 (5'-GTC TAA CCC TAA AGC ATT GG-3') and H950g (5'-GTC TCG GAT TTA GG GGT TT-3') (Abreu-Grobois et al. 2006). PCR amplifications were carried out in a 25 µl reaction volume following the protocol described by Shamblin et al. (2015a). The quality of amplifications was verified by electrophoresis on 2% agarose gel in 1X TAE Buffer using a 100 bp DNA ladder (PROMEGA) as molecular weight marker for confirmation of the amplified fragments length. PCR products were purified and sequenced by MACROGEN INC (Seoul, South Korea).

DNA sequence analysis

Haplotype identification and gene diversity

Sequences were edited and aligned using BIOEDIT 7.2.5 (Hall 1999). We compared the sequences obtained to previously described haplotypes and classification was based on nomenclature published on the Archie Carr Center for Sea Turtle Research (ACCSTR) website (https://accstr.ufl.edu/resources/mtdna-sequences) for the longer control region fragment (~817 bp). Gene diversity was assessed for rookeries and foraging aggregations by estimating the haplotype (h) and nucleotide (π) diversity for each locality and over whole data set (named global value) using ARLEQUIN 3.5 (Excoffier and Lischer 2010).

235 *Genetic structure*

236

237 Population genetic structure was evaluated (1) among the rookeries from the Yucatan
238 Peninsula (data from this study), (2) among the foraging aggregations from the Mexican
239 Caribbean (data from this study), and (3) among foraging aggregations from the Mexican
240 Caribbean and Gulf of Mexico (Texas, Shamblin et al. 2017; southern Florida, Naro-Maciel
241 et al. 2017; northeast of Gulf of Mexico, Shamblin et al. 2018). These analyses were
242 performed through pairwise conventional F-statistics (F_{ST}) based on haplotype frequencies
243 (significance *P* values were obtained by computing 10,000 random permutations) and exact
244 test of population differentiation (conducted with 100,000 permutations and 10,000
245 dememorization steps). Additionally, we carried out an analysis of molecular variance
246 (AMOVA; Excoffier et al. 1992) testing different scenarios to optimize the percentage of
247 variation, with aim of identifying the number of management units for the Yucatan
248 Peninsula rookeries (data from this study), and for the foraging aggregations from the Gulf
249 of Mexico (data from Naro-Maciel et al. 2017; Shamblin et al. 2017, 2018) and Mexican
250 Caribbean (data from this study). All of these analyses were performed in ARLEQUIN 3.5.

251

252 *Demographic history of the Yucatan Peninsula rookeries*

253

254 Tajima's D (Tajima 1989) and Fu's Fs (Fu 1997) tests (10,000 replicates) were used to
255 assess how our data fit to the neutral hypothesis. To estimate the patterns of historical
256 population expansion or contraction, we performed a mismatch distribution among pairwise
257 differences of mtDNA control region, under constant population size and population
258 growth-decline models. Goodness of fit was assessed by raggedness index (*rg*; Harpending

et al. 1993) and Ramos-R_2 statistic (Ramos-Onsins and Rozas 2002), and finally, *P* value was calculated by parametric bootstraps (10,000 replicates). All of these analyses were performed using DNASP 5.10.1 (Librado and Rozas 2009).

Because mtDNA is maternally inherited, the effective female population size (N_{ef}) can be calculated using $\theta = 2N_{ef}\nu$ (Tajima 1993), where theta (θ) is estimated from the relationship between the number of segregating sites and sample size under the infinite-site model (Watterson 1975), where the parameter ν was calculated by $m\mu$ where *m* is the sequence length and μ the mutation rate per generation. We used the mutation rate estimated by Formia et al. (2006) for the control region of sea turtles at 0.01751 substitutions/site per million years and generation time estimated for the Yucatan Peninsula populations of 41 years (Seminoff 2004). The historical effective female population size (prior to population expansion/decline) was calculated from initial theta (θ_i), and the timing of expansion/decline events was estimated by the relation $T = \tau/2\nu$, where τ is the population expansion/decline time in mutation units and ν was described above.

Mixed stock analysis (MSA)

We performed a many-to-many Bayesian MSA using the "mixstock" package in *R* 3.4.1 (Bolker et al. 2007) considering haplotype frequencies from rookeries and foraging aggregations characterized only by ~817 bp haplotype data. *Foraging-ground-centric analysis* allowed estimate the stock contributions from the Gulf of Mexico and Yucatan Peninsula rookeries to the Mexican Caribbean foraging aggregations, while the *rookery-*

282 *centric analysis* assessed to which Gulf of Mexico and the Mexican Caribbean foraging
283 aggregations migrate the individuals born in the Yucatan Peninsula region. We included
284 genetic data published for rookeries from Florida, USA (Shamblin et al. 2015a), Aves
285 Island, Venezuela and Galibi, Suriname (Shamblin et al. 2012), and Mexico (Pérez-Ríos
286 2008, Millán-Aguilar 2009; Shamblin et al. 2017) including new dataset of nine Yucatan
287 Peninsula rookeries (this study), and foraging aggregations from the Gulf of Mexico
288 (Texas, Shamblin et al. 2017; southern Florida, Naro-Maciel et al. 2017; and the northeast
289 Gulf of Mexico, Shamblin et al. 2018) and from the Mexican Caribbean (this study). In
290 addition, the nesting population size (estimated annual females) was included in the
291 analysis as an ecological covariate assuming that potential contribution is proportional to
292 the relative size of the rookery (Tables S1-S3).
293
294 # RESULTS
295
296 **Haplotype identification and gene diversity**
297
298 A total of 333 tissue samples were collected for rookeries and foraging aggregations from
299 the Yucatan Peninsula, from which 19 haplotypes were identified (Tables 2 and 3). In the
300 rookeries of the Yucatan Peninsula, 15 haplotypes were identified; CM-A3.1 was reported
301 in high frequencies (67%) in all localities sampled, followed by CM-A1.2 as the second
302 most abundant (7%); finally, CM-A22.1 and CM-A26.1 were reported in lesser proportions
303 for nesting females (5% each). Any remaining haplotypes was considered as rare (< 3%). In
304 the Mexican Caribbean foraging aggregations, 16 haplotypes were identified; as
305 demonstrated with the rookeries samples, the CM-A3.1 was the most abundant haplotype

306 (63%), followed by CM-A1.1 (14%), CMA5.1 (8%), and CM-A26.1 (4%). The rest of
307 haplotypes were identified in less than 3% of samples.
308
309 Haplotype and nucleotide diversity in the rookeries varied from higher values (h = 0.952,
310 and π = 0.0046) in Sian Ka'an (SK, Mexican Caribbean) to lowest values (h = 0.000, and π
311 = 0.000) in El Cuyo and Las Coloradas (CU and CL respectively, Gulf of Mexico) (Table
312 4). When management units were considered, gene diversity was higher for the Mexican
313 Caribbean than the Gulf of Mexico rookeries (Table 4). Gene diversity of foraging
314 aggregations showed a high value (h = 0.738 and π = 0.0040) in Punta Sacrificio, and a
315 much lower value (h = 0.0000 and π = 0.0000) for Banco Chinchorro and Chiquila, with
316 global values of h = 0.548 and π = 0.0031 (Table 4).
317
318 **Genetic structure**
319
320 Pairwise F_{ST} revealed high and significant genetic differentiation for pairs of rookeries
321 between the Gulf of Mexico and the Mexican Caribbean (Table 5). When two regional
322 groups were considered, the F_{ST} value was highly significant (F_{ST} = 0.153, $P < 0.0001$).
323 The AMOVA showed the highest percentage of variation (20%) when two regional groups
324 were considered for the green turtle rookeries: (1) the Gulf of Mexico and (2) the Mexican
325 Caribbean (Table S4).
326
327 No genetic structure was identified among foraging aggregations in the Mexican Caribbean
328 (Table S5), but a significant genetic differentiation among the Mexican Caribbean and the
329 Gulf of Mexico foraging aggregations (southern Florida, northeast Gulf of Mexico and

Texas; Table 6) were shown. AMOVA indicated weak (4%), but significant genetic structure when considering four MU: (1) Mexican Caribbean, (2) Texas, (3) southern Florida, and (4) northeast Gulf of Mexico (Table S6).

Demographic history of the Yucatan Peninsula rookeries

Although Tajima's D and Fu's Fs neutrality test showed negative values in almost all rookeries from the Yucatan Peninsula (except Isla Aguada and Isla Contoy), these values were never significant (Table 7). For the mismatch distributions, Sian Ka'an and Aventuras DIF rookeries were excluded due to small sample size, while El Cuyo and Las Coloradas were excluded because these were fixed for a unique haplotype (CM-3.1). The mismatch distributions were made considering all remaining rookeries as single genetic stock, and considering two MU (Gulf of Mexico and Mexican Caribbean) previously defined by pairwise F_{ST} and AMOVA. Under the two models, multimodal distribution was observed when all rookeries were considered as single unit and in the stock of Mexican Caribbean rookeries, whereas the mismatch distribution was bimodal in the group conformed by rookeries of the Gulf of Mexico (Fig S1). We reported high values of raggedness and R_2 index for all rookeries which discard the population expansion model (Table 7).

Contemporary effective female population size was generally high (N_{ef} > 3000) for rookeries with the exception of Holbox and Isla Aguada which presents a lower values; Isla Contoy presented the highest value. If we considered the whole dataset as a single unit (global value) the population size remained high (Table 7), and for the two previously identified management units the Mexican Caribbean rookeries showed higher values (N_{ef} =

3927 females), while the Gulf of Mexico presented low values (N_{ef} = 361 females). Based on mismatch distributions, estimated values for θ initial was lower than the theta per sequence values in all rookeries from the Yucatan Peninsula, consequently, historical N_{ef} were lower than contemporary N_{ef} (Table 7). Finally, timing of demographic change was estimated from 11,000 to 33,000 years ago for the different rookeries from the Yucatan Peninsula (Table 7).

Mixed stock analysis (MSA)

Foraging-ground centric

Our results allowed inferring the natal origins of 165 individuals (98%) of foraging aggregations from the Mexican Caribbean. Three turtles were identified with orphan haplotypes (haplotypes found only in foraging aggregations, which cannot be tracked back to source rookeries): CM-A3.8 (Velez-Zuazo X. unpublished), CM-A52.1 (Shamblin B. unpublished), and CM-A73.1 (Naro-Maciel E. unpublished), and consequently these samples were excluded from analyses to avoid bias in the MSA.

Foraging-ground MSA showed for the Mexican Caribbean foraging aggregations that (1) Akumal and Isla Contoy localities were composed by a mix of individuals from the Gulf of Mexico rookeries (15% from Isla Aguada and 15% from El Cuyo) and from the Mexican Caribbean rookeries (15% from Xcacel-Xcacelito and 15% from Sian Ka'an), (2) Punta Sacrificios showed important contributions of nearby rookeries as Xcacel-Xcacelito (22%)

and Sian Ka'an (20%), and lesser proportion from Isla Contoy rookery (10%), (3) Xcalak foraging aggregation was composed of individuals from the Gulf of Mexico rookeries (Isla Aguada and El Cuyo with contributions of ~16% and 11%, respectively) and the Mexican Caribbean rookeries (Xcacel-Xcacelito with 13%), and finally (4) Banco Chinchorro and Chiquila revealed a major contribution from Xcacel-Xcacelito (19%) and Isla Aguada (16%) (Fig 2). Other localities analyzed in this study as Florida, Aves Island and Suriname rookeries reported very low contributions to Caribbean Mexican foraging aggregations (< 3%).

Rookery-centric MSA

Estimations of rookery-centric showed the contributions of (1) Gulf of Mexico rookeries to Caribbean Mexican foraging aggregations, mainly to Punta Sacrificios (~20%), Isla Contoy (~16%), and Akumal and Xcalak (~9% each), (2) northern Quintana Roo rookeries to Mexican Caribbean foraging aggregations such as Punta Sacrificio (~23%), Akumal (~15%), and Chiquila (10%), (3) central Quintana Roo rookeries contributes to closer foraging aggregations as Akumal (~25%), Isla Contoy (~10%), and Punta Sacrificios (10%), furthermore, high contributions to southern foraging groups in Banco Chinchorro (~40%) and Xcalak (25%) were identified (Fig 3a).

Rookery-centric MSA for the Gulf of Mexico foraging aggregations (Fig 3b) showed that (1) Texas received major contributions from the Mexican Caribbean rookeries (40%) and less from eastern Gulf of Mexico (28%), (2) southern Florida foraging aggregations were composed of individuals from the Mexican Caribbean rookeries (34%) with a lower

401 proportion from the Gulf of Mexico (25%), and (3) northeast Gulf of Mexico foraging
402 aggregations showed a mixed contribution from the Gulf of Mexico and the Mexican
403 Caribbean rookeries (25% and 40%, respectively).
404
405 # DISCUSSION
406
407 ## Rookeries
408
409 Haplotype composition of green turtle rookeries from the Yucatan Peninsula presented
410 notable differences among the Gulf of Mexico and the Mexican Caribbean localities. This
411 could be explained considering the probable patterns of historical expansion (Reece et al.
412 2005) that occurred from Caribbean rookeries to the populations of the Gulf of Mexico.
413 These rookeries may have been colonized recently in green turtle evolutionary history, and
414 this is supported by low gene diversity of rookeries in the Gulf of Mexico, a consequence
415 of bottleneck or founder events (Encalada et al. 1998). Six endemic haplotypes were found
416 in the Yucatan Peninsula rookeries of which four (CM-A16.1, CM-A17.1, CM-A22.1 and
417 CM-A26.1) are found exclusively in Quintana Roo (Encalada et al. 1996, Pérez-Ríos 2008)
418 and occurred in representative frequencies in central Quintana Roo rookeries, mainly
419 Xcacel- Xcacelito and Sian Ka'an. The presence of CM-A22.1 in Mexican Caribbean
420 rookeries, clarify the origin of this orphan haplotype, which only has been reported in
421 Texas foraging aggregations (Shamblin et al. 2017). According to Millán-Aguilar (2009)
422 and supported by our results, CM-A18.1 could be exclusive to Gulf of Mexico rookeries,
423 whereas CM-A18.2 is endemic to the Yucatan Peninsula rookeries and is probably the

variant identified by Encalada et al. (1996) in Xcacel and Cozumel rookeries These endemic haplotypes represent a genetic signature that allow the identification of turtles in Atlantic foraging aggregations that were born on the coast of the Yucatan Peninsula.

The haplotype CM-A1.4 found in five females from Quintana Roo rookeries has previously been reported in one female in a Florida rookery (Melbourne locality; Shamblin et al. 2017), what could indicate that Mexican Caribbean rookeries could be a source of this haplotype. This hypothesis is supported by the currents oceanic patterns, favoring the movements of females from the Mexican Caribbean to Florida waters (Méndez et al. 2013). In addition, evidence of mark-recapture data showed few recoveries of females tagged in Florida at locations outside of this locality (Seminoff et al. 2015). Two rare haplotypes (CM-A5.1 and CM-A27.1) were identified in the Yucatan Peninsula rookeries. CM-A5.1 was reported previously in low frequencies in Mexican rookeries (Encalada et al. 1996; Millán-Aguilar 2009), but has been reported in high frequencies in Venezuela, Suriname, and Costa Rica (Encalada et al. 1996). Consequently, its presence in Mexican rookeries could be the signal of historical migration from South Atlantic glacial refugia to Great Caribbean rookeries. This hypothesis is supported by the clinal distribution of CM-A5, with high frequencies in the South Atlantic and low in northern rookeries (Millán-Aguilar 2009). Haplotype CM-A27 was identified as endemic for Cuba (Guanahacabibes Peninsula; Ruiz-Urquiola et al. 2010); nevertheless, it has been reported in Mexican rookeries (Arrecife Alacranes in Millán-Aguilar 2009; and Xcacel in this study). Therefore, its presence in green turtle rookeries from the Yucatan Peninsula could be explained by the patterns of ocean currents in the region, which generate connectivity between the northwestern coast of Cuba (Guanacahabibes Peninsula) and the Mexican Caribbean (Carricart-Ganivet &

448 González-Díaz 2009), allowing sporadic arrivals of Cuban females at nesting beaches of
449 the Yucatan Peninsula.
450
451 Our results of pairwise F_{ST} and AMOVA analysis supported population differentiation
452 among the Gulf of Mexico and the Mexican Caribbean rookeries, which is consistent with
453 evidence reported by Pérez-Ríos 2009. This genetic partition could be the result of
454 contemporary factors (e.g., female nesting behaviour and the ocean currents patterns) and
455 historical processes (e.g., population expansion, historical population subdivision). Reece et
456 al. (2005) suggested that the natal homing can affect the dispersal patterns of maternal
457 lineages in marine turtles and determine the geographical scale of genetic differentiation in
458 each species. However, some studies in green turtles have showed discrepancies in
459 establishing the geographic scale at which natal homing defines the genetic structure of the
460 rookeries, either demographically isolated rookeries are separated by large distances (> 500
461 km), or genetic differentiation is evident in rookeries separated by very short distances
462 (Bowen and Karl 2007; Shamblin et al. 2015a). Although these discrepancies could
463 contradict the hypothesis of female natal philopatry to explain the genetic structure of green
464 turtle rookeries, this inconsistency is a possible effect of molecular marker resolution used
465 to evaluate genetic differentiation. Leroux et al. (2012) suggested that longer mtDNA
466 sequences are more informative for describing the genetic variation among populations
467 than short sequences, thus are more probable to resolve genetic structure at finer
468 geographical scales. In addition, the ocean current patterns represent other important factor
469 that can influence the genetic structure of marine turtle rookeries (Reis et al. 2010). The
470 isolation of the Gulf of Mexico rookeries appears to be driven by the influence of the
471 Yucatan Current and Loop Current (Centurioni and Niiler 2003). This hypothesis is

supported by previous observations identifying an oceanographic break at the North Yucatan Peninsula as for populations of the Queen conch (*Strombus gigas*) (Paris et al. 2006; Machkour-M'Rabet et al. 2017).

The genetic segregation identified among North and South of the Atlantic green turtle nesting areas is consistent either using mitochondrial or nuclear markers, and could denote the influence of historical events as glacial refugia and recolonization processes (Encalada et al. 1996; Naro-Maciel et al. 2010; 2014). Contemporary genetic structure of the Mexican Caribbean green turtle rookeries could be explained based on glacial refugia hypothesis; our data suggest that Mexican Caribbean rookeries (principally the central region of Quintana Roo) might have been part of Caribbean refugial population proposed by Reece et al (2005) and Naro-Maciel et al. (2014), and high gene diversity in these rookeries could represent remnants of gene diversity of ancestral populations (Lahanas et al. 1994; Formia et al. 2006). We proposed this hypothesis considering that the Mexican Caribbean rookeries fit the model proposed by Maggs et al. (2008) for identifying refugial populations and understanding post-glacial colonization processes considering: (1) presence of a ancestral haplotype CM-A3.1 reported in high frequencies in Mexican Caribbean rookeries, (2) Mexican Caribbean rookeries reported very high values of endemic (or private) haplotypes compared with others in the Great Caribbean localities, and (3) our results showed low gene diversity in the Gulf of Mexico rookeries which could be evidence that this region was recolonized by females originating from the Caribbean populations. Our results of mismatch distribution do not support the population expansion model, however, gene diversity values in the Gulf of Mexico rookeries (low values of h and π) could be result of recent colonization evidencing the few mtDNA lineages (Grant and Bowen 1998). A

similar pattern was observed in loggerhead turtle rookeries, Encalada et al. (1998) proposed a likely colonization pathway occurred in a northerly direction along the west coast into the Gulf of Mexico, resulting in reduced haplotype diversity in recently colonized nesting areas due to bottleneck or founder events. Estimates of the most recent population expansions from these refugia range from 10,000 to 18,000 ya for green turtle Atlantic nesting populations (Naro-Maciel et al. 2014) which is congruent with the timing of demographic change of Quintana Roo rookeries which was estimated at 16,776 ya (Table 7).

Foraging aggregations

The genetic composition of the Mexican Caribbean presented dominance of the common haplotype of western Atlantic-Mediterranean nesting populations (CM-A3 and CM-A1; Encalada et al. 1996). CM-A3.1 is the widest distributed haplotype in the Great Caribbean region (Encalada et al. 1996; Bjorndal et al. 2006, Ruiz-Urquiola et al. 2010; Shamblin et al. 2017), whereas CM-A1 (includes variants CM-A1.1 and CM-A1.2) is an endemic haplotype of Florida rookeries (Shamblin et al. 2017). Furthermore, low-proportions of haplotype CM-A5, characteristic of Venezuela and Surinam (Encalada et al. 1996), were found principally in Isla Contoy, Punta Sacrificios, and Xcalak foraging aggregations, which may indicate that turtles originating from Southern rookeries migrate to foraging aggregations localized at higher latitudes. Finally, Mexican endemic haplotypes were found in low proportions in the Mexican Caribbean foraging grounds which corroborate that turtles born in the Yucatan Peninsula rookeries migrate to foraging habitats in Florida and northeast Gulf of Mexico waters (Naro-Maciel et al. 2017; Shamblin et al. 2018). Haplotype and nucleotide diversity of Caribbean Mexican foraging aggregations were

520 higher compared with a Brazilian foraging aggregation (Costa-Jordao et al. 2015), but
521 lower (only for haplotype diversity) than southern Florida foraging aggregations (Dry
522 Tortugas and Everglades National Park; Naro-Maciel et al. 2017). This pattern of high
523 genetic diversity has been reported in hawksbill turtle foraging aggregations in the Atlantic
524 basin, and is common in genetically diverse assemblages conformed by individuals from
525 many rookeries (Velez-Zuazo et al. 2008).
526
527 Genetic homogeneity reported in the Mexican Caribbean foraging aggregations is
528 consistent with others genetic studies in marine species from this region (Paris et al. 2006;
529 Machkour-M'Rabet et al. 2017; Labastida-Estrada et al. in press). The lack of genetic
530 structure appears to be associate with high regional connectivity along Quintana Roo coast
531 generate by the Yucatan Current (Paris et al. 2006). Nevertheless, when we evaluated the
532 genetic differentiation in a wide geographic scale (Gulf of Mexico *vs* Mexican Caribbean),
533 significant genetic structure was observed despite dominance of CM-A1.1 and CM-A3.1 in
534 the haplotype profiles of foraging aggregations analyzed. These results suggest that the
535 genetic structure among foraging aggregations are spatially correlated with the genetic
536 composition of rookeries (mainly observed in the Mexican Caribbean and Florida
537 populations), what had been reported previously for Atlantic loggerhead turtle populations
538 (Bowen et al. 2004), and eastern Pacific hawksbills turtles (Gaos et al. 2017). Although the
539 potential mechanisms that generates this pattern could include oceanic currents,
540 geomagnetic imprinting, and other factors, several studies have suggested that the juveniles
541 distribution and genetic structure of foraging ground are strongly determinated by natal
542 foraging philopatry (Bowen et al. 2004; Naro-Maciel et al. 2012; Gaos et al. 2017).
543

544 In view of the aforementioned, define the genetic structure at fine geographic scale in
545 foraging aggregations is complex principally due to overlap of haplotypes with high
546 frequencies; it is therefore necessary improve the resolution genetic valuations through
547 genomic sequencing of abundant and widely distributed haplotypes as CM-A3.1 and CM-
548 A1.1 to identify additional informative variation as it has been demonstrated in juvenile
549 populations from the northern Gulf of Mexico (Shamblin et al. 2017, 2018).
550
551 **Mixed Stock Analysis (MSA)**
552
553 Foraging-ground centric MSA estimations suggest important migratory connectivity among
554 critical habitats of green turtles of the Yucatan Peninsula (small-scale) as well as between
555 rookeries and foraging aggregations within the Gulf of Mexico and Mexican Caribbean
556 (wide-scale). Our results shown that Mexican Caribbean foraging grounds are used by
557 turtles originating from Campeche and Yucatan rookeries (Gulf of Mexico), which
558 coincides with the migration pathways observed through satellite tracking studies in the
559 Yucatan Peninsula region (Cuevas et al. 2012; Méndez et al. 2013). These tracking satellite
560 results and genetic data brought to light the presence of important foraging areas in the
561 Mexican Caribbean, and suggested that the northern area of the Yucatan Peninsula
562 represents a valuable migratory corridor for green and hawksbill turtles (Cuevas et al. 2012;
563 Méndez et al. 2013; Labastida-Estrada et al. in press). The connectivity patterns within the
564 Mexican Caribbean showed a closely linked relationship between rookeries and foraging
565 aggregations, which could be explained considering the following factors: (1) genetic
566 homogeneity among foraging aggregations in this region suggests that self- recruitment
567 processes into these areas is influenced by mixing of juveniles (Velez-Zuazo et al. 2008),

(2) the effect of the Yucatan Current, a strong current originating from the Caribbean Current and flowing along the Yucatan Peninsula (Carrillo et al. 2015), facilitating mixed distribution of juveniles originating from rookeries within the Mexican Caribbean or from others distant rookeries (e.g. Costa Rica), and finally (3) the potential role of philopatry to foraging areas during juvenile state has been reported in green turtles and could explain the use of foraging grounds in proximity to natal rookeries (Gaos et al. 2017). In this context, this dispersal pattern reported for green turtles in Mexican Caribbean foraging aggregations is consistent with those observed in some studies in Eastern Pacific hawksbills, which suggested that the role of natal foraging philopatry, combined with ocean currents and swimming behavior (Naro-Maciel et al. 2012; Shamblin et al. 2018), could provide a better explanation for the dispersal patterns of juveniles than open-ocean dispersal theory (Gaos et al. 2012, 2017).

Considering a large geographic scale, connectivity patterns among northern Gulf of Mexico foraging aggregations and the Yucatan Peninsula rookeries are consistent with other studies (Naro-Maciel et al. 2017; Shamblin et al. 2017, 2018). Our results shown that Mexican green turtle rookeries contribute substantially to the foraging aggregations of southern Florida, which could be explained principally by oceanic currents of the region and swimming behavior (Naro-Maciel et al. 2017; Shamblin et al. 2017). The green turtles originating from the Mexican Caribbean rookeries travel alongside the Quintana Roo coast through the Yucatan Current and enter into the Gulf of Mexico waters where the orientation of the Loop Current generates a deviation to Florida (Méndez et al. 2013; Shamblin et al. 2017). This migration pathway concurs with satellite tracking studies which reported that green turtles migrating from the Mexican Caribbean cross the Gulf of Mexico until arriving

592 at foraging aggregations localized at southern Florida (Garduño et al. 2000; Cuevas et al.
593 2012; Méndez et al. 2013).
594
595 Although this study showed some connectivity among North Gulf of Mexico foraging
596 aggregations (Texas and northeast Gulf of Mexico) and Mexican Caribbean rookeries, other
597 studies have demonstrated that the principal source of green turtles to these foraging
598 aggregations originates from western Gulf of Mexico rookeries such as Rancho Nuevo,
599 Tamaulipas (Mexico), which is supported by tag data, oceanic currents patterns, and
600 dispersal patterns of neritic juvenile Kemp´s ridleys turtles (*Lepidochelys kempii*) along the
601 Gulf of Mexico coast of the United States (Sturges and Blaha 1976; Shamblin et al. 2017).
602 This case illustrates the inaccurate results that could be generated by an overlap of abundant
603 and widespread haplotypes, and suggest that inferences about contributions of source
604 rookeries to foraging aggregations must be interpreted with care considering the following:
605 (1) important nesting populations (e.g., Cuba) do not have a complete baseline for 817 bp
606 haplotype data, which generates a bias in MSA estimations and draws incomplete
607 conclusions related to the migratory connectivity in the region, (2) small populations of the
608 Great Caribbean, such as Belize, have not been genetically characterized, however, it is
609 likely that turtles originating in these rookeries contribute to Mexican foraging aggregations
610 (assumption supported by the capture of a juvenile tagged in Belize in the Isla Contoy
611 foraging aggregation), and (3) the overlap of CM-A3.1 and CM-A1.1 haplotypes among
612 potential source rookeries could produce unrealistic results. Although use of an ecological
613 covariant, such as rookery size, to evaluate contributions has been an effective strategy to
614 minimize this kind of bias generated by the poor resolution of molecular markers, an
615 improvement in the resolution of genetic structure at small geographic scale is essential,

616 developing tools such as mitogenomic sequences and identifying SNPs (single nucleotide
617 polymorphisms) that provide more variations and increase the robustness of mixed stock
618 analysis.
619
620 **Conservation implications**
621
622 Significant genetic differentiation among the Gulf of Mexico and the Mexican Caribbean
623 green turtle rookeries defines two independent management units in the Yucatan Peninsula,
624 which is fundamental for management and conservation purposes. Our results highlight the
625 importance of the Mexican Caribbean rookeries for their level of gene diversity and the
626 presence of endemic haplotypes, important in terms of protection of these rookeries that
627 represent remnants of ancestral gene diversity for the species (Lahanas et al. 1994).
628 Nevertheless, the central and northern parts of Quintana Roo, important nesting habitats for
629 green turtles, are subject to considerable anthropogenic pressures principally the
630 accelerated growth of the tourism industry (for over 40 years), generating a significant loss
631 of natural marine habitats including the nesting beaches used by several sea turtle species
632 (de la Esperanza et al. 2017). For example, a recent study in Kanzul beach (a locality with
633 high nesting density on the central coast of Quintana Roo) had detected that nesting activity
634 is disturbed by tourist presence, artificial beachfront lighting (causing disorientation of
635 females) and by the installation of beach furniture hindering the movement of females or
636 hatchlings on the beach (de la Esperanza et al. 2017). In view of the biological importance
637 of these rookeries, the establishment of strategies that control and mitigate the
638 environmental impact of tourism activities on critical habitats used by sea turtles in the
639 Mexican Caribbean region is fundamental.

Understanding the connectivity patterns among rookeries and foraging aggregations of the Yucatan Peninsula region may highlight local threats to green turtle foraging grounds (e.g., by-catch) which are extremely valuable during the life cycle of turtle species. Conservation and management actions could be then focused on those particular areas and contribute to the protection of green turtles in the Mexican Caribbean. Our study supports the results based on satellite tracking, which suggests that the northern Yucatan Peninsula is an important migratory corridor (Cuevas et al. 2012), connecting the Great Caribbean with the Gulf of Mexico. Therefore, the protection of foraging habitats of the Yucatan Peninsula is fundamental for the conservation of marine turtles in this region, and requires international collaboration, cooperation, and effective decision-making from the Mexican government.

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Figure captions

Figure 1. Sampling site location and mtDNA control region haplotype frequencies (~ 817 pb fragment) for green turtle rookeries of the Yucatan Peninsula (A) and foraging aggregations (B). The solid line shows the possible genetic break among Gulf of Mexico and Mexican Caribbean rookeries. For localities abbreviation see Table 1.

Figure 2. Foraging-ground centric MSA result for Mexican green turtle populations. Rookeries (circles) and foraging aggregations (squares). Yucatan Peninsula rookeries (IA: Isla Aguada, CU = El Cuyo, IC = Isla Contoy, XC-XT: Xcacel-Xcacelito, and SK: Sian Ka'an) that contribute to the Mexican Caribbean foraging aggregations (CO: Isla Contoy, AK: Akumal, PS: Punta Sacrificios, BC: Banco Chinchorro, and XL: Xcalak).

Figure 3. Rookery centric MSA result for Mexican green turtle populations. Rookeries (circles) and foraging aggregations (squares). Contributions of the Yucatan Peninsula rookeries to Mexican Caribbean foraging aggregations (CH: Chiquila, CO: Isla Contoy, AK: Akumal, PS: Punta Sacrificios, BC: Banco Chinchorro, and XL: Xcalak) (A), and contributions of the Yucatan Peninsula rookeries to Gulf of Mexico foraging aggregations (TX: Texas, NGM: northeast of Gulf of Mexico, and SFL: Southern Florida) (B).

Figure 1

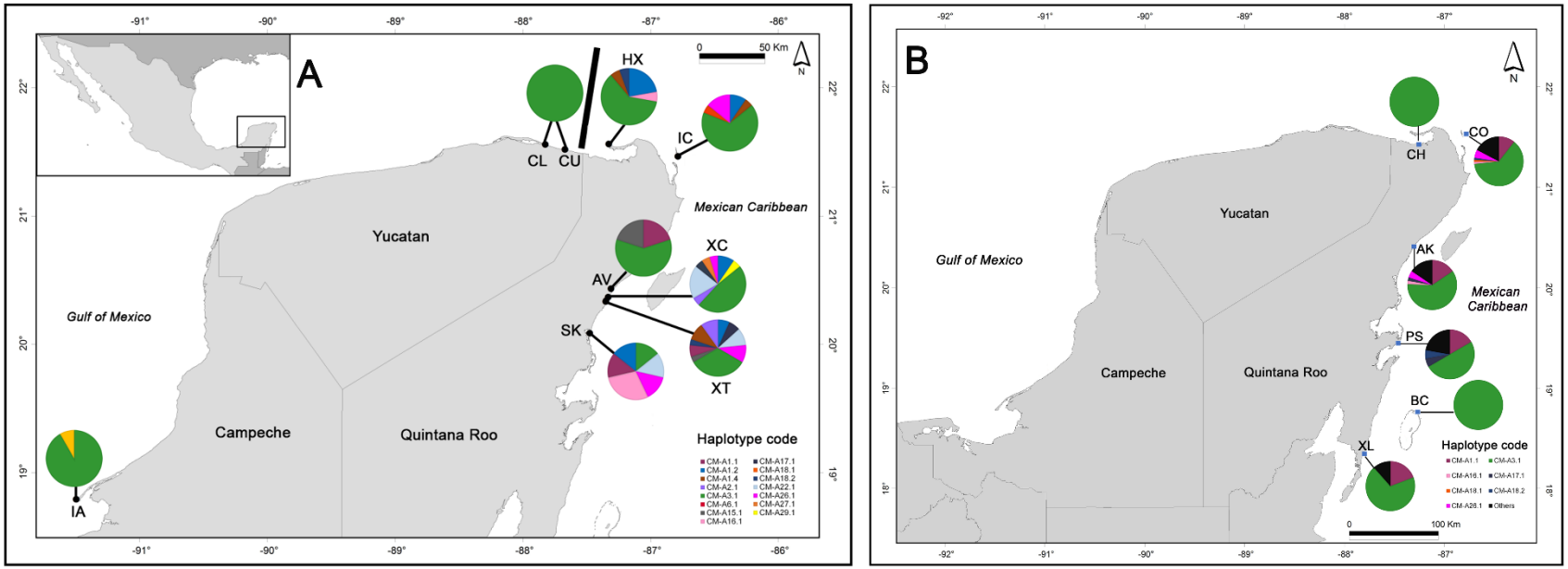
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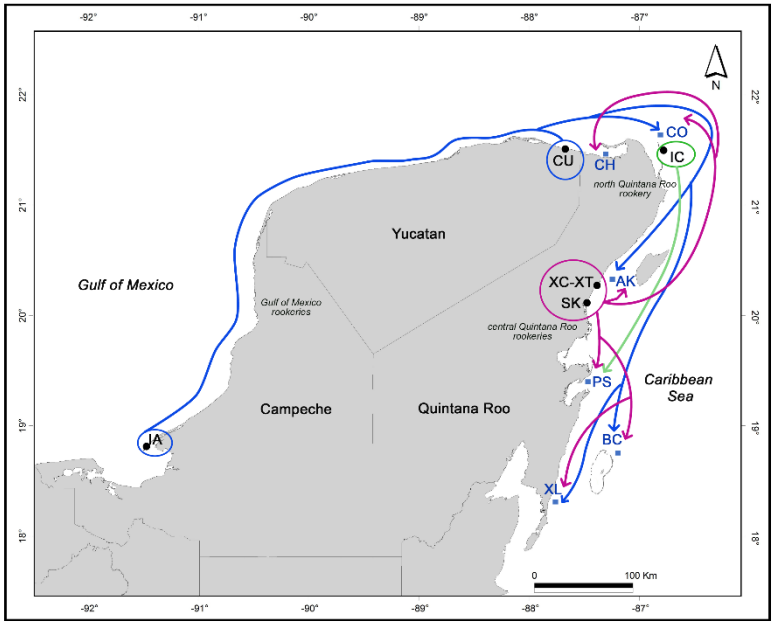
Figure 2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925 **Figure 3**

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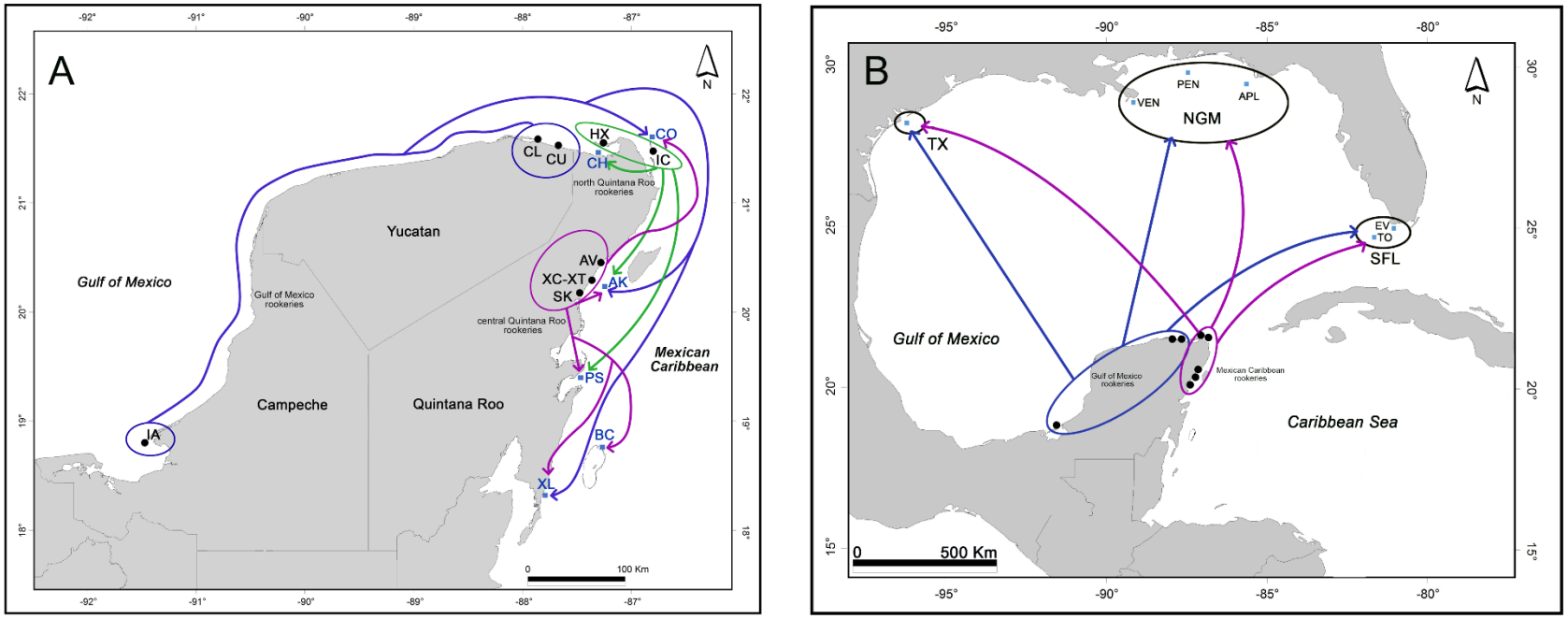

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931 **Table 1**. Sample sites for green turtle rookeries and foraging aggregations from the Yucatan
932 Peninsula, Mexico. N: size sample; GC: geographic coordinates. Note: Sian Ka'an locality
933 includes samples from Kanzul and Caapechen nesting beaches.

Code	Locality / State	N	Collection year	GC
		Rookeries		
IA	Isla Aguada, Campeche	24	2015, 2016	18°47'31"N, 91°29'46"W
CU	El Cuyo, Yucatan	26	2016	21°31'00"N, 87°40'10"W
CL	Las Coloradas, Yucatan	13	2016	21°33'17"N, 87°49'26"W
HX	Holbox, Quintana Roo	18	2016	21°33'33"N, 87°19'36"W
IC	Isla Contoy, Quintana Roo	21	2015	21°27'46"N, 86°47'07"W
XC	Xcacel, Quintana Roo	21	2015, 2016	20°20'18"N, 87°20'53"W
XT	Xcacelito, Quintana Roo	30	2015, 2016	20°19'58"N,87°21'00"W
AV	Aventuras DIF, Quintana Roo	5	2016	20°21'58"N, 87°19'54"W
SK	Sian Ka'an, Quintana Roo	7	2016	20°05'09"N, 87°28'35"W
		Foraging aggregations		
AK	Akumal, Quintana Roo	45	2014-2016	20°23'46"N, 87°18'48"W
BC	Banco Chinchorro, Q. Roo	2	2016	18°44'27"N, 87°15'08"W
CH	Chiquila, Quintana Roo	2	2014	not available
CO	Isla Contoy, Quintana Roo	75	2015, 2016	21°30'36"N, 86°55'36"W
PS	Punta Sacrificios, Q. Roo	18	2014, 2015	19°27'37"N, 87°27'04"W
XL	Xcalak, Quintana Roo	26	2016	18°17'27"N,87°49'14"W

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936 **Table 2**. Mitochondrial DNA control region haplotype frequencies for the Yucatan Peninsula
937 green turtle rookeries. Highest values are in bold. For abbreviation localities see Table 1.
938 Haplotype nomenclature corresponds to longer fragment mtDNA control region (~817 bp).
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Haplotype	IA	CU	CL	HX	IC	AV	XC	XT	SK	Total	%
CM-A1.1	-	-	-	-	-	1	-	2	1	4	3
CM-A1.2	-	-	-	4	2	-	2	2	1	**11**	**7**
CM-A1.4	-	-	-	1	1	-	-	3	-	5	3
CM-A2.1	-	-	-	-	-	-	1	3	-	4	2
CM-A3.1	22	26	13	11	14	3	10	10	1	**110**	**67**
CM-A5.1	-	-	-	-	1	-	-	-	-	1	0.6
CM-A15.1	-	-	-	-	-	1	-	1	-	2	1
CM-A16.1	-	-	-	1	-	-	-	-	2	3	2
CM-A17.1	-	-	-	-	-	-	1	2	-	3	2
CM-A18.1	2	-	-	-	-	-	-	-	-	2	1
CM-A18.2	-	-	-	1	-	-	-	1	-	2	1
CM-A22.1	-	-	-	-	-	-	4	3	1	**8**	**5**
CM-A26.1	-	-	-	-	3	-	1	3	1	**8**	**5**
CM-A27.1	-	-	-	-	-	-	1	-	-	1	0.6
CM-A29.1	-	-	-	-	-	-	1	-	-	1	0.6
N Total	**24**	**26**	**13**	**18**	**21**	**5**	**21**	**30**	**7**	**165**	**100**

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Table 3. Mitochondrial DNA control region haplotype frequencies for the Yucatan Peninsula green turtle foraging aggregations. Highest values are in bold. For abbreviation localities see Table 1. Haplotype nomenclature corresponds to longer fragment mtDNA control region (~817 bp).

Haplotype	AK	BC	CH	CO	PS	XL	Total	%
CM-A1.1	7	-	-	8	3	5	23	**14**
CM-A1.2	1	-	-	3	1	-	5	3
CM-A2.1	-	-	-	-	-	1	1	0.6
CM-A3.1	27	2	2	47	9	18	105	**63**
CM-A3.8	-	-	-	1	-	-	1	0.6
CM-A5.1	5	-	-	6	2	1	14	**8**
CM-A13.1	-	-	-	-	-	1	1	0.6
CM-A16.1	1	-	-	1	-	-	2	1
CM-A17.1	1	-	-	-	1	-	2	1
CM-A18.1	-	-	-	1	-	-	1	0.6
CM-A18.2	-	-	-	1	1	-	2	1
CM-A26.1	2	-	-	4	-	-	6	4
CM-A27.1	-	-	-	2	-	-	2	1
CM-A29.1	-	-	-	1	-	-	1	0.6
CM-A52.1	1	-	-	-	-	-	1	0.6
CM-A73.1	-	-	-	-	1	-	1	0.6
N total	45	2	2	75	18	26	168	100

950 **Table 4**. Summary of population genetic statistics for rookeries and foraging aggregations of
951 green turtles from the Yucatan Peninsula. For abbreviated name of rookeries see Table 1. GM-
952 UM: Gulf of Mexico management unit, MC-MU: Mexican Caribbean management unit, N:
953 number of samples, *h:* haplotype diversity, π: nucleotide diversity, SD: standard deviation, *S:*
954 segregating sites, N hap: number of haplotypes.
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Locality	N	*h* (SD)	π (SD)	*S*	N hap
Rookeries					
IA	24	0.159 (0.094)	0.0003 (0.0004)	2	2
CU	26	0.000 (0.000)	0.0000 (0.000)	0	1
CL	13	0.000 (0.000)	0.0000 (0.0000)	0	1
HX	18	0.601 (0.112)	0.0018 (0.0013)	7	5
IC	21	0.547 (0.118)	0.0025 (0.0016)	14	5
AV	5	0.700 (0.218)	0.0040 (0.0024)	2	3
XC	21	0.752 (0.086)	0.0040 (0.0024)	13	8
XT	30	0.862 (0.046)	0.0036 (0.0021)	15	10
SK	7	0.952 (0.095)	0.0040 (0.0030)	11	6
GM-MU	63	0.062 (0.041)	0.0001 (0.0001)	2	2
MC-MU	102	0.744 (0.042)	0.0032 (0.0020)	24	14
Global value	165	0.546 (0.046)	0.0022 (0.0002)	24	15
Foraging aggregations					
AK	45	0.613 (0.074)	0.0035 (0.0021)	16	8
BC	2	0.000 (0.000)	0.0000 (0.0000)	0	1
CH	2	0.000 (0.000)	0.0000 (0.0000)	0	1
CO	75	0.591 (0.063)	0.0029 (0.0017)	17	11
PS	18	0.738 (0.098)	0.0040 (0.0024)	15	7
XL	26	0.498 (0.103)	0.0017 (0.0013)	13	5
Global value	168	0.584 (0.041)	0.0031 (0.0018)	20	16

Table 5. Pairwise comparisons of genetic differentiation based on 817 bp fragment among Mexican Caribbean and Gulf of Mexico green turtle rookeries. Pairwise F_{ST} value below the diagonal and pairwise exact test of population differentiation *P* values above the diagonal. Locality abbreviations: Isla Aguada (IA), El Cuyo (CU), Las Coloradas (CL), DIF Aventuras (AV), Xcacel (XC), Xcacelito (XT), Sian Ka'an (SK), Holbox (HX), and Isla Contoy (IC). Significant values are indicated in bold.

	IA	CU	CL	AV	XC	XT	SK	HX	IC
IA	-	0.023	0.531	**0.003**	**0.004**	**0.050**	**0.004**	**<0.001**	**<0.001**
CU	0.048	-	-1.00	**<0.001**	**0.001**	**0.022**	**<0.001**	**<0.001**	**<0.001**
CL	0.006	0.000	-	0.089	0.276	0.063	0.118	0.073	**<0.001**
AV	**0.212**	**0.529**	**0.353**	-	0.317	0.313	0.150	0.153	**0.021**
XC	**0.200**	**0.311**	**0.244**	<0.001	-	0.212	0.183	0.212	**0.012**
XT	**0.246**	**0.335**	**0.261**	<0.001	<0.001	-	0.340	0.829	0.520
SK	**0.522**	**0.701**	**0.566**	0.057	0.049	0.002	-	0.638	0.139
HX	**0.152**	**0.277**	**0.187**	<0.001	0.014	0.048	0.130	-	0.259
IC	**0.097**	**0.203**	0.130	<0.001	0.025	0.058	0.180	<0.001	-

Table 6. Pairwise comparisons of genetic differentiation based on 817 bp fragment among Mexican Caribbean and Gulf of Mexico green turtle foraging aggregations. Pairwise F_{ST} value below the diagonal and pairwise exact test of population differentiation *P* values above the diagonal. Locality abbreviations: Mexican Caribbean (MC), southern Florida (SF), northeast Gulf of Mexico (NGM), and Texas (TX). Significant values are indicated in bold.

	MC	**SF**	**NGM**	**TX**
MC	-	**0.022**	**<0.001**	**<0.001**
SF	0.007	-	**<0.001**	**<0.001**
NGM	**0.030**	**0.009**	-	**0.032**
TX	**0.077**	**0.033**	0.008	-

Table 7. Demographic history parameters for green turtle rookeries from the Yucatan Peninsula. For abbreviated name of rookeries see Table 1. GM-UM: Gulf of Mexico management unit, MC-MU: Mexican Caribbean management unit, *D*: Tajima's D, *Fs*: Fu's Fs, *rg*: raggedness index, R_2: Ramos-Onsins and Rozas statistic, θ: theta per sequence, θ_0: theta initial per sequence, N_{ef}: contemporary effective female population size, N_{ef} h: historical effective female population size (after the population growth or decline), τ (tau): expansion/decline time in mutations units, T: time expansion/decline time in generational time, na = not applicable data.

Locality	*D*	*Fs*	*rg*	R_2	θ	N_{ef}	θ_0	N_{ef} h	τ	T
IA	-0.87	0.72	0.36	0.16	0.53	456	0.46	399	0.00	na
CU	na	na	na	na	na	na	na	na	na	na
CL	na	na	na	na	na	na	na	na	na	na
HX	-0.84	-0.18	0.26	0.16	2.0	1731	0.75	640	0.32	11,184
IC	-1.60	0.92	0.19	0.14	3.89	3309	2.70	2385	0.00	na
AV	-0.97	-0.82	na	na	na	na	na	na	na	na
XC	-0.29	-0.41	0.12	0.13	3.61	3072	2.70	1855	0.95	33,204
XT	-0.71	-1.48	0.17	0.12	3.78	3220	1.70	1484	0.72	25,164
SK	-0.81	-0.16	na	na	na	na	na	na	na	na
GM-UM	-1.19	-0.24	0.36	0.16	0.42	361	0.30	282	0.00	na
MC-UM	-1.27	-2.09	0.12	0.09	4.60	3927	2.10	1823	0.48	16,776
Global value	-1.59	-4.07	0.14	0.09	4.20	3593	2.00	1742	0.00	na

SUPPORTING INFORMATION

Table S1. Information for all green turtle rookeries from the Gulf of Mexico and the Caribbean considered in the many-to-many foraging-ground-centric MSA. We considered only haplotype data based on the larger fragment of mtDNA control region (~817 bp). MX: Mexico, FL: Florida, VE: Venezuela, SU: Suriname. The rookery size (estimated annual females) was estimated according to Shamblin et al. 2017.

Code	Locality	Haplotype frequencies references	Rookery size Females/year	Rookery size references
AV	Aventuras DIF, MX	This study	858	Flora, Fauna y Cultura de México, A.C, pers. comm.
CL	Las Coloradas, MX	This study	305	Cuevas et al. 2010
CU	El Cuyo, MX	This study	1738	PRONATURA, Península de Yucatán A.C, pers. comm
HX	Holbox, MX	This study	260	PRONATURA, Península de Yucatán A.C, pers. comm
IA	Isla Aguada, MX	This study	2888	Guzmán y García, 2015-2016, Guzmán 2017, 2018
IC	Isla Contoy, MX	This study	513	Antele-Sangabriel 2017
SK	Sian Ka'an, MX	This study	3619	Flora, Fauna y Cultura de México, A.C, pers. comm.
XC	X'cacel-X'cacelito, MX	This study	3128	Flora, Fauna y Cultura de México, A.C, pers. comm.
AL	Arrecife Alacranes, MX	Millán-Aguilar, 2009	828	Shamblin et al. 2018
AR	Cayo Arcas, MX	Millán-Aguilar, 2009	250	Shamblin et al. 2018
RN	Rancho Nuevo, MX	Millán-Aguilar 2009, Shamblin et al. 2017	715	Seminoff et al. 2015
VE	Veracruz, MX	Millán-Aguilar 2009, Shamblin et al. 2018	1040	Seminoff et al. 2015
BR	Boca Raton, FL	Shamblin et al. 2015	83	Shamblin et al. 2015
CA	Canaveral Nation Seashore, FL	Shamblin et al. 2015	698	Shamblin et al. 2015
DT	Dry Tortugas National Park, FL	Shamblin et al. 2015	115	Shamblin et al. 2015
HP	Hillsboro, Pompano FL	Shamblin et al. 2015	150	Shamblin et al. 2015
HU	Hutchinson Island, FL	Shamblin et al. 2015	211	Shamblin et al. 2015
JU	Jupiter Island northern, FL	Shamblin et al. 2015	234	Shamblin et al. 2015
KW	Key West, FL	Shamblin et al. 2015	18	Shamblin et al. 2015
ME	Melbourne Beach, FL	Shamblin et al. 2015	2383	Shamblin et al. 2015
SI	Singer Island, FL	Shamblin et al. 2015	208	Shamblin et al. 2015
TE	Tequesta (southern Jupiter Island), FL	Shamblin et al. 2015	208	Shamblin et al. 2015
AI	Aves Island, VE	Shamblin et al. 2012	2833	Shamblin et al. 2018
SU	Galibi and Matapica, SU	Shamblin et al. 2012	13067	Shamblin et al. 2018

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Table S2. Information for green turtle foraging aggregations from the Gulf of Mexico and the Mexican Caribbean considered into the many-to-many rookery-centric MSA. We considered only haplotype data based on the larger fragment of mtDNA control region (~817 bp). MX: Mexico, FL: Florida.

Code	Locality	Haplotype frequencies references
AK	Akumal, MX	This study
BC	Banco Chinchorro, MX	This study
CH	Chiquilá, MX	This study
CO	Isla Contoy, MX	This study
PS	Punta Sacrificios, MX	This study
XL	X'calak MX	This study
SFL	southern Florida	Naro-Maciel et al. 2017
TX	Texas, TX	Shamblin et al. 2017
NGM	northeast of Gulf of Mexico	Shamblin et al. 2018

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Table S3. Haplotype frequencies for the larger fragment (~817 bp) of the mtDNA control region for rookeries and foraging aggregations considered in the many-to-many MSA. For localities names see Table S1 and S2.

	Rookeries																								Foraging aggregations									
	RN	VE	IA	AR	CU	CL	AL	HX	IC	AV	XC	XT	SK	CA	ME	HU	JU	TE	SI	BR	HP	KW	DT	AI	SU	TO	EP	TX	NG	AK	BC	CH	CO	PS	XL
CMA1.1	23	83	0	0	0	0	4	0	0	1	0	2	1	22	150	14	10	3	1	0	0	0	0	0	0	22	6	99	53	7	0	0	8	3	5
CMA1.2	0	0	0	0	0	0	0	4	2	0	2	2	1	0	10	1	3	0	0	4	3	0	3	0	0	7	0	3	1	1	0	0	3	1	0
CMA1.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
CMA1.4	0	0	0	0	0	0	0	1	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0
CMA2.1	0	0	0	0	0	0	0	0	0	0	1	3	0	1	4	2	1	1	0	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1
CMA3.1	13	13	22	9	26	13	11	11	14	3	10	10	1	8	76	8	29	9	25	21	14	15	14	5	1	52	10	47	49	27	2	2	47	9	18
CMA3.4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CMA3.8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
CMA5.1	0	0	0	1	0	0	3	0	1	0	0	0	0	0	2	0	0	0	0	0	0	0	4	48	55	7	1	3	4	5	0	0	6	2	1
CMA6.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
CMA8.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	14	0	0	0	0	0	0	0	0	0	0	0
CMA8.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA9.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA10.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA11.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA12.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA13.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
CMA15.1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
CMA16.1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	2	0	0	0	1	0	0	0	0	0	0	5	0	4	0	1	0	0	1	0	0
CMA16.2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CMA17.1	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
CMA18.1	0	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	5	3	0	0	0	1	0	0
CMA18.2	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	3	0	0	0	1	1	0
CMA21.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
CMA22.1	0	0	0	0	0	0	0	0	0	0	4	3	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0	2	1	0	0	0	0	0	0
CMA23.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA24.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

CMA25.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
CMA26.1	0	0	0	0	0	0	0	0	3	0	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	1	2	0	0	4	0	0	
CMA27.1	0	0	0	0	0	0	5	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	2	2	2	0	0	0	2	0	0	
CMA28.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0	0	0	
CMA29.1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	
CMA30.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
CMA32.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CMA47.1	0	0	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	
CMA48.3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	
CMA52.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	
CMA53.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CMA58.1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
CMA68.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	
CMA73.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	
CMA77.1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	

Table S4. Analysis of molecular variance (AMOVA) of green turtle rookeries from the Gulf of Mexico and the Mexican Caribbean. We tested different break hypothesis in order to define the number of management units (MU) in the region. Localities abbreviations: Isla Aguada (IA), El Cuyo (CU), Las Coloradas (CL), Holbox (HX), Isla Controy (IC), Aventuras DIF (AV), X'cacel (XC), X'cacelito (XT) and Sian Ka'an (SK). Groups: **Gulf of Mexico:** IA, CU and COL, **Mexican Caribbean**: HX, IC, AV, XC, XT and SK, **north Mexican Caribbean**: HX and IC, **central Mexican Caribbean**: AV, XC, XT and SK.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation	Fixation indices	*P* value
All the Yucatan Peninsula						
Among populations	8	8.10	0.04	15.59	F_{ST}= 0.15	<0.001
Within populations	156	36.70	0.23	84.41		
Total	164	44.80	0.27			
Gulf of Mexico *vs* Mexican Caribbean						
Among groups	1	5.28	0.062	20.20	F_{CT}=0.20	0.009
Among populations within groups	7	2.82	0.009	3.16	F_{SC}=0.03	0.050
Within populations	156	36.70	0.235	76.63	F_{ST}= 0.23	<0.001
Total	164	44.80	0.307			
Gulf of Mexico *vs* north Mexican Caribbean *vs* central Mexican Caribbean						
Among groups	2	12.71	0.055	18.93	F_{CT}=0.18	<0.001
Among populations within groups	6	1.59	0.001	0.63	F_{SC}=0.007	0.43
Within populations	156	36.70	0.23	80.45	F_{ST}= 0.19	<0.001
Total	164	44.806				

Table S5. Pairwise comparisons of genetic differentiation based on 817 bp fragment among Mexican Caribbean green turtle foraging aggregations. Pairwise F_{ST} value below the diagonal, and pairwise exact test of population differentiation *P* values above the diagonal. Locality abbreviations: Akumal (AK), CO (Isla Contoy), CH (Chiquila), BC (Banco Chinchorro), PS (Punta Sacrificios), and X'calak (XL).

	AK	**CO**	**CH**	**PS**	**XL**	**BC**
AK	-	0.917	1.000	0.559	0.646	1.000
CO	-0.013	-	1.000	0.352	0.584	1.000
CH	-0.191	-0.199	-	1.000	1.000	-1.000
PS	-0.031	-0.020	-0.188	-	0.339	1.000
XL	-0.002	-0.107	-0.226	0.001	-	1.000
BC	-0.191	-0.199	0.000	-0.188	-0.226	-

Table S6. Analysis of molecular variance (AMOVA) of green turtle foraging aggregations from the Gulf of Mexico and the Mexican Caribbean. We tested different break hypothesis in order to define the number of management units (MU) in the region. Locality abbreviations: Akumal (AK), Chiquila (CH), Isla Contoy (CO), Punta Sacrificios (PS), Banco Chinchorro (BC), X'calak (XL), Dry Tortugas (TO), Park National Everglades (EP), Texas (TX), Venice (VE), Ports of Apalachiola (AP), Pensacola (PE). Groups: **Mexican Caribbean**: AK, CH, CO, PS, BC, XL; **north Mexican Caribbean**: AK, CH and IC; **central and southern Mexican Caribbean**: PS, BC and XL; **southern Florida**: TO and EP; **Texas**: Texas; and **northeast Gulf of Mexico** (VE; AP and PE), **northern Gulf of Mexico**: TX, EP, TO, VE, AP, and PE; **southern Florida and north Gulf of Mexico**: EP, TO, VE, AP, and PE

Source of variation	d.f	Sum of squares	Variance components	Percentage of variation	Fixation indices	*P* value
All localities						
Among populations	8	19.96	0.025	2.45	F_{ST}= 0.02	0.005
Within populations	585	586.06	1.00	97.55		
Total	593	606.034	1.026			
Mexican Caribbean *vs* southern Florida *vs* Texas *vs* northeast Gulf of Mexico						
Among populations	3	17.24	0.04	4.37	F_{CT}= 0.04	0.001
Among populations within groups	6	3.30	-0.01	-1.67	F_{SC}= -0.01	0.95
Within populations	584	585.40	1.00	97.30	F_{ST}= 0.02	0.006
Total	593	606.03	0.81			
north Mexican Caribbean *vs* central and southern Mexican Caribbean *vs* southern Florida *vs* Texas *vs* northeast Gulf of Mexico						
Among groups	4	17.65	0.04	4.17	F_{CT}=0.04	0.006
Among populations within groups	5	2.97	-0.01	-1.65	F_{SC}= -0.01	0.890
Within populations	584	585.40	1.00	97.47	F_{ST}= 0.02	0.007
Total	593	606.05	1.02			
Mexican Caribbean *vs* northern Gulf of Mexico						
Among groups	1	10.40	0.03	3.57	F_{CT}=0.03	0.020
Among populations within groups	8	10.22	0.005	0.52	F_{SC}=0.005	0.270
Within populations	584	585.40	1.00	95.91	F_{ST}= 0.04	0.005
Total	593	606.03	1.04			
Mexican Caribbean *vs* southern Florida and north Gulf of Mexico						
Among groups	2	14.87	0.03	3.42	F_{CT}=0.03	0.020
Among populations within groups	6	5.13	-0.003	-0.35	F_{SC}=-0.003	0.711
Whithin populations	585	586.06	1.00	96.93	F_{ST}= 0.03	0.005
Total	593	606.034	1.033			

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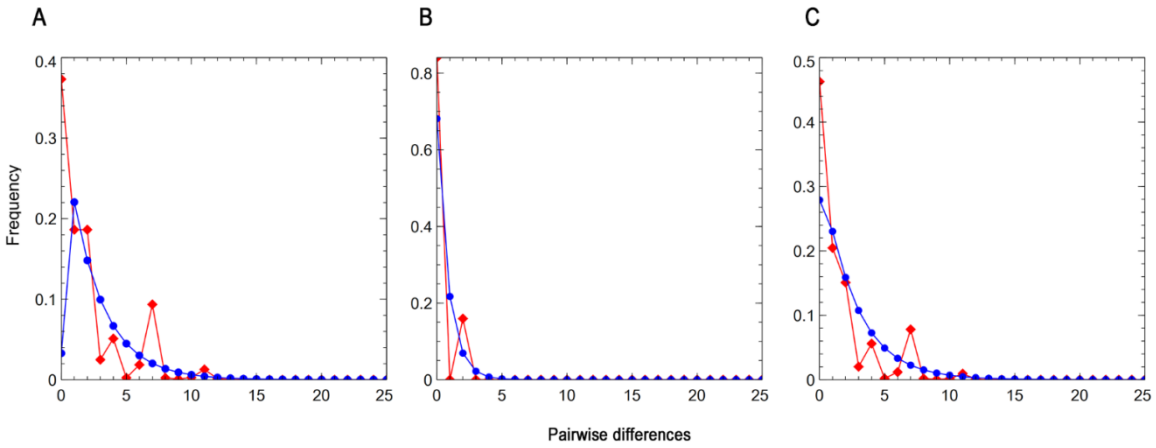
FIGURE S1. Mismatch distribution for the Yucatan Peninsula green turtle rookeries: **(A)** includes all rookeries from the Yucatan Peninsula, **(B)** rookeries that constitute the management unit of the Gulf of Mexico, and (**C)** rookeries that constitute the management unit of the Mexican Caribbean. The blue lines indicate frequencies expected and the red lines indicate the frequencies observed.



CAPÍTULO IV

CONCLUSIONES

El presente trabajo es el primero en examinar la composición genética y origen natal de los individuos que conforman las agregaciones de forrajeo de las tortugas carey y verde en la Península de Yucatán, aportando información novedosa sobre estas especies en los hábitats marinos. De igual manera, a partir de los datos obtenidos en esta investigación se identificaron patrones de conectividad migratoria entre importantes hábitats de anidación y forrajeo a pequeña escala (Península de Yucatán), así como a una escala más amplia (cuenca del Atlántico).

4.1 Tortuga carey

- Las colonias de anidación en la Península de Yucatán tienen un alto grado de endemismo, lo cual resalta la importancia de conservar estos acervos genéticos, con el fin de preservar la diversidad genética de la especie en la región del Atlántico.

- La baja diversidad genética de las colonias de anidación en la Península de Yucatán está relacionada con su aislamiento, resultado de procesos históricos, lo que generó restricción del flujo génico entre las colonias de anidación de México y del Gran Caribe.

- Las agregaciones de forrajeo de la Península de Yucatán se componen principalmente por haplotipos comunes de las colonias de anidación del Atlántico y de haplotipos endémicos de las colonias mexicanas.

- Existe una diferenciación genética significativa entre las colonias de anidación de Campeche *vs* Yucatán/Quintana Roo, y entre las agregaciones de forrajeo del Golfo de México y Caribe Mexicano, lo que indica procesos diferenciales de reclutamiento en cada región.

- La conectividad migratoria en la Península de Yucatán está determinada por los patrones de circulación oceánica, tanto en la región de la Península de Yucatán

como en el Atlántico. Adicionalmente, las tortugas que nacen en la Península de Yucatán utilizan hábitats de desarrollo y alimentación localizados en Florida, Cuba e Isla de Turcos y Caicos, lo que denota importantes patrones migratorios entre las colonias mexicanas y otros grupos de forrajeo del Atlántico.

4.2 Tortuga verde

- Las colonias de anidación en la Península de Yucatán se caracterizan por tener una alta proporción de haplotipos ampliamente distribuidos en el Caribe occidental, y una proporción moderada de haplotipos endémicos, principalmente en las colonias del Caribe. Esto expone la importancia de estas colonias en la región de la Península de Yucatán.

- La diversidad genética de las colonias de alimentación fue baja para las colonias del Golfo de México, lo que puede ser resultado de un efecto fundador. En cambio, en el Caribe Mexicano, la diversidad genética fue alta, lo que sugiere que estas localidades conservan remanentes de la diversidad genética de poblaciones ancestrales.

- La diferenciación genética entre las colonias de anidación del Golfo de México y del Caribe Mexicano se explica por factores contemporáneos, como la conducta filopátrica de la especie y la barrera en la conectividad al norte de la Península de Yucatán, originada por los patrones de corrientes oceánicas; sin embargo, también puede ser explicada por procesos históricos, como la expansión poblacional ocasionada por los periodos glaciales e interglaciares durante el Pleistoceno.

- El alto endemismo y la presencia de un haplotipo ancestral hacen suponer que las colonias de anidación localizadas en la zona central de Quintana Roo pudieron formar parte del refugio glacial localizado en el Caribe.

- El traslape de los haplotipos CM-A3.1 y CM-A1.1 en las poblaciones de tortuga verde de la Península de México y del Caribe occidental muestra la necesidad de mejorar la resolución del marcador molecular, con el fin de definir con mayor especificidad a las poblaciones del Caribe.

- Existen patrones de conectividad migratoria entre colonias de anidación y grupos de forrajeo a pequeña escala (Península de Yucatán), en donde la contribución de las colonias de anidación locales, a los grupos de forrajeo del Caribe, puede ser explicada por aspectos conductuales, como la preferencia de los juveniles por alimentarse en zonas cercanas a su playa natal. A una escala geográfica más amplia (Golfo de México y Caribe Mexicano), las corrientes oceánicas y el comportamiento activo de nado contribuyen a la dispersión de individuos desde el Caribe Mexicano hasta el norte del Golfo de México.

4.3 Implicaciones para la conservación

- La definición de unidades de manejo de las colonias de anidación y agregaciones de forrajeo en la Península de Yucatán a partir de análisis de ADNmt ha permitido clarificar el grado de aislamiento y conectividad entre las poblaciones de tortugas marinas. Por lo tanto, identificar las UM permite priorizar las acciones de conservación a una escala geográfica definida, considerando amenazas específicas en los diversos hábitats de anidación y alimentación.

- Los patrones de conectividad migratoria identificados, resaltan la importancia de los hábitats de alimentación en la Península de Yucatán, los cuales son utilizados por las tortugas carey y verde provenientes de colonias locales y regionales. Esto destaca la importancia de conservar los hábitats críticos que abarcan jurisdicciones nacionales e internacionales, lo cual hace explícita la necesidad de coordinación y colaboración entre diferentes países para lograr estrategias efectivas para la conservación de estas especies.

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